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Food webs in Mediterranean rivers

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Abstract River food webs are subject to two regimes of longitudinally varying ecological control: productivity and disturbance. Light-limited productivity increases as channels widen downstream. Time windows for growth, however, shrink as discharge increases, substrate particle size decreases, and the frequency of flood-driven bed mobilization increases downstream. Mediterranean rivers are periodically reset by hydrologic events with somewhat predictable timing. Typically, a rainy winter with high river discharge is followed by summer drought with little or no rainfall and slowly declining river flow. The magnitude and timing of winter floods and severity of subsequent summer drought can vary considerably from year to year, however. Episodic scouring floods or prolonged periods of drought are experienced as disturbances, stressors, or opportunities by river biota. The timing, duration, and intensity of these hydrologic controls affect performances of individuals, distribution and abundances of populations, and outcomes and consequences of species interactions. These interactions in turn determine how river food webs will assemble, develop, and reconfigure after disturbance. We discuss how spatial variation in solar radiation and spatial and temporal variations in disturbance affects river food webs under Mediterranean climate seasonality, focusing primarily on long-term observations in the Eel River of northwestern California, USA.

Keywords Algal production and fate · Carbon sources · Cross-ecosystem fluxes · Detritus · Disturbance · Drought · Floods · Food quality · Food webs · Hydrology · Insect emergence · Interaction strength · Mediterranean rivers · River-to-ocean fluxes · Seasonality

Introduction

River food webs are periodically reset by flood scour or dewatering, and reassemble repeatedly after these

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events (Fisher et al., 1982; Fisher, 1983; Power et al., 1985; Wootton et al., 1996). The production, distribution, abundances, and fates of organisms and biomass in food webs depend in large part on the timing of hydrologic changes relative to life history events of biota (Resh et al., 1988).

In rivers under Mediterranean climates, seasonal timing of key hydrologic events is somewhat predictable. Typically, a rainy winter season with high river discharge is followed by a summer drought with little or no rainfall and slowly declining river flow (Fig. 1). Important variation occurs from year to year, however, in the magnitude and timing of winter floods and the severity of subsequent summer drought (Gasith & Resh, 1999). Spatial variation in river environments is also partially predictable from their landscape position. Biota in drainage networks, from headwaters to lowland mainstems, experience partially predictable change in radiation regimes and habitat structure and stability. Solar radiation (and therefore potential growth rates of energy-limited organisms) increase as channels widen downstream, but time windows for this growth narrow as coarse bedrock and boulders give way to more mobile cobble, pebble, and gravel bed sediments. As discharge increases and substrate particle size decreases downstream, the frequency of disturbance by flood-driven bed scour increases. Pulsed events like floods, or more prolonged periods of slowly declining seasonal base flows, are experienced as disturbances, stressors, or opportunities by river biota. The timing, duration, and intensity of these events, by affecting performances of individuals, the distribution and abundances of populations, and outcomes and consequences of species interactions will determine how river food webs will assemble, develop, and reconfigure after disturbance.

We use Sousa's (1984) definition of ecological disturbance: a discrete, pulsed event that kills or removes biota, freeing substrates and resources for new colonization and growth. In this sense, flood scour would be a disturbance, occurring over hours or weeks, which are brief and pulsative when scaled to the generation times (weeks, months, or years) of the biota affected. Disturbance resets biological communities to earlier successional states, favoring different types of species over those that dominate during periods of stability. Stress is the reduction in physiological, behavioral, demographic, or ecological performances of individual organisms brought about by suboptimal environmental conditions. Stress can be of any duration, brief or prolonged, and is more specifically defined by tolerances of individual taxa. We follow Lake (2011) in defining drought as a period of prolonged stress imposed on organisms by low river discharge. Drought waxes and wanes in a gradual, ramped fashion, and multi-year droughts can span multiple many generations of common riverine taxa (Lake, 2011). In contrast, flood disturbances (like landslides, fires, or wave-bashing) are pulsed periods of general biomass removal: abrupt and brief relative to life histories of the dominant (or foundational, sensu Dayton, 1971) biota affected.

In this article, we consider how hydrologic disturbance and periods of stress affect biota, and therefore food webs, in rivers under Mediterranean seasonality. We first discuss how Mediterranean seasonality in climate and hydrology affects energy sources from terrestrial and aquatic photoautotrophs: the microbes, fungi, algae, and protists that make up biofilms on river substrates; and the larger turfs or mats of mosses, macroalgae, or macrophytes that occur in less scoured or more sunlit portions of the drainage network. We then discuss how seasonal changes affect the abundance and abilities of primary consumers to feed on these energy sources, and the consequences for secondary consumers that prey on animals. We focus primarily on one case history: how these groups interact under the flood-drought seasonality of the Eel River of Northern California, USA. We briefly highlight some studies illustrating how fluxes of algae or insects can link river food webs longitudinally down rivers, or mediate exchange between channels and their upland watersheds, and or coastal marine environments. We conclude by considering how a few of the pervasive human impacts on watersheds and altered hydrology in Mediterranean rivers affect food webs and the biota and ecosystem services they sustain.

Food webs, food chains, and top-down and bottom-up controls

> "All models are wrong; some are useful."
> G.E. Box 1979

Before exploring how food webs respond to Mediterranean seasonality in rivers, we would like to clarify what "food web" means to us. Food webs are

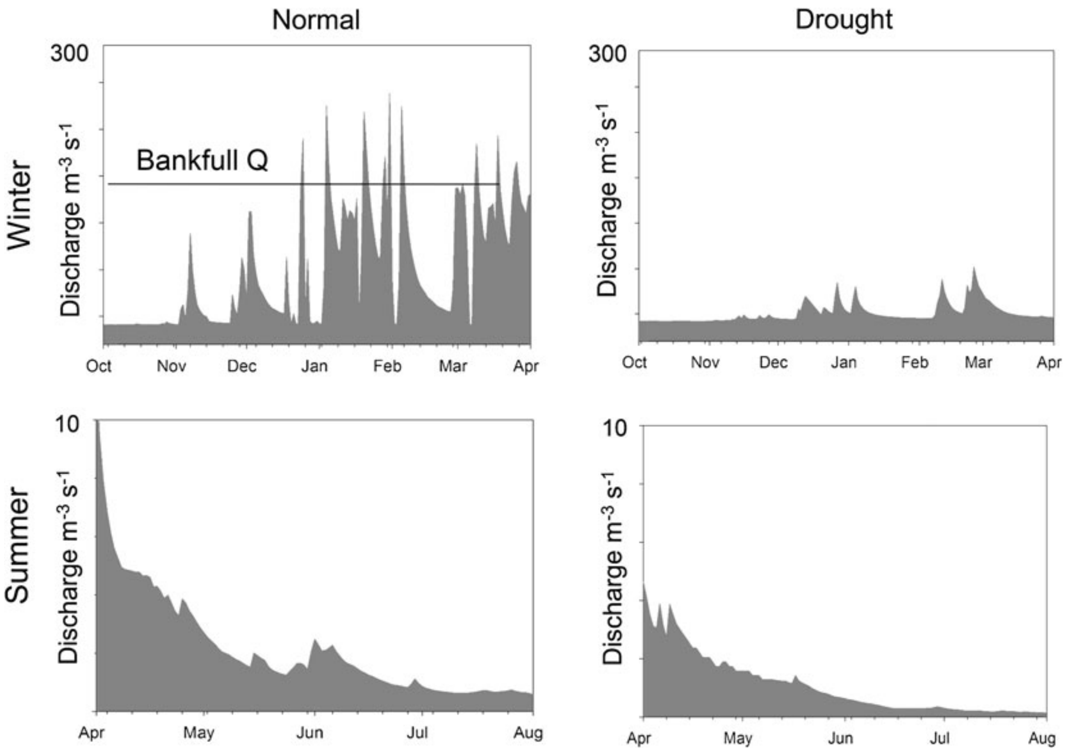

Fig. 1 Winter (*top*) and summer (*bottom*) hydrographs (note Y-scale change) from the South Fork Eel River under normal Mediterranean seasonality (*left*) and during flood-free drought (*right*). During normal wet winters, bed-scouring floods occur at least once. Bed scour occurs in mixed-grain sized gravel bedded channels when discharge exceeds bankfull level (estimated as peak levels reached by floods with >1.5-year recurrence (Leopold et al., 1964)). During drought winters, no bed scour occurs. During normal summers, discharge drops slowly, but stable base flows are maintained. During more severe drought summers (which may be anthropogenic: due to human land use and water extraction, as well as climatic: lack of precipitation), discharge drops to much lower levels, which impose stressful temperatures and reduce habitat for riverine biota

arbitrarily resolved and delimited depictions of some of the feeding interactions of coexisting organisms and resources. Like all models (Box, 1979), no food web accurately represents nature, but some models can be useful. If the goal is to predict how current and future environmental regimes will affect distributions and abundances of biota and consequences for ecosystems, food webs that focus on strong interactions are useful. Strong interactions are those that potentially control flows of energy or materials to consumers ("bottom-up" pathways), or are chains of "top-down" interactions through which consumers potentially limit the biomass of key taxa (dominant space holders or primary producers, top predators, or taxa of management concern) (Paine, 1980; Power et al., 1995). Interaction strength is challenging to measure in the field, as it varies with densities of the interacting organisms, the duration of the period of observation, and the mathematical formula of the index used (Berlow et al., 1999). More fundamentally, species interactions change in strength, and sometimes in sign, as participating organisms encounter different environmental conditions over space and time (Menge et al., 1994; Power et al., 1996).

To forecast real world responses of food webs to change, we must understand the context and context dependencies of species interactions. Where are interacting species or food webs located along gradients of productivity, stress, heterogeneity, or disturbance? When are they assembling or functioning with respect to seasonality and time elapsed as important events like disturbances that reset ecosystems to early stages of successional recovery? Why do these spatial or temporal contexts matter? Rivers, particularly rivers under Mediterranean seasonality, offer iterated opportunities to study, systematically, how different spatial and temporal contexts affect the species numbers, performances, and interactions that structure food webs.

Carbon sources to river food webs: changes down the channel network

Energy can be supplied to river food webs from terrestrial sources (mainly as terrestrial plant detritus and terrestrial insects) and from aquatic primary production. The major primary producers in Mediterranean streams are mosses and vascular plants, green algae (Chlorophyta), blue green algae or cyanobacteria (Cyanophyta), and diatoms (Bacillariophyta). Diatoms generally have the highest nutritional quality, in terms of lipids and polyunsaturated fatty acids (PUFAs), which are necessary to but not synthesized by most animals (Brett et al., 2009). Different functional groups of algae (and other aquatic primary producers) are favored as conditions change down drainage networks.

Algae need both light and time (=substrate stability) to grow. Terrestrial detrital carbon sources are thought to dominate stream food web energy sources in the upper portions of drainages, where channels are narrow and darkly shaded. Terrestrial detritus can also preclude algal growth if it accumulates to cover rocky substrates with organic-rich silts or soft, unstable litter. This occurs following mild (flood-free) winters in the Fuirosos, an intermittent stream draining 16 km^2 with forested riparian areas in the northeast Iberian Peninsula of Spain (Acuña et al., 2005). Detritus in this system is flushed by winter floods, but it reaccumulates as flows drop over the spring and throughout the subsequent stable, low flow interflood periods, particularly in runs and pools (Sabater et al., 2006; Acuña et al., 2007). Algal sources are more important to food webs in these northeastern Spanish streams after wet years when severe winter floods have exported accumulated detritus and organic matter-rich sediments (Acuña et al., 2007). When less of the photosynthetic periphytic community is covered by this stored organic matter, gross primary production increases. Food webs respond to the changing standing stocks of detritus versus algal production in this system under different seasonal regimes.

The role of attached algae in stream food webs is commonly underestimated because scant (macroscopically undetectable) standing crops can support relatively large biomasses of consumers in “inverted pyramids” of trophic level biomass. Consequently, the biomass-specific productivity of diatoms makes them “hidden carbon” whose importance is sometimes revealed only when experimentalists remove access by grazers to algal substrates (Lamberti & Resh, 1983; Power, 1984). Using his own surveys as well as 26 published studies of others, Finlay (2001) analyzed longitudinal trends in δ^{13}C signatures of detritus, algae, dissolved organic carbon (DOC), and various guilds of consumers in food webs in 70 sites in temperate and boreal channels (some but not all Mediterranean). Over the 0.2–4,000 km^2 range of drainage areas surveyed, terrestrial litter (mostly leaves) in streams retained a δ^{13}C signal of *ca.* −28. This flat trend from headwaters to lowland mainstems makes sense if terrestrial vegetation draws carbon from a well-mixed “air shed,” and if within-channel fractionation processes that might change downstream are not important. Algae, in contrast, showed a strong longitudinal trend in δ^{13}C from values in headwaters that were very depleted relative to terrestrial carbon to much more enriched values in large mainstems (Finlay, 2001; Finlay et al., 2011). Finlay hypothesized that headwater algae (sometimes estimated by the isotopic signatures of grazers that ate them) were more depleted in ^{13}C than in terrestrial carbon for two possible reasons. First, much of the DOC that supplied carbon to headwater algae came from very ^{13}C-depleted CO_2 from bacterial respiration in groundwater. Second, the sparse algae in headwater streams would be light-(energy) limited, rather than limited by carbon supply. As a result, algal cells could discriminate in favor of the lighter ^{12}C isotope, which diffuses through physical boundary layers around cell walls more quickly. Moreover, once inside the algal cell, ^{12}C has a higher affinity than ^{13}C for the photosynthetic RUBISCO enzyme. Downstream, as reaches became wider and more sunlit, algal standing crops and productivity increased, and cells became increasingly carbon-limited. As a result, algae had to incorporate more of the less preferred ^{13}C isotope, and their ^{13}C became increasingly enriched, particularly in pool habitats with slower water flow (Finlay et al., 1999). By the time channels drained 100 km^2 or more, algae were much more ^{13}C enriched than terrestrially derived carbon (heavier δ^{13}C). This trend continued over the range of rivers surveyed by Finlay, although he has predicted (personal communication) that in very large channels draining wetland floodplains, subsurface bacterial respiration may once again deplete the δ^{13}C signature in periphyton, consumers, and detritus supplied by this source.

Carbon signatures of stream consumers in Finlay's survey indicated their dietary sources of energy. Carbon signatures of shredders, invertebrates that consume coarse particulate material, typically terrestrial detritus, also hovered around a δ^{13}C of −28, as expected for organisms known to eat terrestrial leaves. But, every other consumer showed significant contribution of algal carbon to their diets over much of the gradient. Collectors, filterers, and invertebrate predators were built of terrestrial carbon only in the smallest headwaters, and took on an increasingly algal signal downstream from *ca* 50 km^2 (although variability in data and overlap between the terrestrial and algal δ^{13}C at channels draining 10–50 km^2 made detection of thresholds for diet switching impossible to determine). Fish predators seemed to have a strong contribution of algae to their diets throughout their ranges in this survey, as they did not occur in very small headwaters. Grazing invertebrates, strikingly, had algal carbon signatures even in the smallest headwater streams in this survey, streams draining <1 km^2 where algae were difficult or impossible to sample or even feel (rocks were not slippery), and stream ecologists would typically assume that algae were excluded by extreme light limitation.

Finlay's (2001) δ^{13}C studies in small headwater streams (0.1–10 km^2 watershed area) of the South Fork Eel River in coastal California (an old-growth forested Mediterranean river system) were supported by subsequent findings of McNeely et al. (2007), who also found that the grazing stone-cased caddisflies *Glossosoma penitum* were built almost entirely of algal carbon as high in the drainage network as they could be collected, even in small channels draining <1 km^2. At this elevation (where channels drained 0.56–10 km^2), other primary consumers like midges and mayflies, and the predators that fed upon them, had δ^{13}C signatures indicating terrestrial carbon energy sources. Experimental removal of *Glossosoma* from replicated pools of a small dark tributary draining 2.6 km^2 shifted the δ^{13}C carbon signal of mayflies toward values indicating increased algal feeding (McNeely et al., 2007). By excluding the dominant algivore for a month, McNeely was able to move some of the heavier algal δ^{13}C signature into primary consumers like mayfly nymphs that were vulnerable to predators (juvenile steelhead, *Oncorhynchus mykiss* and giant salamanders, *Dicamptodon ensatus*), but the signature did not appear in these or in invertebrate stonefly predators in the habitat. It is possible that more prolonged access to algae that would follow a longer term experiment, or the sort of extinction of *Glossosoma* by microsporidian epidemics documented by Kohler and Wiley (1992) in Michigan streams, would shift upstream in the drainage network altering the threshold at which vulnerable grazers, hence predators, could derive their carbon from high quality algal sources. In the headwaters of the South Fork Eel River, all non-armored members of the channel food web: primary consumers like mayfly nymphs, chironomid, and psphenid larvae; invertebrate predators like stoneflies, odonates, and helgrammites; and vertebrate predators like salamanders and fish shift from terrestrial detrital to algal carbon sources where the channels drain >10 km^2 (Finlay, 2001; McNeely & Power, 2007; McNeely et al., 2007). Shifts to algal energy sources would likely occur further upstream in basins lacking the dense forest shading of this watershed (Minshall, 1978).

In the forested upper South Fork Eel, channels that drain 100 km^2 or more are wide enough so that solar radiation reaches the channel surface for 6–8 h or more per day during the summer growing season. With this amount of solar radiation, primary production increases and large blooms of filamentous green macroalgae can proliferate. At this threshold, solar radiation is also sufficient to support a sharp increase in nitrogen fixation, both by free-living epilithic cyanobacteria (*Nostoc* spp., *Rivularia* sp.) and by epiphytic cyanobacteria (*Nostoc* spp., *Anabaena* sp.) and epiphytic and epilithic diatoms in the family Rhopalodiaceae, which contain nitrogen-fixing endosymbiotic cyanobacteria and are active nitrogen fixers. Because of the Mediterranean seasonality of flows, the wetted width of channels that drain >100 km^2 are much narrower than the winter active channel width. Therefore, riparian vegetation along the channels is often offset from the wetted surface by as much as 10–30 m during the biologically active summer low flow season. In addition, along this river many riparian trees (white alders, *Alnus rhombifolia*; big-leafed maples, *Acer macrophyllum*; Oregon ash, *Fraxinus latifolia*, willows, *Salix laevigata, S. lasiolepis*) retain their leaves during the summer and shed them in fall or winter. This flow seasonality and leaf phenology minimizes the access of riverine consumers to terrestrial litter or detritus. Litter is stored along dry rock bars along the channel during the summer active season, and when leaves drop in the fall during cooling, darkening months, they may remain in channels only a short time before being swept downstream by winter floods. As in the Spanish streams studied by Acuña et al. (2005), detritivores (in the Eel, dominated by the shredding caddisflies *Psychoglypha, Lepidostoma* spp., *Heteroplectron*) become abundant and conspicuous (large instars) during autumn, before flood scour. If winter flooding does not occur (during drought years), longer retention of terrestrial litter in deeper pools or behind flow obstacles (e.g., log jams, large bedrock, and boulders) would likely enhance its importance to the Eel River food web.

Vertical and longitudinal fluxes of algae and insects linking rivers to uplands and coastal marine ecosystems

While Mediterranean riparian phenology and flow patterns reduce the access of river consumers to terrestrial leaves, these patterns enhance the importance of algal production for terrestrial consumers. Algal energy is exported to upland consumers (spiders, beetles, lizards, birds, and bats) via insect emergence (Sabo & Power, 2002; Power et al., 2004), and when algae is stranded along shorelines during receding flows (Fig. 2). Algal stranding becomes particularly important downstream near the Eel estuary where low gradient channel bars widen. For example, as river stage dropped in late July 2011, a wide band of algae was stranded along the gravel-cobble shore of the Eel River just upstream of its transition from a river to a brackish estuarine system, near Ferndale CA (Fig. 2). We estimated the amount of filamentous green algae stranded along the river margin by measuring the widths (26–40 m, mean ± 1SE = 30.75 ± 3.3 m) of the deposited band and the dry mass harvested from 0.25 m^2 quadrats whose nearest edges were located 0.5, 1.5, 3.5, 7.5, and 15.5 m from the wetted river margin. There was no change in the thickness of stranded algae with distance from the wetted shoreline (mean ± 1SE = 440.8 ± 52.2 g dry mass m^{-2}, range = 342.4–636.4 g dry mass m^{-2}) (Holomuzki, Lowe & Power, unpublished data). These calculations yielded estimates of 13.7 kg of stranded filamentous green algae and associated epiphytic algae and microbes exported per m shoreline. Stranded algae are consumed by specialist algivores (tetrigid grasshoppers *Paratettix aztecus* and *P. mexicanus*) in which $\delta^{13}C$ signatures indicate that they derive 88–100% of their carbon from epilithic algae rather than terrestrial vegetation (Bastow et al., 2002), as well as dipteran larvae, which in turn feed shoreline predators (carabid and staphylinid beetles, gelastocorid bugs, lycosid spiders), and riparian birds, lizards, and frogs like the abundant Pacific tree toad (*Pseudacris regilla*).

Export from rivers may be even more important in feeding truly arid watersheds. For example, Jackson and Fisher (1986) estimated that 97% of the aquatic insect emergence (22.4 grams carbon m^{-2} y^{-1}) was exported to the watershed of Sycamore Creek, a Sonoran Desert stream, where it fed consumers including ants, birds, and bats. In temperate and Mediterranean streams, terrestrial insects can feed river consumers, particularly where terrestrial vegetation canopy overhangs the wetted channel surface. In the Eel River, this would be true during the biologically active summer in channels draining <10 km^2, about 30% of the total wetted area in the 9,540 km^2 basin during summer baseflow.

Parasitic nematomorphs (horsehair worms which manipulate their terrestrial cricket or beetle hosts to drown themselves) drive terrestrial insects to crawl or drop into Japanese streams, providing a highly significant energy subsidy for fish that indirectly relieves benthic grazing invertebrates from fish predation, reducing algal biomass (Sato et al., 2011). These fascinating parasite-mediated energy flows and trophic cascades are likely to occur around Mediterranean streams as well, where nematomorphs are common.

Fluxes of algae or invertebrates also link river habitats longitudinally. Carbon signatures of hydropsychid caddisflies and simuliid black flies in rapidly flowing sheet wash habitats over boulders indicate that they are collecting sloughed algal particles grown upstream in pools (Finlay et al., 1999). Algal production in shallow pools in the South Fork of the Eel River support invertebrate prey, which emigrate and can be preyed upon by juvenile steelhead trout in riffle habitats. These juvenile trout in turn provide prey for large cannibalistic rainbow trout living in deeper pools (Finlay et al., 2002). *Cladophora* sloughing and transport from upstream habitats to downstream habitats in the Eel can send organic matter subsidies and resident insects downstream, potentially all the

Fig. 2 Export by stranding of filamentous green algae along the Eel River just upstream from its estuary near the Fernbridge, Humboldt County, CA (Latitude: 40°36′58″N; Longitude: 124°12′04″W). *Left* Freshly stranded algae. *Lower right* desiccated "algal paper" with 0.25 m^{-2} plots sampled along a river's edge to upland transect to quantify exported dry biomass (see text). Stranded algae feeds terrestrial primary consumers such as specialist tetrigid grasshoppers and stratiomyid and ephydrid flies, which in turn are eaten by Pacific tree frogs (*Pseudacris* (*Hyla*) *regilla*), wolf spiders, carabid beetles, and other predators (*upper right*)

way to the sea. Because the Eel is a short, steep river with stony substrates almost all the way to its mouth, attached filamentous and adnate epilithic algae flourish throughout most of its length and dominate summer energy inputs to the river food web. They also dominate exports of organic matter. Ng (2012) sampled Eel River organic matter export where the river meets its estuary at Ferndale by placing nets place across the entire cross-section at low flow, and subsampling and normalizing to proportion discharge sampled at higher flows, when the cross-section could not be waded. She found that copious amounts of filamentous green algae were exported during summer and fall 2011. Of 8 monthly surveys (July–November 24) only the last on November 24 contained significant amounts of terrestrial litter (Ng, 2012).

River export of high quality algal food to the estuary may nutritionally important to primary consumers in the estuary. Estuarine or intertidal benthic amphipods and isopods strongly prefer filamentous river algae over local marine green algae (*Ulva* and *Enteromorphora*) that dominate primary producer biomass in the Eel estuarine and intertidal habitats (Ng, 2012). If estuarine grazers rapidly consume this riverine algal flux, the subsidy would be "invisible carbon," important but easy to underestimate.

Disturbance and reassembly under Mediterranean seasonality: succession in primary producers and responses by primary consumers

Down drainage networks, algae and other primary producers grow more rapidly as channel beds receive more sunlight, but their accrual is more frequently interrupted by bed mobilization. Growths attached to dark but stable, rock, or boulder bedded headwaters experience complete bed mobilization only rarely, during debris flows or earthquakes that may recur at given upstream reaches, perhaps less than once every several millenia. In mid-sized tributaries draining 10–100 km^2, large portions of the bedrock and boulder bed stay fixed, as mobile sand, gravel, and small cobbles sediments move around them during floods (Yager et al., 2007). In larger mainstreams (draining >100 km^2), much (70–100%) of the mixed gravel, cobble, and pebble bed mobilizes, typically several times per winter during wet years, although not during drought winters. Channel-forming ("bankfull") flows typically recur every 1–2 years in such channels (Leopold et al., 1964). Further downstream in low gradient lowland rivers, fine sand, or silt substrates may be kept in constant motion, eliminating stable substrates for attached producers, and suspending enough material to curtail light penetration.

With sufficient light and duration of substrate stability (e.g., on bedrock, boulder, or large cobble substrates during summer in Mediterranean channels), algae undergo a pronounced seasonal succession, defined by Tansley (1935) as "…a sequence of phases…subject to ascertainable laws." Throughout the Eel's entire 9,540 km^2 drainage area, algae and cyanobacteria in channels draining >100 km^2 undergo similar successional sequences. The similarity of algal taxa and phenology throughout the basin may be due to the Eel's relatively short, steep drainage relative to its drainage area. It remains gravel–pebble–cobble bedded until a short distance, only 1–2 km, from its mouth (Sommerfield et al., 2007).

Following scouring winter floods, relatively adnate cyanobacteria that have resisted scour persist on larger bedrock and boulder substrates—these include colored skins made of basal cells of filamentous green algae, and adnate diatoms and cyanobacteria: the nitrogen-fixing *Rivularia* and *Nostoc* spp., as well as non-heterocystic epilithic cyanobacteria (*Xenococcus*, *Oscillatoria*). Tough, strongly attached aquatic mosses also survive the winter, although they are usually sheared short.

As the subsiding spring flow continues to warm and clear, skins of epilithic diatoms thicken on larger (bedrock, boulder, cobble) rock substrates, making them slippery and variously colored. As the water continues to warm and clear (mid-spring-early summer), cyanobacteria and diatoms continue to proliferate, and filamentous green algae first become macroscopically conspicuous. By April and May, the first conspicuous attached filamentous green algae appear on bedrock, boulder, and larger cobble substrates. At this time, *Zygnema* is often dominant, but rapidly overgrown by new growths of bright green *Cladophora glomerata* (L.) Kutz. *Cladophora* proliferates at this time to lengths of several (up to 6–8) m in favorable sites. These green algae can proliferate either by mitotic continuous vegetative cell division or by mitotic episodic cloning events (Lowe, 2011). *Cladophora*, an important alga in the Eel River system, exhibits a perennial population on stable substrates, enhanced by annual populations of young filaments that settle in midsummer on smaller substrates that are stable only at low base flow (Power, 1992). Drifting *Cladophora* filaments may also reattach to new substrata and grow. During the long periods of stable flow without scouring events in rivers under a Mediterranean flow regime *Cladophora* can grow to massive proportions with long filamentous streamers occupying large areas of the stream bed (Biggs, 1996; Power et al., 2009). These large growths have both structural and trophic importances in the river. Structurally, *Cladophora* provides habitat for many stream invertebrates (Dudley et al., 1986), including the retreat weaving midge, *Pseudochironomus richardsonii* Malloch (Power, 1991; Gresens, 1997; Furey et al., 2012). The chemistry and structure of the cell wall of *Cladophora* indirectly results in its trophic importance. The coarse cell wall is composed of a thick layer of cellulose overlain with a thin layer of chitin (Smith, 1950). This wall provides a stable substratum for the accommodation of epiphytic cyanobacteria and diatoms. *Cladophora* can be thickly overgrown with epiphytes as it proliferates and matures (Burkholder & Wetzel, 1990; Dodds, 1991; Peterson & Grimm, 1992). Thus *Cladophora*, though of marginal nutritional value itself, provides an important substratum for the growth of nutritionally important algae such as nitrogen-fixing diatoms in the genera *Rhopalodia* and *Epithemia* (Hill & Knight, 1988; Power et al., 2009). In Mediterranean streams, massive growths of *Cladophora* hugely expand benthic surface area and habitat for epiphytes.

Epiphytic assemblages on *Cladophora* also undergo succession, initiated when diatoms and other small organisms colonize the surfaces of the macroalgal host. As these epiphytes accumulate, *Cladophora* loses its bright green color and turns yellow by early July, first in areas of slack flow. The yellow color of *Cladophora* results from the first successional wave of epiphytes, dominated by *Cocconeis placentula* and *C. pediculus*. Other taxa (*Rhoiciosphenia* spp., *Gomphonema* spp.) are also common in these early successional epiphyte assemblages. *Cocconeis* glues its concave valve directly to the convex *Cladophora* host surface; *Gomphonema* and *Rhoiciosphenia* are often attached to this same surface by gelatinous stalks. By and large, these early successional epiphytes cover *Cladophora* as monolayer, conferring a yellow color (Power et al., 2009).

By late July, early August, the *Cladophora* proliferations deepen in color to a rusty red or brown. This color change reflects thicker layers, sometimes 5–10 cells deep, of carotenoid bearing epiphytic diatoms in the family Rhopalodiacea: *Epithemia turgida*, *E. sorex, E. adnata*, and *Rhopalodia gibba* (Power et al., 2009; Furey et al., 2012). All of these Rhopalodiacea contain nitrogen-fixing cyanobacterial endosymbionts and are active nitrogen fixers (Floener & Bothe, 1980; DeYoe et al., 1992). Assemblages rich in Rhopalodiacea can load biologically fixed nitrogen into the generally nitrogen-limited Eel River ecosystem at an aerial rate up to 60-fold higher than occurs before their proliferation (J. Welter et al., personal communication).

Toward midsummer, *Cladophora* fronds detach and float as mats that cover large portions of pool surfaces along slack-water margins. As they drift downstream these mats also hang up on emergent rocks and other substrates like logs that protrude from the river surface. Temperatures in mats can be 8°C warmer than those in the water column during midday, and oxygen is severely drawn down at dawn, when animals must compete with algal respiration for oxygen. The floating mats become “hot spots” for midges (Chironomidae) with hemoglobin, predatory hydrophilid beetle larvae with anal respiratory siphons, thin ceratopogonid larvae, and other taxa with adaptations that allow them to withstand these diel extremes of temperature and oxygen. Rates of emergence of chironomids and ceratopogonids are higher from these mats, which appear to function both as floating food-rich incubators for larvae and as partial refuges from river predators. Besides the extremely small ceratopogonids, hydrophilid beetles (*Enochrus* sp.) are the only common predator observed in mats. While these beetles eat midges, their feeding rates are fairly slow (a hydrophilid larva takes 7–15 min to consume one midge) (M.E. Power, personal observations).

Atmospheric nitrogen fixed by cyanobacteria could be used to synthesize toxins or proteins. The responses of common vertebrate (Kupferberg et al., 1994) and invertebrate grazers (Power et al., 2009; Furey et al., 2012) to *Epithemia*-covered *Cladophora* suggests that these assemblages are producing high quality foods, rather than toxins. Rusty-colored *Cladophora* assemblages are preferentially and rapidly consumed, and support higher growth (Kupferberg et al., 1994) and rates of emergence (Power et al., 2009) by their grazers. In contrast, the detailed observations of Furey et al. (2012) suggested that the midge *Pseudochironomus richardsoni*, (and by inference, other small invertebrate grazers) are less able to detach and remove *Cocconeis* and other adnate, low profile diatoms that dominate early successional (“yellow”) epiphytic assemblages.

Cladophora hosts can sometimes outgrow earlier successional epiphytic diatoms, sending clean green filaments growing out from heavily encrusted proliferations. However, by late summer, *Cladophora* epiphyte assemblages are either grazed back or detaching, floating, or sinking short distances downstream, and senescing, probably as a result of a combination of temperature stress and nutrient (flow) limitation. At this time, algal material and the detritus it generates can be repeatedly regrazed, making its way through guts of organisms several times, as feces of snails, tadpoles, and grazing insects accumulate on the river bed in depositional areas. During these later summer periods, the last successional stages of green algae proliferate, which are dominated by filamentous green taxa like *Mougeotia* and *Spirogyra* that secrete slippery extracellular mucopolysaccharide. These slimy Zygnematales remain free of epiphyte attachment in the Eel as well as in Oklahoma streams under continental seasonality (Power & Stewart, 1987). Mucopolysaccharides that deter epiphytization may simply reflect excretion of excess carbon by algae that become increasingly limited by nutrients like N or P, as flow and supplies subside during summer drought. However, this trait prevents the host from suffering the fate of epiphytized Cladophorales: blockage of light and nutrients by epiphytes and increased consumption by grazers seeking the nutrients supplied by the diatom biofilms, as do invertebrates foraging on the nutritional microbial food source that coats the surfaces of dead leaves in streams (Wallace & Webster, 1996).

Flood disturbance and energy sources to food webs have a somewhat similar interaction in mid-order streams with forested riparian areas in the northeast Iberian Peninsula of Spain. Algal sources are more important to food webs after wet years with severe winter floods. Winter floods remove accumulated detritus and organic matter-rich sediments (Acuña et al., 2007). With lower storage of organic matter (% cover), overall detritivore biomass is lowered, and gross primary production is enhanced because less of the photosynthetic periphytic community is covered by stored organic matter (Acuña et al., 2005). Energy flow to detritivores from organic matter from riparian habitats is more important following mild winters. During such years, detritus can be exported during spates, but it reaccumulates during spring flow reductions and over the subsequent stable, low flow interflood periods, particularly in runs and pools (Sabater et al., 2006; Acuña et al., 2007). Abundance of shredders and collector-gatherer macroinvertebrates is high in these habitats during these periods (Acuña et al., 2007), as is heterotroph (bacteria and fungi) abundance, microbial production, and DOC availability (Sabater et al., 2006). Extended periods of low flows tip the major energy flow paths toward the "brown" (sensu Kaspari & Yanoviak, 2009) food chains, in which decay of organic matter feeds detritivores (Dance et al., 1979).

However, the relative dominance of a feeding group, and hence energy pathways through consumers, depends in part on seasonal flow extremes. In dry years, flow persistence largely determines trophic organization. For example, in the permanent Riera Major, an alder-shaded, 2nd-order stream in northeast Spain, the shredding caddisfly *Halesus radiatus* is dominant in autumn, and high shredder biomass is characteristic year round. Still, from June to August when discharge is low and stable, collector-gatherer and predator abundance increases, as does the periphytic rhodophyte *Hildenbrandia rivularis* and the chlorophyte *Cladophora glomerata* (Muñoz, 2003). In contrast, the nearby intermittent La Solana, a 2nd-order tributary of the Ter River, Spain, typically dries in summer (Muñoz, 2003). Shredding detritivores dominate only in autumn, corresponding with riparian-tree (*Fagus sylvatica*, *Acer* spp.) leaf fall. These taxa significantly decline thereafter with decreases in discharge and benthic organic matter (Muñoz, 2003). Dry conditions also affect allochthonous inputs from the surrounding terrestrial landscape. Drought has accelerated the loss of riparian trees (e.g., especially *Salix alba*) along the Ebro River, Spain, thereby decreasing overall terrestrial detrital subsidies and total carbon supply to the system (González et al., 2012). It is not known how this loss in subsidy affects consumers, but presumably it will decrease shredder abundance and trophic complexity.

Flood effects on food chain length in Mediterranean rivers

After river beds are scoured severely by mobilized sediments, rock-bound organisms (attached algae or mosses, sessile invertebrates, and those with limited mobility) that cannot escape are killed, damaged, or removed. Mobile, strongly swimming fauna, on the other hand, are slightly displaced and diluted as the flooding river expands, but they generally suffer little or no direct mortality from floods. Large fish, for example, can swim above the mobilized bed and may take refuge from high flow in quiet backwaters, in water-filled pore spaces in coarse ("freestone") beds, or up smaller tributaries. Because most aquatic predators are gape-limited, larger organisms tend to occupy higher trophic position. Parasites and pathogens that feed on aquatic predators in food webs would violate this generalization, but their trophic effects remain poorly known in rivers. Larger, strongly swimming organisms at higher trophic positions are likely to persist through flood disturbances that kill or displace most of the immobile or smaller biota at lower trophic positions (Power et al., 1995). For a brief window of time, these predators may experience reduced prey availability, but this can be more than offset if the flood pulse provides them with access to riparian (allochthonous) habitat and prey like terrestrial insects (Junk et al., 1989).

The flood disturbance can also rejuvenate in-channel food webs to early successional states with primary consumer invertebrate prey that are more edible for predators. As food webs recover from disturbance, early successional producer or prey species tend to have high dispersal and growth rates, rather than traits that protect them from consumers, like toxins, armor, or attached retreats (i.e., "r" vs "K" selected traits sensu MacArthur & Wilson, 1967). During these early stages of prey succession, surviving predators encounter relatively edible, vulnerable prey. Therefore, disturbances in rivers (and other habitats) often set the stage for food webs with longer food chains that link predators through primary consumers to plants. These chains operate both through bottom-up energy flow paths, and dynamically through top-down controls mediated through chains (or trophic cascades) in which predators can indirectly influence producer biomass by alternately suppressing and releasing populations at successively lower food chain positions. The length of food chains in webs can determine whether predators (or other focal taxa) get enough food supply to thrive, and also whether plants are protected to accumulate biomass or grazed down (leading to "green" or "barren" environmental states, respectively). We illustrate these general patterns with a case history from one Mediterranean river, the Eel River of the California North Coast (Fig. 3).

Following scouring winter floods, filamentous green algae (first *Zygnema*, followed by *Cladophora*) regenerate vegetatively from basal pads, and proliferate during the late spring and early summer as flows are subsiding, clearing, and warming. During this period, before animals have had a chance to recover numerically from flood scour and while their populations are still diluted by higher flows, *Cladophora* enjoys a window of time when there is only one functional trophic level in the channel, and in the mainstem, turfs of *Cladophora* can attain lengths of several meters during this time (late May–June). In middle (10–100 km^2) reaches where growth is slower, *Cladophora* attains lengths of 10–40 cm, but generally does not grow fast enough to outpace grazing by caddisflies, which also tend to be less severely reset in these relatively stable bouldery channels.

After the winter flood season, soft-bodied primary consumers (mayflies, midges), invertebrate predators (stoneflies, odonates, hemipterans, and coleopterans), and vertebrates (newts, salamanders, fish, and aquatic snakes and turtles) increase in density, initially by concentration in shrinking river habitat, and then by reproduction. Primary consumers can at this stage be controlled by predators, but this may or may not protect algae. For example, the common midge *Pseudochironomus richardsoni* weaves *Cladophora* (or other algae or detrital material) into a protective retreat or "tuft." Larger fish in the Eel do not seem to be able to recognize midges in tufts as prey, although invertebrate predators (lestid, gomphid, and aeshnid nymphs of Odonata) and young of the year roach (*Lavinia* (*Hesperoleucas*) *symmetricus*) and stickleback (*Gasterosteus aculeatus aculeatus*) do, and prey on them (Power, 1990; Power et al., 1992). Predation by these larger predators on small predators sets up a four-level food chain (sensu Fretwell, 1977) in which *Pseudochironomus* are released and infest *Cladophora*. While *Pseudochironomus* ingests mostly epiphytic diatoms harvested from *Cladophora* surfaces (Power et al., 2009; Furey et al., 2012), the midges activities break the macroalga into short, non-viable segments, so they reduce *Cladophora* biomass to prostrate, knotted remnants only 1–2 cm in height. These changes occur in the open river in water deeper than 20–30 cm where larger fishes have densities of 2–3 individuals m^{-2} (and aggregate in higher densities around *Cladophora* turfs on boulders). In summers of 1989 and 1997, following flood winters, *Cladophora* was significantly reduced in experimental enclosures with steelhead and adult roach enclosed at density of 10 (1989) or 2 (1997) individuals. The same change was observed in *Cladophora* albeit in the open river. In fish-free exclosures, small predators (especially lestid nymphs and young of the year roach and stickleback) proliferated and exterminated *Pseudochironomus*, releasing algae from grazing. Under this three-level food chain, *Cladophora* biomass persists but becomes overgrown with nitrogen-fixing cyanobacteria (*Nostoc* spp.) and *Epithemia* spp. As predicted by Hairston et al. (1960) and Fretwell (1977), algae in exclosures that were unlimited by grazers became limited by resources, so the taxa that could fix the limiting nutrient (nitrogen) prevailed.

Following scouring winter floods of 1993, June spates exported *Cladophora* after it had started to grow. The alga did not recover during the summer to levels that produced extensive floating mats. Perhaps for this reason, *Pseudochironomus* was relatively uncommon that summer. The larger fish in enclosures were able to suppress all of the key algal grazers, and maintained a three-level food chain in which some algae (particularly clouds of loosely attached diatoms dominated by *Melosira* and *Cymbella*) proliferated. This year pointed to the importance of the predator-specific defense of *Pseudochironomus* in 1989 in placing larger fish at the fourth trophic level during more normal Mediterranean years with flooding restricted to the winter. Fish were dynamically linked to algae through four trophic levels in 1997 as well, but *Gumaga* rather than *Pseudochironomus* may have mediated this effect through mechanisms that remain obscure. In both years, most invertebrates in fish guts were herbivorous, so diet analysis alone would have suggested that fish should have "protected" algae. This and other experimental analyses of food chains (Paine, 1980; Spiller & Schoener, 1996) have shown that "diet does not predict dynamics" (top-down and bottom-up pathways connecting the same plant biomass to the same predator in webs can vary in length).

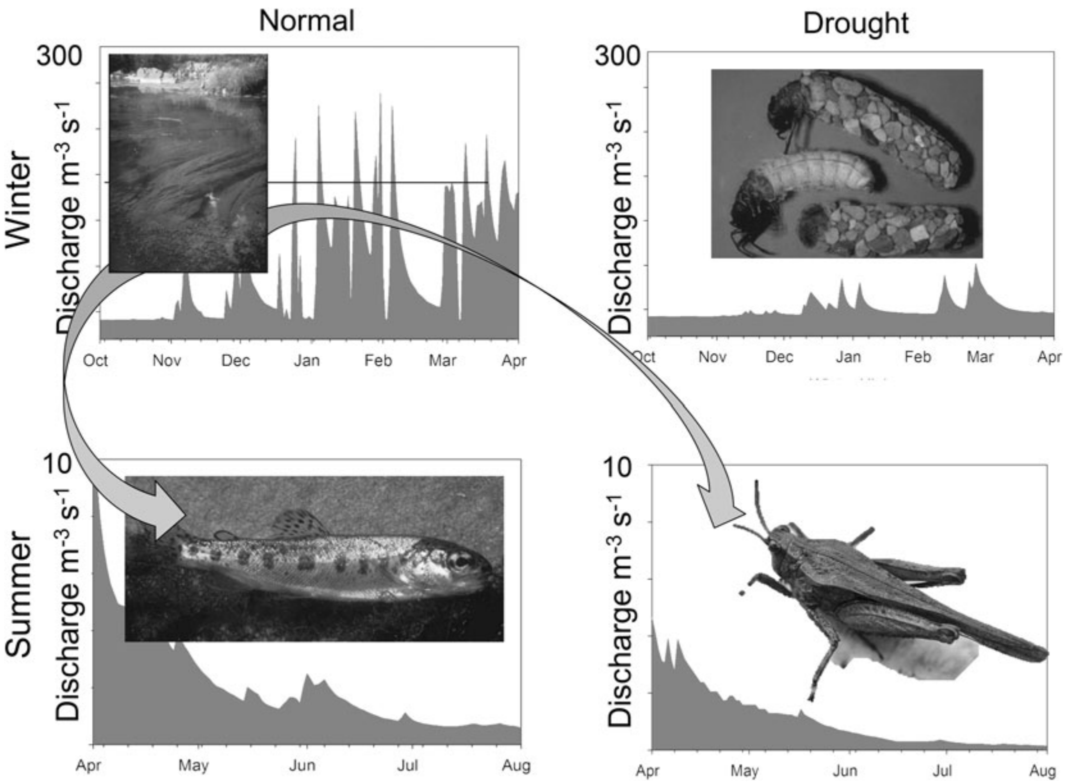

Fig. 3 During wet winters, scouring floods kill or export predator-resistant grazers (e.g., the caddisfly *Dicosmoecus gilvipes* in the Eel River) and large *Cladophora* blooms are released to proliferate the following spring and summer. The fate of this large algal biomass depends on the summer hydrograph. If sufficient stable base flow is maintained during summer (*lower left panel*), algal blooms sustain early successional grazers like mayflies and free-living midges that in turn feed invertebrate predators (e.g., lestid damselflies) and vertebrates (e.g., juvenile steelhead). If summer base flows fall rapidly to low levels, due to severe drought or water extraction, floating mats of senescent algae and stranding may route much of the energy to terrestrial consumers (Fig. 2). Following drought winters (*upper right panel*), dense populations of *Dicosmoecus* persist and graze back *Cladophora*, so little algal accrual occurs. Food webs the following summer have only two functional trophic levels, culminating in this armored, largely invulnerable grazer. Following drought winters, fish exert no top-down influence on algae. Algal productivity (which can remain high at low biomass) is probably largely routed to terrestrial ecosystems when *Dicosmoecus* emerge in late summer and fall

Following two drought winters (1990 and 1991), the story changed. Large fish had no dynamic impact on algae in experimental enclosures. Algae in both enclosures and exclosures collapsed after 3–4 weeks (Wootton et al., 1996; Power et al., 2008). Similarly, algae appear grazer-limited in artificially regulated channels where dams or diversions eliminate scour, setting the stage for food chains with predator-resistant primary consumers and only two functional trophic levels (Power, 1992; Power et al., 1996; Parker et al., 2002) and see below for examples from other Mediterranean rivers. During 1989, two regulated channels (one diversion, one dam release stream) in northern California were surveyed, along with four free-flowing rivers that experienced natural winter bed scour (Power, 1992). In the regulated channels, the grazer guild was dominated by armored, sessile, or retreat-building taxa that were relatively invulnerable to predators (*Petrophila* spp., *Tinodes* sp., hydropsychid caddisflies). Predatory invertebrates and vertebrates including juvenile salmonids were sparse in these two regulated channels, despite the presence of a hatchery on one study reach that drained a dam. In contrast, grazer guilds in four free-flowing river reaches were dominated by soft-bodied, epibenthic mobile grazers like mayfly nymphs, and higher densities of predators were observed. One interpretation is that lack of disturbance in regulated channels (also observed in unregulated channels during drought) allows slower growing defended (armored or sessile) taxa to dominate the food web, rendering top-down control by predators ineffectual.

Food web changes under external anthropogenic forcing

Humans have subtracted water, native biota, wood (living and logs), gravel, structural complexity, and natural disturbance (as described above) from rivers and their riparian zones, and added heat (by water extraction and reduction of riparian shade), excessive loads of nutrients and fine sediments, toxins, and non-native biota (Kupferberg et al., 2009) or genotypes (McClure et al., 2008). All of these activities affect food webs. Such activities rarely occur in isolation, and negative impacts of compounded perturbations can be highly synergistic (Paine et al., 1998). Here, we review only a few of the many documented human impacts on food web interactions in Mediterranean rivers.

Disruption of normal hydrologic regimes

Dams, levees, and diversions of rivers alter natural flood-drought hydrologic cycles in Mediterranean rivers, as well as the normal connection of rivers with their floodplains. Anthropogenic disruptions to flow patterns also affect the resource base and trophic-web structure of Mediterranean river food webs worldwide. Trophic structure in the River Ter, a regulated, anthropogenically disturbed Mediterranean river system in Spain, varies with dam proximity and discharge. Macrophytes are only common in the main stem near dams where annual fluctuations in discharge are controlled and terrestrial detrital subsidies are limited. But even here, benthic diatoms are the dominant primary producer, and grazers and filter-feeders predominate (Sabater et al., 1992). Downstream, shifts in local abundance of feeding groups are related to riparian conditions and availability of food type (Sabater et al., 1992). Likewise, decreased inputs of floodplain carbon following river regulation result in Australian rivers being dominated by algal production and grazing consumers (Robertson et al., 1999). Surface and groundwater abstraction from southwestern Australian rivers for agriculture, particularly during prolonged dry periods, can threaten habitat connectivity and hence foraging/migratory routes for endemic freshwater cobbler (catfish), *Tandanus bostocki*, a common predator of insects, crustaceans, mollusks, and small fish (Beatty et al., 2010). In addition, climate change-induced decreases in rainfall are predicted to amplify the effects of southwestern Australia's river-water extractions, thus further threatening present-day species assemblages and trophic relationships (Morrongiello et al., 2011).

Fine sediments

Excessive loading and storage of fine sediments is one of the most widespread forms of environmental degradation of Mediterranean river ecosystems from land use that removes or disturbs natural vegetation (forest clearing, road construction, agriculture, stock grazing). Water regulation or extraction exacerbates the problem by reducing flushing flows. Fine sediments fill and eliminate critical refugia for fish and mobile invertebrates from high and low flows, such as undercuts beneath banks and water-filled pore spaces in stony substrates (Waters, 1995). They also alter river prey assemblages and predator behavior during periods of stable base flow (Suttle et al., 2004).

As substrates become embedded with fine sediments, benthic invertebrate assemblages shift from epibenthic taxa (e.g., mayflies, stoneflies, free-living or thinly cased trichoptera, chironomids available as prey to fish) to infauna (oligochaetes, sphaeriid clams, elmid, ceratopogonid and tipulid larvae, etc.) inaccessible to fish that feed on epibenthic, surface, or water column prey. When juvenile steelhead trout were reared in a gravel bed Mediterranean river in 24 experimental in-stream channels with bed sediments ranging from 6–90 mm median diameter, and various amounts of sand were added to channels to create six levels of substrate embeddedness (0–100%), their growth (in length and mass) declined linearly with the proportion of sand in the channels substrate (Suttle et al., 2004). Food was less available to fish in more embedded channels, and they needed it more. As fine sediment flattened the bed and obliterated the natural cover—the microtopography offered by freestone cobbles and large pebbles—the steelhead became more active, and fought more with each other. In addition to having severely reduced growth, fish in heavily embedded channels suffered higher rates of mortality from fungal infections of wounds from fights (Suttle et al., 2004). These observations suggest that when land use (timber harvest, careless constructed roads) increases substrate embeddedness in gravel bed rivers, juvenile fish are less likely to rear successfully, and less likely to exert strong top-down impacts on food webs. Anadromous fish that enter the ocean at a small size are much less likely to survive to return and spawn (Bradford & Cabana, 1996). Steelhead trout are particularly vulnerable to this impact, as they spend two years (longer than other types of salmonids) rearing in freshwater rivers before entering the ocean.

Exotic vertebrate species

Trophic structure can be redefined when exotic fish (e.g., *Gambusia*, *Cyprinus*, *Carassius*) displace native fishes, as in rivers in NE Spain (Bernardo et al., 2003), SW Australia (Morgan & Beatty, 2004), Chile (Habit et al., 2006), and California (White & Harvey, 2001). Bullfrogs (*Rana catesbiana*) introduced to California from the Midwestern USA are a major contributor to the decline of native frogs and other native biota, exerting severe adverse effects both as tadpoles (Kupferberg, 1997) and as highly predatory adults (Hayes & Jennings, 1986). Kupferberg (1997) found that native tadpoles had poorer growth and survival in the presence of bullfrog tadpoles, even without evidence of food competition or harmful waterborne substances. She hypothesized that disturbance by the large bullfrog tadpoles might increase native tadpole encounters with predatory insects, such as naucorid bugs that abound during summer in the Eel River.

Eutrophication and heat

When water is extracted and riparian vegetation removed for agriculture or human settlement, loading of nutrients, pesticides and other xenochemicals, and heat to rivers increases. Experimental nutrient loading shifted food webs from heterotrophy to autotrophy, as observed in an Alaska stream (Peterson et al., 1985). The same response was observed in a forested Mediterranean stream, even under low to moderate light levels (Veraart et al., 2008, Sabater et al., 2011). Increases in algal densities increased grazer (*Ancylus* sp.) and detritivore (*Rheocricotopus* and Lumbriculidae) abundances (Sabater et al., 2005), which in turn affect species interactions. For example, changes in prey type and availability at lower trophic levels can cascade to alter trophic diversity (diet breadth) of top predators (e.g., otters) (Remonti et al., 2009).

Cryptic trophic relationships critical to maintaining system food web structure, such as parasite–host interactions, can be altered by human impacts on rivers (Lafferty et al., 2006). A number of pathogens and parasites of freshwater vertebrates appear to be expanding their geographic range, their prevalence, and their virulence in host–parasite interactions with greenhouse warming and eutrophication. Eutrophication that increases densities of snail secondary hosts for the parasitic trematode *Ribeiroia* sp. also increases limb deformities in their primary hosts, California tree frogs (*Pseudacris* (*Hyla*) *regilla*), whose tadpoles suffer damage to their limb buds when the trematodes attach. Deformed frogs are in turn more easily caught by wading birds, the parasite's definitive host (Johnson et al., 1999, Blaustein & Johnson, 2003).

Virulent infectious diseases, such as chytridiomycosis (Berger et al., 1998; Muths et al., 2003; Scherer et al., 2005; Wake & Vredenburg, 2008) appear to be spreading worldwide, independently of warming (Lips et al., 2008). Outcomes of interactions of hosts with pathogens and parasites, however, are particularly sensitive to temperature.

Vertebrates in Mediterranean rivers carry heavy loads of internal and external parasites, but their significance is just beginning to be appreciated (Kaûić et al., 1982; Kupferberg et al., 2009). An introduced Eurasian ectoparasitic copepod, *Lernaea cyprinacea*, commonly referred to as Anchor Worm, attacks native minnows, roach, and tadpoles in the Eel River. During an unusually warm summer, larvae and recent metamorphs of the river breeding foothill yellow-legged frog, *Rana boylii*, suffered much higher levels of *Lernaea* parasitism than previously observed, and exhibited the first leg deformities seen in 20 years of investigation of this river's food web (Kupferberg et al., 2009). The authors warn that such outbreaks associated with warm and dry conditions in the South Fork Eel River of northern California may foreshadow changes following climate change across the range of *R. boylii* in California.

Conclusion: the predictive mapping approach for forecasting the future of Mediterranean river ecosystems

In any river drainage, light, flow, substrate size and stability, offset of riparian vegetation, and other key environmental controls vary downstream, somewhat predictably, with marked change over conveniently short spatial scales in steep portions of the drainage network. In Mediterranean rivers, the seasonality of flow is more predictable than under other climates, with winter floods and summer drought. These partially predictable temporal and spatial changes in environmental factors can be used to probe the effects of environmental context on food webs and ecosystems. How do species performances and, consequently, their interactions with other species change down drainage networks, with downstream changes in conditions, energy sources, and food quality? Where in the landscape do functionally significant "regime changes" occur? It is particularly instructive to locate thresholds where changes in environmental factors correspond to changes in ecological regimes of local processes or interactions that control response variables of interest. Regimes change dramatically when food web or other ecosystem processes respond nonlinearly to environmental controls, triggering dramatic state changes in the outcomes of interactions of these processes. In this article, we have reviewed downstream changes in carbon sources fueling river consumers, how trophic fluxes may link rivers to their upland terrestrial watersheds and to coastal oceans, and the impact of floods, droughts, and human land use on Mediterranean river food web connections. As our understanding of the relationship between environmental boundaries or gradients and food web regime change grows, we should be better able to forecast the local and basin-wide consequences of changes in land use, climate, or biota (e.g., invasions, disease spread, or extinctions that change the strengths of interactions or food web membership) that lie ahead for Mediterranean rivers on all five continents where they occur.

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