Ecology and Management of the Spring Snowmelt Recession

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We present a conceptual model for the ecology of the spring snowmelt recession based on the natural flow regime that relates the quantifiable components of magnitude, timing, and rate of change to abiotic and biotic factors that govern riverine processes. We find that shifts in the magnitude of the recession largely affect abiotic channel conditions, whereas shifts in the timing of the snowmelt primarily affect biotic conditions. Shifts in the rate of change affect both abiotic and biotic conditions, creating the largest observed changes to the stream ecosystem. We discuss these components with regard to the success of riverine species in California's Mediterranean-montane environment. We then present two scenarios of change to the spring snowmelt recession—effects of flow regulation and climate warming—and discuss their potential implications for riverine ecology. Our conceptual model can help guide watershed stakeholders toward a better understanding of the impacts of changing spring recession conditions on stream ecosystems.

Keywords: stream ecology, Mediterranean-montane, climate change, regulated rivers, natural flow regime

Over the past decade, the natural flow regime paradigm (Poff et al. 1997) has garnered widespread study, discussion, and general acceptance in the scientific community as a guide for the conservation, restoration, and management of rivers (Marchetti and Moyle 2001, Arthington et al. 2006, Richter et al. 2006). However, one fundamental aspect of the natural flow regime is the spring snowmelt recession and its effect on both geomorphic and ecological stream processes, the importance of which has received little attention in both scientific study and resource management. In mountain regions, the spring snowmelt constitutes the bulk of the total annual discharge, often delivering more than 70% of annual streamflow (Hauer et al. 1997). In Mediterranean-montane environments, where summer low flows dominate for up to six months of the year, and where at least 65% of annual precipitation falls in the three months of winter, the physical, chemical, and biological impact of this large springtime pulse of water is profound (Gasith and Resh 1999). Yet little research has addressed the direct and indirect effects of the spring snowmelt recession on the biotic and abiotic processes necessary to sustain aquatic and riparian ecosystems.

Here, we present a conceptual model for the ecology of the spring snowmelt recession, with an emphasis on Mediterranean-montane systems. We delineate those components of the natural flow regime most relevant to the recession hydrograph and their relation to physical and biological stream processes. Specifically, we relate the quantifiable components of magnitude, timing, and rate of change to abiotic and biotic stream factors. We discuss these components with regard to the success of riparian and riverine species such as cottonwood (*Populus* spp.) that are native to streams throughout the western United States, and to the foothill yellow-legged frog (*Rana boylii*), an indicator species for in-stream biota of California's Mediterranean-montane aquatic ecosystems. We then present two scenarios of change to the spring snowmelt recession and discuss their potential implications for general stream ecology. Changes resulting from flow regulation that produce a recession with a very high rate of change between two extremes of flow—flood and base flow—contribute to homogeneous channel conditions and a lack of diversity in aquatic and riparian species. Similarly, changes resulting from climate warming, which shift the timing and decrease the magnitude of the snowmelt recession, ultimately alter in-stream and riparian species compositions and increase the abundance of nonnative species. We believe our conceptual model can help guide water resource managers and watershed stakeholders toward a better understanding of the impacts of changing spring recession flow conditions on stream ecosystems.

The spring snowmelt recession

Stream ecology is multifaceted, with the diversity and abundance of species dependent upon conditions and processes occurring at multiple spatial and temporal scales (Imhof et al. 1996). Governed by regional and basin-scale characteristics, the flow regime plays a key role in determining abiotic and biotic conditions at subbasin scales (Poff et al. 1997, Lytle and Poff 2004). A primary feature of the natural flow regime in snowmelt-dominated mountain basins is the

BioScience 60: 114–127. ISSN 0006-3568, electronic ISSN 1525-3244. doi:10.1525/bio.2010.60.2.6

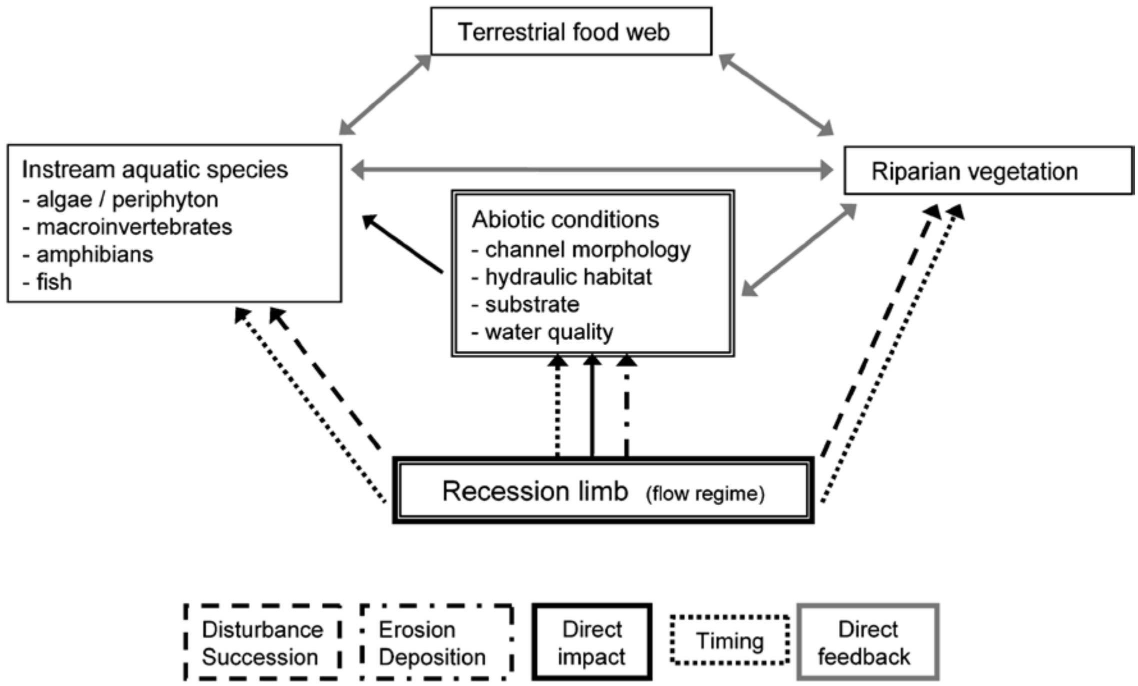

Figure 1. Conceptual model for spring snowmelt recession dynamics. Arrows indicate direction of impacts from physical and ecological processes and feedback relationships.

spring snowmelt recession: It shapes abiotic and biotic processes, such as erosion, deposition, and riparian succession; and dictates reproductive timing cues for in-stream biota (figure 1). Resulting changes in abiotic conditions directly affect the habitat of in-stream aquatic species, whereas changes in biotic conditions create feedbacks between riparian vegetation, in-stream habitat, and terrestrial food webs (Nakano et al. 1999).

The shape of the spring snowmelt recession hydrograph affects not only the availability and quality of water throughout the spring but also how sediment is transported, sorted, and ultimately deposited, thereby determining the abiotic and biotic conditions within the channel. Changes to the shape of the spring snowmelt recession hydrograph can be quantified using three primary components of the natural flow regime (Poff et al. 1997): magnitude, timing, and rate of change (figure 2). The magnitude is the level of discharge (often denoted Q) at the start of the recession, most simply defined as the last significant flow peak of the runoff season. The timing is the date at which the recession starts (t_s), and the rate of change is how quickly the flow changes from one discharge to the next (dQ/dt). Each of these components is easily quantified, and each can have independent effects on stream condition. Changes to the magnitude, for example, can create a different response within the stream system from changes to the timing.

The remaining two components of the natural flow regime, duration and frequency, can also be related to the spring snowmelt recession, and in some cases deserve specific consideration. The duration, or the length of time for the recession to reach summer base flow ($t_s - t_b$), is a function of the magnitude and rate of change. Generally, a slower rate of change will result in a longer-duration recession and vice versa. However, similar rates of change might occur in low-magnitude, short-duration recessions, and high-magnitude, long-duration recessions, though the abiotic and biotic effects of one can be very different from the other. Therefore, it is important to consider the duration of the recession in tandem with the rate of change when evaluating the impacts to stream conditions. By definition, the frequency of the snowmelt recession is annual; however, the frequency of a particular value of each hydrograph component varies on an interannual basis, producing different hydrograph recession

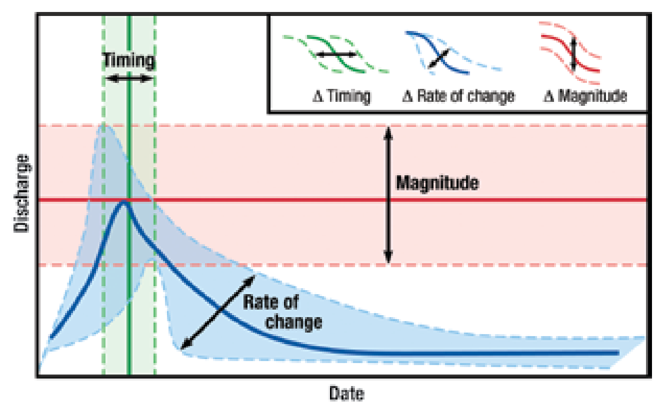

Figure 2. Primary quantifiable components of the spring snowmelt recession. Arrows indicate the direction in which increases or decreases in a component will shift the hydrograph.

shapes each year, depending on climate conditions. For example, in dry years, magnitudes may be lower, timing may be earlier, and the rate of change may be lower than in wet years. In this article, we focus specifically on quantifying and evaluating a single annual spring snowmelt recession; however, it is important to recognize the range of interannual variability in spring runoff conditions, and how that variability contributes to ecological diversity (Naiman et al. 2008).

Role of the spring snowmelt recession in creating and maintaining stream diversity

The spring snowmelt pulse and recession dominates the annual discharge of rivers emerging from winter snowpack headwaters (figure 3). These flows can provide the majority of the annual total flow volume in high-elevation basins and a substantial contribution of flow in mid-elevation basins subject to both rain and snowmelt runoff (Jarrett 1990, Hauer et al. 1997). In most snow-dominated mountain basins, the peak magnitude of the snowmelt pulse typically corresponds to the annual peak flow, even in systems subject to periodic rain events (Jarrett 1990). As a result, the snowmelt pulse is the primary disturbance that mobilizes channel sediments and drives riparian and aquatic successional processes. As the timing of snowmelt is largely a function of increasing day length, the corresponding receding hydrograph provides predictable flows for the reestablishment and population expansion of aquatic and riparian species prior to the low-flow season.

In Mediterranean-montane climates—characterized by dry, hot summers and wet, cool winters—winter floods provide an extreme contrast to summer drought; thus, the spring recession provides the singular annual event during which favorable habitat conditions occur and in-stream biota can recover (Gasith and Resh 1999). With gradually declining flows and a low frequency of pulses, the spring recession provides a stable transition from high abiotic pressures (e.g., scour, turbidity) during winter high flows to high biotic pressures (e.g., competition, predation) during late-summer and fall low flows (figure 4). During the recession, predictable flow conditions coincide with high resource availability, resulting in high reproductive success, growth rates, and survivorship for species adapted to this seasonal flow regime (Gasith and Resh 1999).

Whether in snowmelt-dominated systems or mixed rain-snow systems, the processes of disturbance, erosion, and deposition associated with the spring recession directly and indirectly affect certain biotic and abiotic conditions. Typified by a gradually decreasing discharge regime that extends for several months into summer, the spring snowmelt recession modifies channel morphology and substrate, provides diversity in hydraulic habitat, alters water quality, promotes recruitment for riparian vegetation, sets reproduction cues for fish and amphibians, and increases diversity in benthic producers (figure 5).

Effects of the spring snowmelt recession on abiotic conditions result primarily from the flow dynamics of gradually receding discharge. The peak discharge of the snowmelt

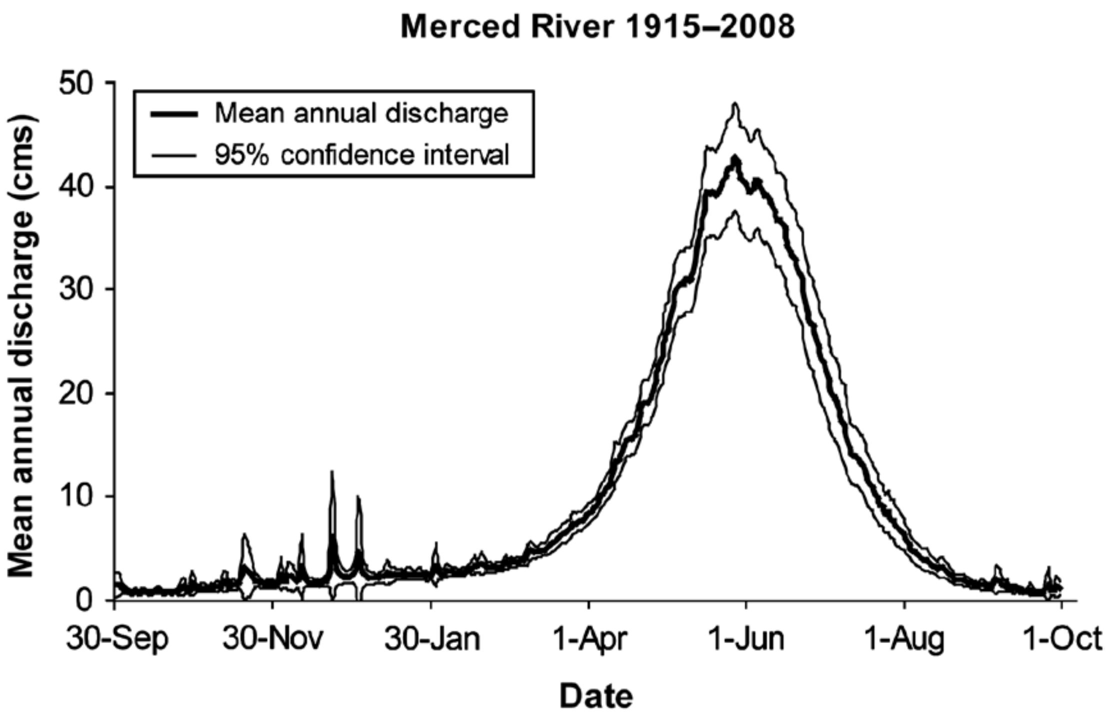

Figure 3. Annual hydrograph of a snowmelt-dominated Mediterranean-montane basin. Discharge is expressed in cubic meters per second (cms). Source: Data are from the Merced River, Yosemite National Park, California, US Geological Survey gage 11264500, elevation 1224 meters. In the Northern Hemisphere, spring typically occurs between March and June.

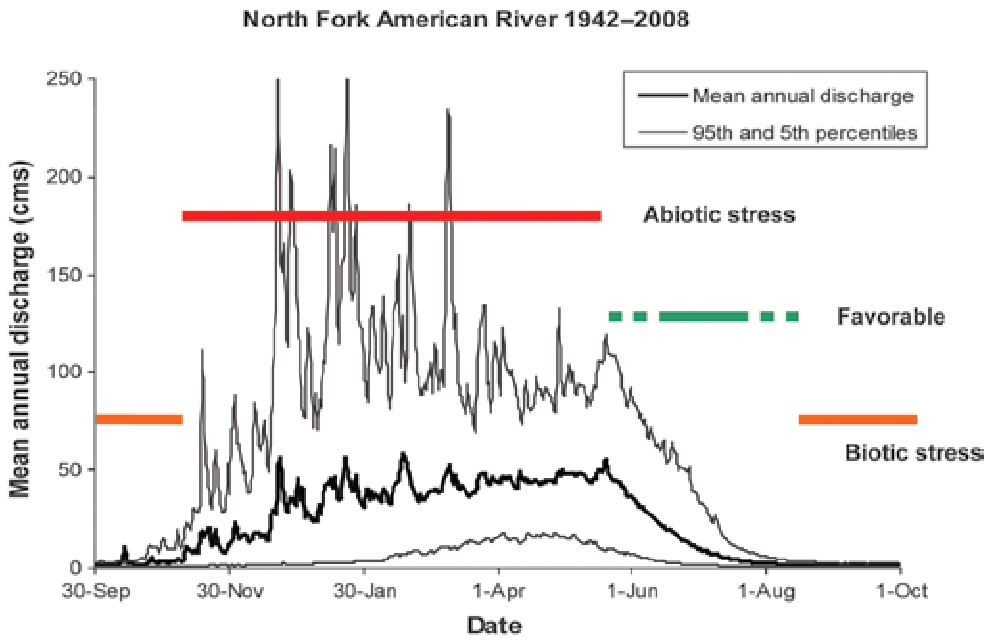

Figure 4. Annual hydrograph of a mixed rain-snow-dominated Mediterranean-montane basin. Discharge is expressed in cms, cubic meters per second. Source: Data from the North Fork American River, California, US Geological Survey gage 11427000, elevation 218 meters. In the Northern Hemisphere, spring typically occurs between March and June.

pulse is a primary driver for the extent and magnitude of sediment mobilization and transport (Madej 1999); however, as discharge decreases and sediment deposits, channel bars form and bedload is sorted into a variety of substrate patches. The geometry, size, and composition of these features are dependent upon local morphology and sediment supply (Ashworth 1996). Longitudinally, high flows redistribute sediment from tributaries and other supply locations, but as flows decrease, continued movement of smaller sediments increases the variability in channel elevation (Madej 1999). As flow gradually recedes, inundation of the floodplain slowly declines, creating a "moving littoral" that provides a high diversity of habitat patches with varying hydraulic conditions (Ward and Stanford 1995). This connectivity with the floodplain also results in greater export of nutrients and producers to the channel (Bowen et al. 2003, Ahearn et al. 2006), while the gradual decrease in volume of low-temperature, snowmelt-derived water results in colder water temperatures later into summer (Leland 2003).

Effects of the spring snowmelt recession on biota can be indirect, through changes in abiotic habitat conditions, or direct, through physical disturbance (e.g., scour) or changes in the timing of reproductive cues. As spring flows mobilize and deposit sediment, both aquatic and riparian habitats are modified through changes in channel morphology and substrate composition, creating shifts in availability and configuration. For example, newly reworked bars provide open, bare surfaces for colonization of riparian plants (Scott et al. 1996), while sorted and flushed substrates provide fresh surfaces for algal growth, niches for macroinvertebrate colonization, and clean spawning gravels for fish (Peterson 1996, Milhous 1998, Osmundson et al. 2002). High flows that cover floodplains increase both the availability and diversity of hydraulic habitat, and as flows recede, changing hydraulic conditions further increase habitat variability over time (Ward and Stanford 1995). Greater variability in hydraulic habitat has been associated with higher species diversity in fish and macroinvertebrate assemblages, which contributes to ecosystem biodiversity (Pastuchova et al. 2008).

For species adapted to the strong seasonality typical of temperate mountain rivers, the spring snowmelt pulse and recession create a predictable disturbance that not only resets riparian succession through scour but also provides timing cues for reproduction and growth (Naiman et al. 2008). Riparian communities are strongly influenced by spring flow regimes, where moderate disturbance enhances species diversity through succession (Merritt and Cooper 2000) and gradually receding flows provide the required conditions for seedling recruitment (Shafroth et al. 1998). As a result, the timing of seed dispersal for many species, such as cottonwoods, is tightly linked with this brief, but opportune, time (Rood et al. 2005, Stella et al. 2006). For primary producers, disturbance from high-snowmelt discharges that reduce algal and grazer densities is followed by a predictable flow recession with elevated nutrients, which promotes rapid growth, greater grazer densities, and higher diversity (Peterson et al. 2001). These riparian and aquatic successional processes, coupled with elevated food resources, create conditions conducive to higher-level trophism and greater niche space for species, such as spring spawning fishes and river-breeding amphibians. As a result, aquatic and semi-aquatic vertebrates often synchronize their reproductive

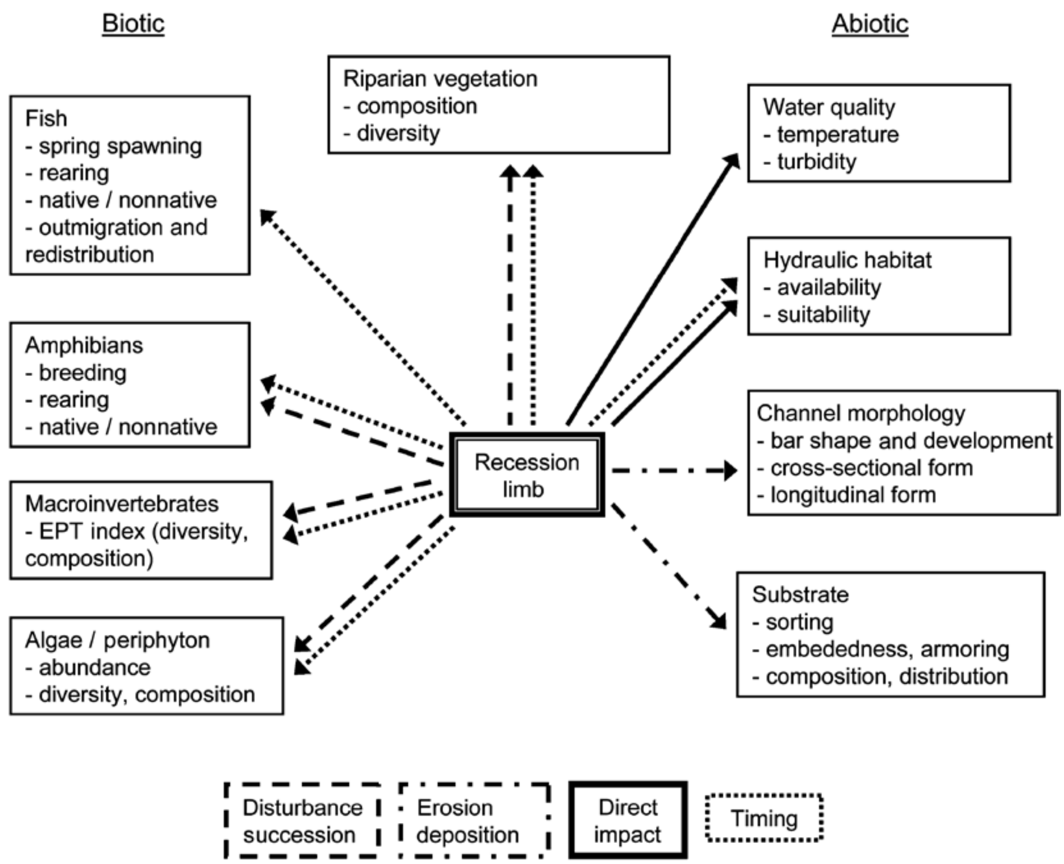

Figure 5. Detailed environmental relationships for spring snowmelt recession dynamics. Arrows indicate ecological and physical processes (described in the legend) acting upon each stream condition.

activities with the spring recession, such that suitable habitat conditions, temperature regimes, and abundant resources allow for optimal reproduction and growth (Kupferberg 1996, Freeman et al. 2001). These cues are primary drivers in population dynamics such that shifts in the timing of the spring recession can alter aquatic community composition and diversity (Jager et al. 1999, Marchetti and Moyle 2001, Jowett et al. 2005).

Over time, natural variability alters the shape and position of the spring snowmelt recession hydrograph. Wet years can produce large-magnitude recessions with a low rate of change and long duration, whereas dry years may result in earlier, smaller-magnitude recessions with a higher rate of change and shorter duration. In some snowmelt-dominated systems, the range in flow variability might be quite small and linked primarily to fluctuations in annual snowfall and temperature (figure 3). In contrast, the rain-dominated stream systems or combination rain-snow systems most typical of Mediterranean-montane climates can exhibit a much larger range in natural flow variability driven by confounding variations in precipitation, snowfall, and air temperature (figure 4). In each of these cases, however, the range of natural variability in unimpaired systems is governed by the natural fluctuations in climate patterns. As a result, species adapt in synchrony to the general predictable cycle of seasons, with these variable year-to-year conditions benefiting different species and promoting biodiversity (Naiman et al. 2008).

Species adaptations to the spring snowmelt recession

In a highly dynamic stream environment, many aquatic species have evolved their life-history strategies to take advantage of high flood predictability and associated seasonal processes (Lytle and Poff 2004, Naiman et al. 2008). The timing of the spring snowmelt recession and the shape of the recession hydrograph contribute to reproductive cues for many riparian and aquatic species, such as cottonwoods, willows, mayflies, amphibians, and salmonids (figure 6a). As flows gradually decrease through spring, the hydrograph passes through these windows of reproduction or biotic thresholds at magnitudes that support habitat (i.e., availability) in sufficient condition (i.e., suitability) for species persistence. Shifts in the timing of the recession or changes to the shape of the recession hydrograph that preclude suitable habitat during a particular species' window of reproduction can lead to a lack of success (Rood et al. 2005, Stella et al. 2006).

For many species, certain abiotic conditions are also required for successful reproduction, such as clean, scoured

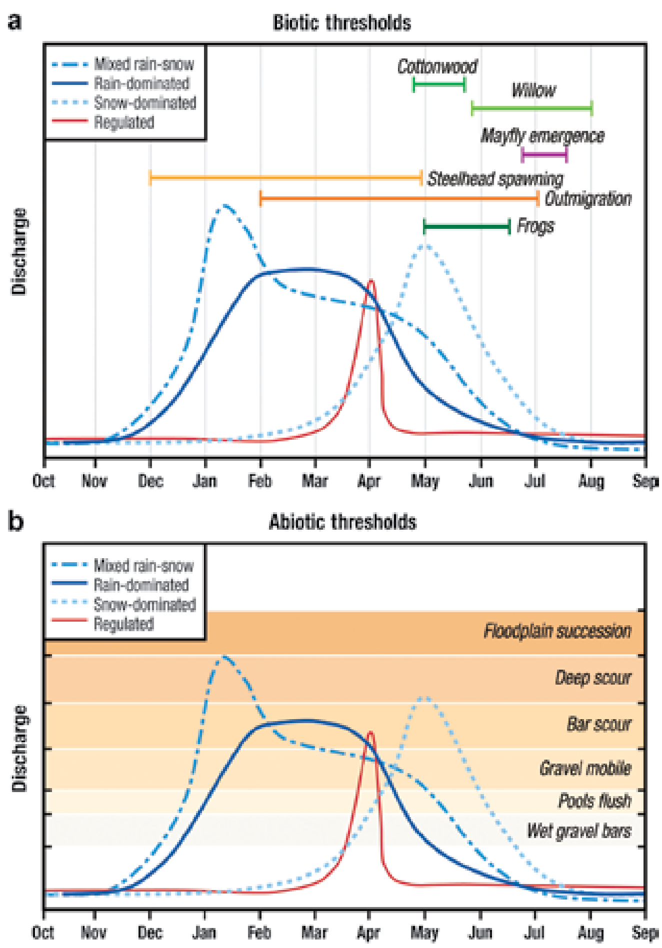

Figure 6. Examples of (a) biotic thresholds and (b) abiotic thresholds for rivers with varying hydrologic conditions. Exact threshold values will vary by species and river location.

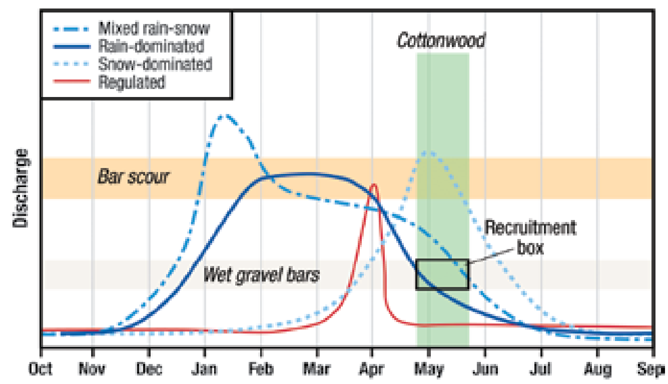

*Figure 7. Abiotic and biotic thresholds for cottonwood (*Populus *spp.). Before but not during the reproduction window (green band), flows must be high enough to initiate bar scour (orange band). During the reproduction window, flows must be high enough to wet gravel bars (pink band) and recede slowly enough to allow for germination of seeds. Where these abiotic and biotic thresholds cross under the hydrograph is the "recruitment box" (Rood et al. 2005).*

channel bars for riparian species and amphibians, emergent cobbles and boulders for macroinvertebrates, or newly flushed gravel substrates for salmonid redds (Harper and Peckarsky 2006, Stella et al. 2006). These conditions are largely governed by the magnitude of flow (figure 6b). In some cases, abiotic thresholds must be crossed before or at the start of the spring recession to create suitable habitat conditions within a given species' reproductive window. In other cases, certain abiotic conditions must be met during a species' reproductive window. The combined abiotic and biotic thresholds for a particular species of interest in relation to the components of the hydrograph can inform a better understanding of potential reproductive success and potential limiting factors.

Where abiotic and biotic thresholds for individual species intersect under the spring recession hydrograph, in-stream physical habitat conditions can be suitable for reproductive success, creating a window of opportunity. Recruitment needs for woody riparian species, such as cottonwood (*Populus* spp.), require certain abiotic conditions to be met at certain times (figure 7; Rood et al. 2005, Stella et al. 2006). High-magnitude flows during winter or early spring are required to scour substrates and create open, bare channel bars free from vegetation. In late spring, seeds disperse for approximately three to four weeks, and those that land on open, inundated, or wet gravel bars are likely to germinate. Thus, the timing of wet gravel bars must coincide with the timing of seed dispersal for successful germination. The rate of change in the discharge following germination must be slow enough to allow for roots to establish and grow in tandem with the receding water level. If the dimensions of the hydrograph are such that (a) this "recruitment box" is missed (Rood et al. 2005), (b) the magnitude of winter flows is too low to create scour on bars, or (c) the rate of recession is too steep to allow for root growth, then cottonwood recruitment will be reduced or unsuccessful (Rood et al. 1995).

Abiotic and biotic effects of changes in magnitude, timing, and rate of change

To date, research has rarely focused on the integrative effects of the spring snowmelt recession on stream ecology; however, ample research exists regarding the effects of flow on particular aspects of stream systems. We have compiled results from these studies to describe expected responses in stream ecosystems to shifts in each of the primary recession components (magnitude, timing, and rate of change) that result from natural or managed changes within a stream system (tables 1, 2, 3). While some responses are well studied, such as the effect of shifts in timing on cottonwood recruitment, others, such as changes to the cross-sectional shape of channel bars as flow duration changes, can only be surmised at this time.

Shifts in the rate of the spring snowmelt recession create the largest impacts on the stream system (table 1).

Table 1. Expected responses to shifts in the rate of change of discharge during the spring snowmelt recession.

Shift	Expected response	Reference
Decreased rate of change	Increased channel surface and subsurface sorting and armoring	Hassan et al. 2006
	Increased spatial patterns in channel substrate sorting	Ashworth 1996
	Development of shallow-sloped graded channel bars	Surmised
	Increased diversity of bed load as flood duration increases	Powell et al. 2001
	Decreased water temperatures, increased turbidity	Leland 2003
	Increased connectivity with floodplain resulting in greater diversity of habitat patches and greater export of nutrients and producers to channel	Ward and Stanford 1995, Bowen et al. 2003
	Increased habitat availability for early fish life stages resulting in increased year-class strength and survival	Freeman et al. 2001
	Increased variability in hydraulic habitat resulting in increased diversity in fish assemblage, macroinvertebrate assemblage and general biodiversity	Lambeets et al. 2008, Pastuchova et al. 2008
	Increased habitat stability and resource availability resulting in increased biota	Gasith and Resh 1999
	Increased diversity of riparian vegetation due to increased habitat diversity	Scott et al. 1996, Merritt and Cooper 2000
	Increased riparian species seedling recruitment	Shafroth et al. 1998
	Increased macroinvertebrate diversity following increased algal productivity	Peterson et al. 2001
	Increased riparian arthropod diversity	van Looy et al. 2007
Increased rate of change	Little to no armor layer on deposited material; no vertical grain sorting	Hassan et al. 2006
	Increased armoring in main channel	Ligon et al. 1995
	Increased transport of fines, increased substrate embeddedness	Wood and Armitage 1997
	Development of steeply sloped ungraded channel bars	Surmised
	Decreased habitat availability and variability due to rapid return to base flow	Bowen et al. 2003
	Increased water temperatures due to rapid return to base flow	Inferred
	Decreased salmonid spawning activity during high rates of change in flow	Moir et al. 2006
	Increased stranding of early life stage fish and amphibians	Kupferberg et al. 2008
	Increased temperature stress for fish resulting in decreased success	Jager et al. 1997
	Increased riparian vegetation encroachment	Lind et al. 1996
	Decreased riparian species seedling establishment	Rood et al. 1995
	Decelerated riparian leaf breakdown rates	Langhans and Tockner 2006
	Decreased arthropod abundance and diversity due to increased substrate embeddedness	Paetzold et al. 2008
	Decreased primary productivity due to high variability in flow	Acs and Kiss 1993

Decreasing the rate of change of flow alters the movement and deposition of sediment in the channel such that particles become well sorted and substrate patches become more spatially diverse (Hassan et al. 2006). As discharge gradually declines, subsequently smaller and smaller particles are deposited in different areas of the channel as a result of decreasing flow competence, creating a wide variety of well-sorted habitat patches of differing grain size. Furthermore, we surmise that this gradual deposition of sediment as flows diminish over a channel bar will produce a shallow, graded, cross-sectional shape that provides proportionally larger regions of shallow, in-stream habitat at a variety of flows. Larger duration flows resulting from a slower recession also increase connectivity with the floodplain, which has been shown to have numerous ecosystem benefits (Ward and Stanford 1995, Tockner et al. 2000), including a greater export of nutrients to the channel (Bowen et al. 2003) and greater fish growth and survival (Freeman et al. 2001). As flows slowly drop down into the channel, the variability of hydraulic conditions as water passes over diverse topography and substrate creates a gradually shifting mosaic of habitats that allows (a) a variety of riparian species to establish (Merritt and Cooper 2000, Shafroth et al. 2002), (b) terrestrial arthropods to disperse (Lambeets et al. 2008), and (c) primary producers to flourish (Peterson et al. 2001). The overall result is a highly heterogeneous environment that promotes the biodiversity of fishes, macroinvertebrates, and riparian vegetation assemblages.

Shift	Expected response	Reference
Increased magnitude	Increased sediment transport capacity and redistribution of sediment	Madej 1999
	Increased scour of sediments in depositional sites; flushing of fines	Osmundson et al. 2002
	Increased habitat availability for early fish life stages resulting in increased year-class strength and survival	Freeman et al. 2001
	Decreased water temperature due to larger volume snowmelt	Inferred
	Increased variability in hydraulic habitat depending on channel morphology	Moir et al. 2006
	Increased fish diversity and abundance due to increased habitat diversity and availability	Propst and Gido 2004
	Increased scour/drift of macroinvertebrates and prey availability for fish	Suren and Jowett 2006, Franssen et al. 2007
	Initial decrease in algal productivity due to scour, but subsequent increase in productivity due to release of grazing invertebrate pressure	Peterson 1996, Power et al. 2008
Decreased magnitude	Channel narrowing, loss of backwaters and side channels; channel simplification	Ligon et al. 1995, Van Steeter and Pitlick 1998
	Decreased erosion and deposition, reduced lateral migration rates; decreased channel elevation variability	Shields et al. 2000, Parker et al. 2003
	Increased transport and deposition of fines	Wood and Armitage 1997, Parker et al. 2003
	Increased water temperature due to smaller volume snowmelt	Inferred
	Increased vegetation encroachment, denser vegetation	Lind et al. 1996, Shafroth et al. 2002
	Increased growth in early life stages of amphibians	Kupferberg 1996
	Decreased diversity of macroinvertebrates and abundance of fish due to loss of habitat	Jowett et al. 2005, Dewson et al. 2007
	Shift toward less-specialized riparian arthropod assemblages	Lambeets et al. 2008
	Decreased algal production and increased senescence due to reduced scour and increased deposition of fines	Peterson 1996

Table 2. Expected responses to shifts in the magnitude of discharge at the start of the spring snowmelt recession.

Shift	Expected response	Reference
Later	Decreased water temperatures	Inferred
	Decreased growth of amphibians	Kupferberg 1996
	Increased growth of cold-water fish due to decreased temperatures	Jager et al. 1999
Earlier	Increased water temperature resulting in changes in timing of macroinvertebrate emergence, maturation age for trout, and fish and macroinvertebrate composition	Jager et al. 1999, Marchetti and Moyle 2001, Harper and Peckarsky 2006
	Increased growth for warm water fish and amphibians	Kupferberg 1996, Jager et al. 1999
	Decreased growth for cold water fish	Jager et al. 1999
	Decreased riparian seedling recruitment	Rood et al. 2005, Stella et al. 2006
	Increased low flow duration resulting in decreased arthropod abundance and changes to fish and macroinvertebrate composition	Marchetti and Moyle 2001, Jowett et al. 2005, Suren and Jowett 2006, Paetzold et al. 2008

Table 3. Expected responses to shifts in the timing of the start of the spring snowmelt recession.

Conversely, increases in the rate of change of discharge that produce a “flashy” recession lower the availability and diversity of in-stream habitats, as the duration of the recession is shorter. As flows rapidly decrease, mobile sediment abruptly deposits as unconsolidated substrate with minimal sorting or armoring (Hassan et al. 2006). Fewer substrate patches of varying sizes are created and finer sediments are not flushed from coarser particles, leaving deposits that lack biologically important interstitial space. A quick return to base flow within the main channel most likely creates a steep-sloped, ungraded channel bar that is further steepened by continued erosion along the edge of the main channel at the toe of the bar. The high rate of change in flow can limit the reproductive success of many species, such as salmonids attempting to spawn (Moir et al. 2006), or riparian plants attempting to establish (Rood et al. 1995), and can also reduce the diversity of algal and ground beetle communities (Acs and Kiss 1993, van Looy et al. 2007). A quick return to the base flow limits access to adjacent floodplains, decreasing shallow habitat availability and variability (Bowen et al. 2003), and as a result, reducing overall aquatic primary productivity (Ahearn et al. 2006). Subsequent increases in the duration of sustained low flows within the main channel result in greater transport of fines and substrate embeddedness (Wood and Armitage 1997), increased riparian vegetation encroachment (Lind et al. 1996), higher temperature stress for fish (Jager et al. 1997), and decreased rates of ecosystem processes such as leaf-litter decomposition (Langhans and Tockner 2006). The result is a stream system where the abiotic and biotic conditions reflect only the two extremes of flood and base flow, rather than the full spectrum and diversity of flows occurring in between.

Shifts in the magnitude of flow at the start of the spring snowmelt recession primarily affect the abiotic conditions within the stream (table 2). Greater discharges result in higher sediment transport and redistribution within channels as larger portions of the channel substrate are mobilized, ultimately increasing disturbance and habitat variability. The larger volume of cold snowmelt water in the channel creates greater hydraulic habitat availability and decreases water temperatures, conditions that are both particularly beneficial to fishes (Freeman et al. 2001). Although an increase in magnitude may be detrimental to macroinvertebrate and algal communities in the main channel as a result of scour, additional habitat availability in overbank areas and subsequent rapid recolonization in the channel can lead to greater benthic community species abundance and diversity (Franssen et al. 2007, Power et al. 2008). For communities adapted to a seasonal flood regime, high-magnitude scouring flows can provide the opportunity for producers to flourish during the predictable recession before grazer densities rise and subsequently provide energy to higher trophic levels (Power et al. 2008). For amphibians or riparian species, impacts from an increase in magnitude will depend on local channel conditions. For example, higher flow volume might result in reduced tadpole growth as a result of lower water temperatures and decreased breeding habitat availability if high flows flood suitable habitat, or it might increase breeding habitat availability if high flows provide access to warm, open, overbank areas (Kupferberg et al. 2008).

A lower magnitude of the spring snowmelt recession limits stream channel heterogeneity and aquatic species' productivity in several ways. Decreased erosion and deposition of coarse sediment over time reduces lateral channel migration (Shields et al. 2000), homogenizes channel elevations (Parker et al. 2003), and results in overall channel narrowing and simplification (Ligon et al. 1995, Van Steeter and Pitlick 1998). The subsequent loss of backwaters and side channels depletes habitat variability, and the overall lower-flow volume reduces in-stream habitat availability and macroinvertebrate diversity (Dewson et al. 2007). In addition, lower discharges generally result in higher water temperatures, which can negatively affect fishes by intensifying stress (Jowett et al. 2005), or positively affect the growth of amphibians (Kupferberg 1996). Lower discharges can also lead to increased vegetation encroachment and growth rates if flows are not adequate to scour established seedlings (Shafroth et al. 2002) and decreased algal productivity due to greater deposition of fine sediments (Peterson 1996). Most of these habitat conditions are likely to be amplified over time if low-magnitude discharges persist.

Shifts in the timing of the start of the spring snowmelt recession alone will have little impact on the abiotic conditions in the channel, with the exception of water temperature (table 3). If the timing of snowmelt occurs earlier in the season, there will be a longer duration of the warm-water conditions associated with the low-flow season. This might be beneficial to tadpole growth rates, for example, but detrimental to cold-water fish species (Jager et al. 1999). Conversely, shifts to timing that provide cold snowmelt runoff later into the summer will aid in sustaining lower water temperatures and shortening the duration of the low-flow season.

Biologically, shifts in timing can have profound impacts on population dynamics, particularly for species that have adapted to reproduce during the relative stability of the snowmelt recession (table 3). For example, cottonwood establishment is notable for its dependence on numerous factors (figure 7). If the timing of the recession shifts such that conditions do not coincide with the seed dispersal window, seedlings will not establish (Rood et al. 2005). Similarly, river-breeding amphibians time egg laying to optimize a balance between the risk of scour from early spring high flows and the benefits of increased growth prior to winter floods (Kupferberg 1996). Mayfly (Order: Ephemeroptera) emergence has been shown to occur during the tail end of the spring snowmelt recession when both water temperatures are higher and cobbles are first emerging, providing ideal conditions for egg-laying and hatch success (Harper and Peckarsky 2006). An earlier recession in the spring will lengthen the duration of warm summer and fall low flows. Although this might benefit warm-water species, it also intensifies stress to cold-water species, leading to changes in fish composition over time as warm-water and cold-water species vie for available habitat (Marchetti and Moyle 2001). Longer durations of low flows and related temperature changes may also affect macroinvertebrate and arthropod diversity, as habitat conditions clash with life-history strategies (Suren and Jowett 2006, Paetzold et al. 2008).

Although specific impacts from shifts in each of the three primary hydrograph components of the spring snowmelt recession can be described through thoughtful analysis of

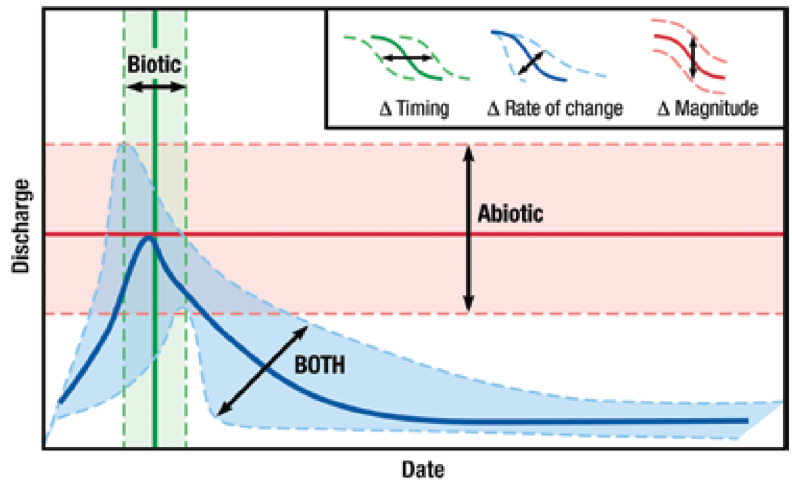

Figure 8. Dominant type of ecological impact resulting from shifts in the primary quantifiable components of the spring snowmelt recession.

a particular stream system, several general conclusions also emerge. Shifts in the magnitude of flow at the start of the recession that reflect a change in the volume of water in the channel will have the largest impacts on the abiotic conditions in the channel. Conversely, shifts in the timing of the recession will primarily affect biotic conditions. Shifts in the rate of change during the recession will profoundly affect both abiotic and biotic conditions, creating the largest observed changes to the stream ecosystem (figure 8). Which of these components requires the most focus in an analysis of the flow regime will depend on the stream system and the nature of the problem to be addressed.

River regulation and the spring snowmelt recession

It is well established that the damming of rivers for hydropower generation and water diversion alters in-stream habitat conditions and habitat connectivity by modifying discharge and sediment movement (Ligon et al. 1995). While most riverine species are adapted to natural variations in stream conditions, changes to the flow regime in managed systems often fall outside the range of natural variation, and thus have detrimental effects on native species. Efforts to minimize negative impacts on a species resulting from regulation have included prescribed “environmental” flows that mimic certain aspects of a natural flow regime and that provide discrete geomorphic or ecological functions such as substrate-flushing flows or minimum in-stream flows (Milhous 1998). More recent environmental flow efforts have moved beyond such discrete functions to a more holistic approach that incorporates greater flow variability by assessing the frequency and duration of low flows, high flows, and natural pulsed flows (Richter et al. 2006); however, quantifying the degree to which a managed hydrograph meets ecological requirements, and determining expected responses from shifts in managed hydrographs, remains elusive (Arthington et al. 2006). An assessment of the spring snowmelt recession in a managed hydrograph can not only show potential ecosystem responses from observed shifts in the hydrograph as described above but can also, if reference data are available, provide additional quantifiable recommendations for environmentally beneficial flows.

One example of a species that is directly affected by changes to the spring snowmelt recession is the foothill yellow-legged frog (*R. boylii*), a river-breeding amphibian native to mid-elevation streams in California and southern Oregon that was designated a California Species of Special Concern (Jennings and Hayes 1994). Individuals breed annually in early spring following the start of the spring snowmelt recession, timing their reproduction so as to minimize the risk of egg scour caused by unpredictable late-spring storms, and also to maximize growth during summer low flows (Kupferberg 1996). Frogs lay egg masses on open, newly scoured cobble bars, where the eggs must remain submerged for up to two weeks until tadpoles hatch. After hatching, tadpoles graze in shallow, warm, near-shore environments throughout the summer until metamorphosis occurs in fall. Although they are well adapted to the natural seasonal cycle of flow in Mediterranean climates, egg masses are still vulnerable to scour from late-season storms and to desiccation from rapid decreases in spring flow, whereas tadpoles are vulnerable to scour from rapid changes in flow during the summer (Kupferberg et al. 2008). As a result, frogs have been found to associate with river reaches of high habitat heterogeneity where a variety of suitable habitats exist for all life stages across varying flows (Yarnell 2008).

Regulated rivers in California (i.e., rivers with discharge largely controlled by dams, weirs, and diversions) often exhibit a spring flow regime that is markedly different from a natural spring snowmelt recession. As winter rain and snowmelt flows are captured behind dams and fill reservoirs, streams receive constant base flows that are periodically interrupted by high-magnitude, high rate-of-change events (i.e., spills). This bimodality of flow extremes results in a

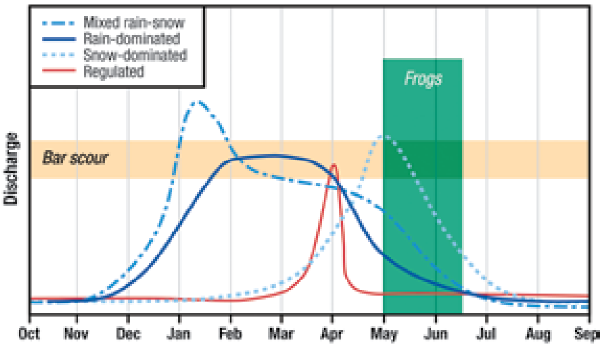

Figure 9. Abiotic and biotic thresholds for foothill yellow-legged frog (*Rana boylii*). Before but not during the reproduction window (green band), flows must be high enough to initiate bar scour (orange band). During the reproduction window, flows must recede slowly enough to avoid desiccation of eggs.

more homogeneous channel with limited habitat availability (see references in table 2). In addition, the timing of these spill events is highly variable, coinciding only occasionally with natural peaks in spring runoff. For species such as the foothill yellow-legged frog, the timing of these spill events and the high rate of recession directly determines its annual reproductive success (figure 9). High-magnitude winter storms and early spring storms provide the required benefit of newly scoured cobble bars for egg deposition, but spill events that occur in late spring either during or after breeding can cause widespread scour and mortality (Kupferberg et al. 2008). Conversely, flows that are abruptly diminished during or after the breeding season, such as might occur when a spill event has concluded, will desiccate eggs and newly hatched tadpoles. Prescribing a spring flow regime that gradually ramps down from a spring spill event or that mimics the timing and rate of change of a natural spring snowmelt recession will reduce the potential for egg or tadpole mortality while also providing high habitat availability for multiple native species.

Climate warming and the spring snowmelt recession

The effects of climate warming on water resources in temperate latitudes will be profound: Many studies in western North America show contemporary shifts in the seasonality of snowmelt runoff (Maurer et al. 2007, Stewart 2009). The Mediterranean-montane climate of California is expected to warm by between 2 degrees Celsius (°C) and 6°C over the next 50 to 100 years (Young et al. 2010). Higher air temperatures will reduce the proportion of precipitation that falls as snow and increase the amount of winter rain, subsequently resulting in greater variability in the shape and position of the spring snowmelt hydrograph (Maurer et al. 2007). While shifts in the timing, magnitude, and rate of the spring snowmelt recession may not be as extreme as observed in some regulated systems, the shifts are likely to move beyond the historic range of natural variability (Maurer et al. 2007). As a result, the spring recession hydrograph in a typical, mixed rain-snow-dominated Sierran mountain basin will exhibit shifts in timing, magnitude, rate of change, and duration (figure 10). Depending on the basin, the timing of the spring snowmelt recession is predicted to occur two to four weeks earlier, the magnitude to be reduced as more precipitation falls in the form of rain, and, as a result of only slight decreases in the rate of change, the duration of the snowmelt recession may be shorter (Stewart 2009). Determining how each component of the spring hydrograph will shift in response to climate warming is basin-dependent and complex, but even knowledge of general trends in how the spring hydrograph might change can provide some information on potential ecosystem impacts. The specific impacts of these shifts on a stream's ecology will vary by elevation, latitude, and the degree of overall temperature increase (Young et al. 2010), but several general conclusions can be reached on the basis of current available data (tables 1–3).

As climate warming shifts the timing of the spring snowmelt recession to earlier in the season, and decreases the magnitude of flow at the start of the recession, we expect to see a longer duration of the warm, low-flow season as less snowmelt is delivered downstream. Although the rate of the recession may decrease slightly, significant reductions in magnitude negate this effect, resulting in an overall shorter duration of cold water within the system. An earlier start to the recession will provide longer time for growth of some species, such as amphibians and native warm-water fishes; however, the resulting increase in low-flow duration will also expand the abundance of nonnative species (Marchetti and Moyle 2001). Consequently, an elevational shift in the distribution of cold- and warm-water fish species will occur as cold-water species are limited to higher elevations (Jager et al. 1999). An earlier and shorter spring recession will also limit the extent of suitable habitat and recruitment success for woody riparian plant species, as adequate flow conditions occur less often during times of seed dispersal (Rood et al. 2005, Stella et al. 2006). The resulting lower diversity and abundance in the riparian vegetative community and the associated changes in channel habitat, compounded by an increase in sustained low flows, will diminish riparian arthropod diversity and change the aquatic macroinvertebrate community (see references in tables 1–3). These changes in the riparian and aquatic communities will have cascading impacts to the adjacent terrestrial ecosystem (Nakano et al. 1999).

A decline in the magnitude of flow at the start of the spring snowmelt recession will also cause less redistribution of sediment, creating large abiotic changes in stream systems. The abiotic impacts will be more complex in Mediterranean-montane basins, where a decreased snowmelt pulse is confounded by higher magnitude and frequency of winter rain events. High-magnitude winter rain events will mobilize extensive amounts of sediment and create high levels of disturbance; however, the rapid recession rate of these flashy winter storms in contrast to the slower recession rate of the snowmelt pulse will create changes in how the sediment is sorted and deposited. Channel substrates will be more homogenous, as

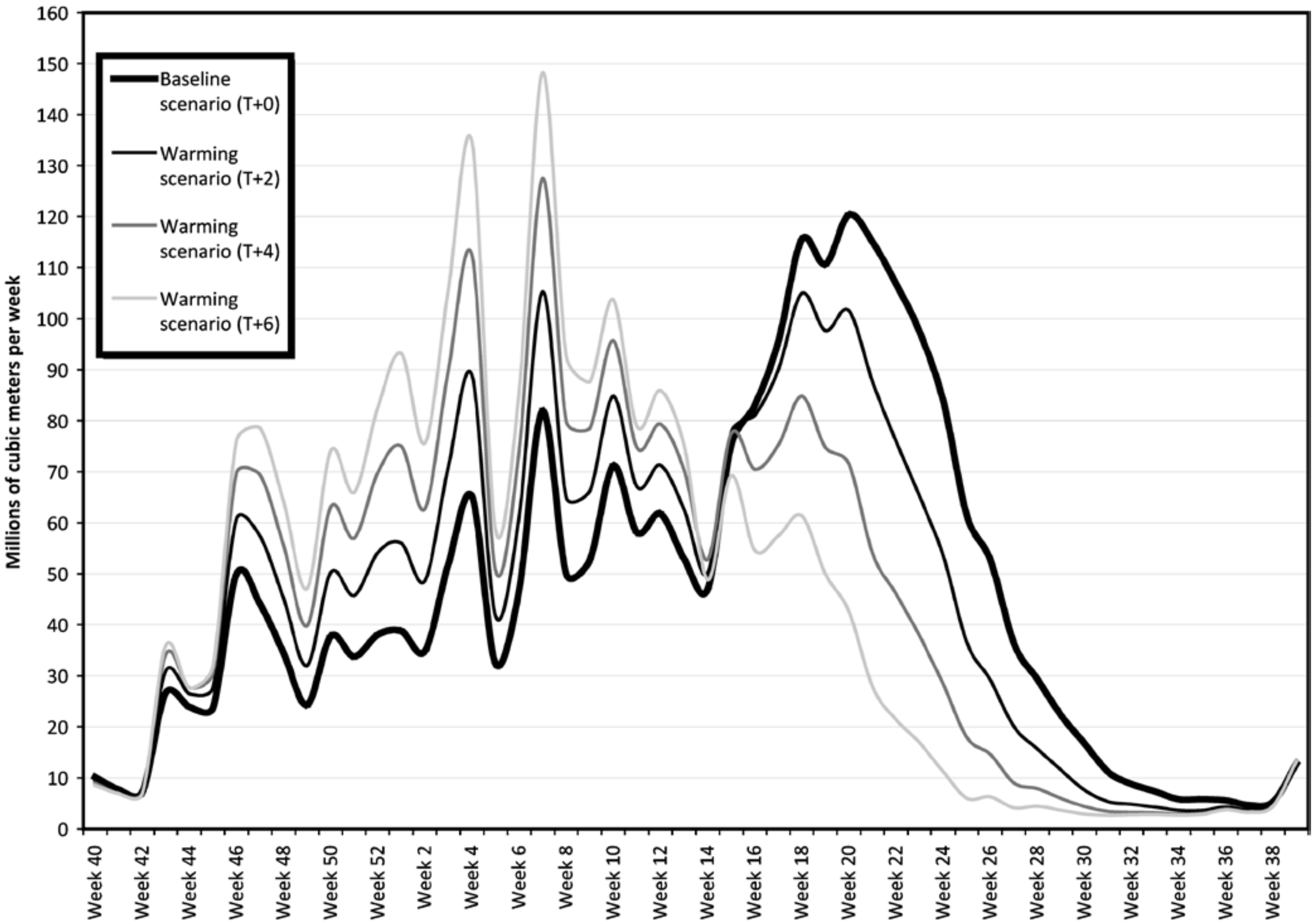

Figure 10. Simulated weekly hydrograph of Tuolumne River under warming scenarios. Snowmelt recession progressively decreases in magnitude and rate of change as air temperature increases. Weeks refer to California water year, beginning October 1 (week 40). Source: Data from Young and colleagues (2010).

rapidly deposited sediment is not redistributed and sorted over time; channel bars may be more steeply sloped, creating less habitat availability as flows fluctuate (see references in table 1). Similar to conditions observed in regulated systems, a flashier spring hydrograph as a result of climate warming may create channel habitat conditions reflective of two dominant flow stages, flood and low-flow, rather than of multiple flow stages ranging between the two extremes. The overall result is a stream system with greater homogeneity in habitat conditions, and thus less overall biodiversity.

Although the extent of stream and riparian ecosystem alteration as a result of climate warming is not yet fully understood, we do know that the western United States (Stewart 2009), and California's Sierra Nevada in particular (Young et al. 2010), is undergoing a shift in its hydrologic regime, unprecedented in recent human history. The ability of aquatic and riparian organisms to adapt to changing habitat conditions will be limited by the rapid pace of change. Further, most aquatic and riparian ecosystems are heavily degraded, and sentinel species are already at risk (Marchetti and Moyle 2001). Thus, there is a pressing need to better understand the complexities of stream ecology, as changing hydrologic conditions will alter the composition, behavior, and function of aquatic and riparian ecosystems that currently depend on spring snowmelt.

Conclusions

From the basis of the natural flow regime paradigm and general conclusions regarding the effects of flow on geomorphic and ecological stream processes, we were able to develop a conceptual model of the ecology of the spring snowmelt recession that specifically relates the quantifiable hydrograph components of magnitude, timing, and rate of change to abiotic and biotic stream factors. This conceptual model is particularly suited to the Mediterranean-montane environments, but is also applicable to other regions with similar hydroclimatic conditions.

Our conceptual model indicates that changes in the shape of the spring snowmelt recession hydrograph can have both direct and indirect effects on aquatic and riparian species. For example, shifts in the timing of the start of the recession coupled with higher rates of change can directly affect cottonwood recruitment or foothill yellow-legged frog egg survival, whereas decreases in flow magnitude could adversely affect the availability of suitable habitat for both species. In general, we found that shifts in the magnitude of flow at the start of the recession have the largest impacts on abiotic conditions in the channel, whereas shifts in the timing of the recession primarily affect biotic conditions, pushing many species' periods of reproduction out of phase with the availability of suitable habitat. Shifts in the rate of the recession affect both abiotic and biotic conditions, creating the largest observed changes to the stream ecosystem (figure 8).

We also investigated two scenarios of change to the spring snowmelt recession and discussed their potential implications for general stream ecology. The effects of climate warming on aquatic ecosystems in Mediterranean-montane climates will be profound, with shifts in each of the three primary components of the recession (magnitude, timing, and rate of change). Shifts in the timing at the start of the recession and decreases in the magnitude of the flow, coupled with a shorter duration resulting from a relatively small increase in the rate of change, will alter in-stream and riparian species compositions, forcing cold-water aquatic species to inhabit higher elevations, and leading to a higher abundance of nonnative species. Shifts in the spring recession as a result of flow regulation can create similar patterns. On the basis of our conceptual model, we found that managed hydrographs with a flashy, short-duration spring snowmelt recession overlying a steady base flow can create channel conditions reflective of the two observed extremes in discharge, flood and base flow. Aquatic and riparian species will be reflective of the homogeneous channel conditions and lack diversity.

We believe that there is an opportunity to mitigate the better-documented negative impacts of flow regulation through dam operations (e.g., manipulation of ramping rates), such that the bounds of the spring snowmelt recession do not exceed those of unimpaired systems. Restoration of the spring recession, with the diversity of flows and predictable resources it provides, will help to create a wide variety of channel habitats that contribute to increased species diversity and abundance. We believe our conceptual model can help guide water resource managers to more effectively maintain key ecosystem services in regulated rivers, and help watershed stakeholders form adaptation strategies for anticipated changes in the nature of flow regimes in lotic environments as a result of climate warming.

Acknowledgments

We would like to thank the Center for Watershed Sciences at University of California, Davis, for generously supporting this work. Insightful discussions with Peter Moyle, Carson Jeffres, Rob Lusardi, and Gerhard Epke greatly improved the body of this work, and comments from Karen Goodwin improved the manuscript. We also extend special thanks to Janice Fong for her creativity and input regarding the figures and illustrations.

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