



THIRTY-THREE

Rivers

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Introduction

The diverse ecosystems in and around California's river networks reflect their large latitudinal range and extreme topographic and geologic heterogeneity. California's sixty major and more than a thousand smaller river drainages contrast sharply in the amount of annual precipitation they receive (from $>500 \text{ cm y}^{-1}$ in the northwest corner of the state to $<5 \text{ cm y}^{-1}$ in its southeast corner in the Colorado Desert) (Mount 1995). The timing of runoff from this precipitation also differs markedly between coastal basins watered by rain from Pacific storms and interior basins whose runoff is derived in large part from snowmelt. In this chapter we describe watershed ecosystems of the California rivers that drain to the Pacific Ocean (Figure 33.1). We discuss how native riverine and RIPARIAN biota have adapted, or at least adjusted, to the wide variability in flow and temperature that characterizes various natural (UNIMPAIRED) HYDROLOGIC regimes (Figure 33.2). Knowing how the riverine biota and food webs once assembled and functioned is important for understanding the profound nineteenth- and twentieth-century ecological

impacts of humans on California's water systems, "one of the most massive re-arrangements of Nature ever attempted" (Kahrl et al. 1979, p. iv).

We also hope to inform predictions of how California's riverine ecosystems might change, or be sustained, through shocks and directional changes in climate, land use, and biological communities faced by the state's natural and human systems. We survey general changes in river environments and biota as one travels downstream from headwaters to lowland mainstems and estuaries, and we discuss general attributes of California's riverine biota. We conclude with a description of past, current, and projected human interactions with, and impacts on, California's river systems. Four California basins or regions (Table 33.1) are used to illustrate temporal and spatial variation in natural riverine food webs (the Eel River); water quality patterns through a large river system (the Klamath River); and the impacts of land and water development on rivers and their native species (the Sacramento-San Joaquin-Lake Tulare system; and southern and central coastal rivers).

General Tendencies in River Networks and Ecosystems

Every river basin is unique, and those in California are particularly diverse, but all river networks share fundamental characteristics that constrain how their habitats and ecosystems change over space and time. From headwaters of drainage networks to lowland mainstems, rivers change in partially predictable ways that strongly influence the organisms and ecosystems they support. Streams usually begin at springs or seeps near basin divides (Montgomery and Dietrich 1988) and gather **RUNOFF** from larger and larger **DRAINAGE AREAS** as they flow from headwaters to lowlands. As discharge (flow) increases downstream, river channels widen and deepen, and average flow velocities increase. At a single site, width, depth, and velocity also increase or decrease as river flow rises and falls. These changes in width, depth, and flow velocity vary more or less predictably according to a set of empirical relationships known, respectively, as “**DOWNSTREAM**” and “**AT-A-STATION HYDRAULIC GEOMETRY**” (Leopold et al. 1964). These hydraulic adjustments with flow result in changes in sediment erosion, transport, and deposition that alter channel morphology, bed texture, and disturbance regimes (i.e., bed mobilization during floods).

As channels widen, streams receive more solar radiation, which increases water temperature and the potential for aquatic primary production (growth of aquatic plants and algae) (Vannote et al. 1980). Substrata and channel morphology change systematically downstream, with steep headwaters typified by coarse boulder and bedrock substrata, and mid-elevation rivers with gentler gradients having gravel, pebble, and cobble substrata, with occasional boulders and bedrock formations emerging as habitat islands (Dunne et al. 1991, Montgomery and Buffington 1997). Near river mouths (e.g., estuaries, confluences) and in low-gradient lowland rivers, beds are composed of mobile sands and silts. Disturbance from bed mobilization therefore increases in frequency downstream. In steep headwaters, debris flows sometimes fill channels, but these are rare events, recurring at century to millennial time scales. Lower in the drainage network, floods mobilize beds and scour rock-bound organisms, sometimes several times a year, when flows exceed **BANKFULL**. In lowland rivers, sand and silt beds are in constant motion, except where sediments are stabilized by large debris jams and flood-tolerant vegetation or are stored in off-channel water bodies.

As river discharge fluctuates, local (“at-a-station”) habitats expand and contract, connect and fragment, and environmental gradients within and along channels change. Drought may leave channels completely dry, whereas sediments carried by large floods scour, move, and bury river beds, killing or removing the sedentary benthic (bottom) biota. Some organisms can survive scouring disturbances. Mobile organisms, such as fish, can seek refuge in channel backwaters, under banks, behind logs, bedrock formations, or large rocks. Generally only the surface layer of the river bed, about as deep as the median diameter of bed particles, is mobilized during floods. Water-filled spaces below this layer serve as refuges for organisms that seek cover there. These **HYPORHEIC** habi-

tats are also refuges during droughts if they provide access to underlying groundwater. They are important refuges for prey from larger predators during biologically active periods. Hyporheic refugia are lost when coarse cobbles and pebbles in rivers become embedded within fine sand, silt, and clay sediments, or when ground water is pumped, withdrawing hyporheic flows. Excessive loading of fine sediments is one of the most widespread forms of environmental degradation of river ecosystems (Waters 1995). In California (Suttle et al. 2004), excessive fine sediments that clog river beds have been introduced by hydraulic mining, deforestation, road building, livestock grazing, construction, and agricultural practices, some of which continue to this day.

Dewatering droughts and bed-scouring floods are natural disturbances that structured stream ecosystems long before humans appeared. Sousa (1984) defined **DISTURBANCE** as an event that kills or removes organisms and frees space and other resources for new biota. Animals that survive drought or flood in refuges, as well as attached algae, mosses, and microbes that are not completely removed from rock surfaces, become the seeds for recovery during ecological **SUCCESSION**, the process that reestablishes biota after disturbance (Connell and Slatyer 1978, Fisher et al. 1982, Power et al. 2008). Surviving organisms are joined by colonists that move from other habitats into recently disturbed, sparsely populated areas. For example, an “air force reserve” of winged, terrestrial adult insects oviposit in rivers, seeding new generations of aquatic larvae to reestablish their populations (Gray and Fisher 1981). Large fish and other predators are more mobile than algae or small invertebrates and often survive disturbances that destroy organisms at lower trophic levels. As food webs recover from disturbance during succession, the first producer or prey species to recover or colonize tend to have traits that favor high dispersal and high growth rates. Later arriving taxa are often more defended against predators (e.g., toxic, armored, or tightly attached). Living within attached retreats is another common adaptation that protects stream animals from predators and parasites but requires organisms to stay in one place (a **SESSILE** lifestyle), and allocate energy, time, and nutrients from reproduction or growth to building protective coverings. During early stages of succession, food webs tend to have surviving predators that encounter relatively edible, vulnerable prey. Therefore, disturbances can often lengthen food chains (Power et al. 1996) by allowing energy from primary producers (algae or plants) to flow efficiently up through herbivores to feed predators. By controlling prey, these predators can indirectly alter the biomass of primary producers by reducing grazers or their predators through chains of direct and indirect interactions called **TROPHIC CASCADES** (Estes et al. 2011, Power 1990b).

Hydrologic Regimes in California's Rivers

Many Californian rivers experience Mediterranean seasonality, with almost all precipitation occurring during the cool winter months, followed by summer droughts with little or no rainfall. In rivers fed by snowpacks in the Sierra Nevada, Klamath, or Cascade mountains, **HYDROGRAPHS** (plots of discharge or flow versus time; see Figure 33.2) are typified by large spring flows during snowmelt that diminish through the summer. In other regions of California with less snow-

Photo on previous page: Unicorn Peak and Tuolumne River at Tuolumne Cascades, Yosemite. Photo: Carson Jeffres.

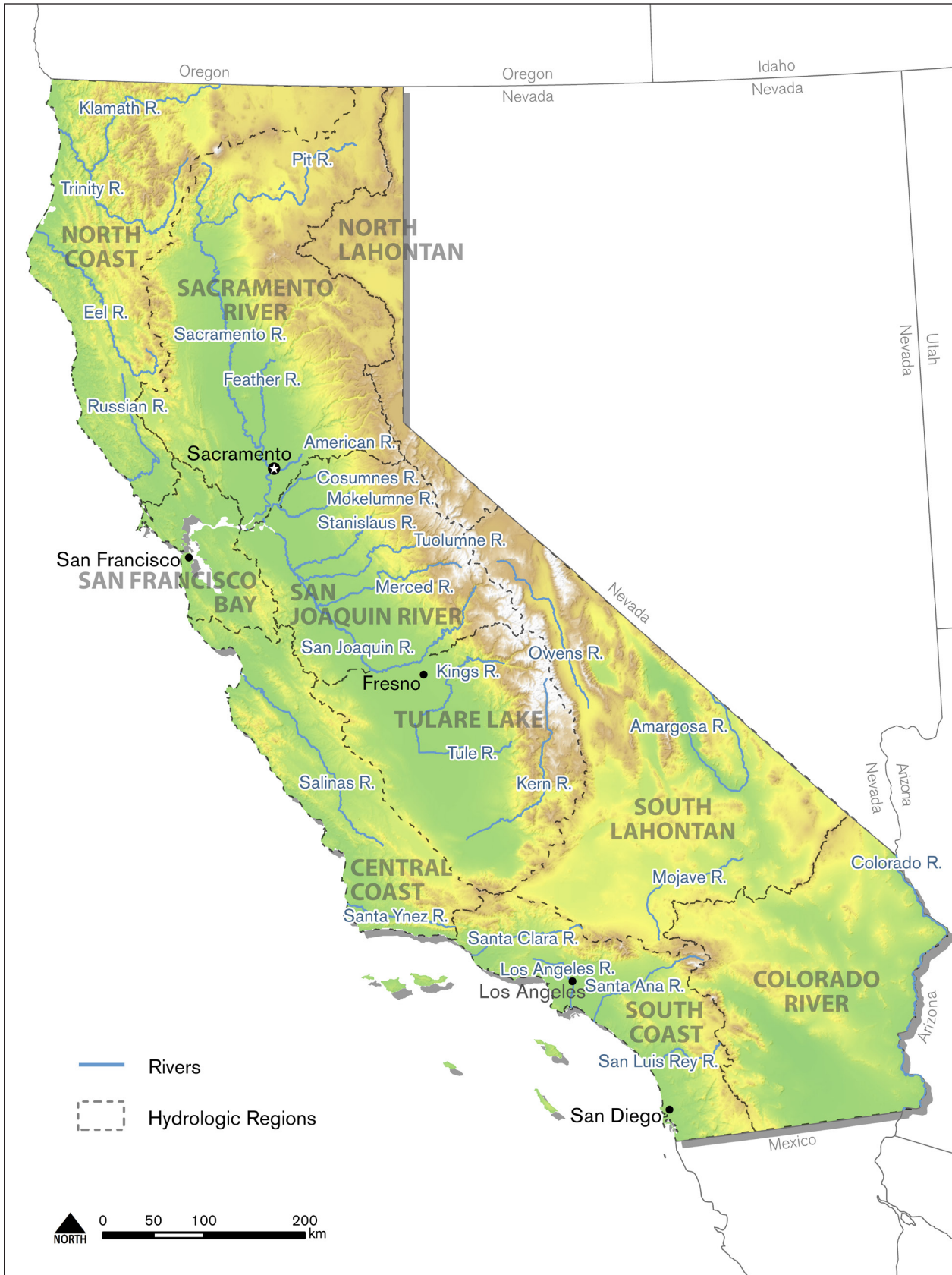


FIGURE 33.1 Major rivers and hydrologic regions of California (with permission after figure in Howard et al. 2013). Source: U.S. Geological Survey, National Hydrography Dataset (NHD). Map: Parker Welch, Center for Integrated Spatial Research (CISR).

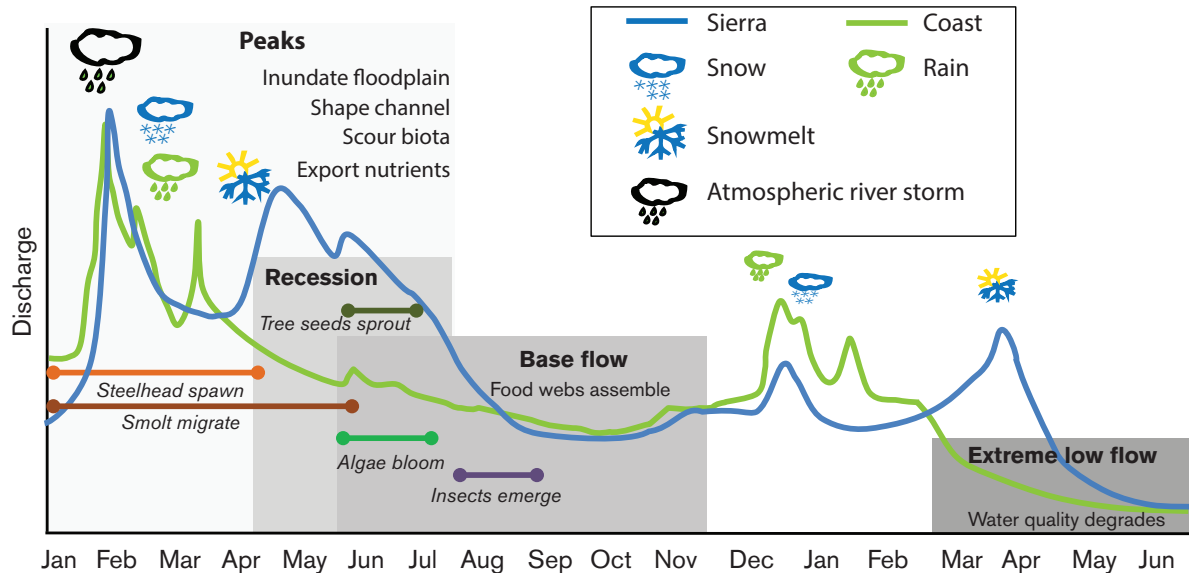


FIGURE 33.2 Stylized hydrographs indicating periods of flooding in a wet year (left); life-cycle events of representative organisms (colored bars placed with respect to time, not discharge); and periods of stress on the biota in a drought year (right) due to drying, high temperatures, and high solute and low dissolved oxygen concentrations. Discharge indicates relative volume rate of water flow. With permission after a figure from Yarnell et al. 2010.

pack, hydrographs of streams and rivers closely follow rainfall patterns, which typically follow the winter-wet, summer-drought “Mediterranean” seasonality of much of the state. On top of this strong seasonality, regions under Mediterranean climates, including California, experience large year-to-year variation in precipitation and flow patterns, ranging from frequent, intense winter storms and unseasonably late spring spates to extreme year-round drought, with many implications for the river biota (Gasith and Resh 1999, Power et al. 2008). The responses of river organisms to hydrologic disturbances depends on the timing of flood or drought events relative to the timing of organismal life history stages. Native riverine species in western North America have many morphological, physiological, and behavioral adaptations to the “deluge or drought” conditions typical of this region, such as behavioral adaptations for seeking refugia during disturbances (Meffe and Minckley 1987, Meffe et al. 1983, Lytle and Poff 2004).

An attempt to subdue and harness the variable flows of California’s rivers motivated the massive rearrangement of the state’s water system for flood management or prevention; for storage, diversion, and transport of water to generate electricity; and to irrigate crops and supply urban areas. By capturing much of the water from winter rains and spring snowmelt and releasing it over the summer, dam operations decrease the average magnitude of high flows, create daily pulsed flows for powerhouses to generate electricity during peak demand hours, and eliminate the gradual decline of river stage when flood waters recede (Figure 33.3). Next, we briefly describe dominant types of organisms—primary producers, invertebrates, and vertebrates—that live in and around California’s rivers. We find repeated evidence that human alteration of the water cycle is a serious threat to California native, river-associated flora and fauna because they are adapted to the region’s natural, albeit extremely variable, hydrologic regimes.

Overview of Key Taxa in Food Webs of Californian Rivers

Primary Producers

Consumers in rivers derive their energy (or carbon) both from terrestrial plant detritus and invertebrates and from aquatic primary producers. Primary production in rivers is carried out by diverse, phylogenetically distant photosynthetic organisms: cyanobacteria or “blue green algae” (Cyanophyta); diatoms (Bacillariophyta); green algae (Chlorophyta); aquatic mosses and liverworts (Bryophyta); and vascular plants (Tracheophyta). All riverine producers have distinct life history traits that affect their distributions and abundances in channel networks, their PHENOLOGIES (seasonal life history cycles), and their ecological roles. Aquatic vascular plants (macrophytes) may become dense in slow-moving or stagnant waters as well as during sustained periods of low, stable flow but are scoured from substrata during floods (Klose et al. 2009). These plants are often important habitats for EPIPHYTON, fish, and invertebrates. Like terrestrial plant material, aquatic macrophyte tissue enters river food webs primarily as DETRITUS (dead organic matter) (Webster and Benfield 1986), which is colonized and broken down by microbes (fungi and bacteria). The simple molecules produced and incorporated by these microbes make important nutritional contributions to the diets of detritivorous invertebrates and fish (Arsuffi and Suberkropp 1984).

“Algae” (an informal term for a diverse array of nonvascular aquatic primary producers, including single-celled and multicellular colonial taxa) are usually the dominant primary producers in sunlit streams and rivers (Box 33.1). During favorable periods, algae grow vegetatively by division of solitary or colonial cells. Spores or other resting stages are produced for dispersal and to endure periods of environmental stress, like drought (Bold and Wynne 1985). Diatoms can divide from

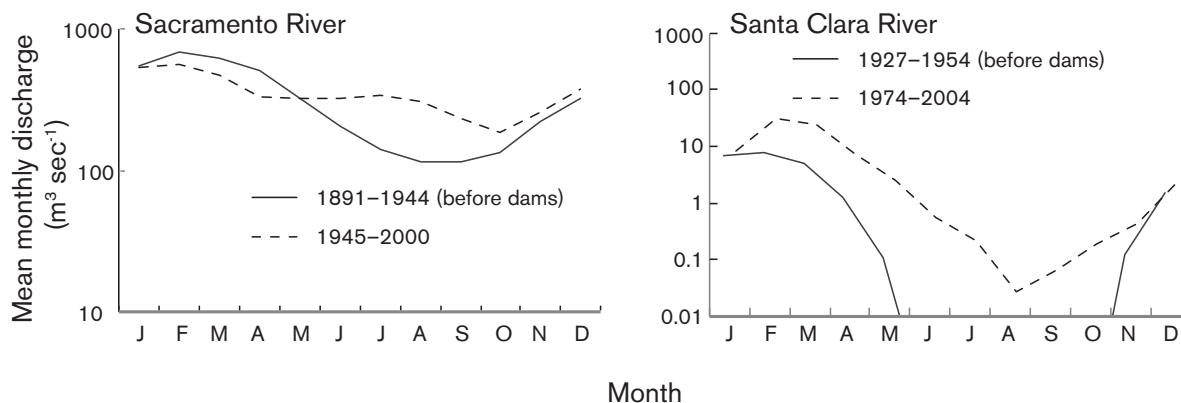


FIGURE 33.3 Seasonal flows in the Sacramento River (left) and Santa Clara River of southern California near Montalvo (right, U.S. Geological Survey gage 11114000), showing the effects of dam operations that capture and store winter precipitation, release flows during the summer, and augment discharge with agricultural return flows. Sources: With permission after figure from Kondolf and Batalla 2005.

once to several times daily, prokaryotic cyanobacteria even faster (Lowe 2011). Green algae, which can attain a high biomass as “macroalgae” in sunlit rivers (Whitton 1970, Dodds and Gudder 1992), can proliferate via cell division or episodic cloning events (Stevenson et al. 1996).

Algae also are characterized by their habitat associations. They can be planktonic (drifting in the water column) or attached. Attached algae, because they resist washout, dominate in flowing streams and rivers and are characterized by the substrata on which they grow, as *EPILITHIC* (on stone), *EPIPELIC* (on clay, sand or silt), or *EPIPHYTIC* (on plants, often on macroalgae) forms. *METAPHYTON* are algae that may initiate growth attached to substrata but then proliferate to become suspended, cloudlike, in the water column. Floating mats of detached algae can become conspicuous after proliferations start to senesce. *PHYTOPLANKTON* are algae suspended in the water column, which can accumulate in river pools, side channels, or floodplain waters during low flow.

Algae have strong impacts in rivers as food sources, as habitat structure, and by influencing and sometimes controlling biogeochemical cycles and water quality. Diatoms generally have the highest nutritional quality, supplying lipids and polyunsaturated fatty acids (PUFAs) that are needed but not synthesized by most animals (Brett et al. 2009). Given their rapid growth and high nutritional quality, low (inconspicuous) standing crops of diatoms can support large biomasses of consumers (Elton 1927). Their potentially high productivity, nutritional quality, and low abundance (often due to high grazing pressure) make diatoms and other edible algae sources of “hidden carbon” whose importance in river food webs is revealed only when scientists conducting experiments (Lamberti and Resh 1983, McNeely and Power 2007), or other circumstances (Kohler and Wiley 1992), remove grazers. In contrast, certain cyanobacteria, particularly those that proliferate under warm, low-flow conditions, can synthesize harmful toxins affecting the liver (e.g., microcystin) (Smith et al. 2008, Miller et al. 2010) and nervous system (e.g., anatoxin) (Kudela 2011, Paerl and Huisman 2009). Whether algae have beneficial (via food web support) or detrimental (via toxin production or oxygen depletion) effects on fish and other vertebrates (Puschner et al. 2008) depends on environmental conditions, particularly flow, light, temperature, and nutrient levels (Klose et al. 2012). In flowing rivers that are sunlit but cooled during summer by groundwater inputs and riparian

shading, edible algae grow rapidly but are also typically suppressed by grazers. These algae can fuel the growth of salmonids (salmon and trout) and other desirable consumers by supporting invertebrate prey. When drought, water withdrawals, or impoundments reduce flow through sunlit California rivers, disconnected pools and backwaters warm, stagnate, and stratify. If warm stagnant habitats are enriched by decaying organic matter or other sources of nutrients, they can support blooms of cyanobacteria, including potentially toxic taxa (Paerl and Huisman 2011).

In contrast, when river flows below dams are kept artificially cold and stable during summer by releases of deep water from upstream reservoirs, other potentially harmful algae can proliferate, such as the benthic diatom *Didymosphenia geminata* (Kirkwood et al. 2009, Kumar et al. 2009). The bedrock geology and snowmelt hydrology of rivers in the mountains of California produce chemical and thermal conditions that allow *Didymosphenia* to cover rocks with a sheath of extracellular mucilage and exclude edible algal species (Rost et al. 2011). *Didymosphenia* may also benefit when hydroelectric dams are managed to follow peak energy demand, causing daily wetting and exposure of river edges (Furey et al. in press). Mucilage may keep these and other algae moist, allowing them to dominate areas that are only periodically inundated (Benenati et al. 1998). Because mucilaginous taxa are often unpalatable or have low nutritional value (Shannon et al. 1994), such algae may lower the nutritional quality of attached algal assemblages and restrict the flow of energy and nutrients up food chains to higher trophic levels (Furey et al. in press).

Invertebrates

California rivers and streams host a wide range of invertebrates: worms (flat worms, round worms, aquatic earthworms, leeches); insects; crustaceans (e.g., crayfish, amphipods or scuds, and microcrustaceans (cladocerans, copepods, and ostracods); water mites; and mollusks (snails, mussels, and clams) (Figure 33.4). Some groups are quite diverse, with at least 100 species of mollusks, 50 species of crustaceans, and more than 1,100 species of aquatic insects, excluding the Diptera (flies, midges, mosquitoes) (Ball et al. 2013). Many additional species, including many that are *ENDEMIC* to Cali-

(continued on page 722)

TABLE 33.1
 Characteristics of river systems described in Boxes 33.1, 33.3, 33.4, and 33.5

Descriptive feature	Klamath	Eel	Sacramento	San Joaquin/ Tulare Lake	Central/southern California
Major river or tributaries (generally listed north to south)	Shasta, Scott, Salmon, Trinity (below Upper Klamath Lake)	South, Middle, North Forks, Van Duzen	McCloud, Pit, Feather, Yuba, Bear, American	San Joaquin: Mokelumne, Stanislaus, Tuolumne, Merced, Upper San Joaquin. Tulare Lake: Kaweah, Tule, Kern, Kings Rivers	Central: Pajaro, Salinas, Carmel, Arroyo Grande South: Santa Maria, Santa Ynez, Ventura, Santa Clara, Los Angeles, San Gabriel, Santa Ana, Santa Margarita, San Luis Rey, San Diego
Drainage area (km ²)	31,339	9,546	71,432	35,065	355–10,774
River length (km)	410	320	1,110 (including Pit River)	589	40–290
Peak discharge (m ³ sec ⁻¹ , date)	15,775 (December 3, 1965)	>21,000 (December 31, 1964)	17,556 (February 19, 1986)	2,237 (December 9, 1950)	680–3,653
Mean annual discharge (m ³ sec ⁻¹)	487	207	665 ^A	127	1.9–10.3
Hydrograph type	Headwaters: Interior: snowmelt Below 1,000 m Coastal: rain	Mediterranean, precipitation as rain with coastal fog	Headwaters: snowmelt Below 1,000 m: rain	Headwaters: snowmelt Below 1,000 m: rain	Rain
Vegetation	Great Basin/High Desert, subalpine forest, mixed conifer and oak woodland, coastal mixed deciduous and conifer	Coastal mixed deciduous and conifer, eastern oak-grassland	High elevations: treeless and subalpine forest, mixed conifers Low elevations: oak savannah, deciduous riparian forest, wetlands	High elevations: coniferous forests Treeless above 3,200–3,500 m Low elevations: wetlands, grassland, chaparral, and oak woodlands	Chaparral, oak woodlands, grasslands, coastal sage scrub; mixed coniferous/redwoods in northern coastal
Land use	High elevations: wildlands, timber, livestock grazing/rangelands. Moderate elevations: timber, agriculture, livestock grazing/rangelands Low elevations: timber, low intensity/sustainable agriculture	Timber, cattle ranching, gardens (marijuana and vegetable) and dairy near the mouth	High elevations: wildlands, timber, livestock grazing Low elevations: intense agriculture, urbanized around cities of Sacramento and Fresno	High Sierra: wildlands, some timber, livestock grazing Low elevations: intense agriculture	Wildlands: high elevations and inland; valley agriculture; heavily urbanized in the south (Ventura, Los Angeles to San Diego)

A. At Freeport.

BOX 33.1 NATURAL FOOD WEBS THROUGH SPACE AND TIME: THE EEL RIVER

The South Fork Eel River and several of its tributaries run through the 3,200 hectare forested Angelo Reserve, where biota and food webs have been studied since the 1980s. Within the reserve, tributary basins are relatively pristine, but the mainstem South Fork bed is clogged with excessive fine sediment from logging and dirt roads upstream of the reserve. Studies of the upper Eel illustrate how food web structure and species interactions change over the annual Mediterranean hydrologic cycle, and up and down drainage networks, in relatively unimpaired coastal California rivers.

Changes over Time: Seasonal Phenology of the Eel River Biota

Under “normal” Mediterranean seasonality, rainy, cool winters precede biologically active summer drought periods. The coarse boulder and bedrock beds in tributaries of the Eel remain stationary during high winter flows, but in mainstem channels with more flow, smaller (gravel, pebble, cobble) bed sediments are mobilized once or several times during winter floods, when discharges exceed bankfull (a frequency-defined discharge corresponding to flows with about 1.5 year RECURRENCE INTERVALS) (Parker 1978).

In springs following winter flood-scour, days lengthen; flows clear, subside, and warm; and attached algae proliferate. Epilithic diatoms, cyanobacteria, and green algae regrow on the river bed. The green macroalga (*Cladophora glomerata*), which dominates PRIMARY PRODUCER biomass during summer, initiates vegetative growth from basal cells that survived winter flood-scour on more stable substrates (e.g., boulders and bedrock). During the late spring/early summer period with high-nutrient fluxes and lengthening days, and before grazer populations have recovered from scour, *Cladophora* streamers can attain several meters in length, peaking in midsummer.

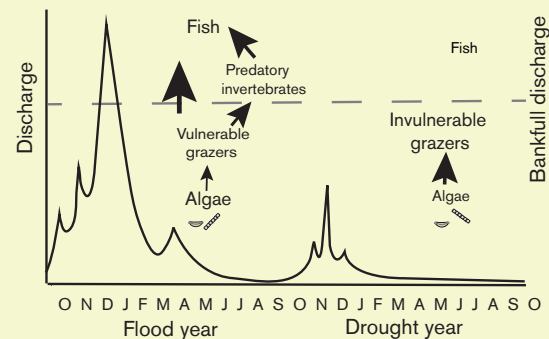
The first invertebrates to colonize after scouring floods are early successional PRIMARY CONSUMERS, primarily fast-growing, mobile, unarmored invertebrates like mayflies and chironomids. These are prey vulnerable to predatory invertebrates (e.g., dragonfly and damselfly nymphs) and fish. At this time, fish influence the persistence of *Cladophora* blooms through trophic cascades (Estes et al. 2011). Large fish in the Eel suppress both herbivores and small predators that eat herbivores, so their indirect effects on algae can be positive or negative depending on which pathway dominates during a given year (Power et al. 2008). In some years, an algivorous midge (*Pseudochironomus richardsoni*) that is consumed by small predators but not large fish becomes abundant enough to suppress *Cladophora*. During these years, fish have negative effects on algal biomass because they reduce small predators, releasing fish-resistant grazers to suppress algae (Power 1990a, Power et al. 2008). In years without substantial recruitment of fish-resistant grazers, fish suppress all important algivores, with a positive indirect effect on algae (Power et al. 2008).

Bed-scouring flows do not happen every winter. During drought winters without flood-scour, large, heav-

ily armored, cased caddis flies (*Dicosmoecus gilvipes*) and sessile, attached grazers such as a common aquatic moth larva (*Petrophila* spp.) overwinter in large numbers. These grazers are susceptible to scouring floods, but not to fish and other predators, and can suppress *Cladophora* growth during the following summer (Power et al. 2008). When *Dicosmoecus* are experimentally removed during drought summers, however, algae can recover to cover substrates and form floating mats (Wootton et al. 1996). In summers following drought (scour-free) winters, fish have no indirect impact on algal biomass, receive little energy from invulnerable grazers, and grow poorly (Parker and Power 1997). Invulnerable grazers are the functionally important apex consumers in two-level food chains. In contrast, floods that remove predator-resistant grazers and release vulnerable grazers and algae are followed by summers with longer food chains, more energy flow from algae to fish, and stronger top-down effects of fish on algal biomass (Power et al. 2008) (Box 33.1 Figure 1).

Cladophora blooms can increase the surface area available for colonization by microbes, stream invertebrates, and epiphytic cyanobacteria and diatoms by approximately five orders of magnitude (Dodds 1991, Dudley et al. 1986, Power et al. 2009). Over the summer months the color of *Cladophora* blooms changes from green to yellow to rusty red as encrustations by epiphytic diatoms thicken (Power et al. 2009). During early to middle epiphyte succession (June through early July), epiphytes are dominated by monolayers of tightly adhering, low-profile taxa. Later in the season, *Cladophora* and its early epiphytes become smothered by diatoms in the family Rhopalodiaceae, a family of diatoms that contain nitrogen-fixing endosymbiotic cyanobacteria that provide a nutrient source in these nitrogen-limited waters (Peterson and Grimm 1992, Hill and Knight 1988, Marks and Power 2001, Power et al. 2009, Furey et al. 2012). Unlike earlier epiphyte assemblages, *Rhopalodia* and *Epithemia* smother their

(continued)



BOX 33.1 FIGURE 1 Dominant food webs in the Eel River over wet and dry years. Text sizes and arrow sizes within the food web diagrams indicate abundances of functional groups and magnitudes of trophic interactions, respectively. Illustration: Sheila Wiseman.

(Box 33.1 continued)

Cladophora host in deep layers, darkening the bloom to a deep rusty red (Power et al. 2009).

Atmospheric nitrogen fixed by cyanobacteria can be used to synthesize toxins or proteins. The endosymbionts in *Epithemia* and *Rhopalodia* appear to produce compounds of high nutritional quality, as they are strongly preferred and rapidly consumed by tadpoles (Kupferberg et al. 1994), estuarine amphipods, and isopods (Ng 2012), snails, and grazing insects (Power et al. 2009, Furey et al. 2012). Areal rates of insect emergence are up to twenty-five-fold greater over rusty-red *Epithemia*-rich *Cladophora* proliferations than over areas lacking these blooms (Power et al. 2009).

By late summer, *Cladophora*-epiphyte assemblages are reduced to short stubbles by grazing, decay, or sloughing. Much *Cladophora* biomass dries along shorelines and on emergent rocks, or floats downstream to accumulate in slack water areas and depositional zones, where it decomposes. Floating mats of algae become hot spots of insect emergence (Power 1990b), diverting riverine energy and nutrients to riparian and aerial insectivores (lizards, spiders, birds, and bats) (Power et al. 2004, Baxter et al. 2005, Ng 2012). Riverine algae that drift (or are experimentally introduced) into the estuary are rapidly consumed by the crustaceans (amphipods and isopods) that abound there. During late summer, palatable algae and algal detritus are repeatedly regrazed, passing several times through guts as the feces of snails, tadpoles, and grazing insects. These repeatedly processed algae accumulate as whitened, flour-like deposits in quiet backwaters and pools along river margins. Late-summer *Cladophora* becomes overgrown by cloudy blooms of bright green Zygnematales (*Mougeotia* and *Spirogyra* spp.) whose slimy extracellular mucopolysaccharide secretions keep them free of diatom epiphytes and, hence, grazers (Power and Matthews 1983, Power and Stewart 1987). Where heavy grazing or abrasion keeps stone surfaces clear of deposits or overgrowth, free-living, tightly attached cyanobacteria like *Rivularia* proliferate.

During the later phases of summer drought, pools and backwaters become isolated and stagnant, condi-

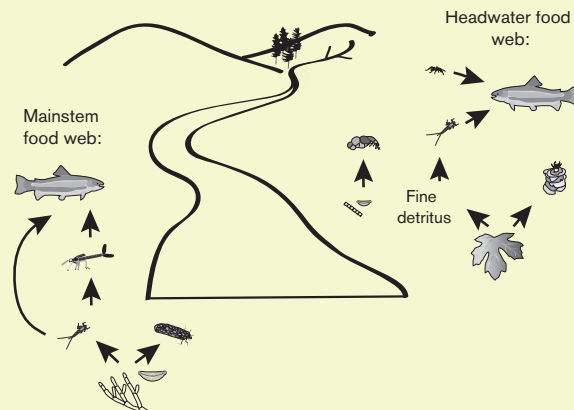
tions exacerbated by water extraction for human use. Rotting algae and detritus trapped in these warm habitats release nutrients, fueling blooms of cyanobacteria (*Anabaena*, *Cylindrospermum*, *Lyngbya* or *Planktothrix*) (K. Bouma-Gregson, R. Lowe, P. Furey, and M. Power personal observations). During extremely low summer flows, isolated mainstem pools can become thermally stratified, engendering harmful blooms of toxic cyanobacteria (Paerl and Huisman 2009). At least eleven dog deaths have been linked to toxic cyanobacteria in the Eel since 2002 (Hill 2006, Puschner et al. 2008). Predicting where and when such problems arise motivates considerations of controls over river food webs and water quality from headwater tips to the terminus of the drainage network.

Spatial Energy Sources to Channel Food Webs down the Drainage Network

Headwater Tributaries

(Drainage Areas = 0.1–100 square kilometers)

Stable carbon isotopes have been used to distinguish terrestrial from aquatic sources of carbon for river resources and consumers (Finlay 2001), although information from other isotopes (e.g., of H and N) is often needed to reduce uncertainty in these analyses (Cross et al. 2013, Tsui et al. 2013) (Box 33.1 Figure 2). Using published and his own data from drainage areas ranging from 0.2 to >4,000 square kilometers, Finlay (2001) analyzed downstream trends in $\delta^{13}\text{C}$ signatures of detritus, algae, and various functional groups of consumers. Over this range, terrestrial leaf litter retained a $\delta^{13}\text{C}$ signal of ca. -28 , but algae showed increasingly enriched $\delta^{13}\text{C}$ values downstream (Finlay 2001, Finlay et al. 2011). As channels widened, productive algae in sunny reaches became increasingly carbon-limited and enriched in the heavier isotope, particularly in pools (Finlay et al. 1999). Where channel drainage areas exceeded 100 square kilometers, algae were clearly $\delta^{13}\text{C}$ -enriched relative to terrestrially derived carbon, allowing clear distinctions between consumer tissues built from terrestrial detritus versus instream algae.



BOX 33.1 FIGURE 2 Longitudinal changes in the Eel River food web from headwaters to mouth. Illustration: Sheila Wiseman.

Carbon signatures of stream consumers, then, can indicate their dietary sources of energy (Rundel et al. 1988). Finlay et al. (1999) found that shredders, as expected, had $\delta^{13}\text{C}$ values consistently similar to those for terrestrial leaves in channels draining areas ranging from 0.2 to 4,000 square kilometers. Deposit and filter-feeders, unarmored scrapers, and invertebrate predators were also built of terrestrial carbon, but only in small headwater streams. Except for shredders, all consumer FUNCTIONAL GROUPS were substantially and increasingly supported by algal carbon downstream (Finlay 2001, McNeely et al. 2007). Fish predators did not occur in very small headwaters and showed increased $\delta^{13}\text{C}$ signatures elsewhere, suggesting substantial contributions of algal-based resources to their diets. Strikingly, armored grazing invertebrates, such as the stone-cased caddis fly (*Glossosoma penitum*), had algal carbon signatures even in the smallest headwater streams (i.e., those draining <1 square kilometers) (McNeely et al. 2007). Experimental removal of this caddis fly from replicated pools of a small, dark tributary of the Eel River shifted mayfly diets from terrestrial detritus to algae (McNeely et al. 2007).

We can use these results to illustrate “predictive mapping” of environmental or biotic changes in river channel networks. If sunlight to the channel increased (e.g., following fire or logging), or if *Glossosoma* were extirpated by parasites, as occurred in Michigan streams (Kohler and Wiley 1992), the threshold above which vulnerable grazers, and hence their fish and salamander predators, could derive their carbon from high-quality algal sources might move upstream in the drainage network. Shifts to algal energy sources should also occur further upstream in basins where riparian vegetation is reduced, either naturally (e.g., in deserts or at high elevations) (Minshall et al. 1997) or by human disturbance.

Mainstems (Drainage Areas = 100–1,000 square kilometers)

Downstream in more sunlit reaches, epilithic and epiphytic algal production is higher (Finlay et al. 2011) (see Box 33.1 Figure 2). South Fork Eel mainstem channels, draining subcatchments more than 100 square kilometers, are wide enough that solar radiation reaches the water surface for six to eight hours or more per day during the summer growing season. As a consequence, primary production increases and blooms of filamentous green macroalgae proliferate. Solar radiation is also sufficient to support a sharp increase in nitrogen fixation (Finlay et al. 2011), an energy-intensive process (Vitousek and Howarth 1991, Marcarelli et al. 2008).

Mediterranean flow seasonality and leaf phenology reduce the access of river consumers to terrestrial litter or detritus during the summer. Because winter scour denudes lateral bars of vegetation and channels are much narrower in the summer than winter, riparian vegetation is set far back from the summer wetted channel, and much of the terrestrial litter is stored on dry bars until the rainy season. In addition, dominant riparian trees along the Eel (white alders, *Alnus rhombifolia* (Nutt.); big-leaved maples, *Acer macrophyllum*

Pursh; Oregon ash, *Fraxinus latifolia* Benth., willows, *Salix laevigata* Bebb, *S. lasiolepis* Benth.) retain most of their leaves until fall or winter. Leaf litter on mainstem lateral bars is swept downstream towards the ocean by the first winter floods. Despite this Mediterranean seasonality and phenology, some mainstem shredder taxa still consume primarily terrestrial detritus.

Fluxes of algae or invertebrates link river habitats longitudinally as well as laterally. The carbon signatures of filter-feeders (net-spinning caddis flies and blackflies) in sheet wash habitats tumbling over boulders indicate that they are collecting algal particles that grew in quiet upstream pools (Finlay et al. 1999, Finlay et al. 2002). Algal production in shallow pools in the South Fork of the Eel River supports invertebrate prey, which emigrate and are eaten by juvenile steelhead in riffles. These juvenile trout, in turn, can move into deep pools, where they become prey for large, cannibalistic rainbow trout (Finlay et al. 2002) and non-native pike minnows (*Ptychocheilus grandis*) that were introduced into the Eel in 1979 or 1980 (Brown and Moyle 1991, 1996).

Lowland Channels to Estuaries

(Drainage Areas = 1,000–10,000 square kilometers)

Although Mediterranean riparian tree phenology and flow seasonality reduce terrestrial subsidies for river consumers in Eel River mainstems, these seasonal changes enhance links from riverine algae to terrestrial consumers directly or indirectly via insect emergence. Emerging insects deliver algal carbon and nutrients to terrestrial invertivores (spiders, beetles, lizards, birds, and bats) (Power et al. 2004, Sabo and Power 2002 a,b), and stranded algae along shorelines become food for terrestrial herbivores. Near the Eel estuary at Ferndale, the Eel Valley opens, and wide, lateral bars retain considerable biomass of locally attached and incoming drift algae stranded during receding summer flows (Power et al. 2013). Stranded algae are consumed by specialist algivores, such as tetrigrad grasshoppers *Paratettix aztecus* and *P. mexicanus*, who derive 88–100% of their carbon from epilithic algae rather than terrestrial vegetation (Bastow et al. 2002). Stranded algae also are eaten by dipteran larvae, which in turn become prey for shoreline predators (carabid and staphylinid beetles, gelastocorid bugs, lycosid spiders) and riparian birds, lizards, and amphibians such as the abundant Pacific tree frog (*Pseudacris regilla*) and the once common western toad (*Bufo* [aka *Anaxyrus*] *boreas*). Frogs and toads, in turn, provide important food for birds and snakes, like the aquatic and common garter snakes (*Thamnophis atratus* and *T. sirtalis*).

Cladophora and other Eel River primary producers may constitute a trophic subsidy to the sea. Because the Eel is a relatively short, steep river, it remains largely gravel-cobble bedded all the way to its mouth. Attached filamentous and low-profile epilithic algae dominate summer energy inputs throughout the river network. They also dominate exports of organic matter to the estuary, except following the first winter storms. Ng (2012) found that copious amounts of filamentous green algae were exported from the river

(continued)

(Box 33.1 continued)

to its estuary during summer and fall, with exports of terrestrial litter becoming important only with the first winter flood. River export of high-quality algal food to the estuary may be nutritionally important to primary consumers (amphipods, isopods) in the estuary, which strongly prefer filamentous river algae over the marine green algae (*Ulva* and *Enteromorpha*) that dominate producer biomass in the estuary (Ng 2012). If estuarine grazers rapidly consume this riverine algal flux, the subsidy would be “invisible carbon,” important but easy to underestimate.

In summary, the amount, composition, and fate of algae and the nutrients they cycle depend on seasonal regimes of discharge and solar radiation as well as on consequent temperatures, nutrient fluxes, and food web interactions (Stevenson et al. 1996, Power et al. 2008, Power et al. 2013). Precipitation and flow are the “master variables” (Resh et al. 1988, Power et al. 1995, Poff et al. 1997) driving temporal changes in food web structure and subsidies across seasons and years. If at least one scouring flood occurs during the winter,

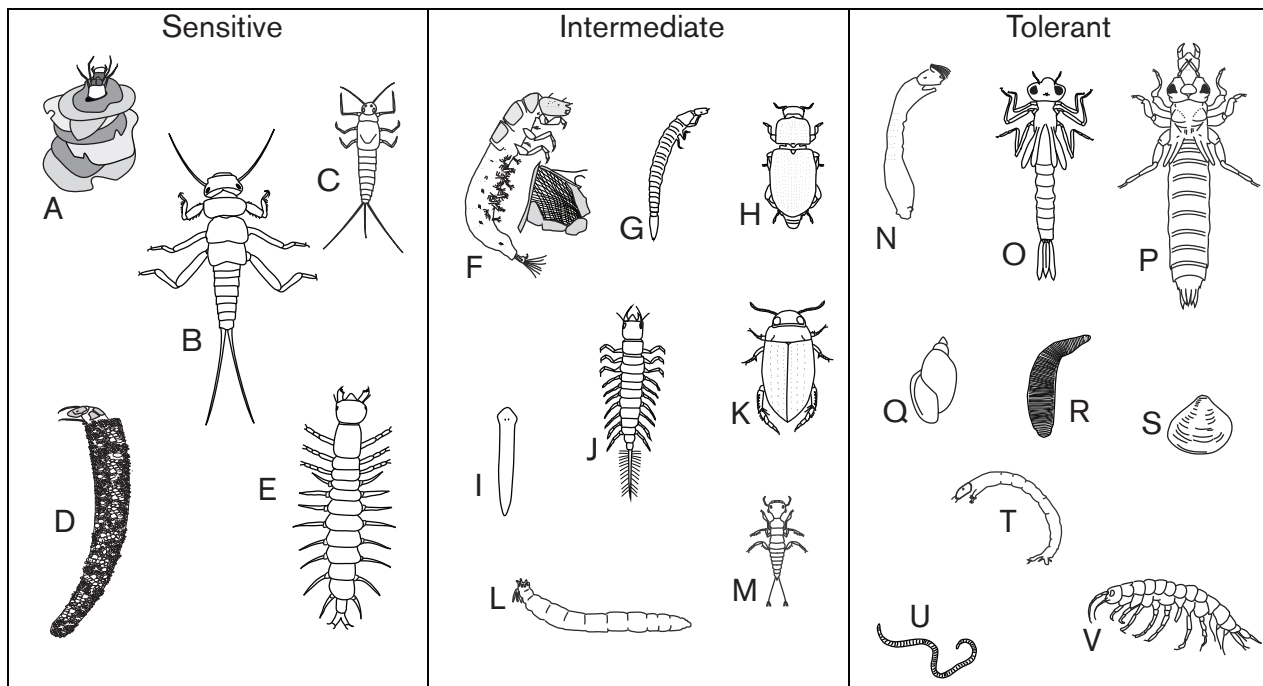
large blooms of algae, released from predator-resistant grazers, can proliferate during the following spring and early summer, before animal densities build up (the food chain has at this time one functional trophic level—producers). This algal biomass may rot on shores or in the water; be grazed and fuel upland, riverine, or estuarine/coastal food webs; or slough off and drift down to the coastal ocean. As time goes on, the fate of algae depends largely on how quickly summer base flows decrease. If relatively high summer flows sustain the longitudinal connection of channel habitats and maintain cooler temperatures, algal production will likely support food webs that produce salmonids and other predators valued by society, either in the river or offshore. If summer base flows drop so that stream reaches become disconnected and pools and backwaters warm and stratify, edible algae will be overtaken by inedible, or even toxic, taxa. The future of the Eel River will depend on how climate, vegetation change, and choices about land and water use affect the river’s light, temperature, chemical, and hydrologic regimes.

California, are likely unknown or undescribed (Ball et al. 2013). Among known species, estimates of endemism in California’s Mediterranean areas range from about 2% for mollusks to 5% for insects to 21% for crustaceans. Within insect groups, estimates of endemism for stoneflies (Order Plecoptera) and caddis flies (Order Trichoptera) were reported to be 11% and 7%, respectively, in Mediterranean areas and 25% and 19% in the Sierra Nevada (Erman 1996, Ball et al. 2013). Several endemic species have become extinct, and a number are very rare and have restricted distributions (Kabat and Hershler 1993, Erman 1996, Silldorff 2003, Herbst et al. 2009, Martin et al. 2009, Ball et al. 2013). Two species, a crayfish and a shrimp, are currently listed as endangered under the Endangered Species Act (Box 33.2). Approximately ten non-native mollusk (e.g., New Zealand mud snail [*Potamopyrgus antipodarum*]), Asiatic clam (*Corbicula fluminea*), Zebra and Quagga mussels (*Dreissena polymorpha* and *D. rostriformis bugensis*), and twenty crustacean species (e.g., the Louisiana red swamp crayfish, *Procambarus clarkii*) have been introduced to California, in some cases with substantial effects on native aquatic species (Klose and Cooper 2012, 2013; Moore et al. 2012a, 2012b).

California’s native and exotic aquatic invertebrates have diverse life styles, habitat preferences, and life histories. Non-insect aquatic invertebrates and a few aquatic insects spend their entire lives in water, but most aquatic insect larvae emerge as flying terrestrial adults (Merritt et al. 2008, Thorp and Covich 2010). During their aquatic phases, many species are more abundant in either depositional (pool, back water) or erosional (riffle, run) habitats and most have one to multiple generations per year (i.e., are UNIVOLTINE to MULTIVOLTINE), with a few completing their life cycles in two or three years (SEMIVOLTINE taxa) (Bêche et al. 2006, Bonada et al. 2007, Merritt et al. 2008). The life histories and/or behavior of stream invertebrates are often timed to seasonal cycles of flooding and drought. Certain groups dominate in the wet season, when flows are high, and are replaced by other invertebrates in the dry season, when diminishing flows dry rivers

to a series of isolated pools or sometimes completely (Bêche et al. 2006, Bonada et al. 2007). Because different invertebrate taxa have different susceptibilities to drying, perennial and nonperennial streams usually have different biotas (Lunde et al. 2013). Variation in river flows from year to year also drive interannual changes in the composition and abundance of invertebrate communities and in stream food webs in California (Bêche and Resh 2007a,b; Power et al. 2008). Stream reaches disturbed by fire, floods, or drying are often quickly colonized by short-lived, dispersive, small, multivoltine insect species, such as some mayflies, midges, and black flies. In contrast, invertebrates that spend their entire lives in streams or have long life cycles (e.g., some predatory stoneflies, dragonflies, and damselflies, some heavily armored caddis flies) are often extirpated by intense disturbances, and their populations may take some time to recover (Bêche et al. 2009, Verkaik et al. 2013). In some cases, early colonists are displaced by later colonists via competition or predation, particularly when colonizing taxa compete for space (Hemphill and Cooper 1983).

California’s stream invertebrates also have diverse food habits (Merritt et al. 2008). Some invertebrates, called SHREDDERS, eat primarily leaf litter and associated microbes (bacteria, fungi); grazing invertebrates either browse or scrape attached algae from substrate surfaces; predatory invertebrates consume other animals; and collectors either filter fine particulate organic material (FPOM) from the water column using nets, head fans, mucus strings, or setae (filter-feeders) or ingest FPOM after it has settled on the bottom (deposit feeders) (see Figure 33.4). One insect family, the Chironomidae (midges), includes almost all of these feeding groups. Midges are generally the most abundant and diverse group of stream macroinvertebrates. Other invertebrate groups (such as the Decapods = crayfish and shrimp) are omnivorous, consuming a variety of algal, detrital, plant, and animal items (Klose and Cooper 2013). Different feeding groups abound in different types of habitats, with shredders more abundant in heav-



(A) and (D): cased caddisflies (Order Trichoptera; A shredder, D shredder/deposit-feeder/grazer)

(B) stonefly (Order Plecoptera, predator)

(C) mayfly (Order Ephemeroptera, grazer/deposit-feeder)

(E) hellgrammite (Order Megaloptera, Family Corydalidae, predator)

(F) net-spinning caddisfly (Order Trichoptera, Family Hydropsychidae, filter feeder: net is shown); larval (G and M) and adult (H, K) aquatic beetles (Order Coleoptera; G and H deposit-feeders, K and M predators)

(I) flatworm (Phylum Platyhelminthes, Class Turbellaria, predator)

(J) alder fly (Order Megaloptera, Family Sialidae, predator)

(L) cranefly (Order Diptera, Family Tipulidae, shredder)

(N) blackfly (Order Diptera, Family Simuliidae, filter-feeder)

(O) damselfly and (P) dragonfly (Order Odonata, predators)

(Q) snail (Phylum Mollusca, Class Gastropoda, grazer)

(R) leech (Phylum Annelida, Class Clitellata, Subclass Hirudinea, predator)

(S) fingernail clam (Phylum Mollusca, Class Bivalvia, Order Veneroida, Family Sphaeriidae, deposit-feeder)

(T) midge or chironomid (Order Diptera, Family Chironomidae, variable)

(U) aquatic earthworm (Phylum Annelida, Class Clitellata, Subclass Oligochaeta, deposit-feeder)

(V) scud or amphipod (Phylum Arthropoda, Subphylum Crustacea, Class Malacostraca, Superorder Peracarida, Order Amphipoda, deposit-feeder/grazer)

A–H, J–P, and T are insects (Phylum Arthropoda, Subphylum Hexapoda, Class Insecta)

FIGURE 33.4 Major riverine invertebrate groups, classified by their sensitivity to pollution and land use change, from sensitive to tolerant. The functional feeding group designations are for the specific taxa shown. Other taxa within the same group (e.g., family) may have different feeding habits. Organisms are not drawn to scale relative to one another. Redrawn by Sheila Wiseman from Herbst et al. 2001.

ily shaded, headwater streams where inputs of leaf litter from riparian vegetation are substantial, and grazers more abundant in sunny, clear streams with adequate nutrient concentrations where algal production is high (Minshall et al. 1983; see Box 33.1).

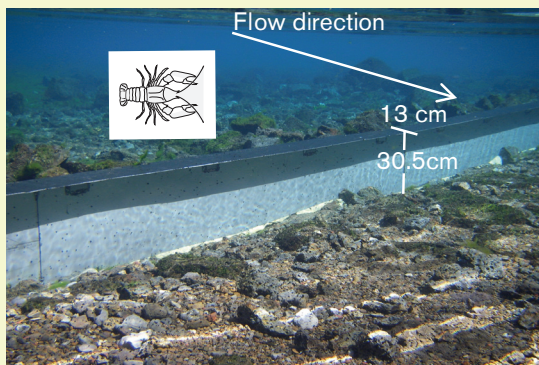
Collectors are common in most streams, consuming detritus generated from leaf litter, algae, or aquatic macrophytes. Aquatic invertebrates, particularly if they lack protective armor and are exposed on substrate surfaces, are fed upon by invertebrate and vertebrate predators. Benthic aquatic invertebrates can enter the water column and drift downstream, presumably to locate new food sources or to avoid benthic predators. However, this drifting behavior makes these invertebrates vulnerable to drift-feeding fish, such as trout or juvenile salmon. Aquatic invertebrates have adapted to predation pressure from these visually-feeding fish by drifting primarily at night (Douglas et al. 1994). In addition to providing a major food source for many aquatic vertebrates (fish, newts,

salamanders), aquatic insects after emergence are an important food source for riparian predators (spiders, predatory insects, salamanders, frogs, lizards, birds, bats) (Erman 1996, Nakano and Murakami 2001, Sabo and Power 2002a, Sabo and Power 2002b, Power et al. 2004, Baxter et al. 2005).

Because invertebrate taxa vary greatly in their tolerances to extreme temperatures, low oxygen concentrations, and high sediment and contaminant loads, they are often used as indicators of human impacts on stream and river systems (California Department of Fish and Wildlife Aquatic Bioassessment Laboratory 2014, SWAMP 2014). The diversity and abundances of many species in the insect orders Ephemeroptera (mayflies), Plecoptera (stoneflies), and Trichoptera (caddis flies) (EPT taxa) are reduced by pollution, excessive sediment deposition, and land use impacts on their food resources (leaf litter, algae), whereas the relative abundances of noninsects and some of the chironomids often increase in the face of human perturbations associated with agricultural, industrial,

BOX 33.2 ENDANGERED STREAM INVERTEBRATES IN CALIFORNIA

The Shasta crayfish (*Pacifastacus fortis*) and the California freshwater shrimp (*Syncares pacifica*) are listed as endangered under the Endangered Species Act (California Department of Fish and Wildlife 2013). The Shasta crayfish once occurred throughout the upper Pit River, which flows into the Sacramento River, and its highly productive tributary, the Fall River (Daniels 1980), but has been largely displaced by the non-native signal crayfish (*P. leniusculus*). The exotic signal crayfish is more aggressive and has higher consumption rates than the Shasta crayfish, so can competitively exclude the native. This invasive species also benefits from dams and flow regulation because it is vulnerable to flood flows but can tolerate warm water (Ellis 1999, Light 2003, Pintor et al. 2009, Pintor and Sih 2011). To restrict further upstream invasion of signal crayfish in the Fall River, Pacific Gas and Electric has installed a migration barrier as a requirement of its operating license on the Pit River (Box 33.2 Figure 1). The California freshwater shrimp, native to lowland streams in Sonoma, Marine, and Napa Counties, has been severely reduced by water quality degradation, habitat loss, and the introduction of predatory fish (U.S. Fish and Wildlife Service 1998, Martin et al. 2009, Wickstein 2012). Because the preferred habitat of California freshwater shrimp is submerged, exposed tree roots; undercut banks; and terrestrial detritus in shaded streams, restoration efforts for this species have concentrated on planting riparian trees and stabilizing banks.



BOX 33.2 FIGURE 1 An underwater fence constructed on the upper Fall River in 2007 to prevent the unrestricted upstream invasion by signal crayfish into habitat occupied by Shasta crayfish. Photograph by Maria Ellis and drawing by Sheila Wiseman.

and urban development (see Figure 33.4) (Brinkman 2007, Carter et al. 2009). As a consequence, biomonitoring programs have used indices based on macroinvertebrate assemblages (composition or diversity) to evaluate environmental gradients or compare perturbed and unperturbed sites (Ode et al. 2005, 2008, Rehn et al. 2007, Rehn 2009). Such indices also are used to monitor the “health” of streams over time and under different watershed conditions or to measure the

success of stream restoration efforts. These indices, however, have been criticized because of ambiguities in their interpretation, limitations in the databases used for their construction, inadequate consideration of temporal and spatial variability, and unclear presentation of basic biological data (Mazor et al. 2011, Lunde et al. 2013, Cooper et al. 2013). Furthermore, indices developed for one set of human perturbations (e.g., land use change) may not be useful indicators of other kinds of stress (e.g., climate change) (Lawrence et al. 2010).

Vertebrates

Vertebrates in California’s rivers include those that are fully aquatic (e.g., fish) as well as those that use both aquatic and terrestrial habitats (e.g., mammals like water shrews, mink). Over 135 species of birds use California riparian habitats during some stage of life (RHJV 2004). Some riparian vertebrates are riverine specialists, such as the bats *Myotis yumanensis* and *M. lucifugus*, which usually feed by skimming above the water’s surface at night (Brigham et al. 1992) and birds such as bank and cliff swallows (*Riparia riparia*, *Hirundo pyrrhonata*), which feed aerially above the water by day. Others, such as the western red bat *Lasiurus blossevillei*, roost in mature sycamores and cottonwoods and forage for insects over gravel bars and along riparian canopy margins (Pierson et al. 2006). These aerial and terrestrial insectivores are reduced by losses of riparian vegetation and declines in water quality that reduce aquatic insects (increasing water temperature, fine sediment, and toxin loading) (RHJV 2004). In Japan, riparian forest loss caused stream salmonids to switch from terrestrial to aquatic prey, reducing the biomass of insects emerging from streams and thereby abundances of streamside predators (spiders, lizards, birds, bats) (Baxter et al. 2004, 2005).

Many terrestrial vertebrate consumers in California, including humans and now-extinct grizzly bears, relied on historically large seasonal runs of ANADROMOUS fish (salmon, steelhead, Pacific lamprey), with Chinook and Coho salmon forming the basis for a commercial fishery. Only small, remnant runs of these fish remained after the construction of dams throughout the state (Moyle et al. 2002, Carlson and Satterthwaite 2011). The Central Valley supported annual runs of one to three million salmon per year, but only about forty thousand to two hundred thousand migrate today (Yoshiyama et al. 2001). Even these depleted runs, however, provide substantial amounts of food to terrestrial vertebrates. Fourteen species, mostly turkey vultures and raccoons but also gray fox, red-tailed hawks, and “herbivores” such as mule deer and squirrels, have been photographed eating Chinook salmon carcasses (Merz and Moyle 2006). These scavengers likely transport marine-derived nitrogen to riparian trees (willows, sycamores, and cottonwoods) as well as to agricultural fields. Wine grapes in vineyards near salmon spawning sites on the Mokelumne River received 18–25% of their foliar nitrogen from marine sources (Merz and Moyle 2006), probably from salmon.

FISH

Among California’s 129 distinct forms of native freshwater fish (including species, subspecies, DISTINCT POPULATION SEGMENTS, and evolutionary significant units, hereafter called

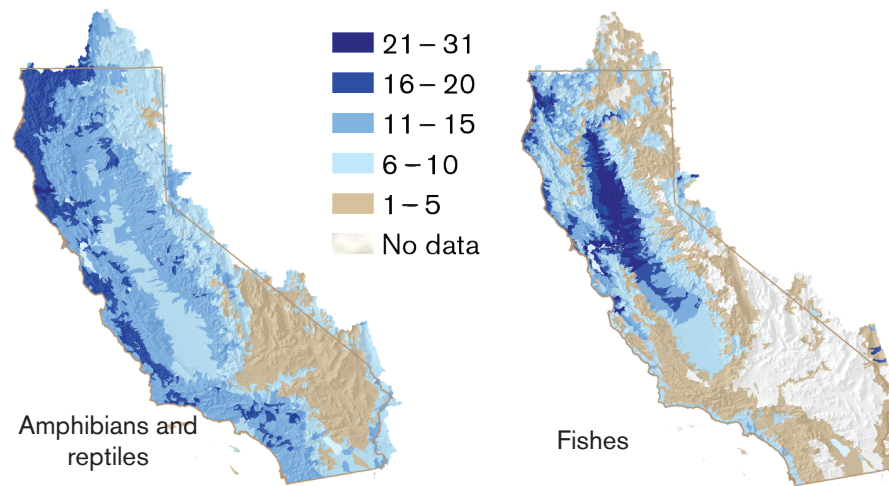


FIGURE 33.5 Total diversity of amphibians, reptiles, and fishes found in California's rivers. Source: Data from Howard et al. 2013. Map: K. Fesenmyer.

"species"), almost two thirds (63%) are endemic. The highest fish diversity occurs in the tributaries and mainstems of the Sacramento and San Joaquin Rivers (Moyle 2002, Moyle et al. 2011) (Figure 33.5). Across the Sacramento and San Joaquin drainage basins, thirty-three distinct habitats based on patterns of fish distribution and endemism occur from montane headwaters to the rivers' confluence in the Sacramento–San Joaquin Delta (Moyle and Ellison 1991). Most native sculpins and cyprinids (minnow family: hitch, roach, hardhead, squawfish, dace) are found at low to middle elevations on the west slope of the Sierra, but native rainbow trout (*Oncorhynchus mykiss*) and Sacramento suckers (*Catostomus occidentalis*) were historically recorded at elevations over 2,000 meters in the Kings River drainage. Rainbow and golden trout subspecies (*Oncorhynchus mykiss* subspp.) in the Kern River drainage reached elevations of 2,400 to 3,000 meters. Because of glacial or volcanic activity and barriers to fish migration, most Sierra waters over 2,000 meters in elevation and many east-side streams originally lacked fish, with the exceptions noted above, but trout have been widely stocked in these waters for a recreational fishery. The unglaciated southernmost portions of the Sierra host three golden trout subspecies including the California golden trout (*Oncorhynchus mykiss aguabonita*), the state fish (Moyle 2002).

Some of the tributaries of the upper Sacramento River, such as the Pit River, drain the Modoc Plateau, a volcanic landscape containing closed basins with historically large lakes that still host a variety of unique fish species. The Lost River system is home to two endangered species, the Lost River sucker (*Deltistes luxatus*) and shortnose sucker (*Chasmistes brevirostris*), which live in warm, eutrophic systems with low dissolved oxygen concentrations. The watershed of Goose Lake, now separated from the Pit River and occasionally dry (Heck et al. 2008), contains four endemic fish taxa: the Goose Lake redband trout (*Oncorhynchus mykiss newberrii*), lamprey (*Lampetra tridentata* ssp.), sucker (*Catostomus occidentalis lacusan-serinus*), and tui chub (*Gila bicolor thalassina*). These fish spend distinct life history stages in the lake and its tributaries, respectively. Similarly, fishes of arid and semiarid areas of the state, although low in number of species, have high levels of local or regional endemism, including species or subspecies of pupfish (*Cyprinodon* spp.), tui chubs (*Siphateles bicolor*

subsp.), and/or speckled dace (*Rhinichthys osculus* subspp.) in the southeastern valleys (e.g., Owens and Death Valleys) and deserts; a variety of sucker (*Catostomus santaanae*), chub (*Gila orcutti*), dace, and stickleback (*Gasterosteus aculeatus* subspp.) along the southern Coast; and the Lahontan fish fauna of the eastern Sierra and western Great Basin including Lahontan tui chubs (*Siphateles bicolor obesa*), redband (*Richardsonius egregius*), speckled dace (*Rhinichthys osculus robustus*), mountain suckers (*Catostomus platyrhynchus*), Paiute sculpin (*Cottus beldingi*), mountain whitefish (*Prosopium williamsoni*), and two subspecies of cutthroat trout (*Oncorhynchus clarki henshawi* and *seleneris*) (Swift et al. 1993, Moyle et al. 1996, Moyle 2002, Lin and Ambrose 2005, Brown et al. 2005, O'Brien et al. 2011). The native fishes of these regions are adapted for dealing with extreme hydrologic events, high summer temperatures, and low dissolved oxygen levels (Swift et al. 1993, Matthews and Berg 1997, Spina 2007, Boughton et al. 2007, Bell et al. 2011, Sloat and Osterback 2013).

Like riverine invertebrates, fish show diverse and distinct foraging modes and food and habitat preferences. Eel-like lampreys, which have cartilaginous skeletons but lack jaws, show ONTOGENETIC NICHE SHIFTS in their habitats and feeding habits. The anadromous Pacific lamprey (*Lampetra tridentata*), the most widespread California lamprey, preys on fish as adults in the ocean, attaching to hosts' bodies with suckerlike mouths and ingesting fluids from wounds made with their rasping tongues. When they spawn in rivers and streams, Pacific lamprey migrate inland as far as 440 kilometers and historically were abundant enough to be harvested by Native Americans (Moyle 2002, Brown et al. 2010, Close et al. 2002). After hatching from eggs, the larval ammocoete stage lives three to seven years within fine sediments, where it filter feeds on suspended particles. Ammocoete growth is enhanced by the presence of western pearl shell mussels (*Margaritifera falcata*) (Limm and Power 2011).

Many fish feed on insects and other macroinvertebrates, with some benthic-feeding fishes (e.g., sculpins, some minnows) relying exclusively on invertebrates for food (Erman 1996). Other fish (such as many salmonids) forage on benthic invertebrates, invertebrates drifting downstream in the water column and at the surface, and terrestrial invertebrates that fall into the water (Rundio and Lindley 2008). Some fishes

that are insectivorous as small juveniles become piscivorous as adults, such as the Sacramento pikeminnow (*Ptychocheilus grandis*) and larger rainbow trout (*Oncorhynchus mykiss*). Fish 3 to 15 centimeters in length are “perfect prey” (Moyle 2002, p. 28), vulnerable in shallow water to predatory birds such as kingfishers and herons and in deep water to larger fish. Threats to small fish from aquatic predators, and to large fish from fishing birds and mammals, can set up a “bigger-deeper” size-depth distribution for fish seeking to avoid size-specific predation (Power 1987). Ontogenetic niche shifts also can shift the trophic position of fishes downward. For example, hardhead (*Mylopharodon conocephalus*), a large (up to 46 centimeters) minnow once widespread throughout Sierran foothill rivers, consume invertebrates as juveniles using hooked teeth. As adults they develop large, molar-like teeth and eat aquatic plants, macroalgae, and hard-shelled invertebrates (*Mylo-phara-don* means “mill-throat-teeth”).

California’s freshwater fish fauna has been severely diminished by human activities, with seven species extinct, thirty-three more (26%) at immediate risk of extinction, and another thirty-three species on a path to extinction if current trends continue (Figure 33.6; Moyle et al. 2011). Native fishes are particularly threatened by flow modifications, especially dams and diversions, the introduction of exotic species, and agricultural and urban development and operations (Box 33.3; May and Brown 2002, Kats and Ferrer 2003, Riley et al. 2005, Moyle et al. 2011). At least fifty non-native species of fish have become established in California’s waterways, including many predatory species from the Mississippi River basin (e.g., black bass [*Micropterus* spp.], sunfish [*Lepomis* spp.], crappie [*Pomoxis* spp.], catfish [*Ictalurus* spp.], bullheads [*Ameiurus* spp.]) adapted to the slack water conditions that follow flow modification, rather than the strong flow variation characteristic of natural western rivers (Brown et al. 2005, Marchetti et al. 2004, Light and Marchetti 2007). The distributions of introduced fish species in California are often determined by the locations of introductions, hydrologic connections, perennial flow patterns, and dispersal limitations (Riley et al. 2005, Marchetti et al. 2006, Moyle and Marchetti 2006). These introductions have reduced native amphibian populations, altered invertebrate assemblages, and, in some cases, released algae from grazing pressure (Knapp et al. 1998, Riley et al. 2005, Herbst et al. 2009). In the case of trout introductions to montane waters that originally lacked fish, it appears that high-elevation, endemic invertebrate and amphibian prey species, which have no evolutionary history with fish, are the most vulnerable taxa (Knapp et al. 1998, Herbst et al. 2009). Introduced brown (*Salmo trutta*), brook (*Salvelinus fontinalis*), and rainbow trout also have affected native golden and cutthroat trout via hybridization, competition, and predation at high elevations, and introduced black bass have reduced native cyprinids at low elevations (Moyle et al. 1996).

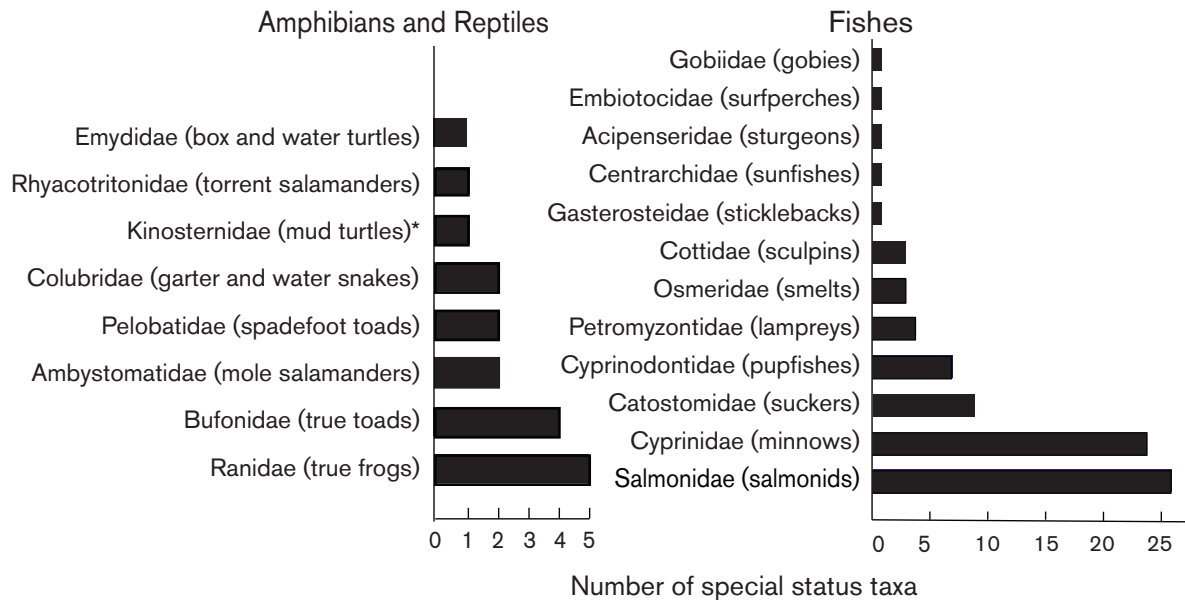
AMPHIBIANS AND REPTILES

Of the more than 150 species comprising California’s herpetofauna, Brode and Bury (1984) estimated that 83% of the amphibians and 40% of the reptiles occupy riparian habitat, with a smaller subset truly aquatic (see Figure 33.6). The river-dwelling frogs, toads, newts, salamanders, snakes, and turtles of California occupy various levels in food chains. Frog and toad tadpoles eat primarily algae, and most species require open sunlit channels where high primary productivity pro-

motes rapid growth. Where locally abundant, tadpoles can reduce benthic algal biomass, but they can also facilitate the growth of less edible *Cladophora* by scraping epiphytic diatoms off this filamentous host alga (Kupferberg 1997). In small, high-gradient streams, salamanders and newts are often the dominant vertebrate predators. In forested coastal streams, larvae of the coastal giant salamander (*Dicamptodon tenebrosus*) and the endemic California giant salamander (*D. ensatus*) are top predators. Both eat macroinvertebrates and sometimes juvenile salmonids (Parker 1994).

Although juvenile salmonids recycle 1.7 times more nitrogen and 1.2 times more phosphorus than salamander larvae per unit mass, salamanders can make up a much larger proportion of total predator biomass in some streams (Munshaw et al. 2013). Salamanders are often overlooked because they are cryptic, sometimes nesting or seeking dry season refuges below the streambed surface (in the hyporheic zone) (Nussbaum 1969, Feral et al. 2005). In central and southern California streams, California newts (*Taricha torosa*) are the dominant salamanders. Newts have flexible food habits, shifting to earthworms after wildfires, which can reduce adult newt cannibalism on newt larvae (Kerby and Kats 1998). Although *Taricha* possess potent neurotoxins (tetrodotoxin) (Bradley and Klitka 1981, Ferrer and Zimmer 2013) as adults, egg masses and larvae are vulnerable to introduced predators like western mosquitofish (*Gambusia affinis*) and Louisiana swamp crayfish (*Procambarus clarkii*) (Kats and Ferrer 2003, Riley et al. 2005, Kats et al. 2013).

River-breeding amphibians illustrate a wide range of flow-regime adaptations (Lytle and Poff 2004), defined as morphological traits and life history strategies enabling persistence through extreme droughts and floods. Some adult amphibians react to seasonally predictable flood-drought cycles by migrating long distances, sometimes several kilometers, from headwaters or terrestrial refugia to specific stream segments in the spring (e.g., California red-legged frogs, *Rana draytonii* [Tatarian 2008]; red-bellied newts, *Taricha rivularis* [Tewitt et al. 1964]; and foothill yellow-legged frogs, *R. boylei* [Bourque 2008]). Breeding adults gather where the channel cross-sectional shape minimizes the risks of flood disturbance or dewatering, providing safe rearing habitats with slow water velocities for sessile eggs and weakly swimming larvae (Kupferberg 1996). Other native anurans (frogs and toads), such as spadefoot toads *Spea hammondi* and *Spea intermontanus*, are adapted to xeric environments, breed in ephemeral streams, and use keratinized patches on their hind feet as “spades” to burrow into sandy sediments during dry periods. There they wait in a state of torpor with low metabolic rates (ESTIVATION) until low-frequency vibrations from rainfall trigger their emergence. The federally protected Arroyo toad (*Anaxyrus californicus*) of southern California forms a cocoon of layers of shed skin to prevent moisture loss while estivating. These toads avoid washout by laying their eggs at the end of the wet season, and their tadpole development can accelerate in response to decreasing water levels to allow early metamorphosis before stream drying (Denver et al. 1998). At the opposite extreme, tadpoles of the tailed frog (*Ascaphus truei*) may take years to reach metamorphosis in the cold, shaded headwaters of northwestern California’s forests, where growth is constrained by light-limited algal productivity (Mallory and Richardson 2005). *Ascaphus* tadpoles are able to persist through multiple growing seasons because their strong suction cup mouths are used to adhere to rocks and withstand winter high flows.



*The Sonoran mud turtle (*Kinosternon sonoriense sonoriense*) was formerly present in the Colorado River but appears to be extirpated.

FIGURE 33.6 Total family-level diversity of special status amphibians, reptiles, and fishes in California's rivers. Included taxa are California State Species of Special Concern or threatened or endangered species under the California or Federal Endangered Species Act. Sources: Moyle 2002, Stebbins and McGinnis 2012, and California Department of Fish and Wildlife 2011.

Despite these adaptations, amphibians are declining in California's rivers and streams. For example, the foothill yellow-legged frog (*Rana boylei*) was historically widespread throughout the Coast Range, the west slope of the Sierra Nevada, and the mountains of southern California but has disappeared from more than half of its range, particularly downstream from large dams (Kupferberg et al. 2012). Untimely pulsed releases from dams (e.g., for recreational whitewater boating) remove eggs and tadpoles, whereas rapid cessation of snowmelt flows blocked by dams kills them by stranding (Kupferberg et al. 2011, 2012). Reservoirs also harbor non-native predators (e.g. American bullfrog, *Lithobates catesbeiana* [Moyle 1973]), and block frog movements, creating genetic isolation (Peek 2011). Water temperature is the best predictor of the yellow-legged frog's breeding abundance (Welsh and Hodgson 2011). When dams release cold water from the depths of upstream reservoirs, frog populations shift to shadier and less productive, but relatively warmer, tributaries (Catenazzi and Kupferberg 2013). Tadpoles comprise a large portion of the diet of young garter snakes (Lind and Welsh 1994) and are a food source for predatory macroinvertebrates and fish, so the loss of tadpoles from river food webs can affect a diverse array of consumers.

California has one extant native turtle, the western pond turtle (*Actinemys marmorata*, previously *Clemmys*, *Emys*) (Stebbins and McGinnis 2012). Western pond turtles forage and mate in water but nest, estivate, and overwinter on land (Pilliod et al. 2013). These opportunistic predators and scavengers (Holland 1985, Bury 1986) show great flexibility in dealing with extreme hydrologic events, traveling far from rivers to avoid floods (Pilliod et al. 2013) and persisting in relic populations in the remnants of the Mojave River (Lovich and Meyer 2002). Western pond turtles are declining due to habitat destruction, dam construction, flow regulation, and introductions of exotic species, such as the American bullfrog

(Moyle 1973, Brattstrom 1988, Reese and Welsh 1998, Bury and Germano 2008, Bondi and Marks 2013). In urban settings, western pond turtles are often outnumbered by alien turtle species such as the more aggressive and fecund reared slider (*Trachemys scripta elegans*) that have become naturalized after being released as unwanted pets (Spinks et al. 2003).

MAMMALS

The legacy of California's fur rush, which preceded the Gold Rush, is just beginning to be appreciated. European exploration and exploitation of inland California during the 1820s were driven by the quest for beaver pelts (Dolin 2011). The California golden beaver, a subspecies of the North American beaver (*Castor canadensis subauratus*), had become rare by 1837 (Skinner 1962). Recent reexaminations of historic, ethnographic, and paleontologic evidence challenge the long-held assumption that beaver were originally absent above elevations of 350 meters, especially from the eastern Sierra Nevada, where they have been recently introduced (James and Lanman 2012, Lanman et al. 2012). Given the significance of beavers as ecosystem engineers, their true historical distribution and abundance have critical management implications. In semiarid habitats of the western United States, the reintroduction of beaver can aggrade incised streams, reconnecting them to their floodplains (Pollock et al. 2007). Beaver dams increase macroinvertebrate production (McDowell and Naiman 1986, Wright et al. 2002), increase habitat heterogeneity, enhance production of salmonid smolts, and provide fish with refuges during both low and high flows without impeding fish passage (Gard 1961, Pollock et al. 2004, Kemp et al. 2012, Lokteff et al. 2013). When managers have removed beaver dams ostensibly to facilitate fish passage, they

BOX 33.3 CHANGES IN WATER QUALITY FROM HEADWATERS TO MOUTH IN A LARGE RIVER SYSTEM: THE KLAMATH RIVER

The Klamath River Basin contains an impressive diversity of peoples, land uses, geology, topography, flora, and fauna, including remarkable anadromous fish runs (Wallace 1983). Some of the native fish species found here include Chinook (*Oncorhynchus tshawytscha*), coho (*Oncorhynchus kisutch*), and chum salmon (*Oncorhynchus keta*), steelhead (*Oncorhynchus mykiss*), coastal cutthroat trout (*Oncorhynchus clarkii clarkii*), Pacific lamprey (*Lampetra tridentata*), eulachon (*Thaleichthys pacificus*), and Green sturgeon (*Acipenser medirostris*) in the middle and lower river, and Lost River sucker (*Deltistes luxatus*), shortnose sucker (*Chasmistes brevirostris*), and redband trout (*Oncorhynchus mykiss newberrii*) in the upper river. Fisheries for these and other species are critical for cultural and subsistence uses by several Native American tribes as well as for commercial and recreational fishers. Wild salmon and steelhead populations have been in continual decline due to modified flow regimes, and degraded habitat and water quality (Moyle 2002) in response to legacy mining, forestry, water extraction and impoundment, agriculture, and other factors, some of which continue today.

The Klamath Basin's hydrology and water quality reflect its geographic, climatic, and geologic setting, as well as modifications by humans during the twentieth century. The Klamath River's headwater tributaries, the Sprague and Williamson Rivers in southern Oregon, flow into Upper Klamath Lake. Upper Klamath Lake is a large (surface area 313 square kilometers), shallow (mean depth 2.4 meters), naturally eutrophic lake that has become hypereutrophic in response to anthropogenic activities (NRC 2004, Eilers et al. 2004). The Klamath River proper then flows from near Klamath Falls, Oregon, over 400 kilometers to the Pacific Ocean south of Crescent City, California. The river has few tributaries but several hydropower impoundments in the first 100 kilometers below the lake. Over the next 300 kilometers, mean annual river flows roughly double every 100 kilometers, increasing from around 1.0 billion cubic meters below Iron Gate Dam to over 1.3 billion cubic meters at the estuary. Major tributaries in this section include the Salmon, Shasta, Scott, and Trinity Rivers, with extensive water development in the latter three.

Water quality affects native fishes either directly (via temperature, turbidity, dissolved oxygen) or indirectly

(via nutrients and associated primary production). Due to unusual landscape and anthropogenic controls over water quality, the Klamath River is often called an "upside-down river" (Rymer 2008), with upper reaches impaired and water quality improving downstream (Kaplan and Newbold 2003) (Box 33.3 Figure 1). The distribution of native fish species reflects water quality conditions, with upstream species (e.g., suckers, redband trout) tolerating eutrophic conditions and downstream species relying on higher water quality.

Although anadromous salmonids typically require cool water temperatures, the Klamath River is not considered a cold-water stream (Bartholow 2005). The Klamath River has cool water temperatures from late fall through spring but warm water temperatures in the summer, although groundwater and other cold-water inputs provide local summer thermal refugia (Sutton et al. 2007). Large mainstem reservoirs stratify during warm seasons and, depending on the depth of reservoir water releases, alter river temperatures (Ward and Stanford 1983). Although temperature responds largely to seasonal changes in climate, dissolved oxygen levels in the upper river are reduced by large organic loads emanating from Upper Klamath Lake (Sullivan et al. 2011), then increase downstream, attaining saturation in lower river reaches. Local deviations in dissolved oxygen occur below large mainstem reservoirs, where hypolimnetic anoxia during summer stratified periods leads to subsaturated dissolved oxygen concentrations immediately below their dams (NRC 2004).

Upper river reaches below Upper Klamath Lake have total phosphorus (TP) and total nitrogen (TN) concentrations three to five times higher than those in the lower reaches in both winter and summer (see Box 33.3 Figure 1). Concentrations of inorganic nitrogen (ammonium, nitrite, nitrate) and phosphorus (orthophosphate), and dissolved and particulate organic carbon, are likewise higher in the upper basin and diminish downstream, although local deviations can occur. Reservoir impacts on river nutrient levels also are evident (Kann and Asarian 2005, Asarian et al. 2010), but their effects are modest relative to the landscape-scale nutrient changes from the upper basin to the estuary.

PERIPHYTON assemblages and aquatic macroinvertebrate distributions reflect these water quality conditions. During spring, nutrients support a wide range

have inadvertently damaged sensitive habitats. For example, when beaver dams were removed from a stream flowing into Lake Tahoe to promote the spawning migrations of introduced Kokanee salmon, stream phosphorus concentrations doubled (Muskopf 2007).

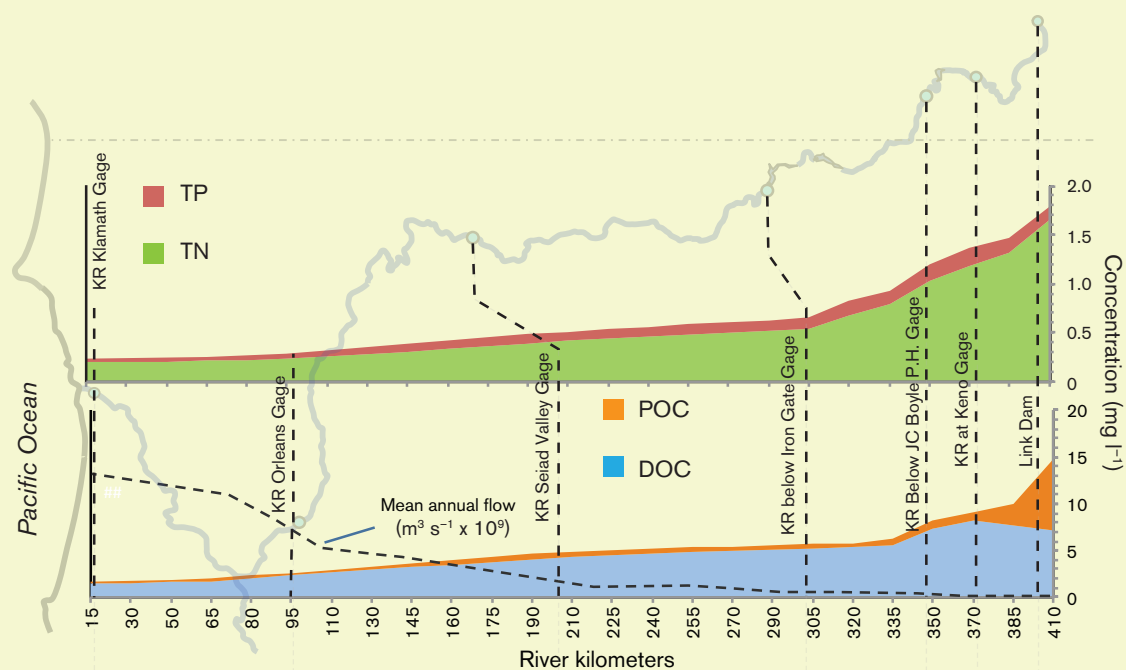
The North American river otter (*Lontra canadensis*), also once prized for its pelt, is recovering its position as the top carnivore of California's rivers as populations rebound (Black 2009). River otters are highly mobile, commonly moving > 4 km d⁻¹, with some tracked individuals moving up to 42 km d⁻¹ (Melquist and Hornocker 1983). In coastal California, river

otters move among freshwater, brackish, and marine habitats, feeding mainly on fish and crayfish (including non-native taxa), as well as on crabs, amphibians, insects, and birds (Grenfell 1974, Penland and Black 2009). In winter, when waterfowl migrate along the Pacific flyway, ducks and coots can make up 21% of otter diets (Cosby 2013). In the Klamath, southern Cascades, and Sierra Nevada mountain ranges, river otters occur above 3,000 meters; however, it is not clear if their occurrence at high elevations is a result of recent expansion into waters now inhabited by non-native fish and crayfish (Garwood et al. 2013).

of benthic eutrophic diatoms, but by late summer, nitrogen limitation in the lower river favors diatoms like *Epithemia sorex* that have nitrogen-fixing ENDOSYMBIOTES. Macroinvertebrates are abundant, but have low diversity, in the upper reaches of the river and in the hydropower peaking reach (PacifiCorp 2004), with diversity increasing with distance downstream of Iron Gate Dam (Malakauskas and Wilzbach 2012). One macroinvertebrate of interest is the freshwater polychaete worm, *Manayunkia speciosa*, which acts as an intermediate host to two myxozoan parasites, *Parvicapsula minibicornis* and *Ceratonova shasta*, that are potentially lethal to salmonids in the Klamath (Bartholomew et al. 1997 and 2006, Stocking and Bartholomew 2007, Nichols et al. 2007, Wilzbach and Cummins 2009).

The Klamath's naturally eutrophic condition has left the basin particularly susceptible to additional im-

pairment from human activities. A particular worry is climate change, which is expected to increase water temperatures by several degrees Celsius in tributary and mainstem reaches that already provide only marginal summer habitat for salmonids. Currently, efforts are under way to remove four mainstem hydropower dams to foster the recovery of anadromous fishes and improve water quality as part of a basinwide agreement among a wide range of stakeholders (KBRA 2010). Additional work is needed to define problems, pose solutions, and develop clear metrics for prioritizing actions, allocating resources, and measuring success. Interim, transitional, and long-term measures, including adaptive management programs, should be developed and implemented as responsible steps towards robustly balancing the needs of aquatic ecosystems, human cultures, and enterprises in this large, complex basin.



BOX 33.3 FIGURE 1 Summertime total nitrogen (TN, green), total phosphorus (TP, brown, top), and particulate (POC, brown, bottom) and dissolved organic carbon (DOC, blue) concentrations in the Klamath River, indicating higher concentrations in headwaters near Link Dam (RKM 400) and decreasing en route to the Pacific Ocean (RKM 0). Mean annual flow is shown as the dashed line in the lower graph. USGS Gage locations identified on map overlay. Klamath, Orleans, and Seiad Valley are communities; Iron Gate, J. C. Boyle, Keno, and Link are dams along the upper Klamath.

The Past and Alternative Futures of Californians and Their Rivers

Humans have had a long, intimate history with California's rivers and streams. For over twelve thousand years, these waterways have been corridors for human colonization, dispersal, and migration as well as sources of water, food, fiber, and shelter. Although early Native Californians attained a population size of more than three hundred thousand (Anderson 2005) by the time of European exploration and, in some cases, developed economies and cultures based on river-

ine resources (e.g., salmon in northern rivers), their environmental impacts were probably muted by their low densities and largely hunter-gatherer lifestyles (Fagan 2003; see Chapter 10, "Indigenous California"). Although the widespread use of low-intensity fire to manipulate forest structure, generate wildlife forage, and encourage useful plants may have affected river flows (Skinner and Chang 1996, Keeley 2002, Stephens et al. 2007, Lightfoot and Parrish 2009), these fires probably had much lower impacts on rivers than the severe wildfires of today (Verkaik et al. 2013). From 1769 to 1823 the Spaniards founded missions and conscripted Native Ameri-

cans to build water-delivery systems, herd livestock, and farm arable land, with probable local impacts on streams. Spanish concessions and Mexican land grants dedicated large tracts to livestock grazing and introduced invasive European grasses and weeds, culminating in the Rancho period (1834–1849). Vegetation cover in catchments affects river conditions, and the conversion of California grasslands to domination by exotic plant species heavily grazed by cattle probably had many, although largely unstudied, impacts on river systems (Minnich 2008, Herbst et al. 2012, Cooper et al. 2013). At the same time, after depleting sea otter populations along the coast, Russian, English, and American fur traders and trappers exploited inland fur-bearers, greatly reducing or extirpating beaver, otters, mink, and other mammals in much of California (Lanman et al. 2012).

In 1848 the discovery of gold by James W. Marshall at Sutter's sawmill on the South Fork American River ushered in a new era of rapid economic growth and land development, shifting California from a bucolic backwater to an economic powerhouse (see Chapter 5, "Population and Land Use"). Over three hundred thousand people migrated to California in the first seven years of the Gold Rush, prospecting for gold deposits and providing the goods and services needed by miners. After depleting placer deposits in Sierra foothill stream beds, miners turned to hydraulic mining, spraying hillslopes with high-pressure jets of water and capturing runoff in sluices for gold separation. Miners denuded riparian zones of much of their timber and introduced massive amounts of sediment to rivers, with river beds, such as those in the American and Yuba Rivers, rising 10 to 30 meters (Mount 1995). Over 40 million cubic meters of sediment flowed into the Central Valley, clogging channels, blocking boat traffic, and flooding downstream floodplain farms. In response, lowland enterprises dredged and realigned channels and built levees to provide flood protection, further modifying flow and sediment conditions in rivers. Conflicts between lowland farmers and upland miners led to an 1884 court injunction that stopped hydraulic mining, signaling the replacement of mining by agriculture and timber harvest as the state's major industries.

Although the Great Flood of 1861 and 1862, followed by the drought of 1863 and 1864, devastated livestock herds and wheat farms in many parts of the state, agricultural enterprises quickly rebounded. Sheep and cattle herds peaked in the late 1800s and early 1900s, grazing most parts of California, while the expansion of row crop, orchard, and vineyard farming fueled agricultural prosperity. Private agricultural development, often based on irrigation from local surface and groundwater supplies, fostered irrigation colonies in southern California and later the Central Valley. Logging accelerated along the North Coast and later in the Sierra Nevada. All of these activities decreased or degraded river habitat for native aquatic biota by altering flow patterns and increasing erosion, sediment loading, and contaminant concentrations (Mount 1995, Cooper et al. 2013). These impacts on habitat, together with overfishing, destroyed commercial riverine fisheries such as the Chinook salmon fishery on the Sacramento River (Lichatowich 1999).

Even these nineteenth-century changes pale in comparison to the rearrangement of landscapes and waterscapes in the twentieth century. As California's human population has grown from about 1.5 million in 1900 to 38 million today, unfettered agricultural, urban, and industrial growth made California one of the ten largest economies in the world. To satisfy demands for wood, logging of private and federal lands

in northern coastal California and the Sierra Nevada peaked by the 1940s and 1950s, destroying most of the old-growth forests. During the 1940s government agencies expanded rangelands using herbicides and fire. Although these practices have been discontinued, grazing still occurs on about half of the state's wildlands, and many of these areas are overgrazed (Mount 1995). Toxic runoff to river networks from nearly 2,500 abandoned mines persists (Domagalski et al. 2004, Kim et al. 2012, Davis et al. 2012). Mining of sand and gravel from river channels and floodplains increases erosion, alters channel morphology, and decreases riparian vegetation (Kondolf 1994, Downs et al. 2013). Despite mitigation measures now in place, many streams and rivers continue to be degraded by logging, grazing, and mining legacies or practices (Box 33.4).

The most massive impacts on rivers and streams in the twentieth century, however, came from the development of water and land resources to support agricultural and urban development (Kahrl 1979, Worster 1985, Mount 1995, Grace 2012). In the early 1900s, as local water supplies became inadequate to satisfy their demands, agricultural and urban interests looked further afield for water resources. Because private resources were not sufficient to construct and maintain storage and long-distance conveyance facilities, public initiatives came to the fore. Municipalities, such as the cities of Los Angeles and San Francisco, developed schemes to tap distant water sources, with Los Angeles completing the 375-kilometer Los Angeles aqueduct to the Owens Valley in 1913 and San Francisco completing the 269-kilometer Hetch Hetchy aqueduct to the Tuolumne River in 1934 (Figure 33.7). In 1928 the state legislature created the Metropolitan Water District (MWD), a consortium of fourteen cities and twelve water districts in southern California, to construct and operate the 389-kilometer Colorado River aqueduct. Both the federal government, under the terms of the 1902 Reclamation Act, and the state government set about to "make arid California bloom" by building dams, diversions, and canals to store and deliver irrigation, domestic, and industrial water, to provide hydroelectricity, and to control floods (Worster 1985, Reisner 1993, Grace 2012). Large water-delivery projects often received impetus from water panics created by drought. To deliver irrigation water from the Colorado River to southern California deserts, the federal Bureau of Reclamation built the All-American Canal and its Coachella spur in the 1940s and 1950s. The Bureau of Reclamation also built the Central Valley Project (CVP), a massive complex of dams, pumps, and canals, to store Sierra Nevada and Klamath Mountains runoff and ultimately divert it to farmlands in the Central Valley.

To circumvent restrictions on water supplied by federal reclamation projects and to serve more of southern California's water needs, the state approved the State Water Project (SWP) in 1960, subsequently constructing dams to collect Sierra Nevada meltwater and regulate downstream Sacramento flows to the northern Delta. The CVP and SWP have intake facilities just outside the southern Delta near Tracy that supply canals (Delta–Mendota Canal, California Aqueduct) that transport water to central and southern California. Although similar in design and now largely operated together, the CVP and SWP differ in their purposes, with the CVP serving agricultural developments and the SWP primarily serving urban interests (Kahrl 1979). Both projects turn an east-west flowing natural system, the Delta, into a north-south conveyance facility, creating many problems for the Delta's farms, fisheries, and ecosystems (Lund et al. 2008).

BOX 33.4 ENVIRONMENTAL CONTAMINANTS THROUGH A LONGITUDINAL CONTINUUM:
THE SACRAMENTO–SAN JOAQUIN SYSTEM

The Sacramento and the San Joaquin are the largest rivers flowing entirely within California and provide water to most of the state. They face the most varied, complex, and difficult environmental problems in the region. Here we illustrate three ways that humans have affected inputs of sediment, heavy metals, pesticides, nutrients, and other contaminants, proceeding longitudinally from river headwaters in the Sierra Nevada to the rivers' mouth in the Sacramento–San Joaquin Delta.

High- and Mid-Elevation Sierra: Sediment and Nutrient Inputs from Logging, Livestock Grazing, and Fire

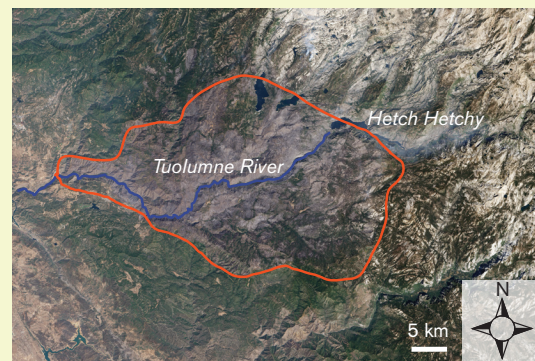
At mid- and high elevations in the Sierra Nevada, logging and livestock grazing have altered aquatic habitats and reduced native species by reducing or removing native vegetation, increasing runoff, erosion, and sediment inputs. Excessive deposition of fine sediment covers benthic organisms and food sources, reduces habitat heterogeneity, clogs gills, and fills interstitial pore spaces, reducing oxygen penetration and hence the survival of benthic organisms including salmonid fish eggs (Graber 1996, Kattelman 1996). Sediment inputs to streams in logged basins depend on the extent and intensity (selectivity) of timber removal, the disposition of slash and debris, and distance of these activities from streams. They can be reduced to some extent by the preservation of riparian buffer strips of adequate width (Newbold et al. 1980, Erman and Mahoney 1983, Mahoney and Erman 1984). In many cases, the roads, skid trails, and yarding areas associated with timber harvest have had larger effects on erosion and sediment deposition than the logging itself.

Sediment and nutrient inputs from cattle grazing accrue because cattle are attracted to streams and their riparian zones for shade, forage, and drink, where they trample and consume riparian vegetation, defecate and excrete nutrients, and compact soils and break down channel banks. Compaction and erosion by cattle can lead to channel incision and a lowering of the water table, desiccating riparian habitats. Streams heavily impacted by livestock often are wider, shallower, and clogged with fine sediment deposits, and they often have bare banks and low riparian shading and inputs. These changes have strong effects on stream algae, invertebrates, and vertebrates including salmonid populations (Knapp et al. 1998, Herbst and Silldorff 2006, Herbst and Blinn 2007). Reversing the effects of livestock on streams may require management on relatively large scales. For example, fencing livestock away from sections of stream, varying in length from several hundred to several thousand meters, had few effects on invertebrate communities, but removing livestock from large allotments restored natural invertebrate communities and diversity (Herbst et al. 2012).

Burned areas are another major source of sediment delivered to Sierran streams (Box 33.4 Figure 1). Although fires are widespread natural disturbances in California, their intensities and frequencies have

changed due to human activities (Miller et al. 2009; see Chapter 3, "Fire as an Ecosystem Process"). By removing upland vegetation and altering soils, wildfires increase erosion and runoff, increasing loading of sediment and nutrients to streams (Jackson et al. 2012, Oliver et al. 2012). Catastrophic disturbances after fire, such as debris or mud slides and scouring floods, can have long-lasting effects on stream communities by removing or smothering most organisms in stream beds (Koetsier et al. 2010). Aquatic ecosystem recovery rates after fires can be prolonged in forested catchments, but faster in shrub or grassland habitats (Verkaik et al. 2013). In one study the geomorphology of drainage channels in forested Sierran catchments returned to prefire configurations within six years, but benthic macroinvertebrate diversity remained lower in burned than in unburned streams for up to seven to twenty-three years (Roby 1989). Although diversity can decline, the density of recolonizing species characterized by short life histories, small sizes, and high dispersal rates (i.e., midges, mayflies, blackflies) can be high. Where riparian vegetation has burned, algal-based food webs dominate, because of high nutrient and light levels, whereas streams with intact riparian vegetation have food webs based on terrestrial detritus, including higher abundances of shredders (Cooper et al. 2015, Verkaik et al. 2013). When macroinvertebrates proliferate postfire, they can provide a rich food supply for aquatic and riparian predators (e.g., fish, spiders, bats, birds) (Koetsier et al. 2007, Malison and Baxter 2010, Buchalski et al. 2013). Because low-severity prescribed fires that do not affect the riparian canopy have far fewer and shorter-lived effects (less than one year) on stream ecosystems (Stephens et al. 2004, Bêche et al. 2005), their increasing use may re-create some aspects of pre-European fire regimes and reduce fuel loads while protecting water quality.

(continued)



BOX 33.4 FIGURE 1: Satellite imagery of Rim Fire burn scar (red) encompassing the Tuolumne River from Hetch Hetchy to Don Pedro Reservoir (blue). Source: < http://www.nasa.gov/sites/default/files/california_a2013270.2105.721.250m_0.jpg>.

(Box 33.4 continued)

Sierra Foothills and Inner Coast Range: Heavy Metal Pollution

Legacy pollution from the California Gold Rush continues to affect the greater Sacramento River Basin. Hydraulic mining on the western slopes of the Sierra from 1853 to 1884 resulted in massive slope failures and sediment inputs, which smothered river beds (Box 33.4 Figure 2). Although these river channels have now returned to their natural forms, sediment deposits remain on terraces (Mount 1995). Eroding sediments and acid mine drainage from mine tailing piles deliver metals, such as copper, at concentrations high enough to alter the production, abundance, and composition of algal and invertebrate assemblages (Leland and Carter 1985, Leland et al. 1989). The exhumation and transport of mercury, in particular, has created widespread environmental problems (Alpers et al. 2005). Cinnabar ore (mercury sulfide, HgS) was mined in the Inner Coast Ranges and transported as liquid mercury to the Sierra Nevada for the recovery of gold. This enterprise transported more than 3 million kilograms of mercury to the northwestern Sierra (Domagalski 2001). Mercury

(Hg), a potent neurotoxin, **BIOACCUMULATES**, increasing at each trophic level in aquatic and riparian food webs.

Periphyton in streams and rivers can **BIOMAGNIFY** mercury and methyl mercury (MeHg), which is converted from mercury by bacterial activity in environments with a high carbon supply and little or low oxygen levels (Bell and Scudder 2007, Moye et al. 2002). Near and downstream of abandoned cinnabar mines, tissue concentrations of mercury for insectivorous consumers, such as cliff swallows, are five to seven times greater than at reference sites (Hothem et al. 2008). Amphibians including the American bullfrog, which may be caught and consumed by humans, had concentrations above the U.S. Environmental Protection Agency's tissue residue criteria for fish (Hothem et al. 2010). In the floodplain wetlands of the Sacramento River, methyl mercury concentrations are highest where inundation is prolonged (Sacramento Slough) and where wetlands receive flow from Cache Creek (see Figure 33.5) that carries runoff from abandoned mercury mines (Domagalski et al. 2004). After the record



BOX 33.4 FIGURE 2 Water cannons at Malakoff Diggings used to erode sediment into sluice boxes for gold recovery. Mine tailings flowed into the South Yuba River. Photo: Courtesy of the Bancroft Library, UC Berkeley.

These large federal and state projects, combined with flood control and navigation projects completed by the Army Corps of Engineers and numerous other private and public water agencies, have massively changed the flow patterns, amounts, and paths of California's streams and rivers (Kahrl 1979, Worster 1985, Reisner 1993, Grace 2012). Water development projects in California, anchored by over fourteen hundred large dams, have captured nearly 60% of the state's runoff, engendering explosive agricultural and urban growth. Some of the

largest components of this water system are the dams on the tributaries and mainstem of the Sacramento and San Joaquin Rivers, which store nearly 30 billion cubic meters of water and produce nearly 24 million megawatt-hours of power (see Figure 33.7). In general, dams inundate upstream areas, converting rivers to reservoirs; trap sediments; and in concert with the land use changes discussed earlier, dams have altered the hydrology, geomorphology, and chemistry of rivers and their riparian zones, often with deleterious effects on sensi-

flood of January 1, 1997, concentrations of mercury were lower than expected in the water and sediments of Sacramento tributaries draining former gold-mining areas, perhaps because reservoirs on these rivers had trapped mercury-laden sediments and the mercury had then bioaccumulated in the tissues of reservoir organisms (Domagalski 2001). Mercury concentrations in game fish in reservoirs on the Yuba and Bear Rivers exceed levels considered safe for human consumption and potentially create neurotoxic effects in piscivorous mammals, such as otter and mink (Saiki et al. 2010, and references cited therein).

Central Valley Pesticides: Nutrient and Metal Contamination

Urbanization and agriculture on the Central Valley floor also deliver contaminants to fresh waters. Airborne pollutants generated in the Central Valley, including pesticides, have increased contaminant inputs to High Sierra waters with uncertain impacts on aquatic organisms (Cahill et al. 1996, Davidson and Knapp 2007, Bradford et al. 2011, 2013). Dust-borne phosphorus appears to have contributed to eutrophication and a shift from phosphorus to nitrogen limitation in High Sierra lakes (Vicars et al. 2010, Vicars and Sickman 2011). More locally, valley floor rivers receive pesticides in urban storm runoff at concentrations toxic to the aquatic biota (Weston and Lydy 2012). Wastewater effluent from urban areas in the watershed have augmented nutrient inputs to the Sacramento and San Joaquin Rivers (Jassby and Van Nieuwenhuysse 2005, Jassby 2008), stimulating problematic phytoplankton production downstream (Parker et al. 2012).

Interestingly, over the past fifty years, phytoplankton community dominance in the Sacramento River has shifted from a diverse diatom flora to small flagellates and green algae (Greenberg 1964, Parker et al. 2012 and references cited therein). The cities of Stockton and Sacramento are both under regulatory scrutiny as they install and implement new systems to reduce their considerable discharge loads to surface waters (California State Water Resources Control Board 2012). Research revealing the toxicity of PYRETHROIDS for aquatic invertebrates (Gan et al. 2008, Weston and Lydy 2012), and the widespread dissemination of antibiotics, endocrine disruptors (Colborn et al. 1993, PAN 2014), and other micropollutants, implicate urban and suburban Californians and their lawns and gardens as additional sources of harmful chemicals to aquatic habitats.

Because of extensive and intensive agriculture and water use in the San Joaquin Valley, most of the dimin-

ished flow in the lower San Joaquin River is agricultural return flow, laden with fertilizer residues, pesticides, herbicides, metals, and other potentially harmful chemicals. Some attempts to deal with environmental impacts created by polluted agricultural return flows have exacerbated the problem. For example, the Bureau of Reclamation (the Bureau) built the 137 kilometer San Luis Drain that in 1971 began delivering wastewater from areas served by the Westlands irrigation district to Kesterson Reservoir in the Kesterson National Wildlife Refuge, a migratory waterfowl refuge administered by the U.S. Fish and Wildlife Service (FWS) (Garone 2011). Drainage tiles were installed under 17,000 hectares of the Westlands service area in 1976 to collect water from saturated soils and contaminated agricultural return flows and channel it to the San Luis Drain. These subsurface waters became the primary contributors to Drain flows by 1981. From 1981 to 1985, federal agency personnel found high selenium concentrations in Kesterson waters, often far in excess of later-developed toxicity thresholds for this element (Wu 2004). In addition, they reported algal blooms and declines in emergent aquatic vegetation, fish, frogs, and waterfowl. Because selenium is incorporated into the tissues of plants and algae then bioaccumulates up the food chain, it often becomes most concentrated in top predators, like birds and fish (Hamilton 2004). Horribly deformed bird embryos associated with high selenium concentrations in tissue were observed at Kesterson (Ohlendrof et al. 1986, Wu 2004).

Because agricultural runoff is exempt from the provisions of the federal Clean Water Act, but not from the provisions of the state's Porter-Cologne Water Quality Control Act, it took the State Water Resources Control Board (SWRCB) to order the Bureau to remedy the environmental damage created by its actions. Under orders from the Department of Interior, which oversees both the FWS and Bureau, the San Luis Drain was closed and Kesterson Reservoir was sealed with a layer of soil to reduce wildlife exposure to selenium hazards (Garone 2011). With the tile drains now plugged, Westlands and other Valley agencies still suffer from soil waterlogging and salinization and have been testing mitigation measures, including drip irrigation, on-site evaporation ponds, HALOPHYTE planting to concentrate salts, and limited retirement of marginal farm lands (Garone 2011). The types of problems encountered at Kesterson now appear more ubiquitous than formerly thought, with high selenium concentrations in other parts of the western San Joaquin Valley and the Tulare Lake Basin as well as in the Salton Sea (Garone 2011, Saiki et al. 2012).

native species and ecosystems (Sabo et al. 2012, Cooper et al. 2013). The direct manipulation of the water cycle through dams, canals, groundwater pumping, and interbasin transfers have devastated migratory and other sensitive species that rely on natural hydrologic cycles to survive and complete their life cycles, and have promoted the spread of alien species adapted to altered conditions (Lichatowich 1999, Moyle et al. 2008, Moyle et al. 2011, Alagona et al. 2012). Moyle et al. (2011) concluded that dams; alien species; and urban, agri-

cultural, and industrial development were the major causes of the extensive loss of native fish species diversity in California (Box 33.5).

Concerns about human-caused damage to the environment provoked the environmental movement of the 1960s and 1970s. In the 1970s state and federal legislation—such as the Clean Water, Endangered Species (ESA), Wild and Scenic Rivers, National Environmental Policy, and California Environmental Quality Acts—inaugurated an era of increased



FIGURE 33.7 Major components of the California water storage and delivery system. Major rivers are shown with solid lines, aqueducts and canals as dashed lines, dams as bars, reservoirs as black bodies without outlines, and lakes as gray bodies outlined in black. Map by Parker Welch, Center for Integrated Spatial Research (CISR).

public awareness and governmental oversight of development activities that harmed natural resources, species, and ecosystems as well as remedies for their conservation. For example, after a decades-long legal battle, a 2006 settlement mandated the rewatering of the lower 150 mile-long San Joaquin channel as well as the construction of a conservation hatchery and reintroduction of Chinook salmon (Matthews 2007, NOAA 2013). Because of environmental concerns, increased construction costs, a scarcity of remaining sites appropriate for dams, and doubts about their economic benefits, large dams are no longer being built, although a number are proposed (e.g., Temperance Flat on the San Joaquin River) and some existing dams are slated for enlargement (e.g., Los Vaqueros,

Shasta). The last large dam built in California was the New Melones Dam on the Stanislaus River in 1979. Furthermore, urban and environmental concerns during recent droughts have challenged agriculture's dominance as a user of the state's water resources. Although agriculture currently represents a small proportion of the California economy, it uses most of the state's water. Although many citizens and non-governmental organizations agitate for the protection or restoration of natural ecosystems, and many governmental agencies are charged with monitoring and enforcing environmental laws, the legacy of massive rearrangements of waterways and landscapes in California has created overwhelming challenges for the state's rivers and their biota.

BOX 33.5 THE STEELHEAD: A DWINDLING ICONIC SPECIES
IN COASTAL CENTRAL AND SOUTHERN CALIFORNIA

Steelhead (*Oncorhynchus mykiss*) precariously persist in the streams and rivers of coastal southern and central California, a region with a benign climate punctuated by catastrophic earthquakes, fires, floods, landslides, and droughts. Geologic faults, including the San Andreas fault on its eastern border, and steep coastal mountains bordered by marine terraces and coastal floodplains characterize the region's geography (Faber et al. 1989, Norris and Webb 1990, Keeley et al. 2012). Short streams drain coastal mountains, whereas longer rivers drain inland areas and flow to the sea through mountain gaps (e.g., Pajaro, Salinas, Santa Maria, Santa Ynez, Santa Clara) or large alluvial floodplains (Los Angeles, San Gabriel, Santa Ana). This topography and latitudinal range have produced strong gradients in rainfall and river flow that typically increase with increasing elevation and latitude and decrease with distance from the coast.

Because of large seasonal and interannual variation in rainfall, driven by large-scale climatic cycles (e.g., EL NIÑO/SOUTHERN OSCILLATION, PACIFIC DECADAL OSCILLATION cycles; see Chapter 2, "Climate") and steep terrain, flow regimes vary from catastrophic winter floods to summer desiccation, when many alluvial, southern, or inland reaches become intermittent or dry completely. These flow regimes also affect the estuaries at the mouths of streams and rivers, which range from conduits for strong winter floods to intermittently closed lagoons separated from the ocean by sand berms during the dry season, sometimes for prolonged periods during dry years (Jacobs et al. 2011, Rich and Keller 2013). Against this extremely dynamic backdrop, the steelhead has maintained populations for thousands of years due to flexibility in its behavior, life history, and physiological tolerances. The steelhead has a complex (nonobligate) anadromous life history, maturing in the ocean, ascending rivers during winter flood flows to spawn in mainstem reaches or tributaries, then developing as juveniles in streams over one to three years (usually two). At the end of their stream residence, juveniles undergo physiological and morphological changes (smoltification), usually in late winter or spring, that allow them to survive in the ocean. The smolts then migrate to the sea where they develop for one to four years (usually two) before returning to rivers as migrating spawners (Moyle 2002, Quinn 2005, Quinn and Meyers 2005, Boughton et al. 2006). Individual steelhead show many variations in life history. Some fish show the typical two-year freshwater, two-year marine cycle; some spend substantial time as juveniles in estuaries, where they grow faster and larger, enhancing their survival in the ocean; and some individuals (usually called rainbow trout) spend their entire lives in streams (Hayes et al. 2011, Kern and Sogard 2013, NMFS 2012, NMFS 2013).

Some studies report that resident fish can produce anadromous offspring and vice-versa, but the conditions and frequency under which this occurs may vary between populations and require more research

(Thrower et al. 2004, 2008, Olsen et al. 2006, Christie et al. 2011, Hayes et al. 2012, but see Zimmerman and Reeves 2000, Pearse et al. 2009). Their remarkable life history variation can buffer steelhead populations from environmental change, for example, by allowing populations to persist as residents where downstream migration is blocked by drying or migration barriers or by allowing upstream areas decimated by severe floods or fires to be repopulated by anadromous fish (Bell et al. 2011, Thorson et al. 2013). Because adult anadromous steelhead are much larger and more fecund than resident forms, they have the potential to disproportionately augment upstream populations where their passage to the sea is maintained.

Steelhead exist near the southern limits of their range in southern California. The native populations occurring in this region have a variety of distinctive behavioral, physiological, and genetic traits warranting their designation as distinct population segments (DPSs) by the NATIONAL MARINE FISHERIES SERVICE (NMFS 2012, 2013). Because of large, interannual variation in lagoon sand berm breaching, some steelhead spawners do not have access in dry years to their natal streams, where they typically spawn, so they can disperse to nearby streams where adequate flows allow access (Boughton et al. 2006, Clemento et al. 2009, Bell et al. 2011, Jacobs et al. 2011). Steelhead populations in this region also show unusual tolerances to low flow, high temperatures, and low oxygen levels, with juveniles often overwintering in isolated or semi-isolated pools with temperatures sometimes exceeding 25°C (occasionally approaching 30°C) and oxygen levels occasionally dropping to <3 mg/L, outside tolerances reported for steelhead in other regions (Carter 2005, Richter and Kolmes 2005, Spina et al. 2005, Spina 2007, Bell et al. 2011, Sloat and Osterback 2013, S. Cooper personal communication). Furthermore, steelhead in this region are adept at seeking out cold water seeps or pockets with more suitable temperature conditions (Matthews and Berg 1997).

Despite this array of adaptations for dealing with a variable and sometimes harsh environment, widespread land conversion and water developments in this region have reduced steelhead from historical runs in the tens of thousands to current runs that amount to a few individuals (probably less than one thousand anadromous individuals regionwide) (Moyle et al. 2008, Moyle et al. 2011, Alagona et al. 2012, NMFS 2012, 2013) (Box 33.5 Figure 1). The extensive construction of dams, in particular, has blocked steelhead migrations, isolated upstream landlocked *O. mykiss* from downstream migrant populations, and altered downstream flow regimes, sometimes producing inadequate flows to breach lagoon sand berms, to provide adequate depths for spawner migrations, or to support juvenile rearing habitat (Boughton et al. 2006, Moyle et al. 2011, Petts and Grunell 2013). Numerous water diversions and intensive groundwater pumping also have dewatered channels and many rivers have been channelized for flood

(continued)

(Box 33.5 continued)

control, destroying the complex habitats, cover, and food sources required by juvenile steelhead (McEwan and Jackson 2003, Hunt & Associates 2008a, Hunt & Associates 2008b, Kier Associates and NMFS 2008).

These water structures were built to serve extensive agricultural, urban, and industrial development, which itself has changed water and chemical cycles, engendering flashier hydrographs with higher flood peaks, lower base flows, simplified stream morphologies, altered shading, and increased nutrient and pollutant loading and temperatures, with many repercussions for steelhead and the food webs that support them (Paul and Meyer 2001, Allan 2004, Ackerman and Schiff 2003, Mazor and Schiff 2008, Cooper et al. 2013). Flood control activities, including the construction and maintenance of debris dams to trap sediments, stream channelization, and clearance of in-stream and riparian vegetation often block steelhead migrations and degrade habitat (NMFS 2012).

Further, urban and agricultural development and gravel and sand mining have directly destroyed or degraded important steelhead habitat, such as estuaries and stream channels, through infilling, dredging, pav-



BOX 33.5 FIGURE 1 What has been lost? 1946 catch of steelhead from the Ventura River at Foster Park. Angler: John B. Colla. Photo: Robert Phelan.

ing, construction, and/or the diversion of flows through pipes or tunnels (Ferren et al. 1995, Ferren et al. 1996, Kier and Associates and NMFS 2008, Grossinger et al. 2011). Although dams and diversions decrease downstream flows in some cases, depending on the time of year and operational schedules, many urban rivers of southern California have increased flows throughout the year compared to historical times. This is due to increased runoff from impervious surfaces in the wet season and return flows of water imported from other parts of the state (Delta, Colorado River, Owens Valley) for irrigation, industrial, and domestic uses in the dry season (White and Greer 2006, Townsend-Small et al. 2013). In some cases, waste water treatment plants supply most of the flow in the lower reaches of southern California's rivers in the dry season (Spina et al. 2005, Lyon and Sutula 2011). They can produce effluent water laden with nutrients, producing algal blooms that decrease oxygen at night to levels potentially harmful to steelhead (Klose et al. 2012).

Increased flows in these rivers have not enhanced steelhead stocks because existing channels do not have the complexity, cool temperatures, riparian inputs, cover, depths, or high water quality needed to support steelhead. Further, these modifications to flow regimes (dams, more perennial flows) often promote the introduction and spread of exotic fish species, which may prey on or compete with steelhead (Riley et al. 2005, Marchetti et al. 2006, Cucherousset and Olden 2011). Irrigation return flows in agricultural areas, such as those along the Pajaro, Salinas, Arroyo Grande, Santa Maria, Santa Ynez, and Santa Clara Rivers, and urban runoff in rivers such as the Los Angeles, San Gabriel, and Santa Ana can carry high loads of herbicides, pesticides, metals, oil residues, nutrients, hormones, antibiotics, and other contaminants with potential lethal and sublethal effects on aquatic life (Ackerman and Schiff 2003, Moeller et al. 2003, Busse et al. 2006, Macneale et al. 2010, Cooper et al. 2013, Sengupta et al. 2014). Many of these stresses are exacerbated in estuaries, which become downstream sumps for contaminants originating in their watersheds.

The expansion of human populations into wildland areas has increased the incidence of wildfires, which can extirpate steelhead from some reaches via accidental drops of toxic fire retardants, extreme scouring flood flows, and sediment deposition from erosion and landslides. Subsequent steelhead recolonization can then be blocked by stream barriers (dams, road crossings) (Kier and Associates and NMFS 2008, Verkaik et al. 2013). Although the California Department of Fish and Wildlife has restricted angling for listed steelhead, it still continues to stock reservoirs in this region with hatchery strains of this species (California Department of Fish and Wildlife and U.S. Fish and Wildlife Service 2010, California Department of Fish and Wildlife 2013). Genetic studies have established that hatchery

stocks generally do not interbreed with native stocks (Nielsen et al. 1994, Girman and Garza 2006, Clemento et al. 2009), but concerns exist about competition with or the introduction of disease by hatchery strains.

Given all the human impacts on steelhead stocks in central and southern California, near their southern range limits where their existence was already precarious, is there hope for their restoration? Because of their unique characteristics and the numerous threats to their continued existence, NMFS designated the south-central California steelhead, ranging from the Pajaro River to Arroyo Grande Creek, as threatened and the southern California steelhead, ranging from the Santa Maria River to the U.S.-Mexico border, as endangered under the U.S. Endangered Species Act. In their recovery plans for these steelhead stocks, NMFS called for a variety of measures to protect and restore key populations, including fish passage structures around dams, removal of barriers, water regulation to ensure adequate flows for spawning migrations and nursery and rearing habitat, improvements in water quality, appropriate fuel and fire management, and restoration of in-stream and riparian habitat (NMFS 2012, 2013). Extensive research and monitoring plans assessed the changing status of the species and addressed unanswered questions regarding the species' life history and relationships between anadromous and resident *O. mykiss* (NMFS 2012, 2013). Fish passage facilities around dams and dam removal are promising because many headwater streams on federal lands in this region support resident steelhead (trout) populations (Bell 1978, O'Brien et al. 2011, NMFS 2012, NMFS 2013). Steelhead populations above and below dams are more closely related to each other than to those in other watersheds (Clemento et al. 2009), indicating that effectively reconnecting upstream and downstream populations could rehabilitate anadromous runs.

Currently, however, it is not clear that the few fish passage facilities that have been installed (e.g., around the Ventura River's Robles Dam and the Santa Clara River's Freeman Diversion Dam) are effective for both adult and juvenile migration. Plans to remove dams, such as Matilija Dam on a tributary of the Ventura River and Rindge Dam on Malibu Creek, have foundered on problems associated with the disposal of trapped reservoir sediment and concerns about impacts on downstream resources; however, the removal of San Clemente Dam on the Carmel River has begun (Capelli 1999, 2004, 2007). Recent hearings before the State Water Resources Control Board (e.g., over releases from Bradbury Dam on the Santa Ynez River) indicate that agencies are struggling to find a balance between in-stream and off-stream uses of water, particularly while considering natural resources like steelhead that are protected under California's Public Trust Doctrine. Although the State Water Resources and Regional Water Quality Control Boards have set standards and identified impaired water bodies in this region (California

State Water Resources Control Board 2007a, 2007b, 2007c, 2007d), the process of setting total daily maximum load (TMDL) targets for contaminants and permitting effluent discharges from waste water treatment plants and other point sources takes many years. This has produced a large backlog of cases without addressing large contaminant loads resulting from nonpoint sources.

In short, threats to steelhead continue to grow, solutions remain elusive, basic ecological data are lacking, and many governmental agencies work at cross-purposes. Competing interests among private citizens, nongovernment groups, and a variety of government agencies over river resources in this region are likely to grow with climate and land use change. Expected increases in droughts, wildfires, sea level, storm intensity, and human population size will increase human demands for water, flood control, and coastal protection to the detriment of protecting and restoring river and estuarine ecosystems and their native biotas and natural ecological processes (Keeley et al. 2012, NMFS 2012, NMFS 2013). Further, warming water may push southern steelhead to their lethal limits, with weakened steelhead being more prone to disease.

A note of hope involves the efforts of government agencies and citizens' groups to restore river habitat and protect steelhead. For example, the City of San Luis Obispo has restored the reach of San Luis Obispo Creek passing through the heart of the city, and The Ojai Land Conservancy has acquired a large portion of the Ventura River and established the first Southern California Steelhead Preserve. Many citizens' groups have adopted particular rivers to promote their environmental qualities, expand outdoor education, and protect and restore natural resources. For example, although the Los Angeles River has been called the largest storm drain in the world with 80% of its channel paved, the FRIENDS OF THE LOS ANGELES RIVER (FOLAR) are working to restore habitat, develop recreational facilities, modify flood control practices, educate students and the public, coordinate cleanup efforts, improve water quality, participate in planning, and influence policy to better steward this river's natural and historical amenities (Gumprecht 1999). These local-scale efforts need to be better complemented by basinwide planning and management efforts to ensure adequate flows for native species and to reduce contaminant inputs (Bernhardt and Palmer 2007, 2011).

It is a testament to the steelhead's natural resilience that this species continues to persist in central and southern California, given the numerous natural and human threats it has faced. They represent precious genetic resources for maintaining salmonids in a warming world (IPCC 2014a, 2014b). Concerted, coordinated research and data-driven action by private citizens, environmental groups, and governmental agencies at all levels are needed to prevent this natural treasure from becoming an environmental tragedy.

The future of California's rivers is inextricably linked to climate change. Climate models project warming of streams and rivers, earlier peak flows, more prolonged or lower summer base flows, and autumnal and winter discharge peaks due to increased rain and rain-on-snow events, the latter associated with "pineapple express" storms (Singer 2007, Dettinger et al. 2009, Dettinger 2011, Weller et al. 2012). Hydrologic models further predict that overall river discharge will decline with increasing temperature, with more pronounced changes in the northern than the southern Sierra (Null et al. 2010). Many Sierran glaciers are expected to melt away within the next 50 to 250 years, removing water supplies during dry periods for high-elevation streams and lowland valleys (Basagic and Fountain 2011, Stock and Anderson 2012). Changes in water temperature and in the timing, duration, and magnitude of floods and droughts are likely to alter habitats and elevational distributions of organisms, challenge cold-water taxa, and shift the composition of communities (Herbst and Cooper 2010, Herbst 2013, Kadir et al. 2013). Over 80% of California's native fishes could be extinct in one hundred years if present climate trends continue (Moyle et al. 2013). Climate change also will increase human demands for water, and more calls for storing and transporting water will likely intensify competition among interest groups for increasingly limited, variable, and altered water supplies.

As a final example of California's water problems, we turn to the Sacramento–San Joaquin Delta, which is both the linchpin for California's largest water projects (CVP, SWP) and a complex agricultural, wetland, and aquatic ecosystem supporting high biodiversity and productive farms. The Delta receives half of the state's runoff, drains over 40% of the state's land area, and has been radically altered by diking and draining, island (polder) subsidence, pollution, local and regional development, upstream dams and diversions, and the introduction of many alien species (Lund et al. 2008, Whipple et al. 2012, Alagona 2013; see also Chapter 19, "Estuaries: Life on the Edge"). Water quality deteriorates as it flows from the Sacramento River through the Delta, and federal and state water agencies have faced the challenge of delivering large quantities of high-quality water from the Sacramento River in the north to intake systems for the Central Valley and State Water Projects near Tracy in the south. Past proposals to divert Sacramento water around the Delta to the Tracy intakes were opposed by groups who believed that such developments would harm the Delta's remaining wetlands, rich agricultural areas, and endemic species, such as the endangered Delta smelt, while damaging northern California ecosystems and economies to benefit primarily southern California (Lund et al. 2008, Alagona 2013).

Droughts exacerbate such conflicts, preventing the CVP and SWP from meeting their contractual water deliveries while creating conspicuous environmental impacts (e.g., saline intrusion, reduced fish habitat). Attempts to develop coordinated state, federal, and private actions to deal with the Delta's water and environmental problems, such as the CALFED Bay-Delta Program, have made little progress due to political, organizational, and funding problems (Little Hoover Commission 2005, Legislative Analyst's Office 2006, Hanemann and Dyckman 2009, Alagona 2013). The rapid decline of the Delta's pelagic fish and invertebrates and subsequent lawsuits under the ESA led to court orders to shut down the Tracy pumps for short periods, exacerbating conflicts between environmental groups and development, agricultural, and urban interests. The state Delta Reform Act of

2009 addressed wetland restoration, protections for listed species, the repair of aging levees, and new conveyances to ensure the quality and reliability of water supplies for users. Nevertheless, detailed proposals to carry Sacramento water to Tracy via tunnels or canals, even with associated environmental protection and restoration programs, have reignited concerns about the environmental and economic impacts of rerouting Delta flows.

Are there solutions to the ecological problems of California's rivers generated by water development and land use changes? Environmental laws and industry regulation have led to management changes and reduced sediment and pollutant loading to some streams and rivers, and some upland and riparian zones have been preserved or restored. Selective and/or rotational logging and changes in harvest practices (e.g., yarding methods) in the timber industry; rotational grazing and changes in the intensity (number of animals), duration, and timing of livestock grazing allotments; and preservation of riparian buffer strips also have helped to reduce environmental damage to streams (Erman and Mahoney 1983, Herbst et al. 2012). Some of the legacy and current effects of mining have been reduced by remediation practices and controls on sand and gravel mining (Kondolf 1994, Davis et al. 2012). Local zoning restrictions and regional water constraints can also affect the patterns and extent of urban and agricultural development and associated water use, although the effectiveness of these measures varies widely and is often challenged by development interests. The state's water quality is overseen by the State Water Resources Control Board, which through its regional boards aims to meet the provisions of the Clean Water Act by setting standards, identifying impaired waters, developing TOTAL MAXIMUM DAILY LOAD (TMDL) allocations for pollutants, and regulating pollutant discharge (http://www.waterboards.ca.gov/water_issues/programs/tmdl/).

Although new developments are subject to environmental review under federal and state laws (e.g., the California Environmental Quality Act [CEQA]), it is often difficult to mitigate environmental damage legacies from past developments. An exception is the process used to renew hydropower dams operating under thirty- to fifty-year licenses from the Federal Energy Regulatory Commission. In California, where hydropower accounts for approximately half of all renewable energy generation in the state (U.S. Energy Information Administration, Annual Energy Outlook 2013), approximately fifty multidam licenses were scheduled for review and renewal between 2005 and 2020 (Rehn 2009). This relicensing process provides one of the only formal opportunities to evaluate the effects of flow schedules on river ecosystems and reconfigure dam operations to achieve conservation goals. Recent court decisions have demonstrated that the California Department of Fish and Wildlife has considerable statutory authority to improve flows for fish below dams (Bork et al. 2012), as does the State Water Resources Control Board in regulating water allocations and dam operations. Other biota besides fish also are now being considered (Kupferberg et al. 2012).

Considerable recent attention has focused on the operations of dams to achieve environmental objectives. The native riverine biota of California, as in much of western North America, has had a long evolutionary history with extreme hydrology, characterized by large seasonal and interannual variation in discharge including megafloods and droughts (Moyle 2002, Waples et al. 2008). Over the long term, hydrologic variation and extreme events can enrich ecosystems

and diversify habitat structure (Waples et al. 2009). As a consequence, many river scientists have postulated that native riverine species and diversity can be restored by operating dams to mimic natural hydrologic regimes (Waples et al. 2008, Poff and Zimmerman 2010). Although it could be impossible to replicate natural flow variation while meeting human water demands, it could be possible to operate dams to produce some seasonal flow characteristics required by critical life history stages (Kiernan et al. 2012, Kupferberg et al. 2012). In some cases, dams have outlived their usefulness while prolonging environmental damage, leading to calls for their removal (e.g., Searles Dam on San Francisquito Creek; Matilija Dam on Matilija Creek, a tributary to the Ventura River). The largest such demolition project in California history is currently under way on the Carmel River, where the seismically unsafe San Clemente Dam is being removed (<http://www.sanclementedamremoval.org/>). Because of sediment stored behind dams, however, dam removal has to be done carefully to minimize impacts on downstream areas (Stanley and Doyle 2003). Discontinuing water diversions could also recreate natural conditions that support natural communities.

Stream and river restoration has become a focus for many governmental agencies and environmental groups. By reestablishing more natural stream contours, planting native vegetation, removing exotic plant and animal species, providing passage for migratory species, reestablishing historical flow regimes, and instituting sediment and contaminant controls, restoration projects can rebuild ecosystems more hospitable for native species. Most current restoration projects lack follow-up studies to measure their effectiveness and are too small in scale (e.g., in short reaches) or with too little water to be effective (Bernhardt et al. 2005, Palmer et al. 2005, Kondolf et al. 2007, Bernhardt and Palmer 2011). Nevertheless, some effective river restoration efforts have been well documented. One example is the reestablishment of the native fish fauna in Putah Creek, a tributary to the Sacramento flowing through the Yolo Bypass (Kiernan et al. 2012). After 32 kilometers of the creek was dewatered in 1989, a lawsuit and subsequent court order mandated releases of water from Lake Berryessa / Monticello Dam to feed the creek. Flow was manipulated to provide sufficient water for spring spawning species to reestablish and to allow Chinook salmon to migrate upstream from the Yolo bypass. Native fish now numerically dominate > 20 kilometers of this reach, compared to < 2 kilometers under the old regime.

Another particularly heartening example is the restoration of Big Springs Creek, a tributary to the Shasta River in the Klamath basin. Despite contributing less than 1% of the Klamath's mean annual flow at the estuary, the Shasta River historically produced roughly half of the Chinook salmon in the lower Klamath River watershed because of cool spring flows that feed the Shasta River from Big Springs Creek (Wales 1951, NRC 2004). Poor land management practices degraded the area around Big Springs Creek, increasing daily maximum water temperatures from 11°C near the creek source to over 25°C in just 3.5 kilometers, and restricting oversummering anadromous salmonids to only about 10 meters at the head of the creek (Jeffres et al. 2009). In 2008 the Nature Conservancy purchased lands adjacent to Big Springs Creek and the Shasta River and initiated active restoration. Today, anadromous salmon again oversummer down the entire length of Big Springs Creek as well as in several kilometers of the downstream Shasta River (Nichols et al. 2013).

Lowland river floodplains are particularly promising foci for future restoration efforts. Once teeming with rich communities of native species including juveniles of valued fish, active river floodplains have been largely lost or degraded by urban and agricultural development. Originally, floodwaters in Central Valley rivers would spill over natural levees onto extensive floodplains. Flows are now diverted into canals or channels, and floodplains drained and converted to agriculture. One of the few exceptions is the 24,000 hectare Yolo bypass basin (Figure 33.8) that floods annually when the Sacramento River overtops the Fremont Weir, a 2-mile long concrete structure (Sommer et al. 2005). Because the Yolo basin has natural flood cycles, it supports fifteen native fish species and twenty-seven non-native taxa, providing appropriate seasonal habitats for several species of special concern including a recently delisted species, the cyprinid splittail (*Pogonichthys macrolepidotus*) and runs of Chinook salmon (Sommer, Harrell et al. 2001; Sommer, Nobriga et al. 2001; Feyrer et al. 2006). A complex Bay Delta Conservation Plan is under development (CALFED 2005, Mount et al. 2013). Recommendations to enhance the Yolo basin's floodplain function include placing notches or gates in the Fremont Weir to improve fish passage. Lowering the height of the weir would increase the frequency and duration of inundation, expanding the area of flooded agricultural fields. A challenging mix of grassroots environmental activism, landowner input, evolving frameworks of governance and management, and scientific research is under way to expand the successes of floodplain restoration, while addressing the economic costs of lost agricultural revenues (Salcido 2012, Howitt et al. 2013).

California's central water problem—that most of the state's precipitation falls in the north but most of its water is consumed in the central and southern regions—was addressed with the construction of one of the largest water storage and delivery systems in the world. The California water system has been vital to the state's economy but has had profound and far-ranging effects on its landscapes, waterscapes, and ecosystems. Revised dam operations or removal, the integrated management of ground and surface waters, the preservation of sensitive habitats (e.g., cold water streams, springs, oases) and species, and management practices tailored to California's unique array of freshwater ecosystems can all help to address environmental concerns (Moyle 2013). At base, however, there simply is not enough high-quality freshwater to serve all of the state's projected economic and environmental needs. This is particularly true given the current use of subsidized water by agricultural interests. Even along the relatively well-watered North Coast, rivers are overtaxed by summer withdrawals and drought and have approached thresholds at which they may flip between salmon-supporting and cyanobacterially degraded ecosystems (see Box 33.1). Some water conflicts could be reduced by conservation and recycling measures, a shift to more efficient, unsubsidized water pricing, and transfer of water contracts from low- to high-value uses (Gleick et al. 1995). Rising sea levels, altered fire intensities and frequencies, and climate change and human uses that alter hydrological cycles and thermal regimes will have many repercussions for rivers and the natural and human ecosystems they support (Hayhoe et al. 2004, Kadir et al. 2013). Native Californian cultures endured and survived droughts and megafloods as severe as those predicted to recur over the years and decades ahead (Ingram and Malamud-Roam 2013). Modern Californians will require similar adaptability, flexibility, tenacity, and

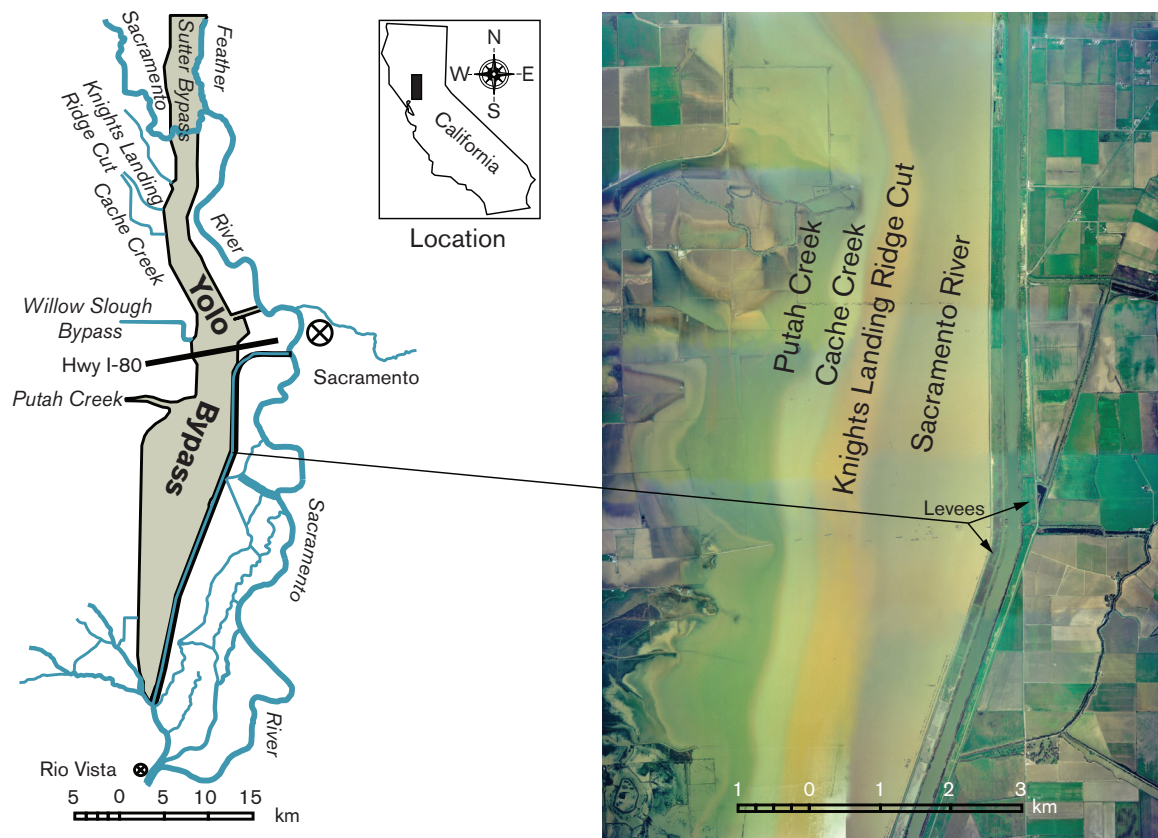


FIGURE 33.8 Schematic map and high-resolution photomosaic of the central 10 kilometers of the Yolo Bypass during a March 1998 flood event. Source: With permission from Sommer et al. 2008.

ingenuity, as well as a shift in values toward (in Wallace Stegner's phrase) "making a living not a killing" within our home watersheds.

Summary

California's river networks harbor diverse ecosystems due to their large latitudinal range and extreme topographic and geologic heterogeneity. California's sixty major and more than a thousand smaller river drainages contrast sharply in annual precipitation, from $>500 \text{ cm y}^{-1}$ in the northwest corner of the state to $<5 \text{ cm y}^{-1}$ in the southeast corner in the Colorado Desert. Coastal Californian rivers, watered by rain from Pacific storms, experience Mediterranean seasonality with almost all precipitation falling during the cool winter months and with summer droughts. Rivers of interior basins fed mainly from snowmelt have large spring flows that diminish through the summer. The native riverine biota has adapted behaviorally, morphologically, and physiologically to these seasonal rhythms and to "deluge or drought" year-to-year hydrologic variation, including superfloods and megadroughts that have occurred over centuries and millennia in this region. Repeatedly, human alterations have suppressed and rearranged this flow variation, creating more of a threat to the native flora and fauna of California's rivers than extreme natural variation to which the biota has adapted.

In "one of the most massive re-arrangements of Nature ever attempted" (Kahrl et al. 1979), humans during the nine-

teenth and twentieth centuries have subdued, diverted, and harnessed California's rivers, transforming them into the largest plumbing system in the world and managing it for flood protection, water storage and diversion to irrigate crops, supply urban areas, and generate electricity. Although early logging, grazing, and mining damaged river watersheds and channel networks, the most massive impacts on rivers and streams came from development of water and land resources to support agricultural and urban growth. Despite increasing demands on water supplies, encouraging cases of river restoration and improved stewardship are building on the natural resilience of some riverine landscapes and their biotas. The future of California's rivers, however, is inextricably linked to climate change and intensifying land use. Climate models project warming of streams and rivers, earlier peak flows, more prolonged or lower summer base flows, and autumnal and winter discharge peaks due to increased rain and rain-on-snow events—the latter associated with atmospheric rivers. Climate change will increase human demands for water, intensifying competition between interest groups and natural ecosystems for increasingly limited, variable, and compromised water supplies. Using the Eel, the Klamath, and the Sacramento–San Joaquin River systems as well as rivers draining the central and southern California coast, we discuss the adaptations of the native biota to variation through seasons, across years, and from headwaters to mouth. This chapter emphasizes that the state's rivers are among the most dynamic, critical, altered, and vulnerable components of California's ecosystems.

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Glossary

- ANADROMOUS** Organisms that migrate up rivers from the sea to breed in freshwater, spend early stages of their life histories in freshwater, but return to the ocean to grow and mature.
- BANKFULL** Discharge or stage (river depth) at which river flow in channels is level with the floodplain, which recurs on average about every 1.5 years. In rivers where there is no obvious floodplain, bankfull discharge is estimated as that delivered during the 1.5-year recurrence discharge.
- BIOACCUMULATION** The accumulation of a substance inside the bodies of organisms.
- BIOMAGNIFICATION** Increasing concentration of a substance from lower to higher trophic levels up food chains when consumers or predators accumulate and don't excrete the toxic loads of their resources or prey.
- COLLECTORS** Functional group of invertebrates that make their living by feeding on fine particles that they either filter from the water column (filter-feeders) or collect from deposits (deposit-feeders).
- DETRITUS** Dead organic matter of plant, algal, microbial, or animal origin.
- DISTINCT POPULATION SEGMENT (DPS)** Defined in the Endangered Species Act as a population of a species that has distinctive genetic, behavioral, physiological, and/or morphological traits.
- DISTURBANCE** A discrete event that kills or removes biota and frees space or other resources for recolonizing organisms (Sousa 1985). OR 1984 AS IN REFS?
- DRAINAGE AREA** The area of the basin (also known as catchment or watershed) that collects the water that drains into a given site within a river network. Delimited by drainage divides or ridges between basins.
- EL NIÑO/SOUTHERN OSCILLATION (ENSO)** El Niños result when high pressure over the western Pacific weakens equatorial trade winds, increasing sea surface temperatures in the eastern Pacific, resulting in the cessation of upwelling off Peru and California. La Niña is the reverse. On average, El Niños produce wet conditions and La Ninas produce dry conditions in California.

- ENDEMIC** A species that only occurs within a defined geographic location.
- ENDOSYMBIONT** An organism that lives within a host organism of a different species.
- EPILITHIC** Living on the surface of stones.
- EPIPELIC** Living on the surface of sand or mud.
- EPIPHYTIC** Living on the surface of plants, including macroalgae.
- EPIPHYTON** Plants that live on the surface of other organisms.
- ESTIVATION** A state of torpor with lowered metabolic rates in which animals endure seasonal periods of stress.
- FRIENDS OF THE EEL RIVER (FOER)** A citizens group concerned with management and restoration of the Eel River.
- FRIENDS OF THE LOS ANGELES RIVER (FOLAR)** A citizens group concerned with management and restoration of the Los Angeles River.
- FUNCTIONAL GROUPS** Arbitrary groupings devised by ecologists to classify organisms into guilds that make their living in particular ways.
- HALOPHYTE** Salt-loving (or at least tolerant) plant.
- HYDROGRAPH** The graph of discharge over time (measured as volume time⁻¹, e.g. m³s⁻¹); the amount of water flowing past a specific cross-section of a river or other channel versus time. Sometimes discharge is estimated from river stage, or depth, if rating curves that relate stage to discharge are available for the cross-section.
- HYDRAULIC GEOMETRY** Empirical power-law relationships that scale flow velocity (v), depth (d), and width (w) to river discharge (Q), discovered by Luna Leopold and Tom Maddox:
- $$w = a Q^b$$
- $$d = c Q^f$$
- $$v = k Q^m$$
- Where exponents $b+f+m = 1$ and coefficients $a*c*k = 1$. (Eq 33.1)
- DOWNSTREAM HYDRAULIC GEOMETRY** At a discharge with the same recurrence interval, discharge and width and depth increase from upstream to downstream locations according to hydraulic geometry relationships with approximately these exponents:
- $$b \sim 0.50; f \sim 0.40 \quad m \sim 0.10$$
- AT-A-STATION HYDRAULIC GEOMETRY** At a given cross-section, changes in discharges of different recurrence frequencies will be related to depth, width, and velocity with these exponents:
- $$b \sim 0.05; f \sim 0.35, m \sim 0.60$$
- HYPORHEIC** Below the streambed, in interstitial pore water flow.
- METAPHYTON** Macroscopic cloudy proliferations, often algal, that accrue suspended in the water column.
- NATIONAL MARINE FISHERIES SERVICE (NMFS)** The federal agency within the National Oceanic and Atmospheric Administration (NOAA) in the Department of Commerce. Among other things, NMFS is responsible for overseeing provisions of the Endangered Species Act for marine and anadromous species.
- NITROGEN FIXATION** The reduction by bacteria or cyanobacteria of atmospheric nitrogen N₂ to ammonia (NH₄)—a form that can be used by nonfixing microbes, plants, and fungi.
- ONTOGENETIC NICHE SHIFT** The changes in the niche of an organism as it grows and develops.
- PACIFIC DECADAL OSCILLATION (PDO)** Warm and cool cycles of sea surface temperature in the northern Pacific, shifting

typically at twenty- to thirty-year intervals. Discovered by Nate Mantua, a scientist trying to determine why salmonid oceanic survival was so variable across years.

PERIPHYTON An assemblage of attached algae and associated micro-organisms that live on stream plant, detrital, or mineral substrates.

PHENOLOGY The seasonal patterns of life history events of organisms.

PHYTOPLANKTON Microscopic algae that drift in the water column.

PRIMARY PRODUCERS The organisms (also known as “autotrophs”) that fix their own carbon from solar radiation (photosynthesizers) or chemical bonds (chemosynthesizers).

PRIMARY CONSUMERS The organisms that eat (primarily) primary producers or their dead cells or tissues.

PYRETHROIDS A class of synthetic, organic compounds that comprise the majority of current household insecticides.

RECURRENCE INTERVAL The probability of a hydrologic event; the chance that an event during any given year will equal or exceed some given value. The hundred-year flood is a flood of a magnitude that has a 1% probability (calculated from a fairly long record) of being equaled or exceeded during any given year.

RIPARIAN Along the banks of a body of water.

RUNOFF Overland flow of water from rain, snowmelt, or surfacing groundwater.

SECONDARY CONSUMERS Animals that prey on primary consumers.

SESSILE Organisms attached permanently or semipermanently to substrates.

SHREDDERS Primary consumers that feed on particulate organic matter (e.g., dead tree leaves) that is larger than 1 millimeter in diameter.

SUCCESSION The sequential recovery of biota that recolonize habitats after disturbance.

TOTAL DAILY MAXIMUM LOAD (TMDL) The estimated amount of a pollutant that a body of water can receive per day and still meet water quality standards specified by regulatory agencies enforcing the U.S. Clean Water Act.

TROPHIC CASCADE The indirect effects of top-down changes in food web control. The alternate release and suppression of populations at odd versus even numbers of levels below trophic position x that would occur if an important consumer or predator at position x is extirpated from a food web. For example, predators may reduce grazers, causing increases in primary producers.

UNIMPAIRED HYDROGRAPH A hydrograph that depicts the natural discharge through the river that would flow without human interventions like dams or diversions. Often computed as the sum of known sources of runoff and groundwater reaching river drainages at a given point.

VOLTINISM Describes the numbers of generations per year in the life history of a species, most commonly used with aquatic invertebrates. **UNIVOLTINE** refers to one generation per year; **BIVOLTINE**, two generations per year; **MULTIVOLTINE**, more than two generations per year; and **SEMIVOLTINE** refers to organisms whose generation time is more than one year.

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