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NOVEL AQUATIC ECOSYSTEMS: THE NEW REALITY FOR STREAMS IN CALIFORNIA AND OTHER MEDITERRANEAN CLIMATE REGIONS

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ABSTRACT

Temporary streams in California and other Mediterranean climate areas are among the aquatic habitats most altered by human actions and by invasions by alien species. They typically support novel ecosystems, defined as ecosystems dominated by new combinations of organisms in highly altered habitats. Although these new ecosystems have many attributes of the ecosystems they replaced, such as native species, they typically contain many new interactions among species. Managers need to recognize this reality to find ways to direct change towards novel ecosystems with desirable features, including native species. The concept of reconciliation ecology is a practical approach to living with the new reality; it includes actively guiding ecosystem change, as illustrated by Putah Creek, Cosumnes River, Eel River and Six Bit Gulch in California. The first three waterways are all highly altered and managed with varying degrees of success to favour desired aquatic species, whereas Six Bit Gulch experiences such extreme conditions that the original ecosystem is still largely intact. The examples illustrate that most aquatic ecosystems in California are so highly altered that attempting to restore them to an earlier condition or stable state is largely not possible. Where more or less intact systems persist, it is usually because extreme environmental conditions restrict both alien invaders and human use in small watersheds. This pattern appears to be fairly typical of streams in Mediterranean climate areas. Copyright © 2013 John Wiley & Sons, Ltd.

KEY WORDS: freshwater fishes; temporary rivers; intermittent streams; reconciliation ecology; water management

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INTRODUCTION

Streams and rivers are among the most highly altered ecosystems worldwide. Those in arid and Mediterranean climate areas have an especially high degree of alteration, because most streams are dammed and diverted to provide scarce water for human use (Marr *et al*., 2009; Kondolf *et al*., 2012). In these regions, some of the most extreme cases of alteration occur in seasonal streams that are either intermittent or are entirely dry (i.e. temporary rivers) during the low rainfall season. Such streams are part of the complex array of aquatic habitats found in most watersheds (e.g. in California, Moyle and Ellison, 1991), especially in the more arid regions (Levick *et al*., 2008). In recent decades, many natural temporary streams have become drier for longer periods in most years, through the building of dams and diversions to capture seasonal flows. Alternately, they have been converted to permanent streams by using once seasonal channels to deliver water to downstream users during dry months. Under either scenario, the channels become highly altered. Levees are typically built and channels straightened to prevent flooding. The channels also become repositories of waste materials, such as old concrete, used to stabilize banks.

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Today, an additional type of temporary stream has been created by converting permanent streams to temporary streams through diversion of water from their channels. Much of the 240+ km of the lower San Joaquin River in central California was dewatered or became seasonal in flow from the capture of flow by upstream dams (Rose, 2000; Moyle, 2002); as a result, it became a temporary river with its channel converted to a leveed floodway. Many of the river's tributaries, however, are either natural temporary streams, with seasonal tributaries that support rich insect and amphibian faunas (e.g. Abel, 1984) or intermittent tributaries, with permanent summer pools that support native fishes, such California roach, *Lavinia symmetricus* (Moyle and Nichols, 1973; Moyle, 1984, 2002). Such temporary streams are found throughout California (e.g. Cooper *et al*., 1985) but they are often highly altered because they have low value for fisheries and recreation and because they are subject to extreme, if infrequent, high-flow events that result in flooding of rural communities and lands. In periods of no flow, they are easy to channelize or otherwise modify.

The streams with altered flows and channels become new habitats that are easily exploited by alien species, as do the reservoirs that capture much of the water (Moyle and Marchetti, 2006; Hermoso *et al*., 2011; Ribiero and Leunda, 2012). Lomnicky *et al*., (2007), for example, found that over half of over 213 000 km of streams in the arid western USA contained non-native (alien) vertebrates, mostly fishes, and the aliens were dominant species in many streams, especially where habitats had been altered. Alien species are particularly likely to dominate in rivers downstream of dams where operations tend to reduce natural flow variability, creating uniform conditions that favour aliens (Moyle and Mount, 2007) and discourage native species adapted for less stable conditions, such as the California roach. Alien species often cause further changes to stream fish assemblages and presumably to the ecosystems of which they are part (Hermoso *et al*., 2011; Kiernan and Moyle, 2012).

Interactions between altered river systems and alien species are creating novel ecosystems, which have new combinations of species in habitats often quite different from the original habitats (Seastedt *et al*., 2008). In this paper, (1) the concept of novel ecosystems is applied to temporary rivers, especially in California; (2) reconciliation ecology (Rosenzweig, 2003) is described as a basic approach to managing these ecosystems; and (3) examples are provided of temporary rivers and their floodplains in a Mediterranean climate region, California. The focus of this paper is to describe the new reality for temporary rivers: that social and natural systems are tightly coupled (Kareiva and Marvier, 2012), as well as to discuss ways to manage novel ecosystems to favour native fishes and other desirable elements of aquatic ecosystems.

NOVEL ECOSYSTEMS

"In managing novel ecosystems, the point is not to think outside the box but to recognize that the box itself has moved…" Seastedt *et al*., 2008, p. 548.

In a sense, every ecosystem was novel at one time, reflecting both the difficulty of precisely defining ecosystems and the fact that no place on earth is static. Changes in species and habitats at any given place are continuous and inevitable. What is different today, of course, is the rate at which change is happening. New assemblages of interacting organisms are being thrown together in streams and lakes that are vastly different habitats from what they were a century ago, or less (Marchetti *et al*., 2001). The novelty of the new assemblages is greatly increased by rapid and frequent movement of organisms across biogeographical boundaries by humans and their transportation systems. Thus, most streams in California, the Iberian peninsula and other Mediterranean climate regions have been both highly altered and invaded by alien fishes or invertebrates (Marchetti *et al*., 2001; Moyle, 2002; Hermoso *et al*., 2011), creating novel ecosystems. This is especially true of temporary rivers.

Although new assemblages of organisms in highly altered environments are well documented, the conservation significance of novel ecosystems, represented by the present state of most temporary streams, depends on ecosystem services they provide and their resemblance to more natural systems (Hobbs *et al*., 2006, 2009). Two key questions that need to be answered for each novel ecosystem are as follows: Does it behave like ecosystems made up of co-evolved organisms, that is, natural ecosystems? And does it represent a new stable state with an ability to persist through time?

The answer to the first question for many novel aquatic ecosystems is a fairly strong 'yes', at least based on the relatively short periods they have been studied (e.g. Mascaro *et al*., 2012). Like natural ecosystems, novel ecosystems have a demonstrable energy-based trophic structure (i.e. primary, secondary and tertiary production) and species organized according to their interactions with the abiotic environment and with each other, more or less following 'laws' of ecology discussed by Dodds (2009). Predation, competition and symbiotic interactions all contribute to observed ecosystem structure, and usually the result is assemblages of species that are quite distinct from one another in morphology and that divide resources much as in a co-evolved assemblage (Moyle and Light, 1996). For example, Martis Creek, a small stream in the Sierra Nevada of California with a long history of alteration, supports a fish assemblage of five native species and two dominant alien species that showed structure, persistence and resilience over a 30-year period (Kiernan and Moyle, 2012). The reservoir upstream, which supports summer flows in the creek, is entirely dominated by alien fishes, especially green sunfish (*Lepomis cyanellus*), but appears to have been much less stable in its species composition over the same period (unpublished observations).

In some instances, a novel predator may eliminate many native species, simplifying the ecosystem, such as what happened in the highly seasonal Cosumnes River, California with the invasion of alien redeye bass (*Micropterus coosae*) (Moyle *et al*., 2003, see later). In other instances, a new species may just be added to the existing array of resident species, increasing complexity of interactions and contributing to assemblages with apparent ability to persist through time. For example, the shimofuri goby (*Tridentiger bifasciatus*) invaded the upper San Francisco Estuary in 1989 and became very abundant; intensive study found no negative interactions with other fishes. It now appears to be integrated into a shifting assemblage of about 50 species, about half aliens (Moyle, 2002).

The question about whether or not novel ecosystems, such as that of Martis Creek, represent new stable states is harder to answer, as is defining exactly what is meant by a 'stable state'. In Martis Creek, the species composition of the mixed-fish assemblage has likely been persistent for 100 years or so, although abundances of individual species over a 30-year study period fluctuated widely in response to variable timing of flows below the dam, built in 1972

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(Kiernan and Moyle, 2012). Historically, the creek would have been recolonized after a dry period by emigration of fish from the Truckee River, to which it is a tributary, or from headwater refuges.

Walker and Salt (2006) indicate that a given ecosystem can have multiple stable states, with a predictable set of interactions and species over a human time scale, but new states can also be irreversible once a threshold is crossed. Hobbs *et al*., (2009) see a trajectory towards a new stable state as being important for defining a novel ecosystem. In the extreme, this trajectory is stated in terms of 'regime shifts' (Scheffer and Carpenter, 2003; Folke *et al*., 2004), where fundamental changes occur, often rapidly, that are probably irreversible. Reversibility in the state of aquatic ecosystems becomes less and less likely as time goes by, because climate change is putting additional stress on these systems, further favouring alien species (Moyle *et al*., 2011, 2013b). Consequently, a stable state in a novel ecosystem could be described as a state where change has slowed relative to change in the recent past. For managers, a logical course of action in such situations is to determine how to maximize benefits to selected native or desirable alien species by controlling the change in various ways (see Putah Creek example later). Hobbs *et al*., (2009) describe this type of management in terms of stabilizing the trajectory of change. Most temporary rivers, at least in California, have been so drastically altered that returning them to a previous state is problematical, so intensive management of flows and habitat to favour desired species is the best option available.

RECONCILIATION ECOLOGY

Standard conservation practice focuses on natural systems that can be set aside as preserves or on altered systems that can be restored to more natural conditions. Alternatively, ecosystems can be managed to favour single species, as is generally required by the state and federal endangered species acts in the USA and as has been traditionally been undertaken in fisheries management. Unfortunately, most ecosystems today are far from pristine, especially those with endangered species, and they require considerable human intervention if they are to support desirable, usually native, species. Increasingly, ecosystems that support desirable species are also novel ecosystems. Rosenzweig (2003) resolves this dilemma through *reconciliation ecology*. This is defined as the 'science of inventing, establishing, and maintaining new habitats to conserve species diversity in places where people live, work, and play' (Rosenzweig, 2003, p. 7). Reconciliation ecology acknowledges that humans increasingly dominate most ecosystems on the planet, which leaves us with the responsibility to determine what we want these integrated ecosystems to look like and what species we want them to contain.

Most aquatic ecosystems, including temporary rivers, have been altered without much consideration for their native biota bringing about increasingly novel ecosystems that bear only superficial resemblance to their historic state. The Sacramento–San Joaquin Delta (the confluence of the Sacramento and San Joaquin rivers), for example, has been transformed from a seasonally dynamic riverine/estuarine environment to one that is more like a lake. As a consequence, California has traded native species such as delta smelt (*Hypomesus transpacificus*), splittail and green sturgeon (*Acipenser medirostris*) for aliens such as Mississippi silverside (*Menidia audens*), largemouth bass (*Micropterus salmoides*) and various sunfishes (*Lepomis* spp.). This ecosystem transformation was the result of ever-increasing diversions of water, new invasions of alien species and many other stressors (Moyle *et al*., 2011). If the Delta is to be a reconciled ecosystem in the future, managers will presumably try to manage the system to favour a well-defined suite of desirable fishes that require more estuarine conditions (Moyle *et al*., 2012). The reconciled ecosystem would still bear only modest resemblance to the historic one, because the physical environment has been irrevocably altered (diked, drained and subsided), some native species have gone extinct, and many species of alien plants and animals continue to be players in the ecosystem. The key for maintaining desirable aquatic species and conditions in this and other ecosystems is active management towards a defined set of goals.

RIVERS IN CALIFORNIA AS NOVEL ECOSYSTEMS

Rivers and streams in Mediterranean climate regions, such as California, are characterized by extreme flow patterns, often drying up in long reaches during rainless summers but then experiencing sudden flood flows during winter and spring rains (Figure 1). Such systems have fishes adapted for living with this basic flow regime, surviving in pools during summer and quickly recolonizing dry reaches when flows return (Moyle, 2002; Bernardo *et al*., 2003; Aparicio *et al*., 2011). This hydrograph makes the streams especially susceptible to alteration because dams can store winter flows and channels are easy to modify when dry. Today, these temporary rivers tend to support fish and invertebrate faunas, in whatever water remains, that are mixtures of tolerant native and alien species. California is typical of other regions with Mediterranean climates both in the extreme alteration of its waterways (Kondolf *et al*., 2012) and in the development of novel ecosystems with many alien species (Moyle, 2002). In the following sections, three quite different examples of novel aquatic ecosystems

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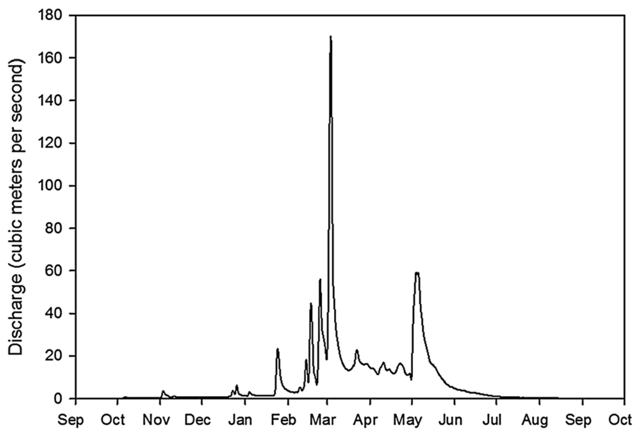

Figure 1. Hydrograph for the Cosumnes River at Michigan Bar, 2008–2009. The Cosumnes River is one of few in California without a dam on its main stem, so the hydrograph reflect once typical patterns of flow for California streams. The peaks of flow represent major winter and spring rain events. During rainless summers, much of the river in this reach is dry, reflecting both natural hydrology and high rates of groundwater pumping for agricultural and urban use

are discussed, that reflect different aspects of temporary rivers in central California (Figure 2). Putah Creek, the Cosumnes River and the Eel River are all clearly novel ecosystems that present challenges for application of reconciliation ecology as a management approach. Also provided is an example of a temporary stream, the Six Bit Gulch, that still retains its original ecosystem because it flows through a harsh landscape in which few non-native organisms survive.

Putah Creek

Putah Creek flows out of the Vaca Mountains in the Coast Range, flowing east into the Sacramento Valley of central California (Figure 2). Historically, it was an intermittent stream for much of its length, but it supported a diverse native fish fauna. These fishes either persisted in remnant summer pools or migrated upstream from the Sacramento River for seasonal spawning (Moyle *et al.*, 1998). Winter–spring floods created a vast swampy area through which the creek meandered in multiple channels. Today, this floodplain region is mostly productive farmland. In the 19th century, the creek was diked and forced into a single channel, which became greatly incised. Groundwater pumping eliminated in-channel pools that were once summer habitats for many fishes. In 1957, the 93-m-high Monticello Dam was built, which resulted in the formation of Berryessa Reservoir, for irrigation, urban water supply, and flood control; the reservoir drowned formerly intermittent reaches in more mountainous regions. The Putah Creek Diversion Dam was built 13 km below Monticello Dam to send nearly all water released from the reservoir down the Putah South Canal to water users. The once intermittent reach between the dams, now with cold water flows year around, became the site of a high-value trout fishery (Moyle *et al.*, 1998). The 27-km reach between the diversion dam and the creek's mouth in the Yolo Bypass, however, was neglected, becoming dry in many years and subject to activities such as gravel mining and trash dumping. However, flows were provided to a 3 km reach immediately below the diversion dam to satisfy local riparian water rights; as a result, this reach inadvertently served as a native fish refuge. This entire 27-km reach is now actively managed as a reconciled ecosystem that favours native fish, plants and other organisms.

Reconciliation came about because of the growing interest, starting in the 1980s, in stream conservation by local citizens and by the University of California, Davis, which is adjacent to the stream. Prompted by an extended drought, which dried up the lower creek, the Putah Creek Council, the university, and the City of Davis sued the dam operator, Solano County Water Agency, to follow state law and provide flows for fish below Putah Creek Diversion Dam (Moyle *et al.*, 1998). An accord among the litigants was reached in 2000, which stipulated a flow regime designed to favour native fishes, including maintaining the creek as a living stream at all times from the diversion dam to mouth and providing timed releases for spring spawning flows. As a result, 10 species of native fishes became dominant in much of the stream (Kiernan *et al.*, 2012), although most of the alien fish species remained (Figure 3). These alien species still dominate the warm lowermost reaches of the creek, supporting a fishery for largemouth bass, common carp (*Cyprinus carpio*) and other alien species.

With the establishment of permanent flows, riparian plants, birds and other organisms began to flourish (Truan, 2004), as did restoration projects, such as removing large amounts of trash, planting native vegetation and undertaking large-scale improvements of the stream channel. These major changes were the result of a combination of factors: (1) enthusiastic citizenry, led by the Putah Creek Council; (2) a full-time stream keeper to manage the creek and restoration projects; (3) a cooperative water agency; (4) cooperative riparian landowners; and (5) annual monitoring of both aquatic and terrestrial organisms.

Despite these efforts, the creek bears little resemblance to the historic Putah Creek, an intermittent stream with long dry reaches. The stream is now permanent, flowing through a narrow corridor of riparian habitat in an agricultural landscape. Importantly, all major groups of terrestrial and aquatic organisms in the corridor are mixtures of native and alien species, with origins from all over the globe (Truan, 2004). Overall, Putah Creek is demonstrably a novel ecosystem with persistence of desirable features determined in part by constant human interventions to discourage alien species (e.g. removing invasive plants) and to encourage

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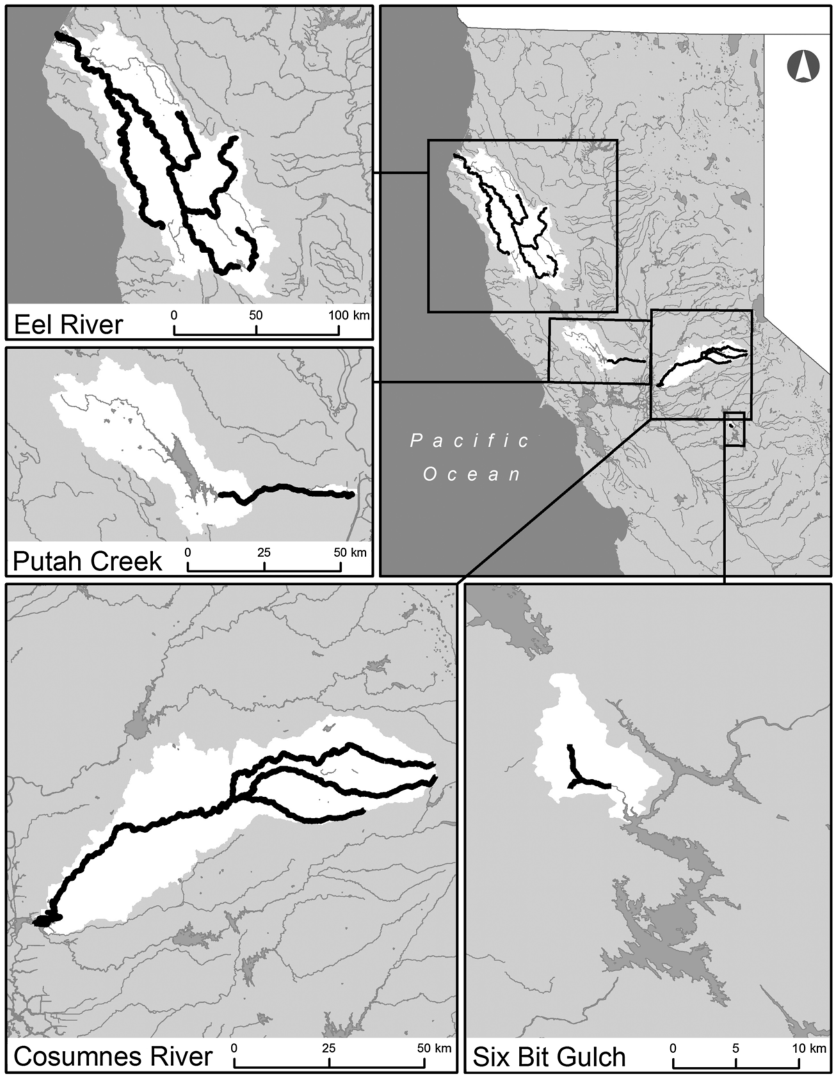

Figure 2. Locations of example streams mentioned in the text; note the differences in scale among the maps

native species (e.g. maintaining stream flows). Likewise, Bernardo *et al*., (2003) report that some Portuguese streams and their fishes behave in a similar fashion, with periodic high flows favouring native fishes.

Cosumnes River

The Cosumnes River is the largest river flowing out of the Sierra Nevada that does not have a dam on its mainstem (Figure 2). This means it is unusual for a California stream in having a relatively unimpaired hydrograph, which is driven largely by seasonal rainfall patterns (Figure 1). Moyle *et al*., (2003) divided the watershed into eight segments on the basis of geology and determined that each segment had a distinctive fish assemblage. The four uppermost segments (600–2000 m in elevation), permanent alpine streams, contained only various combinations of rainbow trout (*Oncorhynchus mykiss*), brown trout (*Salmo trutta*) and brook trout (*Salvelinus fontinalis*); the latter two species are aliens. The next two segments were permanent streams in the foothills (elevation, 15–52 m). In summer months, flows become extremely low ($<0.3 m^3 s^{-1}$) and large, deep bedrock pools support most of the fish. The dominant fish in most of this region is the alien redeye bass (*M. coosae*), which seems to have driven at least two native species to extinction in the river and greatly depleted populations of other native species. It co-occurs primarily by itself or with low numbers of other non-native centrarchids (*Lepomis spp*. and *Micropterus spp.)* present in low numbers.

Below the foothill segments, the river enters the valley floor, where its incised channel is confined by levees that keep farm fields from flooding (Moyle *et al*., 2003). Long reaches of this segment go dry each summer, partly from pumping water for irrigation, although a few large pools

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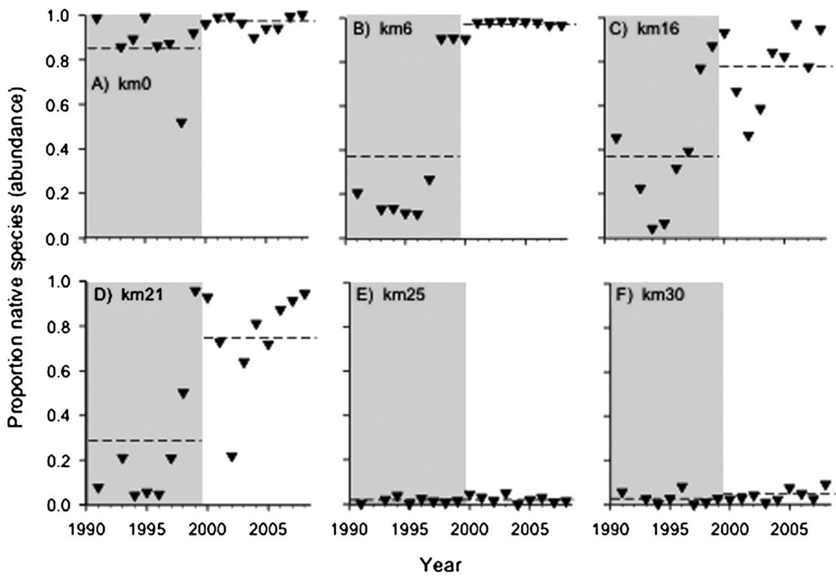

Figure 3. Change in the proportion of native fishes in Putah Creek, 1991–2008, showing the response to the 'natural' flow regime instituted in 2000. The graphs show the response at six stations at differing distances (km) below the Putah Creek Diversion Dam. 1998 and 1999 were high-rainfall years in which flows spilling from the dam were consistent with the natural flow regime. Horizontal dashed lines indicate the mean proportion of native species during each period. Based on Kiernan *et al*. (2012)

persist; the pools mostly support redeye bass and other alien fishes, as well as a few large (>25 cm total length) individuals of Sacramento pikeminnow (*Ptychocheilus grandis)* and Sacramento sucker (*Catostomus occidentalis*). When the dry reaches fill with water in winter and spring, they are used for spawning by runs of pikeminnow, sucker and Chinook salmon (*Oncorhynchus tshawytscha*); usually, large numbers of juveniles are stranded as the river dries, because groundwater pumping results in abnormally rapid desiccation of the riverbed (C. Jeffres, UC Davis, personal communication, 2013).

The two lowermost segments are nontidal and tidal floodplains, respectively. Both floodplains hold water only during extended periods of high flows, which vary in timing from year to year. The use of the tidal floodplain (<1 m elevation) by fish was studied for 7 years by Moyle *et al*., (2007). The Cosumnes floodplain had been re-established by breaching levees that separated the river from agricultural fields, although agriculture continued on large parts of the floodplain. There were 18 species that used the floodplain for spawning and/or rearing of young, 8 natives and 10 aliens. Most spawning took place in fields dominated by non-native annual plants, although some species entered the floodplain as juveniles moving downstream, the product of spawning in the seasonal foothill reach. Chinook salmon juveniles were documented as having exceptionally rapid growth on the floodplain (Jeffres *et al*., 2008). The two groups showed segregation in use of floodplain habitat. The native fishes used the floodplain in February–April, whereas aliens used it April–June. The natives showed strong adaptations for leaving the floodplain as the water receded, whereas aliens tended to become stranded in remnant pools, where they attracted large flocks of piscivorous native birds (Moyle *et al*., 2007). However, the alien species also maintained large populations in permanent tidal waters present in the floodplain. Curiously, redeye bass were largely absent from both these habitats and the floodplain.

Overall, the Cosumnes River watershed can be regarded as supporting an interlinked chain of novel ecosystems, from altered mountain meadows dominated by alien trout (Purdy *et al*., 2012) to the heavily modified temporary reaches with transitory native fishes and pools dominated by alien fishes, to highly modified floodplains used by a diversity of native and alien species (Moyle *et al*., 2003). These ecosystems are not stable in species composition, however, as the environment continues to change (e.g. more water diversions) and as predatory redeye bass continue to spread. Natives seem to persist in floodplain reaches mainly because they show strong adaptations for early season use of floodplains that alien fishes lack. The overall result, however, is use of the floodplain by a wider array of species than would have been possible historically and the domination of fish assemblages of the tidal fresh waters by alien fishes, especially centrarchids and common carp.

Historically, flows in the river would typically have persisted for longer in the lower valley floor reach, providing more opportunities for movement of native fishes between the seasonal floodplain reaches and more permanent headwater reaches. Today, the intermittent reach separates two distinct regions with different novel

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ecosystems: the upstream areas dominated by redeye bass and the floodplain/tidal reach with a mixture of alien and native species.

Eel River

The Eel River is a large (9542 km^2) watershed on the north coast of California (Figure 2), with relatively low elevation (500–600 m) headwaters (Yoshiyama and Moyle, 2010). Its hydrograph is entirely driven by winter rains resulting in rapid rises and falls, and very low flows during the rainless summer (May–October), with many tributaries becoming either dry or intermittent. In reaches close to the Pacific Ocean, water is kept cool in summer by fog, which maintains the forests of coastal redwoods (*Sequoia sempervirens*) and other large trees. Most of the watershed, however, has a classic Mediterranean climate, with hot, dry summers. The vegetation of the upper watershed is a mixture of pine forest, oak woodlands, grasslands and chaparral. The watershed drains a geologic region of rapid uplift and easily erodible rocks, so annual suspended sediment loads (21–23 million metric tons/year) are among the highest in the USA. The sediment is mostly delivered in a few winter storms. Historically, dense vegetation stabilized the hillsides, reducing erosion rates, allowing deep pools to develop and providing partial shade for the summer low-flow channels (Yoshiyama and Moyle, 2010). The classic user of the temporary river habitats is the summer steelhead (*O. mykiss*), an anadromous trout that migrates up to intermittent stream reaches in headwater canyons during spring high flows; the adults spend the summer in these pools and then spawn in the fall when temperatures decrease and streams start flowing again (Moyle, 2002).

The watershed is greatly changed today. Industrial logging, starting in the 1940s, resulted in clearcutting of trees and extensive road building, destabilizing the hillsides. This set up the watershed for massive erosion from record rainfall and floods in 1955 and 1964 (Sloan *et al*., 2001); 10–20 m of sediment was deposited in the channels and most deep pools were filled in, resulting in a wide, shallow, exposed channel with a narrow ribbon of water meandering through it in summer. Although not systematically recorded, summer temperatures in mainstem channels are likely warmer at present than they were historically, with maximum temperatures exceeding 20–22°C on many summer days. The streams in the watershed are largely free flowing, however, despite numerous small diversions. The only large dam on the mainstem Eel River is Scott Dam, built in 1922 to store water for diversion into the neighbouring Russian River. There are no urban areas in the watershed, and the only major area for legal agriculture, aside from grazing, is former estuarine land around the mouth of the river. Unknown quantities of water are removed each year from small tributaries by marijuana growers, which could have significant effects on fishes.

Historically, the Eel River was one of the most important salmon streams in California, supporting large runs of anadromous Chinook salmon, coho salmon (*O. kisutch*) and steelhead, totaling perhaps one million fish per year on average (Yoshiyama and Moyle, 2010). Nine of the 11 other native species are also anadromous or amphidromous, reflecting a fauna highly adapted for taking advantage of a river system with highly variable flows and long intermittent or dry reaches during periods of drought. All of these native fishes are much less abundant than they were historically (Yoshiyama and Moyle, 2010). The salmon runs suffered large declines from overfishing in the early 1900s and their ability to recover was depressed by the massive habitat changes caused by logging, erosion and sediment deposition. Present annual runs are typically less than 5000 fish of all three species combined, a decline of 99%.

An additional change to the watershed has been introduction of 10 species of alien fishes. Five of these species are largely confined to Pillsbury Reservoir behind Scott Dam. Three are present in the larger channels of the river but are uncommon. Sacramento pikeminnow and California roach, however, are now the most abundant and widely distributed species in the watershed (Brown and Moyle, 1997). Both species are well adapted to the clear warm waters and summer pools that now characterize much of the Eel River, which are similar to their native habitats in the nearby Sacramento–San Joaquin River system (Moyle, 2002). The roach, a small (up to 10 cm) minnow, now occupies small, often-intermittent, tributaries that once supported juvenile salmonids, as well as main channel habitats where ever there is sufficient cover for protection from predation. The pikeminnow is a large (up to 50+ cm) piscivore that is assumed to be preventing recovery of anadromous salmonids and lampreys, even as the habitat recovers, through its predation on juveniles (Yoshiyama and Moyle, 2010).

Is the Eel River a novel ecosystem? Its physical habitat has changed enormously but has potential to be restored at least partially if the landscape is allowed to recover from the devastating effects of logging and if predatory alien fish are controlled. The four forks that join to form the mainstem Eel are now either intermittent or have summer flows so low that fish are effectively isolated in permanent pools. The semelparous salmon species, which once delivered enormous amounts of ocean nutrients to the ecosystem, are reduced to very low populations but could also recover if historic channels and summer flows re-established themselves. The fish fauna is now dominated by non-native species but with dominant species coming from nearby watersheds, suggesting the present ecosystem is similar to that found in some Central Valley rivers. However, there

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is no other river so completely dominated by all life stages of the predatory pikeminnow (Moyle, 2002). Right now, pikeminnow and roach domination of the ecosystem seem likely to persist, especially as climate change increases temperatures and reduces late summer flows even more.

The present ecosystem is a difficult one for reconciliation. Despite the conservation significance of restoring threatened salmon and steelhead populations and the potential value of healthy fisheries (likely millions of dollars per year), the effort and expense required to eradicate or reduce pikeminnow populations is generally viewed as prohibitive (Yoshiyama and Moyle, 2010). A similar situation exists in the Cosumnes River, just discussed, where the native fish community, including pikeminnows, has been completely replaced by a single alien predator, the redeye bass (Moyle *et al*., 2003). In both systems, a reconciled ecosystem with the most favourable characteristics would require continuous human intervention for controlling predatory fish numbers and for improving habitats to favour native fishes, including returning now-temporary river reaches to more permanent flows.

Six Bit Gulch

The Six Bit Gulch is one of the most extreme habitats for fish in California. It is the principal drainage of the Red Hills region (Tuolumne County, near China Camp), which has one of the largest outcroppings of serpentine rock in the Sierra Nevada (Figure 2). Serpentine soils contain high concentrations of iron and magnesium, which inhibit plant growth; as a result, serpentine-soil regions are inhabited by predominantly endemic organisms that have evolved tolerances for extreme conditions in both the chemical and physical environment (Harrison, 2013). There is little riparian vegetation, and streams are exposed to the hot sun during the day. Most of the streams dry up by midsummer but water remains in less than 1 km of intermittent stream, fed by small springs (Jones *et al*., 2002, Moyle *et al*., 2013a). The undescribed but distinctive Red Hills roach (*L. s. subsp*.) is endemic to these streams. It persists mainly because of the extreme habitat conditions, given that the Six Bit Gulch now drains into Don Pedro Reservoir (Tuolumne River), which is dominated by alien fishes that can invade the streams. Even so, green sunfish have been observed in one section of the creek, a species that has eliminated the California roach from other intermittent streams (Moyle, 2002). The Six Bit Gulch is an example of a rare stream ecosystem that still retains its original characteristics, despite flowing through a landscape that contains roads, is grazed by cattle, and is subject to use by off-road vehicles (Moyle *et al*., 2013a). If the Red Hills roach is eliminated and replaced by green sunfish (most likely after a wet year makes all habitats accessible), it will qualify as a novel ecosystem, because the sunfish is much more predatory than the roach, which is omnivorous (Moyle, 2002). A sunfish invasion will therefore likely result in a shift in fundamental ecosystem characteristics.

CONCLUSIONS

The examples presented here illustrate that most temporary streams and other aquatic ecosystems in California are likely so highly altered that returning them to an earlier condition or stable state is just not possible. Most temporary streams have either had most of their flows removed, had their channels converted into permanent streams to convey water stored in dams or have been converted to drainage ditches. Not surprisingly, they are often invaded by alien species, creating novel ecosystems. Where more or less intact temporary stream ecosystems persist, it is usually because extreme environmental conditions in small watersheds restrict both alien invaders and human use. This pattern appears to be fairly typical of temporary streams in Mediterranean climate areas (e.g. Bernardo *et al*., 2003; Marr *et al*., 2009; Aparicio *et al*., 2011).

Once aquatic ecosystems are recognized as being novel, they have a more realistic basis for management. Thus the success of management of Putah Creek suggests that applying reconciliation strategies to altered rivers in California is both possible and can promote conservation of native species. Indeed the success of Putah Creek was a factor for returning flows to 240 km of the lower San Joaquin River in the south Central Valley to restore habitat for salmon and other fishes (Börk *et al*., 2012). In some cases, such as the Cosumnes and Eel rivers, reversing decades of human damage to develop a reconciled ecosystem dominated by desired species can be carried out only with great difficulty. Determinations as to which novel ecosystems should also be reconciled will depend on thoroughly understanding the costs and benefits, both economic and non-economic, of alternative scenarios. But the decision process should start by asking the question ‘what kind of ecosystem do we want?’ The answer to the question will depend on societal values (e.g. favouring native fishes of low economic value versus fisheries for alien game fishes) and on views of what is actually possible as climate and other change occurs.

Reconciling novel ecosystems involves the following: (1) setting realistic policy goals (including which species to favour); (2) understanding the basic ecology of the managed systems; (3) taking into account the needs of diverse segments of society; and (4) managing river flows and infrastructure on a more holistic basis (Moyle and Mount, 2007; Geist, 2011; Grantham *et al*., 2012). It also requires policy makers and managers who are willing to take risks with management actions because novel ecosystems may react

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to manipulation in unexpected ways. This is especially true of streams in Mediterranean climate regions, which are facing rapid alteration because of climate change and growing human demand for water.

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