

1 THE THIRSTY EEL: SUMMER AND WINTER FLOW THRESHOLDS THAT TILT THE EEL
2 RIVER OF NORTHWESTERN CALIFORNIA FROM SALMON-SUPPORTING TO
3 CYANOBACTERIALLY-DEGRADED STATES

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27 Running head: Discharge-mediated food web states

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31 Although it flows through regions of Northwestern California that are thought to be relatively well-
32 watered, the Eel River is increasingly stressed by drought and water withdrawals. We discuss how critical
33 threshold changes in summer discharge can potentially tilt the Eel from a recovering salmon-supporting
34 ecosystem toward a cyanobacterially-degraded one. To maintain food webs and habitats that support
35 salmonids and suppress harmful cyanobacteria, summer discharge must be sufficient to connect mainstem
36 pools hydrologically with gently moving, cool base flow. Rearing salmon and steelhead can survive even
37 in pools that become isolated during summer low flows if hyporheic exchange is sufficient. But if the
38 ground water discharge that sustains river flow during summer drought drops below critical levels, warm
39 stagnant conditions will kill salmonids, and cyanobacteria will thrive. Challenges and opportunities for
40 restoring the Eel and increasing its resilience to climate extremes, water diversions, and excessive loading
41 of fine sediments point towards exploring how land use and terrestrial vegetation affect delivery from
42 uplands of water, heat, sediments, solutes, organic matter, and organisms—in ways that either heal or
43 damage rivers.

44 **INTRODUCTION**

45 Hydrologic extremes--droughts and deluges--are predicted to intensify under climate change, particularly
46 in arid and semi-arid regions (IPCC 2011, 2014). These trends are already apparent in the western US
47 (Hayhoe et al. 2004, Kadir et al. 2013). Although shifts or anomalies in annual averages still dominate
48 climate change projections, flow variability (maxima and minima) matters more to aquatic ecosystems
49 (Poff et al. 1997, Stafford-Smith and Cribbs 2010). The timing and duration of significant highs and lows
50 in discharge are important as well, particularly in river ecosystems like the Northern California's Eel
51 River, where native biota are adapted to Mediterranean seasonality (Kupferberg et al. 2012, Power et al.
52 2014).

53 Regions under Mediterranean seasonality, including California, have cool rainy winters and hot,
54 dry summers. In the Eel River of northwestern California, most precipitation falling from October
55 through March, followed by summer droughts with little or no rainfall. Despite somewhat predictable
56 seasonality, Mediterranean rivers experience large year-to-year variation in precipitation and flow
57 patterns, with many implications for the river biota (Gasith and Resh 1999, Power et al. 2008). The
58 responses of river organisms to hydrologic disturbances will depend on the timing of flood or drought
59 events relative to the timing of organismal life history events (Table 1). Winters can be relatively dry or
60 wet, and either of these may be followed by summers with relatively high, sustained base flows, or base
61 flows lowered by drought or human water extraction. Native riverine biota of western North America
62 have many morphological, physiological, and behavioral adaptations to the “deluge or drought”
63 conditions typical of this region, such as behavioral adaptations for seeking refugia during disturbances
64 (Meffe and Minckley 1987, Meffe et al. 1983, Lytle and Poff 2004). However, the limits of these
65 adaptations will be tested under climate change and water extraction that increase the duration of the
66 drought season and decrease the magnitude of summer low flows.

67 Here we propose that the best scenario for summer salmonid production occurs when scouring
68 winter floods (which release large algal proliferations during the following summer) are followed by
69 summers with relatively high base flows, under which nutritious epilithic and epiphytic diatoms
70 dominate. These high flows also stimulate up-river migrations of anadromous salmon and allow them
71 access to upstream breeding grounds in tributaries. The worst case appears to be when bed-scouring
72 winter floods are followed by extreme low-flow summers, because then the algae that bloom early in the
73 summer rot later, fueling overgrowths of cyanobacteria, some toxic, that proliferate as channel pools
74 warm and stagnate. The basis for this prediction is the hydrologic mediation of the length of functionally
75 significant food chains—those through which predators, by suppressing prey or predators of prey, can
76 either control or suppress algal biomass—in the largely algal based food webs of the Eel.

77 **WATERSHED CONTEXT AND HISTORY**

78 *Location, vegetation, and climate*

79 The Eel River is the third largest river flowing entirely within California (the Sacramento and the San
80 Joaquin are larger), draining 9546 km² watershed (Fig. 1). It flows northward through tectonically
81 uplifted terrain covered by conifer forests, oak savannahs, and grasslands. The headwaters of the
82 mainstem Eel River originate near Bald Mountain in Mendocino County. The Mainstem Eel River is
83 joined from the west by the South Fork, and from the east by three other major tributaries: the Middle and
84 North Forks and the Van Duzen River (Fig. 1). Forestry has been the principal land-use since European
85 settlement, with dairy and small-scale agriculture near the estuary.

86 While the area is generally characterized by Mediterranean-climate seasonality, geographic
87 climate gradients across the basin are pronounced. From north to south, from west to east, and from high
88 to low elevations, summers are drier and hotter. Near the ocean, fog ameliorates summer heat. In coastal
89 watersheds that run east-west, marine fog moves up the basin and supports moisture-loving plants like
90 ferns and redwoods distributed across basin valleys from the river to the ridge. Along the north-south
91 running rivers like the Eel however, ridges of the California Coast Range can block maritime fog. In the
92 upper South Fork Eel River, redwoods are generally restricted to swales near the river channel, due to the
93 fog-blocking coast range ridges to the west. Despite microclimatic differences between the cooler coastal
94 and warmer interior portions of the Eel watershed, summer temperatures peak ~20-22°C in headwaters,
95 ~26°C in upper mainstems, and reach ~30°C at sites in the lower drainages (Lewis et al. 2000), unless
96 these are cooled by marine fogs.

97 The Eel and all of its tributaries are largely free-flowing, except for 890 km² of the mainstem Eel's
98 upper watershed that are impounded by two dams creating the artificial Lake Pillsbury and the smaller
99 Van Arsdale reservoir. The Potter Valley diversion reroutes some of this stored Eel water south to
100 Sonoma and Marin Counties (Fig. 1, inset). The rest of the Eel's water flows ~253 km northwest to its
101 estuary on the Pacific Ocean.

102 *Geologic setting*

103 Tectonic uplift at the mouth of the Eel River, near the Mendocino triple junction of three continental
104 plates, has steepened the mouth of the Eel River relative to its headwaters. The river has periodically cut
105 down into its over-steepened mouth, sending waves of incision propagating upstream as nick points (Lock
106 et al. 2006). These episodes of bed incision has left much of the upper Eel basin canyon-bound, and
107 flanked by strath terraces [river floodplains cut into bedrock, then abandoned] (Seidl and Dietrich 1992).
108 Because of its steep incised topography and soft geologic parent materials, during intense winter storms,
109 the Eel delivers one of the highest sediment yields per watershed area of any river in the co-terminous
110 United States, and among the top ten worldwide (Brown and Ritter 1971, Lisle 1990). It is naturally prone
111 to erosion and landslides, which have been severely exacerbated by post-European land use. With soft
112 rocks and steep slopes, the Eel River basin receives large pulses of sediment episodically from deep-
113 seated landslides (Mackay et al. 2011). Impacts of natural landslides on fish habitat would, however, be
114 buffered if mature forests and large woody debris in channels trapped and stored fine sediments.

115 *Human history in the Eel Watershed*

116 Native Californians, including Cahto, Pomo, Wailaki, Yuki, Weott, and Sinkyone tribes, lived as
117 hunter-gatherers for thousands of years in the Eel basin. When white settlers first arrived in the mid 1800s,
118 they saw the giant redwood forests, whales, sturgeon, and impressive runs of anadromous lamprey and
119 salmonids that had sustained these tribes. Before white settlement, road building and logging, the Eel
120 River supported annual spawning runs estimated as high as 800,000 fall-run chinook (*Oncorhynchus*
121 *tshawytscha*), 100,000 coho (*Oncorhynchus kisutch*), and 150,000 winter and summer steelhead
122 (*Oncorhynchus mykiss*), with abundant populations of coastal cutthroat trout (*Oncorhynchus clarki*),
123 Pacific lamprey (*Lampetra tridentata*), and green and white sturgeon (*Acipenser medirostris*, *A.*
124 *transmontanus*) (Yoshiyama and Moyle 2010). Sturgeon, lamprey, and salmon started to decline in the
125 Eel River with late 19th and early 20th century overfishing (see Anderson 2005, p. 115: Fig. 12), but

126 decreased much more after road construction and logging (with tractors, following World War II) ravaged
127 the naturally fragile watershed.

128 Massive deforestation began in the late 19th century shortly after white settlement, and accelerated
129 during the postwar years 1950-1970 when heavy equipment began to be widely used. Road building
130 further destabilized the steep slopes along the Eel, and increased the impacts of the great floods of 1955
131 and 1964 (Yoshiyama and Moyle 2010, Lisle 1990). Long-term residents along the South Fork Eel report
132 that “Humboldt Bridges” (giant felled logs used to bridge creeks) were lifted out of tributaries during
133 these floods to rush downstream, battering and ripping out mature alders and other riparian trees along the
134 river banks (J. and J. Siebert, personal communication). Bank scour and collapse left Eel mainstems much
135 wider and shallower, with beds clogged with huge loads of fine sediments. Aggradation flattened the bed
136 of these streams, scoured or buried their riparian zones and filled pools. Heavy loads of deposited fine
137 sediments degrade riverine habitat for spawning, incubating (Bjorn et al. 1974) and rearing salmonids and
138 the invertebrate assemblages that support them (Suttle et al. 2004). As channels widened and shallowed,
139 they also warmed, particularly where stripped of riparian gallery forests. The legendary salmon
140 populations and other native vertebrates are additionally threatened by reduced summer base flows and
141 elevated temperatures (Katz et al. 2012, Catennazi and Kupferberg 2014). Legacy and some ongoing
142 loading of excessive fine sediments into channels damage Eel River ecosystems to this day (Collison et al.
143 2003).

144 *Water diversions from the Eel*

145 The largest water diversion from the Eel is through the Potter Valley Project, licensed to Pacific Gas and
146 Electric by the Federal Energy Regulatory Commission. A tunnel with a maximum capacity (since 1950)
147 of 9.77 cms (345 cfs) diverts flow from the upper mainstem of the Eel River to the Russian River
148 headwaters (Fig. 1). Water is captured and stored in two reservoirs, the Van Arsdale reservoir (impounded
149 by Cape Horn dam) and the larger Lake Pillsbury (impounded by Scott Dam). In general, water is
150 captured from the headwaters of the mainstem Eel during the rainy winter season, and released to the

151 Russian during the dry season. From spring through fall, the project diverts up to 9.2 cms (325 cfs) of the
152 Eel's runoff into the neighboring Russian River watershed. This diversion occurs high in the watershed
153 on the mainstem Eel. The Cape Horn and Scott dams on the Eel, and the Coyote Dam on Lake
154 Mendocino that receives Eel flow then releases it to the upper Russian River, eliminate spawning habitat
155 in upper reaches of both the Eel and the Russian Rivers. In 1981, the Eel River and its major tributary, the
156 Van Duzen, were designated as Wild and Scenic Rivers, protecting the watershed from future dam
157 building, but not from diversions.

158 *Signs of recovery and possible futures*

159 After fifty years, however, the Eel River, and other rivers of the California North Coast, are
160 beginning to recover from the damaging decades of logging (1950-1970) and the 1955 and 1964 mega-
161 floods. The river's recovery has been aided by regrowth of relatively mature riparian forests that produce
162 habitat complexity for salmonids (Yoshiyama and Moyle 2012), as well as augmented strategically-timed
163 releases back to the Eel from the reservoirs above Potter Valley (discussed below). With sufficient winter
164 and summer flows, observations over the last few years made by environmental non-profits, government
165 agency, and academic biologists are yielding encouraging counts of spawning Chinook, coho, and
166 steelhead (ERRP 2013). But an alternative future for the Eel may arise if a new environmental threat, the
167 California "Green Rush", lowers summer flows below levels needed to maintain cold temperatures and
168 adequate flow velocity. An epidemic of new, numerous, dispersed marijuana gardens is drying up
169 tributaries and diminishing mainstem summer baseflows (Bauer et al., unpublished data and personal
170 communication). In addition, road building and forest removal for careless marijuana cultivation is
171 exacerbating erosion of fine sediments into channels. Ridge-top water impoundments for gardens have
172 failed, triggering landslides that load massive amounts of fine sediments into channels, rendering them
173 wider, shallower, and easier to warm or dewater at low flow. As stressed above, severe low summer
174 baseflows in the Eel have the potential not only to warm mainstems to temperatures lethal to rearing or
175 outmigrating salmon, but also to promote conditions releasing blooms of toxic cyanobacteria. Below we

176 describe flow seasonality in the Eel, climate and watershed conditions and food web responses that favor
177 salmon vs. cyanobacteria, and discuss challenges and opportunities for tilting the Eel back towards
178 salmon-supporting states.

179 **FLOW SEASONALITY, PHENOLOGY AND FATE OF KEY ALGAE, INVERTEBRATES, AND** 180 **FISH IN THE EEL FOOD WEB**

181 In the mixed gravel – bedrock channels of the Eel mainstems, most of the smaller bed sediments
182 (gravels, pebbles, cobbles) are mobilized when winter discharges exceed ‘bankfull.’ In canyon-bound,
183 bedrock-constrained rivers like the Eel, geomorphological evidence for channel bankfull depths is elusive,
184 so we rely on a frequency-defined bankfull discharge threshold corresponding to flows with ~ 1.5 year
185 recurrence intervals (Parker 1978) over a 30-year record of river discharge (Power et al. 2008). During
186 transport, mobile sediments pass by stationary larger boulder and bedrock particles, which only move
187 during megafloods (50-100 year recurrence interval) (Yaeger et al. 2012a,b).

188 Winter scour crushes or exports downstream overwintering cohorts of grazing stream insects, like
189 the caddisfly *Dicosmoecus gilvipes*, releasing algae to proliferate during the following late-spring, early-
190 summer growth season (Power 1992, Wootton et al. 1996, Power et al. 2008). Through early summer,
191 algae enjoy good growth conditions (longer days, cool flowing water and higher levels of nutrients), and a
192 window of time before grazer densities build up. In the Eel and many other temperate rivers, spring-
193 summer blooms are dominated by the filamentous, attached green macroalga *Cladophora glomerata*.
194 *Cladophora* blooms can attain lengths of several meters, and their rough, branching filaments increase the
195 surface area available for colonization by epiphytes: microbes, small stream invertebrates, and
196 cyanobacteria and diatoms, by ~5 orders of magnitude (Dudley et al. 1986, Dodds 1991, Power 1991;
197 Power et al. 2009). If summer baseflows remain high enough to keep mainstem pools hydrologically
198 connected, both *Cladophora* and rock substrates will become covered by highly edible diatoms. Of all the
199 primary producers fueling riverine food webs, diatoms have the highest nutritional quality, supplying

200 proteins and lipids, including essential polyunsaturated fatty acids (Brett et al. 2009). Their high food
201 quality and rapid growth rates under favorable conditions allow scant standing crops of diatoms to
202 support large biomasses of consumers – leading to a counter-intuitive food web structure with more
203 consumer than producer biomass, called an “inverted pyramid of trophic level biomass” (Elton 1927).
204 Under these circumstances, diatoms that are highly productive but held in low abundance by grazing. As
205 such, they are “hidden carbon” sources to food webs, likely to be overlooked because their importance is
206 revealed only when experimentalists (Lamberti and Resh 1983; Power 1984, McNeely and Power 2007)
207 or circumstances (Kohler and Wiley 1992) remove grazers.

208 Food chain length also affects the persistence of algal biomass over the summer. As months go by
209 and animal populations increase and become concentrated by waning flow, food webs develop longer
210 food chains which direct more energy from algae through vulnerable grazers and predatory invertebrates
211 to fish. The first invertebrates to colonize after scouring floods tend to be fast-growing, mobile,
212 unarmored invertebrates, like mayflies and chironomids. These prey are vulnerable to predatory
213 invertebrates (e.g. stonefly, dragonfly and damselfly nymphs) and fish. Large fish in the Eel suppress both
214 herbivores and small predators that eat herbivores, so their indirect effects on algae can be positive or
215 negative, depending on the length of food chains that dominate during a given year (Power et al. 2008). In
216 some years, an algivorous midge (*Pseudochironomus richardsoni*) that is consumed by small predators
217 but not larger fish, becomes abundant enough to suppress *Cladophora*. During such years, fish have
218 negative effects on algal biomass because they reduce small predators, releasing fish-resistant grazers to
219 suppress algae in four-level food chains (Power 1990a, Power et al. 2008). In years without substantial
220 recruitment of fish-resistant grazers, fish suppress all important algivores and protect algae indirectly as
221 predators in three-level food chains (Power et al. 2008).

222 Winter peak flows do not scour channel beds every winter, however. During dryer winters in
223 which flows never reach thresholds that mobilize scouring floods (or downstream of dams and diversions
224 where flows are artificially regulated), dense populations of large, heavily armored cased caddisflies

225 *(Dicosmoecus gilvipes)* or sessile (attached) grazers (such as a common aquatic moth larva (*Petrophila*
226 spp.)) persist over the early algal growth season. These grazers are not susceptible to predation, so when
227 dense, they suppress *Cladophora* growth. During such summers, stream substrates appear relatively
228 barren (Wootton et al. 1996, Power et al. 2008). When *Dicosmoecus* are experimentally removed during
229 these summers, however, algae can regrow to cover river substrates and form floating mats (Wootton et
230 al. 1996). In summers following dry, scour-free winters, fish receive little algal energy from invulnerable
231 grazers, reducing their growth (Parker and Power 1997). The indirect impacts of fish on algal biomass
232 disappear, as fish are functionally irrelevant as top-down controls when two-level food chains connect
233 invulnerable grazers to algae.

234 By late summer, even during “big algae” years, *Cladophora*-epiphyte assemblages are reduced to
235 short stubbles by grazing, decay, stranding or sloughing. Senescing, detached mats float downstream to
236 accumulate in slack water areas and depositional zones, and become hot spots of insect emergence (Power
237 1990b), diverting riverine energy and nutrients to riparian and aerial insectivores (lizards, spiders, birds,
238 and bats) (Nakano and Murakami 2001, Power et al. 2004, Baxter et al. 2005). As flows wane,
239 *Cladophora* stranded along shorelines and on emergent rocks dries as algal “paper” (Power et al. 2013).
240 This stranded riverine algal drift from upstream along with local, attached biomass enters the terrestrial
241 food chain via specialist algal detritivores, such as tetrigid grasshoppers *Paratettix aztecus* and *P.*
242 *mexicanus*, who derive 88–100% of their carbon from epilithic algae rather than terrestrial vegetation
243 (Bastow et al. 2002). Stranded algae are also eaten by dipteran larvae, which, in turn, become prey for
244 shoreline predators (carabid and staphylinid beetles, gelastocorid bugs, lycosid spiders) and riparian birds,
245 lizards, and amphibians such as the abundant Pacific tree frog (*Pseudacris regilla*), and the western toad
246 (*Bufo (aka Anaxyrus) boreas*). Stranded algae also fuel spiders, beetles, lizards, birds, and bats that feed
247 on emerging insects (Sabo and Power 2002 a,b, Power et al. 2004).

248 If late summer baseflows remain sufficiently high, less stranding occurs, and exported sloughed
249 *Cladophora* and other Eel River macroalgae may deliver a significant trophic subsidy to its estuary.

250 Because the Eel is a short, steep river, it remains largely gravel-cobble bedded all the way to its mouth.
251 The attached filamentous and adnate epilithic algae that dominate summer energy inputs throughout the
252 river network also dominate summer exports of organic matter to the estuary. Ng (2012) found that the
253 Eel exported 58 to 844 kg dry weight h⁻¹ of filamentous green algae, some covered with epiphytic
254 diatoms, to its estuary during summer and fall, 2010-2011, with significant exports of terrestrial litter only
255 during the first large winter flood. Primary consumers in the estuary (amphipods and isopods) strongly
256 preferred filamentous river algae over the marine green algae (*Ulva* and *Enteromorpha*) that dominated
257 visible producer biomass there (Ng 2012). If estuarine grazers rapidly consume riverine algal drift, this
258 subsidy also would be “hidden carbon”: an important basal resource for the estuarine food web, but easy
259 to underestimate.

260 But if summer base flows drop precipitously, algal production that is not consumed by aquatic
261 organisms or exported to land or sea may simply rot in stagnant, warming pools. Human water extraction
262 can trigger or accelerate this outcome. Low flows and high algal production increase pH and water
263 temperatures (through albedo and trapping of sun-warmed waters, Power 1990b), as they lower dissolved
264 inorganic carbon concentrations, conditions that can favor cyanobacterial growth over green algal growth
265 (Zhang et al. 2012). Heat stress and nutrient limitation cause the green macroalgal blooms from the spring
266 and early summer to senesce and rot, releasing nutrients that fuel blooms of benthic cyanobacteria
267 (*Anabaena*, *Cylindrospermum*, *Phormidium*, or *Nodularia*), some of which are toxic (Bouma-Gregson,
268 K., Lowe, R. Furey, P., and M. Power personal observations). At least eleven dog deaths have been linked
269 to toxic cyanobacteria in the Eel since 2002 (Puschner et al. 2008, Hill 2010, Backer et al. 2013).

270 **CONSEQUENCES OF WET SEASON-DRY SEASON FLOW SEQUENCES FOR SALMON AND** 271 **CYANOBACTERIA**

272 The most favorable type of water year for salmonid-supporting food webs in the Eel appears to be
273 a winter with at least one scouring flood, followed by a summer with high, sustained base flow (Fig 2a,

274 2c). Also, higher summer base flows maintained by elevated ground water are more likely to provided
275 temperatures, flows, and hydrologic connectivity favorable for juvenile fish survival during late summer
276 (e.g., Grantham et al. 2012).

277 Elevated winter flows during their winter spawning migrations will determine the spatial extent
278 of tributary spawning habitats that returning adult salmonids can access. Each fall, several thousand fish
279 are counted in the lower pools in the river as they wait for winter rains to increase discharge and access to
280 headwater tributaries. During drought winters, like the winter of 2013-14, salmon were limited in their
281 ability to access tributary spawning habitat. The timing of high flows (allowing access into small
282 tributaries) relative to the timing of spawning is critical. Within the Eel River's three species of
283 anadromous salmonids, Chinook initiate the earliest spawning migration (e.g., November-December),
284 followed by coho (December through January), and then steelhead (January-March). During winter 2013-
285 14, the dry early winter meant that Chinook were forced to spawn in mainstem habitats (Higgins 2014a,
286 Allan Renger, CDFW, personal communication). Early February rains allowed coho and steelhead to
287 access tributary habitats, though the low water levels overall hint that the smallest tributaries might have
288 been inaccessible across the entire spawning season for these two species.

289 As explained above, scour-free winters may be followed by “hungry” summers for salmonids and
290 other predators, because much of the primary production is sequestered by large armored or sessile
291 grazers defended from most predators (Fig. 2b, 2c). The worst scenario for salmonids and water quality in
292 the Eel, however, may be when winter flood scour occurs, but is followed by a summer with precipitously
293 dropping base flow (Fig. 2a, 2d). In such years, (which have become more common with expanded water
294 withdrawals during the summer), large blooms of algae proliferate in spring and early summer. Instead of
295 being grazed or exported to the estuary, however, these mats detach and senesce in mainstems as pools
296 disconnect hydrologically, warm and stagnate. Floating algal mats trap sun-warmed water, and are
297 considerably warmer by day than are algae that remain attached underwater (Fig. 3). As floating algal
298 mats and stranded algae rot, formerly benign cells like diatoms leak nutrients that may support the

299 proliferation of heat tolerant (Paerl and Huisman 2011) cyanobacteria. Certain cyanobacteria that
300 proliferate under warm, slack-water conditions can synthesize harmful hepatotoxins (e.g., microcystin)
301 (Smith et al. 2008, Miller et al. 2010) and neurotoxins (e.g., anatoxin) (Dittman et al. 2012, Kurmayer and
302 Christiansen 2009). To date, the main cyanotoxins found in the Eel River (K. Bouma-Gregson,
303 unpublished data) and in stomachs of dogs that died after swimming in it (Hill 2010) are neurotoxic.
304 Hepatotoxins (microcysteins) have also been detected, however, at lower concentrations (K. Bouma-
305 Gregson, unpublished data). Whether algae have beneficial (via food web support) or detrimental (via
306 toxin production or oxygen depletion) effects on fish, stock, dogs (Puschner et al. 2008) humans, and
307 other vertebrates depends on what environmental conditions are maintained, particularly during low
308 summer flows.

309 Spring spates, predicted to increase with climate change along the California North Coast by the
310 Canadian Centre for Climate Modeling and Analysis (CCM1, National Assessment Synthesis Team
311 2000), are yet another factor. In summer 2013, a “perfect storm” of hydrologic events and conditions led
312 to the largest proliferation of cyanobacteria ever observed in a reach of the upper South Fork Eel River
313 that has been intensively studied by river ecologists every summer since 1988. On Dec. 2 2012, the first
314 and last scouring flood of the 2012-13 water year extirpated many overwintering armored grazers
315 (*Dicosmoecus*, then in early instars) (Fig. 4). But following that single flood, severe drought conditions
316 resumed, creating favorable growth conditions for filamentous green algal recovery as flow decreased,
317 warmed, and stabilized over the remaining winter and spring months. Given this seasonal ‘head start’, the
318 green macroalga, *Cladophora glomerata*, in sunlit sites with stable (boulder, bedrock) substrates, grew
319 streamers up to 8-10 m long (the longest ever observed in 25 years by stream ecologists working in the
320 upper South Fork Eel River). But on June 26, a small spate (that elevated stage ~15-20 cm and discharge
321 by 2.5 cms (Fig. 4, inset upper right)) detached *Cladophora*, but did not export it very far downstream.
322 Over the subsequent summer months, most of the detached *Cladophora* rotted as floating mats along
323 slack river margins (Fig. 5a). By July, the diatoms and filamentous green algae in sun-warmed floating

324 mats were dying, and leaking their cell contents (Fig. 5b). Their released nutrients appeared to support the
325 growth of colonies of heat-tolerant cyanobacteria such as *Cylindrospermum* (Fig. 5c,d), *Anabaena*, and
326 *Nodularia*. Proliferations of *Anabaena* and *Cylindrospermum* spread vegetatively, blanketing the
327 remaining stubble of diatom-covered *Cladophora* with black, grey, or dark blue-green mats (Fig. 6). The
328 cyanobacterial colonies detached from these benthic algal substrates if oxygen bubbles from their
329 photosynthesis were trapped in mats and exerted sufficient buoyancy. Flow or wind would then launch
330 flotillas of cyanobacterially dominated clumps, 5-20 cm in diameter as potential propagules, enabling
331 long-distance dispersal and spread of the cyanobacterial infections (Fig. 6, inset, upper right).

332

333 In summary, our present understanding (and predictions) of the ecological impacts of winter-
334 summer flows are as follows: If one or more bed scouring floods occur over the winter, removal of over-
335 wintering grazers will release large algal blooms during the following summer. The fate of this production
336 depends on summer flows. If summer baseflows remain high and cool enough to prolong conditions that
337 favor filamentous green algae and diatoms in river mainstems, these algal assemblages will provide
338 energy, nutrients and essential biomolecules (e.g. 'PUFAs' (poly-unsaturated fatty acids)) to food webs
339 that support productive growth of juvenile salmonids. Higher late summer flows, of course, will also
340 support salmonids physiologically, and provide more over-summering habitat. If no winter floods exceed
341 the 'bankfull' threshold necessary to scour the mobile component of the riverbed, large numbers of
342 algivores that grow into predator resistant (armored or attached) grazers will survive and suppress algal
343 growth during the spring-summer low flow period. Salmonid growth will be reduced if soft-bodied,
344 mobile, edible grazers are out-competed by predator-resistant grazers during such summers. If dry winters
345 are followed by dry summers, salmonids will be heat-stressed as well as hungry. The worst case appears
346 to be if scouring winter flows release algal blooms, but abrupt decreases in summer baseflows cause these
347 to rot in the channel as pools warm and stagnate. These are the conditions that can severely reduce water
348 quality as well as quantity, and trigger blooms of harmful cyanobacteria. In recent years, these conditions
349 have been exacerbated by extensive, dispersed summer water extraction for marijuana cultivation.

350

351 **RECOVERING THE EEL**

352 While watershed residents and stakeholders have limited power to affect globally changing
353 climate, they can practice and promote land uses that will make the Eel Basin more resilient to impacts
354 anticipated under scenarios forecasting more extreme climate: prolonged drought, alternating with more
355 intense flooding. What combinations of land cover and seasonal flow discharges would keep channel
356 habitats and food webs favorable for salmon rearing? What land cover and hydrologic regimes would
357 keep cyanobacterial proliferations in check? How do different sub-basins of the Eel vary in their
358 vulnerability to ecosystems flips from salmon to cyanobacteria? Are adverse human impacts primarily
359 from legacy land uses, or are contemporary practices, such as intensified marijuana cultivation,
360 threatening the recovery of the Eel ecosystem?

361 Keeping the Eel “swimmable, fishable, and drinkable” (ERRP 2014 www.eelriverrecovery.org),
362 will require maintaining adequate flows and reducing excessive loading and bed deposition of fine
363 sediments. More severe summer droughts coupled with summer-time water extraction activities have
364 fragmented rivers, leading to warmed, stratified conditions that can trigger harmful cyanobacterial
365 blooms. The challenge will be to manage water diversions and withdrawals to keep enough water in the
366 river channel to maintain productive river food webs and habitats suitable for salmonids. Water
367 withdrawals and diversions range tremendously in size from large-scale federal projects to small private
368 riparian withdrawals. At every scale, projects vary along a spectrum of sustainability, with some water
369 users striving to be responsible watershed stewards with their water consumption and land use, and other
370 users being less forward-looking. In addition to water withdrawals, improving forestry and road building
371 practices to reduce erosion and fine sediment loading into the river will also provide spawning habitat and
372 deeper pools for salmonids.

373 Communities throughout the Eel basin, and in other North Coast rivers (e.g., Klamath Basin
374 Monitoring Program) are organizing to monitor watersheds and alter land uses and restoration measures
375 to move the future trajectories of their watersheds towards salmon-bearing rather than cyanobacterially-
376 degraded states. Well-organized and active citizens groups committed to sustaining the health of human
377 and natural communities in the Eel basin are partnering with academics, agency and private sector
378 scientists, non-profits, and each other to learn about hydrologic, geomorphologic, climate, microbiologic,
379 and ecological processes that can be enlisted to guide basins towards recovery. Below we discuss some of
380 the challenges and opportunities for guiding the Eel towards a resilient, salmon-supporting state.

381

382 *Large scale water diversions: challenges and opportunities*

383 Water diversions, both large and small, create challenges for managing the Eel as a salmon-
384 supporting system. As discussed earlier, the largest diversion within the Eel is the Potter Valley Project,
385 which diverts water from the upper mainstem of the Eel to the Russian River, with consequences for
386 downstream flows within the Eel. Much of this water is released to the Russian during the dry season.
387 While the importance of summer base flows for supporting salmon has long been appreciated, winter base
388 flows in the Eel may also be more important than formerly realized, as freezing may kill incubating
389 salmon eggs if winter discharges are too low, conditions that may have occurred during December the
390 severe drought winter of 2013 in the upper mainstem Eel during Dec 2013 (Higgins 2014b).

391 While the Potter Valley diversion reduces base flows and fish passage to spawning areas, the
392 reservoirs, particularly the larger 106.6 million m³ (86,388 acre-foot) Lake Pillsbury, also create
393 opportunities for environmental flow management. Reservoir releases to the mainstem Eel during critical
394 bottleneck periods have been successfully used to augment flows needed for spring salmonid migrations
395 (P. Kubicek, personal communication). Releases from the Potter Valley project are also starting to be

396 used to ameliorate mainstem Eel conditions for salmonids over-summering during drought (D. Mierau,
397 CalTrout, personal communication, Graziani 2013), and could also reduce hazard of egg freezing during
398 critically dry winters.

399 *Small scale water diversions: challenges and opportunities*

400 The Potter Valley flow diversion has been debated for decades, with open negotiations mediated
401 periodically by the Federal Energy Regulatory Commission and the Russian-Eel River Commission.
402 Citizens on both sides of the Potter Valley divide, however, stress the need to recover Eel River salmonid
403 populations as a fundamental, bedrock goal.

404 The California “Green Rush” currently presents a more difficult challenge to the recovery of the
405 river. The current complex legal status of marijuana in Northern California makes documenting and
406 regulating environmental impacts from its cultivation difficult or impossible. A 1996 California law that
407 legalized cultivation of medical marijuana, followed by a California Supreme Court 2010 ruling
408 increasing the number of plants permissible to grow, has left laws governing marijuana cultivation,
409 transport and sale inconsistent among county, state, and federal jurisdictions. In response, burgeoning
410 marijuana cultivation has swept through watersheds throughout forested areas of Northern California (S.
411 Bauer, personal communication and Bauer et al. unpublished data). Marijuana is a thirsty crop, and a
412 single large plant is estimated to require at least 22.7 liters (6 gal) water per day (Humboldt Growers
413 Association (2010) cited in Bauer et al. unpublished data). Bauer and colleagues used aerial
414 reconnaissance ground-truthed during enforcement actions to study four large watersheds in the Eel basin.
415 They estimated that water demand for marijuana cultivation exceeded total dry season stream flow in 3 of
416 4 of these watersheds. As described above, if summer flows are drawn down below flows needed to
417 sustain flow through mainstem pools, the Eel River could tip from a salmon-supporting ecosystem based
418 on diatom production towards an ecosystem impaired by toxic cyanobacteria.

419 Summer water extraction for crop production is a critical challenge for salmonids and other native
420 biota in the Eel. However, opportunities for meeting both societal and ecological demands for freshwater
421 during the summer drought season exist, and include storing winter water for summer use—but in small
422 tanks, not large ponds with liners that can fail and unleash landslides. Growers within watersheds can
423 coordinate to asynchronize water withdrawals, and modify withdrawal schedules to take less per time
424 over longer periods, reducing impacts of summer irrigation and spring frost protection for grapes. Such
425 innovative approaches are being considered in other storage-limited coastal California systems, e.g., the
426 Russian River (Grantham et al. 2010) and the Pine Gulch Enhancement Project, where farmers and
427 vintners are implementing new strategies to capture and store water during the winter to reduce stream
428 diversions during the summer dry season in an effort to conserve summer-rearing habitat for salmon.

429 *River habitat restoration: challenges and opportunities*

430 The Eel River was once a complex habitat with deep pools, cool tributaries, and riparian
431 vegetation providing resources and refuge to many animals. In the late 1800s, pools in the lower reaches
432 supported hundreds of large-bodied (six foot and one hundred pound) green sturgeon (*Acipenser*
433 *medirostris*) (Humboldt Times, 1883). Summer steelhead were abundant in creeks, and the Chinook and
434 coho salmon runs numbered in the hundreds of thousands. However, logging, development, and other
435 watershed disturbances widened, aggraded, embedded and simplified the channel, eliminating the refugia
436 that animals depended on during the long, hot summers, and during winter high flows. Restoring large
437 wood jams or bioengineering with riparian plantings could be used in the mainstem to create flow
438 heterogeneity and refugia, as well as scour deep holding pools that stratify, maintaining cool bottom water
439 for Chinook and other salmon (Nielsen et al. 1994).

440 Reducing sediment loads to the Eel is particularly important for its restoration. When inputs are
441 reduced, the high discharges of the Eel are able to cut through the accumulated fine sediments and expose
442 the gravel below. The river is quite resilient, and over the decades, in tributaries where logging has

443 decreased, reaches once choked with fine sediments now have gravel bars suitable for salmonid spawning
444 (P. Higgins, personal observations). Addition of large wood in channels can also concentrate and store
445 finer sediments, accelerating downstream recovery (Abbe and Montgomery 1996).

446 Reducing fine deposited sediments from river beds also restores important thermal refuges for
447 salmonids. In the absence of large riparian woody vegetation, as described above, excessive fine sediment
448 deposition widens and flattens channels, and embeds stream substrates, eliminating pool habitat,
449 decreasing hyporheic connectivity and increasing temperatures. Where fines are stabilized by large,
450 woody vegetation, however, sediment deposition can have quite the opposite effect. Early white settlers
451 wrote of remarkable stands of redwoods in “alluvial flats” (unusually flat areas along the generally steep
452 Eel River profiles, where large trees or large woody debris can trap and retain deep deposits of fine,
453 organic-rich sediments). These were not only rich growth habitats for trees, but low and high flow refugia
454 for rearing salmonids. The few “alluvial flats” that persist today sustain cool summertime flows in deep
455 but narrow multi-thread channels that cut through meters of deposited sediment trapped among mature
456 woody, deep-rooted vegetation. As an example, in Redwood Creek, a tributary of the upper South Fork
457 Eel near Branscomb CA, a reach that flows through an alluvial flat can maintain temperatures of 13°C
458 when the nearby South Fork mainstem temperatures peak daily at 26°C (M. E. Power, personal
459 observations). Most of the juvenile coho that biologists observed during summer in the upper South Fork
460 watershed were in this critical summer refuge (M.E. Power and J.A. Sabo, unpublished data).
461 Additionally, the richly vegetated creeks also serve as refuges for juvenile fish from scouring high winter
462 flows. Reconstruction of alluvial flats or some facsimile of them that restored cool, deep narrow channels
463 during summer baseflow, while also reducing winter scour, could greatly benefit coho and other rearing
464 salmonids.

465

466 *Forest habitat restoration: challenges and opportunities*

467

468 Critical to the restoration of the Eel and other mountainous, forested rivers are the processes on
469 hillslopes through which vegetation—in the Eel basin, tall conifer and broad-leafed trees, as well as
470 chaparral and savannah—regulate water storage and release during drought periods. When tended by
471 Native Californians, these were forests of very large trees, spaced well apart, sheltering understories of
472 forest forbs, ferns, and grasses. Native elders taught that this type of forest management kept river flows
473 higher and cooler through prolonged drought (Ron Reed, Karuk tribe, personal communication). Simply
474 on the basis of leaf area indices, lower evapotranspirative losses would be expected from mature forests
475 with open understories than from choked, brushy Douglas fir forests that regrow after hillslopes are clear
476 cut, and then subject to fire suppression (Anderson 2005). This difference has been observed in the
477 Mattole Basin on the California North Coast (Stubblefield et al. 2012). In addition, large, deep-rooted
478 trees can vertically recirculate water, prolonging storage of soil or rock moisture high on the landscape,
479 and therefore prolonging its gradual release as runoff that sustains streamflow during drought. Tall trees
480 along coasts also can harvest fog, and increase recharge to soils from fog drip by considerable amounts
481 (Dawson 1998). Mature forest canopies affect near-boundary atmospheric circulation, retaining and
482 locally recycling water (e.g., Schwartz 2013). Evaporative cooling from tall forest is another very
483 important control ameliorating local air (and river) temperatures (Link et al. 2014), complementing the
484 important shading effects on water temperature of tall riparian galleries.

485 Finally, forests of large, well-spaced trees with strong, deep roots better retain sediments on
486 hillslopes, and are less likely to spread or succumb to insect outbreaks or catastrophic megafires. Forests
487 managed for mature stands seem key to enhancing the resilience of the Eel through warming and drought,
488 particularly in its western basins, where the South Fork and mainstem Eel flow through sedimentary
489 sandstones, mudstones, and shales of the Franciscan coastal belt, composed of highly fractured rocks with
490 high water holding and releasing capacity.

491 To the east, the Middle and North Fork Eel flow through Central Belt, underlain by clay-rich
492 *mélange*. Here, the dry soils and rocks exert greater negative water potentials during summer drought,

493 and vegetation shifts from the coastal conifer or mixed conifer-deciduous forest cover to more drought-
494 tolerant grass-oak savannah. Historic grazing in the late 1800s on the prairies of the Central Belt mélange
495 in the upper watershed changed grasses from deeply rooted perennial native species to shallower rooted
496 non-native annual grasses. In the 1964 flood, these meadows proved vulnerable to gully erosion and the
497 sediment supplied at the upper end of the watershed system in the 1964 rain-on-snow event then triggered
498 inner gorge failure of the middle reaches of the river. The USGS measured aggradation of 5.2 m (17 feet)
499 during this event. Restoration of native deep-rooted, perennial bunch grasses might enhance resilience of
500 these watersheds against erosion, floods, fires, and drought in the more arid eastern portions of the Eel
501 basin, protecting habitat quality in the river channels.

502

503 **CONCLUSIONS**

504

505 Not only salmonid populations, but algae at base of their food webs are depend critically on both winter
506 and summer flow regimes in the Eel River (Power et al. 2008, Power et al. 2013). If at least one scouring
507 winter flood occurs, large blooms of algae, released from grazing by predator-resistant grazers, can
508 proliferate during the following summer. The biomass accrual of algae depends on winter flows; the fate
509 of algal biomass depends largely on summer base flows. If high summer flows sustain the longitudinal
510 connection of channel habitats and maintain relatively cool temperatures, algae will be dominated by
511 edible diatoms on rock and macro-algal substrates, and this production will fuel food webs that support
512 salmonids and other predators valued by society, either in the river or offshore. If summer base flows
513 drop enough to isolate, warm and stratify pools and backwaters, the more edible algae will sensesce and
514 be overgrown by inedible, sometimes toxic, taxa. This impact of flow and temperature on algae in the Eel
515 River is a key switch mediating impacts of climate, land cover, and water withdrawals on native fishes.

516

517 Despite the 1981 federal designation of the Eel River and its major tributary the Van Duzen as
518 Wild and Scenic Rivers, the entire basin has suffered from deforestation and other erosive land use that
519 began the late 19th century and continue today. Drawdowns to critically low summer flows have been
520 greatly exacerbated by the new California Green Rush (Bauer et al. 2014, Howard et al. in review),
521 driving both summer-time water extraction and increased winter sediment yields, primarily from new
522 access roads and forest clearing. Yet the natural recovery of the Eel following recovery of its riparian and
523 hillslope forests has inspired an “organized and well informed citizenry”: settlers, tribal members, agency
524 employees and non-governmental organizations, and strong citizen-science and community forestry
525 organizations (www.eelriverrecovery.org, www.eelriver.org, www.riffi.org). Recent years have seen large
526 returns of salmon that have renewed optimism that the Eel can be restored as a largely free-flowing,
527 salmon-supporting river. Volunteer groups of Eel River citizens, tribal members, environmental scientists,
528 and policy makers are mobilizing to study the natural underpinnings of this river ecosystem. As these
529 people study ways to guide the Eel and other rivers of the California North Coast towards recovery and
530 resilience, they will figure out how, to paraphrase Wallace Stegner (1971), to “make a living, not a killing”
531 in its watershed. Societal engagement and broad understanding of a watershed’s landscapes and natural
532 history are both crucial for guiding the Eel and similar rivers back towards a more resilient future.

533

534

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536

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731 **FIGURE LEGENDS**

732

733 Fig. 1. Map of the entire Eel Watershed, showing Potter Valley diversion where headwaters of the
734 mainstem Eel are diverted through a 3.2 km tunnel south across the basin divide to the Russian River.
735 The small Van Arsdale reservoir is just above the diversion on the Eel. To the west and slightly north, the
736 larger reservoir serving the diversion, Lake Pillsbury lies at the confluence of the mainstem Eel
737 headwaters and its small Rice Fork tributary, joining from the southeast. These are the only two
738 reservoirs on the Eel. Squares show locations of dog deaths associated with cyanobacterial blooms since
739 2002.

740

741 Fig. 2. Water year 2012-2013, which produced the largest proliferations of **Cladophora glomerata**,
742 followed by the largest cyanobacterial blooms, ever observed in 25 years of field work in the upper South
743 Fork Eel River within the Angelo Coast Range Reserve. On Dec. 2 2012, the first and last scouring
744 flood of the 2012-13 water year (that exceeded the 120 m³/s bankfull threshold at this site) scoured out
745 many early instar *Dicosmoecus gilvipes*, reducing subsequent summer densities of the large, armored
746 instars that, if abundant, can suppress macroalgae blooms. After the single flood, stable, clear, warming
747 flows gave *Cladophora* a long seasonal ‘head start’. But on June 26, a small spate (that elevated stage
748 ~15-20 cm and discharge by 2.5 cms (inset upper right)) detached *Cladophora* streamers that had attained
749 lengths of up to 8-10 m. This biomass was not exported far downstream, but accumulated as large floating
750 mats along the slack-water pool margins of pools, and at pool tails where they stranded around emergent
751 rocks (Fig. 5a).

752

753 Fig. 3. Temperature (i-Button) records from the river bed where benthic algal turfs remained attached, and
754 adjacent floating mats of *Cladophora* from two adjacent river pools, GirlyMon and Merganser Pool,
755 downstream. Floating mats, which trap sun-warmed water, showing the high amplitude fluctuations and
756 high peak day-time temperatures in floating mat microsites, compared to the greater thermal stability of

757 the benthic turfs. Floating mats attained temperatures above 30°C that stress or kill common green algae
758 and diatoms, but are tolerated by or even favorable for some cyanobacteria (Paerl and Huisman 2011).

759

760 Fig. 4. Water year 2012-2013, which produced the largest proliferations of *Cladophora glomerata*,
761 followed by the largest cyanobacterial blooms, observed in 25 years of field work in the upper South Fork
762 Eel River within the Angelo Coast Range Reserve. On Dec. 2 2012, the first and last scouring flood of
763 the 2012-13 water year (that exceeded the 120 m³/s bankfull threshold at this site) scoured out many early
764 instar *Dicosmoecus gilvipes*, reducing subsequent summer densities of the large, armored instars that, if
765 abundant, can suppress macroalgae blooms. After the single flood, stable, declining flows gave
766 *Cladophora* a seasonal ‘head start’. But on June 26, a small spate (that elevated stage ~15-20 cm and
767 discharge by 2.5 m³/s (inset upper right)) detached *Cladophora* streamers that had attained lengths of up
768 to 8-10 m. This biomass was not exported far downstream, but accumulated as large floating mats along
769 the slack-water pool margins of pools, and at pool tails where they stranded around emergent rocks (Fig.
770 5a).

771

772 Fig. 5. (a) Decaying mat of *Cladophora* and its epiphytes, dominated by diatoms, at the tail of GirlyMon
773 Pool. Healthy fresh *Cladophora* is a bright green color, and becomes yellow, then red as it gets encrusted
774 with deeper and deeper layers of epiphytic diatoms. Diatom-covered *Cladophora* assemblages are
775 extremely high in food quality for riverine grazers. As these mats warmed in the sun, however,
776 *Cladophora* hosts and diatom epiphytes perished. (b) Cell contents leaking from a dying diatom,
777 *Epithemia adnata*, one of the dominant summer epiphytes on *Cladophora*, and highly preferred by
778 vertebrate and invertebrate grazers (micrograph taken at 400x). (c) In the organic matter released by dying
779 diatom and filamentous cells (orange debris is due to released carotenoids), balls of dark, olive-green
780 filamentous cyanobacteria appeared (micrograph taken at 100x). (d) The terminal positions of their
781 heterocytes suggest that these were colonies of *Cylindrospermum sp.*, a cyanobacteria known to be
782 neurotoxic (micrograph taken at 400x). Photographs by M.E. Power.

783

784 Fig. 6. Merganser Pool, downstream from the floating mats described in Fig. 5, where a stubble of
785 *Cladophora* epiphytized by diatoms remained attached. These remnant turfs were initially green (new
786 *Cladophora* growth), and became yellow or rusty-red over the summer, depending on stage of epiphyte
787 succession and thickness on hosts. After floating mats proliferated upstream, these turfs turned dark olive-
788 green to black as they became thickly overgrown with cyanobacterial mats dominated by
789 *Cylindrospermum*. Photographs by M.E. Power. Inset upper right: Late summer *Cladophora*-epiphyte
790 filaments completely overgrown with dense darkly-colored cyanobacterial mats, bouyed by oxygen
791 bubbles from photosynthesis. Some clumps have pulled loose and are floating downstream as potential
792 propagules that can be advected by river flow or wind for many meters to infect downstream habitats. The
793 blue thermometer lying on the riverbed is 15 cm long. Photograph by K. Bouma-Gregson.