

23 **ABSTRACT:** Bycatch impacts on non-target species present significant management
24 problems in diverse fisheries throughout the world. Despite successful efforts to
25 minimize bycatch in US West Coast Pacific Hake fisheries, these impacts remain a
26 concern, particularly for sensitive populations of Chinook Salmon. NOAA Fisheries
27 needed predictive models to estimate proportions of Chinook Salmon Evolutionarily
28 Significant Units (ESUs) expected in bycatch. We used genetic mixture analysis to
29 estimate ESU proportions from at-sea bycatch between 2008 and 2015. Using latitude as
30 a predictor and applying jackknife cross validation, we found Dirichlet regression more
31 accurately estimated abundant ESUs, whereas multinomial logistic regression performed
32 better with rare ESUs. This targeted, ESU-specific approach showed the spatial
33 distribution of sensitive stocks in bycatch and supported NOAA's obligations to forecast
34 impacts on listed ESUs. The overarching goal of this continuing work is to maximize
35 sustainable harvest while protecting threatened and endangered Chinook Salmon ESUs.

36

INTRODUCTION

37 Pacific Hake¹ (*Merluccius productus*) are distributed from the Gulf of Alaska to
38 the Gulf of California (Quirollo et al. 2001). This abundant marine resource supports a
39 large-scale trawl fishery off the US West Coast. Trawling in this region began slowly in
40 the 1870s but increased in the 1920s with implementation of diesel engines and other
41 technological advances (Easley 2001). By 1966 harvest reached 137 kMT and now
42 represents an important economic resource to the region and to the nation (Hamel et al.
43 2015). In 2016, commercial landings of Pacific Hake totaled more than 260.8 kMT
44 valued at over US\$42 million (NOAA 2019).

45

Incidental Take Statement for the US West Coast groundfish fisheries

47 Despite much effort and management action to reduce impacts on non-target
48 species, bycatch remains a concern in this commercially important fishery (Somers et al.
49 2015). There is special concern for bycatch of Chinook Salmon (*Oncorhynchus*
50 *tshawytscha*) protected under the US Endangered Species Act (ESA). By international
51 treaty (PSC 2020), management of coastal Pacific hake fisheries is shared among
52 Canadian Department of Fisheries and Oceans, NOAA Fisheries, and the Joint
53 Management Committee. In cooperation with the Pacific Fishery Management
54 Council (PFMC), NOAA manages the Pacific Hake fishery on the US West Coast in
55 Federal waters (3 to 200 miles offshore). Federal agencies must consult with NOAA on
56 activities that might jeopardize the continued existence of protected marine species
57 (essentially any action that involves “take”). As part of the 2017 ESA Consultation for
58 the West Coast Groundfish Fishery Management Plan salmon biological opinion (BiOp),

¹ Also referred to by the industry name “Pacific whiting”

59 the PFMC and NOAA faced a series of questions related to alternative fishery regulation
60 scenarios. For example: What would be the actual number of Chinook Salmon
61 individuals in bycatch from each Evolutionarily Significant Unit (ESU), if the current
62 restriction were rescinded on processing Pacific Hake south of latitude 42? What if there
63 was a resumption of the tribal mothership fishery off the north coast of Washington
64 State? Ultimately, NOAA's Incidental Take Statement needed to forecast the actual
65 number of Chinook Salmon from each ESU taken in bycatch, given predicted spatial
66 distribution of fishing effort (Matson and Erickson 2018) and under different
67 management scenarios (NMFS—WCR 2017).

68

69 *Limited CWT recoveries in bycatch*

70 Tiny coded-wire tags (CWTs) are implanted in the snouts of juvenile hatchery
71 fish, and much has been learned about Chinook Salmon migration patterns and ocean
72 distribution from CWT recoveries (Weitkamp 2010; Riddell et al. 2018; Shelton et al
73 2019). We know that particular stocks have characteristic patterns of tag recovery,
74 primarily in commercial salmon harvest. Importantly, these patterns of migration were
75 shown to be surprisingly stable across years, despite high interannual variation in ocean
76 conditions and relative abundance (Weitkamp 2010). In spite of broad utility in harvest
77 management and basic research, coded-wire-tag recoveries in bycatch have generally
78 been inadequate to estimate relative abundance and distribution of 17 ESUs (identified in
79 Appendix 1). In parallel with tissue sampling, only 687 CWTs were recovered from
80 among 9,862 Chinook Salmon sampled by NOAA At-Sea Observers over the 8 years of
81 this study (2008 – 2015). Therefore, genetic analysis, where every fish, hatchery and wild,

82 is effectively “tagged,” presented an opportunity to significantly augment what was
83 known from sparse CWT recoveries (NMFS—WCR 2017).

84

85 In the current study, we used genetic mixture analysis to characterize stock
86 composition of Chinook Salmon ESUs in the US West Coast, at-sea, Pacific Hake fishery.
87 We also tested accuracy and precision of different predictive regression models used to
88 forecast ESU impacts in a management context; the goal being to provide the most
89 powerful forecasting tool requiring the simplest possible inputs. Beyond specific interest
90 to salmon conservation and Pacific hake harvest, our results are relevant to broader
91 studies of more general statistical challenges of multinomial regression modeling and
92 measures of forecasting accuracy—both common problems in ecology and natural
93 resource management.

94

95

MATERIALS AND METHODS

96 NOAA’s At-Sea Hake Observer Program (A-SHOP) collected Chinook Salmon
97 tissue samples from the catcher/processor, mothership, and at-sea tribal sectors (NWFSC
98 2021). Rayed fin-clip samples were folded in Whatman 3MM chromatography paper,
99 dried immediately, and stored in barcoded coin envelopes at ambient temperature.
100 Samples were deposited in the Northwest Fisheries Science Center (NWFSC)
101 Conservation Biology Division’s Genetic Tissue Archive (accession numbers in Table 1).
102 All samples were collected during the normal fishing season beginning 15 May and
103 ending 31 December. Tissue samples selected for genotyping (4,498) were drawn
104 randomly each year between 2008 and 2015. Annual sample sizes were dictated by
105 project resources available in a given year, not total bycatch. Table 1 illustrates the

106 filtering process and identifies the following: total estimated bycatch, samples collected
107 by observers, random sub-sample for genotyping, and filtered for genotyping quality and
108 filtered for ≥ 0.8 assignment probability. The latter two sample sets provided the primary
109 input data for this study and reflect two distinctly different statistical approaches; 1)
110 modeled genetic stock composition estimates based on all individuals for all ESUs
111 simultaneously, and 2) discrete individual assignment of each fish to population of origin.
112 Our sample was intended to accurately reflect ESU-specific, spatial and temporal bycatch
113 impacts over the course of each year in the fishery. That was the essential focus of
114 NOAA's BiOp as related to Chinook salmon impacts (NMFS—WCR 2017).

115

116 [Table 1 near here]

117

118 ***Genotyping, genetic mixture modeling, and individual assignment***

119 DNA was extracted and purified by using Qiagen® DNeasy™ membrane capture.
120 Purified DNA was amplified and genotyped for 13 internationally standardized
121 microsatellite loci (see below). Microsatellite products were sized using an Applied
122 Biosystems Incorporated (ABI) 3100 Genetic Analyzer. Genotypes were inferred from
123 electropherograms by using ABI Genescan and Genotyper software. We used conditional
124 maximum likelihood mixture modeling (CMLMM) to simultaneously estimate stock
125 compositions and make individual assignments to population of origin (Rannala and
126 Mountain 1997; ONCOR, Kalinowski et al. 2007), with bias correction (Anderson et al.
127 2008). Population-level allocation was then aggregated by ESU reporting group. Genetic
128 mixture analysis using ONCOR was replicated and confirmed with the R package 'rubias'
129 (Moran and Anderson 2019). The two sets of genetic results from ONCOR, 1) modeled

130 proportions and 2) individual assignments, were used for the two different classes of
131 statistical analysis, 1) Dirichlet regression (DR; Maier 2014) and 2) multinomial logistic
132 regression (MLR; Hilbe 2009). CMLMM is taken to be the best possible estimate of ESU
133 proportions in a given year. We use the term “observed” in reference to observed
134 genotypes and observed latitudes that are compared to “predicted” ESU proportions from
135 the regression models. We calculated credibility intervals for CMLMM proportions,
136 however, we relied principally on cross validation of predictions and evaluation of
137 accuracy with scale-dependent and -independent metrics (see below).

138

139 CMLMM depends on a baseline dataset of known-origin reference samples that is
140 assumed to represent all potentially contributing populations. In this study, we used the
141 most comprehensive Chinook Salmon baseline available, the internationally standardized,
142 microsatellite dataset (i.e., common loci and consistent allele designations, Moran et al.
143 2006) that was developed by the Genetic Analysis of Pacific Salmonids consortium
144 (GAPS; Moran et al. 2005; Seeb et al. 2007). The GAPS baseline was designed for
145 eastern Pacific fishery mixtures, primarily harvest, but the geographic coverage of
146 potential source populations is complete from Southeast Alaska to Central Valley,
147 California. The version of the baseline we used included more than 20,000 known-origin
148 fish from 163 populations representing all ESUs and major Canadian and Alaskan stocks
149 that contribute to these fisheries (Appendix 1). The GAPS baseline is thoroughly vetted
150 by the salmon genetics community and has been widely used in studies of harvest
151 impacts (Bellinger et al. 2015; Satterthwaite et al. 2015; Moran et al. 2018).

152

153 *Predictive regression models and cross validation*

154 Input data for our preliminary exploration included the ESU to which each fish
155 assigned, collection year, ordinal day of the year, latitude (decimal degrees), fork length
156 (cm), and fishing depth (m). Akaike information criterion (AIC) was used to evaluate
157 different predictive models. Focusing on mean latitude of an annual bycatch sample, we
158 compared two multinomial regression methods for predictive forecasting. DR was used to
159 relate observed proportions for an annual sample of individuals relative to the mean
160 latitudes over which those individuals were taken. MLR was also used to estimate an
161 expected proportion for each ESU as a function of latitude but was based on individual
162 fish rather than annual means. Compositional proportions are bounded by zero and one,
163 and not normally distributed or homoscedastic. This class of proportions violates
164 assumptions of linear regression and common parametric analyses such as t-tests and
165 ANOVA, when used as a dependent variable. To evaluate the absolute and relative
166 accuracy and precision of the two regression methods, we conducted sequential,
167 independent, cross-validation analyses holding out each of 8 individual years, one at a
168 time, as test datasets and using all remaining years as training data. We used a similar
169 jackknife approach for both regression methods. In each case, we evaluated the accuracy
170 of the prediction (based on the training data set) against the independent, cross-validation,
171 test set (the “actual” or “observed” ESU proportions derived from observed genotypes).
172 Central Valley Spring ESU only occurred in one test set (annual sample), so that ESU
173 was omitted from the jackknife. To the extent possible, the jackknife is a sequential test
174 of forecasting accuracy, “predicting” the composition of each annual sample as if it were
175 a new observation.

176

177 To quantify accuracy and precision of our forecast predictions compared to
178 observed genotypes, we used scale-dependent and scale-independent error metrics. For a
179 scale-dependent metric we selected the widely used and easily understood mean squared
180 error (MSE),

181

$$182 \quad \text{MSE} = 1/N \sum (y_t - f_t)^2.$$

183

184 Where N = number of tests, y_t = observed composition in the t^{th} test, and f_t = the t^{th}
185 forecast.

186

187 For a scale-independent metric we chose the less widely known mean arctangent
188 absolute percentage error (MAAPE),

189

$$190 \quad \text{MAAPE} = 1/N \sum (\arctan(|y_t - f_t| / f_t)).$$

191

192 MAAPE can be interpreted intuitively as an absolute percentage error like the commonly
193 used mean absolute percentage error (MAPE). However, MAAPE is less biased in greater
194 penalties for positive errors than negative (Makridakis 1993). Moreover, the bounded
195 range of the arctangent function ($\lim_{x \rightarrow \infty} \tan^{-1} x = \pi / 2$) overcomes the MAPE's limitation
196 of going to infinity as the observed value approaches zero (Kim and Kim 2016).

197

198 For context, we compared the accuracy of our modeled estimates with interannual
199 variability between members of paired samples (observed data) that had similar mean
200 latitudes. We selected pairs of annual samples that differed by less than 0.25 degrees in

201 mean latitude (2013 and 2014 at latitudes 43.8 and 43.5, respectively; and 2013 and 2015
202 at latitudes 43.8 and 43.9). This interannual variability should represent the minimum
203 error possible in a forecast estimate. We used the R statistical package (R Core Team
204 2017) for most of our analyses and figures.

205

206

RESULTS

207 NOAA fishery observers from the A-SHOP collected 9,862 individual tissue
208 samples, which represented 41% of the total estimated Chinook Salmon bycatch between
209 2008 and 2015 (Table 1). Samples were stratified by year, and a total of 4,498 fish were
210 randomly subsampled for DNA extraction and analysis (19% of total bycatch).

211 Geographic distribution of individual tissue samples extended from Shelter Cove (41.43°),
212 north to the Canadian border (48.48°); fishing depth 46 - 507 m (mean 246, SD 90.4);
213 bottom depth 66 - 2,743 m (mean 427, SD 217.4), and fork length 24 - 113 cm (mean
214 58.7, SD 11.9). A slight female bias was observed (0.54). Mean latitude values for each
215 annual bycatch sample ranged over 4.4 degrees (43.5° - 47.9°). A general shift to the
216 south was observed in fishing effort and bycatch beginning in 2011 (Table 1). Clearly,
217 similar values for mean latitude might produce very different stock compositions if they
218 have different distribution, e.g., non-normal. Through practical application and cross
219 validation, our results demonstrate the sensitivity of our models to those violations of
220 normality.

221

222

Genotyping and genetic mixture modeling

223 Of 4,498 fish subsampled for genotyping, 96% met genotyping quality criteria. In
224 addition to high genotyping success, high individual fish assignment probabilities were

225 also observed. About 78% of fish successfully genotyped met the assignment probability
226 criterion of ≥ 0.8 (N = 3,360, 14% of total bycatch; see Moran et al. 2014 for sensitivity
227 analysis). Modeled genetic estimates of overall proportions derived from all fish
228 successfully genotyped (“observed”) showed that most of the Chinook Salmon bycatch in
229 this period came from Upper Klamath-Trinity River and S. Oregon and N. California
230 Coastal ESUs (Fig. 1). Those two ESUs accounted for more than 50% of all bycatch in
231 the study period. Secondary contributors included the Oregon Coast and Puget Sound
232 ESUs and Southern British Columbia (lower Fraser River, data not shown).

233

234 [Fig. 1 near here]

235 Managers often focus on fishery management areas. Differences in ESU
236 composition between fishery management areas north and south of Cape Falcon (45.77°)
237 showed the effect of latitude (See figs. 2 and 3 for area boundaries). The two southern
238 ESUs—Upper Klamath-Trinity Rivers and S. Oregon/N. California—dominated bycatch
239 south of Cape Falcon but dropped to only ~5% each to the north of Cape Falcon. The
240 opposite was true of the northern ESU, Puget Sound, and Southern BC populations.
241 Spatial variation was also reflected when comparing the annual samples, which were
242 each taken at different mean latitudes and showed different ESU proportions (see
243 Jackknife cross validation below).

244

245 [Fig. 2 near here]

246

Individual assignment

247 Again, our analysis included two fundamentally different approaches, modeled
248 proportions versus individual assignment. The ESU stock composition results above

249 describe fitted genetic models to all observed genotypic data simultaneously (Koljonen et
250 al. 2005). At this point we shift to analyses based on individual fish assignment. First, we
251 simply created a scatter plot of individually georeferenced fish, color coded by ESU, and
252 overlaid on a map of the US West Coast (Fig. 3). That heuristic presentation also showed
253 strong effects of latitude on ESU composition. No fish assigned to Sacramento Winter
254 ESU, preventing inclusion of that ESU in the exploratory regression analysis described
255 below.

256

257 [Fig. 3 near here]

258 Individual assignment was used to explore the ESU-specific predictive power of
259 multiple sample attributes (e.g., latitude, depth, fork length, etc.). Previous simulations
260 using the GAPS baseline showed that individual assignment with a threshold of ≥ 0.8 for
261 inclusion, and regressing traits on ESUs is a robust and generally unbiased approach to
262 inferring ESU-specific phenotypes (Moran et al. 2014). However, we recognize that
263 individual assignment for compositional prediction raises issues of potential bias that go
264 beyond the scope of this article. Nevertheless, our cross-validation approach subsumes
265 those errors, allowing meaningful comparisons between disparate statistical methods.
266 According to AIC evaluation of MLR models in particular, latitude was by far the most
267 powerful single predictor of ESU origin (similar GAM results not shown). Other factors,
268 most notably year, clearly explained additional variation, but Burnham and Anderson's
269 (2004) Δ AIC values for individual factors, relative to latitude alone, were compelling:
270 year 1505, depth 1574, ordinal day 2271, and fork length 2544. More complex models
271 gave lower AIC values, but were less suitable as predictors and as practical fishery
272 management regulatory elements.

273

274 Plotting DR and MLR curves further illustrated the importance of latitude for
275 most ESUs (Fig. 4). Consistent with the plot of fishery management areas (Fig. 2),
276 northern ESUs were encountered primarily in the north, whereas southern ESUs were
277 concentrated in southern and central coastal areas. Cape Falcon marked an abrupt
278 transition in ESU composition of Chinook salmon bycatch.

279

280 [Fig. 4 near here]

281

Jackknife cross validation

282 The estimated regression curves in Figure 4 can be compared with observed
283 proportions in each annual sample (points in Fig. 4). However, the regression estimates
284 include all data and are therefore not independent from the point observations in Figure 4
285 (i.e., potentially presenting an overly optimistic interpretation of predictive power). By
286 contrast, the jackknife, cross-validation analysis provided an independent observation for
287 every ESU proportion in every year. Figure 5 compares observed ESU proportions for
288 each year with independently derived estimates from the two regression methods and
289 latitude alone. Figure 6 almost perfectly summarizes all individual years (Fig. 4) by
290 averaging over jackknife iterations. Despite a major difference in the MLR estimate for
291 Upper Klamath/Trinity Rivers, estimates for both regression models were close to one
292 another and close to observation for most ESUs.

293

294 [Fig. 5 and Fig. 6 near here]

295

Annual replicates at similar latitude

296 By chance, some annual samples had very similar mean latitudes. Consistent with
297 latitude being more important than year in the AIC, similar ESU proportions were
298 observed in those annual samples that had similar mean latitudes (i.e., 2013, 2014, and
299 2015; Fig. 5). Comparison of variation between years with the accuracy of our forecast
300 was mixed. Forecast predictions for large contributors showed substantially greater errors
301 than variation observed between years at similar latitude (MSE = 0.0005 for DR and
302 0.0008 for MLR compared with only 0.0001 for the annual replicates). However, the
303 scale-independent metric suggested that prediction errors were quite similar to
304 interannual variation (MAAPE = 0.670 and 0.564 for DR and MLR versus 0.572 for
305 interannual replicates).

306

307 *Accuracy of DR vs MLR, overall and by ESU*

308 In predicting the ESU composition obtained from CMLMM in a given year, DR
309 outperformed MLR for most ESUs that contributed more than 2.5%; however, the
310 distribution of errors was complicated. For all contributors, MSE (most sensitive to large
311 contributors) was 38% lower for DR than for MLR. Yet DR errors were more than three
312 times as variable across years (CV = 56% for DR versus 21% for MLR). By contrast
313 MAAPE (sensitive to small contributors) was 16% lower for MLR but nearly twice as
314 variable (CV = 27% for MLR versus 14% for DR). So in each case, the more accurate
315 regression method was less precise. A few patterns were evident in the accuracy and
316 precision of individual ESU estimates. DR underpredicted Upper Klamath-Trinity Rivers
317 ESU, in contrast to MLR that substantially overpredicted that ESU in nearly all years.
318 Large MSE values for MLR were driven largely—but not entirely—by the extreme
319 overprediction of Upper Klamath-Trinity Rivers ESU (Fig. 6; omitting Klamath/Trinity

320 only reduced MSE from 0.0008 to 0.0007, still greater than 0.0005 for DR, and much
321 greater than 0.0001 observed between years at the same latitude). With the notable
322 exception of S. Oregon and N. California Coastal ESU, which MLR estimated almost
323 exactly, southern ESUs were overestimated by MLR, whereas northern ESUs were
324 underestimated. DR underestimated all larger contributors (>5%), but consistently
325 overestimated smaller contributors, e.g., Washington Coast, Upper Willamette River,
326 Mid-Columbia River Spring, Upper Columbia River Spring Snake River Spring/Summer,
327 Snake River Fall ESUs [all years except 2009], and Central British Columbia and Alaska).
328 Extensive additional analyses did not show an obvious effect of omitting fish that failed
329 to meet the 0.8 probability criterion for MLR.

330

331

Discussion

332 We succeeded in developing useful predictive models for Chinook Salmon ESU
333 stock composition estimates in a fishery management context. Latitudinal clines and
334 stock-specific distributions observed here were generally consistent with distribution of
335 CWT recoveries in harvest fisheries (Weitkamp 2010; Shelton et al. 2019; Shelton et al.
336 2021). However, the current study, is the first we know of to describe pre-season
337 prediction of ESU-specific impacts based simply on anticipated latitude of a proposed
338 fishery. Given estimated bycatch numbers and latitudes (Matson and Erickson 2018),
339 NOAA needed to parse total numbers by ESU to give predictions of actual fish counts,
340 based on forecast proportions. These models were used previously in support of the 2017
341 Chinook salmon ITS and BiOp for the West Coast Groundfish Fishery Management Plan
342 (NMFS—WCR 2017). This paper is an extension of the ground truthing that went into
343 the BiOp. Because management needed to estimate ESU-specific impacts at various

344 levels of take, our application required estimating proportions. Our approach was dictated
345 by specific management needs, but the challenges of compositional forecasting and
346 characterization of errors are ubiquitous in fields as disparate as ecological genetics and
347 economic market research (Aitchison 1986). Even more broadly, the analysis of
348 individuals versus aggregates is a fundamental statistical dichotomy.

349

350 *Broadly similar results between methods*

351 We evaluated the performance of two accepted multinomial regression models
352 representing two different analytical approaches, one based on genetic mixture modeling
353 and DR, and the other based on individual assignment and MLR. We observed broadly
354 similar results, despite differences in both the treatment of genetic data and in the
355 regression. Independent cross validation showed that both analysis methods gave
356 surprisingly accurate estimates despite a range of potential challenges. Not least, that
357 different distributions of bycatch, with different stock compositions, might have similar
358 means, thus confounding our prediction.

359

360 On initial inspection, Dirichlet regression appeared more accurate than MLR, but
361 neither method provided a clear advantage across both rare and abundant ESUs. For
362 example, MLR consistently overestimated the abundant Upper Klamath-Trinity Rivers
363 ESU, especially in 2008 and 2011, whereas DR was much more accurate. DR was clearly
364 more accurate than MLR in estimating large contributors; however, DR consistently
365 overestimated small contributors, such as Upper Willamette River, Snake River
366 Spring/Summer, and Snake River Fall—all listed as Threatened under the US
367 Endangered Species Act. MLR was much more accurate than DR in estimating those

368 small contributors at all latitudes and in nearly all years. Essentially all prediction errors
369 for large contributors were greater than observed between members of paired annual
370 samples at similar mean latitude—clearly room for improvement. However, for small
371 contributors, prediction accuracy was extremely good. For example, 8 of 17 ESUs
372 showed less variation between MLR prediction and observed ESU proportions in a given
373 year than between years at similar latitude (6 of 17 for DR). In other words, prediction
374 error with MLR was no larger than interannual variation for these small contributors.

375

376 Prediction accuracy is often critical for small contributors to mixed fisheries.
377 Overprediction of sensitive or ESA-listed ESUs can lead to elevated concern, fishery
378 restrictions, and needless forgone harvest. Moreover, a scale-independent metric like
379 MAAPE could be considered a more appropriate measure of general forecasting accuracy
380 than MSE. So, the recommended method depends on specific application and relative
381 concern for abundant versus rare stocks. Harvest allocation might call for DR, whereas
382 conservation might be better served by MLR. Managers are advised to examine both DR-
383 and MLR-based take estimates and weigh the implications of specific inconsistencies.

384

385 *Comparison of Chinook Salmon stocks in bycatch versus directed harvest*

386 We noted interesting differences from stock compositions previously reported for
387 harvest. Direct comparison is difficult, but it appeared anecdotally that the Bellinger et al.
388 (2015) study of commercial troll observed substantially higher proportions of Central
389 Valley Fall ESU and lower proportions of Klamath-Trinity ESU than the current study.
390 Also, Columbia River populations were more abundant in troll than in bycatch (Fig. 5 e, f,

391 and g in Bellinger et al. 2015 compared to our Fig. 1). Similar results were seen in
392 harvest studies (commercial and recreational fisheries) that sampled areas farther south
393 (Winans et al. 2001; Satterthwaite et al. 2015).

394

395 With respect to latitude, the most direct available comparison between harvest and
396 bycatch comes from the Washington commercial troll fishery (Moran et al. 2018). The
397 mean latitude for all samples observed in that study between 2012 and 2015 was 47.4°,
398 which was similar to the annual bycatch sample that we analyzed in 2009 (47.9°).

399 Despite that similarity in latitude, the observed stock compositions were quite different.

400 The relative abundance of Lower Columbia River and Upper Columbia River

401 Summer/Fall was much higher in Washington troll than in bycatch from similar latitude.

402 By contrast, proportions of Puget Sound and Southern British Columbia were much

403 lower in troll than in bycatch. A difference worth noting is that at-sea bycatch tends to be

404 unimodal in latitude within years (either north or south) but bimodal among years,

405 whereas Washington coastal troll is strongly bimodal every year (Moran et al. 2018).

406 There are also differences in depth and distance offshore. These anecdotal stock

407 composition differences among disparate studies are difficult to interpret without broader

408 spatial overlap and temporal replication. Eventually, however, the hope is that meta-

409 analyses among fisheries can help discriminate where fish are caught from exactly where

410 they are and how different populations use the marine environment in time and space.

411

412 ***Fishery-dependent focus: Opportunities and limitations***

413 Satterthwaite et al. (2014:128) pointed out that, for management purposes,

414 “variability in interactions with the fishery is more relevant than ecological distribution.”

415 The focus of the current study was not stock-specific, ecological distribution. Instead, we
416 measured fishery impacts explicitly, and we limited most of our analysis to high-level
417 spatial and temporal strata (i.e., coast-wide, annual). We chose both the scale and the
418 compositional forecasting approach to provide fishery managers with a tool that required
419 only simple inputs and would help meet obligations for predicting ESU impacts. In the
420 context of depressed populations, it's worth recognizing the inherent challenge in
421 estimating very small bycatch numbers. Some ESUs were rare or absent in our analysis.
422 Fewer than 10 fish were observed for each of six ESUs, and no Sacramento Winter fish
423 were observed. Despite small numbers of observations for some ESUs, the expected
424 proportions for those rare ESUs are not independent and are partially informed by the
425 proportions of all other ESUs, including abundant ESUs for which estimates are much
426 more confident. Despite concerns about interannual variability, non-normal latitudinal
427 distributions, and the utility of mean latitude, our cross validation showed that error in the
428 MLR estimate was essentially indistinguishable from interannual variation between
429 samples taken at the same latitude. Again, we point out that “errors” in our regression
430 estimates are relative to “observation” that is also an estimate but is based on observed
431 genotypes and is our best estimates of ESU proportions in a given year. We use the term
432 observation to emphasize the distinction between estimation and prediction, an observed
433 mixed fishery versus a compositional forecast.

434

435 Results of Weitkamp (2010) suggested stable Chinook Salmon stock distributions
436 across years, despite different ocean conditions and relative stock abundance (but see
437 Satterthwaite et al. 2012; Shelton et al. 2019; Shelton et al. 2021). Seasonal variation in
438 bycatch composition is substantially dampened, relative to directed harvest, because of

439 the broad distribution of age classes in bycatch. For future genetic bycatch data, we will
440 conduct a detailed exploration of stock-specific associations with oceanographic
441 variables (sea-surface temperature, chlorophyll, etc.). Irrespective of spatial changes in
442 fishing activity, if Chinook Salmon change their distribution or relative abundance in
443 response to climate change, will the curves remain the same, shift uniformly north (or
444 south), or will shapes and relative relationships of the curves change fundamentally, as
445 predicted by Shelton et al (2021)? Climate effects on these latitudinal distributions could
446 go beyond Chinook ESU impacts and conservation, to the extent ESA-listed southern
447 resident killer whales target preferred Chinook salmon stocks (Hanson et al. 2010).

448

449 These questions are important, as the fishing industry becomes increasingly
450 sophisticated in their requests for data on salmon distribution. Not only do fishing fleets
451 want to avoid Chinook Salmon bycatch, they especially want to avoid protected or
452 sensitive ESUs like Puget Sound, Lower Columbia River, Upper Klamath-Trinity Rivers,
453 California Coast, and Central Valley Fall. Our figures 3 and 4 summarize what we know
454 about where these ESUs are most likely to be caught. An obvious measure to avoid
455 particular ESUs is to avoid nearby latitudes. The trouble is, moving north to avoid the
456 threatened California Coast ESU, for example, would likely shift impacts to Puget Sound
457 and Lower Columbia River, also listed as threatened under the US ESA. Moreover,
458 moving fishing pressure north or south has a big effect on ESUs like Upper Klamath-
459 Trinity Rivers or Puget Sound that have steep latitudinal clines, but less effect on ESUs
460 like California Coast that have broader, flatter distributions. Despite that practical
461 limitation to active avoidance of sensitive stocks, our regression models successfully

462 address thorny statistical challenges and offer practical tools that are useful in evaluating
463 ESU-specific impacts under different fishery management scenarios.

464

465

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646 Northwest: Test fisheries in California. *Reviews in Fisheries Science*, 9:213–237.

647 Table 1. Chinook Salmon bycatch in the at-sea sectors of the US West Coast Pacific
648 Hake fishery (where >0.8 is the number of individual fish that met that assignment
649 probability threshold, and Mean latitude is derived from all fish genotyped)

Year	Bycatch¹	Collected	Subsampled	Genotyped	>0.8	Mean lat.	Accession #²
2008	875	271	271	258	178	46.32	34801
2009	1,142	403	403	390	326	47.89	34592
2010	1,364	680	680	664	548	46.89	34927
2011	4,360	1,837	1,835 ³	1,693	1,284	44.77	90517
2012	4,209	2,013	288	288	215	44.43	90598
2013	3,739	1,542	288	285	218	43.78	90601
2014	6,695	2,368	384	381	295	43.54	90627
2015	1,806	748	349	345	296	43.91	90654
Total	24,190	9,862	4,498	4,304	3,360	45.21	

¹Estimated total Chinook bycatch

nwfsc.noaa.gov/research/divisions/fram/observation/xls/SalmonBycatch_Expanded_2002-2015.xlsx

²NWFSC Conservation Biology Division Tissue Archive

³Essentially all collected samples were selected for genotyping in 2012

650

651

652 **APPENDIX**

653 Reference populations and reporting group structure for genetic mixture analysis based
654 on Evolutionarily Significant Units (J. Myers, pers. comm. January 2016). Populations
655 modified from Seeb et al. (2007). Status: E = Endangered, T = Threatened, C = Candidate,
656 NW = Not Warranted, N/A = Not Applicable, stock aggregates that are not ESUs, which
657 are only defined for the conterminous, US West Coast states. Carson Hatchery is a
658 mixed-origin broodstock that is not listed under the ESA.

Genetic baseline population	ESU reporting group	Status
Sacramento Hatchery	Sacramento Winter	E
Butte Creek sp	Central Valley Spring	T
Deer Creek sp	Central Valley Spring	T
Mill Creek sp	Central Valley Spring	T
Feather Hatchery sp	Central Valley Fall	C
Feather Hatchery fa	Central Valley Fall	C
Butte Creek fa	Central Valley Fall	C
Stanislaus River	Central Valley Fall	C
Battle Creek	Central Valley Fall	C
Russian River	California Coastal	T
Eel River	California Coastal	T
Trinity Hatchery fa	Upper Klamath-Trinity Rivers	NW
TrinityHatchery sp	Upper Klamath-Trinity Rivers	NW
Klamath River fa	Upper Klamath-Trinity Rivers	NW
Chetco River	S. Oregon and N. California Coastal	NW
Applegate Creek	S. Oregon and N. California Coastal	NW
Cole Rivers Hatchery	S. Oregon and N. California Coastal	NW

Genetic baseline population	ESU reporting group	Status
Elk Hatchery	Oregon Coast	NW
Sixes River	Oregon Coast	NW
Coquille River	Oregon Coast	NW
Coos Hatchery	Oregon Coast	NW
S Umpqua Hatchery	Oregon Coast	NW
Umpqua Hatchery	Oregon Coast	NW
Siuslaw River	Oregon Coast	NW
Alsea River	Oregon Coast	NW
Yaquina River	Oregon Coast	NW
Siletz River	Oregon Coast	NW
Salmon River fa	Oregon Coast	NW
Nestucca Hatchery	Oregon Coast	NW
Trask River	Oregon Coast	NW
Wilson River	Oregon Coast	NW
Kilchis River	Oregon Coast	NW
Nehalem River	Oregon Coast	NW
Necanicum Hatchery	Oregon Coast	NW
Forks Creek Hatchery	Washington Coast	NW
Humptulips Hatchery	Washington Coast	NW
Queets River	Washington Coast	NW
Hoh River	Washington Coast	NW
Sol Duc Hatchery	Washington Coast	NW
Makah Hatchery	Washington Coast	NW
Lewis Hatchery sp	Lower Columbia River	T

Genetic baseline population	ESU reporting group	Status
Kalama Hatchery sp	Lower Columbia River	T
Cowlitz Hatchery sp	Lower Columbia River	T
Cowlitz Hatchery fa	Lower Columbia River	T
Sandy River	Lower Columbia River	T
Lewis River fa	Lower Columbia River	T
Spring Creek Hatchery	Lower Columbia River	T
McKenzie Hatchery	Upper Willamette River	T
N Santiam Hatchery	Upper Willamette River	T
Warm Springs Hatchery	Mid-Columbia River Spring	NW
John Day River	Mid-Columbia River Spring	NW
U Yakima Hatchery	Mid-Columbia River Spring	NW
Wenatchee River sp	Upper Columbia River Spring	E
Wenatchee Hatchery sp	Upper Columbia River Spring	E
Carson Hatchery	Upper Columbia River Spring	N/A
U Deschutes River	Deschutes River Summer/Fall	NW
L Deschutes River	Deschutes River Summer/Fall	NW
Hanford Reach	Upper Columbia River Summer/Fall	NW
Wenatchee River su/fa	Upper Columbia River Summer/Fall	NW
Wells Hatchery	Upper Columbia River Summer/Fall	NW
Methow River	Upper Columbia River Summer/Fall	NW
Lyons Ferry Hatchery	Snake River Fall	T
EF Salmon River	Snake River Spring/Summer	T
WF Yankee Fork	Snake River Spring/Summer	T
Secesh River	Snake River Spring/Summer	T

Genetic baseline population	ESU reporting group	Status
Rapid River Hatchery	Snake River Spring/Summer	T
Minam River	Snake River Spring/Summer	T
Imnaha River	Snake River Spring/Summer	T
Newsome Creek	Snake River Spring/Summer	T
Tucannon Hatchery	Snake River Spring/Summer	T
Tucannon River	Snake River Spring/Summer	T
Clear Creek Hatchery	Puget Sound	T
Voights Hatchery	Puget Sound	T
S Prairie Creek	Puget Sound	T
Soos Hatchery	Puget Sound	T
George Adams Hatchery	Puget Sound	T
Hamma Hamma River	Puget Sound	T
Snoqualmie River	Puget Sound	T
Samish Hatchery	Puget Sound	T
Elwha Hatchery	Puget Sound	T
Elwha River	Puget Sound	T
Dungeness River	Puget Sound	T
NF Nooksack Hatchery	Puget Sound	T
White Hatchery	Puget Sound	T
Hatcheryupp Sp Hatchery	Puget Sound	T
Skykomish River	Puget Sound	T
Wallace Hatchery	Puget Sound	T
NF Stillaguam Hatchery	Puget Sound	T
Skagit River	Puget Sound	T

Genetic baseline population	ESU reporting group	Status
U Sauk River	Puget Sound	T
Suiattle River	Puget Sound	T
L Sauk River	Puget Sound	T
Marblemount Hatchery sp	Puget Sound	T
Marblemount Hatchery su	Puget Sound	T
U Cascade River	Puget Sound	T
U Skagit River	Puget Sound	T
W Chilliwack Hatchery	Southern BC	N/A
Maria Slough	Southern BC	N/A
Birkenhead Hatchery	Southern BC	N/A
M Shuswap Hatchery	Southern BC	N/A
L Thomson River	Southern BC	N/A
L Adams Hatchery	Southern BC	N/A
Clearwater River	Southern BC	N/A
Riveraft River	Southern BC	N/A
Spilus Hatchery	Southern BC	N/A
Nicola Hatchery	Southern BC	N/A
Louis Creek	Southern BC	N/A
Deadman Hatchery	Southern BC	N/A
U Chilcotin River	Southern BC	N/A
Chilko River	Southern BC	N/A
Quesnel River	Southern BC	N/A
Nechako River	Southern BC	N/A
Stuart River	Southern BC	N/A

Genetic baseline population	ESU reporting group	Status
Swift River	Southern BC	N/A
Morkill River	Southern BC	N/A
Salmon River sp	Southern BC	N/A
Cowichan Hatchery	Southern BC	N/A
Nanaimo Hatchery fa	Southern BC	N/A
Big Qualicum Hatchery	Southern BC	N/A
Puntledge Hatchery fa	Southern BC	N/A
Quinsam Hatchery	Southern BC	N/A
Nitinat Hatchery	Southern BC	N/A
Sarita Hatchery	Southern BC	N/A
Tranquil River	Southern BC	N/A
Robertson Hatchery	Southern BC	N/A
Conuma Hatchery	Southern BC	N/A
Tahsis River	Southern BC	N/A
Marble Hatchery	Southern BC	N/A
Porteau Cove Hatchery	Southern BC	N/A
Klinaklini River	Southern BC	N/A
Wannock Hatchery	Central BC-AK	N/A
Atnarko Hatchery	Central BC-AK	N/A
Kitimat Hatchery	Central BC-AK	N/A
Ecstall River	Central BC-AK	N/A
L Kalum River	Central BC-AK	N/A
Bulkley River	Central BC-AK	N/A
Sustut River	Central BC-AK	N/A

Genetic baseline population	ESU reporting group	Status
Kincolith River	Central BC-AK	N/A
Kwinageese River	Central BC-AK	N/A
Damdochax River	Central BC-AK	N/A
Owegee River	Central BC-AK	N/A
L Tahltan River	Central BC-AK	N/A
Nakina River	Central BC-AK	N/A
Kowatua Creek	Central BC-AK	N/A
Tatsatua Creek	Central BC-AK	N/A
U Nahlin River	Central BC-AK	N/A
Chickamin/White Hatchery	Central BC-AK	N/A
Chickamin Hatchery	Central BC-AK	N/A
Chickamin River	Central BC-AK	N/A
Keta River	Central BC-AK	N/A
King Creek	Central BC-AK	N/A
Clear Creek	Central BC-AK	N/A
Creekipple Creek	Central BC-AK	N/A
Andrew Creek	Central BC-AK	N/A
Andrew/Mac Hatchery	Central BC-AK	N/A
Andrew/Med Hatchery	Central BC-AK	N/A
Andrew/Cry Hatchery	Central BC-AK	N/A
King Salmon River	Central BC-AK	N/A
Big Boulder Creek	Central BC-AK	N/A
Tahini River	Central BC-AK	N/A
Tahini/Mac Hatchery	Central BC-AK	N/A

Genetic baseline population	ESU reporting group	Status
Klukshu River	Central BC-AK	N/A
Situk River	Central BC-AK	N/A

659 ¹Feather River spring run brood stock was extensively hybridized with fall run in that
660 program and the two are now genetically indistinguishable.

661 ²Brood stock from Cole M. Rivers Hatchery on the Rogue River in Southern Oregon is
662 currently propagated and released in Young's Bay at the mouth of the Columbia River.

663 **Figure captions**

664 Figure 1. Overall Chinook Salmon ESU proportions observed in at-sea Pacific Hake
665 trawl fisheries for all years combined 2008 - 2015. ESUs and two stock aggregates are
666 ordered from south to north.

667 Figure 2. Chinook Salmon ESU proportions, stratified by fishery management area,
668 ordered from south to north. Area 1: North of Cape Falcon, Oregon (45.77°); Area 2:
669 Cape Falcon, Oregon to Cape Blanco, Oregon (42.75° to 45.77°); Area 3: Cape Blanco,
670 Oregon to Cape Mendocino, California (40.16° to 42.75°). See Figure 3 for area
671 boundaries.

672 Figure 3. Individual Chinook Salmon taken in bycatch, color coded by most likely ESU
673 of origin, from red in the south to blue in the north. Fishery management area boundaries
674 are shown as red lines with associated latitudes (see Fig. 2 for area descriptions).

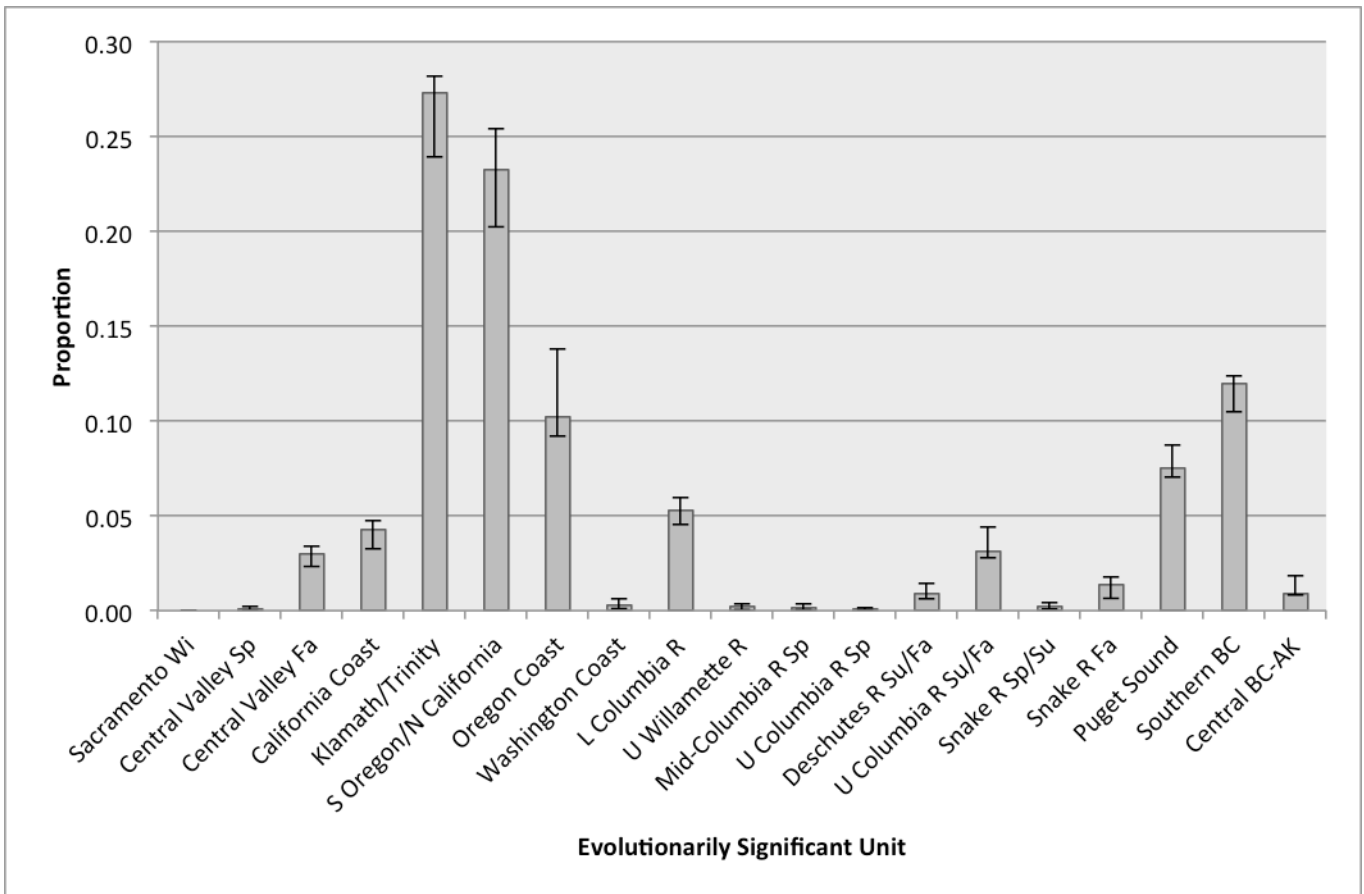
675 Figure 4. Dirichlet regression (solid) and multinomial logistic regression (dashed) with
676 observed proportions (summing to one over all four panels) and mean latitudes of annual
677 samples (points). Data ranges differ because DR is based on mean latitudes, whereas
678 MLR is fitted to individual fish, their observed latitude, and the ESU to which they were
679 assigned. Regional divisions simply facilitate interpretation.

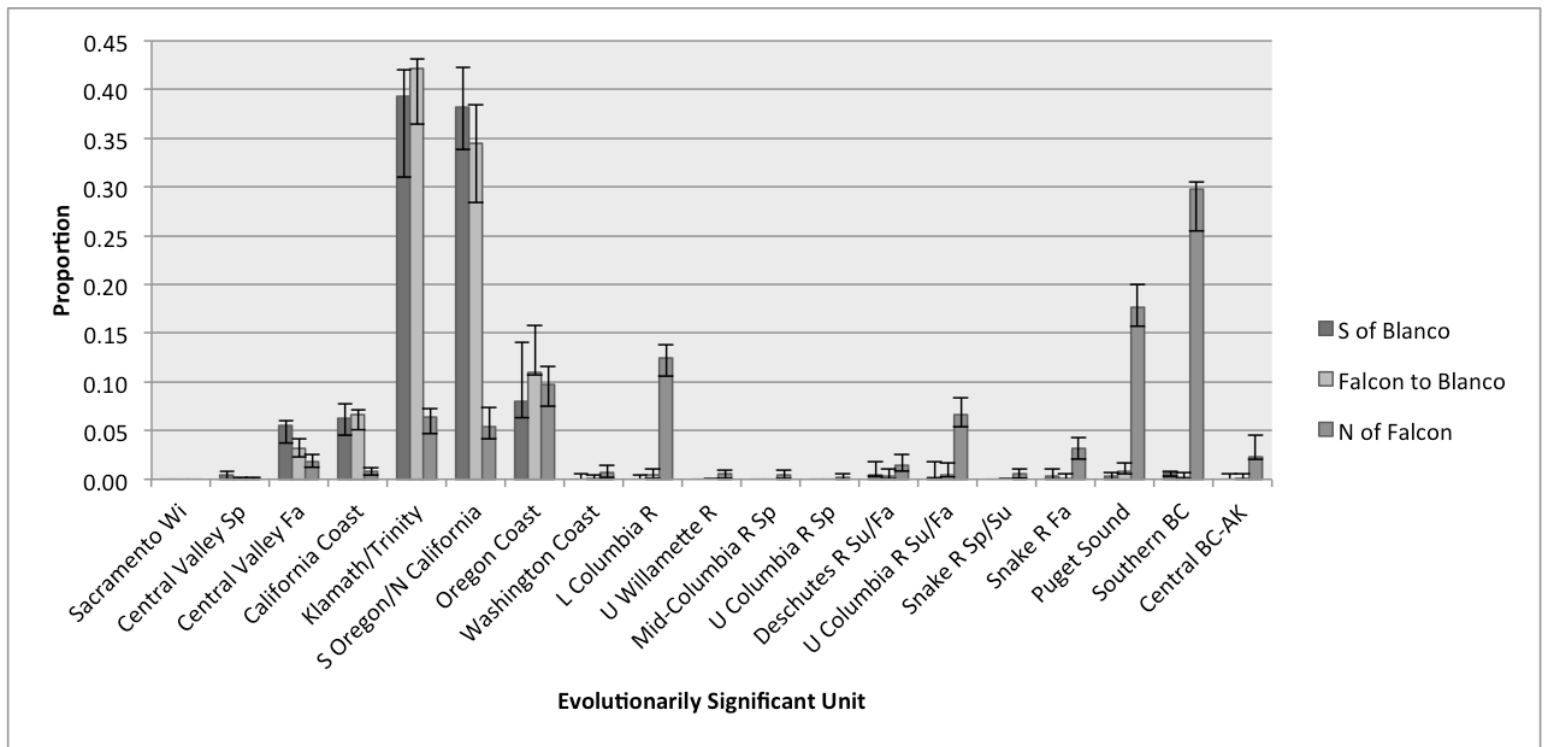
680 Figure 5. Selected realizations of the jackknife analysis are shown in each panel, where
681 one entire annual sample (identified in title) was held out as a cross-validation test set
682 (Obs). The remaining years were used as a training set to estimate ESU proportions given
683 the observed latitude. Those proportions shifted beginning in 2011 and from 2012 to

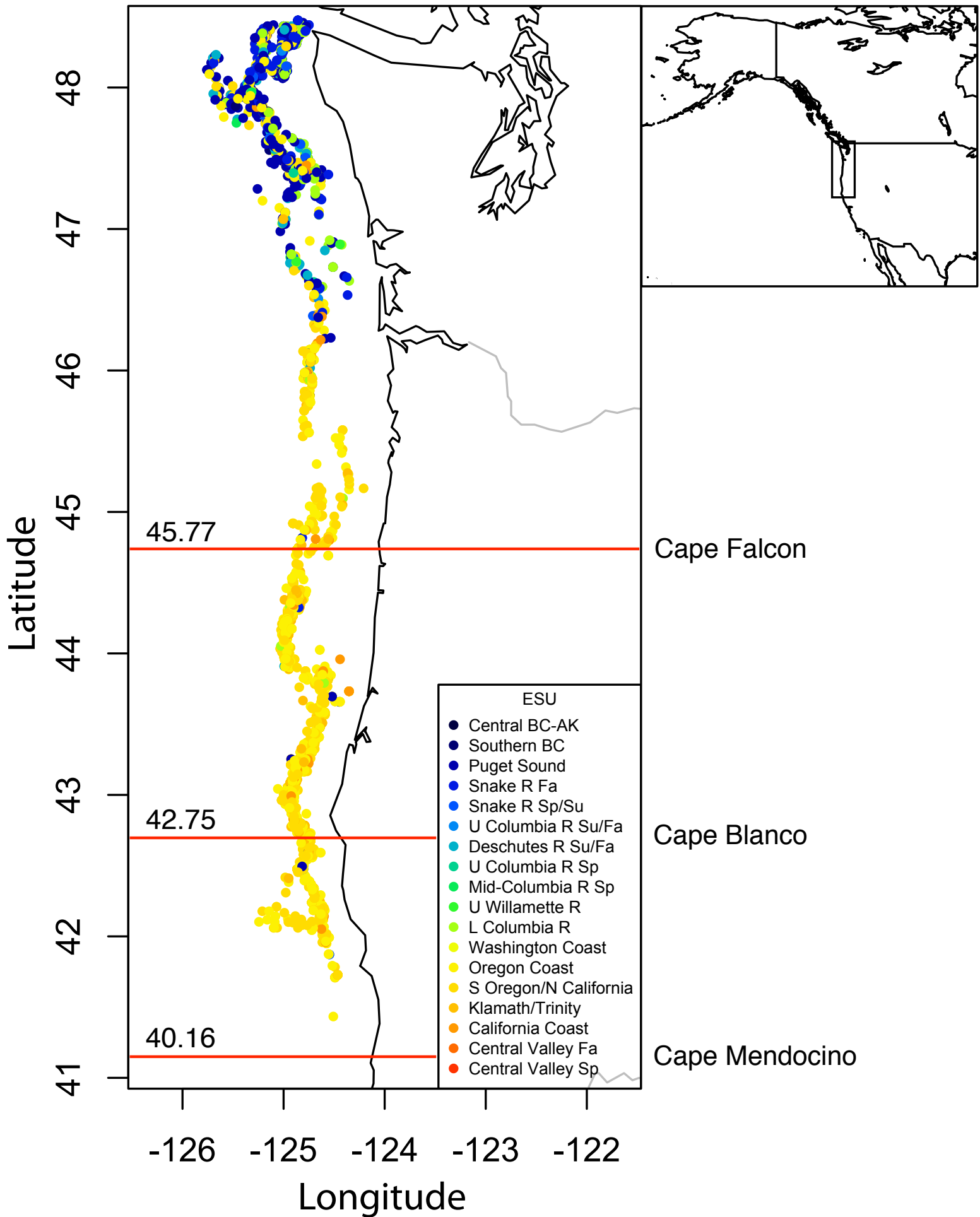
684 2015 northern ESUs nearly disappeared. Note that observed proportions were similar
685 between 2013 and 2015, when mean latitudes were also similar ($\sim 43.8^\circ$, Table 1).

686 Figure 6. Model cross validation, summarized from Figure 5, comparing observed ESU
687 proportions (Obs) with values predicted from Dirichlet regression (DR) and multinomial
688 logistic regression (MLR), independent of observation.

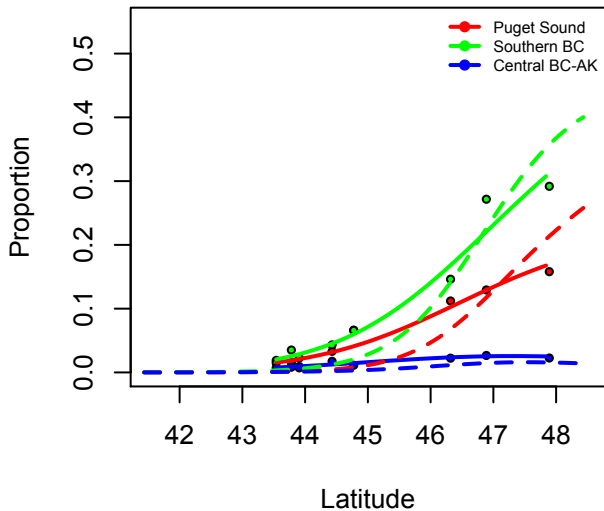
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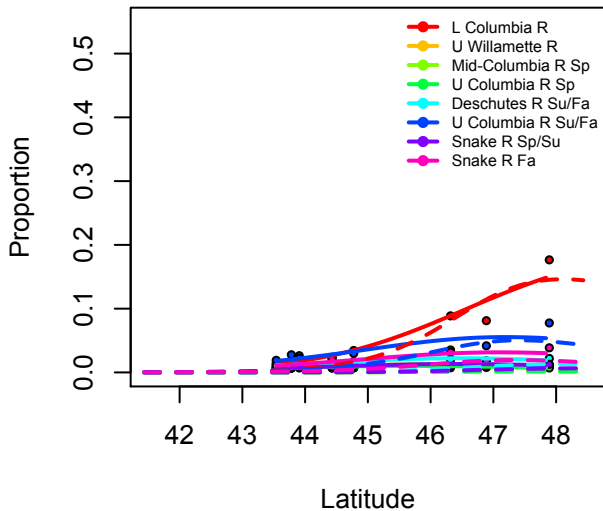




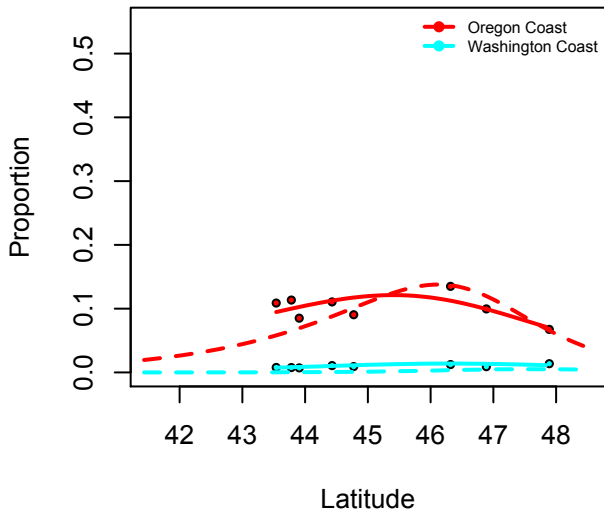
Northern ESUs



Columbia ESUs



Coastal ESUs



Southern ESUs

