

1 **Effects of flow-related variables on oversummer survival of juvenile Coho Salmon in**
2 **intermittent streams**

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31 [A]Abstract

32 While many studies have established the importance of streamflow as a driver of fish
33 population dynamics, few have examined relationships between survival of juvenile salmonids
34 and flow-related variables in intermittent streams. With predictions for higher frequency of
35 drought conditions due to climate change, and the associated increasing human demand for
36 water during the dry season, understanding fish–flow relationships is becoming increasingly
37 important for the protection of sensitive aquatic species. To examine the effects of low
38 streamflow on juvenile salmonids rearing in small intermittent streams, we estimated survival
39 and collected environmental data in four coastal California watersheds from 2011 to 2013. We
40 used an individual-based mark-recapture modeling approach to evaluate the influence of flow-
41 related variables on oversummer survival of PIT-tagged juvenile Coho Salmon stocked into eight
42 stream reaches. Survival was positively associated with streamflow magnitude, wetted volume,
43 and dissolved oxygen, and negatively associated with days of disconnected surface flow (days
44 of disconnection), and temperature. Days of disconnection best explained survival, though the
45 relationship varied by geomorphic reach type. Survival was lower in alluvial reaches as
46 compared to bedrock and clay reaches, and showed a faster rate of decline with increasing days
47 of disconnection and drought condition. In all reaches, the onset of pool disconnection
48 represented a turning point at which water quality, water quantity, and survival declined. For

49 this reason, we suggest that days of disconnection (or the flow magnitude at which pools
50 become disconnected) is a useful metric for identifying flow-impaired reaches, informing
51 streamflow protection strategies, and prioritizing streamflow enhancement efforts designed to
52 benefit sensitive salmonid populations in intermittent streams.

53 [A]Introduction

54 Streamflow is a well-known driver of fish population dynamics, and changes in flow
55 regime have severely impacted freshwater ecosystems over the last century (Power et al. 1995;
56 Bunn and Arthington 2002; Meybeck 2003; Poff et al. 2007; Moyle et al. 2008). Numerous
57 studies have documented relationships between streamflow and fish habitat metrics,
58 particularly in regulated systems (Poff and Zimmerman 2010; Konrad et al. 2011), yet only in
59 recent years have studies begun to quantify the impacts of low streamflow directly on fish
60 population metrics in unregulated intermittent streams (May and Lee 2004; Hodges and
61 Magoulick 2011; Grantham et al. 2012; Hwan and Carlson 2016; Woelfle-Erskine et al. 2017).

62 Intermittency occurs in over half of the streams in the United States (Nadeau and Rains
63 2007), reducing the quantity of habitat available to aquatic biota and potentially compromising
64 water quality conditions in remaining habitat. For fish, stream contraction can reduce food
65 availability, restrict movement, increase population density, cause physiological stress due to
66 compromised water quality conditions, and/or cause acute mortality due to stranding (Labbe
67 and Fausch 2000; Magoulick and Kobza 2003; Hakala and Hartman 2004; May and Lee 2004;
68 Harvey et al. 2006; Stradmeyer et al. 2008; Irvine et al. 2009; Hwan and Carlson 2016). Despite
69 these risks, fish are found occupying residual pools of intermittent streams (Bogan et al. 2015)
70 and some studies have found that, while there are high mortality risks during the summer dry
71 season, intermittent streams can offer preferred habitat for juvenile rearing (Wigington et al.
72 2006) and/or adult spawning (Erman and Hawthorne 1976; Boughton et al. 2009) during the fall
73 and winter wet seasons. Presumably, if fish can survive the high mortality risks of the summer
74 season in intermittent streams, they may gain an advantage of higher survival and growth
75 during the winter season. Understanding such tradeoffs is important in the context of
76 protection and recovery of sensitive species dependent upon these systems.

77 For threatened steelhead *Oncorhynchus mykiss* and endangered Coho Salmon
78 *Oncorhynchus kisutch* populations at the southern extent of the species' range in coastal
79 California, low streamflow has been identified as a limiting factor to survival (Grantham et al.
80 2012; NMFS 2012). In tributaries of the Russian River, California, Grantham et al. (2012) found a
81 positive relationship between streamflow and apparent survival of juvenile steelhead, and
82 Woelfle-Erskine et al. (2017) found that flow-related variables (pool size and conductivity) were
83 strongly associated with survival of juvenile steelhead and Coho Salmon rearing in tributaries of
84 Salmon Creek, California. In Woelfle-Erskine et al. (2017), survival of both species was positively
85 associated with pool size (depth for Coho Salmon and surface area for steelhead) and
86 negatively associated with conductivity, which they considered a proxy for dissolved oxygen
87 (DO) levels. These studies take critical steps towards expanding our limited understanding of
88 the complex relationships between streamflow, habitat, and salmonid population responses,
89 but additional work is needed to identify flow-related variables important for the persistence of
90 fish populations and to inform the development of flow management strategies that support
91 salmonid population recovery.

92 In the Mediterranean climate of the central California coast, low streamflow typically
93 occurs during the summer dry season at a time when human water demand is high, and surface
94 water diversions and groundwater withdrawals from shallow streamside wells can exacerbate
95 seasonal reductions in discharge (Deitch et al. 2009a; Deitch et al. 2009b; Grantham et al.
96 2010). Grantham et al. (2012) found that as vineyard cover increased in four California
97 watersheds between 1994 and 2002, there was an associated decrease in apparent
98 oversummer survival of stream-rearing juvenile steelhead, presumably due to increased water
99 extraction. Human water demand is expected to increase with increasing population growth
100 and exurban expansion (Konieczki and Heilman 2004; Laraus 2004; Thompson 2007; Grantham
101 et al. 2010), and climate change is expected to further jeopardize summer streamflows in
102 Mediterranean systems as a result of increased temperatures, reduced precipitation, and
103 changes in rainfall timing (Mannion 1995; Moyle et al. 2008; Karl et al. 2009; MacDonald 2010).
104 Quantifying the relationship between juvenile salmonid survival and streamflow will help us

105 evaluate the impacts of water withdrawals on fish populations and prepare for the anticipated
106 changes resulting from human population growth and climate change.

107 Addressing widespread streamflow impairment is critical for recovery of stream
108 ecosystems and sensitive species such as threatened and endangered salmonid populations
109 along the West Coast. Over the last few decades, resource managers, non-profit organizations,
110 and private landowners have invested tremendous resources in enhancing habitat for
111 endangered salmonid populations in coastal salmonid streams (NRC 2004; Nielsen-Pincus and
112 Moseley 2010; Roni et al. 2010), yet efforts to improve streamflow have only begun in recent
113 years (Deitch and Dolman 2017). Competing demands for water, as well as the challenges
114 associated with quantifying the effects of low streamflow on fish populations, have thwarted
115 progress in addressing instream flow as a bottleneck to the recovery of imperiled salmonid
116 populations. While many strategies have been developed to identify relevant thresholds that
117 protect streamflow for fish (Reiser et al. 1989; Richter et al. 1997; King et al. 2003; Poff et al.
118 2010), they are typically aimed at regulated, snow-melt driven systems with continuous flows
119 throughout the summer season. Such strategies do not readily apply to the small coastal
120 streams inhabited by juvenile Coho Salmon, where late summer streamflows are so low that
121 collecting accurate measurements presents a challenge. Further, most models for predicting
122 instream flow requirements are based on discharge–habitat relationships and do not directly
123 consider fish population responses (Stalnaker 1979; McKinney and Taylor 1988; Bovee et al.
124 1998; Annear et al. 2009; Beecher et al. 2016). This poses a problem for intermittent streams,
125 where streamflow magnitude can fall to zero while residual pools still support rearing fish
126 through hyporheic flow or groundwater inputs. In these cases, surface flow magnitude may not
127 accurately reflect habitat suitability for fish, and other variables such as pool size, water quality
128 parameters, and thermal regimes become more relevant.

129 To aid in the identification of flow-impaired stream reaches, set management targets,
130 and prioritize and evaluate streamflow improvement projects, creative approaches are needed
131 to link flow-related variables (i.e., streamflow, water quantity, water quality) to fish population
132 responses in intermittent, salmonid-bearing streams. Between 2011 and 2013, we evaluated
133 oversummer survival of juvenile Coho Salmon in relation to flow-related variables in four

134 tributaries of the Russian River watershed in coastal California. For survival estimation, we used
135 an individual-based mark-recapture approach with a common population of hatchery Coho
136 Salmon stocked in equal densities into eight stream reaches representing three geomorphic
137 reach types. Environmental data were collected in these stream reaches over the same time
138 period and survival was related to specific flow-related variables, including flow magnitude,
139 days of surface flow disconnection, wetted volume, water temperature, and DO.

140 The following questions were addressed at the reach scale:

- 141 1. Does oversummer survival of juvenile Coho Salmon vary by stream, reach, and/or year?
- 142 2. Which flow-related variables most influence survival of juvenile Coho Salmon?
- 143 3. Do relationships between survival and flow-related variables differ among geomorphic
144 reach types?

145

146 [A]Methods

147 [B]Study area

148 Between 2011 and 2013, we sampled reaches of Dutch Bill, Green Valley, Mill, and
149 Grape creeks, tributaries of the lower Russian River located along the central coast of California
150 in Sonoma County (Figure 1). Watershed size of the four streams ranges from 8–58 km², and
151 elevations range from 4–39 m above sea level at the stream confluences to 76–214 m at the
152 upper extent of anadromy. Upland areas within the watersheds are generally characterized by
153 Californian Moist Coastal Mixed Evergreen Forest, Californian Coastal Redwood Forest,
154 Californian Broadleaf Forest and Woodland, Californian Coastal-Foothill Seral Scrub, and
155 Californian Annual and Perennial Grassland (USNVC 2016). Vegetation within the riparian
156 corridors consists of coast redwood, Douglas fir, California Bay Laurel, bigleaf maple, white
157 alder, and *Salix* spp., with understories of native and non-native shrubs and grasses. Santa Rosa
158 (population 175,155; (USCB 2016)) is the major population center in the Russian River
159 watershed, and vineyards and rural residential homes occupy much of the landscape in the
160 lower basin. There are no major dams regulating flows on these streams; however, streamflow

161 in Russian River tributaries is frequently influenced by water withdrawals from small-scale
162 direct diversions and streamside wells (Deitch et al. 2009a).

163 The study area is characterized by a Mediterranean climate in which nearly all
164 precipitation occurs in the form of rainfall between November and April, resulting in peak
165 streamflows during the winter season that slowly recede through the spring and summer and
166 commonly reach an intermittent state during the dry season. Air temperatures drop to an
167 average low of 2.5°C in winter and reach an average high of 28.5°C during summer (NOAA
168 2017).

169 Over the study period (2011 to 2013) drought conditions in the Russian River watershed
170 progressed from no drought in 2011, to abnormally dry in 2012, to severe drought in 2013
171 (NDMC 2017), and annual streamflow in the Russian River also decreased progressively over
172 that period (USGS 2017). In all four study streams, we observed a general decline in streamflow
173 conditions between June 15 and September 30 over the years studied, with total discharge
174 decreasing each year from 2011 to 2013 (Figure 2).

175

176 [B]Study reaches

177 Within each of the four study streams, two reaches were selected (Figure 1) based on
178 Coho Salmon habitat suitability and accessibility to streams across privately-owned land. Target
179 reach length was 250 m; however, because reach boundaries were placed at habitat unit breaks
180 which did not always fall at 250 m, this varied somewhat (range 210–310 m; Table 1).
181 Catchment area among reaches ranged from 7.4–43.0 km², and slope ranged from 0.3–1.9%.
182 Due to the potential influence of geomorphic setting on oversummer survival (May and Lee
183 2004), we assigned each reach to one of three geomorphic categories based on visual
184 observations: alluvial (all pools characterized by loose alluvial material), bedrock (bedrock
185 visible beneath gravel/cobble substrate in the majority of pools), or clay (clay visible beneath
186 gravel/cobble substrate in the majority of pools).

187 For each reach, we classified channel types based on geomorphological characteristics,
188 including entrenchment, gradient, width–depth ratio, sinuosity, and bed substrate (Rosgen
189 1994). We also conducted an initial survey each year in June to classify habitat units as pool,
190 riffle, or flatwater habitat types (Flosi et al. 2004). As a measure of relative habitat suitability for
191 rearing juvenile Coho Salmon, we assigned a shelter value to all pool and flatwater units based
192 on the composition and quality of available shelter (0–3, with 3 being the highest complexity),
193 and multiplied this value by the estimated percentage of instream cover in the unit to calculate
194 an instream shelter rating (Flosi et al. 2004). We also assessed over-channel canopy cover on all
195 habitat units greater than six meters in length using a handheld, spherical densitometer.

196 In general, reaches were similar in both channel type and habitat quality (Table 1). All
197 but one reach was characterized as an F channel type (relatively entrenched, meandering, low
198 gradient, riffle–pool channels with high width–depth ratios, generally subject to high erosion
199 rates), and dominated by small cobble (F3) or gravel (F4) substrates. One reach on Green Valley
200 Creek (GRE-13.40) was classified as B4; a moderately entrenched, moderate gradient, riffle-
201 dominated channel with infrequently spaced pools, very stable banks and channel profiles, and
202 gravel substrate. Average canopy cover \pm SD was high in all reaches, ranging from $81.3 \pm 2.4\%$
203 to $98.1 \pm 0.9\%$, and instream cover was available in all reaches, with shelter rating \pm SD ranging
204 from 10.2 ± 2.0 to 34.3 ± 17.3 . The total number of pool and flatwater units varied among years
205 and ranged from 7–8 in MIL-6.10 to 12–16 in GRP-1.14. Over the three study years, average
206 discharge between June and October in the study reaches ranged from 0–44 L/s (0–1.6 ft³/s).
207 Common fish species occurring within the study reaches include Coho Salmon, steelhead,
208 Sculpin *Cottus* spp., and California Roach *Lavinia symmetricus*.

209

210 [B]Study Population

211 The Russian River watershed falls within the Central California Coast Evolutionarily
212 Significant Unit for federally-endangered Coho Salmon and is near the southern extent of the
213 species' range. In the early 2000s, fewer than 10 adult Coho Salmon were known to return to
214 the Russian River watershed each year. In response to this decline, a multiagency partnership

215 initiated a conservation hatchery program in which juvenile Coho Salmon were captured each
216 year from Russian River tributaries, raised to the adult stage, and spawned at Don Clausen Fish
217 Hatchery at Warm Springs Dam. Broodstock were genotyped and spawned according to a
218 matrix that maximizes genetic diversity of offspring. Beginning in 2004, progeny of these
219 broodstock were released annually into Russian River tributaries. Releases of juvenile Coho
220 Salmon during the spring season provided an opportunity to compare oversummer survival in
221 relation to flow-related variables among specific stream reaches using a common population of
222 experimental fish similar in size and genetic composition.

223 In late May or early June each year, hatchery-raised age-0 Coho Salmon were measured
224 for fork length and weight, and fish ≥ 56 mm and ≥ 2 g were tagged with 12.5 mm full-duplex
225 passive integrative transponder (PIT) tags using the methods of Gries and Letcher (2002).
226 Following tagging, the fish were held in tanks for two weeks before approximately 500 fish
227 were released into each study reach in mid-June. Average fork length \pm SD and average weight
228 \pm SD at the time of tagging were 68.7 ± 5.8 mm and 3.9 ± 1.2 g, 66.4 ± 6.5 mm and 3.6 ± 1.4 g,
229 and 66.1 ± 6.4 mm and 3.5 ± 1.1 g in years 2011, 2012, and 2013, respectively. During each
230 stocking event, the fish were transported in aerated backpack containers from the hatchery
231 truck to the target stream reaches and stocked into individual pools and flatwater units. The
232 stocking density (approximately two fish per meter) was consistent with stocking densities
233 applied by the conservation hatchery program in tributaries to the Russian River. Prior to
234 stocking fish, an initial snorkeling survey was conducted in each reach to determine the
235 presence of wild juvenile Coho Salmon. If wild fish were present in a reach, the number of
236 hatchery fish released was reduced for that reach to maintain a similar density of two fish per
237 meter. Wild fish were not included in the survival estimates.

238

239 [B] Juvenile Coho Salmon surveys

240 In order to estimate survival of experimental fish between June and October, we
241 completed a series of surveys on each reach using a portable PIT-tag detection system, or
242 “wand” (O'Donnell et al. 2010). We used the robust design mark-recapture model in which

243 secondary sampling occasions are conducted within primary sampling occasions (Kendall et al.
244 1997). This approach allowed for estimation of abundance on each primary sampling occasion
245 and estimation of survival between primary occasions.

246 Primary sampling occasions occurred approximately monthly between June and late-
247 September or early-October. The number of primary occasions varied from three to six per
248 year, depending on reach and year. Each primary occasion was comprised of a pair of wand
249 surveys (secondary sampling occasions) conducted in each reach over two consecutive days
250 (one wand survey/day). Each pair of wand surveys was conducted close in time in order to
251 satisfy the assumption of the robust design model that there is no mortality between the
252 secondary sampling occasions comprising a given primary sampling occasion. On each wand
253 survey, we waded every pool and flatwater habitat unit in each reach from downstream to
254 upstream, moving the wand through the water column in an attempt to detect PIT-tagged fish.
255 Detected tags were recorded on a PIT transceiver attached to the wand.

256 We placed stationary PIT antennas at the downstream end of each stocked reach for the
257 duration of the study in order to account for downstream emigration from the study reaches.
258 When resources allowed, we also operated antennas at the upstream boundaries of stocked
259 stream reaches (6 of 17 reach/year combinations). To account for upstream movement out of
260 the reaches at times when an upstream antenna was not operated, we conducted additional
261 wand surveys upstream of the reach to a point where PIT tags were no longer detected.

262 In previous stocking events in these tributaries, we often observed fish exhibiting a
263 “flight” response in which up to half of the fish moved either upstream or downstream of the
264 stocking reach during the first few days following the release. To prevent this from occurring in
265 our study reaches, we placed block nets at the boundaries of each reach to prevent the fish
266 from immediately leaving. The nets were kept in place and tended daily for 15–17 days, after
267 which we considered any fish movements to be for reasons other than an initial flight response.

268 Because mortality of fish and PIT tag loss can result in tags that become lodged in the
269 streambed (“ghost tags”), on each sampling occasion we identified PIT tag codes of individuals
270 thought to have perished (or shed a tag) since the previous sampling occasion. We recorded a
271 tag as a ghost tag when it remained stationary despite vigorous disturbance with the wand

272 immediately above an open streambed surface. Because we had no way of determining
273 whether or not the fish had died or shed its tag, we assumed that all ghost tags were
274 mortalities. Although misclassification of shed tags as mortalities could lead to survival
275 estimates that are biased low, for two reasons we are confident that tag loss was negligible.
276 First, we employed the PIT-tagging methods of Gries and Letcher (2002) who observed high tag
277 retention rates (99.8%) in juvenile Atlantic salmon tagged and subsequently held in a hatchery
278 for approximately 9 months. Second, tag retention data based on a secondary mark (collected
279 in our study reaches at the end of each season during subsequent electrofishing surveys)
280 indicated that PIT tag retention rates were 99.4%.

281

282 [B]Environmental data collection

283 Between June and October of years 2011 through 2013, we collected streamflow, water
284 temperature, DO, and wetted volume data in each reach. Streamflow and temperature data
285 were collected at the reach level. DO and wetted volume data were collected at the habitat unit
286 level (DO for pools and wetted volume for pool and flatwater units) and averaged for all units
287 within the reach for reach-scale analyses.

288 For streamflow data collection, we deployed and operated Azonde 2220 or In-Situ Level
289 TROLL 500 pressure transducers in or near (within 300 m of) each reach. Each gauge recorded
290 water stage every fifteen minutes for the duration of the study period. Streamflow was
291 measured approximately one time each month in every reach using a USGS Price Pygmy
292 Current Meter. Measured streamflow values were correlated with stage data at the time of
293 measurement to create rating curves according to standard USGS protocols (Rantz et al. 1982),
294 and the equations of these curves were used to estimate streamflow (L/s) at fifteen-minute
295 intervals for all stage data.

296 To document stream temperature, we deployed Onset HOBO U22 Water Temp Pro v2
297 continuously-recording temperature loggers in a representative pool within each of the study
298 reaches between June 15 and October 15 each year. Temperature loggers were calibrated using
299 a NIST thermometer prior to deployment and recorded water temperature at 60-min intervals.

300 DO surveys were conducted on the same dates as PIT-tag wand surveys in each study
301 reach using a YSI handheld DO meter with a polarographic sensor (YSI 55D or YSI Pro20,
302 depending on year). We measured DO concentrations between 0850 and 1130 hours at a
303 consistent depth (approximately 25 cm below the water surface) at the location of the
304 maximum depth in each pool. DO sensors were calibrated prior to each survey and membranes
305 were inspected and changed, as needed, following guidelines in the manufacturer's operations
306 manuals.

307 Data for estimating wetted volume in each pool and flatwater unit were collected during
308 habitat surveys conducted within one to two days of PIT-tag wand surveys. Following habitat-
309 type classification of individual units (pool, flatwater, or riffle) during initial habitat surveys in
310 June of each year, we established transects within each unit at two to six points (depending on
311 unit size and configuration) that served as fixed locations for measuring wetted width and
312 depth. Wetted length, average wetted width, and average depth were multiplied to calculate
313 the wetted volume of each pool and flatwater unit.

314 Observations of surface flow disconnection during habitat surveys were related to
315 discharge data to estimate a flow level at which pools become disconnected (connectivity
316 threshold). Although connectivity thresholds appeared to vary by stream, we found that in
317 almost all reaches, pools were disconnected when discharge dropped to 0.28 L/s (0.01 ft³/s).
318 This threshold was used to estimate the number of days that pools were disconnected in each
319 reach.

320

321 [B] Data Analysis

322 [C] *Survival estimation approach.*—PIT tag detections recorded during each paired wand survey
323 were used to construct an encounter history for each individual detected during the June
324 survey. We used the robust design mark-recapture model (Kendall et al. 1997) in Program
325 MARK (White and Burnham 1999) to estimate survival at the reach scale. Program MARK uses
326 general linear modeling to estimate beta parameters, and these beta parameter estimates are
327 combined using a sub-model (e.g., sin link, logit link) to estimate real parameters of interest
328 (i.e., survival). This statistical approach allowed for incorporation of environmental covariates in

329 the robust design models. By using the principals of multimodel inference (Burnham and
330 Anderson 2002), we were able to formally evaluate the relative influence of covariates on
331 survival.

332 Individuals that were detected leaving (or upstream of) the study reach during the
333 oversummer period were assumed to have permanently emigrated and were removed from
334 the model likelihood following the date of their last wand detection within the study reach.
335 We accomplished this by changing the frequency of each emigrant's encounter history to
336 negative one. This allowed us to fix the movement parameters in the robust design to zero for
337 all intervals. Additionally, all detections classified as ghost tags were converted from detections
338 (1s) to non-detections (0s) beginning on the sample in which the presumed mortality was
339 documented.

340 Prior to evaluating our study questions, we were interested in understanding the range
341 in survival among reaches and years. To accomplish this, we ran a robust design model for each
342 reach/year combination (eight reaches x three years = 24 individual models) to estimate reach-
343 and year-specific survival. To compare among reaches and years, we standardized the survival
344 interval to June 15 through October 15 (122 days) by adjusting the survival estimate for a given
345 reach to the desired timeframe (standardized $\hat{S} = \text{unstandardized } \hat{S}^{1/(i/122)}$), where i = the actual
346 number of days in the study interval for the given reach.

347 [C]*Statistical evaluation of study questions.*—Our general statistical approach was to construct
348 model sets to evaluate specific study questions. We evaluated the strength of models within a
349 given model set based on Akaike information criteria (AIC). To evaluate model support, we used
350 the following guidelines (Burnham and Anderson 2002): ΔAICc within 0–2 indicated substantial
351 support for both models; differences of 4–7 indicated considerably less support for the model
352 with the higher ΔAICc ; and differences greater than 10 indicated essentially no support for the
353 model with the higher ΔAICc .

354 For environmental covariate models with high AIC support, we examined the beta
355 associated with that covariate to determine whether the 95% confidence interval overlapped
356 zero. For covariates where 95% confidence intervals did not overlap zero, we used the betas to
357 estimate a function describing the relationship between that covariate and survival.

358 [C]Survival in relation to stream, reach, and year (Objective 1).—To determine whether survival
359 varied among streams, reaches, and/or years, we evaluated a model set that included six
360 general models: a model that constrained variation in survival among streams, reaches, and
361 years ($S_{*,*}$), models that allowed for variation in survival among streams, reaches, or years ($S_{s,*}$;
362 $S_{r,*}$; $S_{*,y}$), a model that allowed for variation in survival among both streams and years ($S_{s,y}$),
363 and a model that allowed for variation in survival among both reaches and years ($S_{r,y}$). Because
364 the number of primary sampling occasions varied by reach and year (range 3–6), we limited our
365 dataset for this analysis to the first and last primary sampling occasions of each reach/year
366 combination.

367 [C]Survival in relation to flow-related variables (Objective 2).—We calculated multiple
368 hydrologic metrics from the streamflow dataset to characterize the magnitude and duration of
369 flow conditions hypothesized to impact survival. Multiple hydrologic metrics from Olden and
370 Poff (2003) were considered for representation of critical attributes of the summer flow regime.
371 These included average, minimum, and maximum flow conditions, as well as duration of
372 surface flow disconnection. We also considered metrics to represent three additional flow-
373 related variables known to influence stream salmonid populations; water temperature, DO, and
374 wetted volume (Herrmann et al. 1962; Bjornn and Reiser 1991; Welsh et al. 2001; Woelfle-
375 Erskine et al. 2017).

376 Our first step was to select a single metric to represent each of the seven flow-related
377 variables of interest (average flow, minimum flow, maximum flow, duration of surface flow
378 disconnection, DO, wetted volume, and water temperature). To accomplish this, we proceeded
379 by constructing a covariate model for each candidate metric using the robust design model as
380 previously described. For each covariate model we included the data for a given metric
381 summarized by reach and year and used the same wand dataset as was used for the general
382 models.

383 To select the metric that best represented each flow-related variable, we considered
384 variable-specific model sets that included candidate metric models for each variable. For
385 example, to select a metric to represent minimum flow, we considered eight models; one

386 model for each of eight candidate metrics normalized by catchment area: average minimum
387 daily flow; minimum 7-, 15-, and 30-day average flows; minimum 7-, 15-, and 30-day minimum
388 flows; and 10th percentile average daily flow. The covariate in the model with highest AIC
389 support was selected as the metric to represent minimum flow. This process was repeated for
390 each of the seven flow-related variables resulting in seven representative metrics used for
391 further analyses.

392 Our second step was to evaluate which of the seven flow-related variables had the
393 strongest influence on survival. We used a standard normal transformation to standardize each
394 metric and the resultant transformed values (Z scores) were included as covariates in a single
395 robust design model that included all reaches and years as well as multiple covariates. Prior to
396 transformation and inclusion in the model, each metric representing a given flow-related
397 variable was tested for correlation with the remaining six representative metrics, and we
398 excluded those that were highly correlated. For each covariate included in the final model, we
399 examined the estimated beta for each covariate and its 95% confidence interval to evaluate
400 whether it influenced survival ($\beta \pm 95\% \text{ CI} < > 0$) and, if so, whether the relationship was
401 positive ($\beta > 0$) or negative ($\beta < 0$).

402 [C]Comparison of alluvial, bedrock, and clay reaches (Objective 3).—To evaluate whether
403 geomorphic setting affected survival, we compared a model that included geomorphic reach
404 type (alluvial, bedrock or clay; $S_{g,*}$) with the general model $S_{*,*}$. For this analysis, we used the
405 same wand dataset as was used for the general models representing all reaches and years (first
406 and last primary sampling occasions only).

407 To further explore variation in survival among geomorphic reach types, we developed
408 reach- and year-specific survival models for reaches representing alluvial (GRP-0.16), bedrock
409 (GRP-1.14), and clay (GRE-13.40) geomorphic types. For this analysis, we included wand and
410 environmental data from all reach/year combinations in which we collected data on five
411 primary sampling occasions (four survival intervals) over the summer period (2011 to 2012 for
412 the alluvial reach, and 2011 to 2013 for bedrock and clay reaches). For each reach, we modelled
413 survival as a function of metrics that demonstrated a strong influence on survival from the

414 Objective 2 analysis. For each covariate model, we combined the point estimates of the betas
415 through the logit link to depict survival over a range of covariate values.

416

417 [A]Results

418 Approximately 500 juvenile Coho Salmon were stocked into each reach in each year,
419 with the exception of GRE-13.40 in 2012 and 2013, and GRP-1.14 in 2013 when the number of
420 fish released was reduced due to the presence of wild fish (Table 2). In 2013, we did not stock
421 GRE-8.69 and GRP-0.16 because we presumed that water in all habitat units would disappear
422 due to progressing drought conditions; as expected, these two reaches became completely dry.
423 Because environmental data was collected for these two reaches in 2013, we were able to
424 include them in our model sets by fixing survival to zero.

425 The average proportion (range) of fish that emigrated from the study reaches over all
426 three years was 0.07 (0.01–0.36); in only three cases, the proportion that emigrated was > 0.10
427 (Table 2). Ghost tags were documented in all reaches and the number detected in each
428 reach/year combination ranged from 15–97 (Table 2).

429 Capture probability averaged 0.66 over all wand surveys and ranged from 0.45–0.88.
430 Survival of juvenile Coho Salmon between June 15 and October 15 ranged from 0–0.88 over
431 reaches and years and decreased progressively with decreasing summer discharge from 2011 to
432 2013 (Figure 2, Figure 3).

433

434 [B]Survival in relation to stream, reach, and year (Objective 1)

435 The reach- and year-specific model ($S_{r,y}$) had the highest AIC support when compared
436 with all other general models in the model set (AICc weight = 1.0), indicating that survival was
437 influenced by both reach and year. For all other models, Δ AICc was greater than 100.

438

439 [B]Survival in relation to flow-related variables (Objective 2)

440 For six of the seven flow-related variables, a single metric demonstrated high support
441 when compared with other candidate metrics within that variable (Table 3). The exception was
442 temperature, in which MWMT and MWAT demonstrated similar support.

443 Survival of Coho Salmon increased as streamflow, DO, and wetted volume increased, and
444 survival decreased with increasing days of disconnection and increasing temperature; however,
445 the relationship with temperature was weak (Figure 4).

446 Following tests for correlation among flow-related variables, we chose to include days of
447 disconnection, maximum flow, and wetted volume in the model with multiple covariates. DO
448 was excluded because it was correlated with days of disconnection ($r = 0.82$, $P < 0.001$) and had
449 a weaker relationship with survival than days of disconnection. Temperature was excluded
450 because it was correlated with wetted volume ($r = 0.51$, $P < 0.05$) and had a weaker relationship
451 with survival than wetted volume. Because of strong correlations among average, minimum,
452 and maximum flow, we selected maximum flow as the metric to representative flow magnitude
453 because it had a stronger relationship with survival than average or minimum flow. Correlations
454 for all other comparisons were low ($r < 0.5$). When the three remaining flow-related variables
455 were included in a single model, the betas for days of disconnection, maximum flow, and
456 wetted volume all differed from zero, and days of disconnection had the strongest effect on
457 survival (Figure 5).

458

459 [B]Comparison of alluvial, bedrock, and clay reaches (Objective 3)

460 Overall, we observed lower survival in the three alluvial reaches (GRP-0.16, GRE-8.69,
461 and DUT-3.87) as compared to their upstream counterparts in bedrock or clay reaches (GRP-
462 1.14, GRE-13.40, and DUT-6.51, respectively) (Figure 3). There was strong support for the model
463 that included geomorphic reach type (S_{g*} ; AICc weight = 1.0), and the point estimate for the
464 probability of survival in alluvial reaches was 0.16 lower than in bedrock reaches and 0.38 lower
465 than in the clay reach.

466 Because days of disconnection demonstrated the strongest effect on survival in our
467 Objective 2 analysis, we explored the influence of this metric in the reach- and interval-specific
468 survival models for the alluvial (GRP-0.16), bedrock (GRP-1.14), and clay (GRE-13.40) reaches in

469 which primary sampling occurred on five occasions each year. Because it is likely that DO is one
470 of the driving mechanisms behind the negative relationship between survival and days of
471 disconnection (Figure 4), we also explored reach and interval-specific relationships between
472 survival and DO.

473 With the progression of drought conditions from 2011 to 2013 (Figure 2), the number of
474 days of disconnection increased each summer in each reach; in 2011 all reaches remained
475 connected by surface flow, but by 2013 all reaches had extended periods of pool disconnection
476 (Figure 6). Disconnection occurred most extensively in the alluvial reach, was intermediate in
477 the bedrock reach, and occurred only in 2013 in the clay reach.

478 We also observed a general decline in DO levels in each of the different geomorphic
479 reach types between 2011 and 2013, as well as an overall decrease in DO levels within each
480 study season (mid-June to late-September) (Figure 7). DO levels were highest in the clay reach
481 in nearly all intervals and years, and lowest in late-season intervals in the alluvial reach. Annual
482 and seasonal declines in DO were most pronounced in the alluvial reach.

483 In general, survival remained above 0.5 in all reaches during intervals when surface flow
484 was present, and fell below this level during intervals with extended periods of surface flow
485 disconnection (i.e., surface flow < 0.28 L/s) (Figure 8). In most reaches and years, the lowest
486 survival occurred during the last interval of the season, between late-August and mid-
487 September. The clay reach had the highest survival in years 2011 and 2012, and in 2013 survival
488 remained high until the last interval when it fell precipitously following an extended period of
489 disconnection. Though survival in the bedrock reach was more variable than in the clay reach, it
490 showed a similar pattern, with an extreme decline during the last interval in 2013. The alluvial
491 reach responded differently than the other reaches; in 2011 survival fluctuated among intervals
492 and was generally lower than in the clay and bedrock reaches, and in 2012 there was a general
493 decline in survival over the study period even when surface flow was present. No survival data
494 was collected in the alluvial reach in 2013; however, the reach was intermittent in June and dry
495 in September so we can assume that, had fish been released, they all would have perished.

496 While the relationship between survival and days of disconnection was negative in all
497 cases, the shape of the relationship varied among reaches and was lower in the alluvial reach

498 (Figure 9). For example, based on our data, the model predicted that survival in the alluvial
499 reach would drop to 0.5 following two weeks of disconnection, whereas in the bedrock and clay
500 reaches it would take over four weeks before survival dropped to 0.5. If disconnection persists
501 for a long enough period of time, however, we expect survival to drop to 0 regardless of reach
502 type. We found a positive relationship between survival and DO in all reaches (Figure 9) but
503 survival in the alluvial reach was always lower for a given DO concentration when compared to
504 the bedrock and clay reaches.

505

506 [A]Discussion

507 The results of this study advance our understanding of which flow-related variables are
508 appropriate for describing fish–flow relationships in intermittent streams, and offer insight to
509 managers for the development of flow-related recovery and protection strategies for sensitive
510 salmonid species in small coastal streams. By stocking experimental fish of similar size and
511 genetic composition at common densities, we controlled for some of the potential confounding
512 factors affecting survival (e.g., prior residence, size, genetic composition) and we were able to
513 look more directly at the influence of flow-related variables on survival. In almost all reaches
514 and years, emigration from the study reaches was minimal, and our ability to account for
515 emigration using PIT tag detection systems allowed us to estimate true rather than apparent
516 survival.

517 Our finding that oversummer survival of juvenile Coho Salmon is positively associated
518 with streamflow magnitude, wetted volume, and DO concentrations is consistent with the
519 results of recent studies in coastal California streams (Grantham et al. 2012; Woelfle-Erskine et
520 al. 2017). In addition, we found that the number of days of surface flow disconnection was the
521 strongest driver of survival of juvenile Coho Salmon at the reach scale, with survival decreasing
522 as a function of increasing days of disconnection. Furthermore, survival and its relationship to
523 days of disconnection varied by geomorphic reach type; in an alluvial reach, survival was lower
524 and declined more rapidly following surface flow disconnection than in either a bedrock or clay
525 reach. Though our multiple-interval study was limited to one reach of each geomorphic type,
526 this outcome verifies the results of May and Lee (2004) who showed higher apparent survival of

527 juvenile salmonids in bedrock-dominated pools where more water remained for the duration of
528 the summer season than in alluvial pools.

529

530 [B] Influence of flow-related variables on survival of juvenile Coho Salmon

531 For each flow-related variable in which multiple candidate metrics were considered,
532 with the exception of temperature, a single metric demonstrated high model support (Table 2),
533 and we suggest using these top metrics for future studies in intermittent streams. Most notable
534 was the high support for the model that included the number of days that *minimum* flow fell
535 below 0.28 L/s (flow level at which habitat units disconnected from surface flow) when
536 compared to the model that included the number of days that *average* flow fell below 0.28 L/s
537 (Table 2). This suggests that even daily fluctuations to flow levels that disconnect habitat units
538 can have a negative influence on survival, thus highlighting the importance of maintaining
539 continuous surface flow connection to support summer-rearing salmonids.

540 Similar to Grantham et al. (2012), we found that variables representing streamflow
541 magnitude (average, minimum, and maximum) are positively associated with oversummer
542 survival of juvenile Coho Salmon. Our analysis, however, revealed a potential problem with
543 relying on flow magnitude alone to explain fish population metrics in intermittent streams. The
544 issue is evident in the estimated relationships between survival and flow-related variables
545 (Figure 4) in which survival was greater than zero when flow magnitude variables were zero.
546 This can be explained by our observation that pools held water even after surface flow dropped
547 to zero, allowing fish to survive in residual pools. For this reason, other flow-related metrics
548 (i.e., DO, wetted volume, and temperature) are more likely to accurately represent the
549 conditions that fish continue to experience even after surface flow drops to zero. Indeed, we
550 found that survival was positively associated with DO and wetted volume and negatively
551 associated with temperature (Figure 4).

552 In our study, days of disconnection best explained survival (Figure 5). This metric likely
553 represents an integration of multiple environmental and biological factors that fish directly
554 experience, including water quality, water quantity, predation, food availability, and
555 competition. Presumably, the longer that pools are disconnected from surface flow, the greater

556 the probability that fish will experience mortality due to physiological stress, predation,
557 resource availability, and/or stranding.

558 DO, which was highly correlated with days of disconnection, also demonstrated a strong
559 positive relationship with survival. However, relationships between survival and wetted volume
560 and survival and temperature demonstrated lower model support than expected given that
561 they represent factors directly experienced by fish. We suspect this was due to increased
562 habitat unit-level variability in these metrics following surface flow disconnection. Because our
563 analysis was at the reach scale, important relationships occurring at the habitat unit-level may
564 have been obscured. Further studies are needed that examine fish–flow relationships at the
565 habitat unit-, reach-, and watershed-scales representing a broader range of streamflow,
566 temperature, and geomorphic reach types. This would likely strengthen some of the
567 conclusions and allow for broader management application.

568 Surprisingly, we found juvenile Coho Salmon surviving in pools with DO concentrations
569 below documented daily minimum tolerance thresholds of 3.8–4.3 mg/L (WSDE 2002; Carter
570 2005) and, at times, below lab-based survival thresholds of 3.0–3.5 mg/L (Davison et al. 1959;
571 Herrmann et al. 1962; Warren 1973; WSDE 2002). It is important to recognize that our DO
572 measurements, while consistent in terms of measurement location and time of day, only
573 represented reach-scale averages of point location measurements and did not account for
574 spatial variation within pools or diel fluctuations that might vary over the course of the
575 summer. It is also possible that when DO levels declined in study reaches, juveniles were keying
576 in to locations in pools with higher DO levels than those observed at our spot measurement
577 locations. In other stream systems, fish have been documented moving to locations of
578 preferred temperatures (Nielsen et al. 1994; Matthews and Berg 1997), and it would be
579 informative to learn whether similar behavior occurs in relation to DO. While we are confident
580 in our result that there is a positive relationship between survival and DO, further study is
581 needed to examine microhabitat-scale relationships between continuous DO levels and fish
582 survival, growth, and movement.

583

584 [B]Implications for management

585 The results of this study have important implications for streamflow management and
586 salmonid recovery efforts. Our observation that juvenile Coho Salmon were able to survive at
587 flows below 3 L/s (approximately 0.1 ft³/s), so long as pools remained hydrologically connected,
588 suggests that streamflow improvement projects contributing even a few L/s could allow rearing
589 juveniles to survive the summer bottleneck in intermittent streams. Our findings also
590 underscore the importance of considering the size, character, and geomorphic context of a
591 watershed when estimating the benefits of a potential streamflow improvement project on fish
592 populations. For larger, snowmelt-driven systems, a streamflow enhancement project that
593 repurposes a few L/s to the stream is likely trivial; however, in small, coastal headwater streams
594 that have a tendency towards intermittency, this small quantity of water could mean the
595 difference between complete loss of a year-class of endangered salmonids versus survival to
596 seasons of higher opportunity.

597 Based on the results of this study, we conclude that the number of days of surface flow
598 disconnection is a potentially useful metric for setting management targets to prevent
599 extirpation of juvenile salmonids rearing in intermittent streams. Although we observed reach
600 variation in the rate at which survival declined in relation to pool disconnection, in all reaches
601 the onset of pool disconnection represented a turning point for which water quality, water
602 quantity, and survival all declined. In cases where flow magnitude thresholds are being
603 developed with the goal of sustaining or recovering salmonid populations, we suggest
604 identifying the flow (or stage) at which pools become disconnected in the stream or reach of
605 interest and using that value as the threshold at which the risk of mortality substantially
606 increases.

607
608 [B]Survival versus thrival

609 Although survival is a useful metric for examining how environmental variables affect
610 fish populations, survival should not be the single biological response considered in the context
611 of population recovery. Ensuring that sufficient flow is available for growth and production is
612 also important. In this study, we determined that streamflow magnitude is positively associated
613 with oversummer survival of juveniles and that, given suitable habitat and water quality

614 conditions, maintaining stream connectivity has the potential to allow juvenile Coho Salmon to
615 persist through the summer. We did not evaluate the size or condition of the fish, nor
616 determine their fate to the smolt and/or adult stages.

617 We view the minimum streamflows required to maintain pool connectivity as flow levels
618 that should be sustained in order to minimize flow-related mortality; however, such flows are
619 likely not high enough for achieving target size thresholds or production goals. Studies have
620 shown that reductions in streamflow decrease drift rates of invertebrate prey (Poff and Ward
621 1991), and that there is a positive correlation between streamflow and juvenile salmonid
622 growth (Harvey et al. 2006; Nislow et al. 2004). Summer growth opportunity may result in
623 larger size which, in turn, can have implications for survival to later life stages (Quinn and
624 Peterson 1996; Ebersole et al. 2006; Bond et al. 2008; Claiborne et al. 2011). To inform the
625 development of flow thresholds that support sufficient growth and production in intermittent
626 streams, further work is needed to track the size and condition of summer-rearing fish, as well
627 as their fate following the summer season. An individual-based approach that uses PIT tags and
628 PIT tag detection systems lends itself to this type of evaluation. With the expected increase in
629 drought frequency due to climate change and the associated increasing demand on water
630 supply, such studies will be essential for informing strategies aimed at protecting and restoring
631 threatened and endangered salmonid populations in intermittent streams.

632

633 [A]Acknowledgments

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645 for constructive comments on earlier drafts of the manuscript.

646

647 [A]List of Tables

648 Table 1. Characteristics of study reaches within Dutch Bill (DUT), Green Valley (GRE), Mill (MIL),
649 and Grape (GRP) creeks.

650

651 Table 2. Summary of juvenile Coho Salmon released, number and proportion emigrating during
652 the study period, and number of ghost tags (i.e., mortalities or shed tags) detected in each
653 study reach/year combination.

654

655 Table 3. Flow-related variables and metrics evaluated for use as covariates in juvenile Coho
656 Salmon oversummer survival models. Metrics highlighted in bold had the highest AIC support
657 within each variable and were used as covariates in subsequent analyses.

658

659 [A]List of Figures

660 Figure 1. Locations of juvenile Coho Salmon survival study reaches (black lines) and study
661 watersheds in the Russian River basin, California. Study reach codes refer to stream name (DUT
662 = Dutch Bill Creek, GRE = Green Valley Creek, MIL = Mill Creek, GRP = Grape Creek) and the
663 distance of the downstream end of each reach along the stream course (river kilometers) from
664 the confluence.

665

666 Figure 2. Total stream discharge between June 15 and September 30 by study stream, years
667 2011–2013. Stage and streamflow data were collected at river kilometers 4.37 (Dutch Bill
668 Creek), 9.39 (Green Valley Creek), 6.44 (Mill Creek), and 0.54 (Grape Creek).

669

670 Figure 3. Estimated juvenile Coho Salmon survival ($\hat{S} \pm 95\% \text{ CI}$) based on PIT-tag wand data
671 collected in study reaches between June 15 and October 15, years 2011–2013. Reach codes
672 refer to stream names (DUT = Dutch Bill Creek, GRE = Green Valley Creek, MIL = Mill Creek, GRP
673 = Grape Creek) and the distance of the downstream end of each reach along the stream course
674 (river kilometers) from the confluence. Alluvial, bedrock, or clay indicates the geomorphic
675 setting of the reach.

676

677 Figure 4. Estimated Coho Salmon survival as a function of flow-related variables based on data
678 collected in Dutch Bill, Green Valley, Mill, and Grape creeks between June 15 and October 15,
679 years 2011–2013. Solid lines represent estimated survival functions and dashed lines represent
680 the 95% confidence intervals of estimated survival functions. Specific metrics are defined in
681 Table 2. Covariate ranges reflect empirical ranges during the study period.

682

683 Figure 5. Estimated beta values ($\hat{\beta} \pm 95\% \text{ CI}$) of flow-related covariates showing positive (above
684 x-axis) or negative (below x-axis) relationships with oversummer survival of juvenile Coho
685 Salmon, years 2011–2013 in Dutch Bill, Green Valley, Mill, and Grape creeks.

686

687 Figure 6. Days of disconnection in alluvial (GRP-0.16), bedrock (GRP-1.14), and clay (GRE-13.40)
688 reaches between June 15 and September 30, years 2011–2013.

689

690 Figure 7. Average \pm SD DO levels collected on multiple dates in alluvial (GRP-0.16), bedrock
691 (GRP-1.14), and clay (GRE-13.40) reaches during the summer dry season, years 2011–2013.

692

693 Figure 8. Average daily discharge (solid line), and minimum and maximum daily discharge
694 (dashed lines) in relation to juvenile oversummer survival ($\hat{S} \pm 95\% \text{ CI}$; black squares) in an
695 alluvial reach (GRP-0.16), a bedrock reach (GRP1.14) and a clay reach (GRE-13.40), years 2011–
696 2013. Gray vertical lines represent timing of PIT-tag wand surveys.

697

698 Figure 9. Estimated survival of juvenile Coho Salmon as a function of days of disconnection and
699 average DO levels in alluvial (GRP-0.16), bedrock (GRP-1.14), and clay (GRE-13.40) reaches
700 based on data collected between mid-June through September, years 2011–2012 (GRP-0.16) or
701 2011–2013 (GRP-1.14 and GRE-13.40). Solid lines represent estimated survival functions and
702 dashed lines represent the 95% confidence intervals of estimated survival functions. Covariate
703 ranges extend from the minimum value observed in one or more reaches to the maximum
704 value in one or more reaches (see Figure 6 and Figure 7).

705

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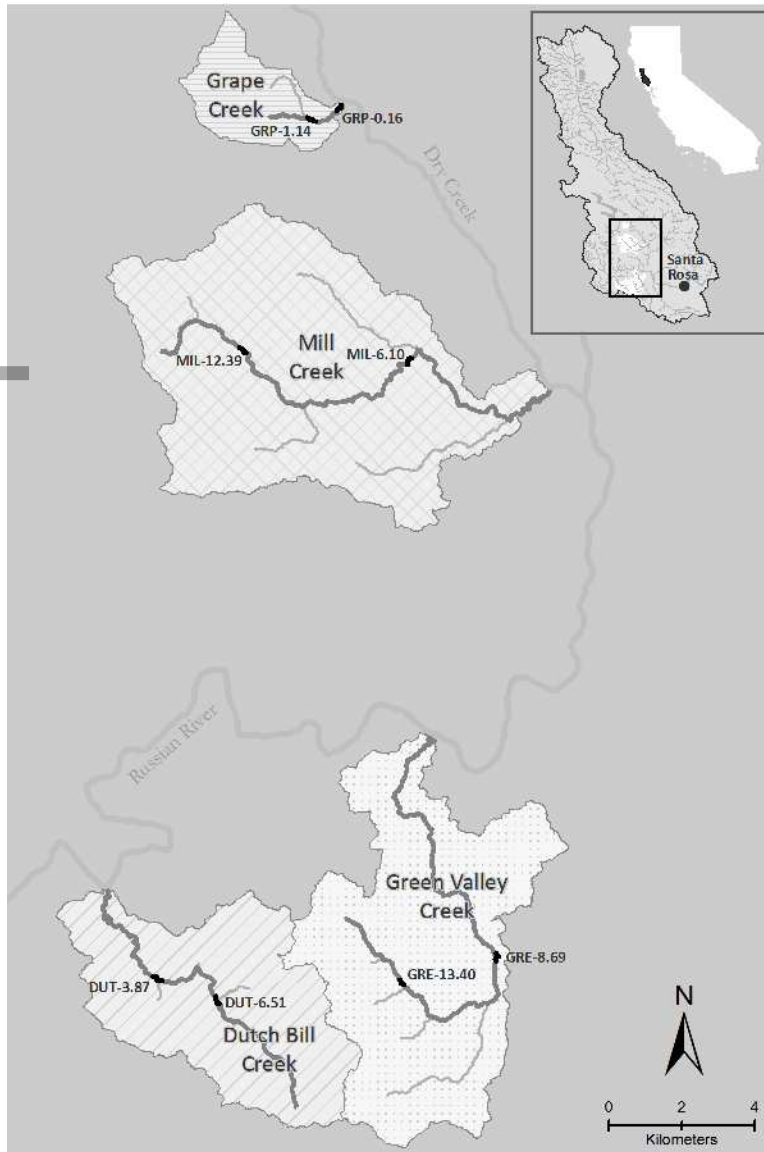
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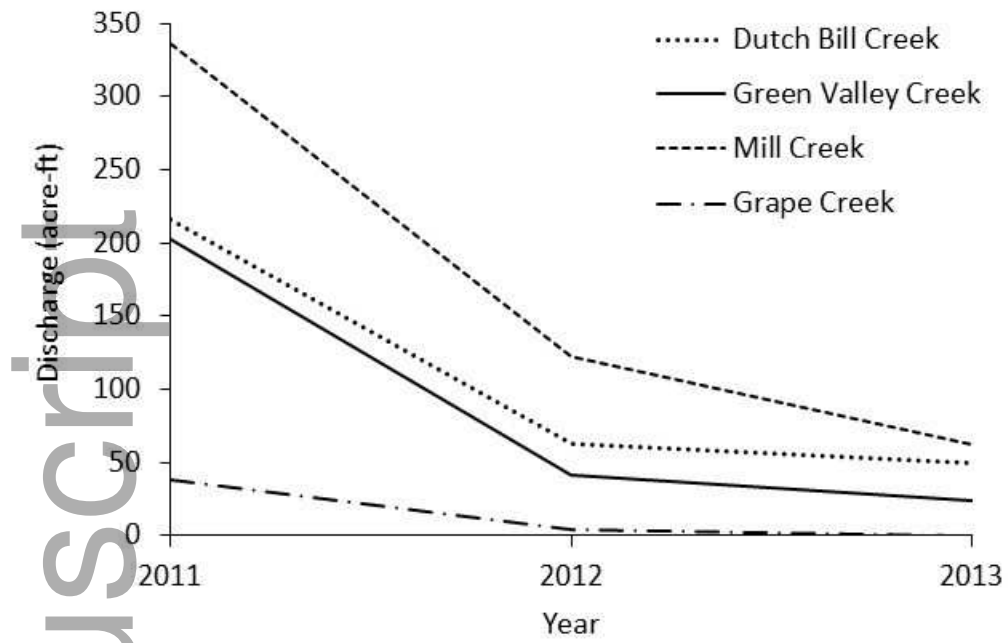
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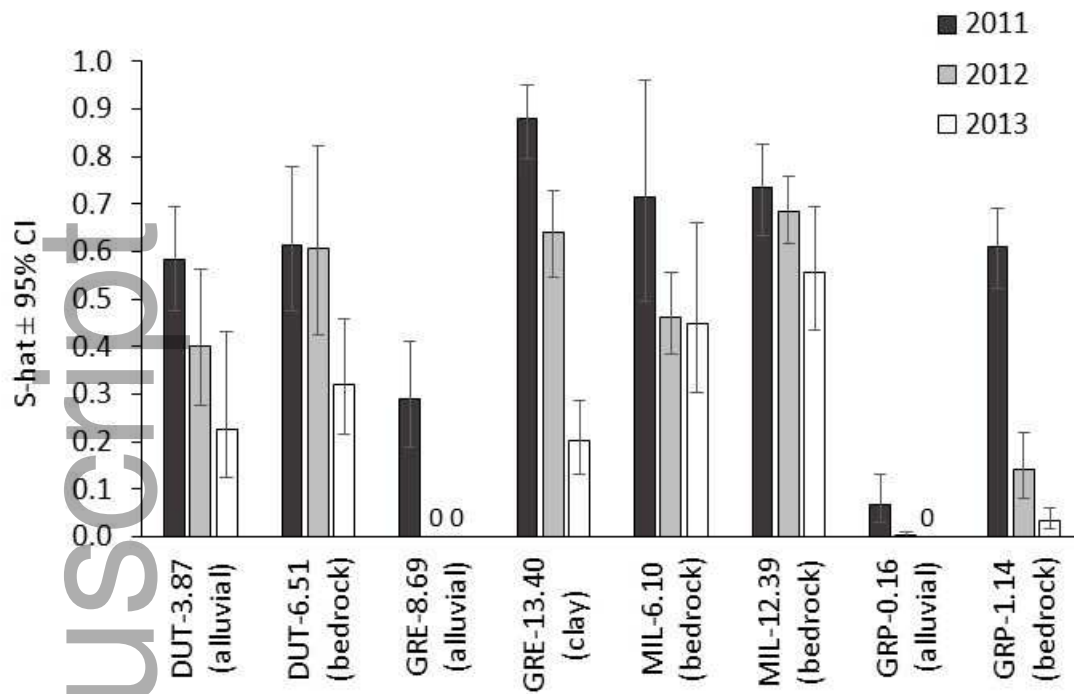


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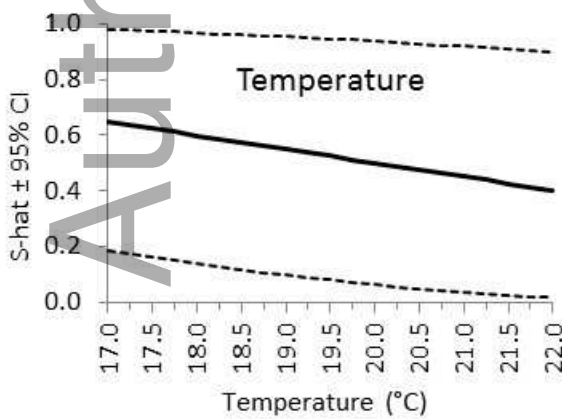
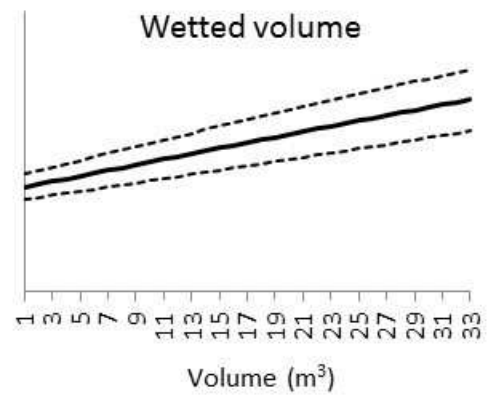
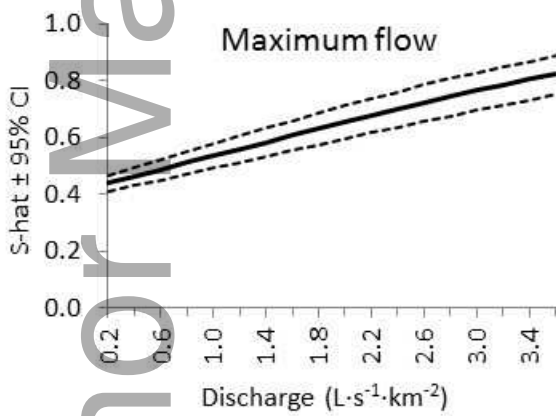
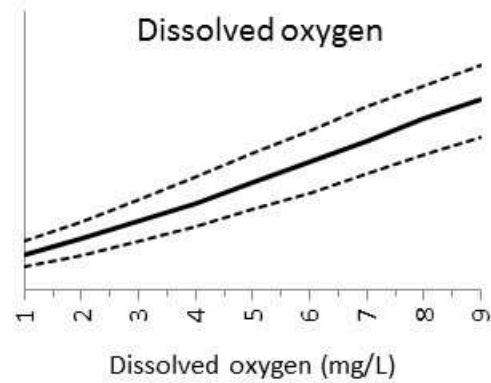
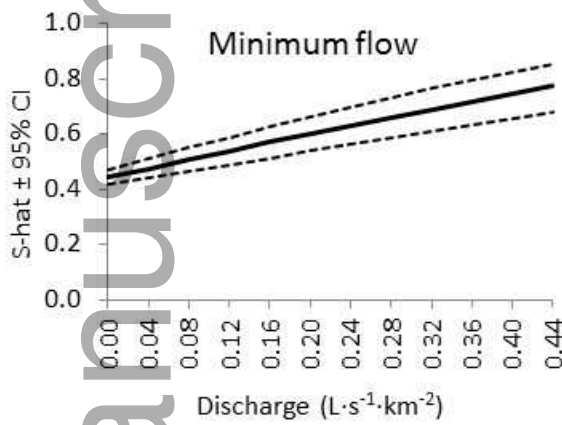
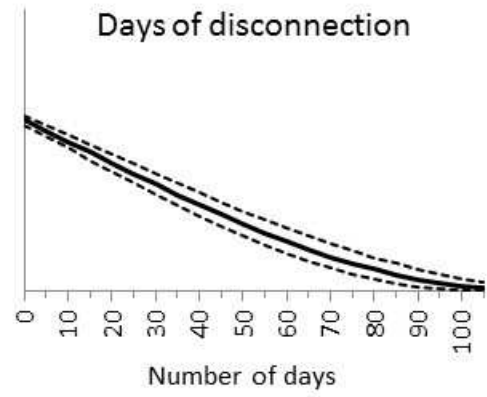
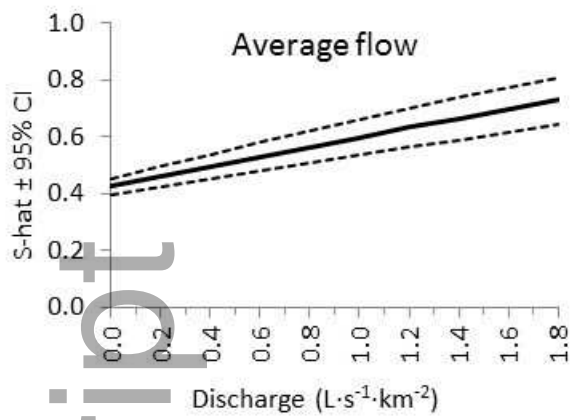


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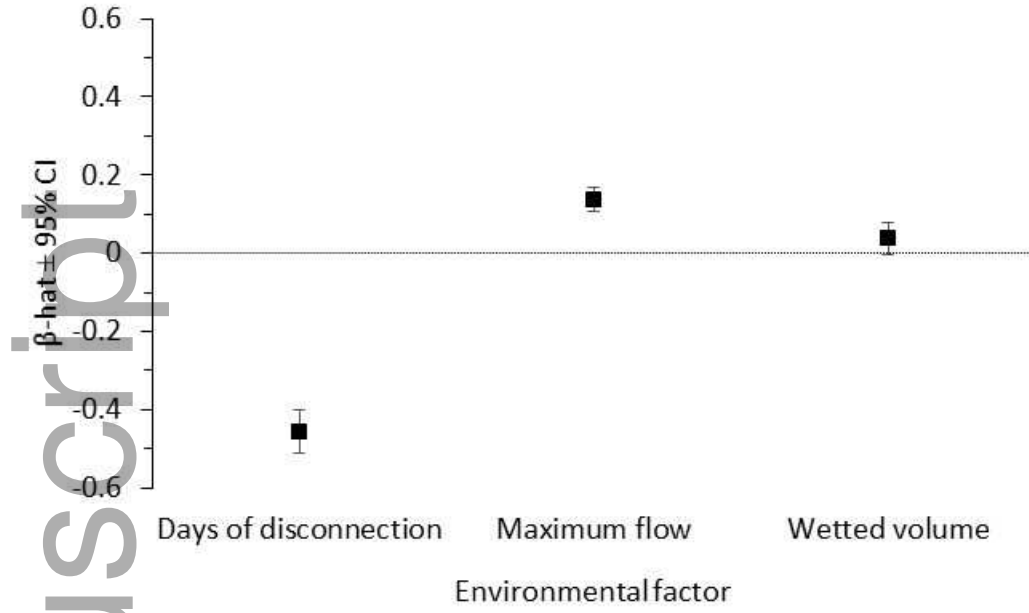
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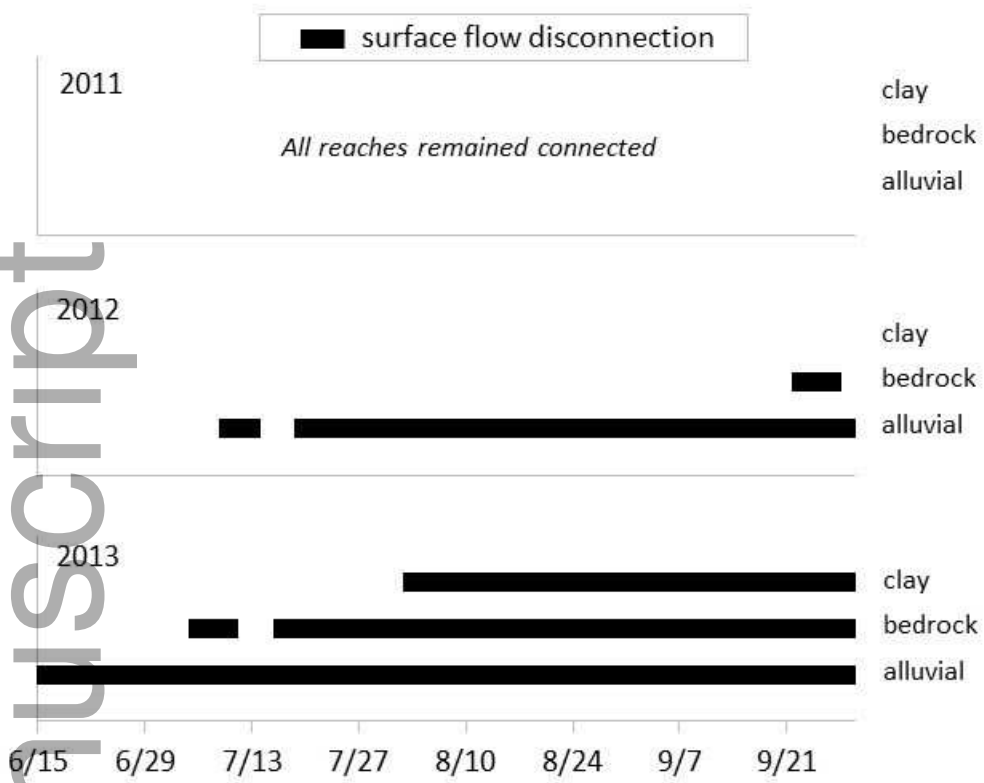


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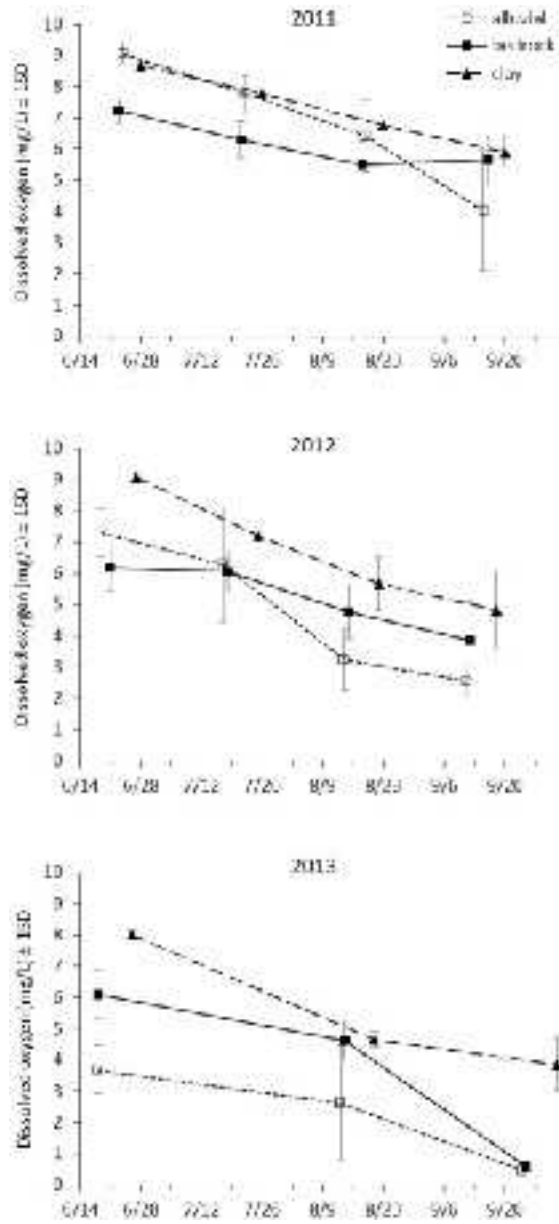


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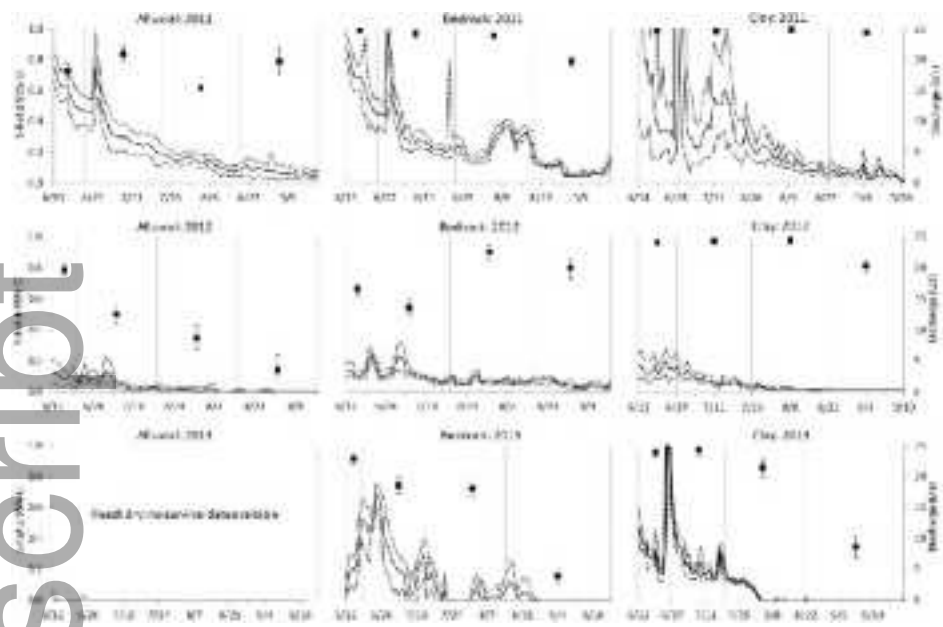
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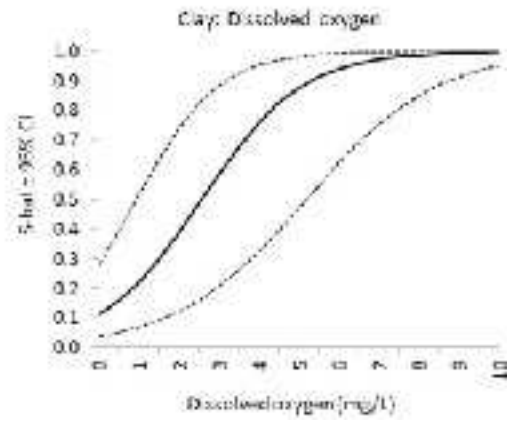
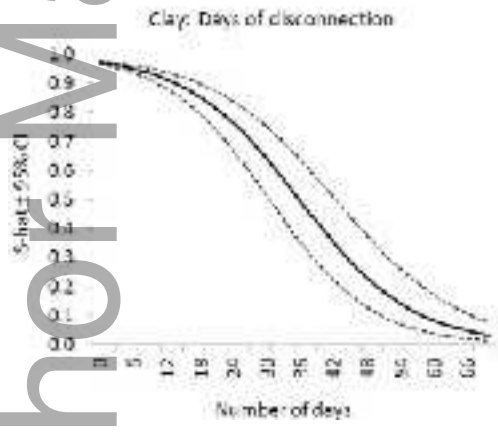
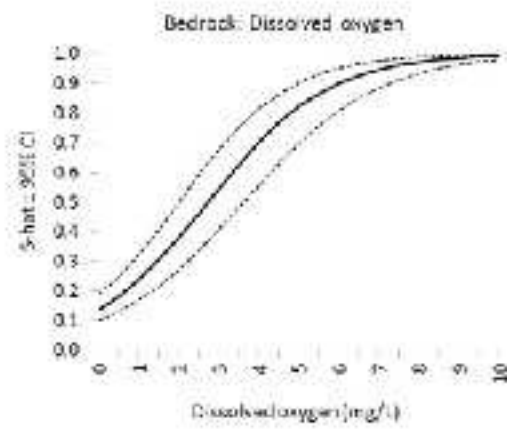
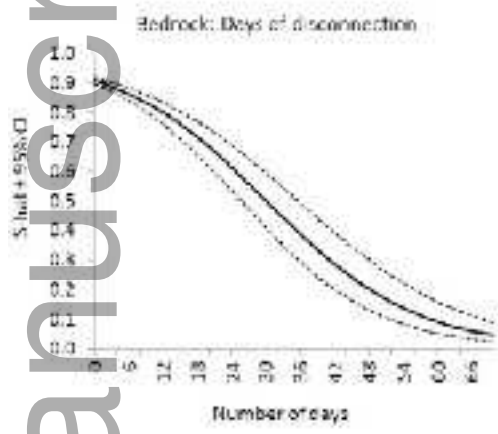
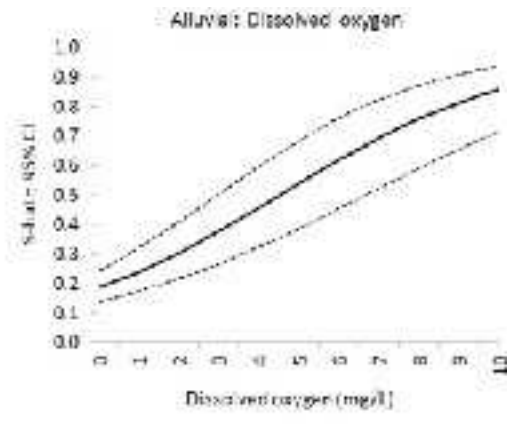
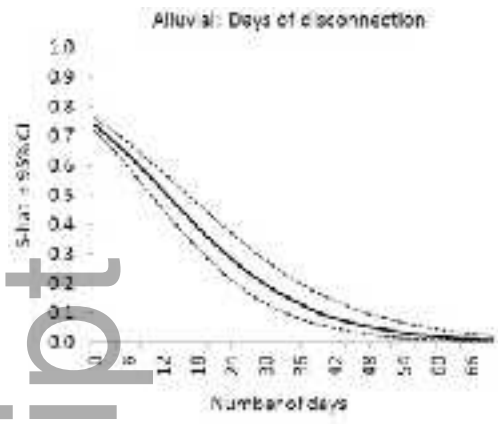


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