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Article type : Article

Resumption of anadromy or straying? Origins of Sockeye Salmon *Oncorhynchus nerka* in the Elwha River

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Key words: homing, straying, dam removal, salmon, genetic stock identification (GSI)

This is the author manuscript accepted for publication and has undergone full peer review but has not been through the copyediting, typesetting, pagination and proofreading process, which may lead to differences between this version and the [Version of Record](#). Please cite this article as [doi: 10.1002/TAFS.10294](https://doi.org/10.1002/TAFS.10294)

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Abstract

25
26 When barriers to migration are removed, anadromous fishes from other rivers may colonize
27 accessible habitat, or landlocked forms of the species may resume anadromy if conditions
28 allow. For example, two large hydroelectric dams on the Elwha River, in Washington, USA, were
29 removed, between 2011 and 2014, to restore Pacific salmon populations after a century of
30 isolation. Immediately prior to and following dam removal (2010 – 2017), upstream migrating
31 adult Sockeye Salmon, *Oncorhynchus nerka* were sampled, and DNA was extracted and
32 compared to samples from the local Lake Sutherland population (above the lower dam's former
33 location) and a coast-wide genetic baseline to determine each salmon's probable origin.
34 Genetic analysis indicated that none of the 45 Sockeye Salmon sampled had originated from
35 the local population or other populations nearby in the genetic baseline, and only a single fish
36 originated from the abundant and proximate Fraser River populations. The strays reflected two
37 different sources and processes: 22 were from the west coast of Vancouver Island (all in 2015,
38 when these populations were very abundant and encountered conditions unfavorable for
39 upstream migration in their natal system). Another 22 assigned to more northerly populations,
40 mostly to riverine populations from the Stikine River. Test fishery samples collected in the Strait
41 of Juan de Fuca contained very few fish with assignments similar to these northern rivers. It is
42 not clear whether these individuals originated from the distant riverine populations, or from a
43 closer population not in the baseline that resembles them genetically. Taken together, the
44 findings indicate that the genetic composition of any future population in the Elwha River may
45 reflect signatures from diverse sources, and subsequent selection in the new habitat.

47 Introduction

48 Anadromous fishes tend to return to their natal site for reproduction, as shown by
49 tagging studies and analysis of the distributions of genetic markers, including American Shad
50 *Alosa sapidissima* (Hasselman et al. 2013; Melvin et al. 1986), other clupeid fishes (Martin et al.
51 2015), and salmonids such as Atlantic Salmon *Salmo salar* (Dillane et al. 2008) and Pacific
52 salmon of the genus *Oncorhynchus* (Beacham et al. 2006; Keefer and Caudill 2014; Quinn 1993).
53 However, much of the habitat currently occupied by these and other species in the Northern
54 Hemisphere was glaciated repeatedly over their evolutionary history. Consequently,
55 recolonization by straying (i.e., entry into and spawning in a non-natal river) has strongly
56 affected the zoogeography and population genetics of these fishes (Hasselman et al. 2013;
57 Petrou et al. 2013; Petrou et al. 2014).

58 Recolonization of rivers after glacial retreat can be studied in such locations as Glacier
59 Bay (Milner et al. 2007) and Kenai Fjords (Milner and York 2001) in Alaska, where newly
60 accessible habitat is colonized within decades by various organisms including salmonids (Milner
61 et al. 2008). Such new populations might be expected to show genetic bottlenecks resulting
62 from founder effects. However, if the colonizing salmon come from many sources (Kondzela
63 and Gharrett 2007; Scribner et al. 2017), genetic diversity may be high if those sources
64 contribute to the new blended population. In addition to these natural processes, in some cases
65 salmon were excluded by dams but, after the migratory corridor was reconnected, the rivers
66 were recolonized by strays from multiple proximate (Griffiths et al. 2011) or even distant rivers
67 (Perrier et al. 2010). These cases can provide insights into the natural recolonization process, in
68 addition to the valuable information on the restoration of the rivers involved.

69 Rivers can be restored and made suitable for recolonization by water quality
70 improvement, as in the Thames (Griffiths et al. 2011) and Seine (Perrier et al. 2010), and the
71 removal of impassable barriers such as dams (Bellmore et al. 2019). Recolonization by
72 anadromous fishes often occurs after dam removal, as populations from parts of the basin
73 below the dam expand upstream (Burdick and Hightower 2006; Pess et al. 2014), and formerly
74 landlocked populations resume anadromy (Godbout et al. 2011; Quinn et al. 2017). However,
75 the new population may be entirely or partially derived from strays that originated elsewhere.

76 The largest dam removal project in the United States, on the Elwha River, on the
77 Olympic Peninsula of Washington (Fig. 1), is providing an opportunity to study the responses of
78 a diverse community of anadromous fishes to dam removal. Two hydroelectric dams completed
79 on the Elwha River in 1912 (Elwha Dam) and 1927 (Glines Canyon Dam) to support economic
80 development throughout the North Olympic Peninsula impacted salmon populations for nearly
81 a century. The Elwha Dam was constructed 7.9 rkm from the river mouth without fish passage
82 facilities and restricted anadromous fishes to the area downstream of the dam. Glines Canyon
83 Dam at rkm 21.6 further restricted fish movements and isolated populations. Prior to dam
84 removal, several salmonids persisted below the lowermost dam: Chinook Salmon *O.*
85 *tshawytscha*, Coho Salmon *O. kisutch*, Chum Salmon *O. keta*, and Pink Salmon *O. gorbuscha*, as
86 well as Rainbow Trout/Steelhead *O. mykiss* (Pess et al. 2008) but Sockeye Salmon were only
87 occasionally observed downstream of Elwha Dam. Rainbow Trout were also self-sustaining but
88 not anadromous above the dams, as were Coastal Cutthroat Trout *O. clarkii clarkii*, Bull Trout
89 *Salvelinus confluentus*, and non-anadromous Sockeye Salmon *O. nerka* (Pess et al. 2008). The
90 removal of the two dams occurred between 2011 and 2014; full fish passage was restored at
91 Elwha Dam in Spring, 2012 and at Glines Canyon Dam in Fall, 2014. Since dam removal, Chinook
92 Salmon, Steelhead, and Bull Trout have ascended to the headwaters of the Elwha River, Coho
93 and Pink Salmon have passed the former Glines Canyon dam site, and Chum Salmon have
94 passed the former Elwha Dam location (Duda et al. 2020; McMillan et al. 2019).

95 Among the Elwha River's salmonids, the pre-dam status and subsequent response to
96 dam removal have been the most ambiguous in Sockeye Salmon, *O. nerka*. The species is
97 characteristically associated with lakes, where juveniles feed for a year or two prior to seaward
98 migration, but some populations spawn in river systems without lakes and either migrate to sea
99 in their first year of life as sea-type or after a year of feeding as river-type (Burgner 1991; Quinn
100 2018; Wood et al. 1987). Wood (1995) hypothesized that these ecotypes, often collectively
101 referred to as riverine (Beacham et al. 2006; Pavey et al. 2007), are the colonizing forms and
102 stray more than does the lake-type form. This hypothesis is consistent with some genetic
103 studies of population structure (Gustafson and Winans 1999), but not in all cases (Beacham et
104 al. 2006), so the connection between freshwater life history and straying is not entirely clear.

105 Lake Sutherland, situated between the sites of the two former dams, is the only natural
106 lake in the Elwha River system. It had a native population of the *O. nerka* but it is unclear
107 whether they were anadromous or not (Hiss and Wunderlich 1994; Quinn et al. 2015). The
108 species commonly exists as a self-sustaining non-anadromous form known as kokanee (Quinn
109 2018; Wood 1995), sometimes in sympatry with the anadromous form from which they evolved
110 independently in each river system (Taylor et al. 1996). Kokanee were transplanted into Lake
111 Sutherland after dam construction from diverse and sometimes uncertain origins, that
112 “probably included British Columbia, Montana, Idaho, and Lake Whatcom [Washington]” (Hiss
113 and Wunderlich 1994). Consequently, it was unclear whether the *O. nerka* would resume (or
114 adopt) anadromy, as has taken place elsewhere (Godbout et al. 2011). Limited genetic sampling
115 prior to dam removal did not resolve their origins (Winans et al. 2008), and Pess et al. (2008)
116 concluded [p. 87], “Whether or not Sockeye Salmon will re-establish a self-sustaining
117 population is perhaps one of the biggest unknowns of all salmonid species in the Elwha River
118 basin.” The capacity of this small (146 ha) lake to produce anadromous Sockeye Salmon may
119 depend on the extent to which there is a remaining non-anadromous (i.e., kokanee) component
120 (Hansen et al. 2016), so the patterns of colonization are important to the future of the species
121 in this system.

122 Sampling in the Elwha River has yielded some adult Sockeye Salmon in the years
123 immediately prior to, during, and after removal of the Elwha Dam in 2011. These fish might be
124 strays from one or more of the many Sockeye Salmon populations in Washington, British
125 Columbia, and Alaska (Burgner 1991). Alternatively, they might have been spawned in the Lake
126 Sutherland system, migrated to sea, and returned as adults, thus representing the reawakening
127 of the dormant life history form, as seen in the Elwha River’s bull trout (Brenkman et al. 2019;
128 Quinn et al. 2017). Each fish is either a native or a stray, but the group might be exclusively or
129 predominantly one or the other, or some mixture, and the strays might be from geographically
130 proximate or distant locations. Strays might have lower reproductive success than native fish
131 (Kitanishi and Yamamoto 2015; Mobley et al. 2019) but in this case the native fish have not
132 been anadromous for a century, and the strays might be from many locations. Consequently,
133 the future population may be a mix of salmon adapted to multiple locations, and might show a

134 higher than expected effective population size and temporal variation in allele frequency
135 distribution until it later stabilized (Walter et al. 2009). The origins will determine the future
136 genetic composition of the population, and, by extension, shed light on the straying and
137 colonization by salmon. Accordingly, the goal of this study was to determine whether
138 opportunistically obtained tissue samples of adult Sockeye Salmon in the Elwha River could be
139 genetically assigned to the Lake Sutherland population, indicating the resumption of anadromy,
140 or to populations from the Columbia River to southeastern Alaska (Beacham et al. 2004;
141 Beacham et al. 2006), indicating that they were strays.

142

143 **Methods**

144 **Site Description**

145 The Elwha River flows 72 km northward on the Olympic Peninsula of Washington, USA
146 (Figure 1), into the Strait of Juan de Fuca (Duda et al. 2008). It has a maritime climate, with high
147 precipitation in fall and winter, falling as rain and, at higher elevations, snow, and mild air
148 temperatures from about 2° C in winter to 22° C in summer. The river has two periods of high
149 flow: from May to July when most of the snow melts, and from November to February when
150 highest rainfall occurs (Duda et al. 2008). Elwha and Glines Canyon dams isolated fish
151 populations and created reservoirs but the only natural large lake in the system is Lake
152 Sutherland: 146 ha in area, draining 21 km², with a mean depth of 17.4 m and 7.8 km of
153 shoreline (Hiss and Wunderlich 1994). Its outlet, Indian Creek, flows 9 km and enters the Elwha
154 River from the west, 5 km above the former site where the Elwha Dam was located (Figure 1).
155 The lake is steep-sided and almost all spawning occurs along beaches (Hiss and Wunderlich
156 1994).

157

158 **Sampling**

159 Samples of 100 adult *O. nerka* from Lake Sutherland were obtained from late August to
160 early October over four years (2010: n = 20; 2011: n = 30; 2013: n = 12; 2015: n = 38) by setting
161 gillnets in areas of the lake where the salmon aggregate for spawning. Many of these
162 specimens had previously been used for studies on the life history of this population (Quinn et

163 al. 2015). All were small-bodied (mean fork length: 304 mm, range 254 – 355), consistent with a
164 non-anadromous life history. A fin clip was removed from each fish and preserved in ethanol
165 for later processing. The DNA from these fish was used to provide a baseline against which
166 adult anadromous fish of unknown origin could be compared.

167 A weir was established at rkm 6.2 and operated by the Washington Department of Fish
168 and Wildlife and adult salmon were trapped, sampled for DNA by removal of a small piece of fin
169 tissue, and the species, sex, and length were recorded. The weir operated from 2010 to 2013
170 (Anderson et al. 2015) but a variety of factors hindered its operation, and the subsequent focus
171 of monitoring adult salmon was conducted using SONAR at rkm 0.8 (Denton et al. 2019; Pess et
172 al. 2020). At this latter site, salmon and other species were sampled in a fine-mesh gillnet for
173 species, sex, and length data, including some Sockeye Salmon sampled for DNA. Other samples
174 were obtained, opportunistically, as moribund salmon drifted down to the counting sites or
175 were seen on other surveys, including sites upstream of Indian Creek. Thus the total sample
176 represented fish in a range of conditions, from upstream migrants to post-spawning, but none
177 from Lake Sutherland. In total, 45 adult Sockeye Salmon were sampled from which attempts to
178 extract DNA, genotype, and assign to probable region or river of origin were successful (Table
179 1). These fish were collected from 2010 through 2017. Another seven fish were sampled but the
180 DNA was too degraded for successful amplification. The observed sex ratio (28 males, 19
181 females, discounting 5 for which sex was not recorded) did not differ significantly from a 50:50
182 ratio ($X^2 = 1.7$, 1 df, $P > 0.10$).

183

184 **Genetic Analyses**

185 Samples were extracted from tissues stored in non-denatured 95% ethanol using the
186 BioSprint (QIAGEN) extraction method. DNA was quantified by spectrophotometry (Tecan) and
187 negative control wells were included. Genotyping was conducted as per Beacham et al. (2006)
188 using a total of 14 microsatellite loci. Data were imported into Microsat Manager (Candy et al.
189 2002), converted to geneclass format, and then prepared as mixture files by separating
190 mixtures based on the year of collection. A coast-wide microsatellite genetic baseline for
191 Sockeye Salmon was obtained from the Molecular Genetics Lab (MGL, DFO) database and

192 prepared for analysis. This Sockeye Salmon baseline has been commonly used for coast wide
193 mixed-stock analysis since 2018, and contained 246 populations from 21 regions (Supplemental
194 Table 1) from the Columbia River to southeast Alaska, including proximate populations in
195 Washington. The newly genotyped Lake Sutherland population was added to this baseline, to
196 which the unknown individuals were compared to identify the potential stock of origin using
197 cBayes (Neaves et al. 2005; Pella and Masuda 2001). We used 20,000 replicate runs, and a
198 maximum of five missing loci, otherwise the fish with poor quality genotyping was removed.
199 Results were reported to the stock and reporting unit (repunit) along with probabilities of
200 assignment. A new version of the baseline was subsequently generated in 2020 using a
201 minimum sample size of $n = 30$ with all of the populations included in 2018, except for several
202 populations that have been removed due to concerns on collection metadata (Supplemental
203 Table 2). This baseline was similarly used in cBayes, including with multiple runs of the analysis
204 with different starting seed values. Further, the baseline and mixed-stock genotype data was
205 then converted to rubias format and run using this second analysis method (Moran and
206 Anderson 2018). The rubias analysis was conducted using rubias (v.0.3.1) in R (v.3.6.3)
207 (RCoreTeam 2020) using 25,000 reps, 5,000 reps burn-in, keeping the final 5,000 reps for
208 analysis. Results were compared among the starting seed variants and the two software
209 methods at the level of individual fish assignment to repunit and any differences among
210 methods were recorded.

211 All populations that received at least 10% of the allocation in any individual were
212 included in a genetic dendrogram based on a genepop exported from the MGL sockeye genetic
213 baseline (Beacham et al. 2006). All populations in the baseline near the Elwha River (e.g.,
214 Washington State populations, Lake Sutherland collection) were also included in the baseline,
215 regardless of whether they received any allocation from the assignment tests. The dendrogram
216 was constructed using the read.genepop function of adegenet v.2.1.3 (Jombart 2008) in R
217 (RCoreTeam 2020), followed by the aboot function of poppr 2.8.6 (Kamvar et al. 2014) using the
218 Cavalli-Sforza and Edwards distance metric (Cavalli-Sforza and Edwards 1967), visualized in
219 FigTree v1.4.4 (Rambaut, A. 2019. FigTree. <https://github.com/rambaut/figtree>).

220

221 Results

222 Of the samples from Lake Sutherland, 81 were successfully amplified and added to the
223 genetic baseline for Sockeye Salmon at the DFO Molecular Genetics Lab (MGL). The Lake
224 Sutherland population did not strongly group with any other Sockeye Salmon population,
225 instead forming its own grouping (Supplemental Figure S1). The Vancouver Island stocks
226 showed strong bootstrap support of their grouping (97%). Lake Sutherland most closely
227 grouped alongside the Fraser and Columbia branches, but did not have a reliable bootstrap
228 support with any other populations, thus its position relative to the other Sockeye Salmon
229 populations is not resolved within the tree. The populations within Washington, specifically
230 Baker Lake and Lake Washington, grouped tightly together (bootstrap support of 95%;
231 Supplemental Figure 1), whereas the Quinault River and Lake Ozette populations had low
232 bootstrap support of the branch (40%), but in general clustered most similarly to the other
233 Washington populations. The Owikeno, Upper Skeena, and Stikine populations all showed
234 strong bootstrap support of their respective groupings (bootstraps of 99.7%, 100%, and 83%,
235 respectively).

236 Not one of the adult Sockeye Salmon sampled in the Elwha River was assigned to the
237 Lake Sutherland population as the primary source or any of the lower probability sources (i.e.,
238 none of the first five probabilities, on average explaining 83% of the assignment probability;
239 median = 0.99), nor was any fish assigned to the geographically proximate populations (e.g.,
240 Lake Quinault and Lake Ozette on the Olympic Peninsula, and Baker Lake and Lake Washington
241 in Puget Sound). Only one fish was assigned to the Fraser River (early summer run, Table 1, with
242 the most probable population being Scotch Creek, in the Shuswap Lake system). The patterns of
243 genetic assignment tended to vary with the year of collection; most of the fish were within
244 years 2010 and 2015 (n = 18 and 24, respectively). Specifically, 22 of the 24 fish sampled in
245 2015 were assigned with high probability to the Vancouver Island region, with population
246 assignments to either Great Central Lake (n = 14) or Sproat Lake (n = 8), both of which drain
247 into Barkley Sound. However, in no other year was any fish assigned primarily to the Vancouver
248 Island region (Table 1). Thus, the assignment of fish to the west coast of Vancouver Island was
249 limited to those collected in 2015, and their assignment probabilities were very high.

250 Two fish collected in 2015 were assigned to riverine Sockeye Salmon populations in the
251 Stikine River system, which flows from the mainland of British Columbia through southeast
252 Alaska. These fish did not assign with as high probability as the Vancouver Island assignments in
253 2015, but they had assignment to the Stikine region with probabilities 0.64 and 0.70. The
254 Stikine region was the primary assignment for another 15 fish from years 2010-2013 and 2016
255 (mean assignment to region = 0.71 for all 17 Stikine assignments). The secondary regional
256 assignments of these fish were from a range of systems, but in general had low probability
257 secondary assignments (Table 1). Other than these 17 fish with primary assignments to the
258 riverine populations in the Stikine River system and the 22 fish from Vancouver Island
259 populations collected in 2015, several had inconclusive assignments to the Taku River ($n = 2$;
260 0.72 and 0.58), Owikeno Lake region ($n = 2$; 0.53 and 0.47), and southeastern Alaska ($n = 1$;
261 0.47). One fish from 2015 had a high probability assignment to the Early Summer Fraser River
262 grouping (0.98).

263 Follow-up analyses with different starting seed values or with a secondary mixed-stock
264 analysis tool (rubias) in general confirmed these findings (Supplemental File 1). Using two
265 different starting seed values compared to the seed values originally applied, and considering
266 assignments to the repunit, 41 and 44 of the total 45 assignments were confirmed in each
267 analysis. Differences included low probability Stikine assignments ($n = 3$; mean = 67%) changing
268 to low probability Owikeno assignments, and an inconclusive SE Alaska assignment (50%)
269 changing to a low probability Owikeno assignment in both seed variants. The use of rubias
270 instead of cBayes resulted in more differences, but primarily involved Stikine assignments
271 (mean = 89%; $n = 5$) changing to Alsek assignments, as well as some minor changes from low
272 probability Stikine or SE Alaska assignments (Supplemental File 1).

273 Examination of the recoveries by date (including the seven from which DNA could not
274 be extracted) revealed a range from late June (1), early July (1), late July (4), early August (4),
275 late August (21), early September (9), late September (5), early October (4) and late October
276 (3). However, analysis of origin with respect to date is complicated by the mix of samples from
277 upstream migrants and those sampled after spawning. The fish assigned to Vancouver Island
278 were sampled primarily in late August (9) and early September (7) but also in early August (2),

279 late September (1), and late October (3). Most ($n = 9$ of 17) fish assigned to the Stikine River
280 were sampled in late August but others were sampled from late July to early October, thus
281 there was no clear separation among regions of origin with respect to sampling date.

282

283

Discussion

284 The most important initial result was that genetic evidence indicated that not a single
285 adult Sockeye Salmon collected from the Elwha River had originated from the local Lake
286 Sutherland population. In the first few years after dam removal, any smolts from the Elwha
287 River would not have had time to go to sea and return, as this species typically spends two or,
288 less commonly, three years at sea before returning to spawn. Thus smolts leaving in the spring
289 of 2012 might have returned in the fall of 2014 and thereafter; in previous years the Sockeye
290 Salmon would have been strays. Interestingly, annual smolt trapping on Indian Creek, Lake
291 Sutherland's outlet, since 2013 has not yielded any *O. nerka* (personal communication, Michael
292 McHenry, Lower Elwha Klallam Tribal Fisheries Office). There is some ambiguity as to whether
293 this population is entirely comprised of the descendants of anadromous Sockeye Salmon that
294 were landlocked, because almost 10 million kokanee were stocked into the lake over the
295 decades (Brenkman et al. 2008; Hiss and Wunderlich 1994). Analysis of egg size and fecundity
296 patterns suggested that the current Lake Sutherland populations descended from anadromous
297 Sockeye Salmon (Quinn et al. 2015) but this line of evidence is indirect and somewhat
298 equivocal. Elsewhere, anadromous Sockeye Salmon that were landlocked for comparable
299 periods resumed anadromy (Godbout et al. 2011), so anadromy by the Lake Sutherland
300 population was possible. Given our small sample, some adults of local origin may have returned
301 undetected or will do so in the future, but the genetic stock identification results indicated that
302 the adults were from outside sources.

303 The inferred sources of the strays reflected neither proximity nor total abundance on a
304 consistent basis. Rather, there were two distinct patterns, reflecting different straying
305 processes. First, the 2015 adults were almost exclusively from lake-type populations of Sockeye
306 Salmon from Great Central and Sproat lakes, which drain into Barkley Sound, on the west coast
307 of Vancouver Island. The entrance to Barkley Sound is about 150 km from the mouth of the

308 Elwha River, and the Somass River, draining both lakes, is about another 70 km from the mouth
309 of Barkley Sound at the head of long, narrow Alberni Inlet. The estimated total run of Sockeye
310 Salmon to these lakes in 2015, 2.041 million, was the highest on record (K. D. Hyatt, DFO, pers.
311 comm.). However, several other recent years have also seen large runs to this system, and from
312 2010 – 2017 they averaged over 1 million (Table 2). Thus abundance alone does not explain the
313 large number from this region in 2015. That year was characterized by very warm marine
314 waters over a large area along the west coast of North America but the anomaly was evident in
315 the previous and following years as well (Di Lorenzo and Mantua 2016; Jacox et al. 2018).
316 However, in 2015 there were very high stream temperatures, low summer flows, and also low
317 dissolved oxygen in the Somass River and upper Alberni Inlet, associated with significant delays
318 in upstream migration by these Sockeye Salmon stocks (K. D. Hyatt, DFO). Thus the large
319 number of strays from the Barkley Sound populations to the Elwha River in 2015 probably
320 reflected the combination of anomalous environmental conditions encouraging straying,
321 magnified by the exceptionally large run in that year, making them prevalent even in the small
322 sample from the Elwha River.

323 The straying from lakes draining into Barkley Sound in 2015 was not the only
324 unexpected result. The Fraser River system is the largest source of Sockeye Salmon in the
325 region, with an average total run of 8.04 million from 2010 – 2017, yet only a single stray from
326 this large basin's diverse populations was detected in the Elwha River samples. A variable but
327 typically large fraction of the Fraser River Sockeye Salmon migrates homeward from the north,
328 travelling southward through the Strait of Georgia between Vancouver Island and the mainland
329 to the mouth of the Fraser River. Such fish would not swim near the Elwha River unless they
330 passed the Fraser River and then moved west along the Strait of Juan de Fuca. However, the
331 fraction of the Fraser River run estimated by the Pacific Salmon Commission to use the Strait of
332 Juan de Fuca (Table 2) still constituted an average of 1.88 million Sockeye Salmon in the years
333 when our samples were collected. These salmon would have to swim within about 20 km of the
334 mouth of the Elwha River. Therefore, the proportion of Fraser River Sockeye Salmon straying
335 into the Elwha River must have been very low for them to be so under-represented.

336 None of the samples from the Elwha River were assigned to the Olympic Peninsula
337 populations in the baseline (Lake Quinault and Lake Ozette), nor the Puget Sound populations
338 (Baker Lake and Lake Washington). These populations were in the baseline, hence would have
339 been identified, but they are not very numerous and so might not contribute many strays in
340 general. The Columbia River is farther away but presumably those returning Sockeye Salmon
341 migrate southward along the coast and thus are not far from the Strait of Juan de Fuca and the
342 mouth of the Elwha River, yet fish from that system were not detected either. Each of these
343 populations has its characteristic timing of migration and spawning (Hodgson and Quinn 2002),
344 and so might not have been equally susceptible to sampling, but their absence is still notable.
345 Regrettably, the collection dates were not informative with respect to the likely origins.
346 Sockeye Salmon populations differ in the phenology of arrival into fresh water and spawning,
347 but the variation is largely at local rather than regional or latitudinal levels (Hodgson and Quinn
348 2002). This fact, combined with the variation in the condition of the fish sampled (e.g.,
349 upstream migrants and post-spawning), limits the use of sampling date for inferring origins.

350 Other than the 2015 strays from Barkley Sound and the single fish from the Fraser River,
351 the strays were exclusively assigned to populations from distant locations rather than any other
352 proximate ones. Surprisingly, most of the strays were assigned the Stikine River system, which
353 originates in British Columbia and flows to the ocean through southeastern Alaska. This system
354 has numerous breeding populations including lake-type and riverine forms (Wood et al. 1987).
355 The populations to which the Elwha fish were assigned to were northern, riverine populations,
356 including some of the largest ones of that type in the baseline, which also included the Harrison
357 and Widgeon Slough, riverine populations, both of which drain into the Fraser River. Wood et
358 al. (2008) hypothesized that the riverine types are more prone to stray and colonize newly
359 available habitat than the lake-type. Consistent with this hypothesis, the riverine Sockeye
360 Salmon populations within the Stikine River system were much less differentiated genetically
361 than were lake-type populations (Wood et al. 1994), following a pattern detected across the
362 species' range North American range using allozymes (Gustafson and Winans 1999). More
363 recent analyses using microsatellites revealed more differentiation among riverine Sockeye

364 Salmon than previously reported, but was not inconsistent with the idea that they may be more
365 prone to stray and colonize new habitat than lake-type conspecifics (Beacham et al. 2004).

366 The 17 Sockeye Salmon with primary assignments to the Stikine River system were all to
367 from riverine populations (primarily Bronson Slough and the Craig River). The Stikine River is
368 distant from the Elwha River (> 1000 km away), and produced a small fraction of all Sockeye
369 Salmon in the region during these years (Table 2). Notwithstanding any elevated tendency to
370 stray by riverine Sockeye Salmon that may exist, the Stikine River seems an unlikely source of
371 such a large fraction of the strays, though we cannot rule this out. An alternative, and perhaps
372 more likely, explanation for the assignments is that the genetic baseline applied here is missing
373 riverine populations near the Elwha River that are genetically similar to the riverine populations
374 in the Stikine River, and therefore the genetic stock identification model assigned the fish to the
375 Stikine River. Several Washington rivers have small numbers of Sockeye Salmon spawning at
376 sites not associated with any lakes, including the Nooksack, Skagit, and Stillaguamish rivers in
377 Puget Sound, the Dungeness River near the Elwha River along the Strait of Juan de Fuca, and
378 the Hoh, Queets, and Quillayute rivers on the west coast of the Olympic Peninsula (Gustafson
379 and Winans 1999; Michael Jr 2004). Some indication of non-ideal fit of the cBayes assignments
380 to the northern populations was also indicated by Gelman-Rubin scores associated with the
381 northern regions in the genetic assignment results, which typically are close to 1.0, but here
382 have slight elevations (Stikine, Taku, Alsek: 1.39, 1.56, 1.37, respectively, for the three regions)
383 relative to the rest of the regions (mean = 1.02; n = 18). A re-analysis with the sample size
384 filtered baseline reduced these elevations, although showed very similar assignment identities.
385 The mixed-stock analyses with rubias also showed very similar assignment results, and did not
386 indicate evidence for a missing population based on poor fit of the model based on z-score
387 traces ([https://github.com/eriqande/rubias#assessing-whether-individuals-are-not-from-any-of-the-](https://github.com/eriqande/rubias#assessing-whether-individuals-are-not-from-any-of-the-reference-populations)
388 [reference-populations](https://github.com/eriqande/rubias#assessing-whether-individuals-are-not-from-any-of-the-reference-populations)), as shown in Supplemental File 1. This provides further evidence that if
389 there is a missing population, it is similar in genetic signature to the Stikine River populations. In
390 genetic stock identification, the population of origin that best fits will be used as the primary
391 assignment, even if the true population is absent from the baseline. A comprehensive baseline

392 is therefore needed, particularly for species like Sockeye Salmon with pronounced genetic
393 differences among even proximate populations (Beacham et al. 2005).

394 Given the alternative explanations for the anomalous proportion of strays assigned to
395 the Stikine River region, data from Pacific Salmon Commission's test fishery in Fishery
396 Management Area 20 (i.e., the Canadian side of the Strait of Juan de Fuca) collected in 2010 (n
397 = 2974), 2011 (n = 2521), and 2013 (n = 3231) and previously processed in the DFO Molecular
398 Genetics Laboratory (MGL) were re-analyzed using the same baseline as the present study. Of
399 these 8726 samples, only 5 fish (0.06%) had highest assignments to the Stikine region (2012: 0,
400 2011: 3, and 2013: 2). The regional assignment probabilities ranged 0.42-0.72 in 2011, and 0.58
401 and 1.0 in 2013 (*data not shown*). We interpret these data to indicate that there were very few
402 adult Sockeye Salmon similar to the Stikine-like fish identified in the Elwha River system
403 migrating in the vicinity of the Elwha River and intercepted by the test fishery in these years.
404 Therefore, the most likely explanation of the far north assignments is that the Sockeye Salmon
405 sampled in the Elwha River were from populations nearer to the Elwha River that resembled
406 the Stikine River fish genetically, perhaps some of the region's small riverine populations
407 (Brown et al. 1979; Gustafson and Winans 1999; Michael Jr 2004).

408 Based on extensive analysis of coded wire tagging data from hatchery-produced
409 populations, Pacific salmon populations vary in the proportions that stray (Candy and Beacham
410 2000; Quinn et al. 1991), as do life history variants within species from a given river (Westley et
411 al. 2013), so riverine Sockeye Salmon might be more prone to stray than lake-type conspecifics.
412 Moreover, some rivers receive more strays than others (Quinn et al. 1991), and strays tend to
413 enter rivers more similar to their natal river than less similar rivers, in addition to a general
414 tendency to stray near their natal river (Pascual and Quinn 1994). Given the genetic population
415 structure of Sockeye Salmon from Washington to southeastern Alaska (Beacham et al. 2005;
416 Beacham et al. 2006), it seems unlikely that every river regularly receives a large number of
417 strays from the Stikine River or other small, unidentified riverine populations. It seems more
418 likely that the Elwha River was especially attractive to strays from these sources, either because
419 it resembled their home river, or had other features (sediment levels, temperature, chemistry,
420 etc.) that attracted them. Given the uncertainty as to what chemicals are learned by juvenile

421 salmon and used by returning adults, and other important aspects of homing (Bett and Hinch
422 2016; Quinn 2018; Salmenkova 2017), we cannot distinguish between these two hypotheses.

423 Notwithstanding the implications of the present results for salmon colonization, they
424 leave unresolved the genetic origins of the current non-anadromous *O. nerka* population in
425 Lake Sutherland. The other Washington populations grouped together as might be expected
426 from their geographical proximity (i.e., the Olympic Peninsula: Ozette and Quinault lakes) or
427 transplant history (Baker Lake was the primary source of the Lake Washington population
428 complex, though native *O. nerka* were apparently there as well (Hendry et al. 1996; Spies et al.
429 2007)). In contrast, the Lake Sutherland population was not strongly grouped with any other
430 population, and had low bootstrap support in general. Expansion of the analyzed baseline to
431 include other kokanee populations that might have been transplanted into the lake might help
432 determine the origins of the Lake Sutherland fish.

433 The origins of Sockeye Salmon straying into the Elwha River may affect the future
434 genetic composition of an amalgamated population that may include proportions of the
435 formerly landlocked Lake Sutherland population, and any strays that successfully reproduce
436 there, or elsewhere in the system. Spawning in Lake Sutherland is almost exclusively limited to
437 shorelines, and the limited tributary and outlet habitat might limit successful reproduction by
438 strays but, if they are riverine, they might spawn in the Elwha River itself. Any such nascent
439 population will probably be small but still can provide insights into the processes that took
440 place countless times as glaciers receded, habitat became suitable, and populations were
441 established from one or more sources. For example, the coho salmon in Glacier Bay, Alaska
442 seem to have relied on large source populations outside the area (Scribner et al. 2017). Straying
443 also enabled the establishment and expansion of salmon outside their native range, such as
444 Chinook Salmon in New Zealand (Quinn et al. 2001) and South America (Gomez-Uchida et al.
445 2018), and Pink Salmon in the Great Lakes (Emery 1981; Kwain and Lawrie 1981) and northern
446 Europe (Armstrong et al. 2018; Mo et al. 2018). Finally, as climate changes alter the suitability
447 and accessibility of Arctic rivers, colonization may occur there as well (Babaluk et al. 2000;
448 Dunmall et al. 2013; Nielsen et al. 2013).

449

Acknowledgments

450
451 We thank Marcia House and others from the Northwest Indian Fisheries Commission, and
452 Michael McHenry, Matt Beirne, Rebecca Paradis, and Mel Elofson with the Lower Elwha Klallam
453 Tribe for providing us with access to fish caught in Lake Sutherland and in the Elwha River.
454 Samples from the Elwha River were collected by Keith Denton, Josh Geffre, Geidi Connor, and
455 also by Joseph Anderson and other Washington Department of Fish and Wildlife (WDFW) staff,
456 and we thank them for both sampling and comments on the draft paper. We thank Brenda
457 McIntosh for genotyping of the Elwha River and Lake Sutherland Sockeye Salmon samples, and
458 Eric Rondeau for analytic support. Estimates of Sockeye Salmon abundance were kindly
459 provided by the following individuals and respective organizations, and we are keenly aware of
460 how much effort is involved in generating these estimates: Kim Hyatt, DFO (Barkley Sound and
461 Long Lake), Pacific Salmon Commission (Fraser, Stikine, Taku rivers), Andrew Piston, Alaska
462 Department of Fish and Game (McDonald Lake; Skeena and Nass river estimated derived from
463 work of the joint PSC Northern Boundary Technical Committee), Larry Gilbertson, Quinault
464 Indian Nation (Lake Quinault), US Army Corps of Engineers (Columbia River), Brett Barkdull,
465 Washington Department of Fish and Wildlife (Baker Lake), WDFW and Muckleshoot Indian
466 Tribe (Lake Washington), Makah Indian Nation (Lake Ozette), Megan Adams and the Wuikinuxv
467 Stewardship Department (Owikeno Lake). We thank the Pacific Salmon Commission for
468 permission to use the Area 20 fishery sample genotypes, and Oleksandr Stefankiv for drafting
469 the maps. Funding for field work was provided by the U. S. National Park Service. Funds were
470 also provided from the Washington Sea Grant program, University of Washington, pursuant to
471 NOAA Award No. NA10OAR4170075, Project R/LME-7, and from the H. Mason Keeler
472 Endowment and Richard and Lois Worthington Endowment to Thomas Quinn at the University
473 of Washington. Finally, we thank the reviewers and editorial staff for very helpful comments.
474

476 Table 1. Adult Sockeye Salmon sampled in the Elwha River, with the year and date collected,
 477 sex and fork length (in mm) if recorded, and the most probable region of origin (“Region 1”,
 478 with the probability in parentheses) and the second most probable region of origin (“Region
 479 2”). For the 21 populations with a third probable origin, the average probability was 0.08 and
 480 the maximum was 0.19 (not shown). The letters RT indicate that the most probable stock within
 481 the region was riverine (i.e., not associated with a lake for rearing, as opposed to the more
 482 typical lake type for this species).

483

Year	Date	Sex	Length	Region 1	Region 2
2010	17-Sep	M	460	Stikine – RT (0.85)	Taku - RT (0.06)
2010	6-Oct	M	650	Owikeno (0.48)	Fraser early summer (0.22)
2010	8-Oct	M	680	Stikine – RT (0.44)	Upper Skeena (0.39)
2011	19-Aug	M	710	Taku - RT (0.72)	Stikine - RT (0.27)
2011	20-Aug	M	690	Stikine - RT (1.00)	
2011	31-Aug	M	670	Taku -RT (0.58)	Stikine - RT (0.25)
2011	20-Sep	F	580	Stikine- RT (0.42)	SE Alaska (0.39)
2011	24-Sep	M	650	Stikine - RT (0.66)	Taku - RT (0.34)
2011	26-Sep	M	380	Stikine - RT (0.87)	Alsek - RT (0.11)
2012	7-Aug	F	590	Fraser early summer (0.98)	Stikine - RT (0.01)
2012	24-Aug	M	570	Stikine - RT (0.75)	Alsek - RT (0.18)
2012	12-Sep	M	640	Stikine -RT (0.71)	Taku - RT (0.27)
2013	9-Aug	M	660	Stikine - RT (0.82)	Alsek - RT (0.12)
2013	22-Aug	M	640	Owikeno (0.53)	Stikine - RT (0.43)
2013	28-Aug	F	610	Stikine - RT (0.97)	Taku - RT (0.02)
2013	28-Aug	F	610	Stikine - RT (0.75)	Upper Skeena (0.08)
2013	30-Aug	M	690	Stikine - RT (0.47)	Owikeno (0.26)
2013	7-Sep	M	550	Stikine - RT (0.93)	Taku - RT (0.04)
2015	5-Aug	M	650	Vancouver Is (1.00)	
2015	5-Aug	F	610	Vancouver Is (1.00)	
2015	18-Aug	M	565	Vancouver Is (1.00)	
2015	18-Aug	M	565	Vancouver Is (1.00)	

2015	18-Aug	F	585	Vancouver Is (1.00)	
2015	18-Aug	F	615	Stikine - RT (0.64)	Vancouver Is (0.13)
2015	20-Aug	F	590	Stikine - RT (0.70)	Babine (0.18)
2015	20-Aug	F	560	Vancouver Is (0.83)	Stikine - RT (0.15)
2015	25-Aug	M	563	Vancouver Is (1.00)	
2015	25-Aug	M	595	Vancouver Is (1.00)	
2015	26-Aug	F	550	Vancouver Is (1.00)	
2015	26-Aug	F	490	Vancouver Is (1.00)	
2015	26-Aug	F	550	Vancouver Is (1.00)	
2015	10-Sep	F	510	Vancouver Is (1.00)	
2015	10-Sep	F	500	Vancouver Is (1.00)	
2015	10-Sep	F	560	Vancouver Is (1.00)	
2015	10-Sep	M	630	Vancouver Is (1.00)	
2015	14-Sep		480	Vancouver Is (1.00)	
2015	14-Sep		584	Vancouver Is (1.00)	
2015	14-Sep		556	Vancouver Is (1.00)	
				Vancouver Is (1.00)	
2015	21-Sep			Vancouver Is (1.00)	
2015	22-Oct	M		Vancouver Is (1.00)	
2015	22-Oct	M		Vancouver Is (1.00)	
2015	22-Oct	M		Stikine - RT (0.51)	Owikeno (0.24)
2016	20-Jul	F	610	Stikine - RT (0.60)	Taku - RT (0.21)
2016	26-Jul	M	620	SE Alaska (0.47)	Owikeno (0.41)
2017	20-Jul	M	590		

486 Table 2. Abundance estimates for major Sockeye Salmon runs from southeastern Alaska to the
 487 Columbia River, averaged from 2010 – 2017, and each system’s contribution (“Annual %”), to
 488 the average total (6,454,449). Most estimates are for the total run but in some cases only the
 489 fish escaping the fisheries were counted, and estimation methods vary greatly among systems.
 490 The rivers are ordered from north to south. Data were provided as follows: McDonald Lake,
 491 Nass and Skeena rivers: Andrew Piston, Alaska Dept. of Fish and Game; Taku and Stikine rivers:
 492 annual reports of the Pacific Salmon Commission’s Transboundary Technical Committee;
 493 Owikeno (= Wuikinuxv) Lake: Wuikinuxv Stewardship Department; Long Lake and Barkley
 494 Sound: Kim Hyatt, Dept. of Fisheries and Oceans, Canada; Fraser River (only the proportion
 495 estimated to have migrated via the Strait of Juan de Fuca): annual reports of the Pacific Salmon
 496 Commission’s Fraser River Panel; Lake Washington: Washington Dept. of Fish and Wildlife
 497 (WDFW) and the Muckleshoot Indian Tribe; Baker Lake: Brett Barkdull, WDFW; Lake Ozette:
 498 NOAA-Fisheries and the Makah Indian Nation; Quinault Lake: Larry Gilbertson, Quinault Indian
 499 Nation; Columbia River: US Army Corps of Engineers counts at Bonneville Dam. These data
 500 should not be used without permission from the original sources, and an understanding of the
 501 caveats in each set. The column on the right is the number of fish among the sample of 45 in
 502 the Elwha River assigned to the population complex or region, for comparison.
 503

Population complex	2010 - 2017 average	Annual % of total	Elwha River
McDonald Lake	94,046	1.5	1
Taku River	191,928	3.0	2
Stikine River	160,341	2.5	17
Nass River	525,418	8.1	0
Skeena River	1,725,183	26.7	0
Owikeno (Wuikinuxv) Lake	198,353	3.1	2
Long Lake	103,624	1.6	0
Barkley Sound	1,048,375	16.2	22
Fraser River (Juan de Fuca)	1,882,056	29.2	1
Baker Lake	35,027	0.5	0

Lake Washington	102,596	1.6	0
Lake Ozette	5,725	0.1	0
Lake Quinault	28,205	0.4	0
Columbia River	353,572	5.5	0

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505 Figure captions

506 Fig. 1. Map of the Elwha River system in western Washington, USA, and the larger area of the
507 west coast of North America showing the mouths of rivers where Sockeye Salmon populations
508 occur that were included in the DNA baseline.

509

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511 Supplemental Figure S1. Dendrogram showing genetic similarity of baseline populations
512 relevant to the study of the origins of Sockeye Salmon in the Elwha River. Populations were
513 included if they were detected in individual assignments with at least 10% of any individual's
514 allocation to show genetic similarity among baseline collections, or were otherwise important
515 as potential sources (e.g., Lake Sutherland and other proximate populations). Values at nodes
516 indicate the percentage of the dendrograms that had the same populations grouped to the
517 right of the node (e.g., 90.2% of trees grouped the Columbia River populations within the same
518 cluster). The scale bar indicates the genetic distance as evaluated by the distance metric
519 applied (see Methods).

520

521

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