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RESEARCH PAPER

Dam removal and anadromous salmonid (*Oncorhynchus* spp.) conservation in California

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Abstract Dam removal is often proposed for restoration of anadromous salmonid populations, which are in serious decline in California. However, the benefits of dam removal vary due to differences in affected populations and potential for environmental impacts. Here, we develop an assessment method to examine the relationship between dam removal and salmonid conservation, focusing on dams that act as complete migration barriers. Specifically, we (1) review the effects of dams on anadromous salmonids, (2) describe factors specific to dam removal in California, (3) propose a method to evaluate dam removal effects on salmonids, (4) apply this method to evaluate 24 dams, and (5) discuss potential effects of removing four dams on the Klamath River. Our flexible rating system can rapidly assess the likely effects of dam removal, as a first step in the prioritization of multiple dam removals. We rated eight dams proposed for removal and compared them with another 16 dams, which are not candidates for removal. Twelve of the 24 dams evaluated had scores that indicated at least a moderate benefit to salmonids following removal. In particular, scores indicated that removal of the four dams on the Klamath River is warranted for salmonid conservation. Ultimately, all dams will be abandoned, removed, or rebuilt even if the timespan is hundreds of years. Thus, periodic evaluation of the environmental benefits of dam removal is needed using criteria such as those presented in this paper.

Keywords Dam effects · Pacific salmon · Steelhead · Climate change · Klamath River · Mediterranean environments

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Introduction

Dams are present in nearly all California watersheds. Whether constructed for flood control, irrigation, urban water use, or hydroelectric power generation, dams alter the movement of water, sediment, nutrients and organisms in riverine ecosystems (Magilligan and

Table 1 Anadromous salmonid taxa found in California, their status and level of impact sustained from dams

Species	Taxa	Federal/state listing	Status	Impact from dams
Chinook salmon, *Oncorhynchus tshawytscha*	Upper Klamath-Trinity spring	–	E	High
	Upper Klamath-Trinity fall	–	V	Critical
	Southern Oregon Northern California Coast fall	–	WL	Moderate
	California Coast fall	T/–	V	Moderate
	Central Valley winter	E/E	V	Critical
	Central Valley spring	T/T	V	Critical
	Central Valley fall	–	V-E	High
	Northern California Coast	T/–	WL-E	Moderate
Steelhead, *Oncorhynchus mykiss*	Klamath Mountains Province winter	–	WL	Moderate
	Klamath Mountains Province summer	–	E	High
	Central California Coast winter	T/–	V	Moderate
	Central Valley	T/–	V	High
	South Central California Coast	T/–	V	Moderate
	Southern California	E/–	E	High
Coho salmon, *Oncorhynchus kisutch*	Central Coast	E/T	E	Moderate
	Southern Oregon Northern California Coast	E/T	E	Moderate
Chum salmon, *Oncorhynchus keta*	N/A	–	E	Moderate
Pink salmon, *Oncorhynchus gorbuscha*	N/A	–	E	Low
Coastal cutthroat trout, *Oncorhynchus clarki clarki*	N/A	–	WL	Low

Most taxa have formal recognition as distinct management units by state and federal agencies. We provide both federal listing status and status from Katz et al. (2013) with *T* threatened, *E* endangered, *V* vulnerable and *WL* watchlist. "Impact from dams" measures the magnitude of adverse impacts on specific runs

Nislow 2005; Graf 2006). This disruption of longitudinal connectivity changes the structure of biotic communities and the function of ecosystems (Ward and Stanford 1983; Knighton 1998; Wohl 2012), frequently with adverse consequences for native species (Marchetti and Moyle 2001).

Anadromous Pacific salmon and trout (salmonids; *Oncorhynchus* spp.) are particularly vulnerable to impacts of dams, especially dams that prevent migration between spawning and rearing habitats (Hanak et al. 2011). Salmonids in California are blocked from about 45 % of historical habitats in major mainstem rivers but percentages vary by location. In California's Central Valley, for example, dams have blocked access to more than 80 % of historical salmonid spawning areas (Yoshiyama et al. 1998; Lindley et al. 2006). Recent status assessments (Moyle et al. 2008; Katz et al. 2013) have highlighted that nearly all of California's native anadromous salmonids are in serious decline (Table 1). Dams negatively affect all of the state's anadromous salmonids (Moyle et al. 2008) and are significant contributors to the decline of 43 % of the taxa (Katz et al. 2013).

Since the 1850s, declining numbers of California's anadromous salmonids have been attributed, in part, to dams that blocked migration (Groot and Margolis 1991; Yoshiyama et al. 1998; Fig. 1). Consequently, there have been many attempts to mitigate for loss of salmon and steelhead *Oncorhynchus mykiss* trout due to dams and their operations. Starting in 1870, the California State Legislature passed a series of clearly-stated laws to protect fish from the impacts of dams (Börk et al. 2012). The present manifestation of these laws is Fish and Game Code § 5937, which states, "the

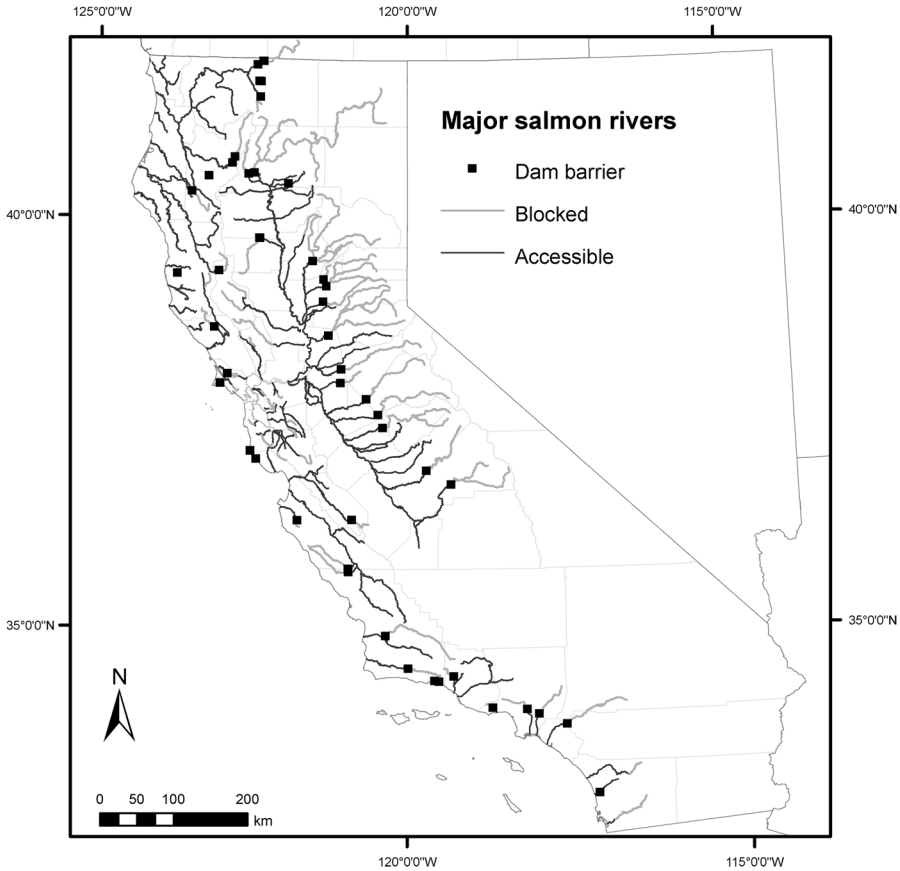

Fig. 1 Anadromous salmonid habitat, accessible and blocked by dams, in major California rivers (modified from Hanak et al. 2011)

owner of any dam shall allow sufficient water at all times to pass over, around, or through the dam, to keep in good condition any fish that may be planted or exist below the dam." Despite this mandate, the majority of dams constructed in California during the last century were designed and operated with little consideration for their impact on fishes (Börk et al. 2012). In particular, most large dams do not provide structures for fish passage. While restoration efforts for salmonid habitat below dams typically focus on reoperation of dams to produce more suitable flows, dam removal is increasingly an option, especially for dams that no longer serve their original purposes well (Kiernan et al. 2012).

Here, we explore the relationship between dam removal and salmonid conservation in California, focusing on dams that act as complete barriers to anadromy (as in Sheer and Steel 2006). Specifically, we (1) review potential positive and negative effects of dam removal on anadromous salmonids, (2) describe factors which must be considered for dam removal in California, (3) propose a method to evaluate benefits and detriments that dam removal poses to salmonids, (4) apply this method to evaluate potential benefits/detriments of removing 24 dams, and (5) discuss the potential impacts of removing four dams on the Klamath River. We recognize there are also socio-economic effects (e.g., Born et al. 1998; Johnson and Graber 2002; Robbins and Lewis 2008) of dam removal and salmonid conservation (e.g., to commercial and tribal fisheries) but do not discuss them here.

Review: effects of dams on anadromous salmonids

Dams disrupt movement of water, sediment, nutrients and biota between upstream and downstream habitats (Knighton 1998; Poff et al. 2007; Arthington 2012), thus altering many key processes in riverine ecosystems that are important to salmonids (Kondolf 1997; Poff et al. 1997; Poff and Hart 2002). The magnitude of these effects on anadromous salmonids depends largely on dam size, location, and operation (e.g., flow

releases), and whether the dam is passable to salmonid migration (Collins 1976; Raymond 1988). Here, we briefly review major effects dams have through the creation of reservoirs and downstream changes in habitat, as well as impacts of hatcheries that are created to mitigate for loss of habitat above dams. Effects that are rare in California are not discussed (e.g., gas supersaturation; Beeman and Maule 2006).

Reservoirs

Although some salmonids have adapted successfully to use reservoirs to complete their life cycle (e.g. Chinook salmon in the Snake River; Connor et al. 2005), changes in stream flow and velocity associated with reservoirs can interfere with migration patterns (Tiffan et al. 2009; Pavlov et al. 2008). Adults migrating upstream through reservoirs can have difficulty finding spawning streams, while downstream migrating juveniles often encounter high predation and limited food resources (Rieman et al. 1991; Beauchamp et al. 1999; Carey et al. 2011). The impact of reservoirs on salmonids differs by location and in some cases they do not impede migration (USDOI and USDOC-NMFS 2012). However, most large dams in California do not have fish passage over them. As an alternative to fish passage, mitigation hatcheries were built downstream of many large dams in California, and at least six species of salmonids have been planted in reservoirs to support in-reservoir fisheries (Moyle 2002).

Downstream effects

The reduction of peak flows commonly observed below dams has a broad range of effects on downstream habitat that adversely affect salmonids and other stream biota. Reductions in peak (geomorphic) flows and resultant encroachment by riparian vegetation can narrow channels and diminish floodplain connectivity (Kloehn et al. 2008). Isolation from floodplains reduces ecosystem productivity by limiting riparian vegetation regeneration (Jacobson et al. 2011; Benjankar et al. 2012) and the lateral movement of nutrients and organic material that support fish growth (Henery et al. 2010; Jeffres et al. 2008). Diminished peak flows limit recruitment of large wood, an important component for habitat complexity, nutrient retention, and channel stability (Bilby and Ward 1991; Naiman et al. 2002). Because sediment from upstream sources is retained by dams, streambeds downstream become coarser or armored, hindering excavation of redds by spawning salmonids (Knighton 1998; Poff and Hart 2002; Morley et al. 2008). In an embedded reach, spawning success is further reduced by accumulation of fine sediment in gravel that is normally flushed out by more frequent and larger flows (Louhi et al. 2011; Jensen et al. 2009). These substrate changes can reduce the abundance of macroinvertebrate prey for juvenile salmonids (Marchetti et al. 2011; Carlisle et al. 2010). In contrast, large flow releases from dams can result in channel incision in which substrates are scoured and sediment recruitment is disrupted by the dam (Kondolf 1997). Large fluctuations in dam releases over short time frames can increase fish mortality through stranding when high flows drop faster than salmonids are able to move (reviewed in Young et al. 2011).

Dam operations often reduce downstream habitat suitability by shifting water temperatures. Reservoirs create a large exposed surface area that absorbs solar radiation. If warm surface water from the reservoir is released, dams will increase downstream water temperatures (Risley et al. 2010), particularly in summer, when flows are lowest. Lower base flows and warm-water releases can reduce the amount of available habitat, increase the metabolic demands of fishes, and disrupt fish migration patterns (reviewed in Bednarek 2001; Olden and Naiman 2010). Warm water can also facilitate the spread of disease (Okamura et al. 2011; Kocan et al. 2009). Some larger dams, however, release cold water from the bottom of reservoirs. Cold-water releases that maintain or increase downstream base flows will usually reduce water temperatures in summer and fall (Huang et al. 2011; Yates et al. 2008), effectively shifting cold-water rearing habitat for juvenile anadromous salmonids from headwaters to below reservoirs (Ward and Stanford 1983). Cold-water releases are often crucial for sustaining remnant salmonid populations. For example, endangered winter run Chinook salmon *O. tshawytscha* in the Sacramento River are maintained entirely by cold-water flows from Shasta Dam, which prevents access to their former habitats (Moyle 2002). However, reliance on cold-water releases to protect salmon can be a problem if there is insufficient cold water in the reservoir to keep temperatures cool during late summer or during periods of drought (e.g., Thompson et al.

2011). Cooler temperatures can also delay juvenile migration cues and slow juvenile growth (Xu et al. 2010; Moyle and Cech 2004).

Hatcheries

Hatcheries are often constructed to mitigate for loss of upstream spawning and rearing habitat when dams obstruct migration or otherwise reduce salmonid populations. Hatcheries have often successfully maintained salmon fisheries for long periods of time, but at a cost of reduced genetic diversity, domestication of hatchery stocks, and major impacts on wild populations. Hatchery supplementation can result in significant differences between hatchery-produced and wild salmonids with respect to evolutionary fitness (Araki et al. 2008; Reisenbichler and Rubin 1999), phenotype (Hjort and Schreck 1982; Knudsen et al. 2006; Kostow 2004), behavior (Dittman et al. 2010; Melnychuk et al. 2010), and physiology (Shrimpton et al. 1994; Chittenden et al. 2008). Abundant hatchery stocks can further impact wild populations by supporting elevated predation (Nickelson 2003) and fishing pressure (Hard et al. 2008). Hatchery operations in California have only partially compensated for the loss of habitat upstream dams and in some cases have contributed to the decline of wild salmonids (Moyle et al. 2008). For example, hatchery practices can contribute (e.g., Klamath River; Hamilton et al. 2011) or introduce disease into the wild (reviewed in Katz et al. 2013).

Review: effects of dam removal

The main goals of dam removal from a salmonid perspective are to restore natural river processes below dams and restore access to upstream habitats (Roni et al. 2002). However, dam removal will likely have short-term adverse effects; the return to geomorphic and biological processes that existed prior to dam construction will not take place immediately but at different temporal scales, assuming other upstream dams and diversions have not also altered the hydrologic regime. In the short term, stream channels are expected to narrow in the location of former reservoirs but widen below the dam as accumulated fine sediment and bedload are redistributed (Pearson et al. 2011). Salmon have spawned in newly deposited gravel just months after dam removal (e.g., Chinook salmon in the Rogue River; Vial 2012), so short-term effects may be minimal. Short-term improvements to benthic habitat in the former reservoir reach will result in recovery of macroinvertebrate abundance and biomass, but standing stocks similar to those prior to dam construction may take many years to achieve (Orr et al. 2008; Hansen and Hayes 2011).

Over the long-term (decades), stream substrate composition will become more heterogeneous (Kloehn et al. 2008). Bed loads of natural materials will encourage lateral migration of the stream channel, increasing habitat diversity and connectivity to the river floodplain (Kloehn et al. 2008), assuming downstream habitats are not constrained by levees and bank armoring. Restoration of naturally dynamic flows can increase native fish abundance where non-native fishes are few or removed (Marks et al. 2010). Upon dam removal, anadromous salmonids will likely recolonize newly accessible habitats (Anderson and Quinn 2007; Brenkman et al. 2008b; Nicole 2012; Engle et al. 2013), facilitating the return of locally extripated species. Dam removal also may increase life history diversity as run-types such as spring run Chinook salmon recolonize upstream reaches or populations isolated above the dams reestablish anadromy (Brenkman et al. 2008b). Life history diversification coupled with increased carrying capacity (Pess et al. 2008) is likely to build more resilient populations with higher fisheries productivity (Burroughs et al. 2010). Restored connectivity and fish migration to diverse habitats, including spring-fed habitats, have the potential to contribute to more resilient populations and buffer the impacts of climate change (Hamilton et al. 2011).

Nonetheless, dam removal also represents a significant disturbance that can adversely affect the ecology of rivers and their watersheds (Catalano et al. 2007; Online Resource 1). Immediately after dam removal, large quantities of impounded fine sediments may mobilize (Mussman et al. 2008) and deposit downstream (Chang 2008). High turbidity from entrained fine sediments can disrupt fish migrations and fill interstitial spaces in the substrate to the detriment of embryos incubating in the gravel (Pess et al. 2008). Moreover, increased fine sediment deposition can decrease benthic invertebrate production in the short term (Orr et al. 2008). Toxic materials (e.g., mercury) locked in reservoir sediments may become suddenly available to contaminate food webs and inhibit nutrient cycling (as in Colas et al. 2013).

Where reservoir releases support cold-water fisheries, dam removal may reduce or eliminate spawning and rearing habitat immediately downstream (e.g., winter Chinook salmon habitat downstream Shasta Dam; Moyle et al. 2008). The draining of a reservoirs results in the loss of lentic habitat and may decrease overall species richness and diversity of the river system (Catalano et al. 2007), although in California most reservoir fishes and many invertebrates are alien species (Moyle 2002). Removal of migration barriers in some situations has the potential to spread disease through interactions of fishes in stream reaches previously separated by dams (Brenkman et al. 2008a) and increase the vulnerability of populations to previously segregated invaders and predators (Stanley et al. 2007).

Review: factors affecting dam removal in California

General frameworks exist to assess the ecological benefits and detriments of dam removal (Hart et al. 2002; Whitelaw and MacMullan 2002; Yang et al. 2011; Zheng and Hobbs 2013). However, not all elements presented in these studies are applicable to dam removal in areas with Mediterranean climate such as California. Here, we discuss the distinct suite of factors that are particularly relevant for evaluating dam removal in California and similar areas: water infrastructure, sediment accumulation, mercury deposition, and climate change effects. The effects from these factors can be significant stressors to salmonid conservation and may be augmented by dam removal.

Water infrastructure

California has been called the 'hydraulic society' due to its vast water infrastructure, designed to move water from places and times of abundance to those of scarcity (Hundley 2001). Most large watersheds contain multiple dams that range in size from small dirt dams on headwater streams to major edifices on mainstem river. When multiple dams occur on a single river, consideration must be given to the location of each dam relative to other dams in order to evaluate removal benefits, because remaining structures may continue to degrade habitats and restrict connectivity to upstream areas (Musil et al. 2012; Grantham and Moyle 2013).

A particular problem in California is transfer of water to other basins via aqueducts. These transfers dramatically alter flow regimes of both diverted and receiving streams. In source basins (e.g., Trinity River), up to 90 % of stream flow is diverted, resulting in hydrographs that are dramatically smaller and less variable relative to historical (natural) conditions (Hanak et al. 2011). In receiving basins (e.g., Sacramento River from the Trinity River), flows are augmented in summer, thus improving water quality for salmonids. Therefore, dam removal may directly benefit salmonids via increased stream flow in the source river, while paradoxically impacting salmonids by removal of water from the receiving basin. Thus, on California's north coast, water diverted from the Eel River to the Russian River is associated with declines of salmonids in the Eel River but increases in the Russian River (Yoshiyama and Moyle 2010).

Accumulated sediment

Reservoirs behind dams frequently contain large amounts of accumulated sediment and this problem is particularly acute in California. While high sedimentation rates in southern California are a natural consequence of the area's erosive geology, in northern California, hydraulic mining, used extensively during the Gold Rush, delivered massive sediment loads to aquatic habitats for nearly 50 years. San Francisco Bay, for example, experienced an order of magnitude increase in sediment transport from 1.5 to 14×10^6 m^3/year (van Geen and Luoma 1999). The excess sediment flooded towns and agricultural fields and impeded river navigation (James 2005). While hydraulic mining was eventually banned, many reservoirs in northern California continue to retain mining sediment from the 19th and early 20th centuries. In addition, natural processes continue to re-work and release mine tailings into streams, adding to the sediment load (Childs et al. 2003).

Given the large quantities of sediment trapped behind many dams, mobilization of this material following dam removal has the potential to be devastating to downstream habitat and all life stages of anadromous salmon, at least in the short-term (Kemp et al. 2011). During migrations, high loads of suspended fine sediment can damage gills, increase physiological stress, and significantly alter behavior patterns (e.g., migration timing; Bjornn and Reiser

1991; reviewed in Newcombe and MacDonald 1991). During egg incubation, fine sediment incorporated in redds decreases substrate permeability resulting in reduced growth, disrupted development, and mortality of embryos (reviewed in Jensen et al. 2009). Moreover, fine sediments can cap redds and prevent fry from emerging. During rearing, juveniles feeding in turbid waters are often smaller than conspecifics in less turbid conditions due to decreased prey capture rates (reviewed in Kemp et al. 2011). Gill abrasion from suspended sediment during juvenile development can result in reduced ability to osmoregulate (Shrimpton et al. 2007). Indirect effects of high fine sediment concentrations (e.g., via loss of riparian vegetation, or filling of interstitial spaces) can further impair juvenile survival and growth by increasing the risk of predation due to loss of cover and altering of food web structure and productivity; even modest increases in streambed fine sediment (i.e. 20 %) are harmful to juvenile salmonids rearing in rivers (Suttle et al. 2004). However, in some situations, populations have recovered quickly from catastrophic fine sediment input (e.g., steelhead in Mount St. Helens streams after volcanic eruption; Bisson et al. 1988) and salmonids have been shown to avoid high turbidity (e.g., Bisson and Bilby 1982).

Mercury deposition

Mobilization of mercury that has accumulated in reservoir sediments is a major environmental concern when considering dam removal in California. Although high mercury levels occur naturally in some California watersheds, an estimated 4.5 million kilograms of mercury were released into California streams as a by-product of hydraulic mining during the California Gold Rush (Alpers et al. 2005). Conversion of inorganic mercury to methylmercury, a biological neurotoxin, occurs at particularly high rates in low-oxygen habitats where dissolved organic carbon is available, such as reservoirs (Domagalski 1998). Methylmercury bioaccumulates in tissues of animals (James 2005) and poses a serious health risk to organisms at higher trophic levels. Some dams were built for the express purpose of catching mining debris and have accumulated large amounts of mercury-tainted sediment in their reservoirs (e.g., Englebright Dam). Therefore, the current methyl mercury load as well as conditions that might promote either mercury methylation or de-methylation need assessment prior to dam removal in California (James 2005).

Climate change

California marks the southern end of the geographic range of six species of anadromous salmonids (Table 1), likely exposing them to conditions (e.g., high summer water temperatures) near the limits of environmental tolerances. In California, climate change is degrading aquatic habitats already affected by other stressors (Battin et al. 2007) through increases in temperature, decreases in snow retention, changes in precipitation patterns, and increases in the magnitude of extreme events, such as floods and droughts (Field et al. 1999; Null et al. 2012). These changes threaten the persistence of anadromous salmonid populations (Moyle et al. 2013) and, in some cases, will strongly influence the relative benefits and detriments of dam removal for salmonids.

Although water temperatures under future climate change scenarios may exceed salmonid tolerance limits in the lower reaches of streams during the warmer months of the year, mainstem habitats will continue to serve as migration corridors during winter, with cooler headwater streams offering the only suitable habitat in the system (Crozier et al. 2008). Consequently, habitat connectivity will become as important as habitat quantity or quality (Isaak et al. 2007) in conserving California salmonids. In some instances, dam removal may be the only option to provide anadromous salmonids with access to suitable cold-water habitats including high-elevation tributaries and spring-fed streams that would be buffered from warming impacts of climate change.

Conversely, water releases from cold, thermally-stratified depths present in some existing reservoirs may provide cold-water habitat downstream of dams and mitigate the effect of elevated air temperatures (Poff and Hart 2002). Such water releases can favor cold-water species immediately below the dam (Poff and Hart 2002) and affect riverine community composition for many kilometers downstream (reviewed in Haxton and Findlay 2008). However, cooling effects from dam releases differ by reservoir size and location (i.e. elevation and latitude; Null et al. 2014). Summer water releases can also augment seasonal low flows in areas where groundwater pumping lowers water tables or dries stream reaches (Constantz and

Table 2 Scoring rubric for evaluating benefits of dam removal for salmonid conservation

	Score
1. Characteristics of salmonid taxa	
a. Number of taxa that may benefit or number of endemics	
None	0
1 taxon/≥1 also found in other locations	1
2 taxa/taxa in only one other location	2
3+ taxa/only found in removal watershed	3
b. Status of source population(s)	
Extirpated	0
Most small and or declining	1
Stable or increasing	2
Abundant	3
c. Life history diversity of source population(s)	
Extirpated	0
Single life history pattern dominates	1
Some runs/patterns lost	2
All historic life histories represented	3
2. Quality and quantity of aquatic habitat	
a. Migration barriers below dam	
Barriers exist near or downstream dam	0
Multiple permanent barriers in watershed	1
Seasonal or partial barriers exist	2
No additional barriers	3
b. Habitat suitability above dams	
No suitable habitat exists	0
Limited or degraded habitat exists	1
Suitable but slightly degraded habitat	2
Habitat in good condition	3
c. Amount of spawning and rearing habitat above dam	
None	0
<30 % of former habitat	1
30–50 % of former habitat	2
>50 % of former habitat	3
3. Stressors to salmonid recovery	
a. Number of additional limiting stressors (excluding hatcheries)	
Stressors cannot be overcome	0
>5 additional stressors	1
2–5 additional stressors	2
0 or 1 additional stressor	3
b. Duration of adverse impacts from dam removal	
Indefinite or long-term	0
Longer than 2 years	1
1–2 years	2
<1 year	3
c. Extent of hatchery supplementation	
Entirely reliant on hatcheries	0
>70 % of taxa supplemented	1
30–70 % of taxa supplemented	2
<30 % of taxa supplemented	3

See text for explanation

Essaid 2007). Augmentation of flows may be particularly important for providing suitable salmonid habitat as water demands increase with human population growth (Tanaka et al. 2006). However, if available cold water cannot simultaneously meet human water demands and maintain stream flows in particularly dry years, salmonid populations may be extirpated (e.g., adult spring-run Chinook in Butte Creek; Thompson et al. 2011). Under such conditions, cold water combined with favorable habitat conditions may create an 'ecological trap' in which juvenile salmonids are attracted to cold flows during rearing and later die when cold-water releases are curtailed and temperatures become too warm (Jeffres and Moyle 2012).

Methods

Rating the effects of dam removal

We developed a simple, flexible rating system to rapidly assess the relative magnitude of impacts from dam removal (Table 2), considering both positive and negative impacts that dam removal may have on anadromous salmonids over different spatial and temporal scales (see Online Resource 1). We intend this rating system to serve as a first step in a dam removal evaluation process and as a way to prioritize dams for removal. The system scores nine metrics relating to the characteristics of salmonid populations, habitat quality, and stressors in the watershed of interest. Benefits from dam removal were considered to be none or limited (scores = 0–9), moderate (scores = 10–18), or high (scores = 19–27) based on the sum of metric scores. The system was designed to encompass issues that are generally applicable to

most dams that prevent fish passage in Mediterranean-climate rivers.

Characteristics of salmonid taxa

The first metric in Table 2 considers either the level of endemism or number of native salmonid taxa that could benefit from dam removal. If protection or restoration of endemic salmonids is a desirable goal, this metric scores 0 for no existing endemics, 1 if one or more endemics exist but are found in multiple other drainages in the region, 2 if the endemics are only found in one other drainage, and 3 if the endemics occur only in the dam-removal watershed. If protection of salmonid diversity is the desirable goal, the metric scores 0 for no taxa present, 1 for one taxa, 2 for two taxa, and 3 for three or more taxa. Flexibility in the first metric allows equal consideration between areas characterized by few but highly endemic taxa and areas containing diverse assemblages. The second metric scores the ability of likely source populations to re-colonize the newly accessible areas. A source population is defined as the population that would most likely recolonize available habitats upon dam removal. Extirpated populations score a 0, small populations or those with low densities score a 1, stable or increasing populations score a 2, and abundant or highly dense populations score a 3. Status for California salmonids is evaluated in Moyle et al. (2008, 2011) and Katz et al. (2013). For the third metric, life history diversity, we assumed taxa with multiple life histories (i.e. life history portfolios as in Carlson and Satterthwaite 2011), are more adaptable to changing environmental conditions than those with extirpated or hatchery-dominated runs (as in Greene et al. 2010). Extirpated populations score 0, populations with a single life history score 1, populations with potential to regain lost life histories score a 2, and populations with all life histories intact score a 3.

Habitat quality and quantity

For metrics pertaining to aquatic habitat, we considered accessibility, condition, and quantity of habitat upstream and downstream of dam sites. For the first metric, users must determine if other barriers are present in the system. Removal of a single dam within a basin containing multiple barriers may result in limited benefits unless a large area of habitat is made accessible and all salmonid life-stages benefit. Streams with other barriers immediately adjacent to the dam under consideration, such that little to no additional habitat will be made accessible, score 0; streams with multiple remaining barriers within the range of anadromy, but not immediately adjacent, score a 1; streams with additional seasonal or temporary barriers score a 2; streams with no additional barriers score a 3. For the second metric, the quality of accessible habitat above the dam is considered (Roni et al. 2002). Dam removal may only have limited benefits if the watershed upstream has been irreversibly altered (e.g., by water diversion or urbanization). For example, streams upstream of the dam site with unscreened water diversions can result in high fish mortality due to entrainment or stranding of fish (as in Carlson and Rahel 2007). If a watershed requires extensive habitat restoration beyond dam removal, there will likely be limited benefits. Systems with no suitable habitat made available score a 0, while systems with habitat requiring extensive restoration score a 1, if dam removal provides access to habitat that is suitable most of the year score 2, or habitat in good condition year round (including cold-water springs) score a 3. The third metric scores the proportion of former spawning and rearing habitat reopened to anadromous salmonids. Habitats that function primarily as adult migration corridors are not considered here. In cases where multiple salmon taxa are present, the amount of habitat made available to the furthest migrant is estimated, usually for steelhead in California. Sheer and Steel (2006) used stream gradients to define general and optimal habitat for Chinook salmon and steelhead; Chinook salmon generally will use gradients from 0 to 7 % (optimal at 1–2 %), while steelhead use gradients 0–12 % (optimal at 1–5 %). Coho salmon *O. kisutch* use shallower gradients than Chinook because they do not often migrate as far inland, especially in California (Groot and Margolis 1991). Sheer and Steel (2006) determined that barriers had large, moderate, and limited impacts on steelhead and Chinook salmon distribution in the Willamette and Lower Columbia River basins, Oregon, when they blocked >50, 30–50, and <30 % of optimal habitat, respectively. We therefore used stream gradients above dams for estimating the proportion of high quality habitat accessible to different taxa upon dam removal. We used the thresholds

determined by Sheer and Steel (2006) in our rating system because salmonids in Oregon and California have overlapping habitat requirements (Groot and Margolis 1991). Systems with no spawning or rearing habitat upstream of the dam score a 0, systems with <30 % of former habitat score a 1, systems with 30–50 % of former habitat score a 2, and systems with >50 % of former habitat score a 3.

Stressors

In addition to current habitat impairment, watersheds in California are subject to ongoing anthropogenic stressors that may limit the potential for salmonid populations to recover following dam removal [e.g., stream sedimentation, mercury accumulation, estuarine alteration, etc.; see Katz et al. (2013) for a list of 15 stressors evaluated]. Our stressor metric scores a 0 if one or more stressors clearly prevent habitat recolonization (e.g., chronic source of pollution such as acid mine drainage) or population expansion, scores a 1 where greater than five stressors were identified in the watershed, a 2 for 2–5 stressors, and a 3 for one or no stressors.

A particular stressor that we considered separately is the dam removal process itself which can represent a large disturbance (Stanley and Doyle 2003). Dam removal that is likely to result in permanent unfavorable downstream changes (e.g., scour the stream channel to bedrock) would score a 0. Metric scores increase with decrease in time to recovery. Adverse impacts lasting more than 2 years but expected to disappear over time score a 1, impacts lasting 1–2 years score a 2, and impacts expected to last <1 year score a 3.

The third metric concerns the degree of influence of hatcheries on salmonid populations in the system. We address this stressor separately because hatchery production can alter population characteristics intrinsically (e.g., genetics or fitness) as well as extrinsically (competition with and predation on wild fish). Several studies (reviewed in Katz et al. 2013) have shown that species persistence can be threatened at different levels based on the magnitude of hatchery supplementation (including juvenile releases and adult straying) in a system. In systems where salmon runs are constantly supplemented by hatcheries, dam removal may only have limited initial benefits because fishes may already have lost key adaptations to former habitat (e.g., run timing). In such situations, redevelopment of local adaptations is likely to take multiple generations. Accordingly, benefits may be intermediate in systems with partial hatchery supplementation but high where hatchery supplementation is absent or supplementation has been managed in small conservation hatcheries over short duration (Lackey et al. 2006). Systems with taxa largely reliant on hatchery supplementation score a 0, while systems with >70, 30–70, <30 % hatchery-supplemented populations score a 1, 2, or 3.

Certainty

A score of certainty is also given to each metric. A score of 1 represents limited knowledge based primarily on expert opinion. A score of 2 reflects moderate knowledge supported with a few papers and reports, usually from gray literature. High degree of certainty, a score of 3, is largely based on peer-reviewed publications (e.g., Yoshiyama et al. 2001) and high familiarity of the system by the scorers. An overall certainty score for each dam removal is calculated as the average of the certainty scores for all metrics.

Application of the rating system

We first selected eight dams as case studies of dam removal for salmon conservation, based on recommendations by Hanak et al. (2011; Table 3) and the personal knowledge of one or more of the authors with these sites. These dams have all been considered for removal at one time or another. The eight dams studied in detail were Scott, Englebright, Matilija, Rindge, and the lower four dams on the Klamath River (Iron Gate, Copco 1, Copco 2, and J.C. Boyle dams; Fig. 2). Although J.C. Boyle is located in Oregon, just north of the California border, we include it here because it is part of a complex of four dams formally proposed for removal on the Klamath River. The context of each of the case studies is described below. An additional 16 large dams (see Online Resource 2 for characteristics) which are complete migration barriers to salmonids, but are not currently candidates for removal, were also rated (Online Resource 3). These dams were chosen on the basis of location, size, and their consideration for reoperation to improve habitat conditions for salmonids (i.e. environmental flows; T. Grantham, unpublished data).

Table 3 Evaluation of potential benefits of proposed dam removal in five California watersheds

Dam Watershed	Scott Eel River	Englebright Yuba River	Rindge Malibu Ck.	Matilija Matilija Ck.	Iron Gate + 3[a] Klamath River
Metric					
1a	3	3	1	1	3
1b	1	1	1	1	2
1c	2	2	1	1	2
2a	2	2	3	2	2
2b	2	2	2	2	2
2c	1	3	3	3	2
3a	2	3	2	2	2
3b	1	0	3	1	2
3c	3	1	3	3	1
Score	17	17	19	16	20
Category	M	M	H	M	H
Certainty	3	3	3	3	3

For metrics, see Table 2. Categories of benefits from dam removal: *H* high (scores = 19–27), *M* moderate (scores = 10–18), *L* none or limited (scores = 0–9)

[a] Copco 1, Copco 2, J.C. Boyle dams

Scott Dam

Cape Horn Dam was built in Mendocino County as part of the Potter Valley Project on the Eel River, approximately 290 km from the ocean, to divert water into the Russian River. The reservoir quickly filled with sediment and, in 1921, Scott Dam (Lake County) was constructed upstream of Cape Horn Dam to increase storage capacity and provide hydropower (Pejchar and Warner 2001). Reduced flows in the mainstem river, coupled with widespread habitat degradation by logging, flooding, and mining (Pejchar and Warner 2001) and the introduction of the predatory Sacramento pikeminnow *Ptychocheilus grandis* resulted in a greater than 99 % reduction in historical salmonid populations (Yoshiyama and Moyle 2010). While Cape Horn Dam has a functional fish ladder, Scott Dam does not and it prevents runs of Chinook salmon, coho salmon and steelhead trout from reaching ~93 km of potential habitat (Yoshiyama and Moyle 2010). The amount of accessible habitat, however, is lower during periods of low flow when functionality of the ladder at Cape Horn dam is compromised (Yoshiyama and Moyle 2010). The inter-dam reach (between Scott and Cape Horn dams) is an important rearing area for steelhead even at low flows because cold-water releases from Scott Dam are present all summer (Yoshiyama and Moyle 2010).

Englebright Dam

Englebright Dam, located in Yuba and Nevada counties, was built in 1941 on the Yuba River, just downstream of the point where the North, Middle, and South Yuba rivers join together to form the main river. It is located approximately 314 km upstream from the Pacific Ocean. The dam was constructed for hydropower generation and mining debris containment, although hydraulic mining ceased upstream shortly after construction. Today, its reservoir is 25 % filled with mercury-tainted sediment that continues to accumulate in the reservoir (Childs et al. 2003). Another debris dam, Daguerre Point Dam, 16 km downstream, has a fish ladder allowing fish passage up to Englebright Dam. The absence of fish ladders on Englebright Dam makes it a barrier to anadromous fishes; blocking access to ~160 km of potential spawning and rearing habitat (USGS 2004). Yoshiyama et al. (2001) indicate that 70 % (90 km) of historically available spawning habitat for Chinook salmon and steelhead has been cut off by the dam.

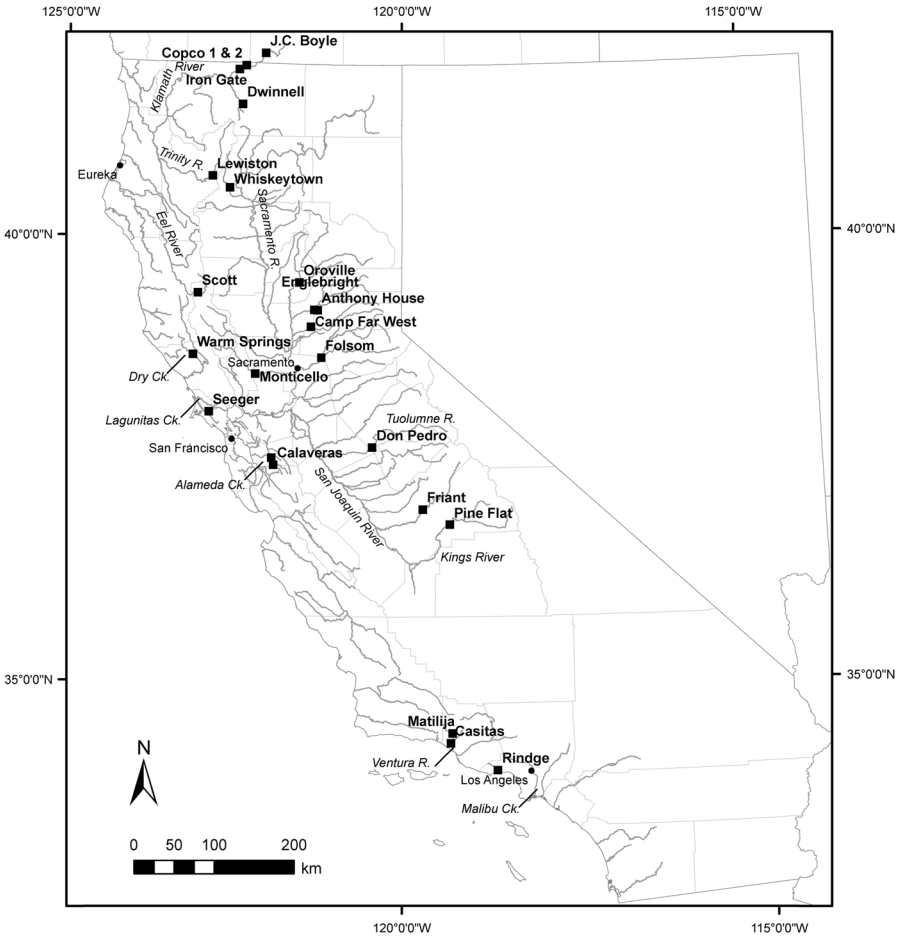

Fig. 2 Dam removal sites evaluated for effects on anadromous salmonid conservation in California

Matilija Dam

Matilija Creek, located in Ventura County approximately 27 km from the ocean, is a major tributary to the Ventura River. Matilija Dam was built in 1947 on Matilija Creek for water storage and flood control. However, due to the high natural erosion rates of the region, the dam has trapped more than 2.5×10^6 m^3 of sediment, completely filling the reservoir (Slagel and Griggs 2008). Trapped sediments were once important for creating and maintaining channel structure and fish spawning habitat downstream (Jenkin 2009). Additionally, use of construction materials of poor quality resulted in structural weakening of the dam (Minear 2003). The Ventura River watershed historically supported large runs of southern steelhead (Allen et al. 2007), but prime spawning and rearing habitat became severely limited following construction of three large dams: Matilija, Casitas, and Robles Diversion dams. Furthermore, altered flow and sediment transport regimes have substantially degraded the quality of accessible habitat (Becker et al. 2010). Matilija Dam is currently the upstream-most barrier to habitats that historically provided more than half of the spawning and rearing habitat in the system (P. Moyle and R. Quiñones, personal observations).

Rindge Dam

Rindge dam was built in 1926 on Malibu Creek in Los Angeles County for private water supply; its reservoir was completely filled with sediment by 1955 (Courter 2002). The estimated $0.6–1.2 \times 10^6$ m^3 of sediment currently trapped behind the dam historically balanced shoreline erosion at the creek's mouth, which supports an estuary that provides habitat for several listed species (e.g., tidewater goby *Eucyclogobius newberryi*, willow flycatcher *Empidonax traillii*; M. Capelli,

NMFS, unpublished observations). Rindge Dam is located just 4.4 km inland from the coast, leaving little spawning and rearing habitat accessible to endangered southern steelhead populations in Malibu Creek. Removal of the dam would about triple the amount of quality habitat available to steelhead (Abramson and Grimmer 2005).

Iron Gate, Copco 1, Copco 2, and J.C. Boyle Dams

Between 1911 and 1962, six dams were built on the mainstem Klamath River: three in Klamath County, Oregon (Link River, Keno, and J.C. Boyle) and three in Siskiyou County, California (Copco 1, Copco 2, and Iron Gate). The downstream-most dam, Iron Gate Dam, is approximately 308 km from the ocean. The primary functions of these dams are to impound and divert water (Link River and Keno dams), or to generate hydropower (J.C. Boyle, Copco 1, Copco 2, Iron Gate dams). Only Link River and Keno dams, the two most upstream structures, have fishways that facilitate salmonid passage. As a result, approximately 675 km of potential migration, rearing and spawning habitat are currently inaccessible to anadromous salmonids in the basin (Hamilton et al. 2011), although not all this habitat is likely suitable (P. Moyle and R. Quiñones, personal observations). As a condition for a hydropower relicensing, the Departments of Interior and Commerce prescribed mandatory fishways at the lower four dams to provide upstream access to migrating anadromous fishes. This has resulted in agreements (USDOI and USDOC-NMFS 2012) to decommission the lower four dams because of the high cost of building fishways.

Results and discussion

Using the rating system, we evaluated the benefits and detriments of removing 24 dams, including potential negative impacts of dam removal not always considered in previous assessments. None of the dams are currently passable for salmon. In our case, the goal was to prioritize dam removal for the conservation of salmonid diversity, as it pertains to metric 1a. Removal of twelve (50 %) of the dams evaluated seems to result in at least a moderate advance in salmonid conservation due to the large number of salmonids that would benefit or the amount of habitat that would become accessible. All eight of the dams with proposals for removal show moderate to high benefits for salmonids. For example, the moderate benefits of removing Scott Dam (score = 17) were largely based on the number of salmonid taxa found in the Eel River (1a), the quantity (2c) of habitat upstream of the dam, and the few negative effects expected from dam removal (3b). Benefits were diminished by the status of declining salmonid populations; for instance, runs of spawning Chinook salmon in the entire Eel River basin have decreased from an estimated 56,000 to 1,000 individuals (Yoshiyama and Moyle 2010). Sacramento pikeminnow are also a major stressor that may inhibit the recovery of anadromous salmonids in the Eel River (Yoshiyama and Moyle 2010). Although several salmonids species exist in the Yuba River (1a), benefits from removing Englebright Dam would likely be moderate (score = 17) due to the status of existing populations (1b; declining), high concentrations of fine sediment already in the mainstem Yuba River (2b) as well as by the large volume of mercury-tainted sediment (James et al. 2009) that would be released upon removal (3b). Additional barriers (2a) and hatchery supplementation (3c) also likely decrease the ability of salmonids to recover. However, large portions of formerly occupied habitat could be made accessible to some taxa upon dam removal (e.g., >80 % for spring-run Chinook salmon; NMFS 2012).

The high and moderate benefits of removing Rindge (score = 19) and Matilija (score = 16) dams were due to the quantity (2c) of habitat upstream of the dams, the limited duration of adverse effects expected from dam removal (3b), usually 1–5 years (as in Hamilton et al. 2011), and the lack of hatchery supplementation in these systems (3c). Removal of the four Klamath dams (score = 20) would likely have high benefits to all existing salmonid taxa (1a), all with intact life histories (1c) due to the short duration of adverse impacts from dam removal (3b; Hamilton et al. 2011). However, net benefits in the Klamath River were diminished by the magnitude of other stressors in the system (3a), including additional barriers (2a; i.e. seasonally poor water conditions in reaches near Kendo dam) and land use practices that decrease the suitability of habitat (2b; discussed below). The degree of hatchery supplementation (3c) for Chinook and coho salmon and steelhead trout also threaten the recovery capability of salmonids in the basin (Quiñones et al. 2013).

Although the eight dams discussed above have been proposed for removal at one time or another, the other 16 dams we rate have not. We evaluate them here for comparison, since all are also large dams that block salmonid migration. The removal of two dams (Seeger, score = 20; Warm Springs, score = 22) could yield high benefits to salmonid conservation in California, while the removal of four (Whiskeytown, score = 6; Monticello, score = 7, Don Pedro Main, score = 8; Folsom score = 8) appear unlikely to have benefits. The other 10 dams were thought to advance salmon conservation at least moderately.

The high benefits of removing Seeger and Warm Springs are largely due to the protected status of these watersheds as important sources of domestic water to Marin County and the city of Santa Rosa. For this same reason, however, their removal is unlikely. The negligible benefits of removing Whiskeytown, Monticello, Folsom, and Don Pedro Main dams are a result of their location. Whiskeytown is located high in the watershed; its removal would afford little new salmonid habitat (2c). Monticello, Folsom, and Don Pedro Main dams are located near other permanent barriers (i.e. Putah Creek diversion, Nimbus dam, La Grange dam) so other dams would continue to degrade habitat and disrupt salmonid migration (2a) upon their removal. However, the likelihood of removing additional dams within the same management complex may increase once operational links between dams (e.g., Putah Creek diversion dam with Monticello dam, Folsom dam with Nimbus dam) are lost. All eight case studies received high certainty scores (3; Table 3) due to the abundance of literature available for each and the familiarity of at least some of the authors with these systems. Most (10 of 16) of the other 16 dams evaluated also received high certainty scores but knowledge of six was considered to be of moderate certainty. Overall, we concluded we had sufficient data to knowingly evaluate all 24 dams.

Of the dams evaluated, the Klamath dams are the only ones being formally proposed for removal at the present time. Consequently, the benefits and detriments of their removal are discussed in additional detail to illustrate the complexities of dam removal even when salmon conservation is the primary consideration. Full evaluation of Klamath dam removal effects are discussed in Hamilton et al. (2011) and USDOI and USDOC-NMFS (2012).

Klamath River case study

The Klamath River basin drains approximately 40,000 km^2 in southern Oregon and northern California (Fig. 2). The Klamath basin once produced an estimated 650,000–1 million adult salmonids per year (Gresh et al. 2000) distributed across multiple species: Chinook (fall and spring runs), coho, chum *O. keta* and pink salmon *O. gorbuscha* and steelhead. However, abundances of runs of wild salmonids have been declining (e.g., spring-run Chinook; Nehlsen et al. 1991; NRC 2004; USDOI and USDOC-NMFS 2012).

Conditions without dam removal

In the absence of dam removal, freshwater habitats above Iron Gate Dam will remain degraded and inaccessible to anadromous fishes, unless major investment is made in fish passage facilities. Stream reaches between Keno Reservoir and Iron Gate Dam (Fig. 2) are characterized by highly-simplified flow regimes (Bartholow et al. 2004) and low water quality (e.g., low dissolved oxygen, algal blooms, high water temperature; reviewed in Hamilton et al. 2011). Furthermore, the sheer volume of water and warm temperatures in reservoirs prevent tributaries from contributing cold water to mainstem habitats (Hamilton et al. 2011). Unmodified, future operation of these dams will continue to limit the viability of fishes in areas upstream of Iron Gate Dam (Hamilton et al. 2011).

Below Iron Gate Dam, the natural flow regime and riverine processes will remain disrupted (reviewed in Hamilton et al. 2011). Construction and operation of the dams has changed the timing and magnitude of peak and base flows in the Klamath River mainstem (Stillwater Sciences 2009; Quiñones 2011), disrupting riparian plant succession, channel formation, and spawning gravel recruitment (KRBFTF 1991; FERC 2007; Varyu and Greimann 2010). These and other dam-related changes to riverine processes have contributed to conditions that foster the spread of fish disease below Iron Gate Dam (Stanford et al. 2011).

Conditions with dam removal

Our rating indicated that removal of these dams will yield benefits, supporting the conclusion of Stanford et al. (2011) that removal of the dams would be

"ecologically beneficial to the Klamath River ecosystem (p. 157)." Our rating is independent of extensive restoration activities proposed concurrent with dam removal that will further benefit fisheries while sustaining agriculture consistent with environmental laws [as in Klamath Basin Restoration Agreement 2010 (KBRA)]. These actions are expected to greatly improve the resilience of Klamath salmonid fisheries over the next few decades (Hamilton et al. 2011). The removal of the four dams is expected to substantially improve water quality and habitat conditions in the upper basin (reviewed in Hamilton et al. 2011 and Stanford et al. 2011). Flow and temperature regimes are expected to more closely reflect historical conditions. Consequently, water that currently evaporates from reservoirs should augment flows after dams are removed (Hamilton et al. 2011). Cyanobacteria blooms, acidity, and problems associated with low dissolved oxygen are expected to diminish because nutrient cycling, uptake and transport rates are greater in lotic systems than in reservoirs (Asarian et al. 2009; Stanford et al. 2011). Water temperatures are also expected to track air temperatures more closely, so will be slightly warmer in summer but cooler in fall and winter than with dams intact (Stanford et al. 2011). There may also be some seasonal or regional cooling due to reduction in hydraulic residence time and increased riparian shading along restored river reaches (Hamilton et al. 2011). The reach that contains Iron Gate and the two Copco dams should provide high quality habitat for holding adult and rearing juvenile salmonids because several large springs provide a continuous source of cool water (Hamilton et al. 2011). Restoration of more natural flow and sediment transport regimes is expected to improve habitat diversity by moving sediment, building bars, eroding banks and toppling large woody debris into the stream channel (NRC 2007). Removal of the dams, in conjunction with KBRA, would provide anadromous salmonids access to approximately 675 km of additional habitat and improve the viability of all species in the system (Hamilton et al. 2011). The suitability of most of this habitat for spawning and rearing has not been closely evaluated so the amount of high quality habitat may be considerably less than the 675 km of accessible habitat. However, even a fraction of the newly accessible habitat could still provide significantly more spawning and rearing habitat, particularly to anadromous fishes eradicated from upstream reaches.

Removal of Klamath dams can also have negative effects on fish, mostly through short-term adverse effects on downstream aquatic habitats (Stillwater Sciences 2011; Stanford et al. 2011). Dam removal may reduce dissolved oxygen and increase turbidity levels in the short term, due to high levels of total suspended organic sediment. The worst-case scenario for salmon exposed to high fine sediment loads is of a one-time loss of production from redds in the mainstem river, potentially resulting in a loss of approximately one-third of adult fall-run Chinook spawners 3 and 4 years after dam removal (Stillwater Sciences 2008). However, the higher than normal fine sediment concentrations are not expected to impact spawning habitats beyond one year, because high flows will clean spawning gravels and remove excess organic sediments from the system. Also, formerly disrupted bedload transport will resume upon dam removal, creating and enhancing spawning habitat in former reservoir and downstream reaches (USDOI and USDOC-NMFS 2012). Over the long-term, benefits of dam removal are expected to outweigh adverse effects such that impacted populations of fall Chinook salmon are predicted to fully recover within 5 years of dam removal (Hamilton et al. 2011).

Conclusions

Dam removal is likely to improve ecosystem function and condition in most cases. However, dam removal is unlikely to restore rivers systems to pre-dam conditions because the effects of dams are amplified through time and dam removal itself is a disturbance. On the other hand, benefits from dam removal can be enhanced by additional habitat restoration and modification of existing resource management strategies. For instance, the magnitude of benefit from the removal of Englebright Dam can be greatly increased if a viable method is found to deal with the mercury-laden sediment stored in its reservoir prior to dam removal and if releases from upstream dams can be adjusted to benefit the restored salmonid populations.

Overall, we found that most dam removals we investigated would result in at least moderate benefits to salmonid conservation. Net positive effects are

most likely in two situations. The first is where salmonid populations below the dams are still large (e.g., fall-run Chinook salmon in the Klamath River), making them more resilient to the temporary negative impacts of dam removal such as sedimentation. The second is where populations are imperiled but adverse effects of dam removal are few (e.g., southern steelhead in Malibu Creek). The magnitude of the benefit from dam removal is therefore expected to be modulated by the conservation status of the impacted species. We assumed that large populations are more stable and able to withstand significant adverse impacts in comparison to small, imperiled populations which are likely more vulnerable. Furthermore, dam removal is likely to produce no or only marginal benefit to salmonids if additional stressors are major causes of a population's decline (e.g., hatchery supplementation, water diversions) or are preventing recovery. The four dams on the Klamath River were given special attention since they are the only ones formally being considered for removal in California at the present time. Our analysis concludes that removal of these dams can be warranted for salmonid conservation.

Our method provides a simple initial assessment of whether dam removal will benefit salmonids. However, dam removal may present benefits to other taxa and river ecosystems as a whole. For example, Bushaw-Newton et al. (2002) found that communities of aquatic insects became more diverse upon dam removal in Manatawny Creek. Freshwater mussels were also expected to benefit from dam removal through the recolonization of upstream habitats by host fishes. In the Carmel River, removal of San Clemente Dam is expected to benefit the imperiled red-legged frog *Rana draytonii* (CDWR 2012). Native riparian vegetation may also benefit from dam removal (Poff et al. 1997), although benefits may only manifest after long periods and in absence of invasive non-native plants (reviewed in Shafroth et al. 2002). River ecosystems overall are expected to become more resilient upon dam removal if they are not so altered as to inhibit restoration of natural conditions (e.g., Hamilton et al. 2011). However, dam removal can also present detriments to river ecosystems. In the Klamath River, dam removal is expected to increase high water temperatures in spring and early summer to harmful levels for rearing juvenile salmonids (Bartholow et al. 2004). Short-term but significant impacts from the release of sediments trapped behind dams may present the largest detriment from dam removal; trapped sediments can degrade water quality and river morphology, and negatively impact salmonids and other aquatic life for several years after dam removal (USDOI and USDOC-NMFS 2012). Consequently, the benefits and detriments of dam removal must be carefully weighed prior to implementation.

While our protocol was developed for anadromous salmonids in California's Mediterranean climate, it could easily be modified for use in other regions and for other taxa, such as freshwater mussels or other anadromous and resident fishes, bearing in mind that the characteristics of the taxa of interest, quality of aquatic habitat, and additional stressors specific to each region and river system must be considered. We can envision such species-based protocols being incorporated into a broader systematic strategy for evaluating dams as operation licenses are evaluated for renewal. Such a strategy would likely include alternative criteria, such as economic considerations, that may reach conclusions contrary to assessments focused on fish.

We recognize that economic benefits and other reasons for maintaining dams are often a priority. Yet when salmon and steelhead conservation are considered in conjunction with other potential benefits, the case for dam removal can out-weigh reasons for maintaining a dam. For example, both Matilija and Rindge dams store large amounts of sediment that, if flushed downstream, would help restore important recreational ocean beaches near their mouths. In exchange for the short-term negative impacts of sediment flushing, there could be long-term benefits to both endangered southern steelhead and to local beach-based economies.

As a final thought, we note that no dam lasts forever and most gradually become reduced in function as the reservoir fills with sediment. Ultimately, all dams will be abandoned, removed, or rebuilt, even if the time span is hundreds of years. Thus, periodic evaluation using criteria such as we have presented in conjunction with economic evaluation is a worthwhile exercise. As dams decline in economic value, the relative benefits of removal will increase.

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Online Resource 1. Potential existing dam effects, and possible positive and negative effects of dam removal on salmon and steelhead in California. Existing dam effects are classified into three types of ecosystem responses: P = physical, WQ = water quality, B = biological effects. Specific effects will vary by location.

			Dam Removal	
Existing Dam Effects	**Type**	**Ecosystem Response**	**Positive Impacts**	**Negative Impacts**
Overall effects	P, WQ, B	reduces resiliency of ecosystem; shifts ecosystem to alternate state; disrupt natural disturbance regimes	increases resiliency of ecosystem to changing environmental conditions; restores natural disturbances regimes	dam removal itself alters form and function of ecosystem; diverges disturbance regimes from fishes' adaptive capability
Reservoir effects: flooding of habitat	P	shifts stream reach from lotic to lentic habitat	regains lotic habitat; narrows channel below reservoir	eliminates lentic habitat and fisheries; widens channel below dam site
Reservoir effects: water temperatures	WQ	creates physiological stress due to high water temperatures; alters growth-temperature relationships of fishes	removes physiological stress for cold-water fishes	removes potential source of cold water to habitats downstream or receiving basin
Reservoir effects: fish movement	B	dilutes signature of natal stream used for homing by adults migrating through reservoir	maintains chemical signal of natal stream in more natural conditions	
Reservoir effects: lentic (non-native) fishes	B	fosters predation and competition with native species inhabiting reservoir and river	reduces mortality from warm-water predators/competitors	increases downstream dispersal of non-native species (temporary)
Loss of high flows: large wood	P	reduces recruitment of large wood to the stream channel	renewal of large wood recruitment as habitat component	may flush existing large wood structures downstream

			Dam Removal	
Existing Dam Effects	**Type**	**Ecosystem Response**	**Positive Impacts**	**Negative Impacts**
Loss of high flows: floodplains	P	reduces wetland/floodplain habitat downstream	regains floodplain/wetland habitat downstream	reduces terrestrial habitats on dry floodplains
Loss of high flows: flow regime	P	alters magnitude, timing, and duration of high flow events	reverts hydrologic regime to a more "natural" state	prevents dampening of harmful high flow events
Loss of high flows: salmonids	B	changes timing of spawning adult and juvenile migration cues associated with changes in flow	allows migration cues to reflect climatic conditions; allows juvenile salmonids to spatially segregate for better survival and growth	eliminates water storage for augmentation of flows in dry seasons
Loss of high flows: alien species	B	promotes persistence of non-native species adapted to altered flow regime	reduces abundance of non-native species	reduces fisheries for alien warm-water species
Loss of high flows: disease	B	creates conditions favorable to pathogens and/or parasites	reduces pathogen/parasite transmission	enables introduction of pathogen/parasites upstream of dam location
Loss of high flows: riparian vegetation	B	allows encroachment of stream channel by riparian vegetation	reduces encroachment of stream channel	inhibits riparian vegetation from establishing on shifting substrates
Reduced base flow downstream: habitat area	P	reduces wetted area of stream channel	increases juvenile rearing and adult holding habitat	may create lower base flows in late summer
Reduced base flow: temperatures	WQ	increases water temperatures	returns river to historic temperature regime	increases temperatures in late summer

			Dam Removal	
Existing Dam Effects	**Type**	**Ecosystem Response**	**Positive Impacts**	**Negative Impacts**
Reduced base flows: fish movement	B	slows or hinders fish movement	increases opportunities for fish movement	hinders reproduction if small populations are highly dispersed
Reduced base flows: fish physiology	B	alters fish physiology, including growth, due to warmer water	decreases incidence of disease and mortality	decreases growth due to lower temperatures
Elevated dry season flows: habitat	P	increases wetted area of stream channel	returns system to more natural flow regime	decreases rearing and holding habitat
Elevated dry season flows: temperatures	WQ	cools water downstream from dam if cold water is released	creates more natural conditions for native salmonids	decreases quality of juvenile rearing and adult spawning habitat; decreases growth of rearing juveniles
Elevated dry season flows: alien species	B	allows non-native predators adapted to altered flow regime to persist	restricts distribution and abundance of non-native predators	permits non-native predator introductions to upstream habitats
Elevated dry season flows: salmonids	B	changes timing of juvenile migration cues associated with changes in flow	allows migration cues to reflect climatic conditions	eliminates water storage procurable for augmentation of flows
Interrupted migration route: fish movement	P	blocks or limits migration to upstream spawning and rearing habitat ; results in loss of habitat connectivity	provides access to upstream spawning and rearing habitat	reduces habitat for resident migratory fishes such as rainbow trout
Interrupted migration route: nutrients	WQ	reduces or precludes delivery of marine derived nutrients to upstream habitats	restores marine derived nutrient delivery	allows delivery of marine-derived toxins bound in salmon tissue

			Dam Removal	
Existing Dam Effects	**Type**	**Ecosystem Response**	**Positive Impacts**	**Negative Impacts**
Interrupted migration route: fish movement	B	blocks or limits migration to upstream spawning and rearing habitat	eliminates stress and mortality associated with passage devices or trap and haul programs; encourages diversification of life histories; increases stream carrying capacity; increases diversity of habitats available to fishes	lures fish into unsuitable habitats upstream (ecological traps); facilitates upstream movement of non-native predators
Interrupted migration route: fish mortality	B	increases mortality due to entrainment into generator turbines or stranding in irrigation diversions	eliminates mortality caused by generator turbines or diversions	increases vulnerability to entrainment in upstream diversions
Interrupted inorganic matter transport: large substrate	P	accumulates larger substrates at upstream end of reservoir	mobilizes accumulated and armored substrates; increases heterogeneity of substrate sizes	impairs migration passage over accumulated substrates due to high channel gradient and loss of surface flow
Interrupted inorganic matter transport: spawning success	B	reduces available spawning habitat	restores recruitment of spawning gravel from upstream habitats	lowers spawning success if redds are dewatered in areas prone to subsurface flows or capped by fine sediment
Interrupted inorganic matter transport: foraging success	B	reduces macroinvertebrate prey abundance and biomass	increases macroinvertebrate prey abundance and biomass	increases turbidities that hamper macroinvertebrate production and reduce prey capture rates in the short-term

			Dam Removal	
Existing Dam Effects	**Type**	**Ecosystem Response**	**Positive Impacts**	**Negative Impacts**
Interrupted inorganic matter transport: fish movement	B	protects migrating fishes from excessive fine sediment loads produced on hillslope	encourages migration patterns that reflect 'natural' sediment fluxes	hinders migration (and osmoregulation) when turbidities are high
Interrupted inorganic matter transport: fine sediment	P	accumulates fine sediment at downstream end of reservoir	mobilizes accumulated fine sediments	increases turbidity and fine sediment in stream substrate
Interrupted inorganic matter transport: channel morphology	P	straightens and simplifies stream channel and armors substrate downstream of dam	allows for migration and diversification of stream channel	scours stream channel and impairs operation of downstream fish ladders in the short term; fills pools and decreases downstream habitat diversity until substrates are mobilized
Interrupted organic matter transport/spiraling: nutrient reduction	WQ	reduces nutrient delivery downstream if nutrients retained in reservoir	restores longitudinal nutrient continuity	causes short-term eutrophication downstream upon release of stored organic matter
Interrupted organic matter transport/spiraling: nutrient increase	WQ	elevates nutrient loads downstream due to eutrophication in reservoir	diminishes eutrophication	reduces stream productivity
Interrupted organic matter transport/spiraling: algal and cyanobacteria blooms	WQ	promotes toxic algal blooms in reservoir and export of toxins downstream	diminishes toxic blooms	causes short-term eutrophication downstream upon release of stored organic matter
Interrupted contaminant transport (heavy metals, PCBs): reservoirs	WQ	accumulates, concentrates or contains contaminants in reservoirs	dilutes contaminants	disperses contaminants

			Dam Removal	
Existing Dam Effects	**Type**	**Ecosystem Response**	**Positive Impacts**	**Negative Impacts**
Interrupted contaminant transport (heavy metals, PCBs): food webs	B	enhances mercury methylation and incorporation of mercury into food web when anaerobic conditions occur	inhibits mercury methylation through aeration of water and substrates	shifts mercury methylation processes downstream
Interrupted large wood transport from upstream to below dam: habitat	P	reduces habitat heterogeneity	restores habitat heterogeneity	increases fine sediment delivery if transported log jams destroy stream crossings (e.g., road fill surrounding culverts)
Interrupted large wood transport from upstream to below dam: nutrients	B	reduces nutrient retention	restores nutrient retention	causes short-term eutrophication downstream upon release of stored organic matter
Warm-water release: fish stress and movement	WQ	acts as physiological stressor or barrier to migration	removes physiological stressor or barrier; increases distribution of migratory fishes	shifts resident fish fauna from cold-water to warm-water species in the face of climate change
Warm-water release: juvenile growth	WQ	increases juvenile growth rates in winter	restores natural growth rates	reduces juvenile growth rates and subsequent adult survival
Warm-water release: adult mobility	WQ	increases adult mobility in winter	restores natural migration cues	reduces extent of adult migration in winter
Warm-water release: alien species	B	creates conditions suitable to warm-water adapted non-native species	restores conditions suitable to cold-water native species	decreases species richness

			Dam Removal	
Existing Dam Effects	**Type**	**Ecosystem Response**	**Positive Impacts**	**Negative Impacts**
Warm-water release: diseases	B	creates conditions favorable to disease or parasites	lessens favorability of conditions for disease or parasites	allows transmission of diseases to upstream populations
Cold-water release: habitat	WQ	creates cold-water habitat in summer	returns flows to more natural regime	reduces cold-water habitat
Cold-water release: habitat: fish growth	WQ	slows juvenile growth and development	allows growth and development to match ambient conditions	creates more stressful conditions in late summer
Interbasin water diversion: habitat	P	increases quantity of juvenile rearing and adult holding habitat in receiving basin	maintains habitat in historical basin	does not augment habitat in receiving basin
Interbasin water diversion: habitat	WQ	degrades habitat in diverted basin; increases water temperatures	restores natural channel processes and thermal regime	
Interbasin water diversion: fish stress	B	stresses native species in receiving basin that are not adapted to altered flow regime	removes physical stressors	
Use of hatcheries to mitigate loss of spawning and rearing habitat: fitness	B	decreases local adaptation and fitness of wild populations interbreeding with hatchery strays	protects genetic and phenotypic diversity of natural stocks	diminishes the use of hatcheries for conservation of imperiled species
Use of hatcheries to mitigate loss of spawning and rearing habitat: mortality	B	increases mortality rates by increasing susceptibility to disease, predation and fishing pressure	decreases mortality rates	decreases abundance of some species to fisheries

			Dam Removal	
Existing Dam Effects	**Type**	**Ecosystem Response**	**Positive Impacts**	**Negative Impacts**
Use of hatcheries to mitigate loss of spawning and rearing habitat: competition	B	increases competition between hatchery and wild fishes for limited natural resources	facilitates population levels that reflect carrying capacity of river system	

Online Resource 2. Characteristics of 21 dams scored for dam removal benefits to salmonid conservation, California. Data was obtained from the ACOE National Inventory of Dams for California and Oregon.

Dam	**Height (m)**	**Storage (10^6 m^3)**	**Upstream catchment area (km^2)**	**No. upstream dams***	**Cumulative storage (10^6 m^3)**
Anthony House	23	4.7	144	4	67.0
Calaveras	64	123.3	255	3	124.0
Camp Far West	56	128.9	731	12	226.5
Casitas	85	313.3	105	2	313.3
Dwinnell Dam (Shasta River Dam)	29	61.7	369	2	62.1
Don Pedro Main	173	2,504.0	3971	28	3,357.7
Englebright	85	86.3	2874	49	1,636.3
Folsom	84	1,202.6	4823	58	2,171.0
Friant	91	642.0	4244	22	1,410.1
Iron Gate	53	71.5	20795	74	2260
James H Turner (San Antonio Reservoir)	59	62.3	99	1	62.3
Lewiston	22	18.1	1861	2	3,037.2
Matilija	50	2.2	141	1	2.2
Monticello	73	1,976.4	1470	27	2,027.0
Oroville	226	4,363.5	9334	43	6,660.2
Pine Flat	134	1,233.5	3998	7	1,536.5
Rindge	30	0.7	212	7	17.2
Scott	41	99.4	749	1	99.4
Seeger	35	27.6	93	1	27.6
Warm Springs	97	470.0	337	1	470.0
Whiskeytown	80	297.4	518	1	297.4

* refers to other large dams in the system only

Online Resource 3. Scores of dam removal benefits to salmonid conservation for 16 dams in California. Refer to text for description of metrics.

			metrics									
	Stream	Watershed	1a	1b	1c	2a	2b	2c	3a	3b	3c	Score/Category/Certainty Comments
Anthony House	Deer Creek	Yuba River	3	1	3	2	2	3	1	1	1	17/M/2 Recreational reservoir
Calaveras	Calaveras Creek	Alameda Creek	1	1	1	2	1	1	3	1	3	14/M/2 Storage of water from sources outside watershed
Camp Far West	Bear River	Yuba River	2	2	2	2	1	2	1	0	0	12/M/2 Scoring includes diversion downstream
Casitas	Coyote Creek	Ventura River	1	1	1	2	3	3	1	1	3	16/M/3 Major regional source of water
Dwinnell	Shasta River	Klamath River	3	1	2	2	3	1	2	2	1	17/M/3 Removal would result in more groundwater pumping
Don Pedro Main (New)	Tuolumne River	Tuolumne River	0	1	2	0	1	2	2	0	0	8/L/2 La grange dam downstream
Folsom	American River	American River	0	1	2	0	1	3	1	0	0	8/L/3 Nimbus dam downstream
Friant	San Joaquin River	San Joaquin River	3	1	2	2	1	1	3	2	2	17/M/2 Ongoing reoperation for salmon conservation
JH Turner	Alameda Creek	Alameda Creek	1	1	1	2	1	3	3	1	3	16/M/2

Lewiston	Trinity River	Klamath River	3	1	3	3	1	1	1	3	1	17/M/3 Trinity dam upstream
Monticello	Putah Creek	Sacramento River	2	0	0	0	1	3	1	0	0	7/L/3 Small historic salmonid runs
Oroville	Feather River	Feather River	3	1	2	3	1	3	1	1	0	15/M/3 Central to state water project
Pine Flat	Kings River	Kings River	3	1	2	1	1	2	2	1	0	13/M/3 Fish passage requires connection to San Joaquin River
Seeger	Nicasio Creek	Lagunitas Creek	2	1	1	3	2	3	3	2	3	20/E/3
Warm Springs	Dry Creek	Russian River	3	1	3	3	3	3	3	1	2	22/E/3 Supports salmon conservation hatchery
Whiskeytown	Clear Creek	Sacramento River	0	1	2	0	1	1	1	0	0	6/L/3 Flows from reservoir maintain salmonids in Clear Creek