



## 23 Abstract

24 Accelerating decreases in survival are evident for northern Hemisphere salmon  
25 populations. We collated smolt survival and smolt-to-adult (marine) survival data for  
26 all regions of the Pacific coast of North America excluding California to examine the  
27 forces shaping salmon returns. A total of 3,055 years of annual survival estimates were  
28 available for Chinook (*Oncorhynchus tshawytscha*) and steelhead (*O. mykiss*). This  
29 dataset provides a fundamentally different perspective on west coast salmon  
30 conservation problems from the previously accepted view. We found that marine  
31 survival collapsed over the past half century by a factor of at least 4-5 fold to similar  
32 low levels (~1%) for most regions of the west coast. The size of the decline is too large  
33 to be compensated by freshwater habitat remediation or cessation of harvest, and too  
34 large-scale to be attributable to specific anthropogenic impacts such as dams in the  
35 Columbia River or salmon farming in British Columbia. Within the Columbia River,  
36 both smolt survivals during downstream migration in freshwater and adult return rates  
37 (SARs) of Snake River populations, often singled out as exemplars of poor survival,  
38 appear unexceptional and are in fact higher than estimates reported from other regions  
39 of the west coast lacking dams. Formal Columbia River rebuilding targets of 2-6%  
40 SARs may therefore be unachievable if regions with nearly pristine freshwater  
41 conditions also fail to achieve these targets. Finally, we present case studies  
42 demonstrating that the historical response to evidence that the salmon problems are  
43 primarily ocean-related was to re-emphasize freshwater actions and to stop work on  
44 ocean issues. With ocean temperatures forecast to increase far further, the failure of

45 management to identify the drivers of salmon collapse and respond appropriately  
46 suggest that the future of most west coast salmon populations is bleak.

47

## 48 Introduction

49

50 The total abundance of salmon in the North Pacific has now reached record  
51 levels [2-4]; however, a dramatic contrast in the winners and losers is obscured by this  
52 milestone. Most of the increased abundance is in the lowest valued species (pink  
53 *Oncorhynchus gorbuscha* and chum *O. keta* salmon) in far northern regions, at least  
54 partly due to major efforts at ocean ranching of these two species [4]. In contrast while  
55 essentially all west coast North American Chinook (*O. tshawytscha*) populations  
56 (including Alaska) are now performing poorly with dramatically reduced productivity  
57 [6]. The situation is similar for most southern populations of steelhead (*O. mykiss*) [7],  
58 coho (*O. kisutch*) [8, 9], and sockeye (*O. nerka*) [10-13]. These poorly performing  
59 species are of higher economic value and the preferred focus of First Nations, sport,  
60 and many commercial fisheries.

61

62 The historical geographic pattern of declines in salmon abundance (greatest  
63 problems in the south, least to the north) were originally assumed to reflect a freshwater  
64 anthropogenic cause because of the greater degree of terrestrial (i.e., freshwater) habitat  
65 modification in the more populous southern regions of the west coast [14, 15]. The  
66 growing appreciation of ocean climate change [16-18] has brought a greater awareness

67 of the role of the ocean in influencing salmon survival. As Ryding and Skalski [19]  
68 noted almost two decades ago, “*It is becoming increasingly clear that understanding*  
69 *the relationship between the marine environment and salmon survival is central to*  
70 *better management of our salmonid resources*” (p. 2374).

71

72            Unfortunately, our scientific understanding of the events occurring in the marine  
73 phase remains severely limited, so there has been little change in management strategy  
74 beyond the essential first step of reducing harvest rates in the face of falling marine  
75 survival. The recent recognition of the decline in Chinook returns across essentially all  
76 of Alaska [20-22] and the Canadian portion of the Yukon River [23], where  
77 anthropogenic freshwater habitat impacts are generally negligible, is another example  
78 of how simple explanations looking at freshwater habitat changes are potentially  
79 flawed. If freshwater habitat disruption across this vast swathe of relatively pristine  
80 territory is severe enough to seriously impact salmon productivity, then there is little  
81 hope that freshwater habitat in more southern regions can be “fixed” to support a newly  
82 productive environment for salmon.

83

84            The same widespread problem of declining survival is also evident for other  
85 diadromous species. Both eulachon [24] and lamprey [25] have undergone sharp  
86 unexplained declines along the Pacific west coast of North America. In the Atlantic  
87 Ocean, both Atlantic salmon [26] and eels [27, 28] are similarly in sharp decline. In the  
88 case of eels, eulachon, and lamprey, the authors attribute the problem to likely marine-

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89 related factors, not freshwater. This point is particularly persuasive for eulachon  
90 because of the very short freshwater phase [24].

91

92            In this paper, we collate Chinook and steelhead time series for the west coast of  
93 North America (excluding California) to look at patterns in survival: (1) freshwater  
94 survival of smolts during the downstream migration phase and (2) smolt-to-adult return  
95 rates (SARs). The SAR is the three-fold product of freshwater smolt survival during  
96 downstream migration multiplied by the marine survival experienced over 2-3 years in  
97 the ocean multiplied by freshwater survival during the final upstream migration by the  
98 returning adults to the final enumeration point. (Depending upon the specific dataset,  
99 adult abundance may be enumerated prior to actual arrival at the spawning grounds; see  
100 Methods). In particular, given the very poor perceived returns of salmon to the Snake  
101 River, many of our analyses compare regional survival to that of Snake River stocks.  
102 We use the term SAR and marine survival interchangeably because, as we will  
103 demonstrate, the majority of the SAR is determined in the ocean.

104

105            For the downstream (freshwater) smolt survival analysis, 46 Chinook and 44  
106 steelhead time series were collated, comprising 531 annual estimates of survival (see  
107 Methods). For the SAR comparison, 101 Chinook time series and 50 steelhead time  
108 series were available (Fig. 1) which equate to 1,729 Chinook and 795 annual steelhead  
109 SAR estimates. Altogether these datasets total 3,055 years of salmon monitoring—  
110 clearly, an enormous effort that likely sums to multiple billions of dollars. As the  
111 breakdown by regime periods will demonstrate, the tremendous increase in resources

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112 devoted to survival monitoring as salmon returns have dwindled over time has perhaps  
113 provided less actual insight into mechanisms (as opposed to numbers) than might be  
114 hoped, a theme we return to in the Discussion.

115

**Figure 1. Map of salmon survival time series used in the analyses.** Numbers inside symbols are keyed to the populations in Supplementary Table S2; yellow circles indicate Chinook populations, pink squares indicate steelhead, and blue triangles indicate locations with data for both species. Acronyms: SEAK (SE Alaska/Northern British Columbia Transboundary Rivers); NCBC (North-Central British Columbia); WCVI (West Coast Vancouver Island); WAC (Washington Coastal); ORC (Oregon Coastal); SOG (Strait of Georgia); PS (Puget Sound).

116

117           The passive integrated transponder (PIT) tag SAR estimates for Chinook and  
118 steelhead are specific to the Columbia River Basin and are reported by the Fish Passage  
119 Center, most recently by [5]. Estimates reported in an earlier paper by Raymond [1,  
120 29] which predate PIT tag estimates for Columbia River basin Chinook and steelhead  
121 were also included. The primary data source for the coded wire tag (CWT) based SAR  
122 time series for Chinook used in this analysis is the official survival estimates submitted  
123 by various State and Federal government agencies to the Pacific Salmon Commission  
124 under the terms of the US-Canada Salmon Treaty. These data include SAR estimates  
125 from OR, WA, BC, and AK. For Washington State steelhead outside the Columbia  
126 River basin, SARs were collected and reported by Kendall et al [7] for Puget Sound, as  
127 well as a number of locations along the coast of Juan de Fuca Strait and the outer  
128 (western) WA coast. In BC, SARs are only available for one steelhead population  
129 (Keogh River). We are unaware of additional steelhead SAR data for Alaska or coastal

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130 Oregon rivers. Individual time series ranged between 2-39 years for Chinook, and 2-37  
131 year for steelhead. (Datasets comprised of only a single year of data were excluded).

132

133           What are acceptable levels of salmon survival? For much of the west coast  
134 outside of the Columbia River basin, formal recovery targets (SARs) have not been  
135 specified, although it is clear in all regions that historical levels of productivity would  
136 be greatly preferred to current return rates. (And, to foretell an underlying theme to the  
137 paper, current SAR levels may in fact be much preferred to what climate change has in  
138 store for salmon in the future). In the extensively dammed Columbia River basin, the  
139 Northwest Power and Conservation Council’s Fish and Wildlife Program (NPCC) set  
140 rebuilding targets for SARs at 2%-6% ([5], p. 4), roughly the survival observed in the  
141 1960s prior to the completion of the 8-dam Federal Columbia River Power System  
142 (FCRPS) [29, 30]. The sharp decrease in salmon returns to the Columbia River (and  
143 most particularly the Snake River) after the completion of the final Snake River dam in  
144 the mid-1970s was widely assumed to be due to the construction of the dams, and great  
145 effort has therefore been devoted to improving in-river smolt survival since that time.  
146 For this reason, we have chosen to contrast survival in other geographic regions to that  
147 of the Snake River as an objective standard of “poor” survival.

148

149           The NPCC SAR objectives did not specify the points in the life cycle where  
150 Chinook smolt and adult numbers should be determined. However, one extensive  
151 analysis for Snake River spring/summer Chinook was based on SARs calculated as  
152 adult and jack returns to the uppermost dam encountered in the migration path [31]:

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153      *“Median SARs must exceed 4% to achieve complete certainty of meeting the 48-year*  
154      *recovery standard, while ... A median of greater than 6% is needed to meet the 24-year*  
155      *survival standard with certainty”* (p. 41). With most current Columbia River basin  
156      SARs on the order of ca. 1%, migratory-phase life-cycle survival would have to  
157      increase 200%-600% (two- to six-fold) to meet these targets. It is unclear whether this  
158      level of rebuilding is actually possible for reasons that we discuss later.

159

160              Unfortunately, as Chinook and steelhead stocks continue to dwindle, progress  
161      on addressing and incorporating ocean impacts on salmon dynamics has been slow,  
162      perhaps due to a combined lack of understanding about how to address marine survival  
163      issues and to pessimism about whether improved understanding of the marine phase  
164      can advance conservation. Therefore, lastly we review two case studies which show  
165      that even when the overriding role of marine survival is identified, there is still a strong  
166      predilection to preferentially identify freshwater factors to study and manipulate. This  
167      has resulted in both the failure to directly address the marine survival problem and a  
168      rather uncritical approach that too readily identifies widely accepted freshwater  
169      stressors as being responsible for the problems evident in specific populations. In our  
170      view, a large part of the difficulty lies in some of the fundamental underlying  
171      assumptions that the fisheries community makes about the nature of the core problem.  
172      Because these assumptions are part of our training and professional ethos, they are  
173      difficult to recognize or question. Nevertheless, given the widespread geographic range  
174      and magnitude of the collapse in survival that is now evident, we view it as urgent that  
175      assumptions about causative agents be carefully assessed.



176

## 177 Results

### 178 Freshwater (downstream) smolt survival

179 To separate and assess what are typical freshwater survival levels for smolts  
180 migrating downstream, we collated the published studies for west coast North  
181 American rivers excluding California (See Methods for a more detailed summary and  
182 Table S1 for reported estimates). We used these data to make regional comparisons of  
183 smolt survival and survival scaled by distance travelled during the downstream  
184 freshwater migration to the sea.

185 Within the Columbia River basin, survival estimates for a range of stocks and  
186 river reaches are available, although the majority are for survival through the  
187 hydrosystem (dammed segment of the river). For yearling Chinook, smolt survival  
188 estimates varied considerably between grouping categories (Fig 2; center column, top

**Fig 2. Freshwater smolt survival for west coast North American rivers.** A total of N=531 annual survival estimates are included. Top row: smolt survival from release to river mouth (and intermediate locations in the case of the Columbia). Bottom row: survival per 100 km of migration distance. The red horizontal line shows the median value for all Snake River data in a given panel (red coloured bars). Data are shown as a box and whisker plot with associated sample size listed above the appropriate boxes. Abbreviations: LRE, Lower Columbia River and estuary (i.e., the river reach from just below the lowest (Bonneville) dam to the river mouth); Release to BON measures Snake River survival from hatchery release through the Snake River above Lower Granite Dam and down through the 8-dam hydrosystem to the last dam (Bonneville). Full river measures survival from release to the mouth of the Columbia River. Data sources and annual survival estimates are reported in Supplementary Table S1.

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189 row); however, when survival is scaled by distance travelled (bottom row), two patterns  
190 become apparent. First, regardless of release location or origin (Snake, Upper, or Mid-  
191 Columbia), all yearling Chinook from the Columbia River basin have remarkably  
192 similar median survival rates of 88% per 100 km of migration distance. Second,  
193 survival rates in the dammed and undammed sections of the river (the hydrosystem and  
194 LRE) are largely similar.

195            For other populations outside of the Columbia River basin which have  
196 published estimates (n=3), survival rates per 100 km varied. Survival rate of the  
197 Nimpkish River (B.C.) population was particularly low: estimated survival to the river  
198 mouth was 60% but the migration distance was only 8.5 km, resulting in only 0.25%  
199 survival per 100 km. Coldwater River (Fraser River/SOG) yearling Chinook survival  
200 rate was 63% and 68% per 100 km. Survival of hatchery-reared Chilko River Chinook  
201 (a Fraser River/SOG population) was the only population similar to the Columbia River  
202 basin; survival was 49% during their 640 km downstream migration in the Fraser River  
203 basin, resulting in a survival rate of 89% per 100 km.

204

205            A similar result is evident for Snake River steelhead which had nearly identical  
206 median survival rates per 100 km of migration distance (87%) as yearling Chinook  
207 irrespective of the section of the Columbia River basin that survival was measured  
208 over. Upper Columbia River steelhead tagged and released at Bonneville Dam in the  
209 lower Columbia River had survival rates of 70-75% per 100 km in the lower river and  
210 estuary, however, steelhead tagged and released at Rock Island Dam (UCOL) had  
211 consistently lower median survival rates, only ~41% per 100 km.

212

213            Survival rates per 100 km in the other regions for which we have steelhead data  
214 (Keogh River, Strait of Georgia, Puget Sound, and Oregon Coast) were generally lower  
215 than either the upper Columbia or Snake River. Keogh River steelhead had particularly  
216 low rates; the release site was located only 300 from the river mouth and survival  
217 ranged between 72-95%, resulting in an estimated survival rate per 100 km close to  
218 zero. Puget Sound and Oregon Coast populations had relatively short migrations to the  
219 ocean (0.3-102 km) and highly variable survival rates; these results suggest intense  
220 losses concentrated in the lowest reaches of these rivers. The only exception was  
221 hatchery-reared Skagit River steelhead which had a survival rate of 90% per 100 km.

222

223            There are no subyearling Chinook survival data available outside of the  
224 Columbia River basin, but within the basin, subyearling Chinook had similar median  
225 survival rates to yearling Chinook and steelhead in the hydrosystem and in the LRE  
226 (~85% per 100 km).

227

228

## 229 **Chinook SARs**

### 230 **Coast-wide trends in adult survival (SARs)**

231            Adult survival data for Chinook salmon are available for a varying range of years.  
232 The most extensive data sets are for the upper Columbia (both subyearling and yearling  
233 Chinook) and Snake rivers (yearlings), which extend back to the 1960s (Table S1).

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234 Data were available for other regions beginning in the 1970s and for all regions by  
235 2001 for yearlings, and 1987 for subyearlings.

236        In essentially all regions where time series extend back to the 1970s or earlier,  
237 survival to adult return has substantially decreased with time (Fig 3). A large drop in  
238 SARs for yearling Snake River Chinook is evident from the 1960s to approximately the  
239 mid-1970s, the time period when Snake River dams were completed [2,28]. Although  
240 the timing varies with region, the collapse in survival is also evident in other regions  
241 with long time series for both yearling (Upper Columbia River and—notably—Alaskan  
242 yearling stocks from SE Alaska), and subyearling Chinook (west coast Vancouver  
243 Island, the Strait of Georgia, and Puget Sound). Raymond [1, 29] (and many  
244 subsequent authors) ascribed the cause of the drop in survival to dam construction;  
245 however, declining SARs are also evident in other regions not affected by the  
246 construction of the FCRPS.

**Fig 3. Time series of smolt to adult survival (SAR) data for west coast Chinook stocks (excluding California).** Left column: subyearlings; Right column: yearlings. Regions are oriented from north (top) to south. Gold dots are SAR measurements based on CWT tags (PSC database), brown dots are SARs reported by Raymond [1], and violet dots are SARs based on PIT tags [5]. A loess curve of survival and associated 95% confidence interval (shaded region) using all available data for each panel is shown as a black line (the smoothing parameter was set to  $\alpha=0.75$ ); the loess curves for Snake River subyearling and yearling survival are overplotted in red to facilitate comparison with other regions. Blank panels indicate regions where the life history type does not occur (for example, Fall (subyearling) Chinook do not occur in Alaska, while Spring (yearling) Chinook do not occur in the low elevation streams on the west coast of Vancouver Island or Oregon coast). The major regime shift years of 1977, 1989, and 1998 are indicated by vertical lines. In this and subsequent figures the pale red band delineates the official Columbia River SAR rebuilding targets of 2-6%.

247 From the time of the major ocean regime shift in 1977 forwards, no substantial  
248 recovery in SARs is evident in any region. As more monitoring programs were  
249 initiated in the 1980s, SARs for all these regions were either declining or essentially  
250 fluctuating around a low mean value closely approximating the Snake River SARs (red  
251 lines) in all regions apart from the Oregon Coast; here, SARs were also roughly flat  
252 over time but at a persistently higher mean level relative to the Snake.

253

## 254 Regional survival differences

255 When compared by region (Fig 4), median Snake River yearling (Spring) Chinook  
256 SAR (1%) is higher than the regional median SARs for Puget Sound (0.55%) and the  
257 Strait of Georgia (0.53%), and is virtually identical to median survival for the Upper  
258 (0.96%) and Lower (1.08%) Columbia River populations. Regional yearling SARs are  
259 higher than the Snake River values only for three geographic areas: the mid-Columbia  
260 River region (1.49%), Northern & Central BC (2.31%), and Alaska (1.88%). Within a

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261 few of these geographic regions, striking population-specific differences are also  
262 evident which we consider later.

**Fig 4. Box and whisker plot of SARs by population (all available years).** The black horizontal line within each bar is the median of the SAR data available for each population. Median survival across all available data for each region is shown as a blue line; median Snake River survival for all populations combined is shown as a red line and overplotted on all panels for comparison. The number of years of data is shown to the right. To save space, abbreviated population names are used here along with the map code from Figure 1; full names for the populations are listed in Supplementary Table S2.

263

264 For subyearlings (Fall Chinook), Snake River median SARs (0.81%) are similar to  
265 or higher than median survival in other regions of the west coast apart from coastal  
266 Oregon (ORC: 2.07%) and the west coast of Vancouver Island (WCVI: 1.34%; Fig 4).  
267 As the time series plot (Fig 3) makes clear, the higher median survival evident for  
268 WCVI (Robertson Creek) Chinook relative to the Snake River may not actually be due  
269 to persistently better SARs, but rather to the longer time series of data for Robertson  
270 Creek that extends back to the period of particularly high SARs in the 1970s. Data for  
271 this time period are lacking for Snake River subyearling Chinook; we consider this  
272 issue further below.

273

274 In addition to the high median SARs for Oregon Coast and WCVI Fall Chinook,  
275 two specific subyearling hatchery populations from farther north (University of  
276 Washington Accelerated Fall Chinook in Puget Sound (3.96%), and Chilliwack Fall  
277 Chinook from the Strait of Georgia (lower Fraser River; 4.56%)) are also of note  
278 because of the strikingly large survival difference (~4X) of these stocks relative to the

279 majority of populations within each region. The higher median SAR for yearling  
280 Chinook from the Mid-Columbia region (1.49%) is similarly due to two wild  
281 populations (Yakima: 2.21% and John Day: 4.12%) and one hatchery population (Cle  
282 Elum: 1.57%) having higher SARs while two other hatchery populations have lower  
283 SARs (Carson 0.62% and Warm Springs 0.66%) than both Snake River and Lower  
284 Columbia River median SARs (SNAK=1; LCOL=1.08%).

285

286        Strikingly, although there are some exceptional populations, no region outside the  
287 Columbia River now achieves the Columbia River basin's official SAR recovery  
288 targets of 2%-6%. The Alaskan stocks attained these target survival levels in the early  
289 1980s, but since that time Alaskan SARs have fallen below the Columbia River basin  
290 rebuilding targets, and in the most recent years have essentially reached the current  
291 survival rates of Columbia basin stocks (Fig 2).

292

293

### 294 **3. Relative survival (scaled by Snake River)**

295        The regional-scale aggregation of SAR data provides a useful overview of  
296 survival between regions. However, important population-specific differences are  
297 potentially obscured because small numerical differences may in fact reflect large  
298 differential impacts on survival when SARs are low. For example, when regional  
299 SARs are only 1%, a population-specific SAR of 0.5% actually represents a population  
300 whose survival rate is only half that of the other populations. In addition, regional

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301 comparisons may be distorted because of trends in survival over time, and differing  
302 lengths to the various time series.

303           The potential influence of these factors can be reduced by normalizing the SAR  
304 estimates. In Fig 5, we divided each annual SAR estimate by the median of all Snake  
305 River SAR data available for the same year. This approach removes the potential  
306 confounding caused by temporal trends in SAR when time series with different lengths  
307 are compared. When SAR data for all available years are normalized in this way, SARs  
308 for Snake River yearling Chinook are higher than Puget Sound and Strait of Georgia  
309 and virtually indistinguishable from those for the Lower Columbia River (Willamette  
310 R) and the Upper Columbia River. Only normalized SARs for mid-Columbia, North &

**Fig 5. Normalized Chinook SARs.** Values are calculated by dividing individual SAR estimates for each stock and each year by the median Snake River SAR for the same year and aggregating by region. Vertical lines show the median SAR for the Snake River (red) and other regions (blue). Note the logarithmic scale on the x-axis. As in the prior plots, Columbia & Snake River SAR estimates based on PIT tags do not incorporate above-dam survival (or harvest).

311 Central BC, and SE Alaskan populations of Spring Chinook are higher than the Snake  
312 River populations.

313           The situation is similar for subyearling Chinook when normalized SARs are  
314 compared: Snake River subyearling SARs are either lower (Upper Columbia; Strait of  
315 Georgia, Puget Sound), higher (Mid Columbia; Lower Columbia), or closely equivalent  
316 (Washington Coast, North-Central BC) to SARs observed for all other regions with  
317 data. The only pronounced differences are the nearly 5-fold higher survival of the two  
318 Oregon coast stocks and the roughly 2-fold higher SAR for the Robertson Creek  
319 population (west coast Vancouver Island).



## 320 4. Survival by regime period

321 Significant changes in ocean productivity are known to impact salmon  
322 populations on time scales ranging from decades [16, 18, 32-34] to centuries [35-37].  
323 An alternative approach to comparing survival normalized by year is to break the  
324 survival data into recognized ocean regime periods [16-18, 32, 33, 38, 39] and then  
325 compare the normalized SARs. We defined four periods based on the year of ocean  
326 entry by smolts: 1977 and earlier, 1978-89, 1990-98, and 1999 or later. The results (Fig  
327 6) essentially mirror prior analyses, with the ratio of median Alaskan yearling Chinook  
328 survival relative to the Snake River falling from ~19X the Snake River value in the pre-  
329 1977 period to ~3X the Snake River value in the next two regime periods and then  
330 down to ~2X the Snake River value after the 1990 regime shift. Only the Alaskan,  
331 north-central BC, and Mid-Columbia populations remain ~2X higher than the Snake  
332 River populations' SARs post-1998, but well below their earlier levels of productivity.  
333 (In fact the time series of Alaskan and north-central BC SAR data (Fig 3) show that in  
334 the most recent years SARs have fallen to Snake River SAR levels). Upper and Lower  
335 Columbia, Puget Sound, and Strait of Georgia populations all have similar or lower  
336 survival. An analogous pattern is evident for subyearling Chinook, except here it is  
337 only the Oregon Coastal populations that have persistently higher survival. The  
338 progressive collapse in survival across regimes is notable for each region.

**Fig 6. Comparison of normalized Chinook SARs by regime periods: pre-1977, 1978-1989, 1990-1998, and post 1998.** Boxes and whiskers have the conventional interpretation; the horizontal red line shows the Snake R median SAR value for each regime to facilitate comparison (1.0 by definition). Sample sizes are shown above each group (green font) and the ratio of median SARs relative to the Snake River is shown immediately above the upper whiskers (black font).

339

## 340 Steelhead SARs

### 341 6. Coast-wide survival

342 Data on steelhead survival (SAR) are more geographically limited than for  
343 Chinook (Fig. 1 & Table S2), but share many of the same features (Fig 7). For  
344 simplicity, we have included the Keogh R time series from the extreme NE tip of  
345 Vancouver Island in the Strait of Georgia/Juan de Fuca Strait (SOG) region, although  
346 the population enters Queen Charlotte Strait, not the Strait of Georgia proper.

347 Prior to the 1977 regime shift, data are only available for the Upper Columbia  
348 and Snake Rivers (Fig 7). Similar to Snake River yearling Chinook, steelhead SARs in  
349 both the Upper Columbia and Snake Rivers declined in the period prior to the mid-  
350 1970s (when both FCRPS dam construction was completed and a major marine regime  
351 shift occurred). SAR data becomes available for Washington Coast, Puget Sound, and  
352 Strait of Georgia regions in the period after the 1977 regime shift. The very high SARs  
353 of Keogh R steelhead (northern SOG region) in the early years of the historical record,  
354 which exceeded 20% in some years, compresses the SAR differences with other regions  
355 (indicated by the LOESS curves), making the differences somewhat difficult to see.

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356      However, plotting the data in this way demonstrate that under former climatic  
357      conditions, very high SARs were achieved in some regions.

358              Following ocean entry year 1990, further decline is evident in Washington  
359      Coast and Strait of Georgia steelhead SARs around ocean entry year 1990 (the time of  
360      the subsequent ocean regime shift) as well as a continuing decline in Puget Sound  
361      SARs to levels below that of Snake River steelhead. Although SAR data are not  
362      available for B.C. steelhead stocks other than the Keogh River (northern Vancouver  
363      Island), the pattern of adult returns to other southern B.C. rivers closely matches returns  
364      to Keogh River, supporting the view that the Keogh SAR pattern applies more broadly;  
365      see [40]. Both Washington outer coast (WAC) and mid-Columbia SARs are  
366      substantially higher than those the Snake River (as is Keogh), while Puget Sound SARs  
367      drop to lower values after 1990. Upper Columbia River steelhead SARs are closely  
368      similar to Snake River values.

**Fig 7. Steelhead SARs plotted against ocean entry year.** Regions are oriented from north (left) to south (right); the Keogh R (KEOG) is situated on the NE tip of Vancouver Island (BC). Gold dots are SAR measurements based on PIT tags, brown dots are SARs reported by Raymond [1], and violet dots are SARs based on CWT tags. A loess curve of survival and associated 95% confidence interval (shaded region) using all available data for each panel is shown as a black line (the smoothing parameter was set to  $\alpha=0.75$ ); the Snake River loess curve is shown in red and over plotted on all other panels to facilitate comparison. Steelhead survival data are for British Columbia only available for the Keogh River (see Ward et al 2006) for a description of the monitoring program). The major regime shift years of 1977, 1989, and 1998 are indicated by vertical lines.

369

## 370 7. Regional survival differences

371 A few specific steelhead populations are notable for having anomalously high  
372 survival (all three mid-Columbia River and three of eight Washington Coast  
373 populations; Fig 8). Median SARs for the Snake River region (1.7%) are comparable  
374 to the Upper Columbia (1.9%) and the Washington Coast regions (2.3%), but more than  
375 double that of Puget Sound steelhead populations (0.8%). Only the median SARs for  
376 the mid-Columbia River region (5.5%) and the Strait of Georgia region (Keogh and  
377 Snow Creek; 3.3%) are appreciably higher than Snake River survival.

**Fig 8. Box and whisker plot of steelhead SARs by population (all available years).**

Population names are listed in Supplementary Table S1. The black horizontal line within each bar is the median of the SAR data available for that population. Median survival across all available data for each geographic region is shown as a blue line; median Snake River survival for all populations combined is shown as a red line and overplotted on all panels for comparison. The number of years of data is shown to the right.

378

379

## 380 8. Relative survival (scaled by Snake River)

381 When annual SAR estimates for individual steelhead stocks are normalized by  
382 the Snake River median SAR values in each year, a similar relationship emerges (Fig  
383 9). Median steelhead SARs are either indistinguishable from the Snake River (Upper  
384 Columbia River), slightly higher (Washington Coast), or substantially lower (Puget  
385 Sound). Only the Mid-Columbia River and Strait of Georgia have substantively higher  
386 SARs than the Snake River when compared on a year-for-year basis.

**Fig 9. Normalized steelhead SARs, obtained by dividing each individual SAR estimate (i.e., for each stock and each year) by the median SAR calculated across all available Snake River SARs for that year. The median Snake River SAR is overplotted in red. Note the logarithmic scale on the x-axis.**

387

## 388 9. Survival by regime period

389 This pattern becomes particularly clear when normalized steelhead SARs are  
390 examined by regime periods (Fig 10). The large drop in Strait of Georgia SARs in the  
391 post-1998 regime period is particularly notable, (in absolute terms, the drop in survival  
392 corresponds to a change in median SARs from 8.4% in the 1978-88 period to 2.6% in  
393 the post-1998 period—a three-fold decline). The second aspect to the steelhead data is  
394 the similarity of the other regions. Excluding the Mid-Columbia River, where only data  
395 for the post-1998 period are available, most other regions have median SARs roughly  
396 similar to the Snake River across all regime periods; only the mid-Columbia and SOG  
397 stand out as having consistently higher median SARs, while Puget Sound drops from  
398 higher median SARs than the Snake River to substantially lower SARs (less than half)  
399 in the post-1998 period.

**Fig 10. Comparison of normalized steelhead SARs by regime periods: pre-1977, 1978-1989, 1990-1998, and post 1998.** Boxes and whiskers have the conventional interpretation; the horizontal red line shows the Snake R median SAR value for each regime to facilitate comparison (1.0 by definition). Sample sizes are shown above each group (green font) and the ratio of median SARs relative to the Snake River is shown immediately above the upper whiskers (black font).

400

## 401 Discussion

402 Our analysis shows that over time Chinook and steelhead SARs have declined  
403 to reach approximately the same low level for almost all measured populations across  
404 the entire west coast of North America—with a few important exceptions that we  
405 discuss later. Although we do not have direct measurements of survival for Chinook  
406 stocks located west of SE Alaska or steelhead for regions north of Vancouver Island,  
407 the decrease in the number of adult Chinook returning to the rest of Alaska [20, 21]  
408 shows the broad region over which the conservation crisis now extends. We first  
409 address juvenile survival during seaward migration as a possible cause of the decline in  
410 adult abundance and then demonstrate the importance of the marine habitat.

## 411 The freshwater contribution to SARs

412 Freshwater survival of smolts during downstream migration to the sea has been  
413 assessed for a number of river systems only over the past 15 years following the advent  
414 of miniaturized acoustic transmitters and the expansion of the PIT tag system within the  
415 Columbia River basin. The published studies collated in Table S1 report varying  
416 freshwater survival levels lying mostly within the 25-75% range for yearling Chinook.  
417 When scaled by migration distance, median survival rates of Columbia River basin  
418 yearling Chinook populations are either similar to or better than available populations  
419 from outside of the basin per 100 km of migration distance. Snake River steelhead have  
420 median survival and median survival rates very similar to Snake River yearling  
421 Chinook, and survival rates per 100 km are much better than those of all steelhead  
422 populations located outside the Snake River (Fig 2).

423

424            Within the Columbia River basin survival scaled by distance travelled is nearly  
425 constant for yearling Chinook irrespective of the source population and migration  
426 segment examined. For steelhead, downstream survival rates are lower in the Upper  
427 Columbia than the Snake River, but are still higher than values reported for outside of  
428 the Columbia River basin.

429            Both observations are at odds with conventional wisdom. Given the enormous  
430 focus over the past half century on improving smolt survival within the Columbia River  
431 hydrosystem, our interpretation is that these efforts were successful because survival  
432 rates are now higher than in undammed river systems. This result extends our earlier  
433 finding that Columbia River smolt survival was slightly higher than the adjacent  
434 undammed Fraser River [41], particularly for steelhead where estimates are now  
435 available for a substantial number of river systems. Thus, significant further  
436 improvement is unlikely because the Snake River now boasts the highest measured  
437 freshwater survival rates in the Pacific Northwest.

438

439            If survival rates were in fact low in the Columbia River basin, improvements in  
440 freshwater survival could potentially increase the SAR. For example, Chinook smolt  
441 survival in California ranged from 3-16% for a 516 km migration in the Sacramento  
442 River [42] to an astonishingly low 0-2% through the lower 92 km of the San Joaquin  
443 River Delta [43]. Such low survival provides substantial scope for potential  
444 improvement. This difference is important because the large drop in coast-wide SARs

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445    excluding California to around 1% and relatively high freshwater survival isolate the  
446    main conservation problem as being in the ocean.

447            Our results also indicate that the river mouth is a perilous location for smolts,  
448    something also noted in California [42], because survival rates scaled by distance are  
449    extremely low in rivers where post-release distance to the mouth is short, e.g., Keogh  
450    River and Big Beef Creek steelhead. Losses (presumably to predators) must be  
451    concentrated near the river mouth to result in this pattern, and continued losses from  
452    predation may well occur after ocean entry because smolts are still concentrated and the  
453    migration timing is predictable, conditions which cause predator aggregation in other  
454    situations [44, 45].

455            It is important to outline why past declines in freshwater survival cannot have  
456    been the driver of the observed drop in SARs—put simply, currently measured  
457    freshwater survival levels are too high. The longer SAR time series indicate at least a  
458    4-5 fold decline over time. However, for freshwater survival to be the cause of this  
459    decline in SARs, current values of freshwater survival cannot be more than 20-25%.  
460    That they are substantially higher for many populations (Fig 2) means that it is  
461    mathematically impossible for freshwater survival to have fallen far enough to explain  
462    the decline in SARs. For example, even if downstream survival through the dams was  
463    originally 80% prior to the 1970s and then fell to 40% this would “only” produce a  
464    two-fold decline in SARs, e.g., from 6% to 3%, so the scope for primarily freshwater  
465    regulation of SARs is limited.

466



467 **The importance of marine habitat**

468 Occam's Razor dictates that any coherent theory to explain the large and  
469 geographically widespread drop in survival to similar low levels should be applicable to  
470 all populations. We are unable to identify a consistent mechanism of action because of  
471 the current limits to our understanding of the ocean phase, but some explanations  
472 (various forms of anthropogenic freshwater habitat disruption) are clearly less likely as  
473 explanations of poor salmon survival than others (climate-related changes in the ocean).

474

475 Salmon, as well as other anadromous fish such as lamprey and eulachon,  
476 migrate widely across a complex landscape composed of many successive freshwater  
477 and marine habitats; even something as simple as the number of distinct habitats each  
478 salmon population occupies over the duration of the marine phase is unknown. The  
479 number of returning adults is therefore successively affected by changes in survival in a  
480 complex sequence of freshwater and marine habitats, most of which are poorly  
481 understood, as the product  $SAR = S_1 \cdot S_2 \cdot S_3 \cdot \dots \cdot S_n$ . If survival drops to 1/10th of its  
482 original value in any one of these habitats, the SAR will also decline equivalently  
483 unless density-dependent factors occurring at some later point in the life history buffer  
484 the impact on adult returns.

485

486 Despite this, conventional conservation thinking for Pacific salmon primarily  
487 focuses on freshwater habitat issues. The rationale for this focus can be traced back to  
488 two separate events first occurring in the 1970s. The first was the passage of the U.S.  
489 Endangered Species Act (ESA) in 1973, with its strong focus on protecting and

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490 preserving habitat as the paramount priority for conservation [46]. Canada’s Species at  
491 Risk Act was enacted in 2003, and was partially modeled on the US ESA. The  
492 Canadian legislation provided a remarkably broad definition of habitat, which  
493 essentially prohibited: “damaging or destroying the residence of one or more  
494 individuals”, with residence defined as “...a dwelling-place such as a den, nest or other  
495 similar area or place, that is occupied or habitually occupied by one or more individuals  
496 during all or part of their life cycles” ([47]; p. 227). Unfortunately, “habitat” in both  
497 countries is ill-defined for migratory animals such as salmon which occupy many  
498 different habitats as they complete their life cycle. The larger question, not discussed in  
499 either country’s legislation, is this: to what degree can (or should) habitat related  
500 declines in some part of the ocean phase be compensated for by remedial action in  
501 some other part of the life history? That is, excluding the direct impacts to habitat  
502 which are obvious candidates for correction, can (and should) ocean impacts be  
503 remediated by intervening in other points in the life history?

504

505           The second event, unappreciated at the time, was a major shift in ocean climate  
506 in 1977 which had impacts on a wide range of marine fish stocks as well as salmon  
507 across the entire west coast of North America [38, 39]. The timing of this regime shift  
508 also nearly coincided with the completion of the final Snake River dam forming the  
509 Federal Columbia River Power System (FCRPS) in 1975. Not surprisingly given the  
510 understanding of salmon dynamics in that era, the ensuing decline in adult salmon  
511 returns a few years later was ascribed purely to poor smolt survival through the dams;

512 however, as we have demonstrated, a similar drop in survival is seen in many other  
513 regions after 1977 and in purely marine species as well.

514

515         The decline in marine survival began earliest in the south and then progressively  
516 expanded farther north along the coast with time (Figs 3 & 7). Almost none of the  
517 rivers outside the Columbia have dams, so the argument that the poor performance of  
518 Snake River stocks is primarily due to the completion of the FCRPS is inconsistent  
519 with the broader data. (We are not dismissing the argument that extensive past  
520 modifications to the FCRPS have improved freshwater survival. Rather, we are making  
521 the point that further improvements in freshwater survival will have small or negligible  
522 impact on increasing adult returns and that the very large ocean impacts may in fact  
523 distort our understanding of how adult returns are related to freshwater modifications).  
524 As we will discuss, many other “single factor” reasons for poor salmon survival along  
525 the west coast also suffer from the same logical flaw that survival now seems to be poor  
526 everywhere.

## 527 **Overfishing alone can't explain the decline**

528         Wasser et al [48] cite this blanket statement: “Anadromous salmonids  
529 (*Oncorhynchus* sp.), which hatch in fresh water, migrate to the ocean, and then return to  
530 their natal waterways to breed, are threatened primarily by habitat loss from dams and  
531 overfishing (SOS 2011)” (Lines 98-101 of the SI). The sentiment underpinning this  
532 statement is widespread and reflects a fundamental problem with simply making a  
533 casual association between the assumed cause (freshwater habitat loss) and the effect  
534 (declining salmon stocks). We view the reality as considerably more nuanced: Fall

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535 (ocean-type) Chinook harvest levels of 50%-70% that were formerly sustainable are no  
536 longer sustainable because marine survival dropped 4-5 fold over the past few decades.  
537 The drop in marine survival is too large (75-80%) to be compensated by even the  
538 complete cessation of harvest. The magnitude of the gap is widely unappreciated, and  
539 the relatively small percentage difference between the harvest rate (50-70%) and SARs  
540 (75-80%) is misleading.

541

542           To fully compensate and maintain adult escapements, the initially sustainable  
543 harvests of the 1970s would have to be as large as the drop in marine survival has been.

544 Algebraically,

545

546            $E_1 = N \cdot S_1 \cdot (1 - h_1)$

547           and

548

549            $E_2 = N \cdot S_2 \cdot (1 - h_2),$

550

551           Here  $E_t$  is the escapement at time  $t$ ,  $N$  is the number of smolts beginning  
552 migration to the sea,  $S_t$  is the SAR, and  $h_t$  is the harvest fraction, where  $t=1,2$  is the start  
553 and end of the time series.

554

555           For escapement,  $E_t$ , to remain constant in the two time periods implies that

556

557           
$$\frac{S_2}{S_1} = \frac{(1 - h_1)}{(1 - h_2)}$$

558 or

559

$$h_1 = 1 - \frac{S_2}{S_1}(1 - h_2)$$

560

561 The maximum compensation management can make for declining marine  
562 survival occurs when all fisheries are curtailed completely ( $h_2=0$ ). In this case, ceasing  
563 or reducing harvest can only fully compensate if the initial rate of sustainable harvest is

564  $h_1 \geq 1 - \frac{S_2}{S_1}$ . The key feature of this equation is that it is the ratio of the current to the  
565 initial period marine survival that determines how large the initial sustainable harvest  
566 rate must have been to allow full compensation by harvest rate reduction. If marine  
567 survival drops by almost an order of magnitude, as it has in at least some regions,  
568 sustainability can only be maintained if the initial sustainable harvest rate was at least  
569 90%.

570

571 Taking the Columbia River basin as a less extreme example, marine survival  
572 has dropped from ~6% to 1%, so the initial harvest rate would have to be  $h_1 \geq 83\%$  to  
573 allow full compensation for changing environmental conditions. Historical harvest  
574 rates reported by the PSC [49] suggest that Chinook harvest rates were on the order of  
575 50%-60% for many subyearling stocks, implying that complete harvest rate  
576 compensation for declining marine survival would only be possible for survival ratios  
577 of  $S_2/S_1 \approx 0.4-0.5$  (or  $\sim 1/2 - 1/2.5$ ); far less decrease in survival than has actually  
578 occurred.

579

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580            The same major decline in survival can be seen in British Columbia after the  
581 1977 regime shift, the period when the first real measurements of SARs for other west  
582 coast regions started. Perhaps the best measurements documenting the magnitude of  
583 the drop in British Columbia SARs was reported by Bilton et al [50]. In the early  
584 1970s, SARs for Strait of Georgia coho of  $\bar{S} = 20.8\%$  (SE:  $\pm 0.5\%$ ) and  $S_{\text{median}} = 17.2\%$   
585 were obtained in extensive experimental hatchery releases (six replicates of each of  
586 three size classes of smolts in each of three months (April, May, and June)). The  
587 magnitude of these survival levels (ca. one in five smolts surviving to return as adults)  
588 justified Canada's decision to fund the Salmon Enhancement Program (SEP), a major  
589 investment in hatcheries. Yet less than two decades after the start of SEP in 1977,  
590 average coho SARs for the nearby Big Qualicum hatchery had dropped from 28.6%  
591 (1973-77 ocean entry years) to 5.6% (1990-99) and then to 1.5% (2000-2012) (data  
592 from [8, 51]). As a result, average survival rates dropped from 1 in 3.5 smolts in the  
593 1970s to 1 in 67 smolts—a decrease to 1/20th of the initial value. (See [8] for a  
594 detailed description of the decline over time in Strait of Georgia coho SARs).

595

596            To place the magnitude of this change in perspective, by the 2000s coho SARs  
597 in the Strait of Georgia were the equivalent to surviving through a sequence of  $n =$   
598  $\log(S_{2000s})/\log(S_{1970s}) = 3.4$  successive survival periods, with each time period  
599 equivalent to the entire survival process experienced by cohorts in 1973-77 (a time  
600 when intensive sport and commercial fisheries were operating, unlike recent years).  
601 Whatever the change in the environment was, it was the equivalent to the coho now  
602 remaining at sea for 60 months (five yr) instead of 1.5 yr while experiencing the overall

603 mortality rates characteristic of the 1970s. As coho harvest rates are near zero in recent  
604 years, it is essentially all natural mortality processes that are currently operative.

605

606            Statements about the major role of particular factors in driving salmon declines  
607 (dams in the Columbia River or salmon farming in British Columbia, which developed  
608 in the 1990s) must therefore be assessed critically because salmon from other regions  
609 lacking these specific factors also return from the ocean with very poor marine survival.  
610 Thus, dams or salmon aquaculture may contribute as habitat issues to overall losses, but  
611 the essential policy debate is (1) whether modifying their operation will materially  
612 contribute to improving salmon returns, and (2) whether proposed courses of action are  
613 actually credible and cost-effective given the primary influence of ocean conditions.

614

## 615 **The role of dams**

616            A wide range of west coast rivers lacking dams have similar or worse reported  
617 survival than the Snake River, both in terms of downstream smolt survival and adult  
618 return rates. We interpret this as evidence for a fundamental flaw in our biological  
619 understanding of the conservation factors controlling salmon productivity.

620

## 621 **Direct Mortality**

622            Conventional thinking holds that if average marine survival was 4-6% in  
623 regions without dams, then the four- to six-fold lower survival of Columbia River  
624 Chinook populations (currently ca. 1%) would be clear evidence that the Columbia  
625 River dams were the cause of poor survival. The conclusion would then be that

626 removing or modifying dams lying in the migration path of Snake River basin  
627 populations should increase SARs four- to six-fold, thereby achieving rebuilding  
628 targets. Yet the same conclusion, which has implicitly guided much conservation  
629 thinking, clearly cannot be used in reverse—presumably no one would argue that  
630 constructing eight dams in the Fraser River would double salmon returns, raising  
631 median Chinook survival in the years since 2000 from a mere 0.53% in the Fraser River  
632 to the Snake River’s current 1%. (Median SAR for all other Strait of Georgia yearling  
633 Chinook populations is also 0.53%; none have dams in the migration path).

634

635         A similar conclusion is evident when the level of survival through the FCRPS is  
636 assessed. Spring Chinook smolt survival through the 8-dam FCRPS ranges from 50-  
637 60% (Tables A.1 and A.2 of [5]), so even eliminating all sources of freshwater  
638 mortality during hydrosystem migration—direct impacts of the dams on survival,  
639 predation, and possible losses from disease—could only increase SARs by a factor of  
640  $0.5^{-1}$ - $0.6^{-1}$ , or 1.7-2%. These levels are well below official rebuilding targets. Further,  
641 because a significant fraction of the downstream loss is due to predation by birds [52]  
642 and fish [53], unless all predatory wildlife species are eliminated even an increase to  
643 1.7-2% SARs is unrealistic.

644

### 645 **Indirect (Delayed) Mortality**

646         The mathematical inability of even perfect hydrosystem survival to achieve  
647 minimum rebuilding targets likely underlies the theory that delayed mortality caused by  
648 multiple dam passage contributes to poor ocean survival [5, 54-64]. Three of five



649 Spring Chinook populations (Fig. 4) and all three steelhead populations (Fig. 8) from  
650 the mid-Columbia region not migrating through the Snake River dams have  
651 substantially higher SARs than Snake River populations, supporting this view;  
652 however, when a broader range of populations is considered the delayed mortality  
653 theory is not supported.. For example, most mid-Columbia stocks of subyearling  
654 Chinook and two of five mid-Columbia yearling Chinook have similar or lower SARs  
655 relative to Snake River populations (Fig. 4). A similar pattern of anomalously high  
656 SARs is also seen for two Washington Coast steelhead populations and one (each)  
657 Strait of Georgia and Puget Sound Fall Chinook populations despite the majority of  
658 nearby populations having SARs consistent with the Snake River median (Figs. 4 & 8).  
659 Thus it is unlikely that greater dam passage causes delayed mortality in the estuary or  
660 ocean both because something unrelated to dam passage also causes a few populations  
661 to have substantially higher survival by the time the adults return from the sea in river  
662 systems lacking dams and because many populations lacking dams in the migration  
663 path now have similarly low levels of survival.

664

665 **Misplaced efforts: Case studies where the marine**  
666 **environment was implicated, but fresh water research was**  
667 **initiated**

668         The data analyzed in this paper demonstrate both a long term coast-wide decline  
669 in survival for Chinook and steelhead and that the cause of the low SARs must  
670 predominantly be located during the marine phase of the life history. Although

671 managers have moved to reduce Chinook harvest to partially compensate for the drop,  
672 relatively little has been done to determine the cause of the decrease in marine survival  
673 because much of the focus remains on remediating freshwater habitat.

674

675           Festinger [65] first defined the term “*cognitive dissonance*”. In brief, it can be  
676 described as the inability to recognize the true problem, despite the evidence. More  
677 formally, in psychology the term has come to mean the process by which an individual  
678 manages inconsistent thoughts, beliefs, or attitudes, especially as relating to behavioral  
679 decisions and attitude change, by modifying aspects of their cognitive process to  
680 achieve internal consistency; for example, discounting or diminishing data inconsistent  
681 with the individual’s pre-existing beliefs.

682

683

684           The history of west coast salmon management suggests that cognitive  
685 dissonance concerning the marine survival problem is widespread and the reason  
686 declining salmon stocks are redressed by addressing primarily freshwater habitat issues.  
687 (Interested readers should also consult Janis [66] (especially Chapter 8) for an excellent  
688 summary of the sociological factors leading to “*groupthink*” and the poor decision  
689 making processes that result). We now review three case studies to illustrate how  
690 cognitive dissonance seems to be at play in determining past operational responses to  
691 falling marine survival: (i) Rivers-Smith Inlet sockeye (Central B.C.); (ii) Columbia  
692 River Chinook and steelhead; and (iii) Upper Fraser steelhead.

693 ***Rivers and Smith Inlet Sockeye (B.C.)***

694 The Rivers-Smith Inlet sockeye complex formed the second largest sockeye  
695 fishery in British Columbia for much of the last century (the Fraser River being the  
696 largest). Adult harvest levels averaged around 1M sockeye for six decades (1910-  
697 1970), and escapement (measured from the late 1940s forward) was stable at ca.  
698 400,000 adults [67]. The Rivers and Smith Inlet populations are located in adjacent  
699 watersheds in the remote central coast of BC where there is little anthropogenic impact.

700 Following 1970, the productivity of both the Rivers and Smith Inlet sockeye  
701 populations suddenly collapsed [67-72]. Because escapement remained stable until the  
702 1970s [67], recruitment overfishing did not occur during this period. Probably because  
703 of the isolated location and the lack of any other nearby significant salmon fisheries,  
704 prompt management decisions to reduce harvest to near zero were promptly taken and  
705 were maintained. However, despite harvest being curtailed, the stocks did not recover  
706 as standard fisheries theory would predict, although escapements remained stable.  
707 Following the next ocean regime shift in 1989, escapement levels fell to record lows,  
708 from >1 million spawning adults to ca. 9,500 adults by 1999—a collapse to 1/100<sup>th</sup> of  
709 the original stock size in just over two decades. Because the fishery had already been  
710 curtailed, no further management action was possible to compensate for the second  
711 drop in survival. There was also evidence that additional nearby sockeye stocks were  
712 impacted similarly [72]. Thus, the stock collapsed despite prompt and full action by  
713 management.

714 A study of the management response [67] to the collapse detailed the reasons  
715 for rejecting a freshwater cause (including using data extending back over half a

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716 century to demonstrate that pre-smolt abundance in the lake was above the long-term  
717 mean). The authors noted that “*Poor marine survival is the most parsimonious*  
718 *explanation for the declining fry-to-adult survival in Owikeno Lake, particularly in*  
719 *light of coincident declines in sockeye salmon returns per spawner at Long Lake (a*  
720 *nearby pristine watershed) and declines in adult sockeye salmon abundance in other*  
721 *populations to the north of Rivers Inlet.*”

722

723           The key findings from a joint federal and provincial government technical  
724 committee reviewing the collapse are worth quoting verbatim [68, 70]:

725           “(1) *The drastic declines in abundance appear to be due to an extended period*  
726 *of poor marine survival that cannot be explained by any one event, such as sea-entry*  
727 *during an unusual El Niño year. At least two recent years (1996 and 1997) show signs*  
728 *of near-zero marine survival, but the reasons for those low survival rates are not known*  
729 *at this time.*

730           (2) *There is little evidence to suggest that logging or other human activity in*  
731 *either of the drainage basins has had more than small and localized impacts on sockeye*  
732 *spawning and rearing. The simultaneous declines in both basins – i.e., in Owikeno,*  
733 *where there has been extensive logging and in Long Lake, where there has been very*  
734 *little – is convincing evidence that the cause of the declines does not lie in freshwater*  
735 *habitat disturbance”.*

736

737           The Rivers-Smith Inlet study is to our knowledge unique in North America.  
738 Not only do the twin conclusions state that the problem lies in the ocean, they also state

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739 that freshwater habitat problems were not contributive—something that is generally not  
740 possible to rule out with certainty for most salmon populations.

741

742           The joint technical committee then recommended necessary research to clarify  
743 the cause of the collapse, and regulatory action that might be taken to improve the  
744 situation. Strikingly, despite the conclusions quoted above, marine survival is not cited  
745 in any of the research which the various review committees recommended pursuing  
746 [68-70]. Instead, the committees recommended three research foci:

747           “(1) *determine absolute escapement levels to Owikeno Lake... in order to*  
748 *improve the credibility of stock assessment;*

749           (2) *improve the understanding of habitat use... by sockeye juveniles in Owikeno*  
750 *Lake and smolts in the Wannock estuary; and*

751           (3) *investigate the status of ocean-type and lake-spawning sockeye, which are*  
752 *less familiar and, although not specifically covered in this plan, may require future*  
753 *intervention*”. (The joint committee noted that there was some evidence for an unusual  
754 sockeye life history type that went directly to sea without rearing in the lake for a year  
755 as pre-smolts (the normal life history pattern) [70]; the other committee reports have  
756 similar language).

757

758           No mention is made of addressing the marine survival issue that was at the core  
759 of the collapse; the reference to improving the understanding of smolt habitat use in the  
760 “Wannock estuary” mentions that “*sockeye smolts do not appear to rear in these*  
761 *estuaries for much time*” [69]. The report further mentions that there are numerous

762 estuaries within River and Smith Inlets, with varying sizes and importance to  
763 salmonids. It is unclear why the Wannock was identified as particularly worthy of  
764 investigation, but the report does note that “*approximately 25% of the Wannock estuary*  
765 *was dyked and filled in 1973 for a log dump facility*” (i.e., almost two decades earlier).

766

767           The recommendations under Habitat are even more striking:

768           “5. *Existing conceptual plans for habitat restoration developed by DFO, the provincial*  
769           *Watershed Restoration Program, and other stakeholders should be evaluated*  
770           *for their potential long term benefits to sockeye, and the feasibility of proposed*  
771           *restoration projects should be thoroughly assessed.*

772           6. *Habitat restoration projects could include the reconnection of spawning and early*  
773           *rearing habitats along the margins of floodplains and in side-channels that have*  
774           *been isolated by road construction or degraded by natural and logging-related*  
775           *activities.*

776           7. *Any habitat restoration projects that are undertaken should be monitored to*  
777           *determine their benefits for sockeye.*

778           8. *DFO and other agencies and stakeholders should continue to collaborate on*  
779           *developing habitat protection strategy during resource development planning*  
780           *processes (e.g., CCLCRMP, Forest Development Plans).*

781           9. *The site-specific and cumulative impacts of logging on habitats used by sockeye*  
782           *should be more comprehensively evaluated”. (ref. [70]; the other committee*  
783           *reports have similar language).*

784

785

786 In other words, despite the reports identifying with high certainty that  
787 freshwater habitat issues were not contributory, the committees did not attempt to  
788 understand the marine drivers and instead advocated a series of actions in freshwater.

## 789 ***Columbia River***

790 Two nearly contemporaneous studies identified the importance of either estuary  
791 (lower river) or ocean processes in controlling the poor survival of Snake River salmon.  
792 First, Kareiva *et al.* [73] applied a matrix life cycle model to demonstrate that recovery  
793 of endangered salmon populations in the Columbia River could only be achieved by  
794 improving survival in the lower river/estuary or in the coastal ocean and that (similar to  
795 our own argument) even raising main stem survival to 100% would not prevent  
796 extinction. Second, Marmorek and Peters [74] in a review of the PATH (Plan for  
797 Analyzing and Testing Hypotheses) process, stated “*Importantly, we found that the*  
798 *different models’ estimate of the survival rate of in-river migrants through the*  
799 *hydropower system, a hotly debated value, was NOT an important determinant of*  
800 *overall life cycle survival. Rather, the key uncertainties that emerged from these*  
801 *sensitivity analyses were related to the cause of mortality in the estuary and ocean*”.  
802 (See also [31]).

803

804 Probably owing to the lack of any direct information on juvenile survival in the  
805 lower Columbia River and estuary regions, two initiatives were subsequently funded:  
806 (a) the development of the JSATS acoustic telemetry system [75], and (b) directed  
807 research using commercially available telemetry equipment to formally test the delayed

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808 mortality hypothesis in the lower river and coastal ocean [76]. Both approaches  
809 established that survival was high in the lower river below Bonneville Dam and lower  
810 (but still high) in the estuary/plume region [56, 77-81]. The studies by Rechisky et al  
811 extended these results further, showing that survival was even lower in the coastal  
812 ocean region extending from the Columbia River plume to the NW tip of Vancouver  
813 Island.

814

815            Despite these findings, further work to measure ocean survival and directly  
816 address the conclusions of Kareiva *et al.* [73] and Marmorek and Peters [74] was not  
817 carried out. After the ocean phase was identified as being the likely cause of poor  
818 returns and not the lower river, research shifted to focus exclusively on studying  
819 freshwater survival upstream at the hydropower dams. Although several publications  
820 subsequently identified the presence of smolts in side channels within the estuary and  
821 suggested the potential importance of estuarine wetlands for salmon conservation [82-  
822 86], we are unaware of any studies that have actually identified low survival in the  
823 estuary or established the period of residency—necessary requisites for improving  
824 SARs. In summary, ocean issues remain largely unaddressed by Columbia River basin  
825 salmon managers, and it is unclear whether research solely focussing on freshwater or  
826 lower river/estuary issues will compensate for poor ocean survival.

827

828            Overall, these studies demonstrate a consistent pattern: a strong proclivity to  
829 preferentially identify and work on freshwater habitat, even in cases where marine



830 survival has been identified as either the sole or most serious detriment to population  
831 growth.

832

833           We are not arguing that freshwater monitoring should not be conducted;  
834 monitoring population trends, and particularly survival, is critical to making informed  
835 management decisions. However, monitoring alone is insufficient. As we noted in the  
836 Introduction, the survival data used in this paper amount to a total of more than 3,000  
837 years of sampling effort. Recent work in BC documented a substantial decline in  
838 monitoring effort in north-central BC, and the authors argued that the situation must be  
839 improved if salmon conservation efforts are to be effective [87]. While some degree of  
840 monitoring is necessary, we note that the previously substantial monitoring effort was  
841 insufficient to develop a successful management response. Obviously, if agencies  
842 cannot respond effectively to the already available data indicating a widespread  
843 collapse in marine survival of salmon populations that has been formally submitted to  
844 the PSC on an annual basis, then it is unclear why simply increasing monitoring further  
845 will lead to a more effective response. Clearly, greater monitoring alone does not  
846 necessarily lead to improved conservation outcomes.

847

## 848 **Managing salmon research**

849           We are troubled that the increase in monitoring evident as survival has dwindled  
850 over time was not matched by an equally intensive analysis to assess whether existing  
851 approaches to salmon management are correct. Salmon smolt survival could only be  
852 measured in most river systems after the relatively recent development of acoustic

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853 telemetry, and PIT tags in the Columbia River Basin. Excluding smolt survival data  
854 and focusing only on the adult survival (SAR) data, the number of years of available  
855 data for Chinook and steelhead demonstrates a massive increase in monitoring over the  
856 decades (pre-1975: 117 yrs; 1976-85: 318 yrs; 1986-95: 456 yrs; 1996-2005: 715 yrs;  
857 2006-2014: 918 yrs). Yet, despite a nearly order of magnitude increase in monitoring  
858 outputs, the point that basic aspects of this data set are in fundamental disagreement  
859 with common assumptions about the cause of the “salmon problem” has gone  
860 unrecognized. In brief, a minor industry has developed in salmon monitoring, but the  
861 implications remained unappreciated.

862         We view it as critical that the roles of various proposed deleterious impacts on  
863 salmon returns be rigorously quantified, rather than simply identified as important  
864 without careful thought about other potential contributing factors. As both Lackey [88,  
865 89] and Kareiva and Marvier [90] have noted, there is a widespread implicit assumption  
866 that ecosystems unaltered by human activity are inherently good, and that restoring  
867 anthropogenically altered freshwater ecosystems will help redress the problems (e.g.,  
868 [91]).

869

870         Further, competing economic activities may be unfairly blamed for the ongoing  
871 collapse of several important salmon species and unrealistic expectations placed on  
872 what various recovery options may actually achieve. This is not simply restricted to  
873 dam removal in the Columbia River basin or banning open-net salmon aquaculture in  
874 British Columbia, two current hot button issues, but extends to impacts of forestry,  
875 competing rights to groundwater, or development in general. Policy options for

876 promoting Chinook recovery need to recognize that the wide geographic footprint of  
877 poor salmon survival likely implies that efforts focused on “fixing” possible  
878 contributing factors specific to some regions are unlikely to be effective. At the very  
879 least, these efforts should be held to a significant standard: (a) clearly demonstrating a  
880 real and substantive improvement is possible, and (b) demonstrating a clear benefit  
881 relative to the proposed costs.

882

### 883 **Refocusing on marine migration pathways**

884           The pattern of variation in SARs along the west coast of North America  
885 suggests that a progressive worsening of marine survival with time occurred and was  
886 accompanied by a geographic expansion northward in the region of poor survival.  
887 However, several aspects of this explanation seem to be inconsistent with the roughly  
888 similar coast-wide SARs now observed.

889

890           Fall Chinook are believed to remain shelf-resident for their entire marine phase  
891 while Spring Chinook migrate north on the shelf before eventually moving off-shelf or  
892 into the Bering Sea/Aleutian Islands. Because both groups have poor SARs, this would  
893 imply that the area of poor marine survival might be restricted to the coastal shelf off  
894 Washington, British Columbia, and SE Alaska; however, the large-scale collapse in  
895 adult Spring Chinook returns includes the Yukon and Kuskokwim Rivers (draining into  
896 the Bering Sea) and the Kenai River (Cook Inlet, Gulf of Alaska) [20-23, 92, 93]. This  
897 suggests that either the area of poor marine survival is now simultaneously large, so  
898 that exposure times to regions of poor survival are similar, or that all stocks congregate

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899 at some point in the marine phase into a more geographically confined region where  
900 their survival is similarly affected.

901

902         We have no evidence for the latter possibility. Fall (subyearling) Chinook  
903 stocks only migrate as far north as SE Alaska [94, 95] after one or more years at sea  
904 (and at least some Strait of Georgia and Puget Sound Chinook remain resident in  
905 southern BC waters for their entire marine lifespan [96-100]). The marine movements  
906 of eulachon [24] and lamprey [25], which have also undergone dramatic declines in  
907 abundance, are less well-known but are likely similar to Fall Chinook. Thus, the  
908 conditions leading to poor marine survival must be geographically widespread because  
909 western Alaska Spring Chinook are not known to migrate to the shelf region off SE  
910 Alaska or BC.

911

912         A key prediction is that stocks with the lowest SARs should have greater  
913 exposure to poor ocean conditions in southern regions. The anomalously high SARs of  
914 some specific salmon populations (Fig 4) might provide the basis for an explicit test of  
915 this prediction. Although our understanding of population-specific differences in  
916 marine migration routes is currently very limited, especially for steelhead [101, 102],  
917 there is now some developing evidence for differential salmon survival in the sea; e.g.,  
918 [100, 103-105]).

919         Assuming that the region of poor survival progressively expanded northward  
920 along the coast at the time of successive regime shifts, there are several testable  
921 hypotheses. For example, Strait of Georgia or Puget Sound Chinook populations may

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922 have lower survival than adjacent outer coast stocks (west coast Vancouver Island,  
923 coastal Washington) because they either remain resident for a longer time period in  
924 coastal marine waters with similar survival rates (greater exposure), or because survival  
925 rates per unit time are lower in Strait of Georgia waters (greater rates of loss). This  
926 could also potentially explain why SE Alaska and north-central BC Chinook stocks in  
927 recent years still have SARs ~2X Snake River stocks and ~4X Strait of Georgia stocks  
928 (Fig 6)—Strait of Georgia Chinook stocks remain resident in the Strait of Georgia for  
929 multiple months after ocean entry [106, 107], while Snake River yearling Chinook  
930 juveniles promptly migrate north along the outer shelf to Alaska [55, 56, 108].

931

932            In this context, the consistently low survival of the Dworshak Hatchery  
933 yearling Chinook relative to other Snake River Chinook stocks is noteworthy; mean  
934 survival from Lower Granite Dam to adult return over the 2000-2015 period was only  
935 0.58% for the Dworshak Hatchery stock versus 1.28% for McCall Hatchery and 1.29%  
936 for Imnaha Hatchery fish (ref [5], Tables B.16, B.22, & B.24). The Dworshak SAR is  
937 thus less than ½ that of the other two populations. All Snake River populations migrate  
938 through the same set of dams, so one explanation for the particularly low survival of the  
939 Dworshak population could be a differential migration to an area of the North Pacific  
940 (or Bering Sea) whose relative survival prospects was only one-half that of other  
941 regions (Columbia River Chinook salmon are known to be seasonally present in the  
942 Bering Sea and to overwinter in the Gulf of Alaska [109]). Our tenuous understanding  
943 of where Chinook and steelhead migrate to in the ocean and how long they remain in

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944 various regions (let alone how these patterns differ between populations) clearly needs  
945 urgent improvement if these issues are to be resolved.

946

947            One important possibility for establishing the geographic differences in survival  
948 is if predators increasingly target returning adult salmon. There is now ample evidence  
949 for substantial increases in marine mammal abundance and presumably predation on  
950 returning adults [110-115]. Ohlberger et al [116] reviewed the decline in size and age-  
951 structure of Chinook across western North America. They noted that consistent with  
952 the adult predation hypothesis, the decline was most pronounced in the older age  
953 groups in some (but not all) regions of the eastern Pacific. Recent work has also  
954 demonstrated that in fish, large females may confer higher fitness on their offspring  
955 [117].

956

957            Competition for food may also conceivably play a role. The geographically  
958 widespread decline in salmon growth over time seen for multiple species by the mid-  
959 1990s, and which was potentially attributed to the growth of hatchery production of  
960 pink salmon [118] has apparently continued. Continued increase in pink salmon  
961 abundance has been shown to affect plankton populations [119] and reduce survival of  
962 at least one marine seabird (shearwaters) [120, 121] as well as some salmon species [4,  
963 122]. Thus, geographically variable rates of competition with pink salmon or marine  
964 mammal predation at older ages could both contribute to determining differential rates  
965 of salmon survival.

966

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967            Large differences in SARs point to important directions for future study. A  
968    very few stocks have SARs 3 to 4-fold higher than nearby stocks. At the extreme, the  
969    Chilliwack stock of Fall (subyearling) Chinook has a median SAR of ca. 4%, an order  
970    of magnitude greater than other nearby Strait of Georgia stocks. Oregon Coastal Fall  
971    Chinook also have SARs much higher than any Columbia River basin stocks.  
972    Understanding why only a few populations consistently have high SARs when  
973    returning from the ocean as adults could pay large dividends in understanding what  
974    differences in ocean experience result in those few populations remaining productive  
975    while many others have essentially collapsed. As Peterman and Dorner [13] remarked  
976    for sockeye, “*Further research should focus on mechanisms that operate at large,*  
977    *multiregional spatial scales, and (or) in marine areas where numerous correlated*  
978    *sockeye stocks overlap*”. The markedly higher SARs evident for Oregon coastal  
979    Chinook relative to most other populations (Figs 4 & 5) may provide important  
980    guidance in this context. Riddell et al [123] (p. 580) specifically note the unique  
981    marine distributions of southern Oregon Chinook stocks, which restricts them for their  
982    entire ocean phase to life in the California Current. Nicholas and Hankin [124] (Table  
983    2) report that Fall Chinook from the Salmon and Elk rivers in Oregon are north  
984    migrating stocks and that Oregon coastal stocks show variation in ocean migration  
985    “*with some migrating north, some south, and one stock has a mixed north and south*  
986    *ocean migration*” [14]. Lending credence to the possibility that ocean migration  
987    pathways influence productivity, Nehlsen et al [14] reported that the few “south  
988    migrating” Oregon Fall Chinook stocks were all characterized as having “depressed”

989 runs in 1988 (prior to the 1989 regime shift), whereas the “north migrating” runs all had  
990 no or increasing abundance trends.

991

992           It thus seems plausible that specific salmon populations have genetically  
993 determined migration behaviours that allow them to home to distinct feeding grounds  
994 within the North Pacific, some of which confer better survival [125]. Batten et al [126]  
995 identified at least 10 geographically distinct plankton communities evident in a single  
996 transect across the North Pacific that were temporally stable across years and  
997 demonstrated that geographically distinct seabird assemblages patterned similar to the  
998 plankton communities. An analysis of tufted puffin communities [127] found that  
999 different forage fish communities also were present in different sub-regions of the  
1000 Aleutian Chain. Thus geographically stable and distinct biological communities exist  
1001 within the North Pacific Ocean, including the pelagic offshore. Salmon populations  
1002 homing to different feeding grounds (or a succession of different feeding grounds)  
1003 could therefore have very different fates if these regions develop differently over time,  
1004 for which there is at least some experimental evidence [99, 128, 129].

## 1005 **Columbia River basin policy implications**

1006           A critical policy question for the Columbia River basin concerns whether  
1007 recovery of listed fish stocks is limited by the hydropower system as currently operated,  
1008 or by ocean conditions [130]. The available evidence indicates that smolt survival  
1009 during downstream freshwater migration is not higher in rivers without hydropower  
1010 dams (Fig 1 and Table S1) and that a number of much shorter coastal rivers have even



1011 lower smolt survival than is experienced through the Columbia River hydrosystem,  
1012 particularly when survival is scaled by distance travelled.

1013

1014            Bisbal and McConnaha [130] suggest several ways in which aspects of the  
1015 freshwater habitat might be manipulated to improve ocean survival. However, given  
1016 that recovery targets are specified in terms of attained SARs, current evidence indicates  
1017 that Snake River SARs are roughly equal to (or better) than those currently achieved in  
1018 the nearby Salish Sea region, a region where dams are absent. It therefore seems  
1019 unlikely that recovery can be achieved without an improvement in ocean survival.  
1020 Unfortunately, current scientific knowledge is simply insufficient to understand how to  
1021 promote this.

1022

## 1023 **The future of Pacific salmon**

1024            Salmon are cold water fish living in a rapidly warming world. There are no  
1025 easy answers for maintaining Pacific salmon populations [131] and current problems  
1026 are likely to get much worse. At least eight separate ice ages are recorded in the last  
1027 800,000 years of the ice core record alone [132] and there were likely more than 50 ice  
1028 ages over the past 2.6M year extent of the Quaternary [133]. Climate change is thus the  
1029 norm, not the exception. However, projected levels of future climate change are far  
1030 outside anything experienced in either the last 150 years of industrialization or the  
1031 previous 2.5M years of the Pleistocene Epoch. Recent marine heat waves along the  
1032 Pacific Coast [134] are thought to have had significant negative effects on adult salmon  
1033 returns [135]. The frequency, duration, and intensity of marine heat waves are all

1034 projected to increase dramatically in future [136], further exacerbating already serious  
1035 problems for salmon.

1036

1037           Current CO<sub>2</sub> emission policies are expected to limit warming by 2100 to  
1038 approximately 3.0°C [137], or more than four times greater warming than the total  
1039 warming experienced over the past 150 years of the instrumental record (~0.7°C).  
1040 Even if all countries meet their commitments under the Paris Agreement, these  
1041 emissions scenarios are predicted to see global mean temperatures stabilize at 1.5–  
1042 2.0°C above pre-industrial levels, or ca. 2-3 times the temperature increase so far—and  
1043 an increase achieved in the next 80 years, not 150 years.

1044

1045           Warming rates 4-6 times those experienced in the recent past mean that further  
1046 surprises in how much salmon survival drops are inevitable. Given the past slow and  
1047 erratic response, the likelihood that the fisheries community will identify the correct  
1048 drivers of the problem and then move to successfully address them is not high if current  
1049 practice continues. So far, the response has been to re-double efforts on what we know  
1050 how to study (freshwater) and to largely avoid what we currently have little ability to  
1051 study (the marine phase). There are real economic, social, and biological costs to doing  
1052 so, with many groups now identifying various single issue factors as the primary  
1053 underlying problem that needs to be fixed (hydropower dams, salmon aquaculture,  
1054 forestry, land use practices, water rights). These region-specific issues cannot possibly  
1055 be the drivers of the continental-scale response that we document and to further delay  
1056 not only increases the threat to salmon, but to those species that rely on them, such as

1057 southern resident killer whales. Wasser et al [48] state that “*Low availability of*  
1058 *Chinook salmon appears to be an important stressor among these fish-eating whales as*  
1059 *well as a significant cause of late pregnancy failure, including unobserved perinatal*  
1060 *loss... Results point to the importance of promoting Chinook salmon recovery to*  
1061 *enhance population growth of Southern Resident killer whales.” There are many real  
1062 consequences to ineffective policy responses—lost time, inability to boost salmon  
1063 abundances (for both human and non-human salmon predators alike), and elevated  
1064 costs for many other industries.*

1065

1066         The history of North American marine research on Pacific salmon has been  
1067 described elsewhere [138-140]. In the last decade, small-scale efforts to describe the  
1068 marine life history of juvenile salmon have developed in specific regions of the  
1069 continental shelf (no small feat in itself; e.g., [141-145]). However, life history  
1070 observation is useful to infer possible mechanisms affecting overall biology, not to test  
1071 and validate the mechanisms driving survival. This means that the rapid learning  
1072 characteristic of physics or chemistry, where hypotheses are explicitly tested and  
1073 important scientific advance occurs when theories are rejected (not merely advanced),  
1074 is unlikely because it is difficult to refute observation-based mechanisms. A key issue  
1075 is that if marine survival problems are widespread along the Pacific Coast, mechanisms  
1076 specific to only some continental shelf regions or river watersheds cannot be the major  
1077 driver unless the movements of all the different salmon populations expose them to  
1078 these stressors. Because poor marine survival is demonstrably widespread, research

1079 and policy predicated on the assumption that the problems are geographically specific  
1080 is unlikely to be successful.

1081

1082            Given the massive investment in restoration and monitoring activities for  
1083 Pacific salmon, the development of correct conservation analyses and policy planning  
1084 is critical. Over \$1 Billion is now spent annually in the continental United States alone  
1085 on freshwater habitat restoration [146, 147], and there is great pressure to remove or  
1086 modify hydropower dams in the Columbia River basin to rebuild salmon runs to  
1087 historical levels of abundance and productivity and more recently to help endangered  
1088 orca populations [48]. Within the Columbia River, the total cost of recent conservation  
1089 efforts reaches or exceeds ca. 25% of FCRPS annual revenues (including foregone  
1090 clean power generation), or >\$0.5 Billion per year [148]. Similarly, in British  
1091 Columbia, where dams are not present in the migration paths, much effort has focused  
1092 on removing salmon farms to help restore Fraser River salmon populations [149-151].  
1093 Clearly, it is important to understand the impact of various anthropogenic impacts on  
1094 poor salmon returns, but it is also important that the real prospects for improvement as  
1095 a result of these region-specific actions are carefully assessed.

1096

1097            In the novel “The Sun Also Rises”, the character Bill Gorton is asked how he  
1098 went bankrupt. He replied, “*Two ways. Gradually, then suddenly.*” [152]. The same  
1099 process appears to be playing out in the ways fisheries science has addressed the marine  
1100 survival problem for salmon. In west coast salmon management, the first issue was  
1101 incorrectly diagnosing the problem (poor and worsening ocean survival) as primarily a

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1102 freshwater issue, and the second problem was failing to change behaviour quickly and  
1103 maintaining a focus largely on freshwater issues (which may inflict significant costs on  
1104 other economic activities). As with economic bankruptcy, failing to staunch losses and  
1105 persisting with previously unsuccessful behaviour is a recipe for eventual catastrophic  
1106 loss. Some positive response is certainly evident, in that harvest from Chinook and  
1107 steelhead fisheries was substantially restricted (e.g., [49]). However, harvest rates of  
1108 shelf-resident Fall Chinook were historically in the 50%-60% range. As we have  
1109 demonstrated, even the complete elimination of all harvest can only compensate for a  
1110 roughly two-fold decline in marine survival; for Spring Chinook and steelhead, which  
1111 are much less impacted by saltwater harvest, maximum compensation is far less.

1112

1113           It is not unreasonable to anticipate a further ten-fold decline in the marine  
1114 survival of salmon from climate change in the relatively near future. In fact, the  
1115 survival time series used in this manuscript generally end prior to 2015. The datasets  
1116 therefore do not include more recent years of even worse anticipated survival. An  
1117 overall pattern of low smolt to adult returns of upper Columbia and Snake river Spring  
1118 Chinook salmon and steelhead has been reported for 2015-16 and is considered likely  
1119 to worsen given the apparently poor early ocean survival of juvenile salmon in 2017  
1120 and unprecedented ocean conditions occurring in 2018 in the Northern California  
1121 Current and Gulf of Alaska [153-155].

1122

1123           With the option of reducing harvest rates now almost exhausted, large  
1124 reductions in escapement can now be expected similar to what occurred in the Rivers

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1125    Inlet case study. Without improved understanding of what is happening at sea,  
1126    potentially inappropriate policy recommendations seem likely to continue. As we have  
1127    shown in the case studies, each time salmon research reached the point where it became  
1128    clear that the survival problem was at sea, the ensuing response was to re-focus effort  
1129    on freshwater activities, leaving the marine survival issues unaddressed while often  
1130    increasing potentially costly freshwater interventions. We view this as evidence of  
1131    widespread cognitive dissonance [65] and significant groupthink [66] in salmon  
1132    management. A useful first step towards breaking the current impasse would be to  
1133    determine whether differences in early marine migration pathways and survival of  
1134    geographically close populations cause the strongly disparate SARs that we document  
1135    for some populations.

1136 **Methods**

1137 **Smolt survival data**

1138 To assess freshwater survival levels for Chinook and steelhead smolts migrating  
1139 downstream, we collated all published studies for west coast North American rivers  
1140 (Table S1), excluding California, and then scaled survival by distance travelled. In a  
1141 previous paper [41], we collated data for the Fraser-Thompson and Columbia-Snake  
1142 rivers for comparison. Our current paper includes available survival estimates from  
1143 coastal Oregon to northern Vancouver Island as well as one additional smolt survival  
1144 study for the Fraser River (Chilko Chinook).

1145

1146 Smolt survival during downstream migration was available for several regions,  
1147 but the data are most extensive in the Columbia River basin where PIT tag-based  
1148 studies have been conducted for over two decades and since the more recent  
1149 development of acoustic tags (Juvenile Salmon Acoustic Tracking System (JSATS) or  
1150 VEMCO). In other river systems, survival during downstream migration was estimated  
1151 using VEMCO acoustic telemetry; there are no published PIT tags survival estimates  
1152 outside the Columbia River basin. A total of 531 estimates, representing 73 individual  
1153 populations, runs or release sites, and time series between 1-23 years in length were  
1154 used in the comparison. All survival estimates were calculated using the Cormack-  
1155 Jolly-Seber model or its derivatives. The specific methods can be found in the sources  
1156 listed in Table S1.

1157

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1158            Within the Columbia River, smolt survival was estimated from various release  
1159 points including dams, traps located in rivers, and hatcheries. Downstream census  
1160 points were PIT arrays located at dams or acoustic receiver arrays in the lower  
1161 Columbia River or estuary. In the Columbia River basin, and particularly the Snake  
1162 River, a proportion of smolts are diverted into barges at the dams and then transported  
1163 downstream to below the lowest (Bonneville) dam; these fish were not included in the  
1164 hydrosystem estimates, but may have been included in lower river and estuary  
1165 estimates. Most Columbia River basin smolt survival estimates (N=461) were  
1166 calculated by NOAA or the Fish Passage Centre using PIT tag data. Twenty-eight were  
1167 from JSATS or VEMCO acoustic tag studies. Smolt survival in the basin was measured  
1168 over distances ranging between 144 - 909 km.

1169

1170            In the other regions, smolt survival was estimated from hatcheries or traps, to  
1171 acoustic receiver arrays near the river mouths. In some cases, fish were transported  
1172 either upstream or downstream of their tagging location, e.g., Chilko Chinook were  
1173 reared at a lower Fraser River hatchery but released ~500 km upstream in the Chilko  
1174 River. Migration distances to the sea after release were typically much shorter than in  
1175 the Columbia or Fraser Rivers (see Table S1). Excluding the Fraser and Columbia  
1176 River populations, average smolt migration distance was only 19 km for all other  
1177 regions.

1178

1179            To better compare survival across basins we scaled survival measurements by  
1180 the migration distance. We used distance because travel time was not reported for all of



1181 the studies. We excluded survival estimates from [41] that were based on populations  
1182 where >75% of smolts had fork lengths not meeting current best practices on acceptable  
1183 tag burdens [156-161] (<130 mm for VEMCO V7 and < 140 mm for V9). This  
1184 resulted in the exclusion of three survival estimates from the Nicola and Spius River  
1185 tributaries of the Fraser River because of high tag burden that were included in our  
1186 earlier paper [41].

### 1187 **Data sources for Chinook**

1188            Most survival rates of Pacific salmon are based on mark-recapture efforts,  
1189 where juveniles are “marked” or implanted with a tags--either coded wire tags (CWT)  
1190 or passive integrated transponder (PIT) tags, and recaptured in the fishery or upon  
1191 return to the river. The basic tag technologies are well described elsewhere [162-166].

1192

1193            CWT technology dates back to the 1960s. A review is provided by [167] and  
1194 the application of the methodology to coastal marine migrations of coho and Chinook is  
1195 described by [95, 168] and to measuring harvest and survival by [21, 49, 169].

1196 Because the tag is implanted in the nose cartilage of smolts, the fish must be dissected  
1197 to recover the tag after capture, ensuring the death of that particular tagged animal and  
1198 preventing further study of its movements. CWT technology provides the basis for the  
1199 Pacific Salmon Commission’s Chinook survival database used for coast-wide  
1200 management of Chinook salmon under the Pacific Salmon Treaty [49]. We used this  
1201 database as the source of Chinook survival data for all regions outside the Columbia  
1202 River basin and for a few stocks located in the Columbia River basin (Table S2). The

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1203 data are contributed by the various governments (provincial, state, and federal agencies)  
1204 responsible for conducting the individual monitoring programs.

1205

1206            In contrast, systematic survival data based on PIT tags first came into  
1207 widespread use in the Columbia River Basin in 1997 (Table S2). PIT tags are long-  
1208 lived but extremely short distance radio frequency tags that can successfully transmit  
1209 their unique ID code only when within <0.5 m of a detector. Although there are some  
1210 recent exceptions in small rivers, the short detection range essentially limits the use of  
1211 PIT tags to the Columbia River dams, which channel sufficient tagged individuals close  
1212 to the detectors to generate useful results. Tagging data are contributed to a central  
1213 database (PTAGIS- Pit Tag Information System) by the various agencies (state, tribal  
1214 and federal) and the SARs are estimated by the Fish Passage Center. All PIT tag-based  
1215 SAR estimates reported in this paper are taken from the Fish Passage Center's  
1216 Comparative Salmon Survival (CSS) Study (McCann et al [5]) and are listed in our  
1217 Table S2.

1218

1219            Earlier survival data for Snake River Chinook populations from the 1960s and  
1220 1970s is available from Raymond [1], who noted that "*From the positive relation found*  
1221 *between rates of return of adults and survival rates of smolts, it was apparent that*  
1222 *mortality of smolts migrating downriver through the dam complex was the main cause*  
1223 *of the decline in Snake River salmon and steelhead runs*", a view that has become  
1224 commonplace amongst salmon biologists. We have included these data in our analysis  
1225 because Raymond's pioneering studies [1, 29, 30] are of unique importance owing to

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1226 the documentation of the high SARs occurring in the 1960s and early years of the  
1227 1970s, a time period prior to the completion of the Snake River dams and the 1977  
1228 marine regime shift, and because they defined the focus for much subsequent work in  
1229 the Columbia River basin to improve survival.

1230

1231           The two major tagging technologies available, PIT and CWT, are largely  
1232 geographically discrete, with most recent survival data from the Columbia River based  
1233 on PIT tag technology and most survival data for other regions based on CWT data.  
1234 Although rarely discussed, the differences in the two technologies determine what  
1235 aspects of migration-phase survival are estimated. These difference are discussed  
1236 below, as is a brief description of Raymond's methods. (Raymond's [1] early survival  
1237 analysis was based on direct estimation of the number of smolts migrating downstream  
1238 past Snake River dams, and dividing this value into the number of adults returning  
1239 several years later; see Raymond [1] for details; as such, comments on the extent of the  
1240 migration path monitored also apply to this early study).

1241

1242           ***CWT tags***

1243           The precise technical methods of counting the number of CWT-tagged adults  
1244 returning back to each population are not documented in the Pacific Salmon  
1245 Commission (PSC) database by the various agencies contributing survival data;  
1246 however, an example of the mark-recapture approach used by ADF&G in the  
1247 Transboundary Rivers of SE Alaska and Northern British Columbia for wild Chinook  
1248 stocks can be found in [21]. Most agencies operate hatcheries or (in a few cases) rotary

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1249 screw traps to estimate downstream smolt numbers for wild stocks. In general, CWT-  
1250 based survival estimates are calculated for hatcheries by dividing the total number of  
1251 maturing adults of various ages estimated to return back to the spawning grounds or  
1252 hatchery or caught in the fishery by the number of smolts released in the year of ocean  
1253 entry. CWT-based survival estimates (49 time series) are only available for Chinook,  
1254 not for steelhead.

1255            The PSC database provides several measures of marine survival. In this  
1256 study, we used survival data calculated as the sum of adults returning at all ages or  
1257 caught in the fisheries, uninflated for losses to natural mortality for Chinook remaining  
1258 at sea for longer than two years because these values are most similar to the CSS PIT-  
1259 tag based survival estimates [5]. Survival estimated using this procedure slightly  
1260 underestimates true survival to ocean age two because some two year old Chinook  
1261 destined to mature at older ages die from natural causes prior to maturing and are  
1262 therefore not enumerated. However, in cases where SAR (survival over the migratory  
1263 phase of the life history), is 1%, the instantaneous total mortality rate is  $M_{\text{Total}}=4.6$ .  
1264 Ricker [170] suggested that the loss due to natural mortality between age two and older  
1265 ages was perhaps  $M=0.46 \text{ yr}^{-1}$ , or only 10% of  $M_{\text{Total}}$ . More recent estimates of age-  
1266 specific natural mortality for Chinook are even smaller: age 2, 40%; age 3, 30%; age 4,  
1267 20%; and age 5 and older 10%; ([49], p. 8). Consequently, not correcting for natural  
1268 mortality losses occurring between age 2 and older ages is unlikely to introduce major  
1269 errors into the SAR estimates, particularly as the majority of Chinook return at ocean  
1270 age two, and especially so in recent years [116]. (The PSC database also includes  
1271 survival estimates with age 3+ adults inflated to account for losses at sea; we chose not

1272 to use these estimates because the PIT-tag based survival estimates are not inflated for  
1273 mortality at older ages, so for purposes of comparison uninflated values should be more  
1274 comparable. We highlight it because of our concern (see Discussion) that fisheries  
1275 biologists may be underestimating the magnitude of losses at older ages and thus  
1276 incorrectly assuming that the primary survival issue is in the first year after ocean entry.  
1277

### 1278 ***PIT tags***

1279 PIT tag estimates of SARs are taken directly from Appendix B of McCann *et al*  
1280 [5], who reports SAR in several ways. We selected the SARs covering the greatest  
1281 extent of the migratory life-history (i.e., smolt releases and adult returns to the highest  
1282 dam available in the Columbia River basin), and we generally used SAR estimates that  
1283 included jacks when available. In the mid-Columbia region, SAR estimates with jacks  
1284 were sometimes available only for a shorter migration segment; in these cases we  
1285 selected the SAR data sets representing the longer migration segment but excluding  
1286 jacks because this was most similar to the CWT survival estimates. The extensive PIT-  
1287 tag based SAR estimates for the Columbia River basin total N=45 Chinook SAR time  
1288 series and N=22 steelhead SAR time series [5].

1289 Because returning adults must ascend fish ladders with PIT tag detectors, all  
1290 PIT tagged adults surviving to return can be censused (ignoring tag shedding).  
1291 Dividing adult returns by the estimated number of tagged smolts reaching the most  
1292 upstream dam in the year of ocean entry provides an estimate of the SAR. However,  
1293 the PIT-tag based SAR estimates for the Columbia River basin differ from CWT-based

1294 estimates in three main ways: (i) they exclude losses to harvest (lowering survival  
1295 relative to what is estimated in the PSC database), (ii) they exclude losses occurring  
1296 from smolt release to encountering the first dam in the migration path (raising survival),  
1297 and (iii) they exclude losses occurring from the time the returning adults migrate past  
1298 the last dam until they reach the spawning grounds (raising survival). We review these  
1299 differences in the context of the two major life history groups (yearling and  
1300 subyearling) for Chinook.

### 1301 **Data sources for steelhead**

1302 All steelhead data analyzed in this paper were from Kendall et al [7] updated to  
1303 incorporate more recent years' data, including new information on the actual age-  
1304 structure of the adult returns. Kendall et al [7] should be consulted for a full  
1305 description of these data sets and the data are available directly from Dr Kendall (Dr  
1306 Neala Kendall, pers. comm. [Neala.Kendall@dfw.wa.gov](mailto:Neala.Kendall@dfw.wa.gov)).

1307

### 1308 **Chinook**

#### 1309 ***Division by life history type***

1310 In general, Chinook salmon display two life history types: subyearling and  
1311 yearling. These life history types are identified in our analysis because there are  
1312 important ecological differences between them (see reviews by [123, 171], and  
1313 references therein) which likely influence survival. Subyearling smolts migrate to the  
1314 ocean within a few months of hatching in the spring, while yearlings migrate to sea

1315 after completing one or more full years of life in freshwater, and are thus significantly  
1316 larger at ocean entry and (generally) spend one less year in the ocean. The  
1317 subyearling/yearling smolt life history types also generally correspond with adult run  
1318 timing (“Fall” or “Spring”), but this linkage is somewhat subjective primarily owing to  
1319 hatchery rearing practices.

1320

1321            Spring (yearling) populations are largely found in high altitude headwater  
1322 tributaries of large river systems penetrating well into the interior of the continent such  
1323 as the Columbia and Fraser rivers, and are the only Chinook life history type reported  
1324 for Alaskan rivers [172, 173]. In contrast, Fall (subyearling) populations are widely  
1325 found in low gradient coastal streams or in the lower mainstem of major rivers but are  
1326 absent from Alaska. Early work [174] suggested an ancient genetic divide with  
1327 subyearling Chinook smolts primarily produced by adult runs returning to freshwater in  
1328 the fall and spawning directly after reaching their natal streams, and yearling smolts  
1329 produced mainly by adults that return in the spring and then hold in freshwater without  
1330 feeding until spawning in the autumn.

1331

### 1332            ***Life history & harvest rates***

1333            Spring Chinook are thought to move offshore and become purely open ocean  
1334 residents for much of the marine phase, and thus essentially immune to harvest by  
1335 fisheries until their return. As a consequence, offshore (pelagic) harvest of Spring  
1336 Chinook is likely negligible because a convention banning high seas fishing beyond the  
1337 200 mile EEZ of Pacific Rim countries was signed in 1992

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1338 ([http://www.npafc.org/new/about\\_convention.html](http://www.npafc.org/new/about_convention.html)) and enforcement patrols  
1339 consistently find few illegal driftnet vessels and only in the far western Pacific, well  
1340 beyond the known ocean distribution of North American Chinook stocks [175, 176]  
1341 (but possibly not steelhead). However, some incidental harvest of immature and  
1342 maturing Chinook occurs in the groundfish fisheries of the Bering Sea, with current  
1343 evidence suggesting that Pacific northwest populations form ca.  $\frac{1}{3}$  of Chinook bycatch  
1344 in the Bering Sea/Aleutian Islands region [109]. Unfortunately, owing to a general  
1345 inability to use collected Chinook fish scales to determine the duration of the freshwater  
1346 period (and thus discriminate yearling from subyearling animals), it is unclear which  
1347 life history type the Pacific northwest populations analyzed in [109] represent.

1348

1349            In contrast, Fall Chinook are known to remain as long-term residents of the  
1350 continental shelf off the west coast of North America and are thus exposed to  
1351 commercial and sport harvest in coastal marine waters over multiple years [171].  
1352 Survival of shelf-resident subyearling Fall Chinook populations can therefore be  
1353 significantly reduced by coastal fisheries that can harvest these animals over several  
1354 years of marine life.

1355

1356            In reality, this relatively simple picture is more complicated. Some hatcheries  
1357 hold subyearling (Fall) Chinook for an additional year before releasing them as larger  
1358 yearling smolts, and others release Spring run Chinook as subyearlings (e.g., Nooksack  
1359 and Skagit-See Table S2). Thus some yearling production is of smolts that  
1360 presumably remain shelf-resident for several years because their intrinsic genetic make-



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1361 up dictates this behaviour despite their larger (and older) age at release. Sharma and  
1362 Quinn [171] also document regional differences in migration distribution between  
1363 lower Columbia River and upper Columbia-Snake River Spring yearling populations  
1364 which they attribute to possibly greater interbreeding between Spring and Fall run  
1365 individuals in the lower Columbia River. Clarke et al [177] similarly present evidence  
1366 from breeding trials that the yearling/subyearling smolting pattern follows simple  
1367 Mendelian genetic rules in crosses of Fall and Spring adults (with the added twist that  
1368 the sex of the parent also influences the result)! More recent work by Prince et al [178]  
1369 has potentially identified a single gene in both Chinook and steelhead that controls  
1370 early (spring or summer) re-entry of Chinook and steelhead that then mature in  
1371 freshwater prior to spawning in the autumn; whether and how this gene might also  
1372 influence marine migration behaviour is unknown.

1373           Very recently, Riddell et al [123] have reviewed the literature and made the  
1374 argument that repeated parallel evolution of the yearling and subyearling life history  
1375 types in Chinook may have occurred in different watersheds. If true, this makes  
1376 Healey's [173] earlier assumption that yearling (Spring) Chinook and subyearling (Fall)  
1377 Chinook have strongly dichotomous ocean migration pathways untenable unless  
1378 evolution of age at ocean entry is strongly linked to migratory behaviour in the ocean.

1379           In this paper, we have thus opted to aggregate smolt returns by age at ocean  
1380 entry (yearling, subyearling) for simplicity, but note that in future it would be very  
1381 valuable to disentangle the role of age at release from genetically determined  
1382 differences in marine migration pathways on survival. Unfortunately, a rigorous  
1383 assessment of the genetic origins of each hatchery program would almost certainly

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1384      require a genetic determination of whether each hatchery program was releasing Fall or  
1385      Spring Chinook, and would need to take into account whether or not hybrid populations  
1386      had been created; it is a fascinating research question whose answer is completely  
1387      unclear at the current time to contemplate whether the offspring of an inadvertent  
1388      hybridization between a Fall and a Spring Chinook parent would rear offshore or on the  
1389      shelf and how it would get there!

1390              The difference in likely marine rearing areas is important because in CWT-  
1391      based estimates of survival [49], the commercial and sport harvest of the different age  
1392      groups is added to the escapement to generate the reported SAR. In contrast, PIT tag-  
1393      based survival estimates for the Columbia River basin do not incorporate losses due to  
1394      harvest ([5]; see p. 95). Columbia River survival estimates using PIT tags will  
1395      therefore underestimate survival relative to the PSC's CWT-based survival estimates.  
1396      For example, the PSC (Table 2.7) reports average annual stock-specific harvest rates of  
1397      29-62% for Strait of Georgia Fall (subyearling) Chinook stocks with harvest rates  
1398      declining over time [49]. For some Spring (yearling) Chinook, harvest rates are much  
1399      lower (at the extreme, Willamette Spring Hatchery Chinook are reported as having only  
1400      a 11% mean harvest rate; see Table 2.10 of [49]).

1401

1402              In this report we do not attempt to directly correct for the effects of harvest or  
1403      differences in the proportion of the migratory phase survival is measured over because  
1404      our most important conclusions seem robust to these differences, but it is important to  
1405      recognize that methodological differences exist and influence survival estimates. In a  
1406      few situations, we found both CWT and PIT tag-based survival estimates for the same

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1407 population and the same release year (Supplementary Info S3). Relative to the 1:1  
1408 relationship expected if both methodologies “perfectly” captured the same survival  
1409 process, we find ratios of  $1.5SAR_{CWT}:1SAR_{PIT}$  for three subyearling Chinook  
1410 populations, consistent with expectation as CWT-based SAR estimates incorporate  
1411 harvest, while PIT tag based estimates do not. Unfortunately, we did not find data to  
1412 directly compare yearling Chinook survival estimates but provide some indirect  
1413 comparisons in Supplementary Info S3.

1414

1415            Summarizing, the PIT tag-based survival estimates for the Columbia River  
1416 basin are biased high relative to total migratory phase survival because these estimates  
1417 exclude losses in the initial and final phases of the migration period above the dams,  
1418 and biased low because they exclude harvest (which varies in potential influence  
1419 between large for Fall (subyearling) and low for Spring (yearling) stocks). Finally,  
1420 some of the CWT-based survival estimates for wild stocks are also biased low to some  
1421 degree because they exclude survival losses occurring in the initial and final phases of  
1422 the migration upstream of the enumeration points for smolts and adults. However, at  
1423 least for hatchery-reared populations, smolt numbers used in the denominator of the  
1424 CWT survival estimate are estimated at the time of release from the hatchery, and  
1425 therefore exclude the possibility of migratory losses occurring prior to census.

1426

1427            For these reasons it should be noted that the strongest comparisons are within  
1428 individual survival time series (the coast-wide declining trends in survival) which are  
1429 based on the most consistent methodologies, while comparison between populations

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1430 will be less reliable because of differences in where each populations is censused to  
1431 measure survival over the migration phase. However, the coast-wide convergence of  
1432 survival in recent years to very low levels at a time when most sport and commercial  
1433 harvest has been drastically reduced is strong evidence that a common factor is driving  
1434 the collapse in survival. It is unlikely that a single consistent conversion factor between  
1435 CWT and PIT tag-based SAR estimates can be derived, because survival losses  
1436 incurred upstream of the initial and final census point for calculating SARs can vary  
1437 substantially between rivers and between populations within a river system and only  
1438 CWT-based methods can account for losses to harvest. Only hatchery releases can  
1439 potentially reach this technical standard of measuring survival over the entire migratory  
1440 phase of the life history, and only if adult enumeration takes place on the spawning  
1441 grounds (or at the hatchery).

1442 **Steelhead**

1443           The migration of steelhead is poorly understood, but it is thought that they may  
1444 migrate directly offshore soon after the smolts reach saltwater [102, 179]. Virtually  
1445 nothing is known of their marine migration, although the open ocean distribution  
1446 extends as a band bounded by specific maximum and minimum sea temperatures across  
1447 the North Pacific [180]. This suggests that (similar to Spring Chinook) maturing  
1448 steelhead may return directly from the offshore to their natal river and be little exposed  
1449 to commercial fisheries operating in continental shelf waters except those lying on the  
1450 direct migration path from the offshore. No commercial fisheries target steelhead, so  
1451 harvest is limited to freshwater sport fisheries and saltwater bycatch in other fisheries.  
1452

1453            Although many steelhead rivers and hatcheries are located in B.C., adult returns  
1454 have not been accurately enumerated which prevents direct estimation of survival. As a  
1455 result, SAR data for British Columbia is restricted to the Keogh River (Fig 1), where a  
1456 weir located within ca. 300 m of the ocean has monitored wild steelhead since 1977  
1457 [181]. Despite the lack of SAR data for other populations, it is known that the survival  
1458 trends evident for the Keogh River are mirrored in adult returns for the province of B.C.  
1459 as a whole, with some differences evident between geographic regions [40, 182, 183] in  
1460 more recent regime periods. Importantly, it is broadly recognized that adult steelhead  
1461 returns have been falling for decades (e.g., [40, 184]) and are now at record lows; for  
1462 example, the Thompson and Chilcotin tributaries of the upper Fraser River now each  
1463 have adult steelhead returns of less than 200 adults [185], despite being of roughly  
1464 similar size and biogeoclimatic zone to the Snake River.

1465

1466            For Washington State outside the Columbia River basin, steelhead SARs were  
1467 assembled and analyzed for Puget Sound (Washington State), as well as a number of  
1468 locations along the coasts of Juan de Fuca Strait, and the outer (western) WA coast as  
1469 well as Oregon; see [7] for detailed methods. SAR data for the Columbia and Snake  
1470 rivers were taken from [5]. We are unaware of additional steelhead SAR data for  
1471 Alaskan rivers.

1472

### 1473 **Comparison of relative survival**

1474 Several of our analyses are based on comparisons with the SARs of Snake River  
1475 populations as these are widely considered to be poor owing to the many dams (8) in

1476 the migration path, and in particular the four Snake River dams. Because the various  
1477 survival time series vary in length and sampling methodology, and because survival  
1478 also declines episodically with time, we chose to make the survival analysis as simple  
1479 and clear cut as possible.

1480 As a result, in each year or regime period, we divided all available individual SAR  
1481 estimates by the median SAR for all Snake River populations in the same time period.  
1482 The normalized median SAR for the Snake River region equals one by definition and  
1483 the frequency distribution of individual normalized estimates allows us to directly judge  
1484 the similarity of the SAR values between regions in the selected time periods under  
1485 examination.

1486

## 1487 **Treatment of SAR data**

1488 SAR data for salmon are log-normally distributed [186]; i.e., a time series of SAR data,  
1489  $S_t$ , will have the form  $S_t = e^{\mu + \sigma Z_t}$ , where  $\mu$  and  $\sigma$  are respectively the mean and standard  
1490 deviation of  $\log_e(S)$ , and  $Z_t$  is the standard normal variable  $Z \sim N(\mu, \sigma)$ . This is  
1491 important because the log-normal distribution is skewed, exhibiting occasional rare  
1492 high survivals which increases the expected value above the mean. As a result, the  
1493 expected value of a log-normally distributed SAR time series is neither the simple mean

1494  $\bar{S} = \frac{1}{n} \sum_{i=1}^n S_i$  nor  $\mu$ , but rather  $E(S_t) = e^{\mu + \sigma^2/2}$  (in fact, it is the median value of the log-

1495 normal distribution that is related to  $\mu$ , as  $S_{median} = e^{\mu}$ ). Calculating the average of the  
1496 untransformed survival data, although often reported, does not have a simple statistical  
1497 interpretation.

1498

1499 When comparing survival time series between regions, some important but subtle  
1500 differences should therefore be kept in mind. We have opted to use the median  
1501 (equivalent to the “geometric mean” if the data is truly log-normally distributed,

1502  $\bar{S}_{Geo} = Exp\left[\frac{1}{n} \sum_{t=1}^n \log_e(S_t)\right]$ , used in some literature), as well as the simple average  $\bar{S}$  of

1503 the untransformed SAR data in a number of key comparisons. The simple average is  
1504 what a number of prior studies report, and therefore what most policy makers and  
1505 fisheries managers are likely comfortable interpreting. For example, the NWPPC has  
1506 set a rebuilding target of 2%-6% for SARs and deemed 1% SARs (roughly the current  
1507 average) to be inadequate, but did not define how SAR values should be calculated.

1508

1509 However, when the distribution of SARs are compared between two regions  $i, j$  then if  
1510 the medians are found to be the similar, the implication is then that  $\mu_i = \mu_j$  and that the  
1511 simple means of the log-transformed data are also equal; this does not, however, imply  
1512 that the expected values  $E(S_t) = e^{\mu + \sigma^2/2}$  are equal because this value also depends on the  
1513 variance of the time series. For these reasons, we use both measures of central  
1514 tendency

1515

$$\bar{S} = \frac{1}{n} \sum_{t=1}^n S_t,$$
$$S_{median} = \bar{S}_{Geo} = e^{\mu}$$

1516 in our analysis, and not the expected mean values of the log-normal distribution

1517  $E(S_t) = e^{\mu + \sigma^2/2}$ , owing to the more complex definition and lack of easy interpretation,

1518 which the (simple) mean and the median readily impart.

## 1519 The precision of survival estimates

1520

1521 The standard error on a binomial proportion reported by the CSS and PSC, survival, is

1522  $SE(S) = \sqrt{S(1-S)/N}$ . The precision of a survival estimate,  $\phi(S)$ , degrades as survival

1523 decreases, because

1524

1525

1526 
$$\Phi(S) = \frac{SE(S)}{S} = \sqrt{\frac{1-S}{S \cdot N}}$$

1527 In the limit as survival approaches either 1 or zero,

1528

1529

1530 
$$\lim_{S \rightarrow 1} \Phi(S) = 0$$

*and*

$$\lim_{S \rightarrow 0} \Phi(S) = \infty$$

1531 The relative uncertainty in a survival estimate with a given sample size increases

1532 without bound as survival decreases towards zero. With survival values now at 1% or

1533 less, the relative precision of a survival estimate now relative to several decades ago

1534 when survival was in the 5-6% range is



1535

$$\frac{\Phi(S_1 = 0.01)}{\Phi(S_2 = 0.06)} = \sqrt{\frac{(1 - S_1) / (S_1 N)}{(1 - S_2) / (S_2 N)}} = \sqrt{\frac{S_2 (1 - S_1)}{S_1 (1 - S_2)}} \approx \sqrt{\frac{S_2}{S_1}}.$$

1536

1537

1538 In this numeric example, where survival falls from 6% at the start of the record to 1% at

1539 the end, the uncertainty relative to the point estimate increases almost 2.5-fold ( $\sqrt{6}$ ).

1540 (Taking into account that both the number of outgoing smolts and the number of

1541 returning adults is not known without error, as is implicitly assumed in using the

1542 binomial probability distribution, the actual uncertainty will be even larger when these

1543 uncertainties are taken into account).

1544

1545 It is interesting to note that should survival fall from the current ca. 1% level to 0.1%--

1546 a ten-fold further decline—it would in fact be difficult to recognize this massive decline

1547 (a fall as large as the decline from 100% to 10% or 10% to 1% survival) because of the

1548 limited precision with which survival can be measured at such low levels. Thus for

1549 both purely mathematical reasons as well as the methodological differences between

1550 tagging approaches listed in the prior section, it is likely infeasible to obtain a perfect

1551 conversion ratio between survival estimates calculated using different methodologies

1552 (PIT vs CWT).

1553

1554

1555

1556 **ORCID**

1557 DWW Orcid ID: 0000-0001-8851-5436

1558 ADP ORCID ID: 0000-0002-1258-8265

1559 ELR: ORCID ID: 0000-0002-2811-8399

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1566 from discussions with several of our colleagues, in particular Drs. XXX for early  
1567 discussions on this topic. The vast (>3000 years!) of data that this paper relies upon  
1568 obviously has involved many more individuals; we collectively thank them all for the  
1569 effort required to generate the data used here. All data except the Keogh R steelhead  
1570 SAR data are available without restriction at ??? (or from the authors).

1571 Investigators interested in accessing Keogh SAR data should request these data  
1572 from YYY.

1573 (Individuals XXX and YYY have been requested to indicate their approval to be  
1574 named in the Acknowledgements, as per PLoS ONE stipulation. At time of  
1575 submission, formal responses had not been received. Specific names will be  
1576 incorporated during the review process).

1577

1578      **CRedit (Contributor Roles Taxonomy)**

1579      Conceptualization, DWW (Lead); Methodology, ADP & DWW; Software, ADP; Validation,  
1580      ADP, ELR; Formal Analysis, ADP, DWW; Investigation, DWW; Data Curation, ADP; Writing  
1581      – Original Draft Preparation, DWW; Writing – Review & Editing, DWW, ADP, ELR;  
1582      Visualization, ADP; Supervision, DWW; Project Administration, DWW, ELR; Funding  
1583      Acquisition, DWW, ELR .

1584      **Competing Interests**

1585      DWW is President and owner of Kintama Research Services Ltd., an environmental  
1586      consultancy focused on the development of innovative applications of telemetry to improve  
1587      fisheries management. ADP and ELR are employed at Kintama. All authors received a  
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1594      the Strait of Georgia region had fallen to levels well below those reported for Snake River  
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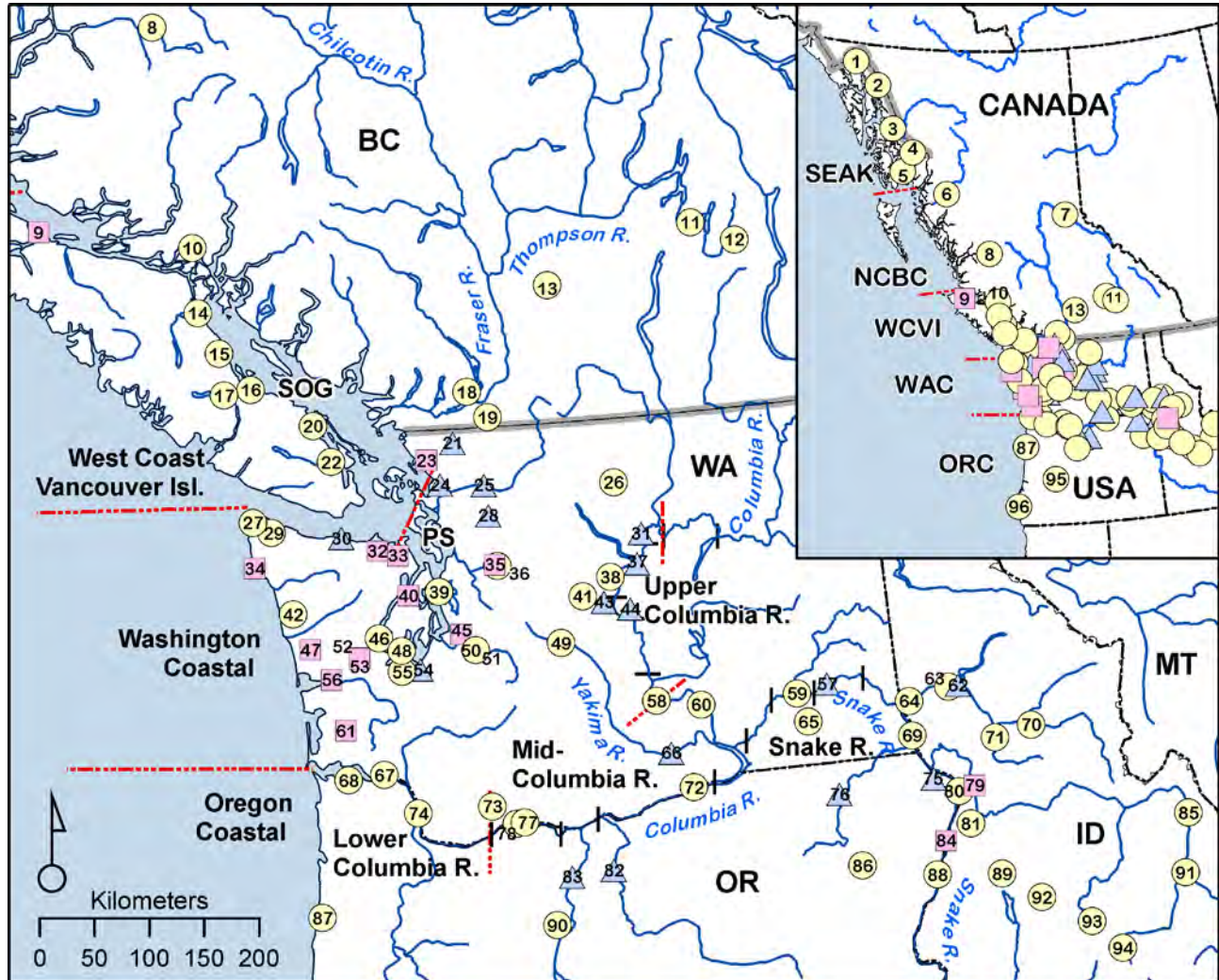
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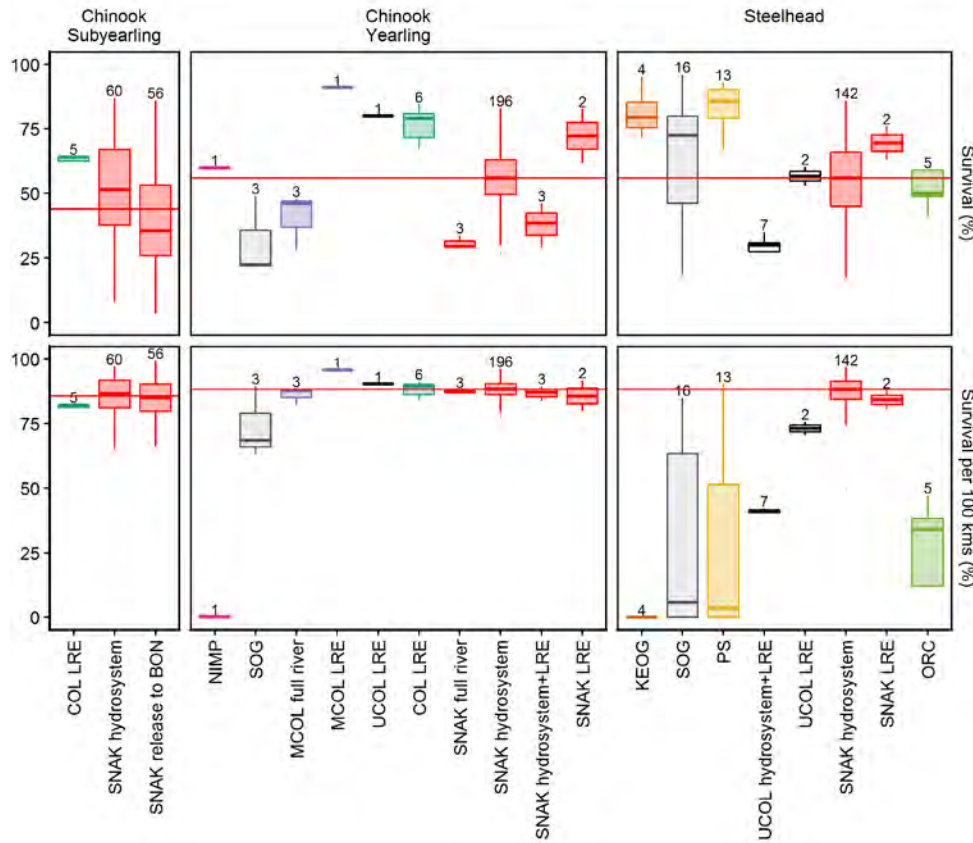


2  
3 **Figure 1. Map of salmon survival time series used in the analyses.** Numbers inside symbols are keyed to the  
4 populations in Supplementary Table S1; yellow circles indicate Chinook populations, pink squares indicate  
5 steelhead, and blue triangles indicate a location with data for both species. Acronyms: SEAK (SE  
6 Alaska/Northern British Columbia Transboundary Rivers); NCBC (North-Central British Columbia); WCVI (West  
7 Coast Vancouver Island); WAC (Washington Coastal); ORC (Oregon Coastal); SOG (Strait of Georgia); PS (Puget  
8 Sound).

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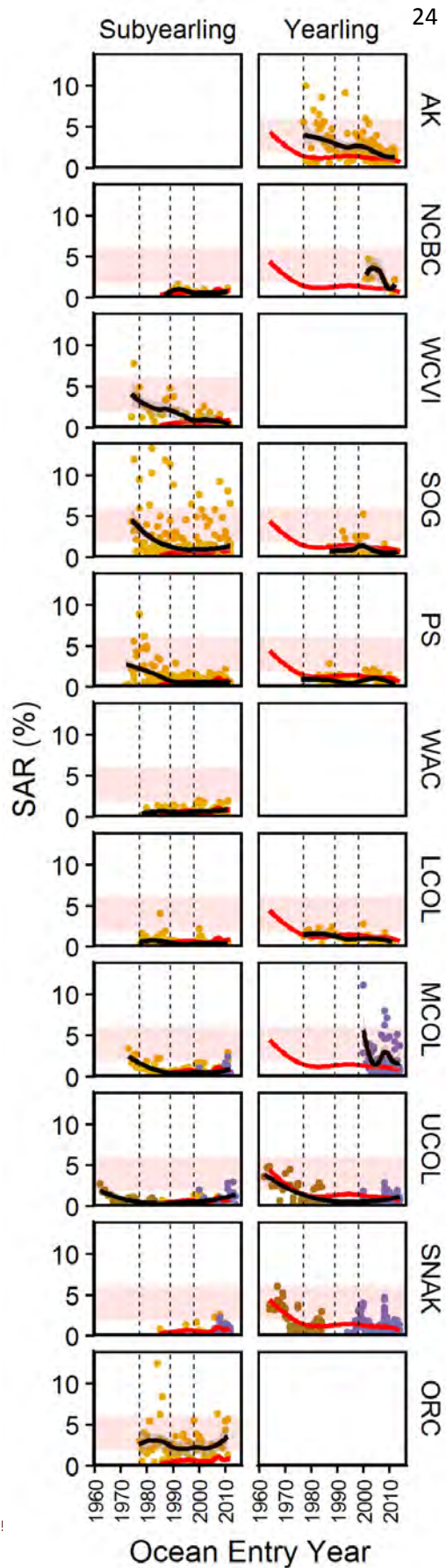
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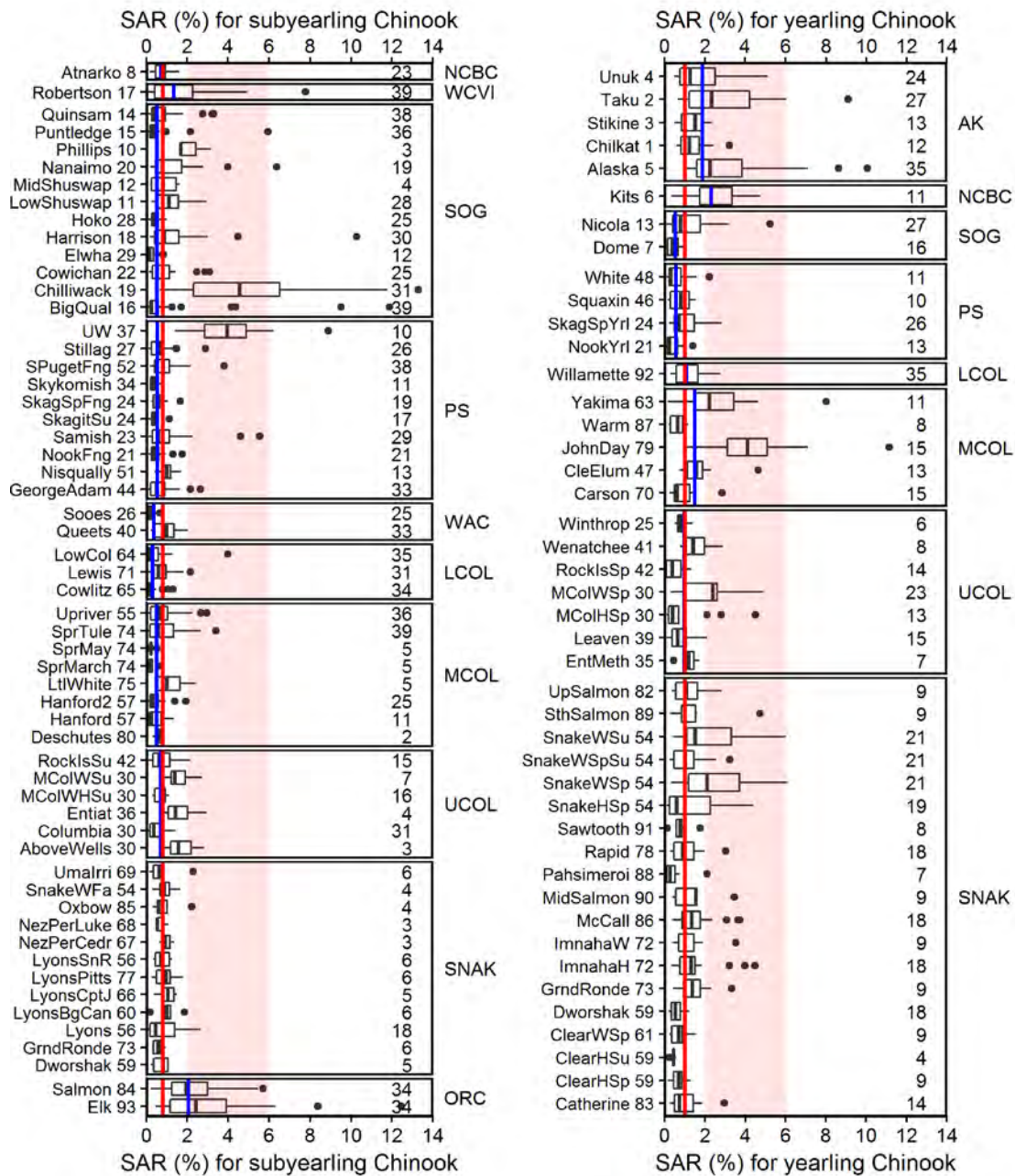
11

12 **Fig 2. Freshwater smolt survival for west coast North American rivers.** A total of N=531 annual survival  
 13 estimates are included. Top row: smolt survival from release to river mouth (and intermediate locations in  
 14 the case of the Columbia). Bottom row: survival per 100 km of migration distance. The red horizontal line  
 15 shows the median value for all Snake River data in a given panel (red coloured bars). Data are shown as a box  
 16 and whisker plot with associated sample size listed above the appropriate boxes. Abbreviations: LRE, Lower  
 17 Columbia River and estuary (i.e., the river reach from just below the lowest (Bonneville) dam to the river  
 18 mouth); Release to BON measures Snake River survival from hatchery release through the Snake River above  
 19 Lower Granite Dam and down through the 8-dam hydrosystem to the last dam (Bonneville). Full river  
 20 measures survival from release to the mouth of the Columbia River. Data sources and annual survival  
 21 estimates are reported in Supplementary Table S1.

22



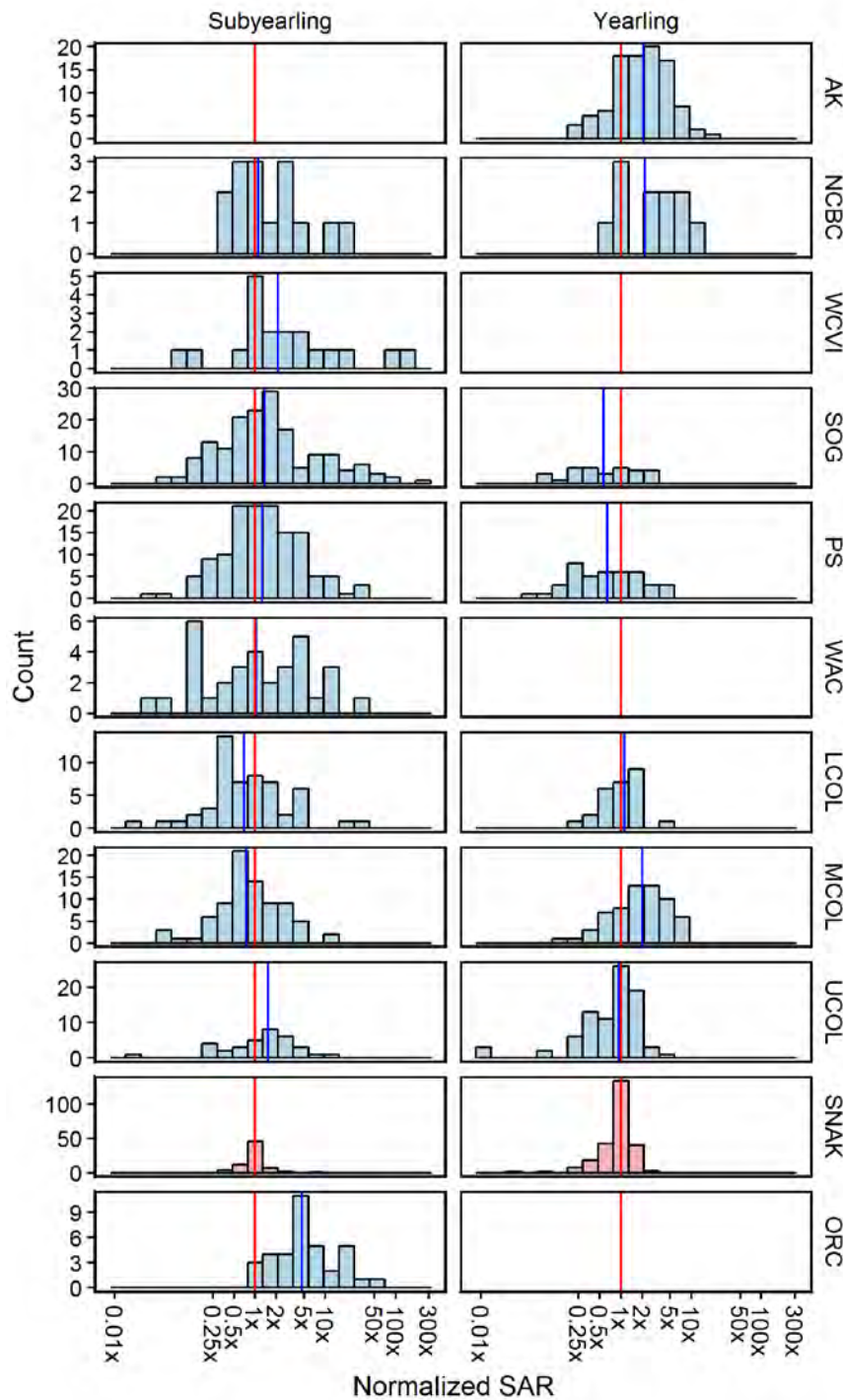
**Fig 3. Time series of smolt to adult survival (SAR) data for west coast Chinook stocks (excluding California).** Left column: subyearlings; Right column: yearlings. Regions are oriented from north (top) to south. Gold dots are SAR measurements based on CWT tags (PSC database), brown dots are SARs reported by Raymond [1], and violet dots are SARs based on PIT tags [2]. A loess curve of survival and associated 95% confidence interval (shaded region) using all available data for each panel is shown as a black line (the smoothing parameter was set to  $\alpha=0.75$ ); the loess curves for Snake River subyearling and yearling survival are overplotted in red to facilitate comparison with other regions. Blank panels indicate regions where the life history type does not occur (for example, Fall (subyearling) Chinook do not occur in Alaska, while Spring (yearling) Chinook do not occur in the low elevation streams on the west coast of Vancouver Island or Oregon coast). The major regime shift years of 1977, 1989, and 1998 are indicated by vertical lines. In this and subsequent figures the pale red band delineates the official Columbia River SAR rebuilding targets of 2-6%.



25  
 26 **Fig 4. Box and whisker plot of SARs by population (all available years).** The black horizontal line within each  
 27 bar is the median of the SAR data available for each population. Median survival across all available data for  
 28 each region is shown as a blue line; median Snake River survival for all populations combined is shown as a  
 29 red line and overplotted on all panels for comparison. The number of years of data is shown to the right. To  
 30 save space, abbreviated population names are used here along with the map code from Figure 1; full names  
 31 for the populations are listed in Supplementary Table S2.

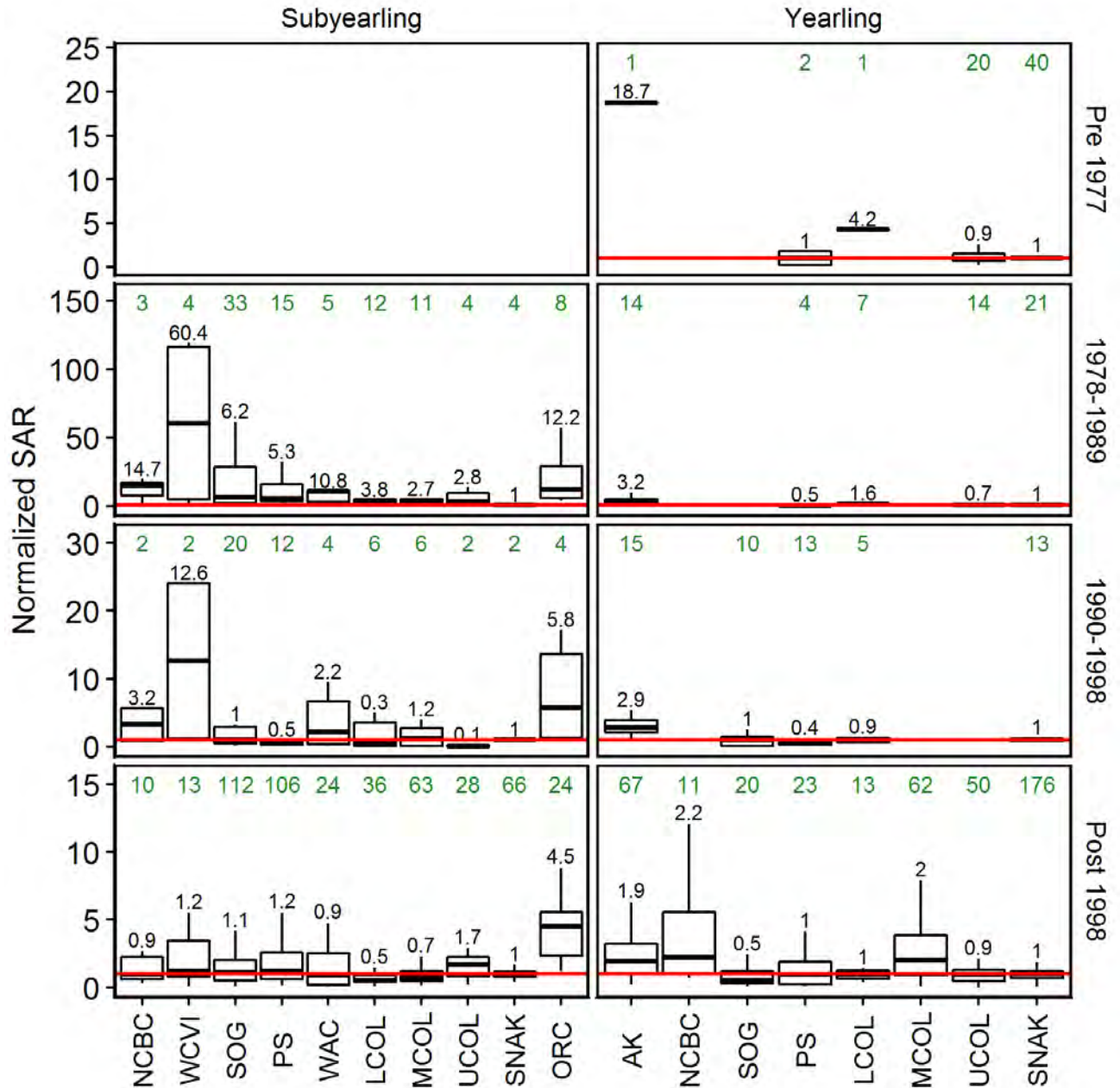
32





33  
34 **Fig 5. Normalized SARs calculated by dividing individual SAR estimates for each stock and each year by the**  
35 **median Snake River SAR for the same year.** Vertical lines show the median SAR for the Snake River (red) and  
36 other regions (blue). Note the logarithmic scale on the x-axis. As in the prior plots, Columbia & Snake River  
37 SAR estimates based on PIT tags do not incorporate harvest or above-dam survival.  
38

39

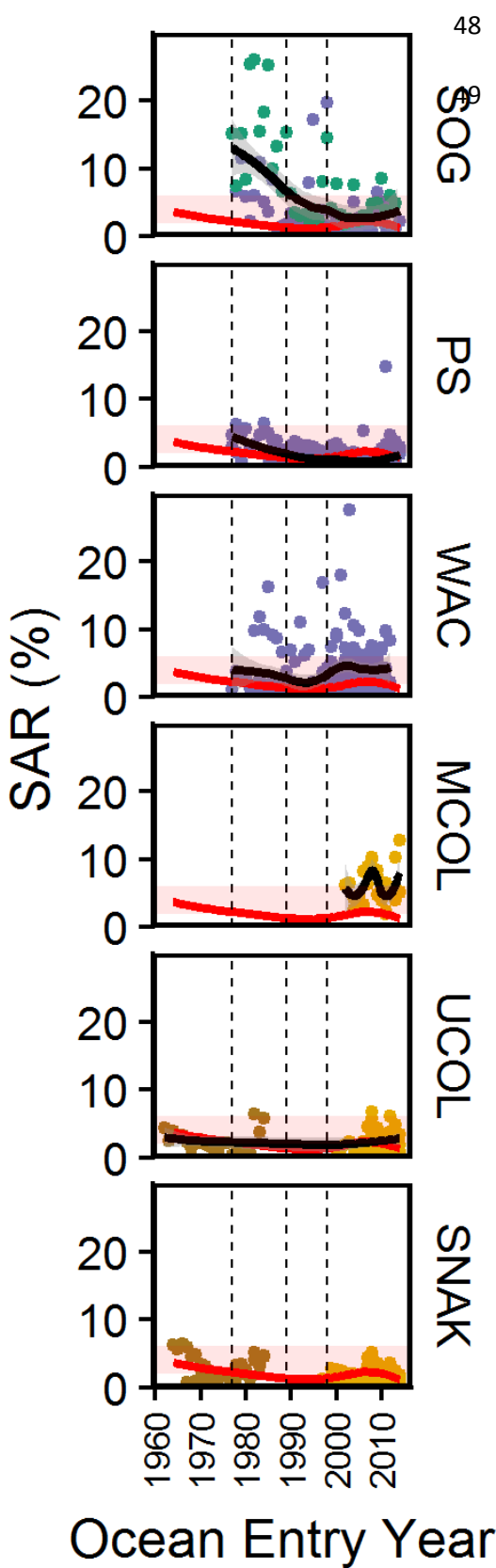


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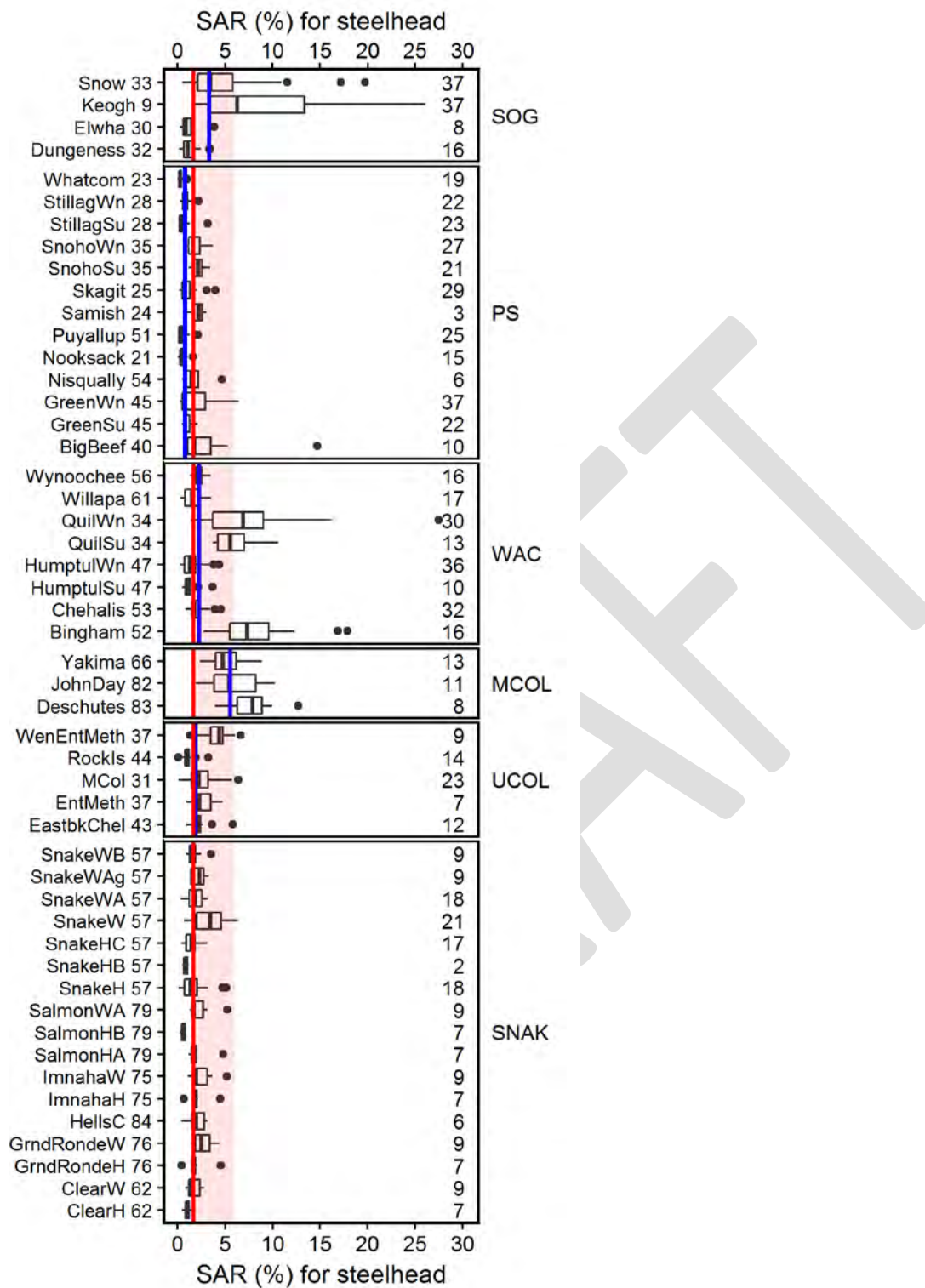
41 **Fig 6. Comparison of normalized Chinook SARs by regime periods: pre-1977, 1978-1989, 1990-1998, and**  
 42 **post 1998.** Boxes and whiskers have the conventional interpretation; the horizontal red line shows the Snake  
 43 R median SAR value for each regime to facilitate comparison (1.0 by definition). Sample sizes are shown  
 44 above each group (green font) and the ratio of median SARs relative to the Snake River is shown immediately  
 45 above the upper whiskers (black font).

46

47

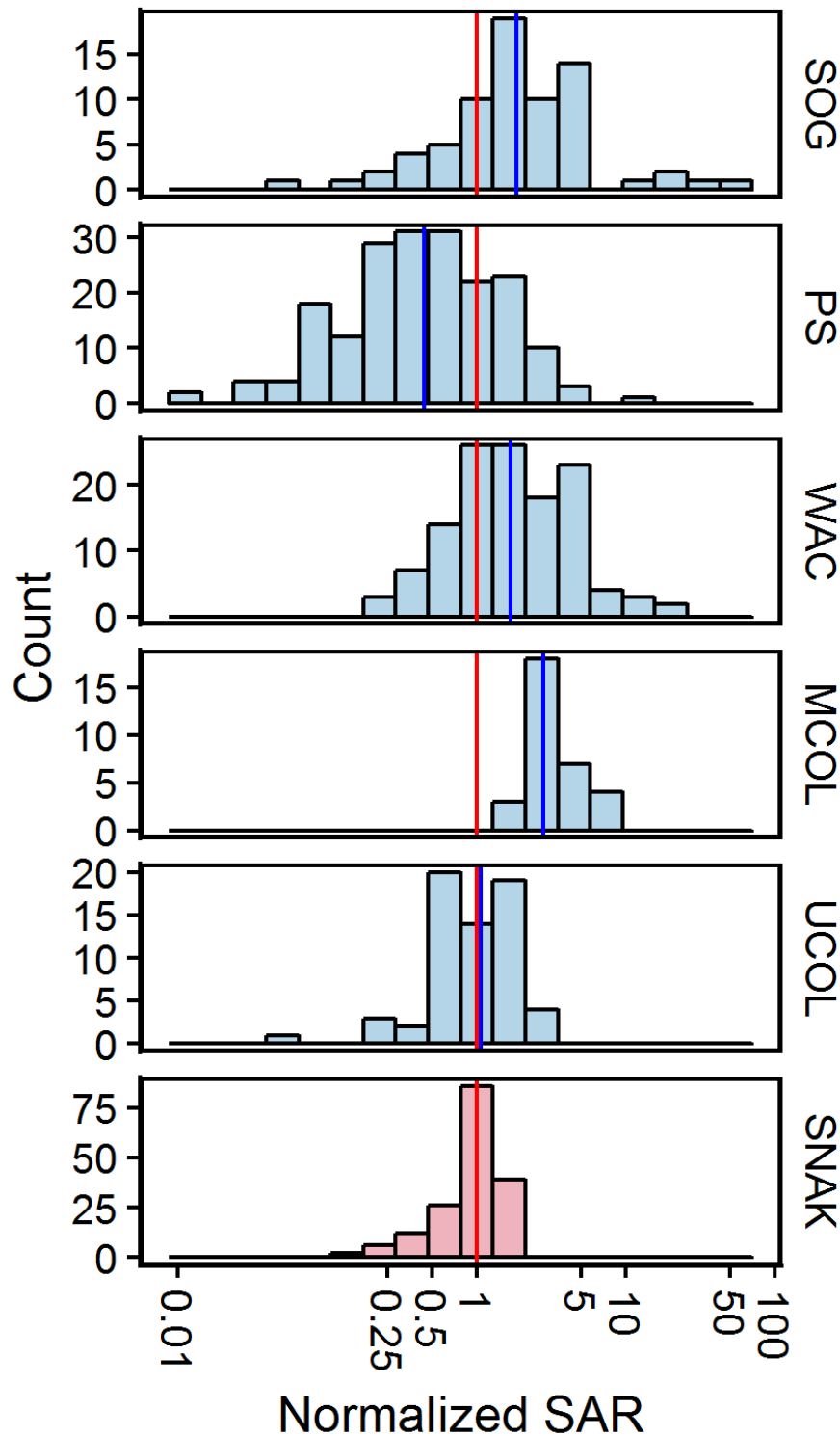


**Fig 7. Steelhead SARS plotted against ocean entry year.** Regions are oriented from north (left) to south (right); the Keogh R (KEOG) is situated on the NE tip of Vancouver Island (BC). Gold dots are SAR measurements based on PIT tags, brown dots are SARs reported by Raymond [1], and violet dots are SARs based on CWT tags. A loess curve of survival and associated 95% confidence interval (shaded region) using all available data for each panel is shown as a black line (the smoothing parameter was set to  $\alpha=0.75$ ); the Snake River loess curve is shown in red and over plotted on all other panels to facilitate comparison. The major regime shift years of 1977, 1989, and 1998 are indicated by vertical lines.



50

51 **Fig 8. Box and whisker plot of steelhead SARs by population (all available years).** Population names are  
 52 listed in Supplementary Table S1. The black horizontal line within each bar is the median of the SAR data  
 53 available for that population. Median survival across all available data for each geographic region is shown as  
 54 a blue line; median Snake River survival for all populations combined is shown as a red line and overlotted  
 55 on all panels for comparison. The number of years of data is shown to the right.

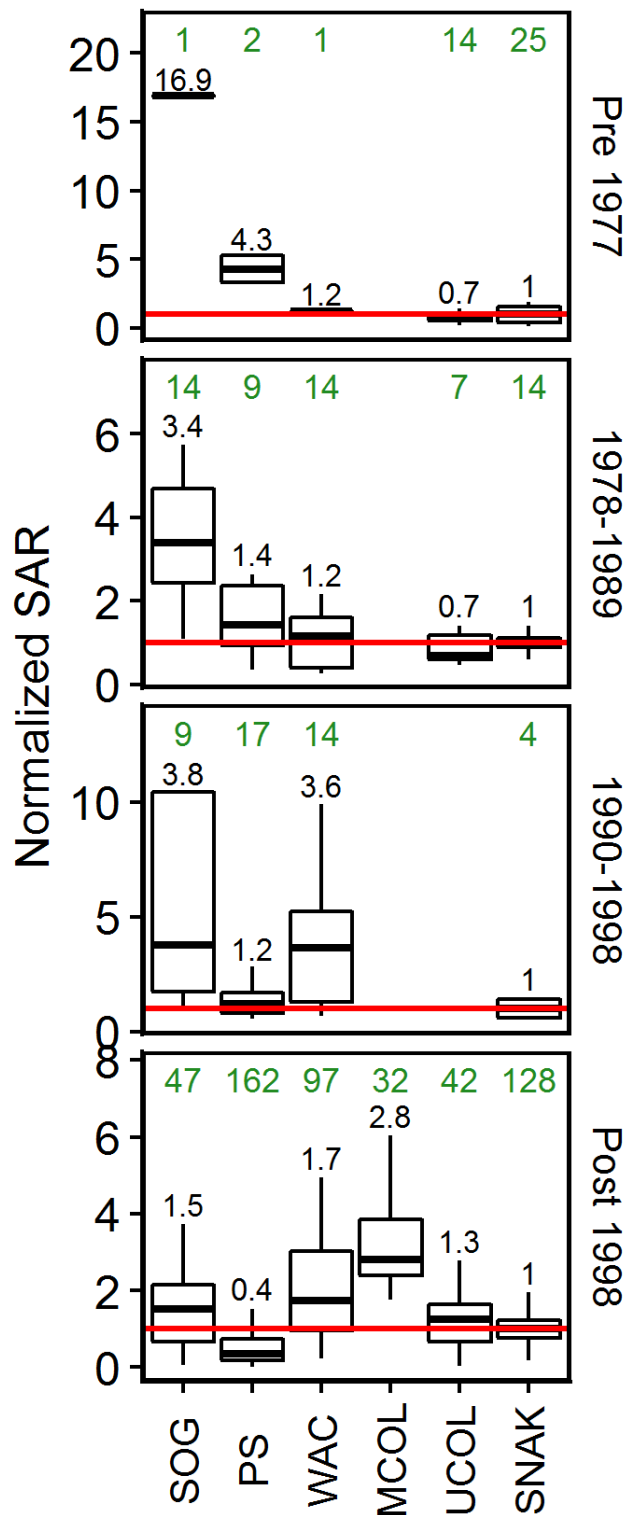


56

57 **Fig 9. Normalized steelhead SARs obtained by dividing each individual SAR estimate (i.e., for each stock**  
58 **and each year) by the median SAR calculated across all available Snake River SARs for that year. The**  
59 **median Snake River SAR is overplotted in red. Note the logarithmic scale on the x-axis.**

60





61 **Fig 10. Comparison of normalized steelhead SARs by regime periods: pre-1977, 1978-1989, 1990-1998, and**  
 62 **post 1998.** Boxes and whiskers have the conventional interpretation; the horizontal red line shows the Snake  
 63 R median SAR value for each regime to facilitate comparison (1.0 by definition). Sample sizes are shown  
 64 above each group (green font) and the ratio of median SARs relative to the Snake River is shown immediately  
 65 above the upper whiskers (black font).

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