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

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Running head: Discharge-mediated food web states

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

INTRODUCTION

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

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

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

WATERSHED CONTEXT AND HISTORY

Location, vegetation, and climate

The Eel River is the third largest river flowing entirely within California (the Sacramento and the San Joaquin are larger), draining 9546 km^2 watershed (Fig. 1). It flows northward through tectonically uplifted terrain covered by conifer forests, oak savannahs, and grasslands. The headwaters of the mainstem Eel River originate near Bald Mountain in Mendocino County. The Mainstem Eel River is joined from the west by the South Fork, and from the east by three other major tributaries: the Middle and North Forks and the Van Duzen River (Fig. 1). Forestry has been the principal land-use since European settlement, with dairy and small-scale agriculture near the estuary.

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

The Eel and all of its tributaries are largely free-flowing, except for 890 km^2 of the mainstem Eel's upper watershed that are impounded by two dams creating the artificial Lake Pillsbury and the smaller Van Arsdale reservoir. The Potter Valley diversion reroutes some of this stored Eel water south to Sonoma and Marin Counties (Fig. 1, inset). The rest of the Eel's water flows ~253 km northwest to its estuary on the Pacific Ocean.

Geologic setting

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

Human history in the Eel Watershed

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

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

Water diversions from the Eel

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

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

Signs of recovery and possible futures

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

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

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

Winter scour crushes or exports downstream overwintering cohorts of grazing stream insects, like the caddisfly ***Dicosmoecus gilvipes***, releasing algae to proliferate during the following late-spring, early-summer growth season (Power 1992, Wootton et al. 1996, Power et al. 2008). Through early summer, algae enjoy good growth conditions (longer days, cool flowing water and higher levels of nutrients), and a window of time before grazer densities build up. In the Eel and many other temperate rivers, spring-summer blooms are dominated by the filamentous, attached green macroalga ***Cladophora glomerata***. ***Cladophora*** blooms can attain lengths of several meters, and their rough, branching filaments increase the surface area available for colonization by epiphytes: microbes, small stream invertebrates, and cyanobacteria and diatoms, by ~5 orders of magnitude (Dudley et al. 1986, Dodds 1991, Power 1991; Power et al. 2009). If summer baseflows remain high enough to keep mainstem pools hydrologically connected, both ***Cladophora*** and rock substrates will become covered by highly edible diatoms. Of all the primary producers fueling riverine food webs, diatoms have the highest nutritional quality, supplying proteins and lipids, including essential polyunsaturated fatty acids (Brett et al. 2009). Their high food quality and rapid growth rates under favorable conditions allow scant standing crops of diatoms to support large biomasses of consumers – leading to a counter-intuitive food web structure with more consumer than producer biomass, called an "inverted pyramid of trophic level biomass" (Elton 1927). Under these circumstances, diatoms that are highly productive but held in low abundance by grazing. As such, they are "hidden carbon" sources to food webs, likely to be overlooked because their importance is revealed only when experimentalists (Lamberti and Resh 1983; Power 1984, McNeely and Power 2007) or circumstances (Kohler and Wiley 1992) remove grazers.

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

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

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

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

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

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

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

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

The most favorable type of water year for salmonid-supporting food webs in the Eel appears to be a winter with at least one scouring flood, followed by a summer with high, sustained base flow (Fig 2a, 2c). Also, higher summer base flows maintained by elevated ground water are more likely to provided temperatures, flows, and hydrologic connectivity favorable for juvenile fish survival during late summer (e.g., Grantham et al. 2012).

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

As explained above, scour-free winters may be followed by “hungry” summers for salmonids and other predators, because much of the primary production is sequestered by large armored or sessile grazers defended from most predators. The worst scenario for salmonids and water quality in the Eel, however, may be when winter flood scour occurs, but is followed by a summer with precipitously dropping base flow. In such years, (which have become more common with expanded water withdrawals during the summer), large blooms of algae proliferate in spring and early summer. Instead of being grazed or exported to the estuary, however, these mats detach and senesce in mainstems as pools disconnect hydrologically, warm and stagnate. Floating algal mats trap sun-warmed water, and are considerably warmer by day than are algae that remain attached underwater (Fig. 2). As floating algal mats and stranded algae rot, formerly benign cells like diatoms leak nutrients that may support the proliferation of heat tolerant (Paerl and Huisman 2011) cyanobacteria. Certain cyanobacteria that proliferate under warm, slack-water conditions can synthesize harmful hepatotoxins (e.g., microcystin) (Smith et al. 2008, Miller et al. 2010) and neurotoxins (e.g., anatoxin) (Dittman et al. 2012, Kurmayer and Christiansen 2009). To date, the main cyanotoxins found in the Eel River (K. Bouma-Gregson, unpublished data) and in stomachs of dogs that died after swimming in it (Hill 2010) are neurotoxic. Hepatotoxins (microcysteins) have also been detected, however, at lower concentrations (K. Bouma-Gregson, unpublished data). Whether algae have beneficial (via food web support) or detrimental (via toxin production or oxygen depletion) effects on fish, stock, dogs (Puschner et al. 2008) humans, and other vertebrates depends on what environmental conditions are maintained, particularly during low summer flows.

Spring spates, predicted to increase with climate change along the California North Coast by the Canadian Centre for Climate Modeling and Analysis (CCM1, National Assessment Synthesis Team 2000), are yet another factor. In summer 2013, a “perfect storm” of hydrologic events and conditions led to the largest proliferation of cyanobacteria ever observed in a reach of the upper South Fork Eel River that has been intensively studied by river ecologists every summer since 1988. On Dec. 2 2012, the first and last scouring flood of the 2012-13 water year extirpated many overwintering armored grazers (***Dicosmoecus**,* then in early instars) (Fig. 3). But following that single flood, severe drought conditions resumed, creating favorable growth conditions for filamentous green algal recovery as flow decreased, warmed, and stabilized over the remaining winter and spring months. Given this seasonal ‘head start’, the green macroalga, ***Cladophora glomerata***, in sunlit sites with stable (boulder, bedrock) substrates, grew streamers up to 8-10 m long (the longest ever observed in 25 years by stream ecologists working in the upper South Fork Eel River). But on June 26, a small spate (that elevated stage ~15-20 cm and discharge by 2.5 cms (Fig. 3, inset upper right)) detached ***Cladophora***, but did not export it very far downstream. Over the subsequent summer months, most of the detached ***Cladophora*** rotted as floating mats along slack river margins (Fig. 4a). By July, the diatoms and filamentous green algae in sun-warmed floating mats were dying, and leaking their cell contents (Fig. 4b). Their released nutrients appeared to support the growth of colonies of heat-tolerant cyanobacteria such as ***Cylindrospermum*** (Fig. 4c,d), ***Anabaena*****, and** ***Nodularia***. Proliferations of ***Anabaena*** and ***Cylindrospermum*** spread vegetatively, blanketing the remaining stubble of diatom-covered ***Cladophora*** with black, grey, or dark blue-green mats (Fig. 5). The cyanobacterial colonies detached from these benthic algal substrates if oxygen bubbles from their photosynthesis were trapped in mats and exerted sufficient buoyancy. Flow or wind would then launch flotillas of cyanobacterially dominated clumps, 5-20 cm in diameter as potential propagules, enabling long-distance dispersal and spread of the cyanobacterial infections (Fig. 5, inset, upper right).

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

RECOVERING THE EEL

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

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

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

Large scale water diversions: challenges and opportunities

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

While the Potter Valley diversion reduces base flows and fish passage to spawning areas, the reservoirs, particularly the larger 106.6 million m^3 (86,388 acre-foot) Lake Pillsbury, also create opportunities for environmental flow management. Reservoir releases to the mainstem Eel during critical bottleneck periods have been successfully used to augment flows needed for spring salmonid migrations (P. Kubicek, personal communication). Releases from the Potter Valley project are also starting to be used to ameliorate mainstem Eel conditions for salmonids over-summering during drought (D. Mierau, CalTrout, personal communication, Graziani 2013), and could also reduce hazard of egg freezing during critically dry winters.

Small scale water diversions: challenges and opportunities

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

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

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

River habitat restoration: challenges and opportunities

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

Reducing sediment loads to the Eel is particularly important for its restoration. When inputs are reduced, the high discharges of the Eel are able to cut through the accumulated fine sediments and expose the gravel below. The river is quite resilient, and over the decades, in tributaries where logging has decreased, reaches once choked with fine sediments now have gravel bars suitable for salmonid spawning (P. Higgins, personal observations). Addition of large wood in channels can also concentrate and store finer sediments, accelerating downstream recovery (Abbe and Montgomery 1996).

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

Forest habitat restoration: challenges and opportunities

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

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

To the east, the Middle and North Fork Eel flow through Central Belt, underlain by clay-rich mélange. Here, the dry soils and rocks exert greater negative water potentials during summer drought, and vegetation shifts from the coastal conifer or mixed conifer-deciduous forest cover to more drought-tolerant grass-oak savannah. Historic grazing in the late 1800s on the prairies of the Central Belt mélange in the upper watershed changed grasses from deeply rooted perennial native species to shallower rooted non-native annual grasses. In the 1964 flood, these meadows proved vulnerable to gully erosion and the sediment supplied at the upper end of the watershed system in the 1964 rain-on-snow event then triggered inner gorge failure of the middle reaches of the river. The USGS measured aggradation of 5.2 m (17 feet) during this event. Restoration of native deep-rooted, perennial bunch grasses might enhance resilience of these watersheds against erosion, floods, fires, and drought in the more arid eastern portions of the Eel basin, protecting habitat quality in the river channels.

CONCLUSIONS

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

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

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FIGURE LEGENDS

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

Fig. 2. Temperature (i-Button) records from the river bed where benthic algal turfs remained attached, and adjacent floating mats of ***Cladophora*** from two adjacent river pools, GirlyMon and Merganser Pool, downstream. Floating mats, which trap sun-warmed water, showing the high amplitude fluctuations and high peak day-time temperatures in floating mat microsites, compared to the greater thermal stability of the benthic turfs. Floating mats attained temperatures above 30^{o}C that stress or kill common green algae and diatoms, but are tolerated by or even favorable for some cyanobacteria (Paerl and Huisman 2011).

Fig. 3. Water year 2012-2013, which produced the largest proliferations of **Cladophora glomerata**, followed by the largest cyanobacterial blooms, ever observed in 25 years of field work in the upper South Fork Eel River within the Angelo Coast Range Reserve. On Dec. 2 2012, the first and last scouring flood of the 2012-13 water year (that exceeded the 120 m^3/s bankfull threshold at this site) scoured out many early instar ***Dicosmoecus gilvipes***, reducing subsequent summer densities of the large, armored instars that, if abundant, can suppress macroalgae blooms. After the single flood, stable, clear, warming flows gave ***Cladophora*** a long seasonal ‘head start’. But on June 26, a small spate (that elevated stage ~15-20 cm and discharge by 2.5 cms (inset upper right)) detached ***Cladophora*** streamers that had attained lengths of up to 8-10 m. This biomass was not exported far downstream, but accumulated as large floating

mats along the slack-water pool margins of pools, and at pool tails where they stranded around emergent rocks (Fig. 5a).

Fig. 4. (a) Decaying mat of ***Cladophora*** and its epiphytes, dominated by diatoms, at the tail of GirlyMon Pool. Healthy fresh ***Cladophora*** is a bright green color, and becomes yellow, then red as it gets encrusted with deeper and deeper layers of epiphytic diatoms. Diatom-covered ***Cladophora*** assemblages are extremely high in food quality for riverine grazers. As these mats warmed in the sun, however, ***Cladophora*** hosts and diatom epiphytes perished. (b) Cell contents leaking from a dying diatom, ***Epithemia adnata*****,** one of the dominant summer epiphytes on ***Cladophora***, and highly preferred by vertebrate and invertebrate grazers (micrograph taken at 400x). (c) In the organic matter released by dying diatom and filamentous cells (orange debris is due to released carotenoids), balls of dark, olive-green filamentous cyanobacteria appeared (micrograph taken at 100x). (d) The terminal positions of their heterocytes suggest that these were colonies of ***Cylindrospermum* sp.**, a cyanobacteria known to be neurotoxic (micrograph taken at 400x). Photographs by M.E. Power.

Fig. 5. Merganser Pool, downstream from the floating mats described in Fig. 4, where a stubble of ***Cladophora*** epiphytized by diatoms remained attached. These remnant turfs were initially green (new ***Cladophora*** growth), and became yellow or rusty-red over the summer, depending on stage of epiphyte succession and thickness on hosts. After floating mats proliferated upstream, these turfs turned dark olive-green to black as they became thickly overgrown with cyanobacterial mats dominated by ***Cylindrospermum.*** Photographs by M.E. Power. Inset upper right: Late summer ***Cladophora***-epiphyte filaments completely overgrown with dense darkly-colored cyanobacterial mats, bouyed by oxygen bubbles from photosynthesis. Some clumps have pulled loose and are floating downstream as potential propagules that can be advected by river flow or wind for many meters to infect downstream habitats. The blue thermometer lying on the riverbed is 15 cm long. Photograph by K. Bouma-Gregson.