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1 **Chinook salmon rearing habitat-discharge relationships change**
2 **as a result of morphodynamic processes**

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26 **Abstract**

27 Relationships between fluvial aquatic habitat availability and discharge are often
28 assumed to remain static when used with hydrologic datasets to analyze
29 changes in habitat availability over time. Despite this assumption, studies have
30 observed significant changes in aquatic habitat availability before and after
31 restoration projects, dam removals, and extreme flood events. However,
32 research is lacking on how aquatic habitat changes as a result of
33 morphodynamic processes during more commonly occurring hydrologic
34 conditions. This study compared Chinook salmon (*Oncorhynchus tshawytscha*)
35 rearing habitat availability at 19 discharges before and after a relatively mild 8-
36 year hydrologic period punctuated with modest floods on the lower Yuba River
37 in California, USA. During this time, the total area of rearing habitat remained
38 relatively consistent at discharges $<2x$ bankfull but decreased by up to 25% at
39 discharges $>2x$ bankfull. Significant decreases in rearing habitat area appeared
40 to be the result of widespread erosion on floodplains, terraces, and lateral bars,
41 even after only modest floods. As a result, spatially delineated areas of lost
42 habitat tended to increase in water depth and velocity at baseflow, bankfull, and
43 floodplain-filling discharges, while areas of gained habitat decreased in depth
44 and velocity. Although these specific results may not apply to all rivers around
45 the world, the finding that habitat-discharge relationships change as a result of
46 morphodynamic processes likely does transfer globally and should be
47 considered when making long-term regulatory and management decisions,
48 such as instream flow requirements and habitat restoration plans.

49 **KEYWORDS**

50 aquatic habitat, habitat change, habitat suitability model, rearing habitat,
51 salmonid habitat

52 **INTRODUCTION**

53 Habitat suitability models have become a common tool used by resource
54 managers to analyze how changes in discharge, substrate, and/or channel
55 topography relate to the abundance and quality of aquatic habitat in river
56 systems (Ahmadi-Nedushan et al., 2006; Dunbar, Alfredsen, & Harby, 2012).
57 These models typically assign relative indices of habitat quality (i.e., suitability
58 values) to spatially explicit maps of physical habitat values (e.g., water depth,
59 water velocity, substrate size, and cover type). Suitability values range from 0
60 (least suitable) to 1 (most suitable) (Bovee, 1986) and are linked to physical
61 habitat values using a variety of methods, including expert judgment, correlative
62 statistics, and bioenergetics (Ahmadi-Nedushan et al., 2006; Dunbar et al.,
63 2012; Naman, Rosenfeld, Neuswanger, Enders, & Eaton, 2019; Rosenfeld,
64 Beecher, & Ptolemy, 2016). Once developed, habitat suitability models are
65 often used to calculate a total habitat area (or “habitat availability”) at a range of
66 discharges and/or with multiple restoration design alternatives and are used to
67 inform regulatory and management decisions.

68 Habitat-discharge relationships developed from habitat suitability models
69 are often applied to actual or theoretical hydrologic time-series data in an
70 attempt to analyze changes in habitat availability over time (Benjankar et al.,
71 2018; Boavida, Caetano, & Pinheiro, 2020; Stamou et al., 2018). However, this
72 method assumes that although the physical habitat conditions within a river may
73 change over time, the relationship between habitat availability and discharge

74 remains static throughout the analyzed time period. Despite such commonly
75 held assumptions, multiple studies have observed changes in habitat-discharge
76 relationships before and after habitat restoration projects (Gard, 2006; Harrison,
77 Legleiter, Wydzga, & Dunne, 2011; Hauer, Unfer, Holzmann, Schmutz, &
78 Habersack, 2013; Wheaton et al., 2010), dam removals (Im, Kang, Kim, & Choi,
79 2011; Mouton, Schneider, Depestele, Goethals, & De Pauw, 2007; Tomsic,
80 Granata, Murphy, & Livchak, 2007), and extreme flood events (Gard, 2014;
81 Harrison, Pike, & Boughton, 2017; Mandlbürger, Hauer, Wieser, & Pfeifer, 2015;
82 Tamminga & Eaton, 2018). However, research is lacking on the stability of
83 aquatic habitat-discharge relationships without major anthropogenic or
84 hydrologic disturbances, particularly at scales larger than a specific project site.
85 Changes in habitat availability induced by fluvial morphodynamics stand out as
86 a particularly important, yet uninvestigated topic in river research and
87 applications. Furthermore, studies related to this topic often lack in-depth
88 analysis of spatial patterns of habitat change and how physical habitat
89 conditions (e.g., depth, velocity, cover) change at specific locations within the
90 river over time.

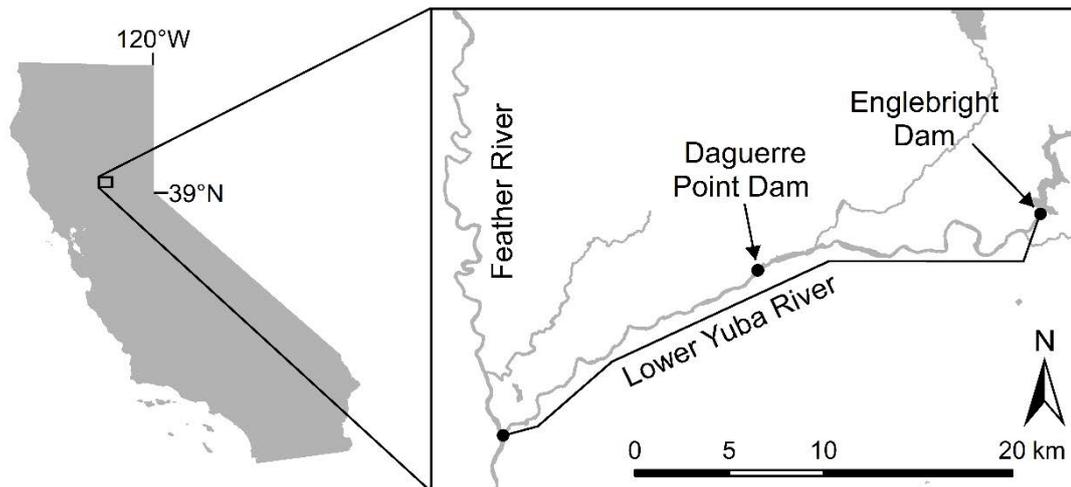
91 The purpose of this study was to evaluate the stability of Chinook salmon
92 (*Oncorhynchus tshawytscha*) fry (i.e., visually observed length < 50 mm) habitat
93 availability in a regulated yet dynamic gravel-cobble river during a relatively mild
94 hydrologic period with modest flooding. The novelty and importance of this
95 study lies in introducing new methods for evaluating changes in habitat
96 availability and linking those changes to morphodynamically induced changes in
97 specific physical habitat conditions. Note that this study does not investigate

98 morphodynamic processes explicitly, but the response of habitat availability to
99 such processes. Specific questions addressed in this study include:

- 100 1. Did key metrics in the habitat-discharge relationship, such as the
101 minimum and maximum habitat availability change in response to
102 morphodynamic changes?
- 103 2. Were morphodynamically induced changes in habitat availability greater
104 at in-channel or overbank discharges?
- 105 3. How did areas of lost, sustained, and gained habitat vary in patch size
106 and longitudinal distribution throughout the river at baseflow, bankfull,
107 and floodplain-filling discharges?
- 108 4. Could changes in Chinook salmon fry rearing habitat availability be
109 explained by changes in channel alignment, hydraulic conditions, and/or
110 cover?

111 **STUDY SITE AND HYDROGEOMORPHIC SETTING**

112 The Yuba River is a tributary of the Sacramento River in northern California that
113 drains 3,480 km² of the western slopes of the Sierra Nevada (Figure 1). The
114 lower Yuba River (LYR), defined as the 37-km segment of the river between
115 Englebright Dam and the Feather River confluence, is a regulated gravel-cobble
116 bed river with a low sinuosity, high width-to-depth ratio, and slight to no
117 entrenchment (Wyrick & Pasternack, 2014). It includes critical habitat for
118 Central Valley spring-run Chinook salmon, currently listed as threatened under
119 the United States Endangered Species Act (National Marine Fisheries Service,
120 2014; US Fish and Wildlife Service, 2010). As one of the most fluvially dynamic
121 regulated rivers in the coterminous United States, the LYR is an ideal testbed
122 for studying morphodynamically induced habitat change.



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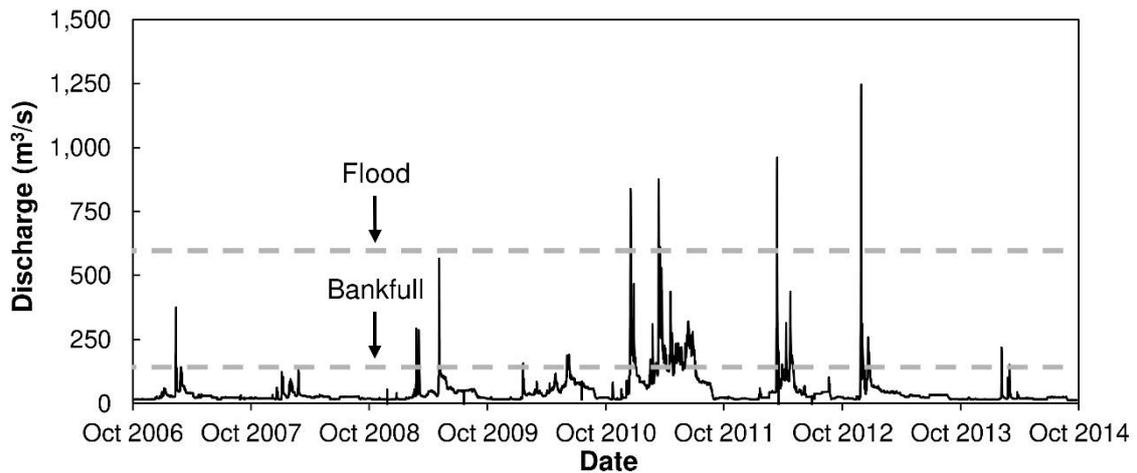
124 **FIGURE 1** Map of the study location in the lower Yuba River

125 Whereas the common expectation for a regulated river is a relatively
 126 static geomorphic state with reduced channel-floodplain connectivity, the LYR is
 127 very different. From 1999–2014, it experienced millions of cubic meters of gross
 128 erosion and deposition (Carley et al., 2012; Weber & Pasternack, 2017),
 129 differentiated among landforms and facilitated by 19 different morphodynamic
 130 processes functioning valley wide (Wyrick & Pasternack, 2015). Further, the
 131 bankfull channel experienced net fill during this time, while the overbank region
 132 experienced net erosion, enhancing channel-floodplain connectivity (Weber &
 133 Pasternack, 2017). This dynamism is driven by a relatively undisturbed flood
 134 regime acting on a massive, anthropogenically derived sediment supply stored
 135 below Englebright Dam (Gilbert, 1917; James, 2005).

136 Discharge into LYR primarily comes from three tributaries: the North,
 137 Middle, and South Yuba Rivers. Although the North Yuba River has a large
 138 reservoir that heavily regulates its outflow year-round, the absence of large
 139 reservoirs on the Middle and South Yuba Rivers allows for hydrologically
 140 dynamic conditions in the LYR. Relatively frequent floods occur when
 141 Englebright Dam is overtopped during winter storms and spring snowmelt and

142 are capable of driving substantial morphodynamic change (Sawyer, Pasternack,
143 Moir, & Fulton, 2010). Daguerre Point Dam (DPD) is an 8-m-high run-of-the-
144 river, sediment-retention dam that also aids flow diversion for irrigation. It is
145 located near the middle of the LYR, 17.8 river kilometers upstream from the
146 Feather River. Storage behind DPD is filled with sediment, allowing bedload to
147 pass downstream during floods.

148 The 8-year hydrologic period covered in this study spanned the 2007
149 through 2014 water years and was considered relatively dry in California. Seven
150 of the 8 years were classified as extremely critically dry, dry, or below normal
151 according to the Yuba River Index, which is calculated based on the current and
152 previous year's unimpaired flows (Yuba County Water Agency, 2012). During
153 this time, the LYR experienced only four modest ~3–5 year flood events of short
154 duration and a maximum instantaneous discharge of 9x bankfull (Figure 2). The
155 total duration of flood events quickly dropped with flood magnitude, with 171.3
156 days of discharges above bankfull, 28.7 days above 2x bankfull, and 4.4 days
157 above floodplain-filling flow. Despite the relatively mild hydrologic conditions,
158 Weber and Pasternack (2017) observed significant topographic change on the
159 LYR during this time, raising the question as to whether and how such changes
160 affected habitat availability.



161

162 **FIGURE 2** Hydrograph of instantaneous discharge in the lower Yuba River from
 163 2006 to 2014 at the Marysville USGS gage (11421000). Bankfull and flood (i.e.,
 164 floodplain-filling) discharges were defined by Wyrick and Pasternack (2012) as
 165 141.6 and 597.5 m³/s, respectively

166 PRECURSORY MODELS

167 The habitat suitability models used in this study were developed using results of
 168 several previously published models of the LYR. A brief summary of the
 169 development and evaluation of these precursory models is provided below, with
 170 relevant details and references presented as a summary table in the Supporting
 171 Information document. A detailed description of the novel methods used in this
 172 study to evaluate and explain changes in Chinook salmon fry rearing habitat
 173 availability in the LYR is then provided in the following section. Spatial analyses
 174 used in this study were performed using ArcGIS v. 10.6 (ESRI, 2018).

175 To characterize the topo-bathymetric conditions of the LYR at the
 176 beginning and the end of the study period, two 0.91-m-resolution digital
 177 elevation models (DEMs) were developed using a combination of ground-based
 178 surveying, boat-based bathymetry, and airborne LiDAR collected in 2006/2008
 179 and 2014. The 2006/2008 model was a combination of 2 years of topo-

180 bathymetric data, with the uppermost 20% of the LYR's length mapped in 2006
181 and the other 80% mapped in 2008. Survey and interpolation errors estimated
182 for both DEMs for bare ground, water, and vegetated ground were 0.039, 0.074,
183 and 0.30 m, respectively (Weber & Pasternack, 2017). Details of 2006/2008 and
184 2014 DEM development and uncertainty evaluation can be found in Carley et al.
185 (2012) and Weber and Pasternack (2017), respectively.

186 From these DEMs, two-dimensional (2D) hydrodynamic models were
187 produced for the study site using SHR-2D for 2006/2008 hydraulic conditions
188 and TUFLOW GPU for 2014 conditions. A model comparison study of 2014
189 river conditions found minimal difference between these solvers for this river
190 (Pasternack & Hopkins, 2017). The result of these models was two sets of 0.91-
191 m-resolution depth and velocity rasters for the LYR. Extensive hydrodynamic
192 validation found that the performance of both models far exceeded peer-
193 reviewed journal norms (Pasternack, 2011). For example, the coefficient of
194 determination (R^2) between predicted and observed values for depth, velocity
195 magnitude, and velocity direction were >0.65 for both models. Details of
196 2006/2008 and 2014 hydrodynamic model development and validation can be
197 found in Barker et al. (2018) and Hopkins and Pasternack (2018), respectively.

198 Cover features were digitized into 0.91-m rasters throughout the study
199 site. Vegetation presence/absence was mapped using airborne LiDAR collected
200 in 2008 (Abu-Aly et al., 2014; Burman & Pasternack, 2017) and 2014 (Weber &
201 Pasternack, 2016; Weber & Pasternack, 2017). Permeant human-built detritus
202 (e.g., rip-rap, cement blocks) were mapped using a combination of 0.3-m-
203 resolution aerial imagery from 2008 and boat-based field reconnaissance in
204 2012 (Vaughan & Pasternack, 2014). Other permanent cover features (e.g.,

205 bedrock outcrops, weirs, bridge piers) were mapped using 0.3-1-m resolution
206 aerial imagery from 2008 and 2012. Detailed field surveys were conducted in
207 2010 and 2011 confirming widespread cover of large cobble substrate
208 throughout the LYR (Jackson, Pasternack, & Wyrick, 2013).

209 Habitat suitability criteria (HSC) functions for depth, velocity, and cover
210 type were developed and bioverified for Chinook salmon fry by Moniz,
211 Pasternack, Massa, Stearman, and Bratovich (2020). HSC functions were
212 applied to 2014 depth, velocity, and cover rasters, resulting in a set of univariate
213 depth, velocity, and cover habitat suitability rasters at a range of discharges
214 between 14.16 and 42.48 m³/s. These rasters were then combined cell-by-cell
215 using the geometric mean function, resulting in a combined habitat suitability
216 raster of the entire LYR for each modeled discharge. Moniz et al. (2020) used
217 bootstrapped electivity indices to classify ranges of suitability values into
218 preferred, avoided, and randomly selected microhabitat. Mathematically,
219 preferred microhabitat was defined as a range of suitability values in which fish
220 were observed at a disproportionately higher percentage than the area of river
221 available having that same range of suitability values. Statistical bootstrapping
222 was used to calculate a 95% confidence interval for each of these ranges to
223 more accurately differentiate preferred and avoided microhabitat from randomly
224 selected microhabitat. Details of the development and bioverification of HSC
225 functions and 2014 habitat suitability models can be found in Moniz et al.
226 (2020).

227 **METHODS**

228 **Delineating preferred microhabitat**

229 To evaluate and explain changes in Chinook salmon fry rearing habitat
230 availability in the LYR, this study applied the HSC functions developed and
231 bioverified by Moniz et al. (2020) to a subset of the 2006/2008 depth, velocity,
232 and cover rasters summarized above. Using the preference threshold observed
233 by Moniz et al. (2020) for Chinook salmon fry in the LYR, cells in the 2006/2008
234 and 2014 habitat suitability rasters with suitability values ≥ 0.5 were classified as
235 preferred microhabitat and converted into polygon features to be further
236 analyzed in this study.

237 Minor modifications had to be made to the 2014 preferred microhabitat
238 polygons to make them comparable to the 2006/2008 polygons. Because the
239 2014 LiDAR coverage extended beyond the 2006/2008 coverage, 2014 models
240 included several features (e.g., tributaries and off-channel ponds) that may have
241 been present in 2006/2008 but were not included in the 2006/2008 models. To
242 make the two datasets exactly comparable, 2014 microhabitat polygons were
243 clipped by the 2006/2008 model boundary. Additionally, because the upstream
244 canyon section of the river known as Englebright Dam Reach was not modeled
245 for discharges between 8.50 and 16.9 m³/s in 2006/2008, the reach was clipped
246 from 2014 maps at these discharges.

247 **Preferred microhabitat-discharge relationship**

248 The total areas of preferred microhabitat were calculated for both years and
249 plotted at 19 discharges, chosen to span a wide range of rearing conditions
250 from 0.06 to 8.5x bankfull. Although more than 19 discharges were originally

251 modeled for the 2006/2008 and 2014 datasets, only 18 matched between them.
252 Those 18 matching discharges and one additional discharge representing the
253 maximum available habitat for either dataset were selected and compared in
254 this study. Percentage changes in overall minimum and maximum habitat
255 availability were computed, and changes in in-channel and overbank habitat
256 availability were compared between years. It should be noted that the same
257 depth, velocity, and cover HSC functions were used for all 19 discharges. This
258 assumes that Chinook salmon fry will change locations within the LYR to
259 maintain suitable depths and velocities as discharge changes, which has been
260 observed for other juvenile Pacific salmon species (Beecher, Carleton, &
261 Johnson, 1995; McMahon & Hartman, 1989; Shirvell, 1990; Shirvell, 1994).

262 **Lost, sustained, and gained preferred microhabitat**

263 This study introduces the scientific concept and methods for computing and
264 analyzing lost, sustained, and gained preferred microhabitat using geospatial
265 analysis of 2D habitat suitability model results. Polygons of 2006/2008 and 2014
266 preferred microhabitat were clipped and intersected to create areas of lost,
267 sustained, and gained microhabitat. Areas of preferred microhabitat available in
268 2006/2008 but not in 2014 were considered “lost,” while areas of preferred
269 microhabitat not available in 2006/2008 but available in 2014 were considered
270 “gained.” Areas of preferred microhabitat that overlapped between years were
271 considered “sustained” microhabitat.

272 The total area, size, and spatial distribution of spatially explicit patches of
273 preferred microhabitat that were lost, sustained, and gained between 2006/2008
274 and 2014 were evaluated at baseflow, bankfull, and floodplain-filling discharges,
275 as defined by Wyrick and Pasternack (2012). A representative baseflow

276 discharge above and below DPD was defined to be 24.92 and 15.01 m³/s,
277 respectively, with the difference accounting for irrigation withdrawals. Bankfull
278 and floodplain-filling (hereafter referred to as “flood”) discharges were defined to
279 be 141.6 and 597.5 m³/s, respectively.

280 These discharge-dependent areas of lost, sustained, and gained
281 preferred microhabitat were compared for the entire LYR in three ways. First,
282 the total area of lost, sustained, and gained preferred microhabitat was
283 compared for the entire LYR. Second, individual polygons of lost, sustained,
284 and gained microhabitat were grouped by size, and the total areas of each
285 polygon type were compared by group. Third, longitudinal profiles of the
286 cumulative areas of lost, sustained, and gained microhabitat were compared to
287 better understand their distribution throughout the river. This was done by
288 computing the areas of lost, sustained, and gained microhabitat within discrete
289 cross-sectional rectangles stationed every 6.1 m (20 ft) along the river valley’s
290 centerline (methods in Pasternack & Wyrick (2017)).

291 **Changes in physical habitat conditions associated with lost,**
292 **sustained, and gained microhabitat**

293 To determine whether changes in Chinook salmon fry rearing habitat availability
294 could be explained by changes in specific physical habitat conditions, more
295 detailed analyses of lost, sustained, and gained microhabitat were performed at
296 baseflow, bankfull, and flood discharges. Changes in channel alignment were
297 examined by computing percent differences in wetted area between 2006/2008
298 and 2014, the percentages of 2006/2008 microhabitat lost by becoming dry
299 land, and the percentages of 2014 microhabitat gained by dry land becoming
300 inundated.

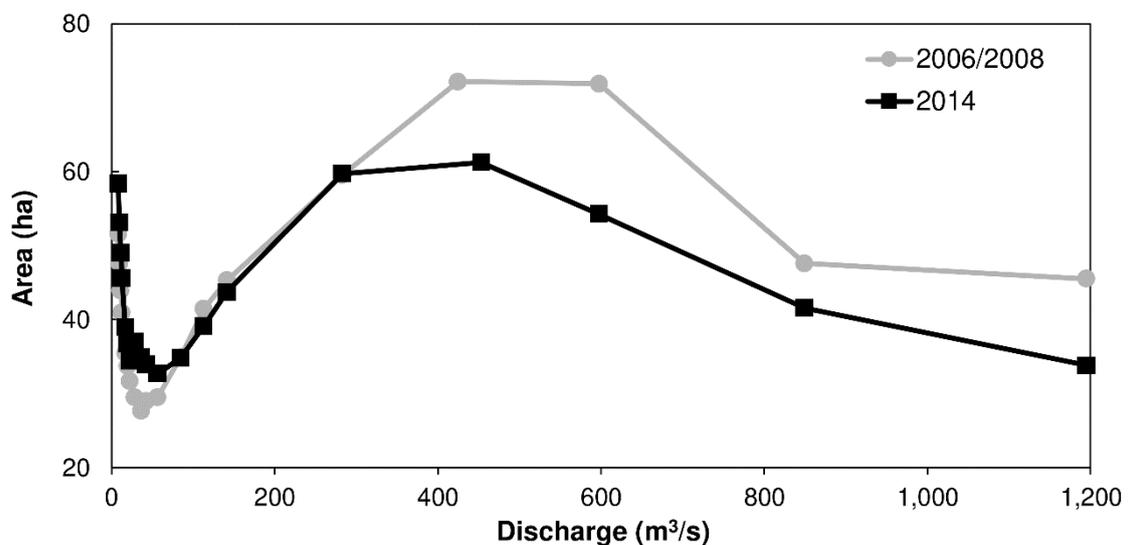
301 To determine whether changes in individual physical variables could
302 explain changes in habitat availability, numerical differences in depth, velocity,
303 and cover were computed between 2006/2008 and 2014 within areas of lost,
304 sustained, and gained microhabitat. Specifically, 2006/2008 depth and velocity
305 rasters were subtracted cell-by-cell from their respective 2014 rasters. Rasters
306 of these differences were then clipped by the lost, sustained, and gained
307 polygons associated with each discharge and grouped by every 0.2 m and m/s,
308 respectively. The total area of lost, sustained, and gained microhabitat within
309 each grouped difference was then computed. Given that permanent instream
310 cover features (e.g., bedrock outcrops, rip-rap, bridge piers, and weirs) could
311 not change between years, cell-by-cell differences in cover conditions could be
312 associated with either no change, a loss, or a gain in vegetative cover, which
313 could change over time. To better understand these changes, percentages of
314 areas where there was a loss, gain, or no change in vegetative cover were
315 computed for lost, sustained, and gained Chinook salmon fry rearing
316 microhabitat polygons.

317 **RESULTS**

318 **Preferred microhabitat-discharge relationship**

319 Preferred microhabitat-discharge relationships for Chinook salmon fry rearing
320 showed the same general pattern between years but had different minimum and
321 maximum areas of preferred microhabitat at different discharges (Figure 3).
322 Results reflect a noticeable increase in in-channel preferred microhabitat habitat
323 area and a decrease in overbank habitat area. From 2006/2008 to 2014, the
324 minimum area of preferred microhabitat increased by 18% (from 27.7 ha at 36.8

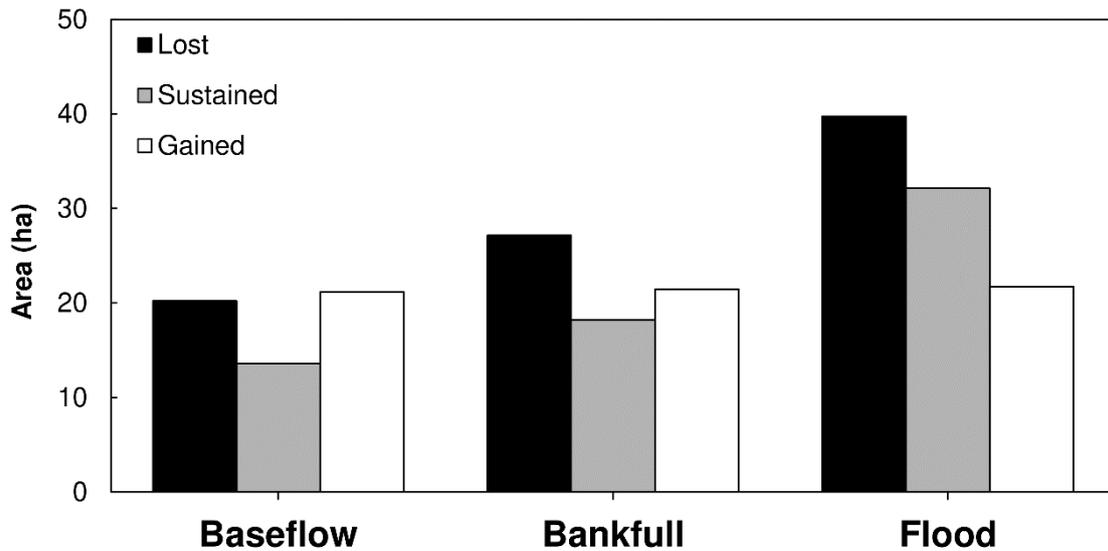
325 m³/s to 32.7 ha at 56.6 m³/s). Meanwhile, the maximum area of preferred
 326 microhabitat decreased by 15% (from 72.2 ha at 424.8 m³/s to 61.2 ha at 453.0
 327 m³/s). Areas of preferred microhabitat were slightly higher in 2014 at discharges
 328 below 56.3 m³/s and remained relatively similar at discharges between 56.3 and
 329 283.2 m³/s, or 2x bankfull. However, a significant divergence in preferred
 330 microhabitat occurred at discharges above 283.2 m³/s, with more habitat
 331 available in 2006/2008 than 2014.



332
 333 **FIGURE 3** Preferred Chinook salmon fry rearing microhabitat area as a function
 334 of discharge during 2006/2008 and 2014

335 **Lost, sustained, and gained preferred microhabitat**

336 There was 5% more Chinook salmon fry rearing preferred microhabitat gained
 337 from 2006/2008 to 2014 than lost at baseflow discharge (Figure 4). However,
 338 during the same time period, the total area of lost habitat was 27% and 83%
 339 higher than the area of gained habitat at bankfull and flood discharges,
 340 respectively. The total area of lost and sustained microhabitat increased with
 341 discharge, while the total area of gained microhabitat remained relatively
 342 consistent.

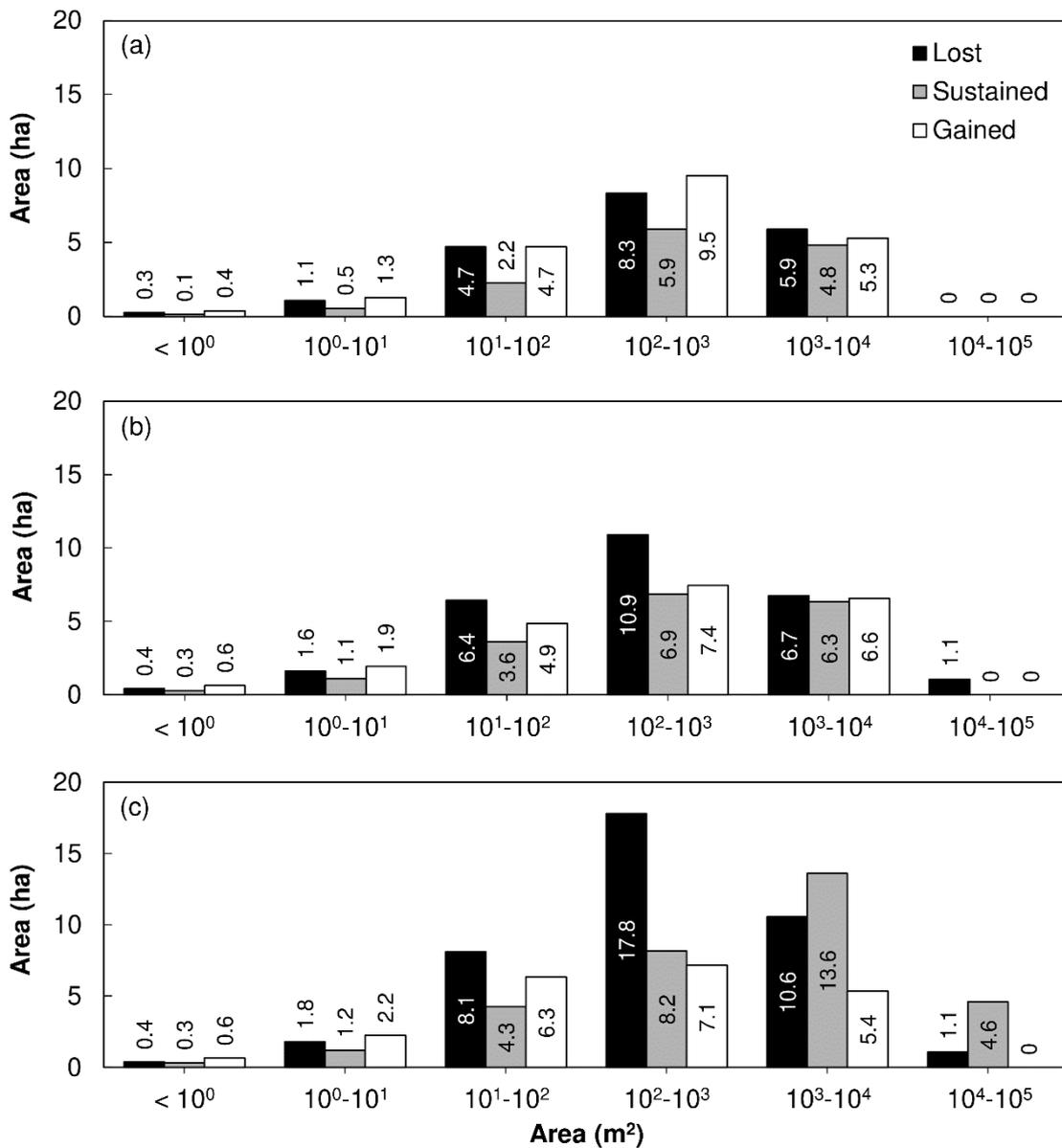


343

344 **FIGURE 4** Changes in preferred Chinook salmon fry rearing microhabitat at the
 345 segment scale between 2006/2008 and 2014

346 Total areas of lost, sustained, and gained preferred microhabitat were
 347 primarily made up of habitat patches between 10^1 – 10^2 , 10^2 – 10^3 , and 10^3 – 10^4
 348 m^2 at all three discharges (Figure 5). At baseflow discharge, the total areas of
 349 lost and gained microhabitat patches between 10^1 – 10^2 and 10^3 – 10^4 m^2 were
 350 relatively similar. However, the total area of gained microhabitat patches
 351 between 10^2 and 10^3 m^2 was 14% higher than the total area of lost patches. At
 352 bankfull discharge, the total areas of lost microhabitat patches between 10^1 – 10^2
 353 and 10^2 – 10^3 m^2 were 29% and 47% higher than the total areas of gained
 354 patches, respectively, while the total area of lost and gained patches between
 355 10^3 and 10^4 m^2 were relatively similar. At flood discharge, the total areas of lost
 356 microhabitat patches between 10^1 – 10^2 , 10^2 – 10^3 , and 10^3 – 10^4 m^2 were 29%,
 357 151%, and 96% higher than the total areas of gained microhabitat patches,
 358 respectively. At baseflow and bankfull discharges, the total area of sustained
 359 microhabitat was highest for patches between 10^2 and 10^3 m^2 , but highest for
 360 patches between 10^3 and 10^4 m^2 at the flood discharge. The 4.6 ha of sustained

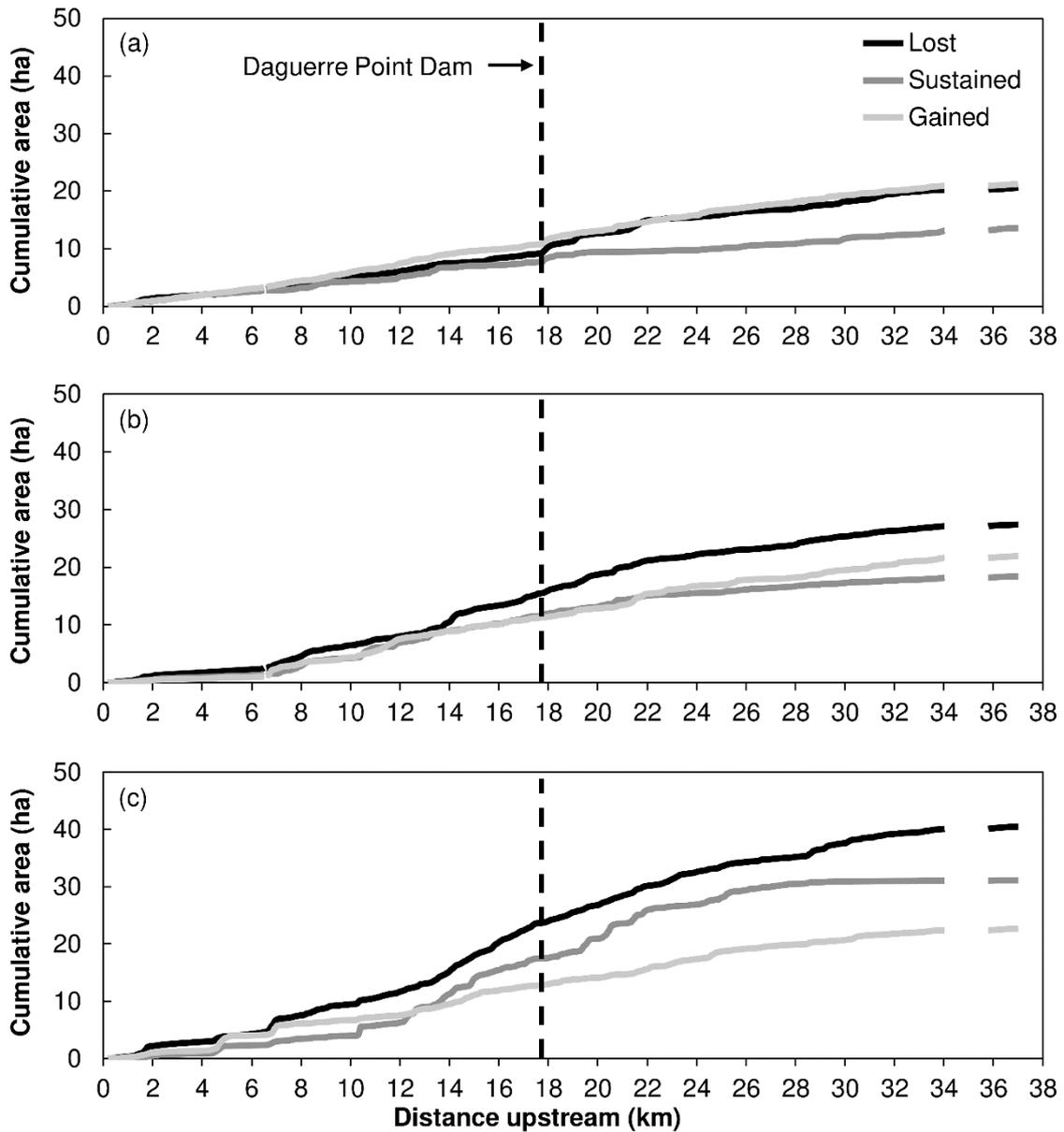
361 microhabitat patches between 10^4 and 10^5 m² were composed of only three
 362 patches at the flood discharge.



363
 364 **FIGURE 5** Size distributions of preferred Chinook salmon fry rearing
 365 microhabitat lost, sustained, and gained between 2006/2008 and 2014 at (a)
 366 baseflow, (b) bankfull, and (c) flood discharges

367 Longitudinal cumulative areas of lost, sustained, and gained microhabitat
 368 varied across the three discharges (Figure 6). At baseflow discharge, the
 369 cumulative area of lost, sustained, and gained microhabitat all steadily
 370 increased upstream until around river-km 14, where the cumulative area of

371 sustained microhabitat flattened out relative to lost and gained microhabitat. At
372 bankfull discharge, the cumulative area of lost, sustained, and gained
373 microhabitat remained relatively flat between river-km 0 and 7 and then
374 increased at approximately the same rate between river-km 7 and 14. Upstream
375 of this point, the cumulative area of lost microhabitat increased at a faster rate
376 than that of gained and sustained microhabitat, with the cumulative area of
377 gained microhabitat slightly outpacing sustained microhabitat upstream of river-
378 km 22. At the flood discharge, there were more distinct “steps” in cumulative
379 areas compare to the other two discharges. These steps in cumulative area
380 indicate more concentrated areas of lost, sustained, and gained microhabitat
381 throughout the river segment, and are most noticeable downstream of river-km
382 22. Sustained microhabitat steps at river-km 10, 12, and 19 were associated
383 with the three patches that were between 10^4 and 10^5 m². Besides the one step
384 at river-km 7, the cumulative area of lost microhabitat at the flood discharge
385 increased relatively smoothly longitudinally up the river, indicating a relatively
386 constant loss of preferred microhabitat throughout the river segment. The rate
387 of increasing cumulative area of lost microhabitat was highest between river-km
388 14 and 22 at bankfull and flood discharges.



389

390 **FIGURE 6** Longitudinal cumulative areas of preferred Chinook salmon fry
 391 rearing microhabitat lost, sustained, and gained between 2006/2008 and 2014
 392 at (a) baseflow, (b) bankfull, and (c) flood discharges. The river was not
 393 modeled between river-km 34 and 36 due to its complex topography and
 394 hydraulics

395 Overall, areas of lost and gained microhabitat remained relatively even
 396 across habitat patch sizes and throughout the river segment at baseflow
 397 discharge. However, higher total areas of lost microhabitat patches, particularly
 398 between 10^2 and 10^3 m², caused an overall reduction in preferred microhabitat

399 at the bankfull and flood discharges. Longitudinal cumulative areas indicate that
400 the areas of lost microhabitat were relatively continuous throughout the river;
401 however, the rate of increasing cumulative area of lost microhabitat appeared to
402 be highest between river-km 14 and 22 at bankfull and flood discharges.

403 **Changes in physical habitat conditions associated with lost,**
404 **sustained, and gained microhabitat**

405 Changes in channel alignment explained a significant but minor amount of the
406 percentage change in preferred microhabitat. There was a 5.1, 4.9, and 0.6%
407 decrease in wetted area between 2006/2008 and 2014 at baseflow, bankfull,
408 and flood discharges, respectively. The percentage of habitat lost between
409 2006/2008 and 2014 as a result of preferred microhabitat becoming dry was 43,
410 38, and 18% at baseflow, bankfull, and flood discharges, respectively. The
411 percentage of habitat gained from dry habitat becoming preferred microhabitat
412 was 37, 38, and 41%, respectively.

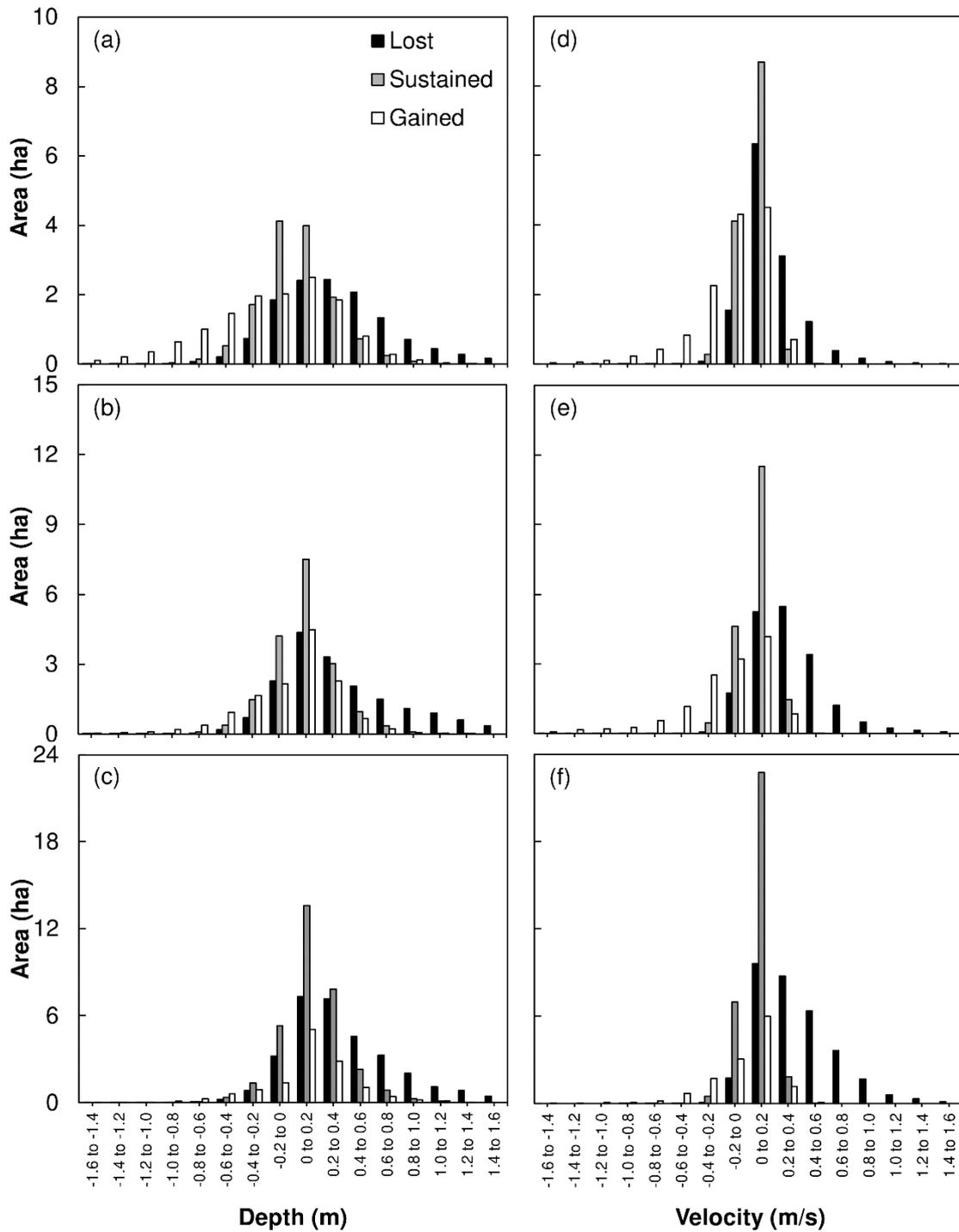
413 In comparison to the effect of wetting and drying, the majority of habitat
414 change is explained by systematic hydraulic changes. Specifically, areas where
415 preferred microhabitat was lost tended to increase in depth and velocity, while
416 areas where microhabitat was gained tended to decrease in depth and velocity
417 (Table 1). Shifts to deeper and/or faster water may have caused microhabitats
418 to become less suitable to Chinook salmon fry (as defined by the depth and
419 velocity HSC functions used in this study), while shifts to shallower and/or
420 slower water may have caused microhabitat to become more suitable. Areas
421 where preferred microhabitat was sustained remained relatively constant in
422 depth and velocity but did become slightly deeper and faster, on average.

423 **TABLE 1** Mean and standard deviation of differences in depth and velocity
 424 between 2006/2008 and 2014 in lost, sustained, and gained Chinook salmon fry
 425 rearing preferred microhabitat. Positive values indicate increases in values,
 426 while negative values indicate decreases

Habitat condition	Lost	Sustained	Gained
Depth (m)			
Baseflow	0.36 ± 0.48	0.02 ± 0.27	-0.18 ± 0.51
Bankfull	0.43 ± 0.55	0.08 ± 0.24	-0.02 ± 0.40
Flood	0.49 ± 0.65	0.14 ± 0.23	0.12 ± 0.33
Velocity (m/s)			
Baseflow	0.19 ± 0.22	0.02 ± 0.09	-0.12 ± 0.30
Bankfull	0.30 ± 0.28	0.04 ± 0.11	-0.18 ± 0.36
Flood	0.36 ± 0.30	0.04 ± 0.10	-0.04 ± 0.23

427

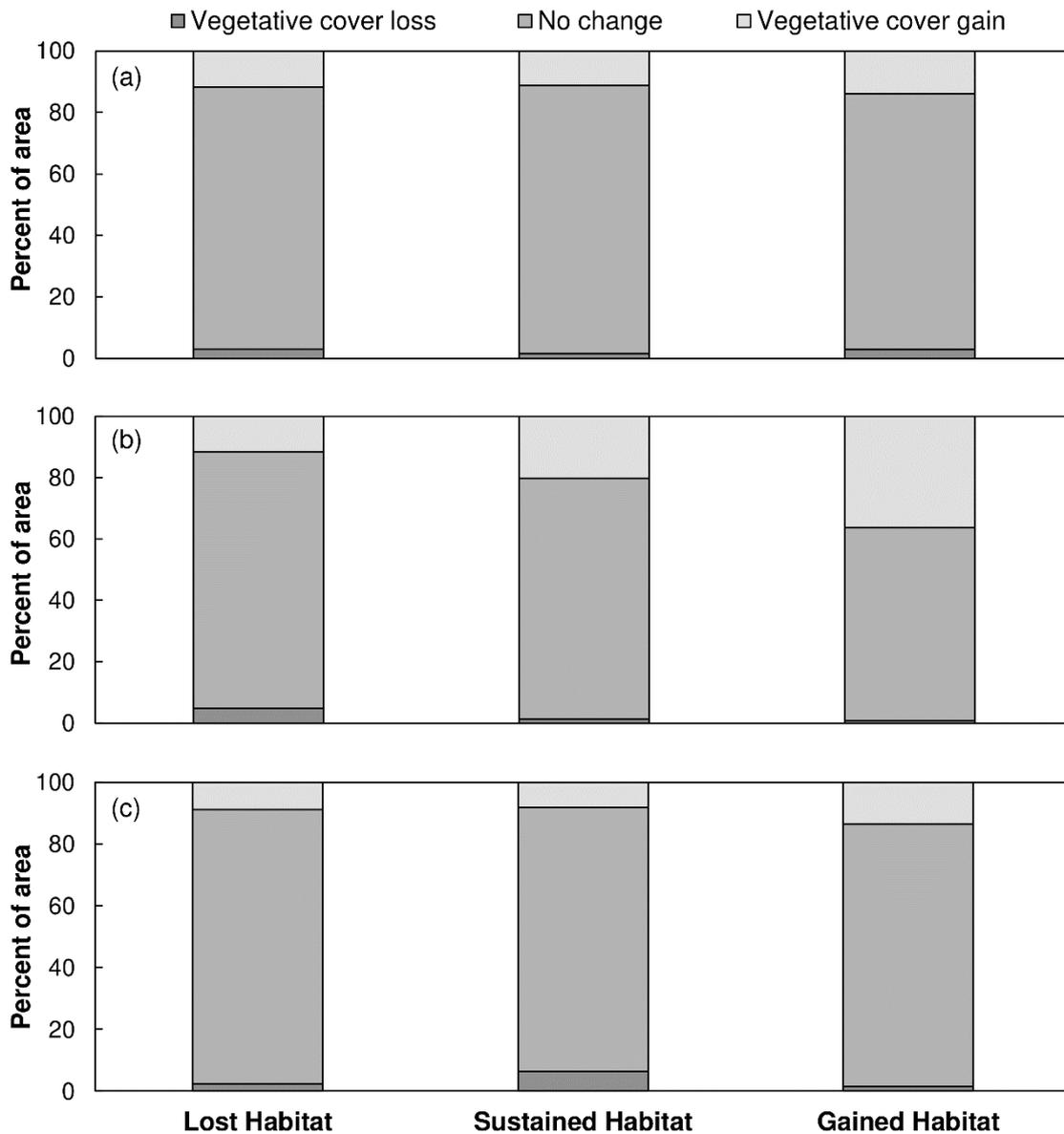
428 The distribution of area of changes in depth and velocity showed similar
 429 results to Table 1 (Figure 7). Changes in depth tended to skew toward positive
 430 values (i.e., get deeper) for lost preferred microhabitat, remained centered
 431 around 0 for sustained microhabitat (i.e., small change), and were mixed for
 432 gained microhabitat. Changes in velocity followed a similar pattern skewing
 433 toward positive values for lost microhabitat, centered around 0 for sustained
 434 microhabitat, and mixed for gained microhabitat.



435

436 **FIGURE 7** Areas associated with changes in depth between 2006/2008 and
 437 2014 at (a) baseflow, (b) bankfull, and (c) flood discharges and with changes in
 438 velocity at (d) baseflow, (e) bankfull, and (f) flood discharges. Positive values
 439 indicate increases in depth and velocity, while negative values indicate a
 440 decrease

441 Percentages of lost, sustained, and gained preferred microhabitat area
442 where there was a loss, gain, or no change in vegetative cover varied with
443 discharge (Figure 8). At baseflow and flood discharges, there were relatively
444 little differences in the percentages of area where vegetative cover was lost or
445 gained within lost, sustained, and gained preferred microhabitat areas.
446 Additionally, at those two discharges, at least 83% of the area within lost,
447 sustained, and gained microhabitat areas had no change in cover. At bankfull
448 discharge, however, the percentage of area where there was a gain in
449 vegetative cover was over 3x higher in gained microhabitat areas compared to
450 lost microhabitat areas. Furthermore, the percentage of area where there was a
451 loss in vegetative cover was over 5x less in gained microhabitat areas
452 compared to lost microhabitat areas. However, based on these results, changes
453 in vegetative cover appeared to play a less significant role in explaining
454 changes in habitat availability compared to changes in channel alignment and
455 hydraulic conditions, particularly at baseflow and flood discharges.



456

457 **FIGURE 8** Percentage of lost, sustained, and gained microhabitat area where
 458 there was a loss, gain, or no change in vegetative cover at (a) baseflow, (b)
 459 bankfull, and (c) flood discharges

460 **DISCUSSION**

461 **Calculating habitat availability**

462 One of the most widely used metrics for deriving habitat availability from habitat
 463 suitability models is the weighted usable area (WUA) index, made popular by
 464 the physical habitat simulation model (PHABSIM; Bovee, 1986; Waddle, 2001)

465 used in the Instream Flow Incremental Methodology (IFIM). This metric is
466 calculated as the product of habitat area (i.e., cell size) and habitat suitability
467 summed across a study domain (Bovee, 1986). Some studies have also
468 nondimensionalized this index by dividing it by the area of the study domain
469 (Benjankar et al., 2018; Mouton et al., 2007; Yao, Bui, & Rutschmann, 2018).
470 Despite its widespread use, the WUA index has been highly criticized for
471 lacking statistical certainty (Williams, 1996), interpretability (Mather, Bason,
472 Purdy, & Silver, 1985), and biological meaning (Railsback, 2016). Unlike those
473 indices, however, bioverified models such as the one used in this study provide
474 biologically meaningful and spatially explicit interpretable areas of preferred
475 microhabitat with known statistical certainty (Moniz et al., 2020). Furthermore,
476 as demonstrated in this study, these areas of preferred microhabitat can be
477 spatially compared over time to determine exactly where and how much habitat
478 is lost, sustained and/or gained, and then compare those changes to changes
479 in physical habitat conditions.

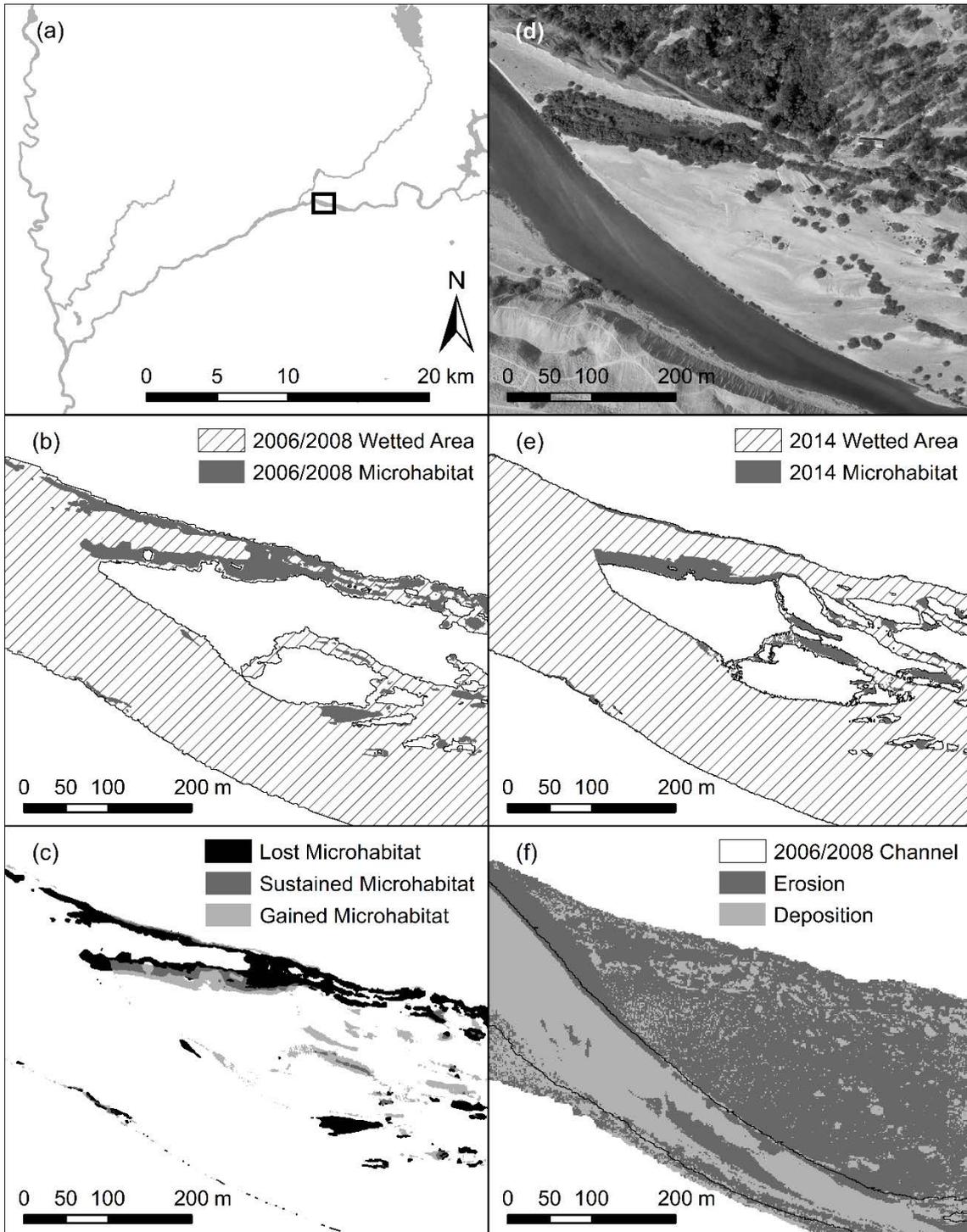
480 **Comparing habitat change with geomorphic change**

481 The period between 2006/2008 and 2014 was relatively dry in California, with
482 the LYR only experiencing four modest ~3–5 year flood events of short
483 duration, albeit with a brief peak discharge up to 9x bankfull. During this time
484 period, the total area of in-channel Chinook salmon fry rearing habitat
485 availability increased slightly, while overbank habitat decreased substantially. At
486 the flood discharge specifically, there was a 25% decrease in preferred
487 microhabitat area. Based on the results of this study, decreases in overbank
488 habitat availability, particularly at the flood discharge, appeared to be
489 associated with increases in depth and velocity (which resulted in diminished

490 habitat suitability), primarily in patches between 10^2 and 10^3 m², and slightly
491 more concentrated between river-km 14 and 22.

492 These results are consistent with findings from Weber and Pasternack
493 (2017), who conducted topographic change detection analysis on the LYR
494 spanning the same time period by calculating vertical differences in the
495 2006/2008 and 2014 DEMs. They found that erosion primarily occurred on
496 floodplains, terraces, and lateral bars between river-km 14 and 22, while
497 deposition occurred within the baseflow channel throughout the river segment.
498 In other words, the channel and floodplain became better connected.

499 Widespread erosion on the floodplain causing deeper and/or faster microhabitat
500 conditions within the 2014 flood discharge wetted area may explain the overall
501 reduction in habitat availability for Chinook salmon fry rearing observed in this
502 study (Figure 9). However, at discharges <2x bankfull, Chinook salmon fry
503 rearing habitat availability remained relatively consistent over this time period,
504 despite significant bank erosion and lateral channel migration (Weber &
505 Pasternack, 2017). These results suggest that despite being
506 hydrogeomorphically dynamic, the LYR can self-sustain Chinook salmon fry
507 rearing habitat during more frequently occurring, within-bankfull channel
508 discharges. Additional research is needed to determine if these results are
509 consistent during more significant flood events on the LYR. Although these
510 specific results may not apply to all hydrologic periods on the LYR or for all
511 rivers, the finding that habitat-discharge relationships can change relatively
512 quickly as a result of morphodynamic processes likely does transfer globally
513 and should be considered when analyzing habitat availability over decades.



514

515 **FIGURE 9** Example maps showing changes in preferred Chinook salmon fry
 516 rearing microhabitat and topography near river-km 22. (d) Aerial imagery was
 517 collected in 2008 and is shown for reference. (b, c, e) Wetted areas and
 518 microhabitat are shown at the flood discharge. (f) Raw topographic change
 519 results are shown with permission from Weber and Pasternack (2017)

520 Other studies have also attempted to relate changes in salmonid habitat
521 suitability with geomorphic changes in rivers using repeat topographic surveys
522 and habitat suitability models. Wheaton et al. (2010) found that Chinook salmon
523 spawning habitat suitability remained relatively stable after gravel augmentation
524 in locations where there were small elevation changes after a major flood event.
525 Furthermore, they found that areas where habitat suitability degraded were
526 dominated by larger magnitude erosion, whereas areas of habitat suitability
527 improvement were dominated by shallow, low magnitude deposition. Harrison et
528 al. (2011) qualitatively related changes in Chinook salmon spawning and
529 rearing habitat availability with geomorphic changes in a restructured gravel-
530 cobble river. They found that Chinook salmon spawning habitat availability
531 increased over time, which they attributed to decreasing velocities over riffles.
532 They also found that rearing habitat availability remained relatively low
533 throughout the study period, which they attributed to high velocities in pools
534 caused by flow constrictions by growing bars. Harrison et al. (2017) observed
535 widespread deposition within the floodplain and erosion within the low-flow
536 channel of a semiarid gravel-bed river after a 10-year flood event. Channel
537 erosion roughly doubled the areal extent of pool mesohabitat, which they
538 predicted would have a positive impact on steelhead trout (*O. mykiss*) habitat.
539 Tamminga and Eaton (2018) observed a decline in the low-flow habitat
540 suitability of adult and juvenile brown trout (*Salmo trutta*) after a 100-year flood
541 event in a gravel-bed river in the Canadian Rocky Mountains. They attributed
542 this reduction in habitat suitability to shallower flow conditions caused by bank
543 erosion and in-channel deposition. Results from these studies and the study

544 presented herein highlight the value of repeat surveys in the assessment of
545 river ecosystem dynamics.

546 **Metrics for evaluating aquatic habitat stability**

547 As repeat topographic surveys and habitat modeling become more cost-efficient
548 with increased availability of remote sensing data (Dimitriou & Stavroulaki,
549 2018; Tamminga & Eaton, 2018), the opportunity for resource managers to
550 support these kinds of repeat studies will become more practical. Repeat
551 studies can help resource managers better understand the dynamics and
552 stability of rivers and their habitats at multiple spatial scales with varying
553 hydrologic conditions, which can lead to more cost-effective long-term decision-
554 making. Having a better understanding of aquatic habitat stability will become
555 increasingly important as rivers continue to adjust to anthropogenic
556 disturbances (Brown & Pasternack, 2017; Gregory, 2006; James, 1991;
557 Leopold, 1973), potentially exacerbated by climate change (Hauer et al., 2013;
558 Meybeck, 2003; Palmer et al., 2009; Praskievicz, 2015).

559 Yet, what constitutes the appropriate method and suite of metrics for
560 evaluating aquatic habitat stability? This study attempts to answer that question
561 with two different conceptual approaches. The first approach involves
562 comparing a typical suite of bulk statistics (including minimums and maximums
563 in the habitat-discharge relationship) for more than one time period, similar to
564 what has been done in other studies addressing changes in habitat availability
565 before and after restoration projects, dam removals, and extreme flood events.
566 The second approach involves a new method in which lost, sustained, and
567 gained microhabitat areas are spatially delineated and used to assess changes
568 in specific physical habitat conditions. This new approach allows resource

569 managers to better understand the locations and potential drivers of habitat
570 change over time. In this case, it was possible to ascertain the size and spatial
571 distribution of changes in Chinook salmon fry rearing habitat availability in the
572 LYR, as well as the relative roles of channel alignment, hydraulic conditions,
573 and vegetative cover in explaining these changes.

574 Although not examined in this study, spatially explicit areas of preferred
575 microhabitat can also be evaluated for multiple species and/or multiple life
576 stages of a single species of special concern. For example, this kind of analysis
577 could be used by resource managers to help evaluate which discharges or
578 restoration design alternatives reduce competition and/or predation of native
579 species by nonnative species by minimizing areas of preferred microhabitat
580 overlap. Furthermore, by overlapping preferred microhabitat for multiple life
581 stages of a single species (e.g., salmonid spawning, embryo development, and
582 rearing), managers could evaluate which discharge or design alternative
583 maximized life stage connectivity throughout the year.

584 **CONCLUSIONS**

585 This study used new and existing methods to evaluate the stability of Chinook
586 salmon fry rearing habitat availability in a regulated, yet dynamic, gravel-cobble
587 river during a relatively mild hydrologic period. Results suggest that despite
588 being hydrogeomorphically dynamic, the LYR can self-sustain Chinook salmon
589 fry rearing habitat during more frequently occurring, within-bankfull channel
590 discharges. At the floodplain-filling discharge, however, decreases in habitat
591 availability were more prevalent, and appeared to be associated with increases
592 in depth and velocity, particularly where widespread floodplain erosion had
593 been previously observed. This study demonstrates the value of using electivity

594 indices and repeat surveys to delineate areas of preferred habitat stability, and
595 highlights the importance of considering morphodynamics in aquatic habitat
596 analysis, even during relatively mild hydrologic periods. As aquatic ecosystems
597 continue to adjust to both natural and anthropogenic disturbances, this
598 consideration will become increasingly important in guiding long-term regulatory
599 and management decisions, such as instream flow requirements and habitat
600 restoration plans.

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610 Unlimited, and Diablo Valley Fly Fishing Club.

611 **CONFLICT OF INTEREST**

612 The authors declare that there is no conflict of interest that could be perceived
613 as prejudicing the impartiality of the research reported.

614 **DATA AVAILABILITY STATEMENT**

615 The data presented in tables and figures that support the findings of this study
616 are available from the senior author (<http://pasternack.ucdavis.edu>) upon

617 request with no restrictions. All 2006/2008 DEM, hydrodynamic models, and
618 microhabitat models/data are available publicly through the Federal Energy
619 Regulatory Commission. Restrictions apply to the availability of the 2014 DEM,
620 hydrodynamic models, and microhabitat models/data, as these were used
621 under contractual agreement from the project sponsor. These are available from
622 the senior author with the permission of Yuba Water Agency.

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850 **SUPPORTING INFORMATION**

851 Additional supporting information may be found in the online version of the
852 article at the publisher's website.

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