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The Abundance and Distribution of Hatchery and Naturally Produced
Chinook Salmon in Columbia River Estuary Nearshore Habitat

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32 Running Head: Hatchery Chinook Salmon in the Columbia River Estuary

33 [A] Abstract

34 Columbia River hatcheries release millions of juvenile Chinook Salmon *Oncorhynchus*
35 *tshawytscha*, to support fisheries and mitigate for historical productivity declines from dam
36 construction and upriver habitat losses. Recent Federal Biological Opinions for Federal
37 Columbia River Power System operations also have mandated restoration of estuarine rearing
38 habitats to mitigate for mortality of naturally produced (NP) salmon at mainstem dams. We
39 compared genetic stock compositions, distributions, abundances, and length frequencies of
40 hatchery-marked and unmarked Chinook Salmon to evaluate the extent of hatchery influence on
41 nearshore estuarine habitat use and the potential for interactions between hatchery origin (HO)
42 and NP salmon. Cumulative Chinook Salmon releases from all hatcheries in 2010 and 2011
43 dictated estuarine stock composition, abundance, and life histories during the spring-summer
44 migration peak. NP salmon from the Lower Columbia River populations, including many fry
45 migrants, were most abundant but larger HO juveniles also frequented nearshore sites, where
46 their total biomass often equaled or exceeded that of NP fish. Large releases of a single stock of
47 origin (Spring Creek Group fall run) in April and May created sharp pulses in the estuary entry
48 timing of fingerling-sized salmon and dominated abundance and stock composition at some sites.
49 Successive releases from scores of hatcheries during spring and early summer ensured a
50 consistent presence of HO salmon near shore, regardless of the habitat-specific residence times
51 of individual fish. Overall, the historical replacement of diverse wild populations with fewer
52 hatchery stocks of a narrow size range and migration timing has intensified nearshore habitat use
53 during the spring-summer migration peak and reduced life history variation of Columbia River
54 Chinook Salmon. Such changes could undermine the fish conservation goals of both hatchery
55 mitigation and estuary restoration programs.

56 [A] Introduction

57 Tidal wetlands and other shallow nearshore habitats provide juvenile rearing areas
58 (Healey 1980, 1982; Levy and Northcote 1981,1982) that contribute directly to the life-history
59 diversity and productivity of Chinook Salmon *Oncorhynchus tshawytscha*, (Reimers 1973;
60 Bottom et al. 2005a, 2005b) and Coho Salmon *O. kisutch* (Craig et al. 2014; Jones et al. 2014).
61 In the Columbia River Basin, juvenile Chinook Salmon occupy both saline and tidal fresh
62 regions of the estuary year-round (Roegner et al. 2012), and many fry (≤ 60 mm FL) and
63 fingerlings (subyearlings > 60 mm FL) utilize wetland channels and other shallow, nearshore
64 habitats to feed and grow before entering the ocean (Lott 2004; Roegner et al. 2010; McNatt et
65 al. 2016). Historically, the Columbia River accounted for the world's largest runs of Chinook
66 Salmon (Van Hyning 1973) but current annual production of this and other salmon species has
67 declined to a fraction of the estimated 11 to 16 million adults that once returned to the basin
68 (Northwest Power Planning Council 1986). The extirpation of hundreds of Columbia River
69 salmon populations and the listing of 13 salmon evolutionarily significant units (ESUs; Myers et
70 al. 1998)—conservation units recognized under the Endangered Species Act—has focused
71 increasing attention on the estuary's role in salmon decline and recovery (Kareiva et al. 2000;
72 Bottom et al. 2005b; Fresh et al. 2005; Gustafson et al. 2007). Salmon access to two-thirds or
73 more of the estuary's historical shallow-water rearing habitat has been lost to diking, shoreline
74 development, and flow regulation (Thomas 1983; Kukulka and Jay 2003; Marcoe and Pilson
75 2017). Recent Federal Biological Opinions have mandated estuary restoration to help mitigate
76 for continued mortality of salmon associated with Federal Columbia River Power System
77 operations (NMFS 2008, 2010, 2020). This mandate takes for granted that estuary restoration
78 will improve survival of naturally produced salmon despite continued releases of millions of
79 hatchery-reared salmon that also congregate in the estuary. To better understand the potential
80 interactions between hatchery origin (HO) and naturally produced (NP) juvenile Chinook
81 Salmon, we compared the abundance, distribution, life history, and genetic stock composition of
82 hatchery-marked and unmarked juveniles in nearshore habitats of the Columbia River estuary,
83 defined as the entire area of tidal influence from the river mouth (rkm 0) to Bonneville Dam
84 (rkm 234) (Simenstad et al. 2011).

85 Columbia River hatcheries have produced salmon for recreational and commercial
86 harvest and to offset basin-wide productivity declines for more than a century (Hilborn 1992;

87 Bottom 1997; Lichatowich 1999; Lichatowich et al. 2006). In 1938 the Mitchell Act established
88 a salmon restoration program that included hatchery facilities to replace freshwater habitat and
89 salmon production losses caused by a series of mainstem dams that eliminated or impeded fish
90 passage to much of the basin, including large areas of the Snake River and upper Columbia River
91 (NRC 1996; Bottom et al. 2005b). When efforts largely failed to relocate interior Chinook
92 Salmon stocks (primarily spring run fish) to tributaries below Grande Coulee Dam (rkm 960),
93 the Lower Columbia Fishery Development Program expanded the production of Lower
94 Columbia River stocks (primarily fall run fish) “to build up the existing runs in the lower basin
95 to the maximum capacity of the streams utilized (Laythe 1950).” Since 1946 as many as 20
96 Mitchell Act hatcheries have released salmon (*Oncorhynchus* spp.) and steelhead (*O. mykiss*)
97 continuously (NMFS 2014). Throughout the Columbia River 82 federal, state, and tribal
98 hatcheries now support salmon mitigation and other fish conservation goals and release on
99 average ~140 million salmon and steelhead annually or approximately 3,700 to 6,000 metric tons
100 (Flagg 2015). Average annual hatchery releases have declined only ~5% in the years since these
101 totals were reported (Pacific States Marine Fisheries Commission 2019).

102 The majority of the adult salmon now returning to the Columbia River basin are hatchery
103 produced, with estimates ranging from 80% (Lichatowich et al. 2006) to between 65% and 75%
104 (NMFS 2011). Chinook Salmon, considered among the most estuarine dependent of salmon
105 species (Healey 1982) and a major target of habitat restoration under the Columbia Estuary
106 Ecosystem Restoration Program (Thom et al. 2013), currently accounts for nearly 75% of all the
107 hatchery fish released in the Columbia River basin (NMFS 2014; Pacific States Marine Fisheries
108 Commission 2020). Hatchery programs often are cited as a factor contributing to natural salmon
109 population declines (NRC 1996; Lichatowich 1999; Williams 2006; Paquet et al. 2011), but the
110 estuarine distributions of HO salmon or their effects on the habitat use or performance of NP
111 juveniles in the estuary have not been investigated.

112 Ecological or behavioral interactions with hatchery juveniles could have negative
113 consequences for NP salmon populations that are the focus of the estuary restoration program.
114 Density-related limitations to salmon foraging or growth have been reported in Pacific coastal
115 estuaries (Reimers 1973; Neilson et al. 1985; Korman et al. 1997) and in Puget Sound
116 (Simenstad et al. 1982; Simenstad and Salo 1982; Beamer and Larsen 2004; Greene and Beamer
117 2012) and often have raised concerns about the salmon carrying capacities of estuaries in basins

118 with large hatchery programs (Reimers 1978; Levings et al. 1986; Korman et al. 1997; ISAB
119 2015). Attraction of avian and marine mammal predators to large concentrations of hatchery
120 smolts in estuaries has been blamed for density-related declines in the productivity of Oregon
121 coastal Coho Salmon populations (Nickelson 2003) and may account for a negative relationship
122 between the survival of wild Snake River Chinook Salmon (from the upper Columbia River
123 basin) and releases of hatchery steelhead (Levin and Williams 2002). Large densities of
124 hatchery fish could undermine salmon recovery efforts in basins already constrained by
125 considerable reductions in estuarine rearing habitat (Marcoe and Pilson 2017; Brophy et al. 2019;
126 Greene et al. 2021). In Oregon's Salmon River estuary, for example, wetland restoration
127 contributed few adult survivors to the local Coho Salmon population until a decades-old hatchery
128 program also was discontinued (Jones et al. 2014; Jones et al. 2018).

129 Genetic or phenotypic differences between HO and NP salmon could have negative
130 consequences beyond the effects of fish density (Flagg et al. 2000; Einum and Fleming 2001;
131 Jonsson and Jonsson 2006). Compared to their wild counterparts, for example, propagated
132 salmonids often exhibit increased levels of aggression (Swain and Riddell 1990; Rhodes and
133 Quinn 1998; Peery and Bjornn 2004; Jonsson and Jonsson 2006), and displacement or mortality
134 of wild salmon following the releases of large sized hatchery-reared juveniles has been reported
135 in some stream environments (Nickelson et al. 1986; Peery and Bjornn 2004). To minimize
136 negative interactions with wild fish, hatcheries often are encouraged to restrict the numbers of
137 fish released and to insure spatial and temporal segregation from wild fish (Flagg et al. 2000;
138 Nickelson 2003; Chilcote et al. 2011; Kostow 2012). To the extent such interactions are
139 unavoidable, however, others recommend that hatcheries release fish at size ranges similar to
140 those of NP salmon to minimize a potential competitive advantage for HO juveniles (Einum and
141 Fleming 2001; Kostow 2009).

142 Hatchery practices in the Columbia River basin vary by program, species, and stock but
143 most juveniles are released at relatively large sizes to encourage rapid seaward migration and to
144 enhance survival (Kostow 2009). Because estuarine residence times and habitat selection by
145 Chinook Salmon tend to vary with fish size (Levings et al. 1986; Healey 1991; Bottom et al.
146 2005b; Campbell 2010), hatchery production of a narrow range of large phenotypes could
147 concentrate estuarine habitat use in time and space, artificially constraining the estuary's salmon-
148 rearing capacity (Bottom et al. 2005b). Tagging studies using acoustic transmitters have

149 measured rapid seaward migration by large subyearling and yearling salmon (including many
150 hatchery-reared juveniles), primarily through deep estuary channels (e.g., McMichael et al. 2011;
151 Harnish et al. 2012; McNatt et al. 2016). Lower-estuary purse seine surveys found that >90% of
152 the Chinook and Coho Salmon and steelhead in deep-water habitats are of hatchery origin
153 (Weitkamp et al. 2012). Hatchery fish also have been collected in some shallow, nearshore areas
154 (Roegner et al. 2012, 2016; Sather et al. 2016) but the combined effects of all hatchery releases
155 on the densities, stock composition, and size characteristics of salmon in these habitats is poorly
156 understood. It is unknown, for example, whether large size at release effectively segregates HO
157 smolts from NP juveniles in most shallow estuarine nursery areas or whether significant overlap
158 enables hatchery fish to dominate or displace smaller NP juveniles (e.g., Nickelson et al. 1986).
159 The potential benefits of restoring estuarine habitat for at-risk Columbia River salmon thus could
160 depend both on the total densities of hatchery salmon that occupy the estuary at any one time as
161 well as the relative phenotypic similarities between HO and NP juveniles where their
162 distributions overlap.

163 Until 2008 it was impossible to distinguish most HO and NP juveniles in estuary surveys
164 because only modest proportions of hatchery salmon were marked. More recently, however,
165 >90% of all hatchery juveniles have received an identifying fin clip or tag prior to release,
166 allowing identification of most (though not all) hatchery fish in estuary collections. This paper
167 takes advantage of these increased hatchery marking rates to compare nearshore habitat use by
168 HO and NP juvenile Chinook Salmon and evaluate the implications for estuary restoration and
169 hatchery production programs. Our analyses address the following objectives:

- 170 (1) Summarize the estuary-wide contributions of HO and NP juveniles to the genetic
171 stock composition and size distribution of juvenile Chinook Salmon.
- 172 (2) Compare the spatial and temporal distribution of HO and NP Chinook Salmon overall
173 and among the major genetic stock groups throughout the estuary.
- 174 (3) Estimate the nearshore densities and biomass of HO and NP salmon across the
175 estuary.
- 176 (4) Determine whether large hatchery releases modify habitat-specific salmon abundance,
177 genetic stock composition, and life history composition (size variation, timing, and
178 estuarine residency).

179

180 [A] Methods

181 We analyzed hatchery release records, Bonneville Dam fish passage data, and recent field
182 survey results to determine the extent of hatchery influence on Chinook Salmon stock
183 composition and nearshore habitat use in the Columbia River estuary. The data sources, field
184 methods, and analyses are briefly described below.

185

186 [C] *Hatchery releases and fish passage at Bonneville Dam.*—We compiled hatchery-release
187 records to compare the cumulative proportions of all Chinook Salmon hatchery stocks released
188 in the Columbia River basin with the stock proportions observed during field surveys of shallow
189 estuarine habitats (Objective 1). For the hatchery records we accessed the Regional Mark
190 Information System database (Pacific States Marine Fisheries Commission 2019) to compile data
191 on releases of juvenile Chinook Salmon from Columbia River Basin hatcheries in 2010 and 2011
192 (Table 1). Release data were summarized by Chinook Salmon ESU. Hatcheries apply several
193 types of marks to fish that can be used to differentiate HO and NP fish. However, not all released
194 fish are marked. For our study, we considered fish with a clipped fin or implanted with a coded
195 wire tag (CWT) to be marked.

196 We tracked the timing of estuary entry for upriver releases of hatchery subyearlings and
197 yearlings based on the Bonneville Dam Fish Passage Index reported by the Columbia River
198 DART for 2009 - 2011 (Data Access in Real Time) (University of Washington 2015). The
199 passage index is measured at a single fish bypass that automatically diverts fish every 10 minutes
200 to a sampling facility below the dam. The index is an indicator of run timing and relative
201 magnitude but not the actual number of fish passing the dam since passage efficiency is not equal
202 across the entire face of the dam and varies with river flow. Because Bonneville Dam marks the
203 upper limit of tidal influence on the Columbia River, the Fish Passage Index depicts the estuary
204 entry of all mainstem migrants (HO and NP). The index does not distinguish HO from NP fish.
205 However, we used the index to determine the estuary arrival of Spring Creek stock hatchery fish,
206 which are released weeks or months earlier than subyearling Chinook Salmon from other
207 hatcheries above Bonneville Dam and has an unambiguous signal in the estuary (Pacific States
208 Marine Fisheries Commission 2019). The passage of Spring Creek fish over the dam provided
209 an indicator of hatchery influence on the life history composition of Chinook Salmon as defined

210 by estuary entry timing and size characteristics (e.g., the initial arrival of fingerling sized
211 salmon) (Objectives 1 and 4).
212
213 [C] *Field surveys*.—We synthesized data from three beach seining surveys to determine the
214 relative use of nearshore, shallow-water (0 – 6m) habitats by HO and NP juvenile Chinook
215 Salmon (Figure 1). The most spatially extensive dataset was a bimonthly salmon Genetics
216 Survey from March 2010 to March 2012 (Teel et al. 2014). The Genetics Survey quantified the
217 distributions of 11 regional Chinook Salmon stock groups across 6 of the 8 hydrogeomorphic
218 reaches (C – H; Simenstad et al. 2011) of the estuary (Figure 1). The analyses here report
219 collections from two habitat types representing a range of nearshore environments to characterize
220 genetic stock diversity within and among estuary reaches: a relatively exposed, nearshore site
221 along the estuary’s main channel (“mainstem” habitat) and a low-velocity, off-channel site on the
222 backside of an island (“backside” habitat). Across the full length of the estuary, nearshore sites
223 encompassed a range of topographies, slopes, sediment types, and depths (< 6m). Columbia
224 River flows in 2010 and 2011 followed a typical seasonal pattern—increasing in the spring to a
225 May or June peak and declining in July to the fall minimum—but the larger spring freshet in
226 2011 started a month earlier (in mid-May) and continued until mid-July. To summarize the
227 estuary-wide genetic stock composition (Objective 1) and distribution of HO and NP Chinook
228 Salmon (Objectives 2 and 3) we supplemented the bimonthly Genetics Survey results with the
229 relevant 2010-11 catch data from a single long-term monitoring site (mainstem habitat only) at
230 Point Adams Beach (rkm 20) in Reach A (Figure 1) (Roegner et al. 2012; Teel et al. 2014).
231 Hereafter, “estuary-wide” results refer to the combined bimonthly data from the Genetics Survey
232 and the Point Adams Beach monitoring (described below).

233 For most sites and time periods during the Genetics Survey we collected fish with a 3- x
234 38-m variable-mesh bag seine (10.0- and 6.3-mm wings, 4.8-mm bag). However, when
235 seasonally high current velocities and water elevations intermittently prevented deployment of
236 the bag seine at upper-estuary sites (i.e., Reaches G and H), we walked a 1.8-m x 4.6-m pole
237 seine (4.6-mm mesh) alongshore to collect juvenile salmon. We collected no March samples in
238 reaches G and H in 2010, but added an additional survey date during the first week of April 2012
239 to provide comparable seasonal data for the six estuary reaches for two full years. We substituted

240 the April 2012 survey data for the missing Reach G and H data to approximate salmon
241 abundance and stock composition for March 2010.

242 Besides extending the spatial coverage of the bimonthly genetics dataset to include Reach
243 A, the more frequent Point Adams Beach monitoring also provided an index of the outmigration
244 timing, stock composition, and size characteristics of HO and NP Chinook Salmon near the
245 estuary mouth (Figure 1; Roegner et al. 2016). We used the biweekly collections at Point Adams
246 Beach to estimate the effects of large hatchery release groups on habitat-specific abundance
247 trends near the river mouth and to estimate the ocean entry timing and overall estuary residency
248 of the selected hatchery release groups (Objective 4). We sampled Point Adams Beach biweekly
249 (March (2011) or April (2010) – July) to monthly (all other months) with a tapered, 3- × 50-m
250 variable-mesh beach seine (19.0, 12.7, 9.5 mm) and a 1.0-cm knotless-mesh bunt. After
251 anchoring one end and stacking the net on the beach, the other end was towed downstream with a
252 small boat, forming a semi-circle along the shoreline. Both ends of the net were then pulled to
253 shore by hand, and all fish were guided into the bunt to sort, identify, and enumerate.

254 A 2009 fish survey at Hayden and Sauvie Island near the Willamette and Columbia River
255 confluence (rkm 163) sampled juvenile Chinook Salmon monthly from February to June (Figure
256 1) (Sol et al. 2009). Sample collections from the six Hayden Island Survey sites approximated
257 the estuary arrival timing for marked and unmarked Chinook Salmon from the mid- and upper
258 basin (i.e., fish above Bonneville Dam) and from the Willamette River. We analyzed these data
259 to evaluate the effects of large upriver releases of HO Chinook Salmon on the habitat-specific
260 abundance, genetic stock composition, and life history composition of juveniles in the upper
261 estuary (Objective 4). Fish samples from the Hayden Island Survey were collected with a 37m
262 Puget Sound bag seine (tapered 0.91 to 2.4 m in the center) with a knotless mesh, stretched
263 measurement of 12.7mm for the wings and 0.31mm for the bag. The net was deployed by
264 extending one tow line from shore and setting the net from the bow of the boat parallel to shore.
265 The opposite tow line was returned to shore and retrieved in a U-shape, funneling all fish toward
266 the center bag.

267 During all three field surveys, we measured, weighed, identified hatchery marks (i.e., fin
268 clips) and scanned for CWTs each of the first 30 juvenile Chinook Salmon; measured and
269 checked the mark status for the next 31-100 individuals; and counted all remaining individuals in
270 each sample. We collected fin tissue samples from up to 30 juvenile Chinook Salmon for genetic

271 stock identification. Additional replicate beach seine hauls were made at sampling sites as
272 needed to approximate the 30 fish target for genetic analysis. When total catches exceeded 30
273 fish, all fish were counted and individuals were selected randomly for genetic sampling
274 regardless of size or presence of a hatchery mark. In sample collections with more than 100
275 individuals, we estimated the total number of marked and unmarked fish based on the
276 proportions counted in each subsample. We assigned age categories (subyearling vs. yearling)
277 for juvenile Chinook Salmon according to standard biweekly to monthly length frequency
278 cutoffs validated from previous beach seining surveys in the lower estuary (Bottom et al. 2011).
279 The cutoff size for yearlings ranged from > 80 mm on March 1 to >145 mm after July 15.

280 For the 2010-11 estuary-wide survey data we used a linear regression model comparing
281 measured lengths to weights of fish to assign weights to individuals that were measured only. We
282 first transformed measured weights and lengths by $\log_{10} + 1$ to linearize the observed relationship
283 and then modeled weight as a function of length, year and mark status, and their two-way
284 interactions. We compared models with all combinations of these variables using AICc
285 (Burnham and Anderson 2002) to find the best and most parsimonious model. Based on this
286 analysis, we pooled years but used separate regression models to estimate the weights of marked
287 and unmarked individuals because their length:weight relationships were significantly different
288 (Table S.1). For individuals that were neither measured nor weighed, we assigned the mean
289 lengths and weights from other marked or unmarked fish captured during the same sampling
290 event. After each fish was assigned a length and weight, the biomass of marked and unmarked
291 groups was estimated by dividing the mean weight by the fish density.

292 Approximately 9% of all the Chinook Salmon were released from hatcheries without an
293 identifiable mark in 2009-11. Since the actual marking rates varied by hatchery, and stock of
294 origin was unknown for all but a random subsample of fish chosen for genetic analysis, we made
295 no attempt to adjust the unmarked fish totals to estimate the true number of hatchery salmon in
296 our sample collections. The results for marked fish reported in this analysis thus should be
297 viewed as minimum estimates of the number, biomass, or proportion of HO Chinook Salmon.

298
299 [C] *Genetic stock of origin.*—We used the genetic stock identification (GSI) methods described
300 by Teel et al. (2014) to estimate the origins of juvenile Chinook Salmon collected during each of
301 the estuary surveys. Accordingly, the terms “stock” or “genetic stock” herein refer to the groups

302 delineated directly from the genetic data. Briefly, GSI was conducted using 13 Chinook Salmon
303 microsatellite DNA loci and genotypic data that were standardized by several west coast salmon
304 genetics laboratories (Seeb et al. 2007; Moran et al. 2013). Genomic DNA was extracted from
305 fin tissues taken during field surveys using Wizard Genomic DNA Purification Kits (Promega
306 Corp.). Polymerase chain reactions (PCRs) were then used to amplify the microsatellite loci and
307 genotyping was conducted using the Applied Biosystems Inc. (ABI) 3700 genotyping platform.
308 The GSI computer program ONCOR (Kalinowski et al. 2007) and a “baseline” representing 45
309 populations were used to assign individual fish to one of 11 regional genetic stocks (Teel et al.
310 2014). Fish with relative assignment probabilities < 0.90 were excluded from the analysis to
311 improve the overall stock assignment accuracy in the data (Teel et al. 2014). The analysis
312 included a coastal region genetic stock to identify estuary-caught juveniles originating from
313 outside the Columbia River basin (Roegner et al. 2012). The 10 Columbia River basin genetic
314 stocks were generally congruent with the basin’s Chinook Salmon ESUs (Table 1). However,
315 because of the lack of genetic differentiation between the Mid- and Upper Columbia River
316 Spring ESUs, genetic assignments were made to a single Mid-Upper Columbia River spring
317 stock. In addition, three genetic stocks were distinct within the Lower Columbia River ESU and
318 assignments were made to West Cascade fall, West Cascade spring, and Spring Creek Group fall
319 stocks. The West Cascade fall and spring stocks include natural spawning and hatchery fish
320 originating in several tributaries to the lower Columbia River and estuary. The Spring Creek
321 Group fall stock is native to tributaries to the Columbia River gorge, upstream of Bonneville
322 Dam. However, the stock’s current distribution also includes populations further downstream
323 resulting from the use since 1901 of fish and eggs from Spring Creek National Fish Hatchery to
324 stock hatcheries and rivers throughout the lower Columbia River (Myers et al. 2006).
325 Assignments to the three stocks were also summed to represent the entire ESU, consistent with
326 the broad conservation and recovery framework applied under the Endangered Species Act.
327 Chinook Salmon from the non-native Rogue River fall genetic stock do not belong to one of the
328 basin’s ESUs, because those fish are descended from stock transfers to Columbia River
329 hatcheries from southern Oregon coastal hatcheries beginning in the 1980’s (North 2006). We
330 included Rogue River fall genetic stock in our GSI analyses, because descendants from those
331 transfers reproduce in some lower river tributaries (Roegner et al. 2010) and are also released

332 from Columbia River hatcheries to support fisheries in off-channel areas of the lower river
333 (North et al. 2006; Table 1).

334
335 [C] *Numerical and biomass densities.*—We estimated the numerical and biomass densities of
336 marked and unmarked salmon for each site and date sampled during the Genetics Survey and the
337 Point Adams Beach monitoring. Gear efficiencies and sample areas were not measured during
338 each sampling event and were undoubtedly influenced by changing hydrological conditions. We
339 estimated salmon densities by the areas swept for each gear type and survey method. A standard
340 set for the survey at Point Adams Beach was a semi-circular haul of the 50-m beach seine, for an
341 estimated area of ~ 397 m². The Genetics Survey employed both “standard” and “towed” beach
342 seine hauls to collect individuals for genetic analysis. A standard semi-circular haul of the 38-m
343 seine enclosed ~ 218 m². When Chinook Salmon abundance was too low to adequately meet the
344 genetics sample goal ($n = 30$) using the standard-haul method, we towed the beach seine for ~ 38
345 m before pulling it to shore, sampling an area approximating twice the area of a standard set
346 (total ~ 436 m²). Finally, in the upper-estuary reaches G and H water velocities and elevations
347 were sometimes too high to effectively sample nearshore habitats with the beach seine. For those
348 periods and locations, we walked a 7.6-m pole seine in an arc sampling approximately ~ 39 m²
349 for each pole-seine effort. We recorded the total sampling effort for each sampling event.

350 For the Genetics Survey we investigated the impact of factors Year (2010/2011), Month
351 (May/July), Location (Mainstem/Backside), and Rearing Type (marked/unmarked) on the mean
352 Chinook Salmon density and biomass for the six estuary reaches (C – H) where both mainstem
353 and backside habitats were sampled. We considered reach as a random rather than a fixed factor.
354 The reaches were a collection of random units of all possible units within the estuary, and each
355 unit contained responses for all levels of all the fixed factors. Therefore, the variability among
356 the reaches could be accounted for in the model and removed for fixed factor comparisons. We
357 compared linear regression models of all combinations of these factors and all two-way
358 interactions between them with reach included in all models. We used AIC to rank the models
359 and chose the model with minimum AICc as the best model unless other models were within 2 of
360 the best. If multiple models were included from this process, we then applied weighted averaged
361 estimates across those models (Burnham and Anderson 2002).

362

363 [A] Results

364 [B] Estuarine stock composition and size characteristics of marked and unmarked salmon

365 Annual releases of hatchery Chinook Salmon in 2010-11 averaged 105 million fish—
366 approximately 75% of all hatchery salmonids released in the basin—with ~2/3 released as
367 subyearlings and ~1/3 as yearlings (Table 1). More than 87% of all hatchery subyearling
368 Chinook Salmon and 98.5% of all yearlings received an identifiable mark or tag prior to release.
369 Two stocks with large subyearling releases were marked at relatively low rates—Upper
370 Columbia River summer/fall (UCR-su/f; 73.9%) and Snake River fall (SR-f; 64.5%). In total,
371 Lower Columbia River (LCR) stocks accounted for nearly 40% of all salmon released from
372 Columbia River hatcheries (Table 1, Figure 2a-b). With the exception of UCR-su/f (25%) and
373 Snake River spring (SR-sp; 13%), each of the remaining Mid and Upper Columbia River stocks
374 constituted less than 10% of the total hatchery production in 2010-11.

375 Together the three LCR stocks—West Cascade fall (WC-f) (44%), West Cascade spring
376 (WC-sp) (4%), and Spring Creek Group fall (SCG-f) (18%)—were responsible for two-thirds of
377 the juvenile Chinook Salmon sampled estuary-wide in 2010-11 (Figure 2c). Most of the
378 remaining fish were identified as UCR-su/f (22%) and Upper Willamette River spring (UWR-sp)
379 (7%). Combining all survey dates and sites, unmarked fish were most prevalent but the three
380 most abundant stocks included significant proportions of marked hatchery fish: LCR (34%),
381 UCR-su/f (23%), and UWR-sp (42%) (Figure 2d). Deschutes River hatcheries released no fall
382 Chinook Salmon in 2010-2011 (Figure 2c). The 19% (n=8) of DR-f stock in estuary collections
383 listed as hatchery marked (Figure 2d) are most likely a mis-assignment of UCR su/f stock, which
384 is genetically similar to DR-f (Teel et al. 2015).

385 Marked and unmarked juvenile Chinook Salmon exhibited distinct estuary-wide size
386 distributions (all months and at all stations combined). The pattern for marked juveniles was
387 bimodal, with a near-normal size distribution centered around ~80 mm FL and a smaller peak at
388 ~120mm FL (Figure S.1). Few marked fish <60mm FL were captured in the estuary. Unmarked
389 fish exhibited a much wider size range and a highly skewed size distribution with a peak at ~40
390 mm FL, ranging upwards to 120 mm FL.

391 The bimonthly size distributions and temporal trends also differed among marked and
392 unmarked juveniles (Figure 3). Groups of marked yearling fish (~120mm FL) were collected in
393 March (Figure 3), and marked subyearlings were prevalent in the May and July collections. The

394 size distributions for marked salmon were nearly identical during the May and July surveys
395 (median ~ 80mm FL). Few marked fish were captured in the fall. Unmarked subyearling salmon
396 were present in the estuary March through November and exhibited a wider range of sizes (30 –
397 120 mm FL) than marked fish (60 – 120 mm FL) (Figure 3 and S.1). In contrast to marked
398 juveniles, the size distributions for unmarked subyearlings increased with each bimonthly
399 sampling period from March through November and may reflect continued growth of estuary-
400 resident juveniles, size-selective mortality of smaller juveniles, the arrival of larger fish from
401 upriver, and a combination of these factors.

402

403 [B] Spatial and temporal distribution of marked and unmarked salmon

404 Use of shallow-water habitats by marked hatchery fish varied considerably among
405 sampling sites in 2010-11 (Figure 4). More than half of the fish sampled in Reach A and more
406 than 30% of the fish collected in reaches E and F (near the Willamette River confluence or
407 immediately downstream) were hatchery marked. The proportions of marked fish were slightly
408 higher along the mainstem channel, averaging 28% compared with 20% for fish collections in
409 the backside habitats. The peak proportions of marked fish in spring and summer reflected
410 hatchery rearing schedules with most hatchery releases occurring from May to July. In both
411 years the relative abundance of marked fish in shallow habitats peaked between 30% and 40% in
412 July (Figure 4).

413 The relative contributions of Chinook Salmon genetic stock groups in the estuary varied
414 geographically in 2010-11 (Figure 5). Lower Columbia River stocks (SCG-f and WC-f) were
415 widely distributed, but the proportional abundance of WC-f was greatest in the mid-estuary
416 (Reaches C – E) (Figure 5). The proportion of UWR-sp stock in nearshore habitats peaked near
417 the Willamette R. confluence (Reach F) and declined downstream while the percentage of UCR-
418 su/f was greatest in upper estuary reaches, G and H. The influence of hatchery programs on
419 estuary-wide distributions and proportional abundances also varied by salmon stock. Hatchery
420 programs increased the proportional abundances of SCG-f and UWR-sp in nearshore habitats but
421 made relatively smaller contributions to the total abundance of WC-f and UCR-su/f stocks. The
422 low proportion of marked UCR-su/f subyearlings at estuary survey sites may reflect the
423 relatively low hatchery marking rate (74%) for this stock, the abundance of UCR-su/f fish

424 naturally produced in an undammed stretch of the mainstem Columbia River (i.e., Hanford
425 Reach), or a combination of factors.

426

427 [B] Nearshore density and biomass

428 Estuary-wide peak densities and biomass of Chinook Salmon ranged from .07 to 1.35
429 fish/ m⁻² and 0.15 – 5.18 g m⁻² in May 2010 and from .05 to 1.81 fish/ m⁻² and 0.16 to 3.89 g/ m⁻²
430 in May 2011 (Table S.2). Other salmon species, including yearling Coho and subyearling Chum
431 Salmon, also were present near shore in the spring but occurred less frequently at most sites and
432 were not included in our density estimates. Throughout the peak of the May-July salmon
433 migration in 2010 and 2011, marked hatchery fish averaged more than a third of the numerical
434 density and about half of the biomass density of Chinook Salmon sampled near shore (Table
435 S.2).

436 Marked individuals accounted for 39% to 72% of the Chinook Salmon biomass sampled
437 at all nearshore locations and more than half of the total biomass in 8 of the 13 habitats surveyed
438 (Figure 4). Large yearlings dominated the catches of marked fish in March (Figure 3) and
439 contributed almost 90% of the Chinook Salmon biomass in the estuary in March 2010 and
440 almost 60% of the biomass in March 2011 (Figure 4). The biomass contributions from
441 subyearling hatchery Chinook Salmon peaked in May at >50% and declined with each bimonthly
442 sampling event thereafter.

443 The biomass densities of marked and unmarked Chinook Salmon followed similar
444 temporal patterns in most estuary reaches, with bimonthly peaks in May or July and low values
445 during the subsequent September and November surveys (Figure 6). Total biomass density
446 estimates for marked and unmarked salmon in reach H were relatively low during spring and
447 summer months in 2010 and 2011 and in reaches E, F, and G in 2011.

448 The linear regression modeling of factors affecting density showed that the model with
449 month, mark status and their interaction better explained variation in mean density than all other
450 model combinations (i.e., change in AIC >> 2.0, except for the same model with location added
451 for which AIC = 1.8; we chose the smaller model, Table S.3). Density of unmarked individuals
452 in May was much higher (0.39 fish/m², 95% CI (0.35,0.54)) than marked (0.14 fish/m², 95% CI
453 (0.04, 0.23) (Table S.4). Densities decreased in July and were similar for marked and unmarked
454 fish (0.06 and 0.11 fish/m², respectively). Bimonthly densities of subyearling Chinook Salmon

455 broadly paralleled the seasonal hydrograph, which increased through the spring to a May or June
456 peak in both years and declined in July to a fall minimum. Differences among years and habitat
457 locations were small.

458 Similar linear regression modeling of factors affecting biomass showed that the model
459 with only month best explained the variation in mean biomass (i.e., change in AIC > 2.0 for all
460 combinations except the two models adding habitat location and year individually (AIC = 1.48
461 and 1.49, respectively), so we chose the parsimonious month-only model, Table S.5). Biomass in
462 May was higher than in July (0.75g m^{-2} , 95% CI (0.55, 0.96) versus 0.36g m^{-2} , 95% CI
463 (0.15,0.56) (Table S.6). Differences between years, habitat locations, and marked/unmarked
464 group were not significant.

465
466 [B] Habitat-specific abundance, size characteristics, and residency of large hatchery release
467 groups

468 Large releases of hatchery fish above Bonneville Dam directly influenced the estuary
469 entry timing and relative abundance of fingerling Chinook Salmon in the upper estuary. In three
470 successive years (2009-2011) two sharp peaks in the Fish Passage Index for subyearling Chinook
471 Salmon occurred within days of large April and May releases of SCG-f stock hatchery fish,
472 indicating an immediate post-release migration to the upper estuary (Figure 7, Table 2). A more
473 protracted distribution of the Fish Passage Index during June and July coincided with the estuary
474 arrival of all other HO and NP stocks (yearlings and subyearlings) from the mainstem Columbia
475 River (Figure 7) (University of Washington 2015).

476 Early spring releases of SCG-f fish above Bonneville Dam in 2009 directly influenced
477 the composition, abundance, and size distribution of Chinook Salmon stocks sampled at upper
478 estuary sites during the Hayden Island survey (Figure 8). Successive large releases of SCG-f fish
479 occurred on April 13 (8.4 million fish from Spring Creek National Fish Hatchery (NFH) and
480 Little White Salmon NFH above the dam), May 1 (4.8 million from Spring Creek NFH), and
481 May 15 (2.5 million from Bonneville Hatchery) (Table 2, Pacific States Marine Fisheries
482 Commission 2019). The number of marked SCG-f fish at Hayden Island increased substantially
483 in April soon after the first hatchery releases and remained abundant through May. Stock
484 richness and abundance of unmarked salmon declined at Hayden Island in April and May but
485 increased again in June after most HO stocks had vacated the site.

486 Marked Chinook Salmon at Hayden Island averaged >80 mm FL, ~40 to 50 mm FL
487 greater than their unmarked cohorts on most survey dates (Figure 8). A considerably greater size
488 disparity occurred during the March survey, when a large group of Willamette River hatchery
489 yearlings averaging ~140 mm FL were present. The mean size of all unmarked subyearlings at
490 this time was ~50 mm FL.

491 Multiple large releases of SCG-f hatchery fish also directly affected the composition,
492 abundance, and size classes of juveniles in the lower estuary as indicated by the 2011 biweekly
493 sample collections at Point Adams Beach (Figure 8). A total of 20.6 million SCG-f salmon were
494 released above and below Bonneville Dam between March 12 and May 25 (Table 2), and marked
495 SCG-f fish dominated abundance and stock composition at Point Adams Beach from mid-April
496 through mid-June. Marked SCG-f fish averaged >80 mm FL in May and June, considerably
497 larger than the co-occurring unmarked fry (<60 mm FL) (Figure 8). Abundance of unmarked and
498 other marked fish (mostly WC-f stock) declined with the arrival of SCG-f hatchery fish in April
499 and gradually increased as SCG-f fish steadily declined in June. We collected marked SCG-f fish
500 at Point Adams Beach through the end of June, >30 days after the last release group from
501 Bonneville Hatchery entered the upper end of the estuary (Table 2). We also observed large
502 numbers of SCG-f fish at PAB during the May 2010 surveys with a corresponding decline in the
503 abundance of unmarked juveniles. However, the narrow (one-month) release period for all SCG-
504 f hatchery fish (Table 2) and our biweekly sampling frequency limited the temporal resolution of
505 the SCG-f hatchery contributions at PAB in 2010.

506

507 [A] Discussion

508 Increased hatchery marking rates since 2008 have enabled the first comprehensive
509 comparisons of HO and NP Chinook Salmon habitat use in the Columbia River estuary. Our
510 study expanded on site-specific (Roegner et al. 2012; 2016) and reach-scale surveys (Sather et al.
511 2016) to examine the estuary-wide effects of hatchery releases on genetic stock composition,
512 abundance, life histories, and co-occurrence with NP juveniles in shallow, nearshore habitats.
513 We found the life history variations of HO juveniles were simplified, as measured by migration
514 timing and size range, while their distributions overlapped considerably with NP fish in time and
515 space. The combined annual releases of >100 million hatchery Chinook Salmon from all
516 Columbia River hatchery programs dictated the frequency and abundance of fingerling Chinook

517 Salmon in nearshore habitats throughout the peak spring-summer migration period. Large
518 releases from mitigation hatcheries magnified the estuary contributions of LCR fall Chinook
519 Salmon and dominated salmon abundance in some habitats for weeks or months. Marked and
520 unmarked juvenile salmon co-occurred near shore throughout the estuary but the size of marked
521 hatchery subyearlings was much larger than their unmarked (presumably NP) cohorts. Average
522 spring-summer biomass density of marked salmon therefore was about the same as that of
523 unmarked juveniles despite their lower average abundance. Hatchery releases of a narrow range
524 of large subyearling and yearling phenotypes (e.g., freshwater riverine smolts) at the peak of the
525 salmon migration concentrated estuarine habitat use in time and space and increased the
526 likelihood of adverse interactions with smaller NP fry in prime shallow-water rearing areas
527 (Nickelson et al. 1986; Flagg et al. 2000; Einum and Fleming 2001; Jonsson and Jonsson 2006).
528 Hatchery production levels have remained relatively stable in the last decade (Pacific States
529 Marine Fisheries Commission 2019), and therefore, these patterns have not likely changed in the
530 years since our surveys were conducted.

531 Chinook Salmon of the same genetic stock groups exhibited distinct seasonal and spatial
532 distribution patterns, and marked and unmarked fish of the same genetic stock co-occurred in
533 many of the same nearshore habitats (Teel et al. 2014). The temporal overlap between HO and
534 NP juveniles reflected the release timing of each hatchery stock. For example, early spring
535 abundance of both marked and unmarked yearling UWR-sp Chinook Salmon peaked
536 simultaneously at mainstem and backside habitats in reaches C/D and E/F following peak
537 hatchery releases of this stock in February and March; July abundance of marked and unmarked
538 fingerling UCR-su/f stock peaked concurrently at the same sites in reaches E/F and G/H,
539 corresponding to the large hatchery releases in June-July (Teel et al. 2014). Although we
540 captured the greatest number of unmarked WC-f fry and fingerlings in May, overlap between NP
541 and HO fish was maximum in reaches A and C-D during the July survey, consistent with the
542 timing of peak hatchery releases of this stock in June-July (Teel et al. 2014).

543 Despite considerable overlap in their nearshore distributions, hatchery salmon exhibited a
544 much narrower range of life history traits than unmarked fish of the same stock. Hatchery release
545 dates often coincided with the peak abundance period for NP cohorts and dictated the estuary
546 arrival times for marked subyearlings (Teel et al. 2014; Figure 7). In contrast, unmarked fry from
547 LCR fall stocks (e.g., WC-f and SCG-f) appeared in the estuary months earlier and continued to

548 arrive later than their hatchery-reared cohorts, presumably the result of natural variations in the
549 emergence and migration times of individuals from diverse lower-river populations (e.g.,
550 Reimers and Loeffel 1967). Hatchery selection for large size at release also accounted for a much
551 larger size-at-age and narrower length distribution for marked than for unmarked salmon of the
552 same or different stocks. Near identical length frequencies for marked subyearlings captured in
553 May and July suggest a uniform release size for hatchery fingerlings during the spring and early
554 summer. Intensive hatchery selection for release size and timing reduced variation in the life
555 history composition of salmon in the estuary (e.g., estuary arrival size and timing, estuary
556 residency, ocean entry size and timing) and may explain the narrower range in estuarine growth
557 variability for marked than for unmarked juveniles in 2010-11 (Goertler et al. 2016).

558 The nearshore dominance of fall-run juveniles, including many fish produced in
559 hatcheries may reflect the historical decline of interior salmon production (Gustafson et al. 2007;
560 NRC 1996) and its replacement with hatchery fish from the lower basin (Laythe 1950). As
561 recently as 1991, 92.7 million hatchery Chinook Salmon were released in the lower river basin
562 below The Dalles Dam (~rkm 309) compared with just 3.3 million in the entire mid- and upper
563 basin regions above (Cone and Riddlington 1996). The vast majority (92%) of these releases
564 consisted of fall-run stocks. By 2017 and 2018 ~44% of all Chinook Salmon stocks were
565 released above the Dalles Dam, and total hatchery production had declined by ~7 million (Pacific
566 States Marine Fisheries Commission 2020). Nonetheless, ~40 million fall Chinook Salmon
567 fingerlings released each year below the dam still account for the single largest hatchery
568 component and continue to magnify LCR stock contributions to the total estuary abundance and
569 nearshore densities of juvenile salmon.

570 Intensive propagation of relatively few Columbia River salmon stocks and phenotypes
571 has been identified as a likely factor in the apparent simplification of Chinook Salmon life
572 history variation during the last century (Burke 2004; Bottom et al. 2005b; Campbell 2010).
573 Most notable is the paucity of late-season migrants that were once abundant in the estuary during
574 late summer and fall (Rich 1920). Hatchery practices that dictate the timing of estuary entry by
575 subyearling migrants also dictate the timing of ocean entry (Weitkamp et al. 2015) and therefore,
576 the range of growth and survival conditions juveniles will experience during the critical first
577 weeks or months at sea (e.g., Beamish and Mahnken 2001; Beamish et al. 2004; Duffy and
578 Beauchamp 2011; Sharma et al. 2012). Hatchery programs that synchronize the migration timing

579 and size characteristics of Chinook Salmon stock complexes may weaken their overall capacities
580 to buffer the effects of environmental variability through portfolio effects (Hilborn et al. 2003;
581 Moore et al. 2010; Huber and Carlson 2015; Satterthwaite and Carlson 2015). The loss of diverse
582 wild populations and their replacement with few hatchery stocks have been identified as
583 important factors in the collapse of Oregon coastal Coho Salmon (Nickelson et al. 1986;
584 Lichatowich 1999; Bottom et al. 2006) and Sacramento River Fall Chinook Salmon (Lindley et
585 al. 2009; Huber and Carlson 2015).

586 Our results contradict the general characterization that hatchery selection for large
587 “ocean-ready” smolts eliminates the risk of significant interaction with NP juveniles in shallow
588 nursery habitats (Bottom et al. 2005b; NMFS 2014; Flagg 2015). Estuarine habitat use by
589 juvenile Chinook Salmon generally varies with fish length, with the smallest size classes
590 frequenting shallow-water habitats near shore (Healey 1991; Bottom et al. 2005b). However, the
591 relatively large size at estuary entry for most hatchery salmon did not prevent considerable
592 overlap in the nearshore distributions of marked and unmarked subyearlings. Large size could
593 limit the total interaction times between hatchery individuals and other NP juveniles because
594 estuary residence times generally decrease with fish length (Campbell 2010). Nonetheless,
595 successive releases from > 80 Columbia River hatchery programs insured large numbers of
596 hatchery juveniles remained near shore through the spring and summer when NP juvenile
597 Chinook Salmon also were most numerous. Mean nearshore densities of HO salmon were less
598 than for NP fish but marked subyearlings dominated fish abundance at some mainstem sampling
599 sites (Table S.2), similar to the patterns we observed at Hayden Island and Point Adams Beach.
600 With a mean biomass density equal to that of NP juveniles, the nearshore energy demand of HO
601 juveniles could be significant during the spring-summer peak. The relative proportion of HO fish
602 was greater in mainstem than in backside habitats in most reaches but we found no significant
603 difference in the numerical or biomass densities of HO and NP salmon between the two habitat
604 types.

605 The potential for interactions between HO and NP juveniles is illustrated by the
606 abundance and residency of marked SCG-f fish near shore following a series of large hatchery
607 releases. SCG-f fingerlings occupied nearshore habitats soon after the first April release and
608 dominated genetic stock composition and fish abundance at upper and lower estuary sites until
609 June. Repeated inverse trends in the abundances of marked SCG-f fingerlings and unmarked fry

610 at Hayden Island in 2009 and at Point Adams Beach in 2011 may be evidence of competitive
611 exclusion or displacement of smaller NP juveniles from productive shallow-water habitats,
612 although we cannot discount seasonal variations or other factors that might otherwise account for
613 these patterns. Similar displacement of juvenile Chinook Salmon fry from prime rearing habitats
614 has been reported in the Skagit River Delta in years when the abundance of large wild smolts
615 leaving the basin exceeds a threshold level (Beamer and Larsen 2004; Beamer et al. 2005).

616 Juvenile densities in estuarine habitats dramatically increase when large groups of
617 similarly sized individuals of a single hatchery stock are released, synchronizing their estuary
618 arrival and migration timing (e.g., Figures 7 and 8). The combined releases from all hatcheries
619 during the spring-early summer period likely contribute to the pronounced seasonal peak in
620 estuary abundance (Burke 2004; Campbell 2010; Bottom et al. 2011) in contrast to the much
621 more protracted abundance period (i.e., through the fall) reported during the first Columbia River
622 Chinook Salmon study in 1914-16 (Rich 1920; Burke 2004). Loss of wetland rearing habitats
623 combined with large pulsed releases of hatchery fish could concentrate salmon abundance near
624 shore. During the spring peak in 2010 and 2011, estimated nearshore densities for HO and NP
625 Chinook Salmon combined averaged 0.53 fish/m² and >1 fish/m² at some sites, similar to values
626 reported for the Skagit River delta (0.32-1.20 fish /m²; Beamer et al. 2005) but greater than the
627 peak values for tidal marsh channels in the Salmon River, Oregon (0.04 - 0.09 fish/m²; Gray et
628 al. 2002; Hering 2009); a marsh complex in the Fraser River estuary (0.35 fish/m²; Levy and
629 Northcote 1982); and for selected Columbia River sites in the lower estuary (rkm 35-101; 0.05 -
630 0.20 fish/m²; Bottom et al. 2011) and Sandy River Delta (rkm 188-202; 0.12 fish/m²; Sather et al.
631 2016). The average spring-summer Chinook densities in our study were ~ 20 times greater than
632 the capacity estimate (252.7 fish/ha or .0257 fish/m²) for four large tidal river deltas (Nooksack,
633 Skagit, Snohomish, Nisqually) in Puget Sound (Greene et al. 2021).

634 Studies in the Columbia River have provided evidence of density dependence during the
635 juvenile stage but little is known about density effects in tributaries below Bonneville Dam and
636 in the estuary (ISAB 2015). Studies in other estuaries have reported salmon densities during peak
637 periods can limit foraging success and growth (Reimers 1973, 1978; Simenstad and Salo 1982;
638 Neilsen et al. 1985; Korman et al. 1997), increase outmigration, or reduce the mean size of
639 rearing juveniles (Beamer and Larsen 2004; Beamer et al. 2005; Rice et al. 2011). Chinook
640 Salmon densities in Puget Sound tidal deltas surpass the estimated rearing capacity in most

641 years, and in some systems, density limitations imposed by historical wetland loss are
642 compounded by large hatchery releases (Greene et al. 2021). The large number of salmon
643 populations and hatchery programs and variability in the temporal and spatial distributions of
644 different genetic stock groups complicate efforts to estimate rearing capacity for the Columbia
645 River estuary or to demonstrate density-dependent relationships.

646

647 [B] Management Implications

648 Salmon habitat use in the Columbia River estuary occurs at the intersection of two
649 mitigation programs with different management objectives targeting different subareas of the
650 basin and life stages of salmon: a hatchery program to replace lost habitat and fishery production
651 potential from the interior basin caused by the construction of mainstem dams (NMFS 2014),
652 and a habitat restoration program in the estuary to offset the mortality of naturally produced
653 juveniles caused by the operations of the Federal Columbia River Power System (Thom et al.
654 2013; Johnson et al. 2018). The considerable spatial and temporal overlap among HO and NP
655 salmon imply a strong potential for interactions in the estuary that are not anticipated by either
656 program but could undermine the salmon conservation goals of both. Recent efforts to reform the
657 hatchery program elevate the conservation of NP populations to a priority equal to the production
658 of fish for harvest (Paquet et al. 2011; Flagg 2015; NMFS 2014, 2017). These reforms focus on
659 reducing impacts on NP fish at the watershed level by adjusting practices at individual hatcheries
660 to minimize the risks from interbreeding and competition in natal streams (e.g., Levin et al.
661 2001; Zaporozhets and Zaporozhets 2005; Araki 2007a,b; Bailey et al. 2010; Chilcote et al.
662 2011). Our results suggest the balancing of fish production and conservation goals may also
663 require adjustment of hatchery operations to account for ecological interactions in the estuary
664 (Williams 2006), where all HO and NP salmon pass en route to the ocean.

665 The appropriate actions to realign Columbia River fish production and estuary restoration
666 objectives may vary among hatcheries but could include adjustments to the timing, size
667 characteristics, and numbers of fish released. Releasing fish in smaller groups over longer
668 periods rather than in large pulses at an “optimum” time could reduce estuary densities by
669 dispersing migrants in time and space. Strategies for rearing fish in semi-natural environments
670 and allowing volitional rather than forced releases have been used successfully by some
671 hatcheries to produce juveniles more similar in size and behavior to NP fish (Fuss and Byrne

672 2002; Maynard et al. 2004; Fast et al. 2008) and without compromising adult returns (e.g.,
673 Brouwer et al. 2014). Hatchery studies frequently have reported better survival for large smolts
674 compared to smolts released at small sizes (Martin and Wertheimer 1989; Morley et al. 1996;
675 Claiborne et al. 2011) but the definitions for “large” and “small” vary among studies, and a
676 larger size at release does not necessarily increase adult survival or production efficiency
677 (Feldhaus et al. 2016). Releasing hatchery salmon that more nearly resemble the size ranges for
678 NP juveniles at estuary entry would likely reduce the risks of competitive dominance by larger
679 individuals (Einum and Fleming 2001; Kostow 2009) but tradeoffs may exist between fish size
680 and densities in prime estuarine rearing areas. Smaller hatchery fish are more likely to reside in
681 the estuary for longer periods (Campbell 2010; Healey 1991), increasing the proportion of HO
682 juveniles in shallow areas and the relative frequency of interactions with NP juveniles.

683 Controlled studies of the estuarine interactions between HO and NP juveniles could help
684 to establish ecological criteria for managing hatchery practices. Our results reinforce previous
685 recommendations (Rand et al. 2012) for designing hatchery releases as experiments to (1) test for
686 density-related effects on salmon consumption, growth, or residence times in estuarine rearing
687 habitats; and (2) identify any significant behavioral interactions and effects, including whether
688 large pulses of hatchery fish displace NP juveniles from prime rearing areas (e.g., Spilseth and
689 Simenstad 2011). A better understanding of density effects is needed to determine whether
690 hatchery practices are working in concert with estuary restoration to achieve the survival and life
691 history diversity objectives for NP populations (Bottom et al. 2005b; Fresh et al. 2005; Krueger
692 et al. 2017). Otolith chemical methods for reconstructing the estuarine life histories of juveniles
693 and their contributions to adult returns (Campbell 2010; Miller et al. 2010; Volk et al. 2010;
694 Jones et al. 2014; Rose 2015) could provide useful population-level indicators of the
695 effectiveness of estuary restoration actions under particular hatchery production levels.

696 Ultimately, reductions in the aggregate number of hatchery fish may be necessary to
697 decrease the concentrations of hatchery subyearlings in the estuary during spring and summer.
698 The disproportionate contribution of large SCG-f hatchery fingerlings to the abundance and
699 biomass density of Chinook Salmon in shallow-water rearing habitats is a particular concern. A
700 formal system-wide review of this and other large mitigation hatchery programs may be
701 necessary to better align management actions among multiple legal mandates for Columbia River

702 fishery production (NMFS 2014, 2017), salmon conservation (e.g., Myers et al. 1998; NMFS
703 2005), and estuary restoration (NMFS 2008, 2010, 2020).

704

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Table 1. Annual mean number (millions) and percentage of marked (with a clipped fin and/or cwt) Chinook salmon released from hatcheries. Hatchery release data are for January 2010 through December 2011. Evolutionarily significant unit (ESU) status: E = endangered; T = threatened; NW = listing not warranted. Abbreviations for the 10 Columbia River basin genetic stocks are as follows: LCR= Lower Columbia River; WC-f = West Cascade, fall; WC-sp = West Cascade, spring; SCG-f = Spring Creek Group, fall; UWR-sp = Upper Willamette River, spring; MCR-sp = Mid-Columbia River, spring; UCR sp = Upper Columbia River, spring; DR-f = Deschutes River, fall; UCR-su/f = Upper Columbia River, summer/fall; SR-f = Snake River, fall; SR-sp = Snake River, spring, RR-f = Rogue River, fall.

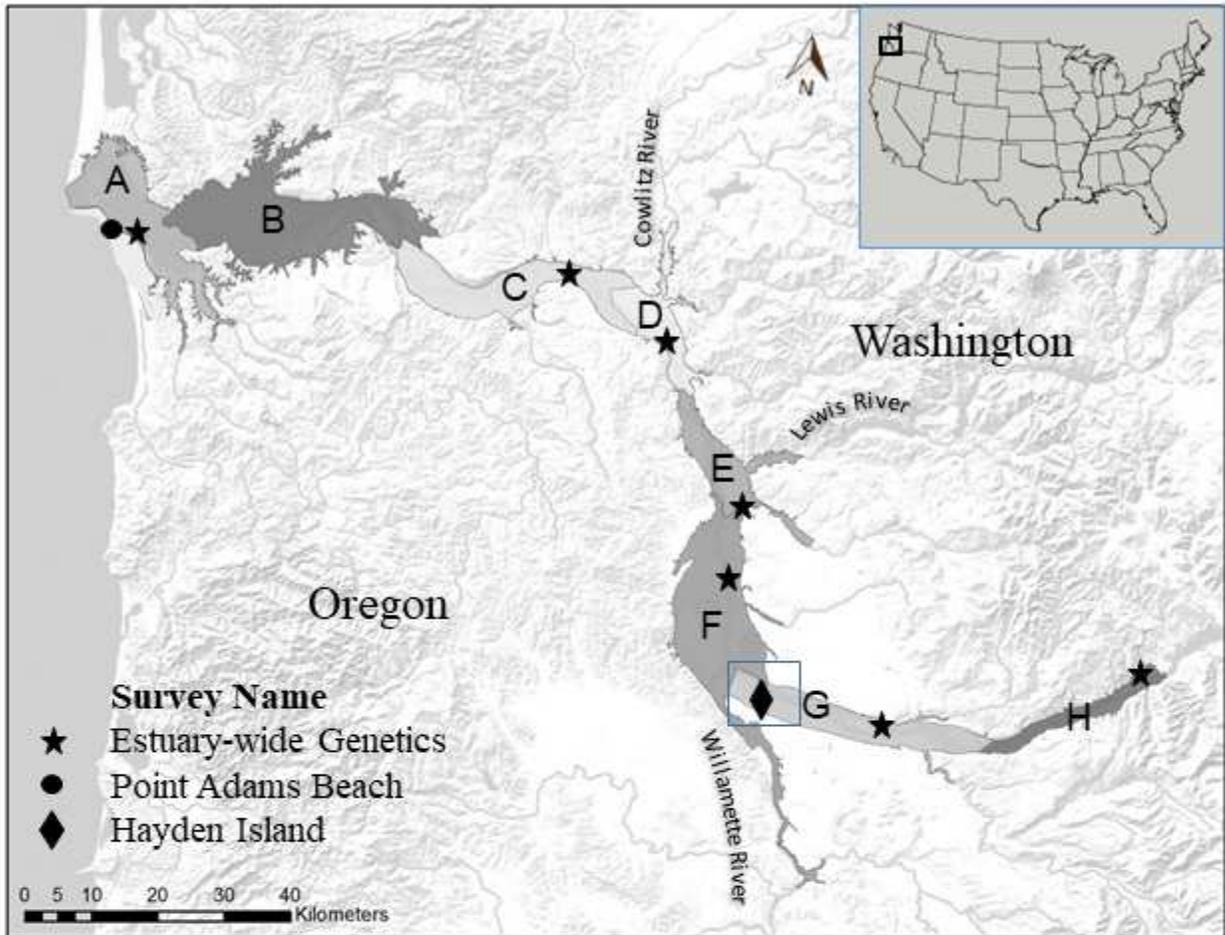
ESU (status)	Genetic stock	Subyearling		Yearling		Total	
		Number (millions)	Percent marked	Number (millions)	Percent marked	Number (millions)	Percent marked
Lower Columbia River (T)	LCR:WC-f	17.0	99.3	0.0	----	17.0	99.3
	LCR:WC-sp	0.3	0.0	2.9	99.3	3.2	89.7
	LCR:SCG-f	21.1	99.6	0.0	----	21.1	99.6
Lower Columbia River ESU total		38.4	98.7	2.9	99.3	41.3	98.7
Upper Willamette River (T)	UWR-sp	2.1	99.9	5.8	99.8	7.9	99.8
Mid-Columbia River Spring (NW)	MCR-sp	0.5	0.0	5.5	93.9	6.0	86.5
Upper Columbia River spring (E)	UCR-sp	0.1	96.4	2.7	98.7	2.8	98.7
Deschutes River Summer-Fall (NW)	DR-f	0.0	----	0.0	----	0.0	----
Upper Columbia River Summer-Fall (NW)	UCR-su/f	23.3	73.9	3.4	100.0	26.7	77.2
Snake River Fall (T)	SR-f	4.8	64.5	0.9	99.4	5.7	70.2
Snake River Spring-Summer (T)	SR-sp	0.9	62.9	12.9	99.1	13.8	96.7

None	RR-f	1.1	100.0	0.0	----	1.1	100.0
All releases		71.3	87.2	34.0	98.5	105.3	90.9

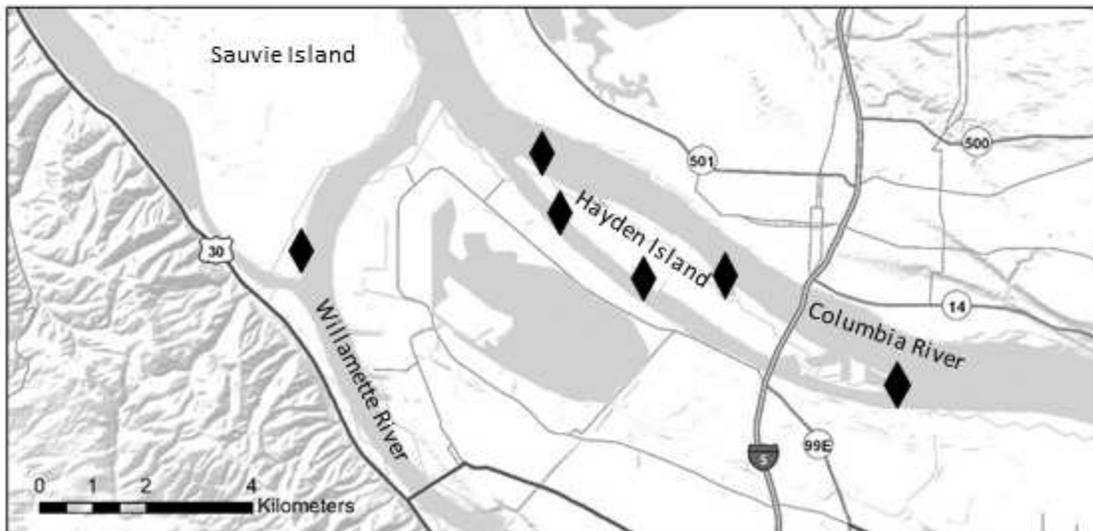
Table 2. Release date, location, and numbers of hatchery origin SCG-f Chinook Salmon released in the Columbia River basin, 2009-11 (Pacific States Marine Fisheries Commission 2019). Fish released into the NF Klaskanine R. (Reach A), Big Cr. (Reach B), and Tanner Cr. (Reach H) enter the estuary below Bonneville Dam. All other releases occurred above the dam.

Year	Release Date	Release Location	Hatchery	Millions Released	Percent Marked	
2009	13-Apr	Spring Cr and	Spring Cr NFH and	8.3	100.0	
		Little White	Little White			
	1-May	Salmon R	Salmon NFH	4.8	100.0	
		Spring Cr	Spring Cr NFH			
	11-May	Big Cr		Big Cr Hatchery	5.7	98.0
Bonneville						
15-May	Tanner Cr	Hatchery	2.5			
Total				21.3	99.4	
2010	12-Apr, 13-Apr	Spring Cr and	Spring Cr NFH and	8.0	100.0	
		Little White	Little White			
	30-Apr, 3-May	Salmon R		Big Cr Hatchery	6.0	98.8
				and Klaskanine		
	10-May	Big Cr and NF Klaskanine R		Hatchery	2.9	98.0
				Bonneville		
3-May	Tanner Cr	Hatchery	4.6	100.0		
Total				21.5	99.4	
2011	12-Mar	Little White	Little White	1.8	100.0	
		Salmon R	Salmon NFH			
	12-Apr	Spring Cr	Spring Cr NFH	6.2	100.0	
		NF Klaskanine	Big Cr Hatchery			
	15-Apr	R		1.9		
	4-May	Spring Cr	Spring Cr NFH	4.6	100.0	
	16-May	Big Cr		Big Cr Hatchery	3.3	99.8
Bonneville						
25-May	Tanner Cr	Hatchery	2.8			
Total				20.6	99.8	

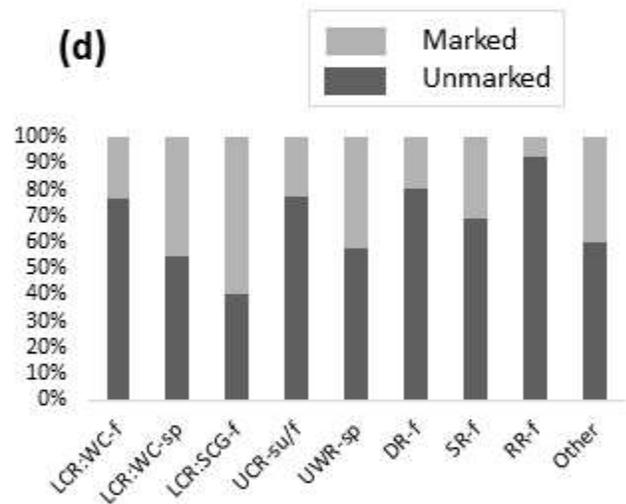
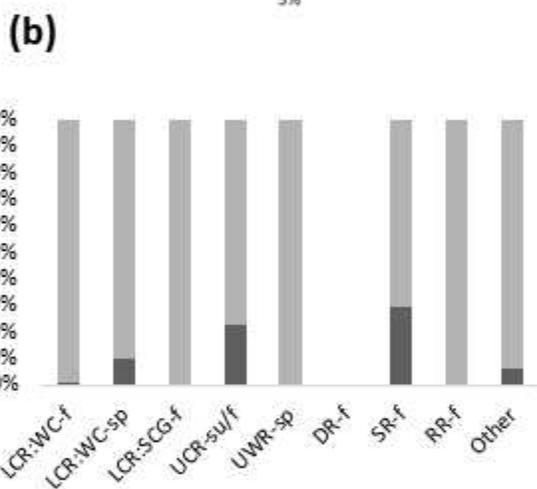
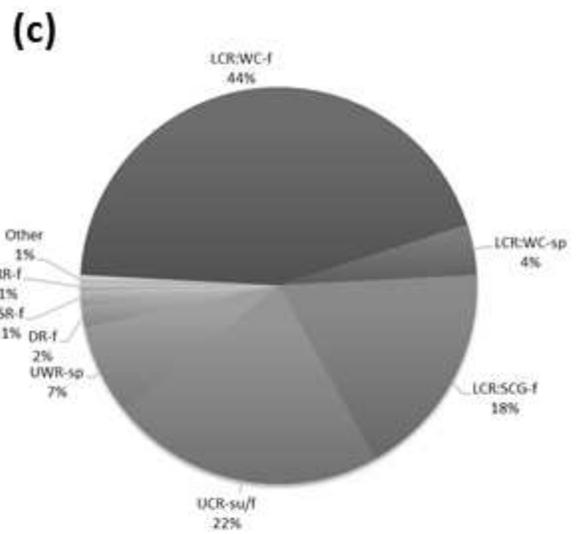
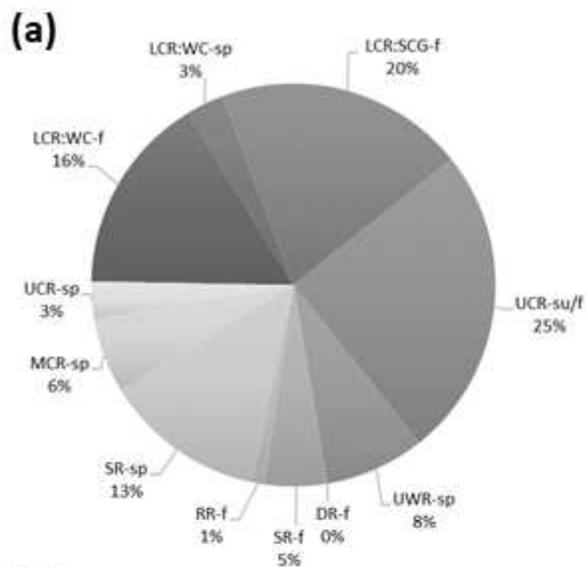
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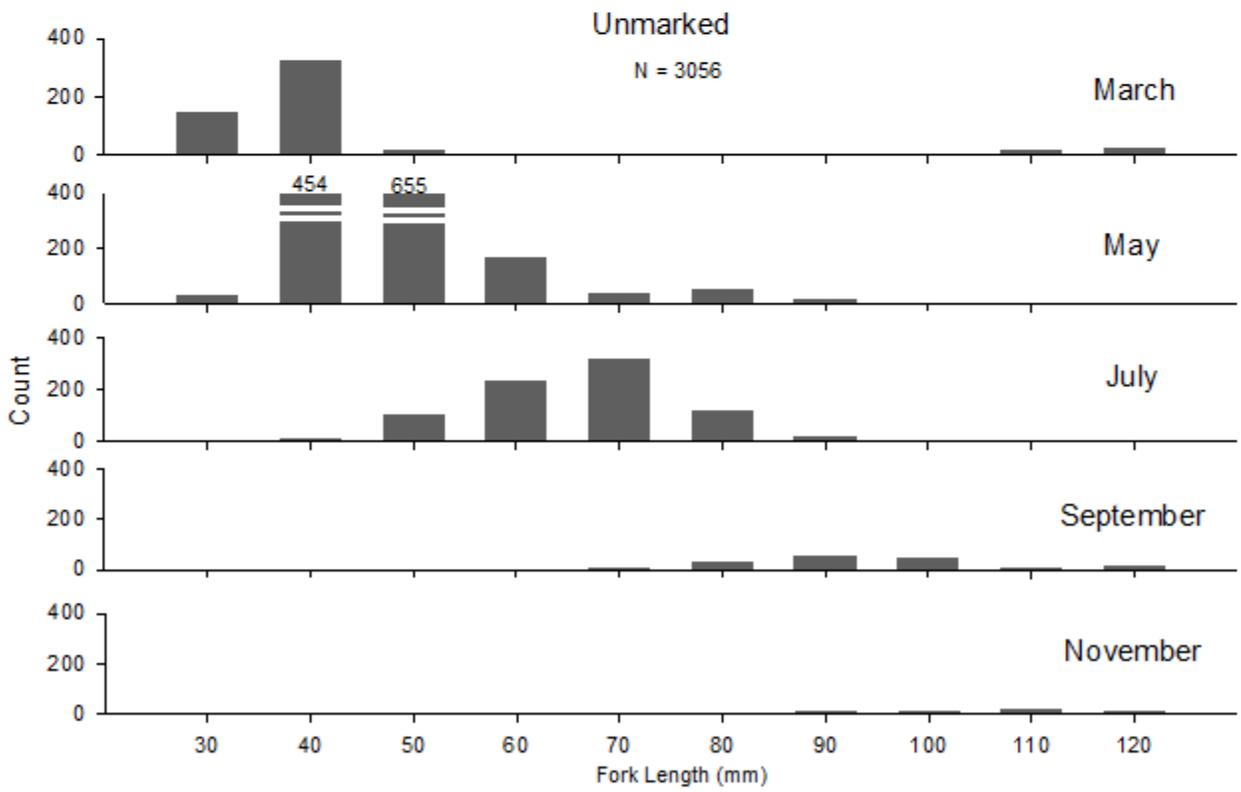
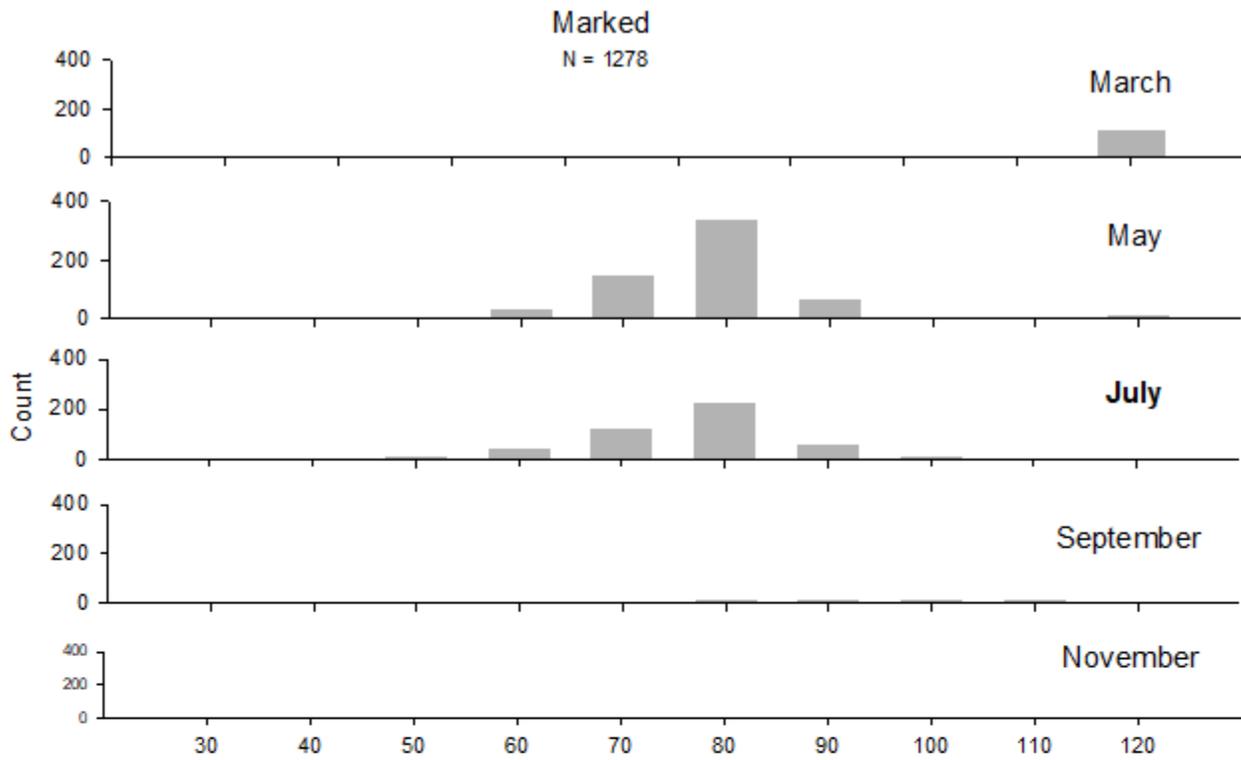


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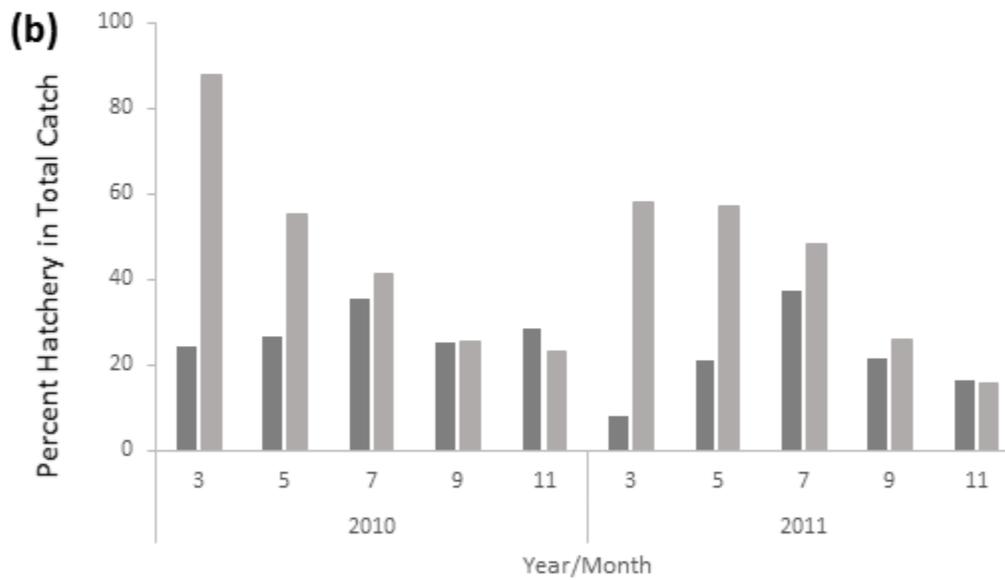
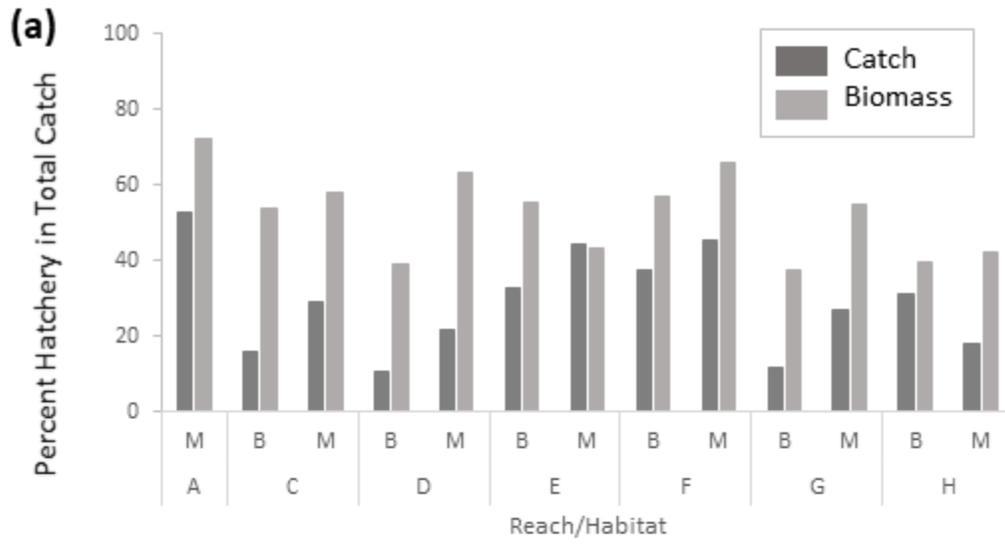


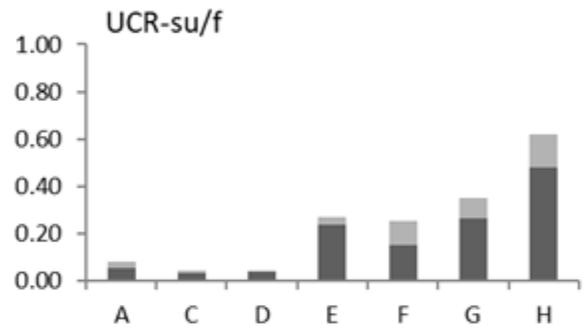
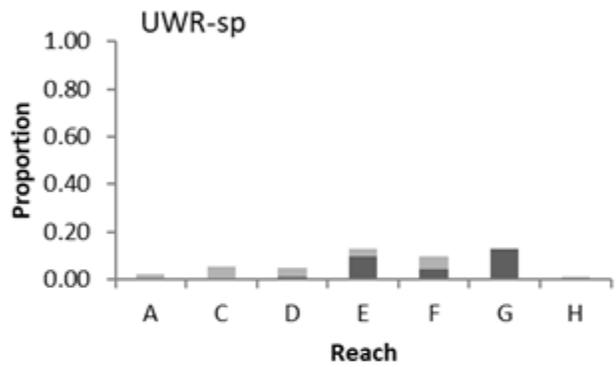
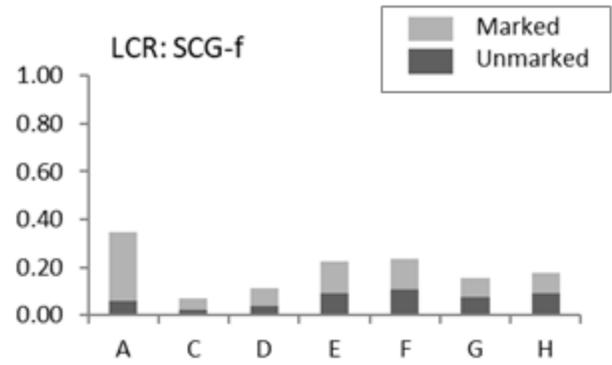
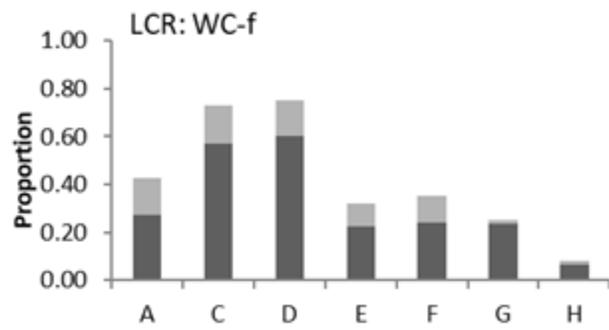
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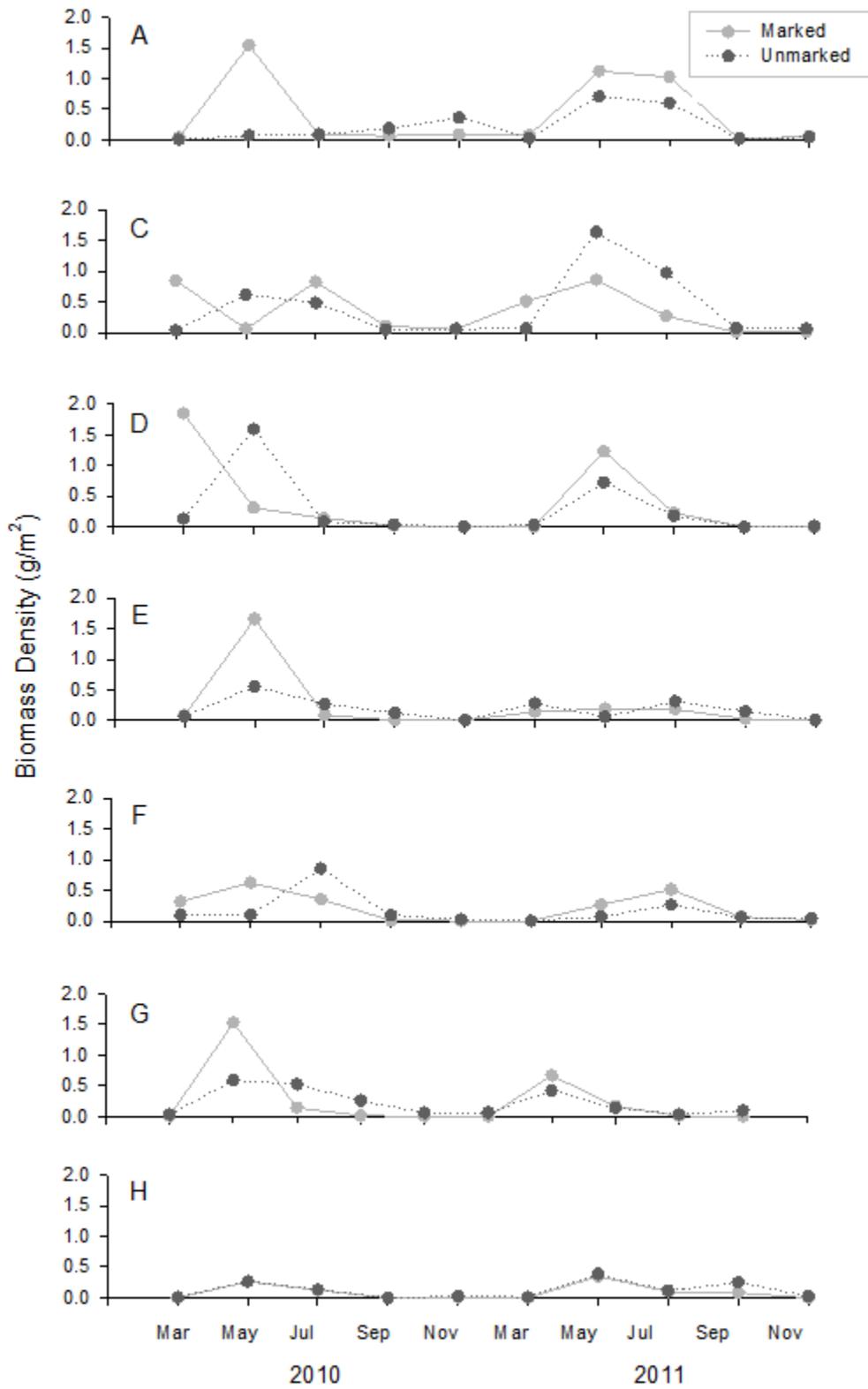




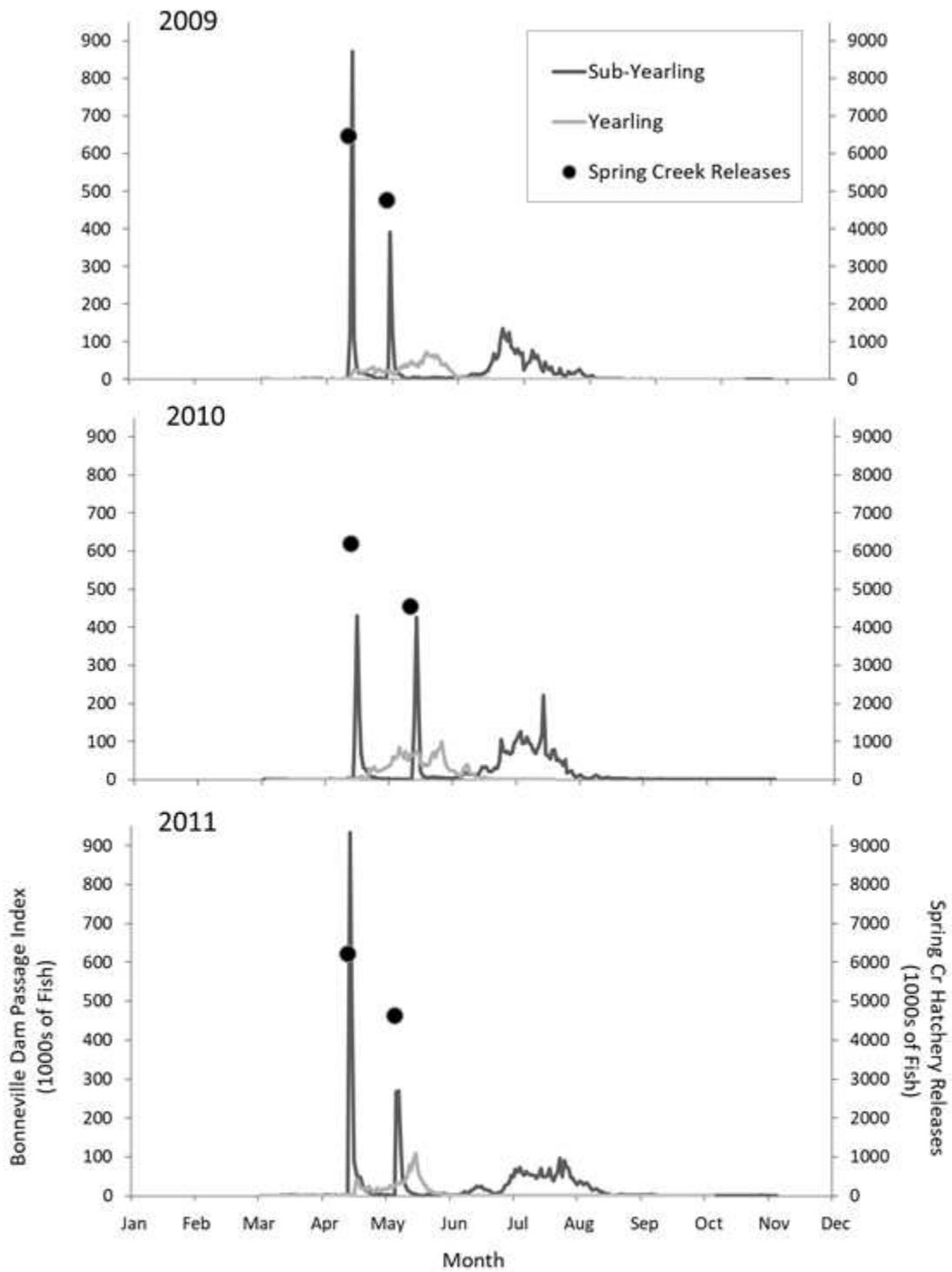
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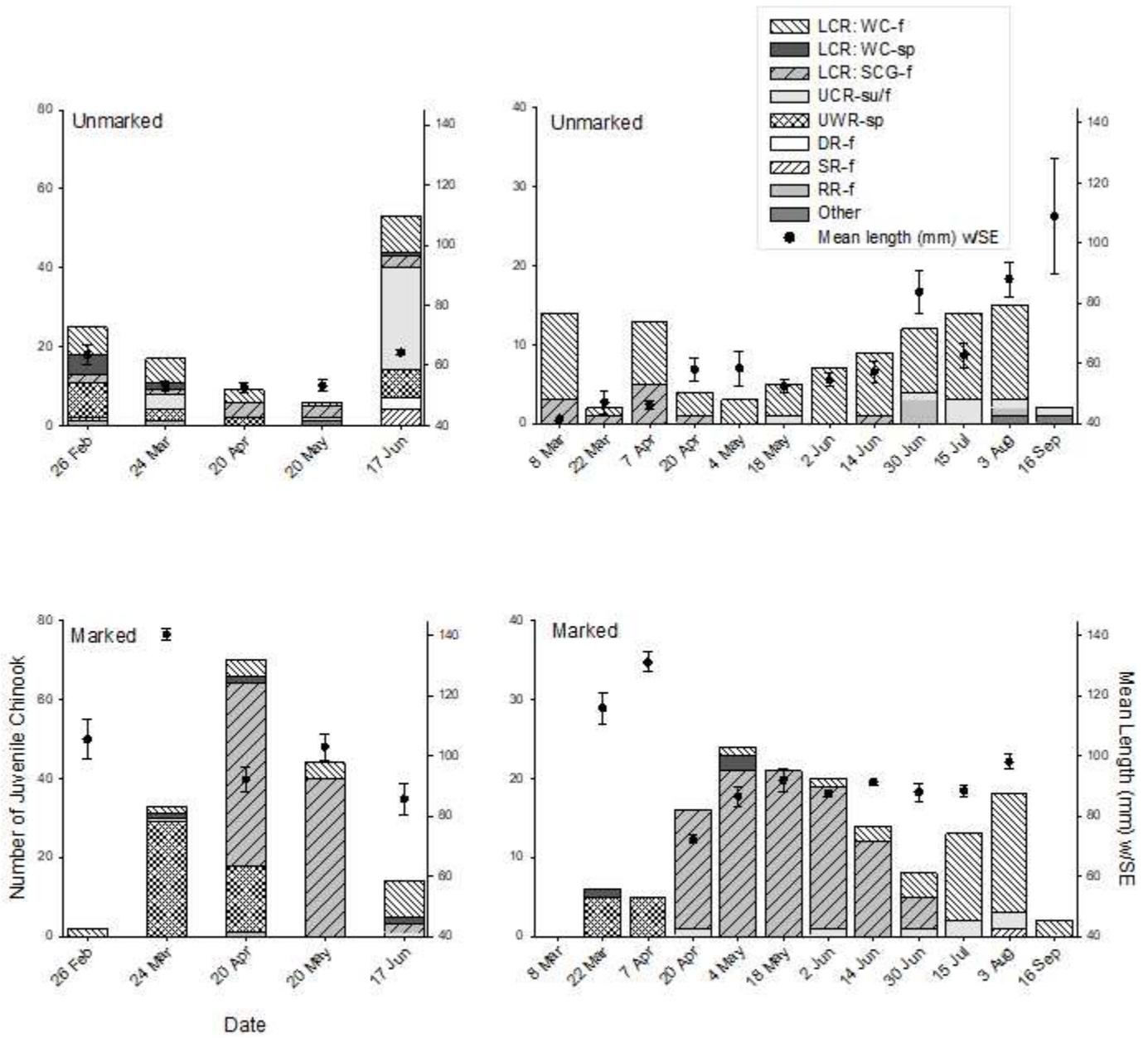
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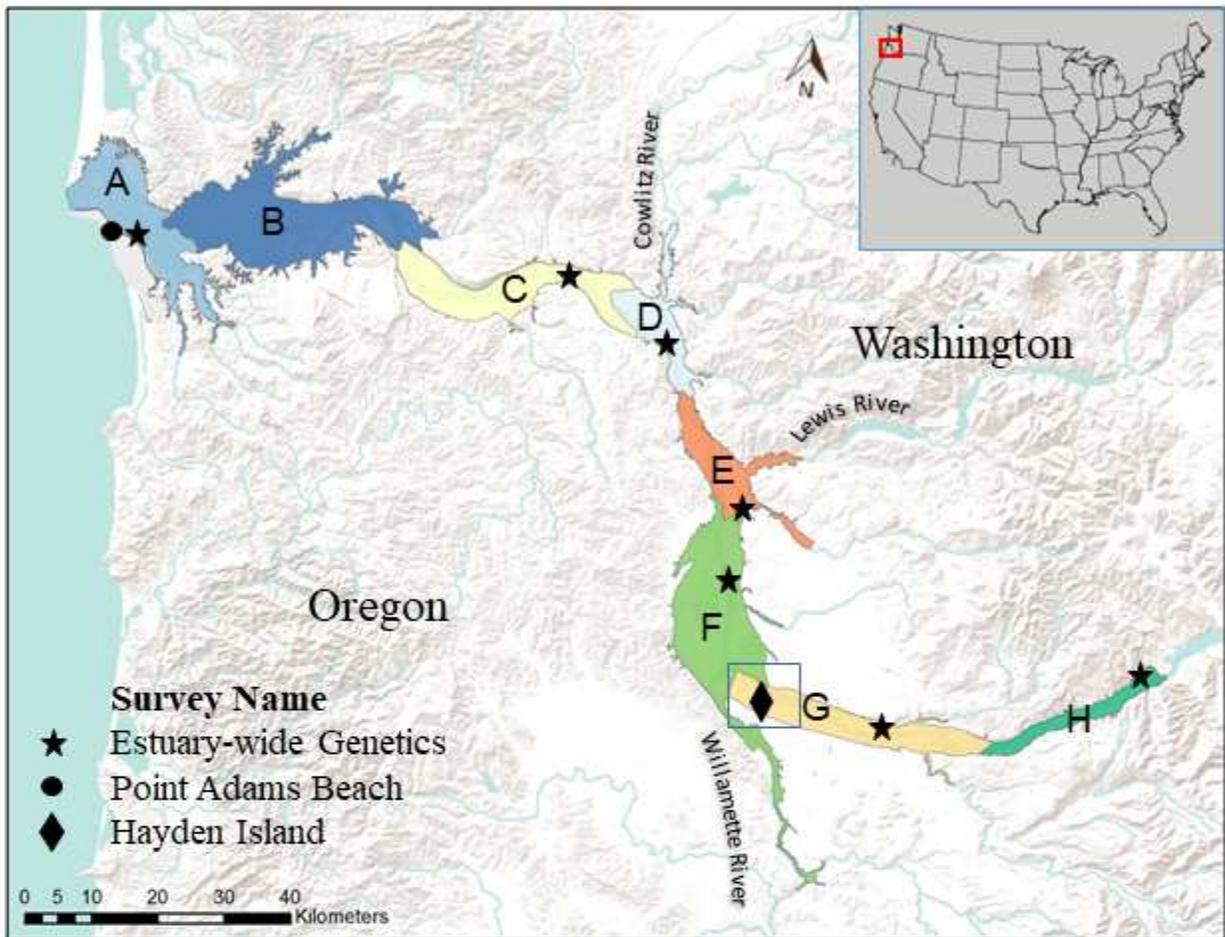
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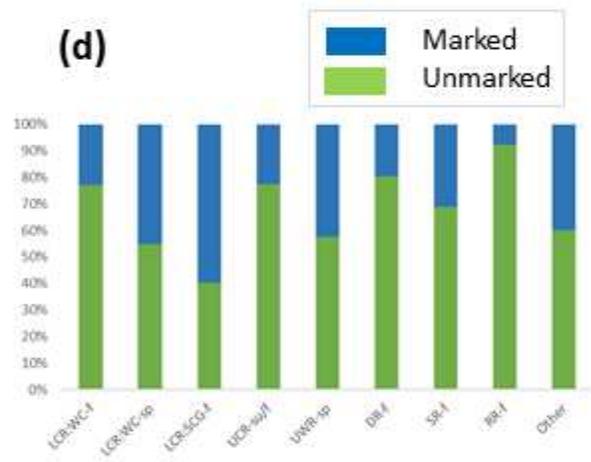
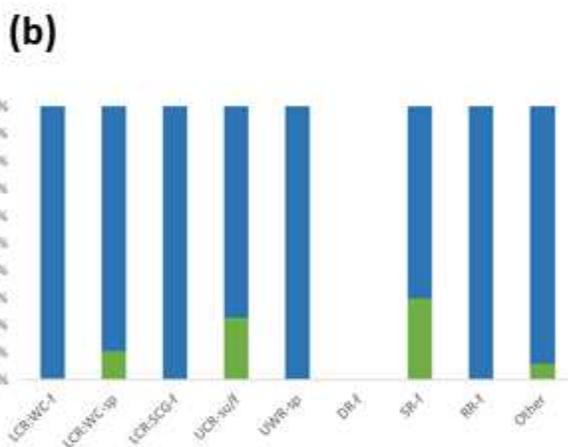
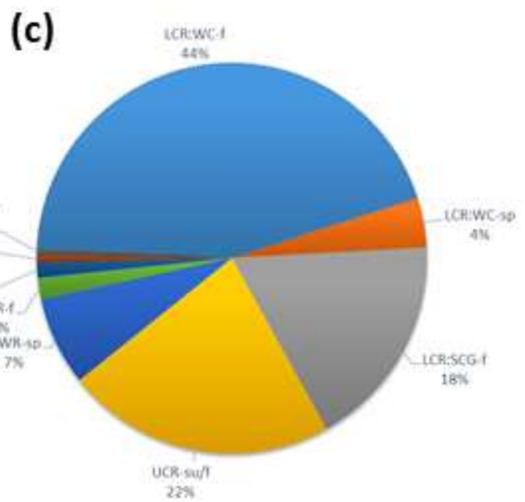
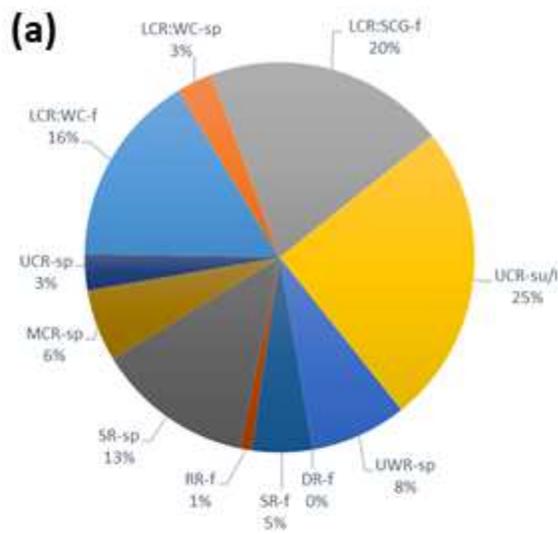
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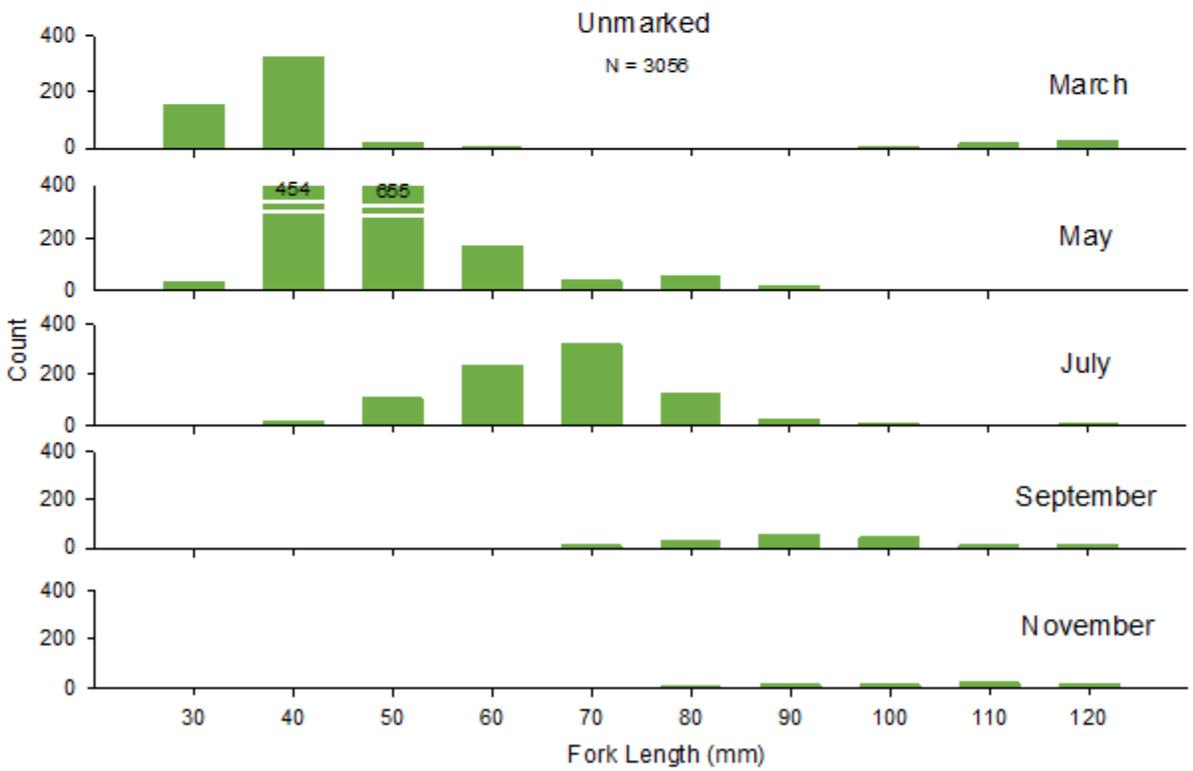
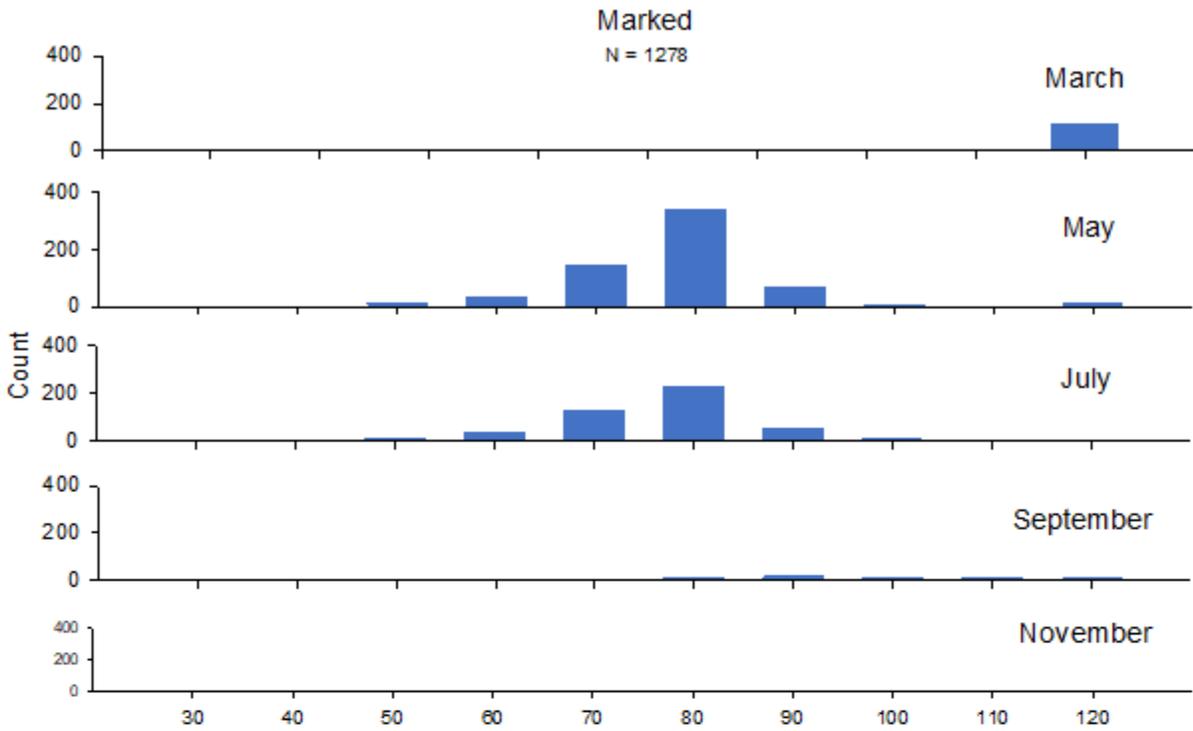


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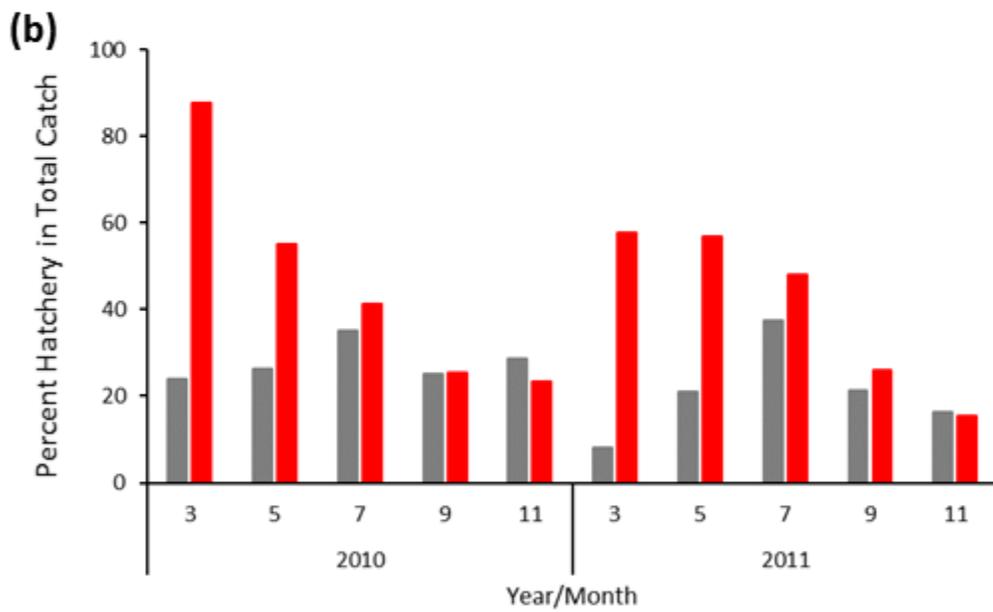
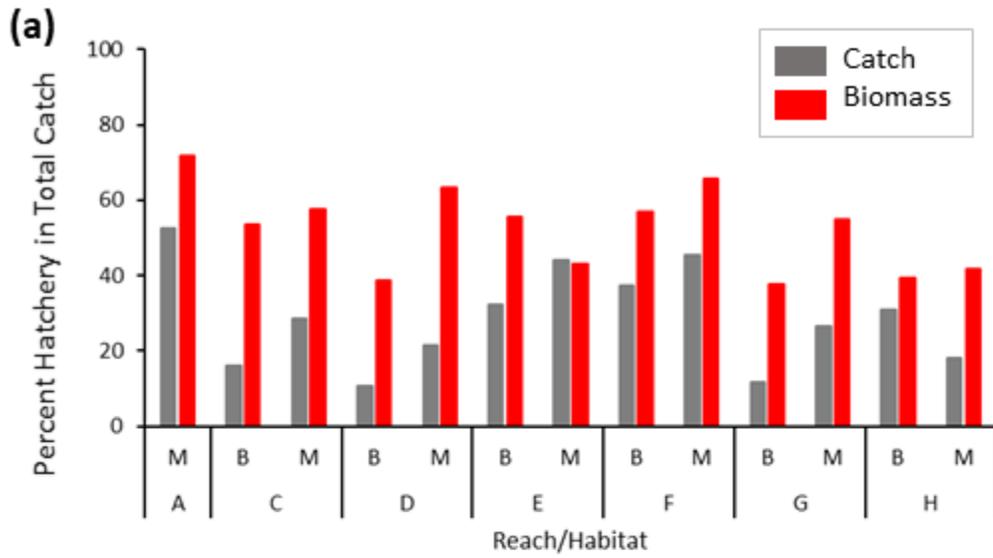


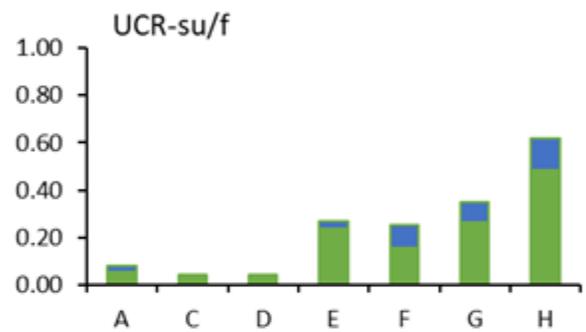
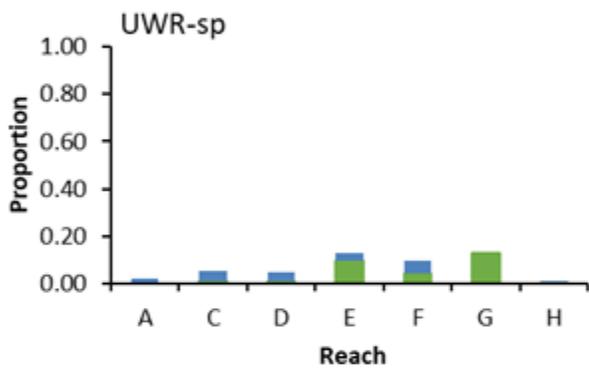
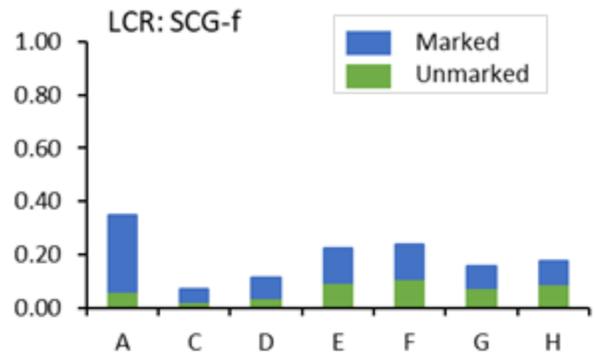
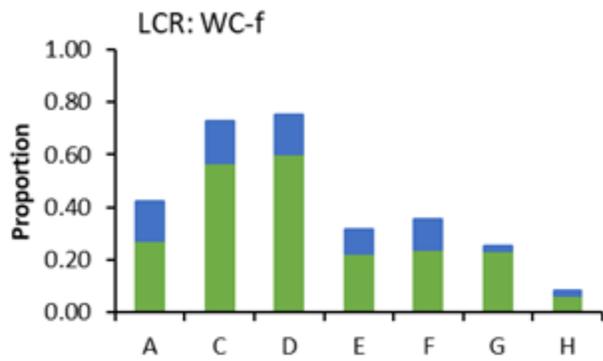
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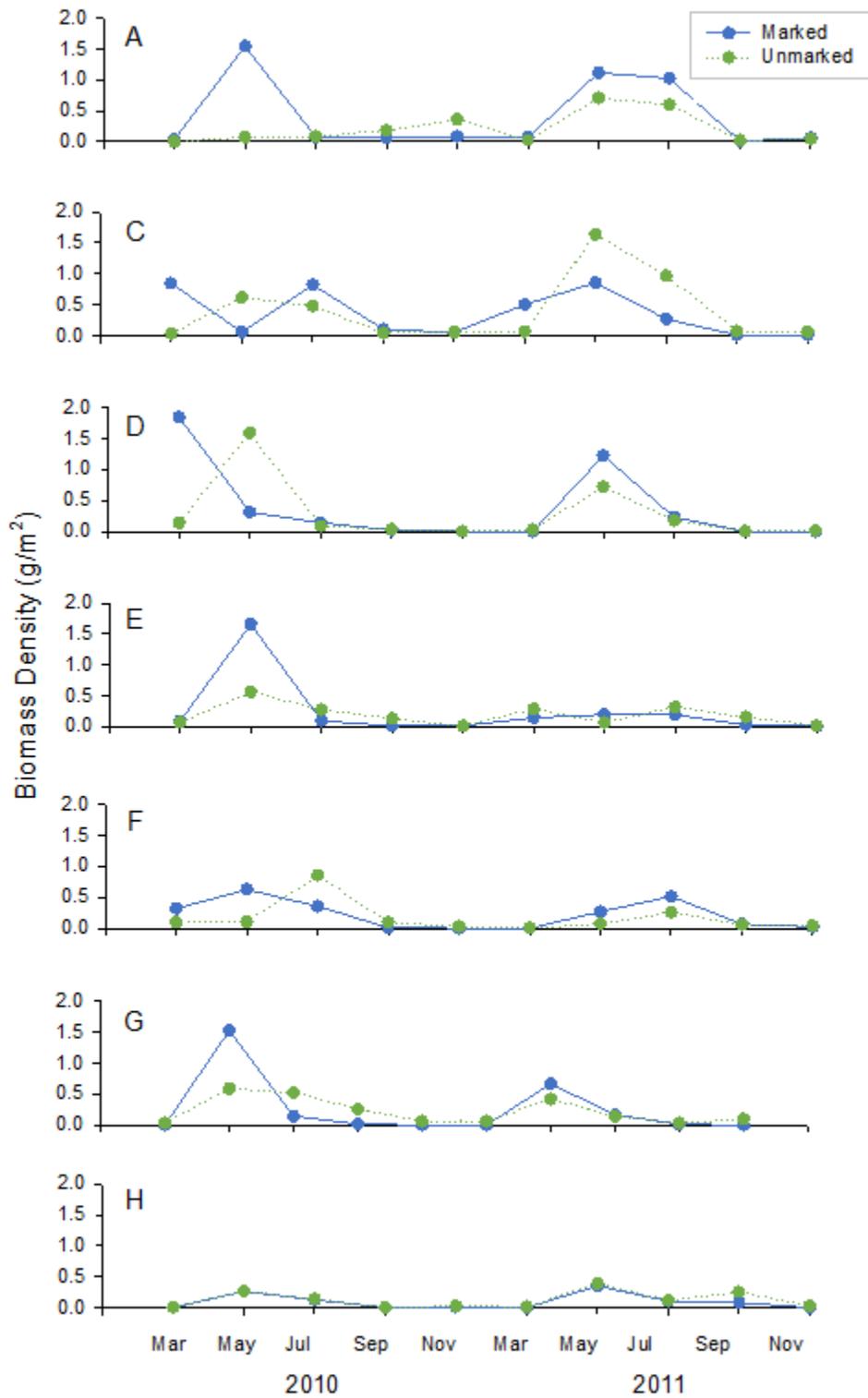




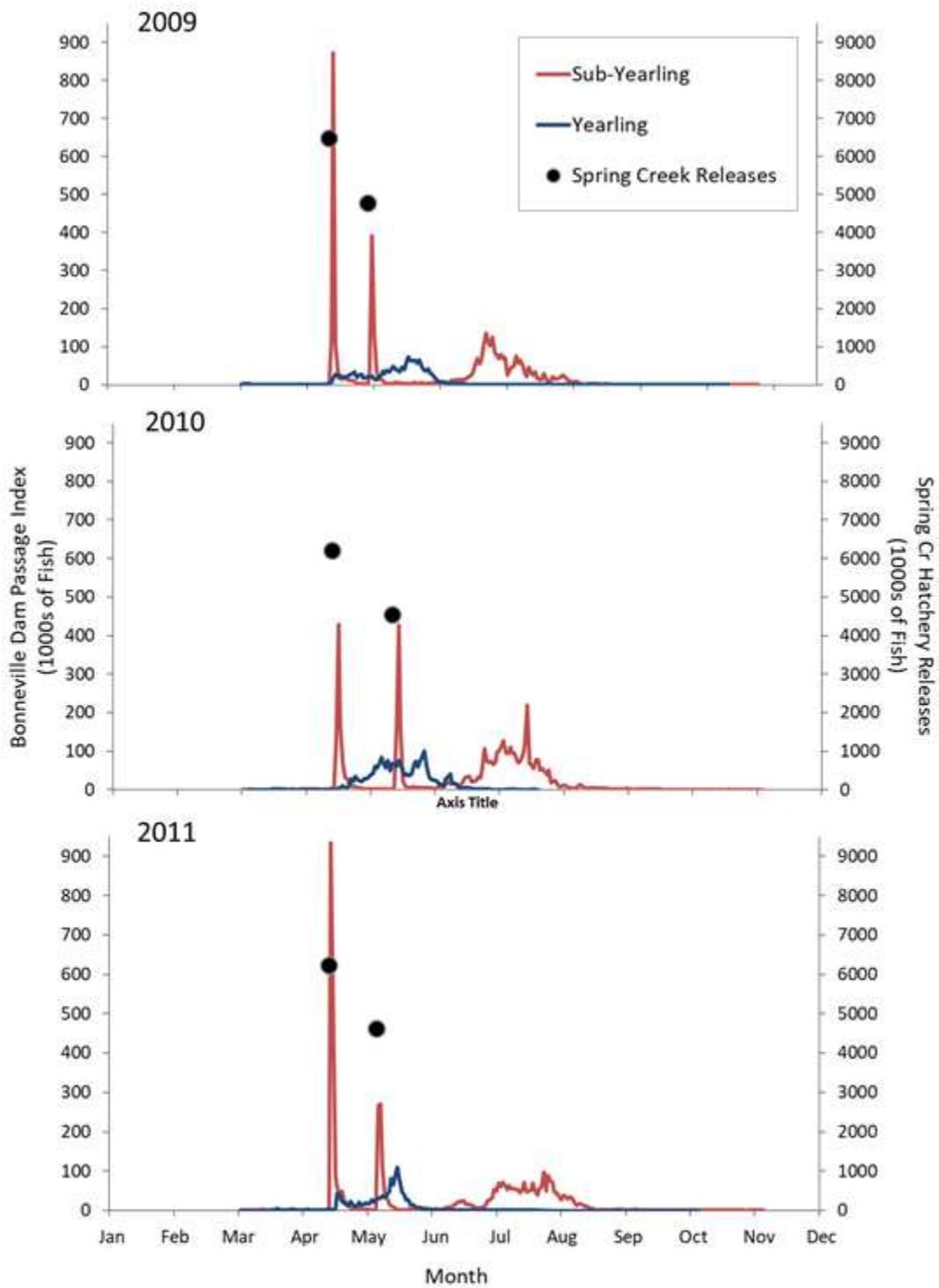
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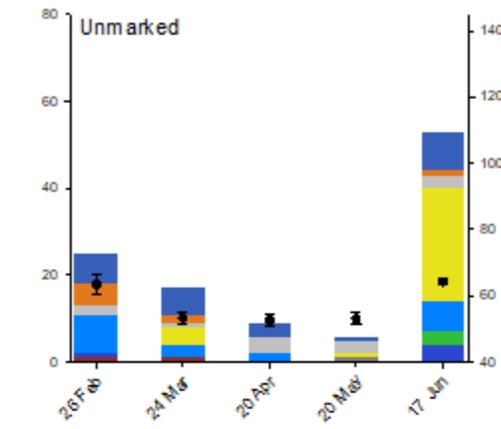


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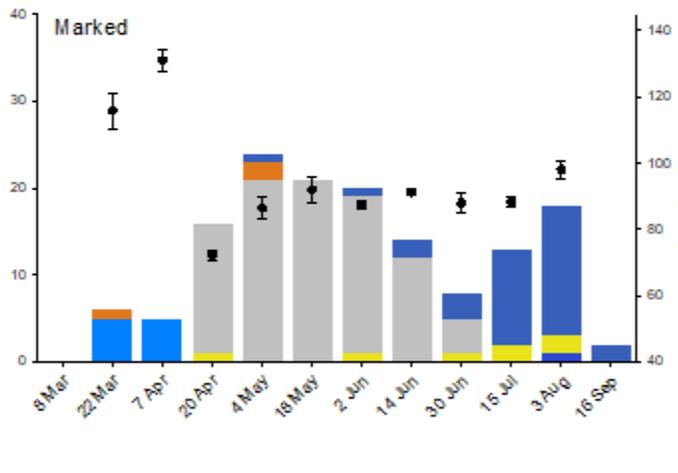
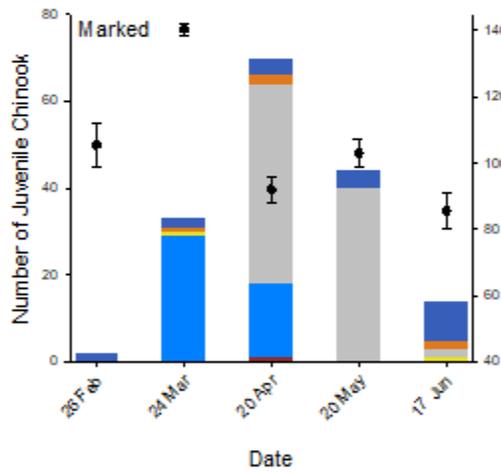
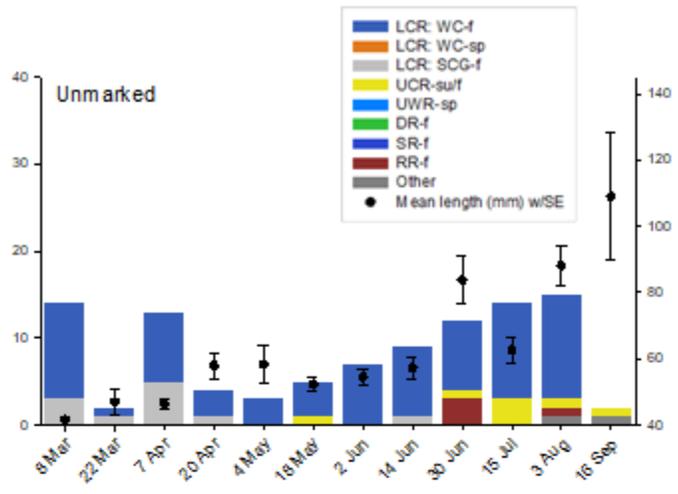


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