Physical and biological constraints on the capacity for life-history expression of

anadromous salmonids: an Eel River, California, case study

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ABSTRACT

Recovery of anadromous salmonid populations is complicated by their complex life-histories. We examined the spatiotemporal interplay of stream temperature, geomorphic features, and a species' thermal sensitivity mediated by biological interactions in a case study of steelhead trout (*Oncorhynchus mykiss*) and Chinook salmon (*O. tshawytscha*) in California's Eel River watershed. We estimated habitat suitability and fish capacity for each salmonid run and freshwater life stage during average, cool, and warm years in each of the watershed's subbasins, including a historically-occupied high-elevation subbasin upstream of an impassable dam. Our estimates varied depending on whether we accounted for exposure to the Sacramento pikeminnow (*Ptychocheilus grandis*), an introduced predator/competitor. Our results indicate that the dammed subbasin has substantial salmonid capacity relative to the rest of the watershed and could provide an important cool-water refuge during warm years and from pikeminnow, potentially improving the productivity and resilience of multiple anadromous salmonid populations. Our approach can be applied in any setting where spatially explicit habitat metrics can be estimated and population specific and life-stage specific habitat criteria can be specified.

19   **INTRODUCTION**

20   Recovery of anadromous salmonid populations is complicated by the fact that these fish

21   have complex life-histories, exposing them to a variety of climatic, physical, and biological

22   impacts throughout their life cycle. A useful framework for sorting through this complexity

23   emphasizes how abundance and productivity (i.e., population growth rate), mediated by a

24   population's interactions with habitat via spatial structure and diversity, impact a population's

25   long-term viability (McElhany et al. 2000). Conceptually, the most straightforward way to apply

26   these ideas has been through quantitative life-cycle models that estimate survival across

27   successive life stages under various climatic and hydrologic conditions. But life-cycle models

28   usually require detailed data on stage-specific survival and abundance over many years (e.g.

29   Scheuerell et al. 2006, Zeug et al. 2011, Crozier et al. 2021), which tends to bias their application

30   to highly impacted populations where collection of such data is mandated. To assess recovery

31   scenarios for understudied or extirpated populations, an alternative approach is to quantify the

32   capacity of the population's environment. Capacity provides an estimate of the potential

33   abundance of a population, and can be accomplished in any setting where spatially and

34   temporally explicit environmental metrics (e.g. monthly temperature, channel gradient) can be

35   estimated and associated criteria (e.g. thermal and gradient thresholds) for populations and life

36   stages can be specified.

37   This alternative approach of assessing the potential abundance of populations from the

38   environment may be particularly useful to evaluate restoration scenarios and potential

39   reintroductions to formerly occupied habitats (Beechie et al. 1994, Pess et al. 2008), a goal of

40   many management action plans (McElhany et al. 2000, NMFS 2013, NMFS 2016, PVP NOI

41   Parties 2020a). Providing fish passage and subsequent recovery efforts can be expensive and are

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42 only practical if ecosystem recovery, including a significant increase in salmonid abundance or

43 productivity, is anticipated (Bellmore et al. 2019, PVP NOI Parties 2020a, PVP NOI Parties

44 2020b). The amount of suitable habitat or carrying capacity of fish is often substituted as a proxy

45 for potential abundance (Burnett et al. 2003, Agrawal et al. 2005, Lindley et al. 2006, Pess et al.

46 2008, Boughton et al. 2018, Cooper et al. 2020). However, while most published studies have

47 focused on physical habitat features such as thermal conditions or geomorphic characteristics,

48 habitat suitability and capacity can also depend on biological interactions (Fausch et al. 1988). In

49 turn, biological interactions such as competition and predation rates may be influenced by

50 physical habitat features. For example, salmonid feeding rates, growth rates, and spatial

51 distributions can be mediated by interspecific competition, and competition can depend on

52 physical features such as temperature and stream gradient (Fausch et al. 1994, Taniguchi et al.

53 1998, Reese and Harvey 2002, de la Hoz Franco and Budy 2005). Similarly, predation rates on

54 juvenile Chinook salmon can be influenced by the environment; for example, based on both

55 experimental and field data, warmer temperatures or low light intensity (e.g., at dusk or dawn)

56 can increase predation rates (Petersen and Gadomski 1994, Marine and Cech 2004, Michel et al.

57 2020). Therefore, to better quantify habitat suitability and capacity as a proxy for potential

58 abundance, there is a need to account for the interplay between the spatial and/or temporal

59 variability in temperature and geomorphic characteristics, the complexities of salmonid life-

60 history diversity, life-stage specific thermal sensitivities, and biotic interactions.

61 In this study, we accounted for this complex interplay in a case study focused on

62 California's Eel River Basin. Historically, the Eel River Basin supported robust and

63 commercially exploited runs of salmon and steelhead trout, but declines in those populations led

64 to their placement on the federal Endangered Species List and subsequent efforts to recover the

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65   populations (U.S. Office of the Federal Registrar 1999, 2000). Drought and climate change may

66   warm stream temperatures to suboptimal or even lethal levels for cold-water salmonids, further

67   impeding salmonid recovery (Eel River Forum 2016). Warmer stream temperatures may also

68   increase predation by and competition with the non-native Sacramento pikeminnow

69   (*Ptychocheilus grandis*), a recent arrival to the Basin that thrives in warmer waters (Rieman et al.

70   1991, Brown and Moyle 1991, Reese and Harvey 2002). These unfavorable climate conditions

71   are predicted to become more frequent and severe throughout the western U.S. because of

72   anthropogenic climate change (Ault 2020, Williams et al. 2020). Cool-water refugia are therefore

73   necessary for salmonid recovery and future resilience, especially those refugia that remain

74   suitably cool throughout warm summers and during prolonged drought periods, conditions that

75   have historically been a normal part of California's climate. Because year-round thermal refugia

76   promote salmonid resiliency, survival, and productivity, it is imperative to explore the spatial and

77   temporal distribution of thermal refugia. In particular, the Upper Mainstem Eel River subbasin

78   (hereafter, Upper Mainstem), which historically hosted multiple populations of salmonids prior

79   to damming (Bjorkstedt et al. 2005), likely harbors more cool-water refugia during summer than

80   most of the rest of the Eel River Basin because of its relatively higher elevation (Isaak et al.

81   2017).

82   A key question addressed here is whether the dammed Upper Mainstem provides a

83   disproportionately large amount of suitable thermal refugia that might protect the productive

84   capacity and resiliency of native salmonids from a warming climate and an introduced warm-

85   water predator and competitor. Although other studies have attempted to quantify the habitat

86   suitability or fish capacity in the Upper Mainstem (e.g. VTN 1982, NMFS 2016, Cooper et al.

87   2020), our study differs from previous evaluations by 1) quantifying capacity and habitat

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88   suitability for multiple salmonid life stages using broad-scale geomorphic features, local habitat

89   characteristics, and thermal criteria based in part on risk of predation or competition posed by

90   Sacramento pikeminnow, 2) assessing how suitability and capacity change throughout a year, 3)

91   comparing suitability and capacity in warm, cool, and average years, and 4) quantifying the

92   value of the blocked subbasin relative to unblocked subbasins in the rest of the Eel River Basin.

93

94   **Study area**

95   The Eel River with its tributaries contains ~ 10,000 total river km on California's north

96   coast, making it California's third largest salmon and steelhead trout watershed behind the

97   Klamath/Trinity and Sacramento/San Joaquin Basins. The Eel River Basin is less negatively

98   impacted by dams than other large watersheds in California, with only two major dams blocking

99   upstream passage. Scott Dam, a 41-meter tall concrete dam operated as a storage reservoir since

100 its completion in 1922, has completely blocked upstream passage to and inundated former

101 habitat in the Upper Mainstem subbasin. Cape Horn Dam, a 29-meter tall dam 20 km

102 downstream of Scott Dam, built in 1908 as part of a diversion project, allows for fish passage

103 with a fish ladder. These two dams are part of the Potter Valley Hydroelectric Project, Federal

104 Energy Regulatory Committee (FERC) Project No. 77, currently operated by Pacific Gas &

105 Electric Company (PG&E) (Eel River Forum 2016). The Potter Valley project is undergoing

106 relicensing in 2022, and removal of Scott Dam and restoring fish passage to the Upper Mainstem

107 is under consideration to increase salmonid productivity and resilience (PVP NOI Parties 2020a,

108 PVP NOI Parties 2020b).

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110 **MATERIALS AND METHODS**

7

Approach

We combined broad- and local-scale habitat suitability and density-at-capacity estimates to quantify the amount of potentially suitable habitat and capacity for each subbasin in the Eel River Basin for winter-run and summer-run steelhead trout (*Oncorhynchus mykiss*) and fall-run Chinook salmon (*O. tshawytscha*). First, we evaluated the extent to which each subbasin retains suitable thermal and geomorphic salmonid habitat in an average, cool, and warm year. For each reach within each subbasin, we determined 1) if a reach is thermally suitable (FitzGerald et al. 2021) and 2) if a reach has a habitable geomorphic channel type (Montgomery and Buffington 1997). As these two data are sparsely measured throughout the entire Basin, we employed a spatial stream network model to estimate mean monthly stream temperature for every river kilometer in the Basin (FitzGerald et al. 2021), and we used channel gradient from a 10-meter digital elevation model to classify geomorphic channel type (Flores et al. 2006) at the same spatial resolution as the stream temperature model. We then calculated the amount (river km) of suitable habitat within each subbasin. Because of the complex life-history diversity of salmonids, reach habitat suitability was calculated separately for each life stage of each run based on life-cycle phenology, thermal tolerances, monthly-varying temperature, accessibility, and channel-type. We also added a temperature-mediated pikeminnow interaction criteria for juvenile rearing habitat suitability. Next, we estimated the relative production capacity of each subbasin based on standard juvenile-rearing and adult-spawning densities adjusted for local stream conditions (Cooper et al. 2020). Finally, we determined the latest month that juveniles could leave each subbasin and outmigrate in thermally tolerable conditions to the ocean. We used these results to determine the potential value for anadromous salmonids in the Eel River Basin if the Upper Mainstem was accessible (e.g., via dam removal or fish passage [PVP NOI Parties 2020a, PVP

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134 NOI Parties 2020b]). Below we detail each of the datasets and approaches used in our analysis.

135

136 **Habitat suitability datasets**

137 *Potentially accessible streams for salmonids*

138 　　　We defined the potential spatial distribution for each run/life stage from historical

139 population boundaries, accessibility of reaches, and channel type. First, historical population

140 boundaries were defined from a study on salmonid biogeographic breaks that showed that

141 steelhead trout and Chinook salmon in the Eel River Basin are divided into historical populations

142 that generally reflect watershed subbasins (Figure 1; Bjorkstedt et al. 2005, Spence et al. 2008).

143 Unless otherwise specified, all river or stream names refer to these subbasins rather than

144 individual rivers or streams. We did not analyze any subbasins that were historically uninhabited

145 for a given run. Next, we removed reaches beyond the limits of anadromy for each species.

146 Anadromous limits were defined as upstream of physical impassable barriers (e.g. large

147 waterfalls) or upstream of species-specific barriers inferred from stream gradient as delineated by

148 Spence et al. (2008). One natural cascade in particular, Bloody Rock Roughs in the Upper

149 Mainstem, has been debated as a full or partial barrier to anadromy (VTN 1982, NMFS 2016,

150 Cooper et al. 2020). For this study, reaches upstream of Bloody Rock roughs were classified as

151 inaccessible for Chinook salmon and potentially accessible for steelhead trout, but note that

152 drought may prevent migration for all salmonids (Cooper et al. 2020). We excluded the currently

153 impassable Scott Dam. However, some habitat in the Upper Mainstem subbasin is downstream

154 of Scott Dam and accessible to salmonids, and so we evaluated the habitat upstream (labeled as

155 'Upper Mainstem') and downstream (labeled as 'Upper Mainstem_ds') of Scott Dam separately.

156 The NMFS regional California Coastal Office provided their most updated file of physical

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157   barriers, and a 10 m digital elevation model (DEM) provided gradient.

158

159   *Stream temperature*

160   Mean monthly stream temperature for each reach was obtained from FitzGerald et al.

161   (2021) (Figure 2A, Supplemental Figure S1). Briefly, FitzGerald et al. (2021) predicted stream

162   temperature using a spatial stream network (SSN) model (Isaak et al. 2017), a specialized

163   statistical regression model that accounts for spatial autocorrelation in temperatures due to

164   stream-network structure and geographic proximity (Peterson and Ver Hoef 2010, Ver Hoef and

165   Peterson 2010, Isaak et al. 2014, Isaak et al. 2017). The SSN model was applied to the National

166   Stream Internet (NSI) network (Nagel et al. 2015) at a 1 km reach resolution for every month of

167   the year. The model was fit with empirical stream temperature from 1993-2015 for the entire

168   Klamath/Northern California region, which includes the stream systems of Eel, Trinity, and

169   Klamath Rivers. The model accurately predicted water temperatures in the Klamath/Northern

170   California region, with an average r^2 of 0.820 and an average mean absolute prediction error of

171   0.705°C across all months for the out-of-sample testing dataset (FitzGerald et al. 2021).

172   Additional modeling details can be found in FitzGerald et al. (2021). The model was then used to

173   predict monthly mean stream temperatures for every river km in the Eel River Basin for every

174   year in the study time period. Reaches classified as manmade lakes and reservoirs were removed

175   because they involve different thermal dynamics that are not well-represented by the SSN model.

176   The temperature predictions and habitat suitability analyses therefore do not include reaches that

177   are currently inundated (e.g. by Lake Pillsbury, created by Scott Dam). A single river km in the

178   Eel River Basin showed abnormally high predictions (sometimes > 10°C higher than the next

179   highest stream temperature in the Basin), and this outlier was removed from all subsequent

180   analyses.

181   Because water temperature can vary substantially among years, we compared thermal

182   suitability during an average year, an exceptionally warm year, and a cool year. For temperatures

183   during an average year, we took the mean monthly stream temperature from 2002-2011; this

184   time period reflects baseline scenario 2 from Isaak et al. (2017) and includes cool, warm, and

185   average years (Table 1, Figure S2). We used 2011 to represent a cool year because this year had

186   the lowest annual mean stream temperature in our study period. Even so, two months during that

187   year (September, October) had higher than average temperatures (Table 1). The warm year is

188   represented by 2015, the year with the highest mean annual temperature. Temperatures in June of

189   2015 were 2.3°C above average (Table 1). Additionally, 2015 was an extreme drought year in

190   California.

191

192   *Geomorphic channel types*

193   We classified each reach by geomorphic channel type. To do this, we generated a fine-

194   grained hydrography with channel gradients and catchment areas from a 10 m DEM using the

195   algorithms of Jasiewicz and Metz (2011). We then spatially joined the finer-grained hydrography

196   to the stream network that was used in the temperature modeling, summarizing the mean

197   gradient and catchment area for each 1 km reach. Then, channel morphology types (Figure 2B)

198   were assigned using channel gradient and catchment area from a classification tree developed by

199   Flores et al. (2006), where channel types are comparable to the process-based classification

200   system of Montgomery and Buffington (1997). The classification algorithm of Flores et al.

201   (2006) had 76% accuracy for the stream systems they examined in other parts of the western

202   USA. We added one additional channel type, low-gradient channel, for segments with mean

203   channel gradients less than 0.0003 m/m, which marks the approximate lower range limit of the

204   training data used by Flores et al. (2006) to develop their classification. We expect

205   geomorphology of these segments to vary between meandering and multithread depending on

206   recent history of flooding and land and water use practices, and to be dominated by sandy

207   substrates with occasional gravel patches characteristic of episodic flow regimes (e.g. Kondolf

208   and Curry 1986).

209

210   *Productivity, phenology, and thermal criteria*

211   We obtained run-specific habitat productivity, phenology, and thermal criteria for each

212   life stage from a review of several published sources. For each life stage of each species, we

213   assigned a qualitative productivity score (ideal, productive, fairly productive, poor) to each

214   channel type based on expert opinion (Table 2). The phenology of each life stage of each run,

215   defined as presence or absence in a month, was obtained from data from the Eel River Basin

216   whenever available (Table 3). For this project, we compared the peak and extended seasons for

217   certain life stages. Peak season indicates when most individuals of that life stage are present,

218   whereas the extended, full season includes all reported months of presence of that life stage.

219   Thermal thresholds are general criteria not necessarily specific to the Eel River Basin

220   (Table 4). We refer to thermal suitability as 'optimal' (the temperatures at which performance is

221   maximized), 'tolerable' (any temperature below the upper thermal limit), or 'intolerable' (the

222   temperature above which significant mortality occurs). We defined thermal tolerance as any

223   temperature below the upper thermal limit, but note that these temperatures may not be optimal

224   and performance may be reduced at some tolerable temperatures. For example, the upper thermal

225   tolerance for steelhead trout juveniles is 23°C, but optimal growing conditions are 10-17°C

226   (Table 4).

227   We developed an additional thermal criterion for rearing juvenile salmonids, accounting

228   for their exposure to pikeminnow predation and competition. The non-native Sacramento

229   pikeminnow is a major predator and competitor of juvenile salmonids in the Eel River Basin.

230   The species was recently introduced (ca. 1979), and native salmonids have been shown to avoid

231   pikeminnow by shifting their habitat use (Brown and Moyle 1991). Adult pikeminnow prefer

232   temperatures above ~18°C, increasing the likelihood of predation on and competition with

233   juvenile salmonids above this threshold (Vigg and Burley 1991, Petersen and Ward 1999, Reese

234   and Harvey 2002). Interspecific competition has been found to have a negligible effect on

235   juvenile steelhead trout at temperatures < 18°C whereas pikeminnow outcompete juvenile

236   steelhead trout at temperatures > 20°C (Reese and Harvey 2002). Thermal effects on

237   interspecific competition between juvenile Chinook salmon and pikeminnow are unknown but

238   are likely similar to steelhead trout. Juvenile salmonids can survive and grow in water

239   temperatures >18°C (e.g Railsback and Rose 1999, Satterthwaite et al. 2010), but for clarity, we

240   use "high-risk" to refer specifically to thermal conditions that expose fish to pikeminnow

241   predation and competition (> 18°C) and "suboptimal" to refer to thermal conditions that expose

242   fish to direct thermal stress or predation. For example, steelhead trout high-risk conditions

243   overlap with tolerably warm rearing temperatures (17-23°C), so we refer to 17-23°C as

244   'suboptimal'. For Chinook salmon, high-risk conditions overlap with optimal (13-20°C) and

245   tolerable rearing temperatures (20-24°C), so we refer to 18-24°C as 'suboptimal'.

246

247   **Estimates of habitat suitability**

248   We combined the datasets described above to evaluate habitat suitability in average, cool,

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249 and warm years for holding adults (summer-run steelhead trout only), incubating embryos, and

250 rearing juveniles for all runs during the time period that each life stage is present. Spawning and

251 incubation are constrained both by channel type and temperature, but we only analyzed

252 incubation because constraints are generally the most stringent for embryos incubating (Table 2,

253 Table 4). We first assessed geomorphic and thermal suitability separately for each potentially

254 accessible reach to give a baseline estimate if only one factor was important for suitability.

255 Second, we assessed the total amount of suitable habitat, combining geomorphic and thermal

256 suitability. Third, we evaluated the suitability for juveniles during outmigration when they leave

257 their natal subbasins and outmigrate to the ocean to continue growing to adulthood.

258   Because outmigrating juveniles need a continuously suitable migration route, we

259 determined the thermal suitability of the most direct pathway between each rearing subbasin and

260 the ocean. Specifically, we classified the downstream migration route as thermally optimal,

261 tolerable, or intolerable for outmigrating steelhead trout smolts or Chinook salmon juveniles for

262 each month in cool, average, and warm years. Classification was based on the least thermally

263 tolerable section of the route; for example, if any part of the outmigration pathway was

264 intolerable during a month, that month was subsequently classified as intolerable, effectively

265 blocking outmigration to the ocean. For steelhead trout, we focused on smolts during

266 outmigration because they are less thermally tolerant than non-smolt juveniles rearing and

267 outmigrating (Table 4). For Chinook salmon, we grouped outmigrating fry, parr, and smolts

268 because juvenile outmigrants in the Eel River Basin may include all of these life stages (JF *pers.*

269 *obs.*). Additionally, multiple factors, including temperature, may affect these life stages

270 differently (VTN 1982, Beak Consultants Inc. 1986, Sturrock et al. 2020), but thermal tolerances

271 for outmigrating Chinook salmon fry vs. parr vs. smolts are not well-known.

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272

273   **Estimates of capacity**

274   To estimate juvenile rearing capacity, we expanded the Unit Characteristic Method

275   (UCM; Cramer and Ackerman 2009a, 2009b), applied by Cooper et al. (2020) to the Upper

276   Mainstem, to all subbasins in the Eel River Basin. The UCM is a capacity model that multiplies

277   baseline fish density by unit area of stream habitat, then adjusts the density by habitat scalar

278   values based on parameters describing local conditions (e.g. cover, depth, pH) for each habitat

279   unit type, such as fastwater, flatwater, and pools (Cramer and Ackerman 2009a, 2009b); note that

280   field measurements in the Upper Mainstem (Cooper et al. 2020) followed the above habitat unit

281   classifications rather than the channel type classification system from our geomorphic analyses

282   (Montgomery and Buffington 1997). Fish density is closely tied to channel types (Rosenfeld

283   2003), and fish of different life stages have specific habitat and thermal requirements (e.g.

284   Hughes 1998, Moyle et al. 2017). Baseline fish densities were from a study calculating the

285   number of juveniles rearing at or near likely capacity in different habitat unit types in "ideal"

286   conditions (Johnson et al. 1993). Following Cooper et al. (2020), we added a temperature scalar

287   based on thermal effects on juvenile Coho density (Cramer et al. 2012), assuming that steelhead

288   trout and Chinook salmon show similar relationships (Cooper et al. 2020). Adapted from Cramer

289   and Ackerman (2009a, 2009b) and Cooper et al. (2020), we calculated parr capacity as:

290

291   (Equation 1) $Capacity_i = \ \ \Sigma(Area_j \times Den_j \times \ Chnl_{ij} \times Dep_{ij} \times Cover_{ij} \times Turb_i \times Drift_i \times$

292     $Fines_i \times pH_i \times Temp_{ij})$

293

294   where:

295   i = stream segment, usually 1 km in length and defined by channel gradient and

296   upstream watershed area (i.e. stream reach category; see below),

297   j = habitat unit type (i.e. fastwater, flatwater, pools),

298

299   *baseline UCM:*

300   *Area* = usable area in segment i of habitat unit type j, the product of length$_i$,

301   wetted width$_i$, and proportion of stream segment i comprised of habitat

302   unit type j,

303   *Den* = standard fish density (fish/m^2) for a given species in habitat unit type j,

304

305   *productivity scalars:*

306   *Chnl* = scalar based on wetted width$_i$, length$_i$ (if applicable), and habitat unit type

307   j,

308   *Dep* = depth scalar based on depth$_i$ and habitat unit type j,

309   *Cover* = cover scalar based on stream segment i and habitat unit type j,

310   *Turb* = turbidity scalar based on depth$_i$ and turbidity$_i$ (measured in NTUs during

311   2016 summer low flow)*,*

312   *Drift* = invertebrate drift scalar, the percentage of reach area in fastwater habitat

313   unit types that produce invertebrates (not well studied so set to 1),

314   *Fines* = fines scalar based on proportion of substrate in riffles of stream segment i

315   composed of fines,

316   *pH* = pH scalar based on pH of stream segment i,

16

317   *Temp* = temperature scalar, based on temperature of stream segment i and habitat

318   unit type j.

319

320   In the Eel River Basin, empirical measures of local conditions (excluding stream segment

321   length, stream temperature, and wetted width; see below) were only available for reaches

322   throughout the Upper Mainstem (Cooper et al. 2020). Cooper et al. (2020) categorized each

323   reach surveyed by channel gradient and upstream watershed area and measured habitat

324   characteristics for each reach to estimate the appropriate scalar for local conditions in the Upper

325   Mainstem. Following their approach, we first applied the same reach categorization scheme

326   throughout the Eel River Basin for each stream segment i. We then assigned the averaged habitat

327   values by reach category (Cooper et al. 2020) to the appropriate stream segment i, given the

328   assumption that habitat scalars measured in the Upper Mainstem could be extrapolated to the rest

329   of the Eel River Basin. Stream segment length and monthly temperature were extracted from our

330   stream temperature modeling.

331   The absolute capacity of a reach is given by the product of its capacity density (*Den*) and

332   the reach area (*Area*), the product of average wetted width and channel length of stream segment

333   i. Wetted width measurements from Cooper et al. (2020) were made in the Upper Mainstem from

334   late June to early August during the warmest time of the year at low flow conditions. Steelhead

335   trout rearing occurs throughout the year, such that low flow conditions give an estimate of

336   capacity when the steelhead trout rearing population may be bottlenecked. However, Chinook

337   salmon have usually outmigrated by late spring (VTN 1982, Beak Consultants Inc. 1986). We

338   therefore modeled wetted width each month in order to better predict how reach area changes

339   throughout the year, enabling us to better estimate Chinook salmon parr capacity. First, we

340   extracted all available measurements of flow and corresponding wetted widths from USGS

341   stream gages (https://waterdata.usgs.gov/nwis/measurements) within the Eel River Basin from

342   2002 through 2015 (to match the approximate time-scale of our temperature predictions) and

343   removed any gage with fewer than 20 measurements. For days with multiple observations at a

344   single location, we averaged these observations such that each gage had a single wetted width

345   measurement per day. This totaled to 16 stream gages and 1,590 wetted width measurements

346   within the Basin. Stream gage locations were linked with bankfull widths, estimated from

347   upstream watershed area and channel gradient. Wetted width observations were right-skewed, so

348   we log-transformed data prior to modeling. We then fit linear models for each month from

349   observed wetted widths and bankfull widths. Monthly models generally performed well (r^2 range:

350   0.61-0.84) and better than an annual model ($r^2 = 0.60$), so we used the fitted monthly models to

351   predict wetted width each month throughout the Basin (Figure S3). We did not have enough

352   wetted width measurements to fit models during the cool year (n = 128) or warm year (n = 96).

353   The UCM model includes a temperature scalar which is based on temperature and

354   juvenile salmonid density but does not include potential negative effects from the pikeminnow.

355   The magnitude of the effect of pikeminnow on juvenile salmonid density is unknown, but

356   temperatures > 18°C are high-risk for juvenile salmonid rearing due to pikeminnow presence.

357   We therefore adjusted all capacity estimates by removing stream segments that were likely

358   conducive to pikeminnow impacts (i.e. > 18°C). We evaluated the effect of pikeminnow on

359   salmonid rearing capacity by comparing these adjusted estimates with the raw, unadjusted

360   estimates calculated by the UCM model.

361   We first ran the parr capacity model for each subbasin for each month of the year to

362   determine which month most limited rearing capacity for each species. We discuss relative

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363   capacity percentages among subbasins because the UCM model includes many assumptions. For

364   example, for the standard densities we used surrogate habitat-specific parr densities from Oregon

365   coastal streams because similar data were not available for the Eel River Basin; see Cooper et al.

366   (2020) for a thorough discussion of UCM model limitations. Then we estimated adult capacity

367   from parr capacity of the bottlenecked month. To estimate the capacity of adults (returning

368   spawners) from parr estimates, we applied several likely parr-to-adult recruitment models to

369   obtain a range of realistic estimates. For steelhead trout, we used a 28% parr-to-smolt

370   recruitment and a 1.5%, 13%, or 20% ocean survival rate (Lister and Walker 1966, Johnson et al.

371   1993, Quinn 2018, Klein et al. 2008, Rawding et al. 2010, Cramer et al. 2012). For Chinook

372   salmon, we applied a 76% parr-to-smolt survival rate and 1.5%, 3%, or 4% ocean survival rate

373   (Cramer and Beamesderfer 2006, Quinn 2018, Cramer et al. 2012, Anderson and Ward 2016).

374   We report adult capacity by subbasin based on each potential ocean survival rate.

375

376   **RESULTS**

377   **Accessibility, thermal suitability, and channel type suitability in the Eel River Basin**

378   The following results assess accessibility, thermal suitability, and channel type

379   separately. Accessibility values include all potentially occupied reaches, regardless of suitability.

380   Thermal suitability did not account for channel type, and channel type suitability did not account

381   for thermal criteria, allowing us to determine how each factor impacts overall suitability.

382   In historically occupied subbasins, winter-run steelhead trout could potentially access

383   5,042 km and summer-run steelhead trout could access 3,996 km. Chinook salmon, which have

384   more restrictive physical constraints than and cannot surmount as steep of gradients as steelhead

385   trout, could only access 2,538 km. Of the potentially accessible reaches in the Basin, Scott Dam

386   blocks 5.7% (144 km) of reaches for fall-run Chinook salmon, 11.6% (584 km) for winter-run

387   steelhead trout, and 14.6% (584 km) for summer-run steelhead trout.

388   Monthly temperature exposure of each life stage of each run was usually tolerable or

389   optimal in each subbasin (denoted by height of each life stage box in Figure 3A). The exception

390   was some steelhead trout subbasins in the summer, which impacted two life stages in particular.

391   First, in some subbasins, late-incubating steelhead trout embryos (incubating into or past May)

392   may have been exposed to intolerable temperatures, especially during warmer than average years

393   ("Incubation" boxes in Figure 3A, Figure S4, Figure S5A-B). Similarly, some subbasins were on

394   average thermally tolerable for juveniles, but were high-risk due to increased pikeminnow

395   presence (i.e. > 18°C; dashed line in Figure 3A). The Upper Mainstem had cooler temperatures

396   than most other subbasins throughout all months, and across cool, average, and warm years (see

397   thick red lines in Figure 3A, Figure S4). From August-September in each subbasin, temperatures

398   were generally similar between cool, average, and warm years. The biggest temperature

399   differences between year types occurred in the late winter and throughout spring (Figure S4,

400   Figure S5).

401   The amount (river km) and proportion of each channel type varied across subbasins

402   (Figure 3B) and by life stage. In particular, spawning and incubation are limited by channel type

403   (Table 2), but most of the Basin was geomorphically classified as ideal (i.e. pool-riffle) or

404   productive/fairly productive (i.e. step-pool, plane-bed, low gradient channel) (Figure 3B). The

405   Upper Mainstem had a similar high percentage of fair or better spawning and incubation habitat

406   (~80-90%, varying by run) relative to the rest of the Basin (~80-93%), indicating that for these

407   life stages, temperature may be more limiting than channel type. In total, the Upper Mainstem

408   offers 129 and 467 km (for Chinook salmon and steelhead trout, respectively) of spawning and

409 incubation habitat geomorphically classified as fairly productive or better, comparable to the Van

410 Duzen (190 and 372 km, respectively).

411

412 **Habitat suitability**

413 *Summary*

414   In summary, reaches were generally thermally and geomorphically suitable for most of

415 the year, but suitability became restricted throughout the Eel River Basin during summer, and

416 more so in the warm year than in the average year. Rearing juveniles were the most impacted by

417 high temperatures due to thermally mediated exposure to pikeminnow. Other life stages –

418 particularly steelhead trout incubating into the late spring – may have experienced poorer

419 conditions during off-peak season and during a warm year, but conditions during peak season

420 were generally productive. Similarly, high temperatures along the migration route may have

421 prevented juveniles outmigrating in the summer, but most outmigration likely occurred in the

422 spring. In general, the Upper Mainstem had a similar or higher proportion of suitable habitat

423 during all life stages relative to other subbasins. In terms of total habitat, the Upper Mainstem

424 had a comparable amount of consistently suitable habitat as the Van Duzen. Below, we discuss

425 results in detail for each life stage. Unless specifically noted below, habitat suitability results

426 account for both thermal and geomorphic habitat constraints.

427

428 *Adult migration*

429   Summer-run steelhead trout usually migrate to the spawning grounds in the spring,

430 whereas fall-run Chinook salmon and winter-run steelhead trout migrate in the late-fall and

431 winter (Table 3). In general for all runs, we found most subbasins during the migration season

432   had tolerable temperatures (Figure 3A, Figure S4). However, some migrant summer-run

433   steelhead trout may arrive in late spring or summer, and some winter-run steelhead trout and fall-

434   run Chinook salmon may arrive in early fall (Table 3). These early or late migrators could

435   experience intolerably warm temperatures along some reaches (Figure S5). Although thermal

436   conditions for off-peak migrants were usually tolerable in the Upper Mainstem even during the

437   warm year, migrants may have to traverse downstream sections that were intolerable. We did not

438   evaluate channel type because we assume adult migrants can traverse all channel types.

439

440   *Adult holding*

441   Summer-run steelhead trout, unlike winter-run steelhead trout and fall-run Chinook

442   salmon, migrate early to the spawning grounds and hold for months prior to spawning in the

443   winter and spring (Table 3). High temperatures in the summer potentially limit their holding

444   distributions, so thermal suitability throughout the Basin was evaluated for June, July, August,

445   and September. We did not evaluate channel type because our geomorphic channel type analysis

446   cannot predict pools formed by exogenous factors like woody debris or rock outcrops (see

447   Discussion). Thermally optimal holding habitat was present in June in most subbasins even

448   during the warm year but became greatly restricted during July and August in all year types

449   (Table S1). Still, most reaches in all historic subbasins were tolerable or better across all summer

450   months and year types, with the exception of the Upper Middle Mainstem (Figure 4, Table S1).

451   During the warm year, the Upper Mainstem – alongside Larabee, South Fork, and the Van Duzen

452   – had suitable cold-water habitat for adults holding, but adults would need to pass through other

453   subbasins before those downstream reaches became unsuitable in June or July (Table S1); most

454   summer-run steelhead trout adults migrate to upriver holding areas in April and May, although

455 some fish migrate in the summer (Table 3). By September across all year types, all reaches were

456 thermally optimal or tolerable, although stream temperatures were slightly warmer than those in

457 June (Table S1). Relative to the rest of the subbasins, the Upper Mainstem had a higher

458 percentage of optimal conditions in August for all year types, second only to the Van Duzen and

459 similar to the South Fork (Figure 4, Table S1). In absolute terms, this translates 216 km of

460 optimal habitat in the Upper Mainstem, comparable to that of the Van Duzen (240 km). No

461 reaches in the Upper Mainstem were classified as thermally intolerable during the summer for

462 any year type.

463

464 *Embryo incubation*

465 Channel type and thermal suitability varied in peak and extended seasons, by species, and

466 by year type. During peak incubation season for all runs across all year types, the Upper

467 Mainstem had 79-90% suitable habitat (i.e., habitat that was thermally tolerable or better and

468 fairly productive or better), comparable to the Van Duzen subbasin (Table S2). Throughout the

469 entire incubation season in cool and average years, the blocked Upper Mainstem had the most

470 (for winter-run steelhead trout) or third most (for summer-run steelhead trout) suitable incubation

471 habitat for steelhead trout runs (Figure 5, Table S2). Steelhead trout had little suitable habitat for

472 the full incubation season during the warm year throughout the Eel River Basin (orange color in

473 top and middle panels in Figure 5, Table S2). Chinook salmon had suitable incubation habitat

474 throughout the Basin. Notably, Chinook salmon suitability was very similar in peak and

475 extended seasons across year types (bottom panels in Figure 5, Table S2). In contrast, very late

476 steelhead trout spawners and incubating embryos (incubating in or past May) could be exposed

477 to intolerably warm temperatures throughout most of the Basin.

478

479   *Juvenile rearing and outmigration*

480   Temperature – either due to physiological constraints or predator/competitor exposure –

481   poses the primary restriction on habitat use for juveniles (Table 2, Table 3). Most reaches were

482   suboptimal or tolerable, but several large subbasins (e.g. Middle Fork, Lower Middle Mainstem,

483   Upper Middle Mainstem, North Fork) all had non-negligible amounts of thermally intolerable

484   habitat in July (Figure 6, Figure S6, Table S3). In contrast, no reaches were intolerable to

485   juveniles in the Upper Mainstem. Still, many reaches were warm enough to expose juveniles to

486   an increased risk of pikeminnow interactions, especially from June-September during all year

487   types. The highest proportions of suboptimal and intolerable conditions occurred in July. Fall-run

488   Chinook salmon in this Basin tend to outmigrate by May (Table 3), avoiding suboptimal or

489   intolerable conditions, whereas steelhead trout rearing occurs throughout the year. The Upper

490   Mainstem hosted a higher amount of optimal rearing habitat for steelhead trout than all other

491   subbasins except the South Fork.

492   Outmigrating juveniles can use the full range of channel types but need a migration route

493   between their rearing subbasin and the ocean that is continuously thermally suitable while

494   transiting through it. Generally, we found that all steelhead trout smolt outmigration routes were

495   thermally optimal or tolerable from October through May (Figure 7A, Figure S7A). Intolerable

496   stream temperatures somewhere along most routes prevented steelhead trout smolts from

497   outmigrating in the summer. During the cool year, some relatively short migration routes were

498   tolerable in June compared to intolerable in average years. In the warm year, many relatively

499   long migration routes shifted from optimal (average year) to tolerable in May, and all routes

500   shifted from optimal to tolerable in October. In contrast to steelhead trout smolts, Chinook

24

501   salmon outmigrants have less stringent thermal limits (Table 4), and juveniles are typically out of

502   rearing areas before mid-summer (VTN 1982, Beak Consultants Inc. 1986). Still, in the summer,

503   long migration routes were sometimes intolerable, depending on the month and year type (Figure

504   7B).

505

506   **Parr and spawner capacity**

507   Parr capacity varied across the year due to changes in usable reach area and temperature.

508   Within the steelhead trout rearing season (full year; Table 3), August was the month most

509   limiting to capacity (Figure 8A). A few Chinook salmon may rear into July (Table 3), but most

510   outmigration occurs by late spring (VTN 1982, Beak Consultants Inc. 1986), indicating that May

511   was likely the month with the most limiting capacity for Chinook salmon parr (Figure 8A).

512   When excluding habitat with pikeminnow exposure, 11.5% of the steelhead trout parr capacity in

513   the Eel River Basin was found in the Upper Mainstem, similar to the Van Duzen; when

514   pikeminnow exposure was ignored, 5.8% of capacity was found in the Upper Mainstem, similar

515   to the North Fork. For Chinook salmon, the Upper Mainstem could hold ~1.4% of the total parr

516   capacity; this value did not change with pikeminnow exposure because temperature throughout

517   the Basin was too cool for pikeminnow in May.

518   Using three parr-smolt-adult survival models per species, we converted parr capacity in

519   the most limiting month to adult returns (Figure 8B). In the Upper Mainstem, estimates of adult

520   capacity ranged from 256-5,370 for steelhead trout and 1,242-3,314 for Chinook salmon, with

521   the large ranges in results stemming from 1) the application of three different survival models

522   and 2) whether parr estimates were adjusted for pikeminnow exposure.

523

DISCUSSION AND CONCLUSIONS

524
525   We compared the habitat suitability and capacity of the Upper Mainstem subbasin that is

526   currently blocked by Scott Dam to all other Eel River subbasins in order to characterize its

527   relative importance to the Basin's Chinook salmon and steelhead trout populations during cool,

528   average, and warm years. For the Eel River Basin as a whole, our analyses found that most

529   reaches within the limits of anadromy were suitable for the salmonid life stage present in each

530   month, but some reaches became suboptimal due to thermally-mediated pikeminnow interactions

531   or even thermally intolerable in the summer months. The amount of suitable habitat was

532   generally higher during the cool year and lower during the warm year relative to the average

533   year, but subbasins showed heterogeneity in how suitability changed by year type. In general, the

534   Van Duzen subbasin had the highest proportion of cool-water refugia and suitable channel type

535   for multiple runs and life stages; the currently inaccessible Upper Mainstem had the second

536   highest proportion of cool-water refugia and suitable channel type of the Eel's subbasins. We

537   found that the Upper Mainstem harbors a significant amount of suitable habitat and could likely

538   sustain anadromous populations of winter-run steelhead trout, summer-run steelhead trout, and

539   fall-run Chinook salmon, even during a warm year. Although we examined suitability and fish

540   capacity in the Eel River Basin, California, our approach can be applied in any setting where

541   spatially explicit environmental metrics can be estimated and habitat criteria for populations and

542   life stages can be specified.

543   Based on our thermal and geomorphic habitat assessments, the blocked Upper Mainstem

544   generally contains a higher proportion of suitable habitat for all freshwater salmonid life stages

545   than much of the rest of the Eel River Basin. Still, suitable habitat was restricted during summers

546   and/or warm years. During incubation, some reaches became thermally intolerable, particularly

547 for late-spawned steelhead trout embryos. Similarly, summer-run steelhead trout migrating in the

548 off-peak summer months would likely be exposed to thermally intolerable reaches. However, if

549 migration timing and spawn timing follow a somewhat normal (Gaussian) distribution (e.g.

550 FitzGerald et al. 2019), it is likely that relatively little migration or incubation for any run

551 actually occurs during these marginal months surrounding the peak. This means that, on the

552 whole, most migration and incubation was still thermally tolerable, even during the warm year. If

553 water temperatures continue to rise in response to global warming, thermally suitable migration

554 and incubation windows of time may become constricted, effectively constraining the non-peak

555 life history strategies. Fringe, rare, and alternative life history strategies can have

556 disproportionate impacts on salmonid abundance and survival during periods of environmental

557 stress (Cordoleani et al. 2021), and within-population diversity is important for salmonid

558 resilience (Greene et al. 2010, Sturrock et al. 2020). In the Eel River Basin, providing more cool-

559 water refugia in the summer could increase survival for these non-peak life history strategies,

560 helping to increase the resilience of the populations.

561   Juvenile rearing was also restricted during summer throughout the Eel River Basin due to

562 the increased exposure to pikeminnow at temperatures above 18°C. For example, the majority of

563 the Middle Fork, the second largest subbasin, became thermally suboptimal or intolerable in the

564 summer. In contrast, the majority of the Upper Mainstem was thermally optimal during summer

565 months of all year types. This blocked subbasin had a similar amount of thermally optimal

566 habitat (km) as the Van Duzen and Lower Mainstem during July of the warm year, the most

567 limiting case. For steelhead trout, this large amount of optimal rearing habitat was second only to

568 the South Fork subbasin, but the South Fork included reaches with intolerable habitat whereas

569 the Upper Mainstem did not. Therefore, in the summer during warm years, the Upper Mainstem

570 may provide a large amount of cool-water refugia from pikeminnow interactions relative to

571 much of the rest of the Eel River Basin.

572   We calculated habitat suitability in terms of number of river km, similar to the Intrinsic

573 Potential (IP) model (Burnett et al. 2003). Other models have also estimated the number of

574 suitable river km above Scott Dam, with estimates ranging from 94-463 km for steelhead trout

575 and 94-160 km for Chinook salmon (see Cooper et al. [2020] for previous estimates). We

576 estimated that this subbasin (not including potential habitat submerged by Lake Pillsbury) has

577 169-467 km for steelhead trout and 51-129 km for Chinook salmon even during a warm year,

578 with results varying by life stage. Our estimate of 461 km of thermally suitable steelhead trout

579 spawning and incubation habitat in the Upper Mainstem is similar to the 437 km estimated by

580 Cooper et al. (2020) (neither estimate included reaches inundated by Lake Pillsbury). Although

581 our estimates overlap with others, our assessments are more detailed in that they evaluated the

582 dynamics of suitability across three different year types, included monthly-varying stream

583 temperatures and temperature criteria specific to each life stage, and incorporated fish-varying

584 productivity levels in multiple channel types. Additionally, we accounted for an important

585 predator and competitor of salmonids, the pikeminnow, which strongly restricted the amount of

586 suitable habitat for juvenile rearing.

587   Because our thermal and geomorphic habitat assessments suggest that juvenile rearing is

588 likely the most limiting life stage, particularly for steelhead trout, we assessed adult capacity in

589 each subbasin based on the most limiting month for parr capacity (August for steelhead trout and

590 May for Chinook salmon). Within each species, our adult capacity estimates varied substantially

591 – often beyond an order of magnitude – dependent on ocean survival rate scenario and whether

592 we accounted for pikeminnow exposure. Similarly, previous estimates of potential adult capacity

593   above Scott Dam, including those from the Intrinsic Potential (IP) model (NMFS 2016), a similar

594   UCM model (Cooper et al. 2020), and surrogate data from accessible subbasins (Cooper et al.

595   2020), have ranged from 1,499-26,381 for steelhead trout and 1,057-10,117 for Chinook salmon

596   (see Cooper et al. [2020] for previous estimates). For steelhead trout, our estimates overlap with

597   previous estimates when we included moderate and high ocean survival rate scenarios. Our

598   Chinook salmon adult capacity estimates also overlapped with previous estimates. For Chinook

599   salmon, accounting for pikeminnow exposure did not substantially reduce capacity estimates

600   because May temperatures are relatively cool. In contrast, accounting for steelhead trout

601   exposure to pikeminnow negatively impacted capacity estimates from August. Note, however,

602   that our capacity estimates accounting for pikeminnow interactions treated suboptimal reaches as

603   having no salmonid production, such that true capacity may be higher if pikeminnow reduces

604   rather than eliminates salmonid production. To improve our capacity estimates and reduce their

605   uncertainty for both species, we need: a better understanding of pikeminnow impacts on

606   salmonid capacity at different temperatures, ground-truthing throughout the Basin to determine if

607   local conditions measured in the Upper Mainstem are representative of the other subbasins;

608   better estimates or models of wetted width throughout the Basin as flow varies across space and

609   time; more flow and wetted-width measurements in smaller streams; local estimates of parr

610   capacity by habitat unit type; and basin-specific parr-to-adult survival models (Cooper et al.

611   2020).

612   All production capacity models, including the UCM model applied here and the IP

613   model, have difficulty in capturing how production and capacity change in dynamic systems.

614   The Eel River Basin is particularly dynamic, containing a variety of channel types with stream

615   temperatures ranging from near freezing to over 25°C throughout the year. Reaches that are

616   suitable in average water years may become inaccessible or unsuitable during atypical years due

617   to high temperatures or changes in flow. Spatial heterogeneity of habitat can help mitigate

618   extreme flow and temperature changes because aquatic organisms can use alternate habitat types

619   or thermally tolerable reaches as refuges, increasing the resiliency of the population (Hilborn et

620   al. 2003, Brennan et al. 2019). Further, spatial heterogeneity avoids concentrating vulnerable life

621   stages, particularly juveniles, in areas where mortality risk is higher, for example, due to

622   predation (Nakamoto and Harvey 2003). Heterogeneity also allows organisms to better exploit

623   multiple habitat types during cool years when temperature-dependent mortality is lower (Hilborn

624   et al. 2003, Brennan et al. 2019). For example, early- or late-spawned embryos that would be

625   exposed to intolerable conditions during an average or warm year may instead experience

626   tolerable temperatures during cool years and above-average survival rates, increasing the number

627   of juveniles rearing in those years. To avoid areas of high density and increased competition,

628   juveniles during cool years may exploit non-ideal (but still productive) habitat types. Relative to

629   much of the rest of the Eel River Basin, the blocked Upper Mainstem has a greater proportion of

630   thermally suitable habitat that could be readily exploited, even in summer during a warm year,

631   by both steelhead trout and Chinook salmon. This indicates that the Upper Mainstem could be an

632   important and productive subbasin for the Eel River Basin during abnormally warm years, which

633   are expected to increase in frequency with anthropogenic climate change (e.g. Ault 2020,

634   Williams et al. 2020).

635   We did not directly estimate the resilience of cool-water refugia in the Eel River Basin to

636   climate change. However, 2015 was an exceptionally warm and dry year that may represent

637   stressful conditions that will occur more frequently in the future in the western U.S. (e.g. Ault

638   2020, Williams et al. 2020). It is interesting to note that summer/early-fall (i.e. ~July-September)

639   stream temperatures were similar across the cool, average, and warm year cases, indicating that

640   some strong negative feedbacks (e.g. feedbacks stemming from evaporative cooling; Mohensi

641   and Stefan 1999, Boughton et al. 2012) may be limiting peak summer stream temperature.

642   Increased levels of thermal stress for salmonids may instead occur in spring with climate change.

643   In this study, we focused on life stages present in the summer because summer and early fall

644   stream temperatures sometimes were not optimal for these life stages. But if spring stream

645   temperatures warm at a faster rate than summer stream temperatures, life stages present in spring

646   may be more negatively impacted. Still, temperatures were usually well below the thermal

647   thresholds for life stages present in spring, even during the 2015 warm year. However, our work

648   sometimes focused on the upper thermal tolerance limit for each life stage whereas optimal

649   temperatures were often much lower. Additionally, our work used thermal thresholds that were

650   generalized for steelhead trout or Chinook salmon, but populations in the Eel River Basin may

651   have slightly different tolerances.

652   A lack of knowledge of thermal criteria or other important factors precluded suitability

653   assessments for some life stages in this study. We did not evaluate thermal or geomorphic

654   suitability for post-spawned, outmigrating steelhead trout adults (kelts), emergent embryos of

655   either species, or fall-run adult Chinook salmon staging (*i.e.*, holding for short periods of time

656   downstream of spawning grounds while waiting for suitable conditions), all of which could be

657   negatively impacted by climate change. For outmigrating kelts and emergent embryos, upper

658   thermal limits are not well-known. Fall-run Chinook salmon must hold in the estuary in late

659   summer/fall or below spawning grounds if flows are not high enough (Moyle et al. 2017). We

660   did not directly include how changes in flow may affect access to spawning grounds because

661   more flow measurements throughout the Eel River Basin and better models describing how flow

662   varies across space and time are needed. These life stages require further study to determine how

663   flow and temperature variations may affect them in the Eel River Basin.

664   Two life stages that were included in this analysis may also require further study due to

665   additional factors that could impact habitat suitability during those stages. The first is juvenile

666   outmigration. Our modeling results show when outmigration is either precluded or possible

667   based on stream temperature, but outmigration timing is also influenced by flow conditions,

668   food, rate of stream temperature increase, photoperiod, predation risk, and fish size, each of

669   which could increase mortality if outmigration occurred earlier in the spring or later in the

670   summer (Ewing et al. 1979, VTN 1982, Beakes et al. 2010, Larsen et al. 2010, Sharron 2015,

671   Sturrock et al. 2020). Flow conditions are especially important for outmigrating juveniles, such

672   that water is released from the dammed reservoirs in the spring to try to mimic the historical

673   natural hydrograph and stimulate juvenile salmonid outmigration (NMFS 2002, O'Dowd and

674   Trush 2016). Additionally, outmigration strategy (i.e., smolting instream vs. estuary) and age of

675   smoltification vary among and within populations and years such that outmigration can include

676   fry, parr, and yearling smolts in varying proportions each year. Each of these life-history variants

677   likely has different thermal and other selection pressures (e.g. VTN 1982, Beak Consultants Inc.

678   1986, Sturrock et al. 2020), but differences in thermal thresholds are not well-understood. For

679   example, it is possible that predation is size-dependent (e.g. Lorenzen 1996) such that

680   pikeminnow may impact fry or parr more than larger smolts, but this has not been demonstrated,

681   so we did not include a pikeminnow thermal threshold for our outmigration analyses. Future

682   work examining the suitability along juvenile outmigration routes could include other factors

683   such as flow conditions and outmigration timing by fish size.

684   The second life stage in our study that may require further analysis is adult holding for

685 summer-run steelhead. During the summer, summer-run steelhead trout adults usually hold in

686 slow-moving, cool-water pools, which help them to conserve energy prior to spawning. Our

687 results showed that most reaches were thermally tolerable for adults, and the Upper Mainstem

688 was comparable to the Van Duzen in terms of its amount of optimal holding habitat.

689 Additionally, our prediction of extensive tolerable but little optimal holding habitat in the Middle

690 Fork agrees with a study of empirical temperature recordings of known summer-run steelhead

691 trout holding pools, which found that most pool surface and bottom temperatures were tolerable

692 (16-23°C) and very few were optimal (A. Clemento *pers. comm.*). Still, our stream temperature

693 modeling assumes water mixing and cannot predict thermal stratification (Isaak et al. 2017).

694 Steelhead trout may be present in stratified layers of pools that are up to 9°C cooler than the

695 surface (Nielsen et al. 1994), indicating that there may be more cool-water refugia than our

696 model shows.

697   An additional consideration is that our adult steelhead trout holding analysis did not

698 include suitability by channel type. Of our geomorphic classifications, self-formed pools are

699 more likely to be found in step-pool or pool-riffle habitats (Montgomery and Buffington 1997,

700 Buffington et al. 2002). Approximately 63.9% of the currently blocked Upper Mainstem consists

701 of these habitats, and therefore ~373 km are likely to contain pools, similar to 60.9% in the other

702 subbasins. However, adult salmonids may also hold in forced pools, which are formed by

703 exogenous factors such as coarse woody debris or streamside rock outcrops. We cannot currently

704 predict forced pools using geomorphic classification alone, although these types of pools may be

705 identifiable using high resolution aerial imagery or local-scale habitat studies. Our estimates of

706 the amount of suitable habitat for holding adults was therefore based on temperature only. It's

707 important to note that salmonids are more likely to be found in cooler, larger, and deeper pools

708   (Nakamoto 1994, Nielsen et al. 1994, Baigún 2003), but we are currently unable to accurately

709   model the likely presence of thermally stratified pools, pool size, or pool depths from

710   geomorphic classifications or stream temperature modeling.

711   Similarly, our stream temperature model and geomorphic channel type classifications

712   have some limitations regarding spatial scale. Stream temperature was predicted at every river

713   kilometer due to the resolution of the input environmental layers in the model and the regional

714   scale analyzed. However, this spatial scale fails to resolve smaller (< 1 km) cool-water refugia or

715   pools (Fullerton et al. 2018), indicating that more thermally suitable pools may be present than

716   we predict. Previous Eel River Basin studies have modeled stream temperature at finer spatial

717   scales than our study (Asarian and Walker 2016, Asarian et al. 2016, David et al. 2018, Cooper

718   et al. 2020), although these other studies did not predict stream temperature throughout the entire

719   Basin. Regardless, fitting the stream temperature model at finer resolutions may not predict pools

720   that are very deep, thermally stratified, influenced by hyporheic flow, or forced by exogenous

721   factors such as woody debris (Isaak et al. 2017). However, airborne thermal infrared imagery

722   could be used to map surface temperatures at much higher resolution from small planes or

723   unmanned autonomous vehicles (drones) (Fullerton et al. 2018). We predicted geomorphic

724   channel type from gradient and catchment area, estimated from a 10 m DEM. Although a 10 m

725   DEM has accurately predicted channel gradient in some systems ($r^2 = 0.88$; Davies et al. 2007), a

726   10 m DEM may miss finer-scale changes in channel type (Flores et al. 2006). Gradient,

727   catchment area size, and channel type classification accuracy for Eel River subbasins were not

728   assessed here due to lack of training data.

729   Although there is some inherent uncertainty due to the spatial and temporal scale of our

730   analyses and the large ranges in the number of suitable river km and capacity estimated by our

34

731 study and others, we conclude that the Upper Mainstem is comparable to the Van Duzen

732 subbasin based on the amount of thermally and geomorphically suitable habitat for multiple

733 freshwater life stages. But a potentially more important question is: if access was provided to the

734 Upper Mainstem, would these populations rebound? In a similar system, two impassable dams

735 blocking Washington's Elwha River were removed after having been in place for over 100 years.

736 Since their removal, multiple anadromous salmonid populations have recolonized the previously

737 blocked but now accessible upstream Elwha River habitats (Bellmore et al. 2019, McMillan et al.

738 2019, Fraik et al. 2021). In the Eel River Basin, a recent genetic study showed that steelhead

739 trout with summer-run and winter-run alleles still reside upstream of Scott Dam after 100 years

740 of isolation from other anadromous populations due to lack of upstream passage (Kannry et al.

741 2020). If access were provided to the Upper Mainstem, these fish have the potential to "restart"

742 the anadromous populations, potentially without additional reintroductions, recolonizations, or

743 translocations from other subbasins (Kannry et al. 2020). Note, however, that to reach the Upper

744 Mainstem, anadromous fish still have to pass Cape Horn Dam via a fish ladder that is only

745 partially compliant with fish passage regulations (Stillwater Sciences et al. 2021); population

746 recovery in the Upper Mainstem may therefore also depend on downstream improvements. Still,

747 based on our evaluation of the quality and quantity of suitable habitat and potential capacity,

748 enabling access to the blocked Upper Mainstem subbasin could likely support populations of

749 winter-run steelhead trout, summer-run steelhead trout, and fall-run Chinook salmon, even

750 during warm months and during exceptionally warm and dry years like 2015.

751

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761　　**DATA ACCESSBILITY**

762　　Relevant data (monthly stream temperature, geomorphic channel type, and monthly wetted width

763　　for every stream segment in the Eel River Basin) needed to replicate our work are openly

764　　available in the DRYAD data repository at https://doi.org/10.5061/dryad.ksn02v74x.

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Physical and biological constraints on the capacity for life-history expression of anadromous salmonids: an Eel River, California, case study

Alyssa M. FitzGerald, David A. Boughton, Joshua Fuller, Sara N. John, Benjamin T. Martin, Lee R. Harrison, Nathan J. Mantua

TABLES AND FIGURES

TABLES

TABLE 1

Table 1. Mean monthly temperatures (°C) during an average water year (2002-2011), and the temperature difference (°C) from the average for each month during a cool year (2011) and warm year (2015) in the Eel River Basin. Annual mean temperature and standard deviation (SD) for each year type are shown in the bottom row.

Month	Mean temp. (°C) Average	Temp. deficit (°C) from average year Cool	Warm
Jan	6.00	-0.06	0.35
Feb	6.29	-0.82	1.69
Mar	7.33	-0.56	1.42
Apr	9.07	-0.87	1.15
May	11.71	-1.33	1.33
Jun	13.97	-1.39	2.26
Jul	16.92	-1.36	0.27
Aug	16.44	-0.19	0.23
Sep	14.39	0.31	-0.11
Oct	11.11	0.07	1.29
Nov	7.95	-0.53	-0.63
Dec	6.87	-0.66	0.03
Annual mean temp. ± SD (°C)	**10.67 ± 4.36**	**10.05 ± 4.33**	**11.44 ± 4.40**

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TABLE 2

Table 2. Productivity level assumed for different habitat types for several life stages of steelhead trout and Chinook salmon.

Species	Geomorphic habitat types				
Life Stage	Pool-riffle	Step-pool	Plane-bed	Low gradient channel	Cascade
Steelhead trout					
Spawning/Incubation/ Emergence[a,c]	Ideal	Productive	Productive	Fairly prod.	Poor
Rearing[d]	Productive	Productive	Productive	Productive	Productive
Chinook salmon					
Spawning/Incubation/ Emergence[b,c]	Ideal	Fairly prod.	Fairly prod.	Fairly prod.	Poor
Rearing[d]	Productive	Productive	Productive	Productive	Fairly prod.

[a]Pfeiffer and Finnegan 2016; [b]Montgomery et al. 1999; [c]Buffington et al. 2004; [d]Moyle et al. 2017

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TABLE 3

Table 3. Phenology for each life stage for winter-run steelhead trout, summer-run steelhead trout, and fall-run Chinook salmon. Phenology is defined from Eel River Basin steelhead trout populations and from California Coastal fall-run Chinook salmon populations. For phenology, an 'x' indicates presence, and an 'xx' indicates peak (if known). Blanks may represent no presence or a lack of data.

Life Stage	Month											
	J	F	M	A	M	J	J	A	S	O	N	D
Eel River winter-run steelhead trout												
Adult Migration[a,f,g,h]	xx	xx	xx	xx	x	x			x	x	x	x
Holding[b,f]	x	x							x	x	x	x
Spawning[a,f,g]	xx	xx	xx	xx							x	x
Adult Outmigration[f]		x	x	x	x	x						
Incubation[b,c]	xx	xx	xx	xx	x	x					x	x
Emergence[b,c]	x	x	x	x	x	x	x	x				x
Rearing[c]	x	x	x	x	x	x	x	x	x	x	x	x
Juvenile Outmigration[i]*		x	x	x	x	x	x					
Eel River summer-run steelhead trout												
Adult Migration[a,f,g]			x	xx	xx	x	x	x	x	x		
Holding[b,f]	x					xx	xx	xx	xx	xx	x	x
Spawning[a,b]	xx	x	x	x	x							x
Adult Outmigration[b]	x	x	x	x	x							x
Incubation[c]	xx	xx	x	x	x	x	x					x
Emergence[b,c]	x	x	x	x	x	x	x	x	x			
Rearing[c]	x	x	x	x	x	x	x	x	x	x	x	x
Juvenile Outmigration[i]*		x	x	x	x	x	x					
California Coastal fall-run Chinook salmon												
Adult Migration[b,d,e,h]	x								x	x	xx	xx
Holding[b,d,e]												
Spawning[d,f]	x	x								x	x	xx
Adult Outmigration	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
Incubation[b,d,e]	x	x	x	x	x					x	x	x
Emergence[b,d,e]	x	x	x	x	x							x
Rearing[b,d,e]		x	x	x	x	x	x					
Juvenile Outmigration[i]		x	x	x	x	x						

[a]Busby et al. 1996; [b]Moyle et al. 2017; [c]McEwan & Jackson 1996; [d]Myers et al. 1998; [e]NMFS 2016; [f]JF *pers. obs.;* [g]CDFG 1975; [h]Kajtaniak and Easterbrook 2019; [i]VTN 1982
*We did not differentiate between the two steelhead trout runs during juvenile outmigration due to identification difficulty.

4

TABLE 4

Table 4. Temperature thresholds of each life stage for steelhead trout and Chinook salmon, based on literature reviews. 'Optimal' is the temperature at which performance (e.g. growth rate) is maximized. 'Tolerable' implies that temperature-dependent survival will likely occur but performance is reduced relative to the optimal. 'Intolerable' represents the incipient upper lethal temperature, above which significant mortality occurs with prolonged exposure. When sources disagreed, we applied the lowest temperature reported. Blanks represent a lack of data.

Life Stage	Thermal thresholds (°C)			
	Tolerable	Optimal	Tolerable	Intolerable
Steelhead trout				
Adult Migration[a,d]	<10	10-15	15-19	>19
Holding[a,e,f]	<10	10-16	16-23	>23
Spawning[a,d]	<6	6-11	11-15	>15
Adult Outmigration				
Incubation[a,d]	<6	6-11	11-15	>15
Emergence[c,d]	<8.9	8.9-11.1	11.1-15	>15
Rearing[a,b,d]	<10	10-17†	17-23†	>23
Parr Outmigration[g]		<17	17-26.5	>26.5
Smolt Outmigration[d,g,h]		6-16	16-20	>20
Chinook salmon				
Adult Migration[a]	<10	10-20	20-21	>21
Holding[a]	<10	10-16	16-21	>21
Spawning[a]	<13	13-16	16-19	>19
Adult Outmigration	NA	NA	NA	NA
Incubation[a]	<9	9-13	13-17	>17
Emergence[a]				
Rearing[a]	<13	13-20†	20-24†	>24
Juvenile Outmigration[g,h]*	<15	15-20	20-24	>24
Smoltification[a]	<10	10-19	19-24	>24

[a]Moyle et al. 2017; [b]Coates, Hobson et al. 2002; [c]McEwan & Jackson 1996; [d]JF (*pers. obs.*); [e]CDFW 2015 *in* Moyle et al. 2017; [f]Nielson et al. 1994; [g]Beak Consultants Incorporated 1986; [h]VTN 1982

*Chinook salmon juvenile outmigrants may include both pre-smolts and smolts (JF *pers. obs.*)

†The thermal thresholds for rearing juvenile salmonids are additionally affected by the presence of pikeminnow; see text
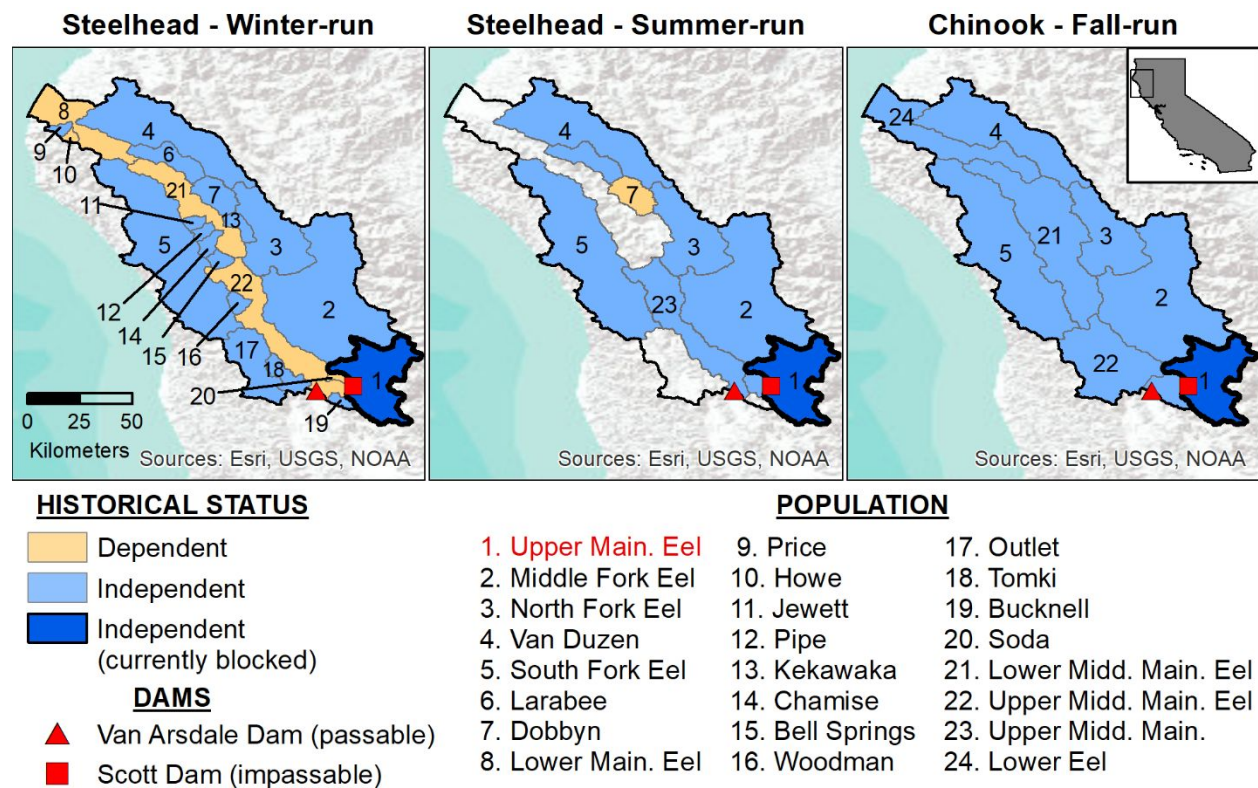
5

FIGURES

FIGURE 1

Figure 1. Steelhead trout and Chinook salmon populations in the Eel River Basin, California. Populations were defined as historically independent (likely to persist over 100-year time scales) or dependent (likely to be extirpated within 100 years without influx from other populations) (Bjorkstedt et al. 2005, Spence et al. 2008). The Upper Mainstem Eel subbasin (population 1, dark blue in figure) is currently inaccessible to anadromous salmonids due to Scott Dam. Maps are in geographic coordinate system North_American_1983.

6

FIGURE 2

Figure 2. Stream temperatures (A) and geomorphic channel types (B) in the Eel River Basin. The Upper Mainstem Eel subbasin, outlined in black, is currently inaccessible to anadromous salmonids. A) Predicted mean monthly stream temperatures from FitzGerald et al. (2021) are shown here for October (average of 2002-2011). Temperatures for every month can be found in Fig. S1. B) Geomorphic channel types in the Eel River Basin were predicted from channel gradient and upstream watershed area, using the classification algorithm of Flores et al. (2006). Maps are in geographic coordinate system North_American_1983.

7
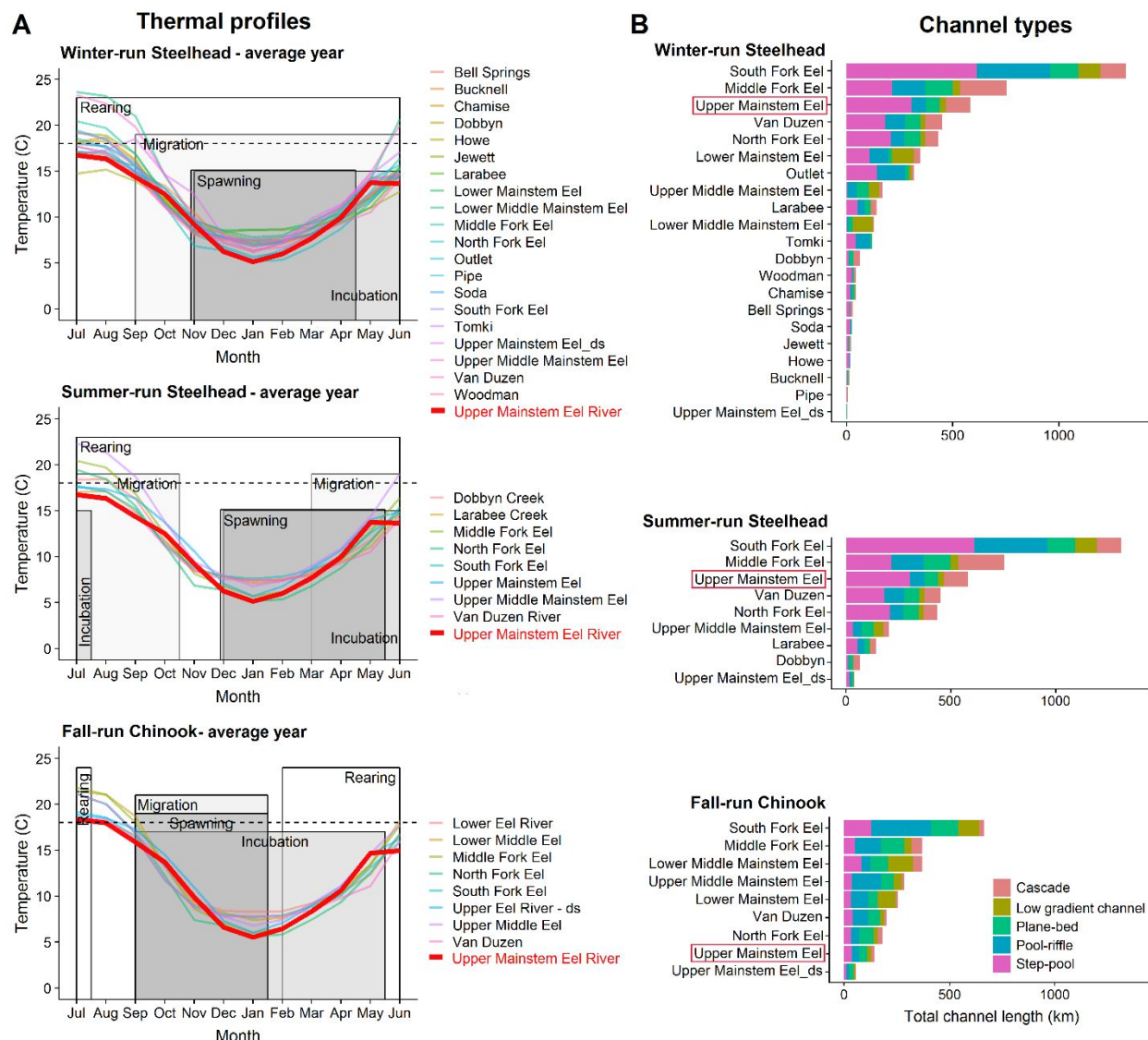
FIGURE 3

Figure 3. Thermal profiles (A) and total length (km) of each habitat type (B) for potentially accessible reaches in winter-run steelhead trout (top panels), summer-run steelhead trout (middle panels), and fall-run Chinook salmon (bottom panels) subbasins in the Eel River Basin. A) Each line shows the average temperature of that subbasin throughout an average year (all year types in Fig. S4); the currently blocked Upper Mainstem is bolded in red. The box for each life stage shows when that life stage is found in freshwater in the Eel River Basin (x axis) and the upper thermal tolerance for that life stage (y axis). To be suitable, the average temperature must be within the box for a specific life stage. The black dotted line shows the lower thermal tolerance (18°C) for pikeminnow, a major predator and competitor of juvenile salmonids. B) Total channel lengths (km) predicted for each geomorphic channel type in each subbasin. The currently blocked Upper Mainstem is outlined in red.

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FIGURE 4

Figure 4. Thermal suitability for holding summer-run steelhead trout in the month of August during cool, average, and warm years within the Eel River Basin. A) The percentage of optimal, tolerable, or intolerable thermal habitat, based on the total amount of accessible habitat, for each summer-run steelhead trout subbasin. Reaches with B) optimal and C) tolerable thermal suitability. Reaches suitable during the warm year were also suitable during the average year, and reaches suitable during the average year were also suitable during the cool year. See Fig. 1 for labeled subbasin names. Maps are in geographic coordinate system North_American_1983.

9
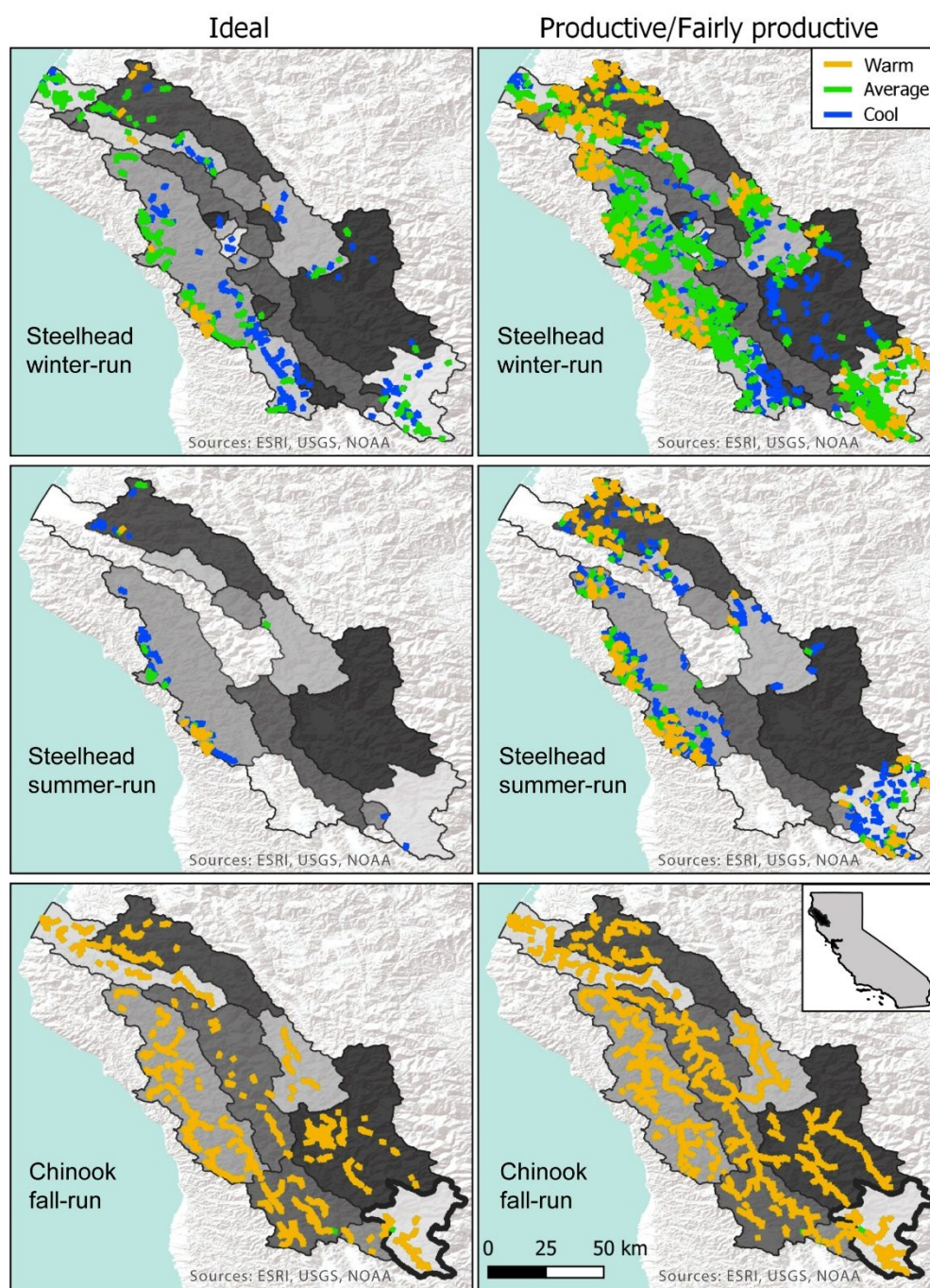
FIGURE 5

Figure 5. Thermal refuges during the entire extended incubation season that are suitable for winter-run steelhead trout (top), summer-run steelhead trout (middle), or fall-run Chinook salmon (bottom) within the Eel River Basin. Suitability is broken up by year type (colors in legend) and habitat type (left/right panels). In general, reaches suitable during the warm year were also suitable during the average year, and reaches suitable during the average year were also suitable during the cool year. Habitat type designations, months of extended season incubation, and thermal tolerability for incubation for each run can be found in Tables 2-4. Maps are in geographic coordinate system North_American_1983.

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FIGURE 6

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Figure 6. Thermal quality of juvenile rearing habitat for winter-run steelhead trout, summer-run steelhead trout, and fall-run Chinook salmon subbasins in the Eel River Basin during the summer of cool, average, and warm years. The size of each box represents the total number of potentially accessible river kilometers in that subbasin for each run, shown in the right column. The Upper Mainstem, currently dammed, is highlighted in red. For clarity, only winter-run steelhead trout subbasins with more than 50 river kilometers are shown. All subbasins and all months are shown in Fig. S6.

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FIGURE 7

13
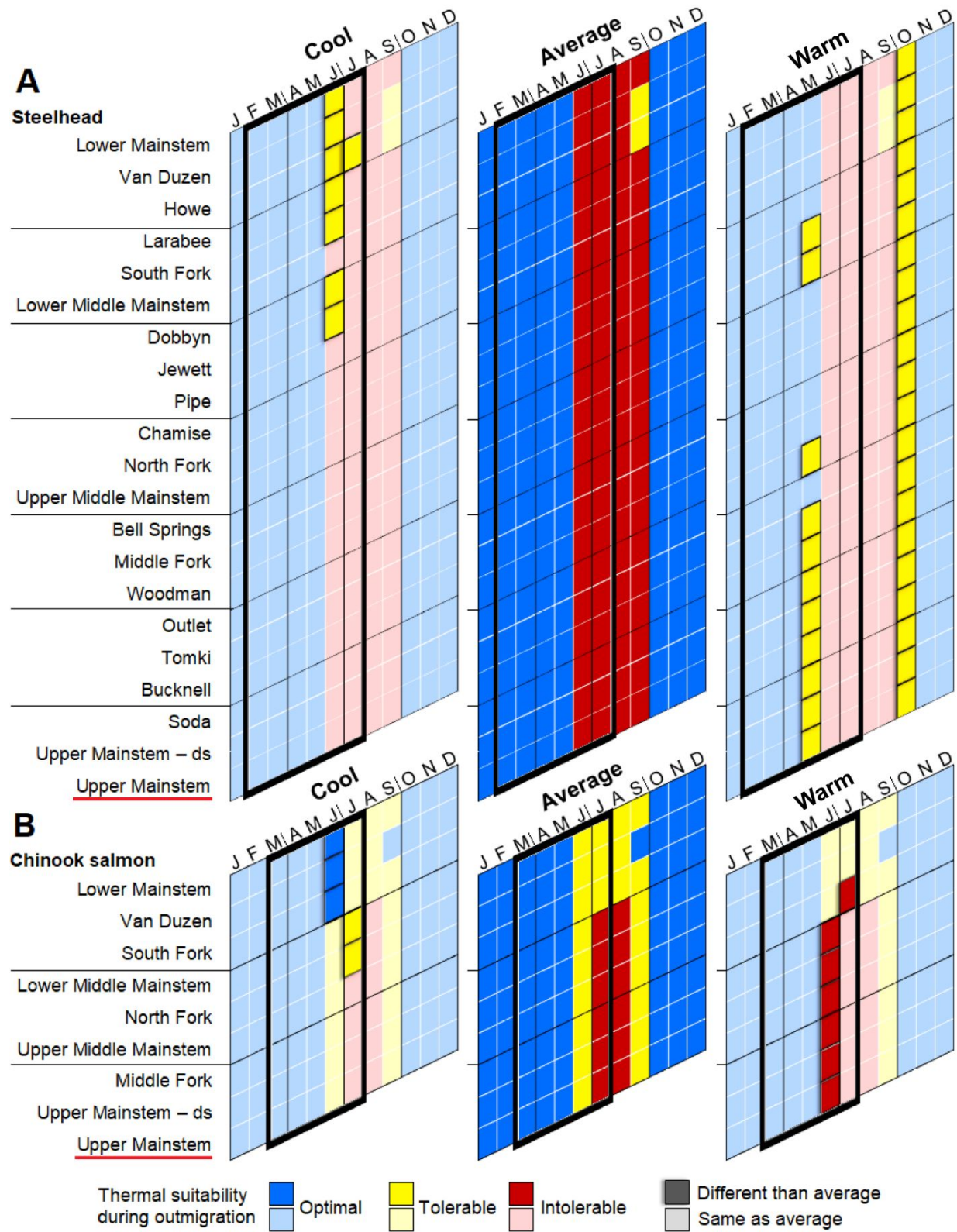
Figure 7. Thermal suitability of downstream outmigration of A) steelhead trout smolts and B) Chinook salmon juveniles. The least suitable section along the route from each subbasin downstream to the ocean defined suitability during each month. The middle panel, bolded, shows an average year. In the cool (left) and warm (right) year types, suitability that differed from an average year is highlighted with dark shading; suitability with the same classification as an average year has light shading. The usual outmigration timing for each run is outlined in black. Subbasins are ordered by approximate distance to the ocean (i.e. Upper Mainstem has longest migration route). The Upper Mainstem, currently dammed, is underlined in red.

14

FIGURE 8

15
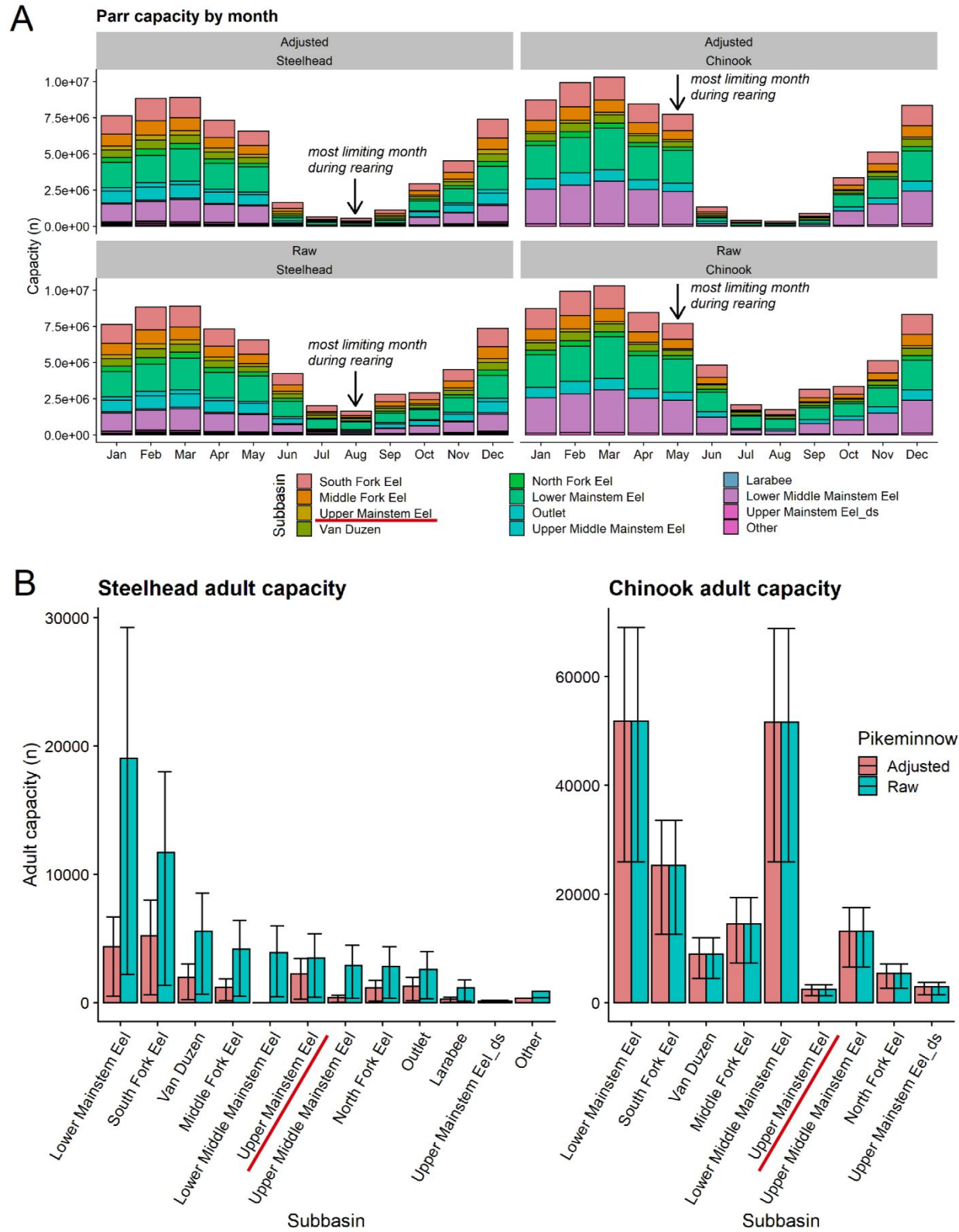
Figure 8. Estimates of steelhead trout and Chinook salmon capacity in the Eel River Basin. 'Adjusted' analyses excluded stream segments conducive to pikeminnow interactions (≥ 18°C); 'raw' analyses included them. A) Parr capacity (n) by month. Steelhead trout juveniles can rear in freshwater throughout the year, so August is their most limiting rearing month. Most Chinook salmon outmigration occurs by late spring, indicating that May is their most rearing month. B) Adult spawner capacity (n), calculated from the most limiting month for parr rearing. The colored bars show estimates based on 13% (steelhead trout) or 3% (Chinook salmon) ocean survival rate. The error bars show capacity estimates calculated from high or low ocean survival models. The Upper Mainstem, currently dammed, is underlined in red. For steelhead trout, small subbasins were grouped as 'Other'.
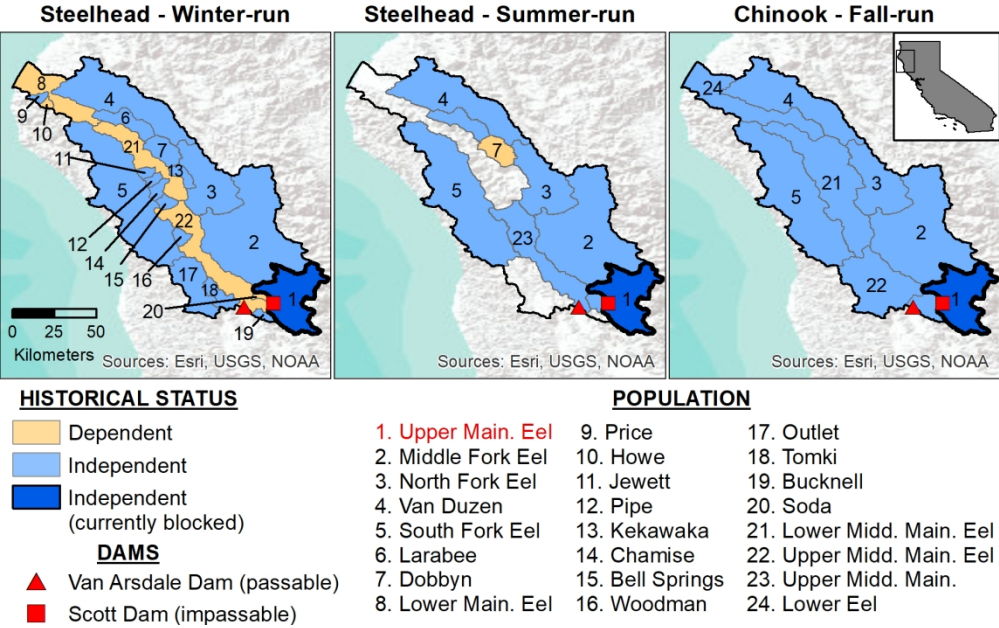
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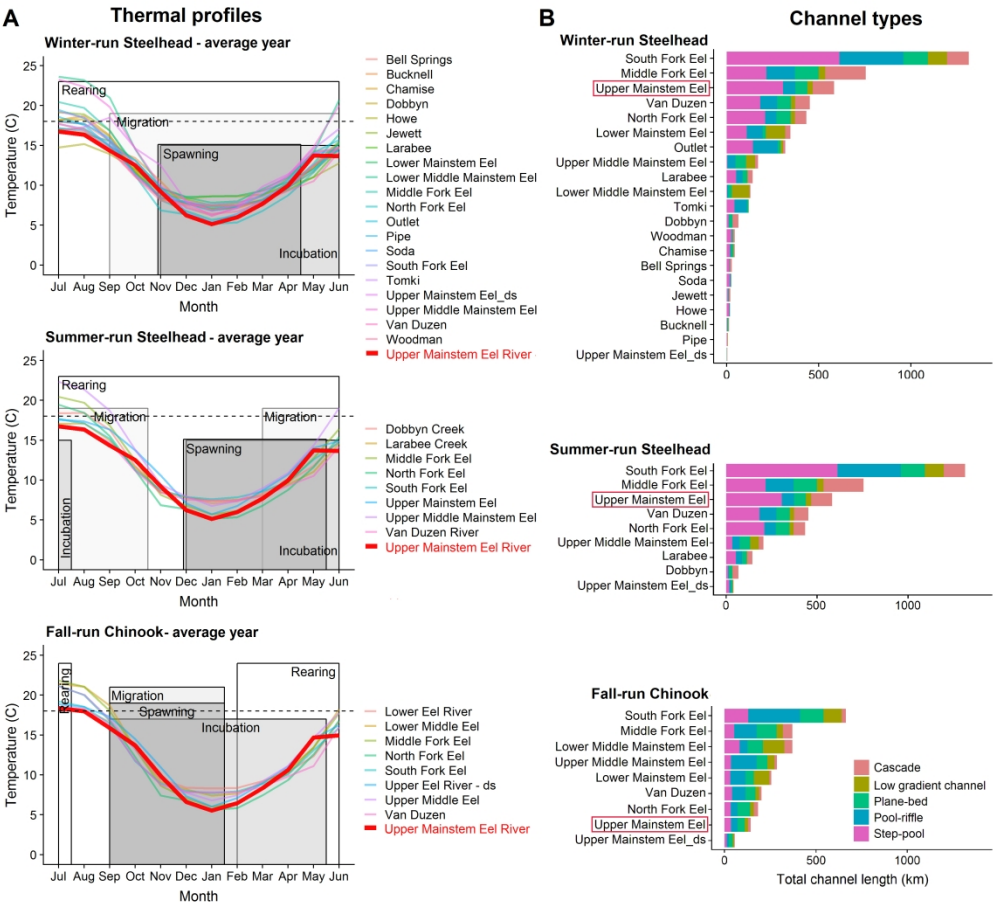
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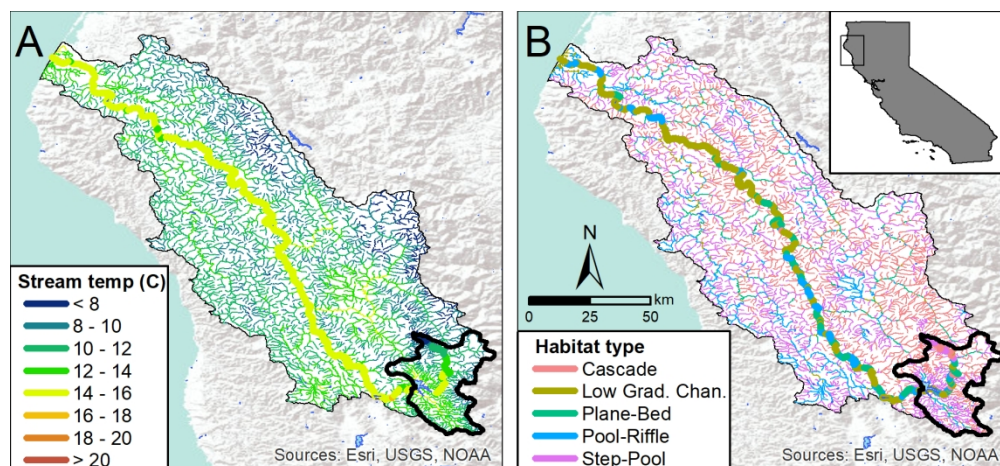
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419x193mm (118 x 118 DPI)

Thermal profiles (A) and total length (km) of each habitat type (B) for potentially accessible reaches in winter-run steelhead trout (top panels), summer-run steelhead trout (middle panels), and fall-run Chinook salmon (bottom panels) subbasins in the Eel River Basin. A) Each line shows the average temperature of that subbasin throughout an average year (all year types in Fig. S4); the currently blocked Upper Mainstem is bolded in red. The box for each life stage shows when that life stage is found in freshwater in the Eel River Basin (x axis) and the upper thermal tolerance for that life stage (y axis). To be suitable, the average temperature must be within the box for a specific life stage. The black dotted line shows the lower thermal tolerance (18°C) for pikeminnow, a major predator and competitor of juvenile salmonids. B) Total channel lengths (km) predicted for each geomorphic channel type in each subbasin. The currently blocked Upper Mainstem is outlined in red.

718x651mm (144 x 144 DPI)