

Ecology and Management of the Spring-Snowmelt Recession

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Abstract

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 impact abiotic channel conditions, while shifts in timing primarily affect biotic conditions. Shifts in the rate of change impact both abiotic and biotic conditions, creating the largest observed changes to the stream ecosystem. We discuss these components with regard to the success of native 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 towards a better understanding of the impacts of changing spring flow conditions on stream ecosystems.

I. Introduction

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 conservation, restoration and management of rivers (Arthington et al. 2006, Marchetti and Moyle 2001, Richter et al. 2006). However, one fundamental aspect of the natural flow regime that has received little attention in both scientific study and resource management is the importance of the spring-snowmelt recession to both geomorphic and ecological stream processes. In mountain regions, the spring snowmelt comprises the bulk of the annual hydrograph, often delivering more than 70% of the annual discharge (Hauer et al. 1997). In Mediterranean-montane environments, where summer low flows dominate for up to six months of the year and at least 65% of annual precipitation falls in the three months of winter, the physical, chemical and biological impact of this large spring-time pulse of water is profound (Gasith and Resh 1999). Yet, little research has addressed the direct and indirect impacts 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 native riverine species, such as cottonwood (*Populus* spp.), native to streams throughout the western U.S., and the Foothill yellow-legged frog (*Rana boylei*), an indicator species for instream 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 due to flow regulation that produce a recession with a very high rate of change between two extremes of flow, flood and baseflow, contribute to homogeneous channel conditions and a lack of diversity in aquatic and riparian species. Similarly, changes due to climate warming that decrease the magnitude, timing and rate of change in the recession, ultimately alter instream and riparian species compositions and increase the abundance of non-native species. We believe our conceptual model can help guide water resource managers and watershed stakeholders towards a better understanding of the impacts of changing spring recession flow conditions on stream ecosystems.

II. 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 (Frissell et al. 1986, 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 sub-basin scales (Lytle and Poff 2004, Poff et al. 1997). A primary feature of the natural flow regime in snowmelt-dominated mountain basins is the spring-snowmelt recession; it shapes abiotic and biotic processes, such as erosion, deposition and riparian succession, and dictates reproductive timing cues for instream biota (Figure 1). Resulting changes in abiotic conditions directly impact the habitat of instream aquatic species, while changes in biotic conditions create feedbacks between riparian vegetation, instream habitat and terrestrial food webs (Nakaono et al. 1999, Power et al. 1996).

The shape of the spring-snowmelt recession hydrograph affects not only the availability and quality of water throughout the spring, but 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 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 than 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, the length of time for the recession to reach summer baseflow (t_s-t_b), is a function of the magnitude and rate of change. Generally, a lower 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, while 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 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 inter-annual basis, producing different hydrograph recession 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 paper, we focus specifically on quantifying and evaluating a single annual spring-snowmelt recession; however, it's important to recognize the range of inter-annual variability in spring runoff conditions, and how that variability contributes to ecological diversity (Naiman et al. 2008, Richter et al. 1998).

III. Role of the Spring-Snowmelt Recession in Creating and Maintaining Stream Diversity

The spring-snowmelt pulse dominates the annual hydrograph of rivers emerging from winter snowpack headwaters (Figure 3). This pulse 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 (Hauer et al. 1997, Jarrett 1990). 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 resets succession. As the timing of snowmelt is largely a function of increasing day length, the corresponding receding hydrograph provides predictable discharge for the reestablishment and population expansion of aquatic and riparian species as they prepare for 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 where non-limiting habitat conditions occur and instream biota can recover (Gasith and Resh 1999). Whether in snowmelt-dominated, rain-dominated or mixed systems, gradually declining flows with a low frequency of pulses provide a stable transition

from high *abiotic* pressures during winter high flows to high *biotic* pressures during late summer and fall low flows (Figure 4). For species adapted to the predictability of this seasonal flow regime, the period of the spring recession allows non-limiting habitat conditions to coincide with high resource availability (Gasith and Resh 1999), resulting in high reproductive success, growth rates, and survivorship.

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 the 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 pulse is a primary driver for the extent and magnitude of sediment mobilization and transport (Madej 1999, Ryan et al. 2005, Trush et al. 2000); 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, Powell 1998). 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), 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 via changes in abiotic conditions or direct via changes in timing of reproductive cues or disturbance regimes. 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 niches for macroinvertebrate colonization and clean spawning gravels for salmonids (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). Increased variability in hydraulic habitat has been associated with increased diversity in fish and macroinvertebrate assemblages (Pastuchova et al. 2008, Rempel et al. 2000).

For species adapted to the strong seasonality typical of temperate mountain rivers, the spring-snowmelt pulse and recession creates a predictable disturbance that not only resets riparian succession, but provides timing cues for reproduction and growth. Riparian communities are strongly influenced by spring flow regimes, where moderate disturbance increases species

diversity through succession (Merritt and Cooper 2000), and gradually receding flows provide the required conditions for seedling recruitment (Bhattacharjee et al. 2006, 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 flows with elevated nutrients, which promote rapid growth, increased densities and higher diversity (Peterson et al. 2001). These successional processes, coupled with elevated food resources, create conditions conducive to spring spawning fish and river-breeding amphibians. Aquatic and semi-aquatic vertebrates often time their reproductive activities to coincide with the spring recession such that suitable habitat conditions, temperature regimes and abundant resources allow for optimal reproduction and growth (Freeman et al. 2001, Kupferberg 1996, Stalnaker et al. 1996). These cues are primary drivers in population dynamics such that shifts in the timing of the spring recession can alter aquatic community composition (Jager et al. 1999, Jowett et al. 2005, Marchetti and Moyle 2001).

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, while dry years may result in earlier, smaller magnitude recessions with a higher rate of change and short 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, 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

temperature (Figure 4). In either case, 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 with the general predictable cycle of seasons, and biodiversity is enhanced as variable year-to-year conditions benefit different species.

IV. Species Adaptations to the Spring-Snowmelt Recession

In a highly dynamic stream environment, many established aquatic species have evolved their life history strategies to take advantage of high flood predictability and associated seasonal processes (Kupferberg 1996, Lytle and Poff 2004, Moyle et al. 2003). 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, 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 timing of the recession or changes to the shape of the recession that preclude suitable habitat during a particular species' window of reproduction can lead to a lack of success (Rood et al. 2005, Rood et al. 2008, Stella et al. 2006).

For many species, certain abiotic conditions are also required for successful reproduction, such as clean scoured channel bars for riparian species and amphibians or newly flushed gravel substrates for salmonids. These conditions are largely governed by thresholds determined by the magnitude of flow (Figure 6b). In some cases, these abiotic thresholds must be crossed prior to 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 cross under the spring recession hydrograph, instream physical habitat conditions can be suitable for reproductive success. Recruitment needs for woody riparian species, such as cottonwood (*Populus* spp.) for example, require certain abiotic conditions to be met at certain times (Rood et al. 2005, Stella et al. 2006) (Figure 7). 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 3–4 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 flow recession 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 either this 'recruitment box' is missed (Rood et al. 2005), the magnitude of winter flows is too low to create scour on bars, or the rate of change in the recession is too steep to allow for root growth, cottonwood recruitment will be unsuccessful (Rood et al. 1995).

V. 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 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 hydrograph components (magnitude, timing and rate of change) resulting from natural or managed changes within a stream system (Table 1). 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 bars as flow duration changes, can only be surmised at this time.

Shifts in the rate of change of the spring-snowmelt recession create the largest impacts on the stream system. Decreasing the rate of change of flow (and subsequently increasing the duration of the recession) alters the movement and deposition of sediment in the channel such that particles become well-sorted and substrate patches become more spatially diverse (Ashworth et al. 1992, Hassan et al. 2006, Powell 1998). As discharge gradually declines, subsequently smaller and smaller particles are deposited in different areas of the channel due to 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 move down a channel bar, will produce a low-sloped graded bar shape that provides larger regions of shallow instream habitat at a variety of flows. Longer duration flows also increase connectivity with the floodplain, which has been shown to have numerous ecosystem benefits (Tockner et al. 2000, Ward and Stanford 1995), including 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 allow a variety of riparian species to establish (Merritt and Cooper 2000, Shafroth et al. 2002) and primary producers to

flourish (Acs and Kiss 1993, Peterson et al. 2001). The overall result is a highly heterogeneous environment that increases the diversity of fish, macroinvertebrate and riparian vegetation assemblages (Table 1).

Conversely, increases in the rate of change of the spring-snowmelt recession that produce a 'flashy' recession decrease the availability and diversity of instream habitats as the duration of the recession is reduced. As flows rapidly decrease, mobile sediment abruptly deposits as unconsolidated substrate with minimal sorting or armoring (Hassan et al. 2006, Reid and Laronne 1995). 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 baseflow within the main channel likely creates a steep-faced ungraded channel bar that is further steepened by continued erosion along the edge of the main channel at the toe of the bar (personal observation). 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). A quick return to baseflow limits access to adjacent floodplains, decreasing shallow habitat availability and variability (Bowen et al. 2003), and as a result, reduces overall aquatic primary productivity (Ahearn et al. 2006). Subsequent increases in the duration of sustained low flows within the main channel result in increased transport of fines and substrate embeddedness (Wood and Armitage 1997), increased riparian vegetation encroachment (Lind et al. 1996) and increased temperature stress for fish (Jager et al. 1997, Walsh and Kilsby 2007). The result is a stream system where the abiotic and biotic conditions reflect only the two extremes of flood and baseflow, rather than the full-spectrum and diversity of flows occurring in between.

Shifts in the magnitude of the start of the spring-snowmelt recession primarily affect the abiotic conditions within the stream, although direct impacts to aquatic organisms can occur. Increased discharges result in increased sediment transport and redistribution within channels as larger portions of the channel substrate are mobilized (Table 1), ultimately increasing disturbance and habitat variability. The increased volume of cold snowmelt water in the channel creates greater hydraulic habitat availability and decreases water temperatures, both conditions particularly beneficial to fish (Freeman et al. 2001, Stalnaker et al. 1996). While an increase in magnitude may be detrimental to benthic macroinvertebrates in the main channel due to scour, increased habitat availability in overbank areas may compensate and even increase prey availability for fish (Franssen et al. 2007). For amphibians or riparian species, impacts from an increase in magnitude will depend on local channel conditions. For example, increased flow volume might result in decreased tadpole growth due to colder water temperatures and decreased amphibian 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 decrease in the magnitude of the spring-snowmelt recession limits stream channel heterogeneity and aquatic species productivity in several ways. Decreased erosion and deposition of 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 decreases habitat variability, and the overall lower flow volume

reduces instream habitat availability. Lower discharges generally result in higher water temperatures, which can negatively impact fish (Jowett et al. 2005) or positively impact growth of amphibians (Sarah Kupferberg, Department of Integrative Biology, University of California, Berkeley, personal communication, February 25, 2009). 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). Most of these habitat conditions are likely 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. Decreases in the timing of snowmelt to earlier in the season, will generally increase the maximum weekly average water temperature as the duration of the low flow season increases. This might be beneficial to larval amphibian growth rates, but detrimental to cold-water fish species (Jager et al. 1999). Conversely, increases in timing that provide cold snowmelt runoff later into the summer will provide lower water temperatures throughout the low flow season.

Biologically, shifts in timing can have profound impacts on population dynamics, particularly for species adapted to reproduce during the relative stability of the snowmelt recession. 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. 2008). Similarly, river-breeding amphibians time egg-laying to optimize a balance between the risk of scour in early spring high flows and the benefits of increased growth prior to winter floods (Kupferberg 1996). Decreases in timing of the recession

will provide a longer period of stable warm low flows and increased tadpole growth. Decreases in the timing of snowmelt may also lead to changes in fish composition over time as warm-water and cold-water species vie for available habitat (Marchetti and Moyle 2001), and changes in macroinvertebrate and arthropod abundance as habitat conditions clash with life history strategies (Evans et al. 1995, Paetzold et al. 2008).

While specific impacts from shifts in each of the three primary components of the spring-snowmelt recession can be described through thoughtful analysis of a particular stream system, several general conclusions emerge. Shifts in the magnitude of the start of the recession reflecting a change in the volume of water in the channel will have the largest impacts to 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 of the recession will profoundly impact 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.

VI. River Regulation and the Spring-Snowmelt Recession

It is well established that the damming of rivers for hydropower generation and water diversion alters instream 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 impacts from regulation have included prescribed ‘environmental’ flows that mimic certain

aspects of a natural flow regime and provide discrete geomorphic or ecological functions such as substrate flushing flows or minimum instream flows (Milhous 1998). More recent environmental flow efforts have moved beyond such discrete functions to a more holistic approach that incorporates a larger range of flow variability by assessing the frequency and duration of low flows, high flows and natural pulsed flows (Mathews and Richter 2007, Richter et al. 2006); however, quantifying the degree to which a managed hydrograph meets ecological requirements or 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 provide not only knowledge of potential ecosystem responses from observed shifts in the hydrograph as described above, but if reference data is available, additional quantifiable recommendations for environmentally beneficial flows.

One example of a species known to be directly impacted by changes to the spring recession flow regime is the Foothill yellow-legged frog (*Rana boylei*), a river-breeding amphibian native to mid-elevation streams in California and southern Oregon and 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 due to unpredictable late spring storms but maximize growth during summer low flows (Kupferberg 1996). Egg masses are laid on open newly scoured cobble bars where they must remain submerged for up to 2 weeks until tadpoles hatch out. Subsequent to hatching, tadpoles graze in shallow warm near-shore environments throughout the summer until metamorphosis occurs in fall. Adapted to the natural seasonal cycle of flow in Mediterranean climates, egg masses are vulnerable to scour from late season storms and desiccation from rapid

decreases in spring flow, while 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 lifestages across varying flows (Yarnell 2005).

Regulated rivers in California 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 reservoirs, streams receive constant baseflows periodically interrupted by high magnitude high rate of change spill events (Figure 9). This bimodality of flow extremes results in a more homogeneous channel with limited habitat availability (see references in Table 1). In addition, the timing of these spill events is highly variable, only occasionally coinciding 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 change of the recession directly determines their annual reproductive success (Figure 10). Similar to cottonwoods, high magnitude winter 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 decreased 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 mimics the timing and rate of change of a natural spring-snowmelt recession reduces the potential for egg or tadpole mortality while providing high habitat availability for multiple native species.

VII. Climate Warming and the Spring-Snowmelt Recession

Climate warming effects on water resources in temperate latitudes will be profound with many studies in western North America showing contemporary shifts in the seasonality of snow-melt runoff (Maurer et al. 2007, Stewart et al. 2005). The Mediterranean-montane climate of California is expected to warm by 2–6 °C over the next 50 to 100 years (Hayhoe et al. 2004). Variability in the shape and position of the spring-snowmelt hydrograph is expected to get larger as climate changes due to an increase in winter rain and an associated loss of snowpack as air temperatures increase (Maurer 2007). While shifts in the timing, magnitude and rate of change 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 11). Depending on the basin, the timing of the spring-snowmelt recession is predicted to occur 2–4 weeks earlier, the magnitude will be reduced as more precipitation falls in the form of rain, and due to only slight decreases in the rate of change, the duration 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 (Null et al. forthcoming), but several general conclusions can be reached based on current available data (Table 1).

The largest impacts on the spring-snowmelt recession from climate warming will occur due to a shift in timing and decreases in magnitude that increase water temperatures and low flow duration as less cold water is delivered downstream. While the rate of change in the recession may decrease slightly, significant decreases in magnitude negate the effect, resulting in an overall decreased duration of cold-water within the system. An earlier start to the recession will provide increased time for growth of warm-water species such as amphibians; however, the resulting increase in water temperatures will cause an increase in the abundance of native warm-water fish and an increase in the number of non-native species (Jager et al. 1999, Marchetti and Moyle 2001). As a result, 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 duration 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 decreased diversity and abundance in the riparian vegetative community, compounded by an increase in sustained low flows will cause a decrease in arthropod abundance (Paetzold et al. 2008). These changes in the riparian community will create cascading impacts to the adjacent terrestrial ecosystem (Robinson et al. 2002).

In general, a decrease in magnitude will result in less mobilization 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 an increase in the 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 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 due to climate warming may create channel habitat conditions reflective of two dominant flow stages, flood and lowflow, rather than that 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 (Moyle and Mount 2007).

Although the magnitude and extent of stream and riparian ecosystem alteration due to climate warming is not yet fully understood, we do know that the western United States (Stewart et al. 2005), and California's Sierra Nevada in particular (Young et al. forthcoming), 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 due to the rapid pace of change. Further, most aquatic and riparian ecosystems are heavily degraded (Poff et al. 2007), sentinel species are already at risk (Davidson 2004), and burgeoning attempts at ecosystem restoration are ambiguous in their success (Bernhardt et al. 2005). Thus, there is a pressing need to better understand the complexities of stream ecology as changing hydrologic conditions will change the composition, behavior, and function of aquatic and riparian ecosystems currently dependent upon spring snowmelt.

VIII. Conclusions

From the basis of the natural flow regime paradigm and general conclusions regarding 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 environment of California, but is 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 increases in the rate of change can directly impact cottonwood recruitment or Foothill yellow-legged frog egg survival, while a decrease in magnitude could adversely affect the availability of suitable habitat for both species. In general, we found that shifts in the magnitude of the start of the recession have the largest impacts on abiotic conditions in the channel, while shifts in the timing primarily affect biotic conditions, placing the period of reproduction for many species out of phase with availability of suitable habitat. Shifts in the rate of change of the recession impact both abiotic and biotic conditions, creating the largest observed changes to the stream ecosystem.

We also investigated two scenarios of change to the spring-snowmelt recession and discuss 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. Shifts in the timing and decreases in the magnitude at the start of the recession coupled with a decreased duration, resulting from a relatively small

increase in the rate of change, will alter instream and riparian species compositions, pushing cold-water species to higher elevations, and increasing the abundance of non-native species. Shifts in the spring recession due to flow regulation can create similar patterns. Based on our conceptual model, we found that managed hydrographs with a flashy short-duration spring-snowmelt recession overlaying a steady baseflow can create channel conditions reflective of the two observed extremes in discharge, flood and baseflow. 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 ramping rate manipulation, 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 due to climate warming.

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Table 1. Summary of expected responses to shifts in hydrograph components based on literature review.

Component	Shift	Expected Response	Reference
Rate of change	Decrease	Increased vertical grain sorting and progressively coarser well-sorted surface	(Hassan et al. 2006)
		Increased spatial patterns in sorting as different grain sizes routed along diff pathways as deposition occurs and flow competence decreases	(Ashworth 1996, Powell 1998)
		Development of shallow-sloped graded channel bars	<i>Surmised</i>
		Increased diversity of bedload 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	(Bowen et al. 2003, Ward and Stanford 1995)
		Increased habitat availability for early fish lifestages resulting in increased year-class-strength and survival	(Freeman et al. 2001, Stalnaker et al. 1996)
		Increased variability in hydraulic habitat resulting in increased diversity in fish assemblage, macroinvertebrate assemblage and general biodiversity	(Dyer and Thoms 2006, Oberdorff et al. 2001, Pastuchova et al. 2008, Rempel et al. 2000)
		Increased habitat stability and resource availability resulting in increased biota	(Gasith and Resh 1999)
		Increased diversity of primary producers	(Acs and Kiss 1993, Peterson et al. 2001)

Component	Shift	Expected Response	Reference
		Increased diversity of riparian vegetation due to increased habitat diversity	(Merritt and Cooper 2000, Scott et al. 1996)
		Increased riparian species seedling recruitment	(Bhattacharjee et al. 2006, Shafroth et al. 1998)
Rate of change	Increase	Little/no armor layer on deposited material; no vertical grain sorting	(Hassan et al. 2006, Reid and Laronne 1995)
		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	<i>Surmised</i>
		Decreased habitat availability and variability due to rapid return to baseflow	(Bowen et al. 2003)
		Increased water temperatures due to rapid return to base flow	<i>Inferred</i>
		Decreased salmonid spawning activity during high rates of change in flow	(Moir et al. 2006)
		Increased stranding of early lifestage fish and amphibians	(Kupferberg et al. 2008, Saltveit et al. 2001)
		Increased temperature stress for fish resulting in decreased success	(Jager et al. 1997, Walsh and Kilsby 2007)
		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)
Magnitude	Increase	Increased sediment transport capacity and redistribution of sediment	(Madej 1999)

Component	Shift	Expected Response	Reference
		Increased scour of sediments in depositional sites; flushing of fines	(Osmundson et al. 2002, Payne and Lapointe 1997)
		Increased habitat availability for early fish lifestages resulting in increased year-class-strength and survival	(Freeman et al. 2001, Stalnaker et al. 1996)
		Decreased water temperature due to larger volume snowmelt	<i>Inferred</i>
		Increased variability in hydraulic habitat depending on channel morphology	(Moir et al. 2006)
		Increased fish diversity, abundance due to increased habitat diversity, availability	(Propst and Gido 2004)
		Increased prey availability for fish	(Franssen et al. 2007)
Magnitude	Decrease	Channel narrowing, loss of backwaters and side channels; channel simplification	(Church 1995, Ligon et al. 1995, Van Steeter and Pitlick 1998)
		Decreased erosion/deposition, reduced lateral migration rates; decreased channel elevation variability	(Parker et al. 2003, Shields et al. 2000)
		Increased transport and deposition of fines	(Parker et al. 2003, Wood and Armitage 1997)
		Increased water temperature	<i>Inferred</i>
		Increased growth in early lifestage amphibian species	(Kupferberg 1996)
		Increased eutrophication	<i>Surmised</i>
		Increased vegetation encroachment, denser vegetation	(Lind et al. 1996, Shafroth et al. 2002)

Component	Shift	Expected Response	Reference
		Decreased abundance of fish and diversity of macroinvertebrates due to increased low flows	(Dewson et al. 2007, Jowett et al. 2005)
Timing	Later	Decreased water temperatures	<i>Inferred</i>
		Decreased growth of primary producers and amphibians	<i>Inferred</i> ; (Kupferberg 1996)
		Increased growth of certain fish due to decreased temperatures	(Jager et al. 1999)
Timing	Earlier	Increased water temperature resulting in changes in maturation age for trout, changes in fish and macroinvertebrate composition	(Evans et al. 1995, Jager et al. 1999, Marchetti and Moyle 2001)
		Increased growth for warm water fish, amphibian species	(Jager et al. 1999, Kupferberg 1996)
		Decreased growth for cold water fish due to high baseflow temps	(Jager et al. 1999)
		Decreased riparian seedling recruitment	(Rood et al. 2008, Stella et al. 2006)
		Increased low flow duration changing fish species composition, decreasing arthropod abundance	(Jowett et al. 2005, Marchetti and Moyle 2001, Paetzold et al. 2008)

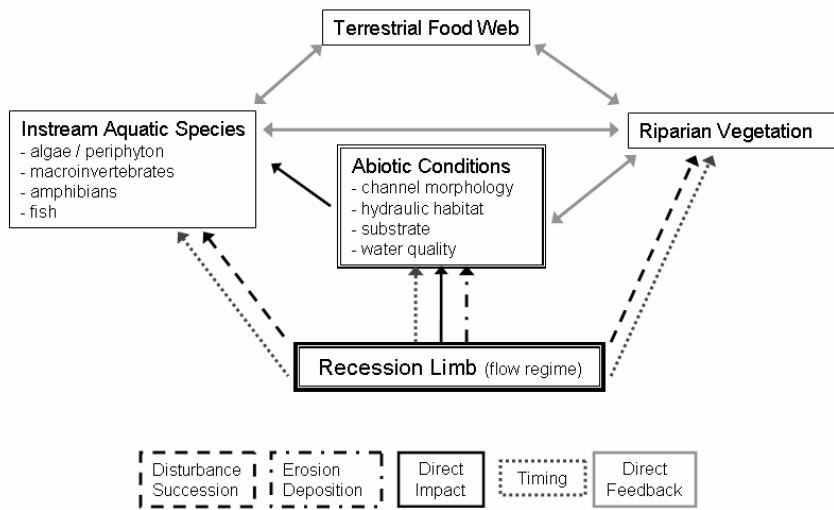


Figure 1. General environmental relationships for spring-snowmelt recession dynamics. Arrows indicate direction of impacts from physical and ecological processes and feedback relationships.

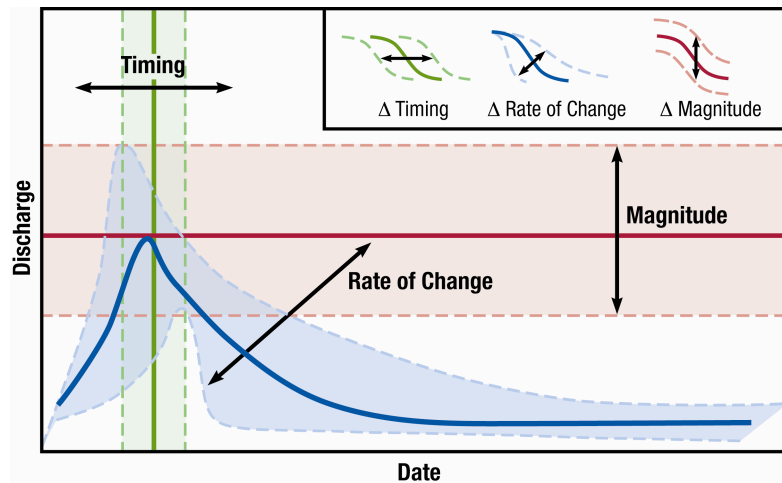


Figure 2. Primary quantifiable components of the spring-snowmelt recession. Arrows indicate the direction in which increases or decreases in a component will shift the hydrograph.

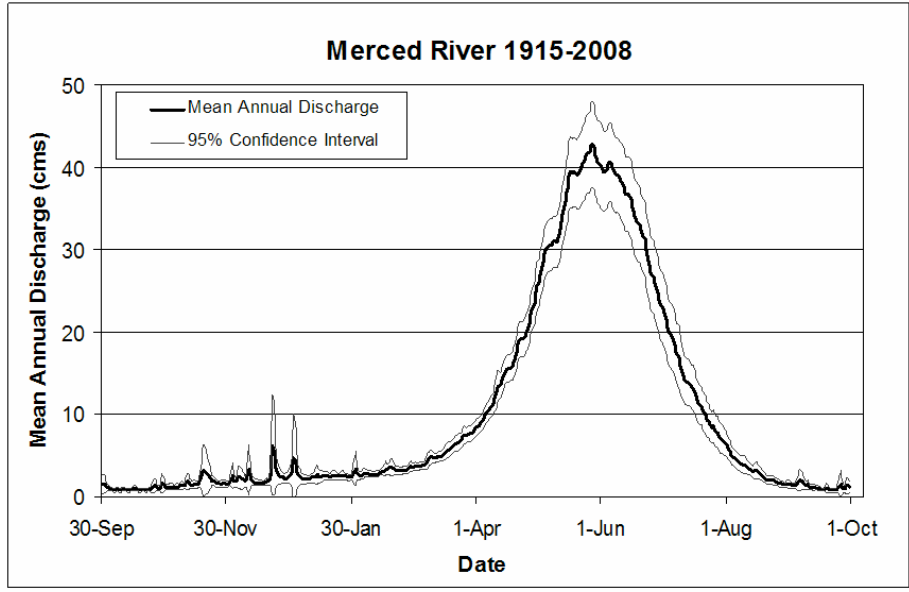


Figure 3. Annual hydrograph of a snowmelt-dominated Mediterranean-montane basin. Discharge is expressed in cubic meters per second (cms). Data from the Merced River, Yosemite National Park, California, USGS gage 11264500, elevation 1224 meters (m). In the northern hemisphere spring typically occurs between March and June.

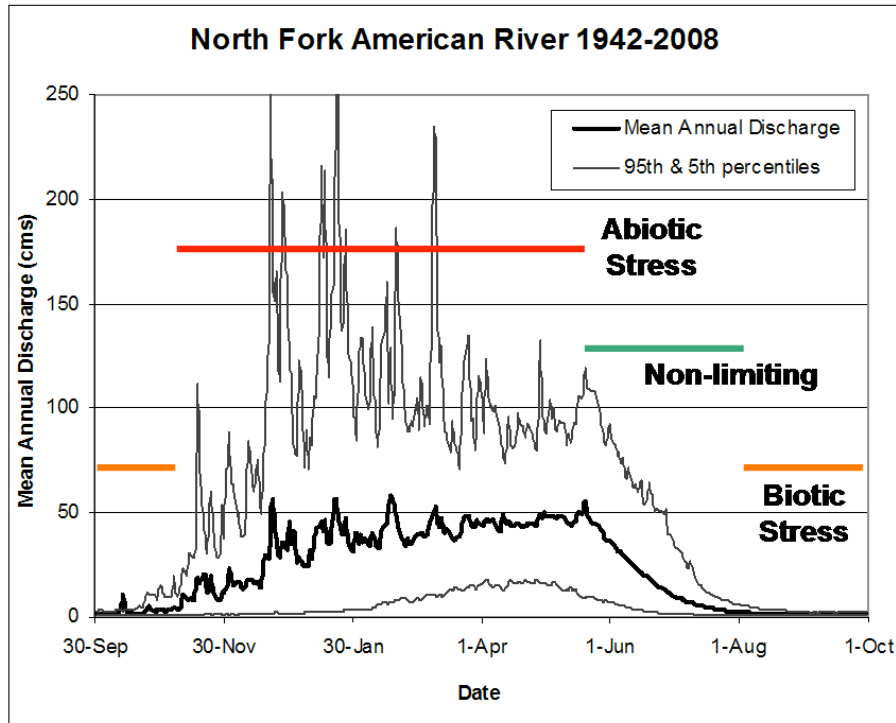


Figure 4. Annual hydrograph of a mixed rain-snow-dominated Mediterranean-montane basin. Data from the North Fork American River, California, USGS gage 11427000, elevation 218 m. In the northern hemisphere spring typically occurs between March and June.

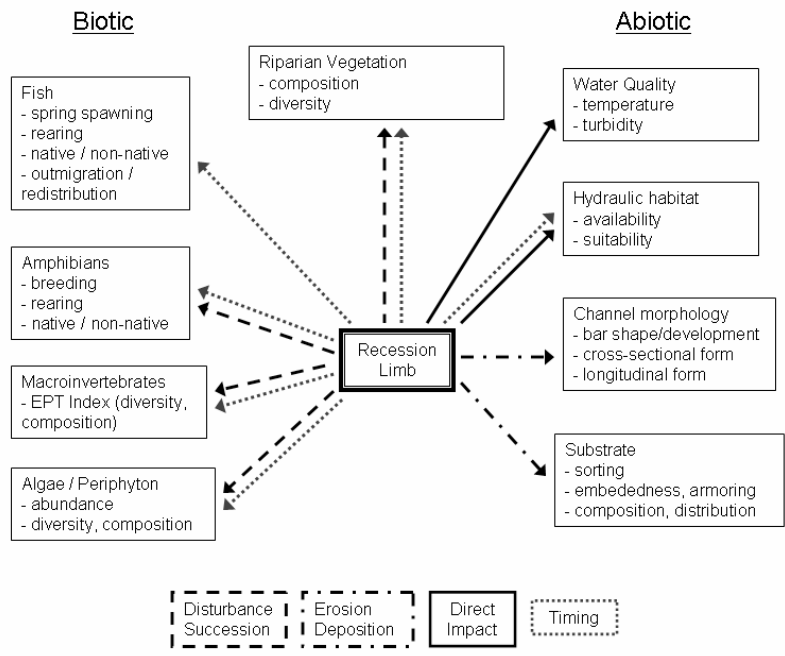


Figure 5. Detailed environmental relationships for spring-snowmelt recession dynamics.

Arrows indicate ecological and physical processes acting upon each stream condition.

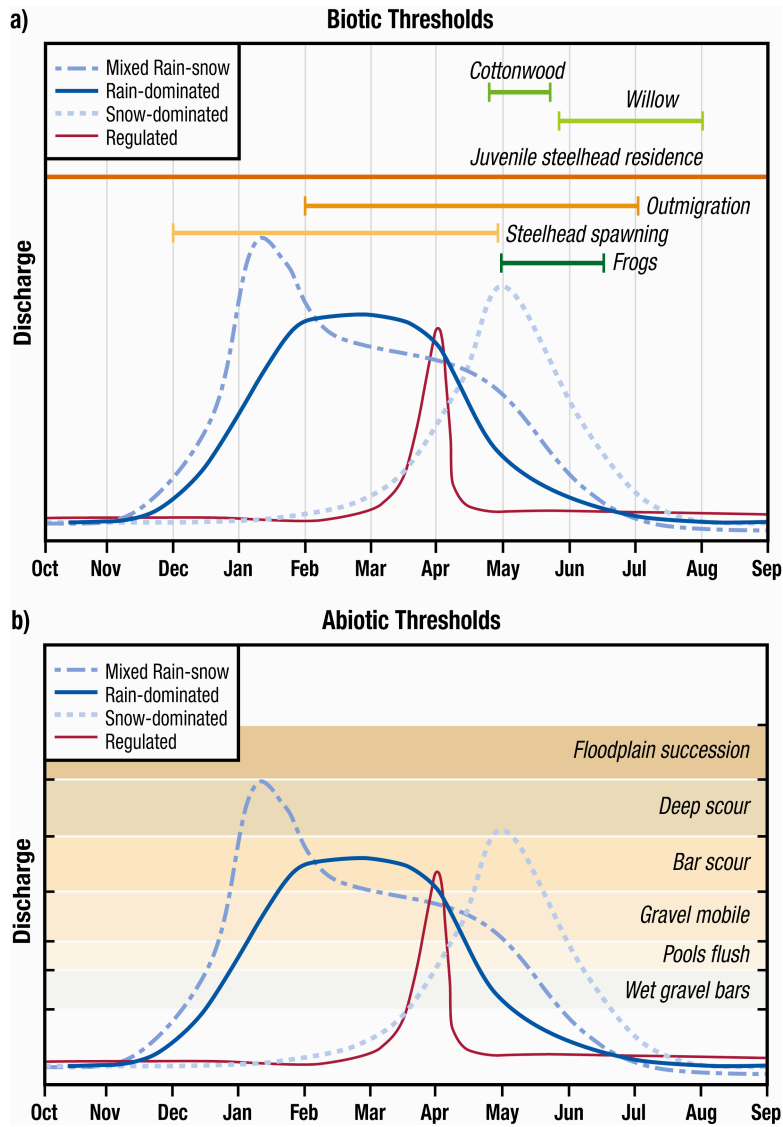


Figure 6. Examples of (a) biotic thresholds, and (b) abiotic thresholds for rivers with varying hydrologic conditions. Exact threshold values will vary by river location.

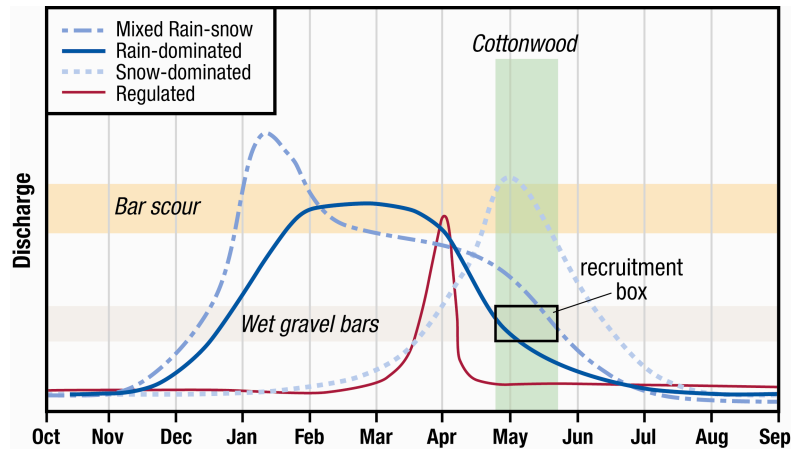


Figure 7. Abiotic and biotic thresholds for Cottonwood (*Populus* spp.). Prior to but not during the reproduction window (orange box), flows must be high enough to initiate bar scour (pink box). During the reproduction window, flows must be high enough to wet gravel bars (yellow box) and recede slowly 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).

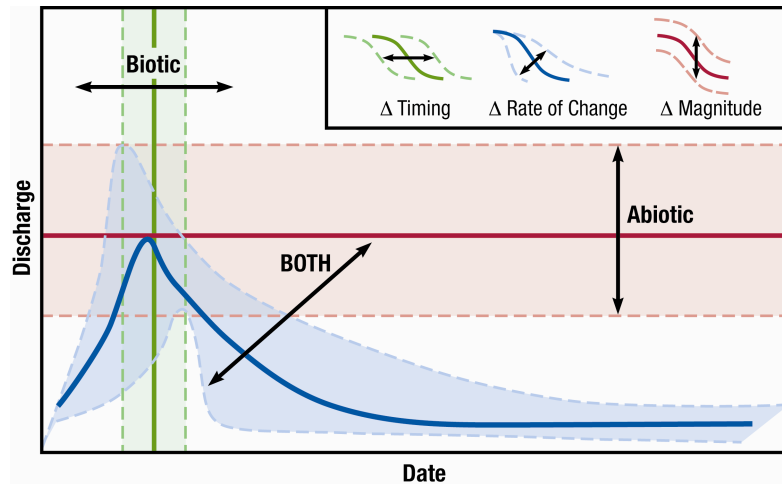


Figure 8. Dominant type of ecological impact due to shifts in the primary quantifiable components of the spring-snowmelt recession.

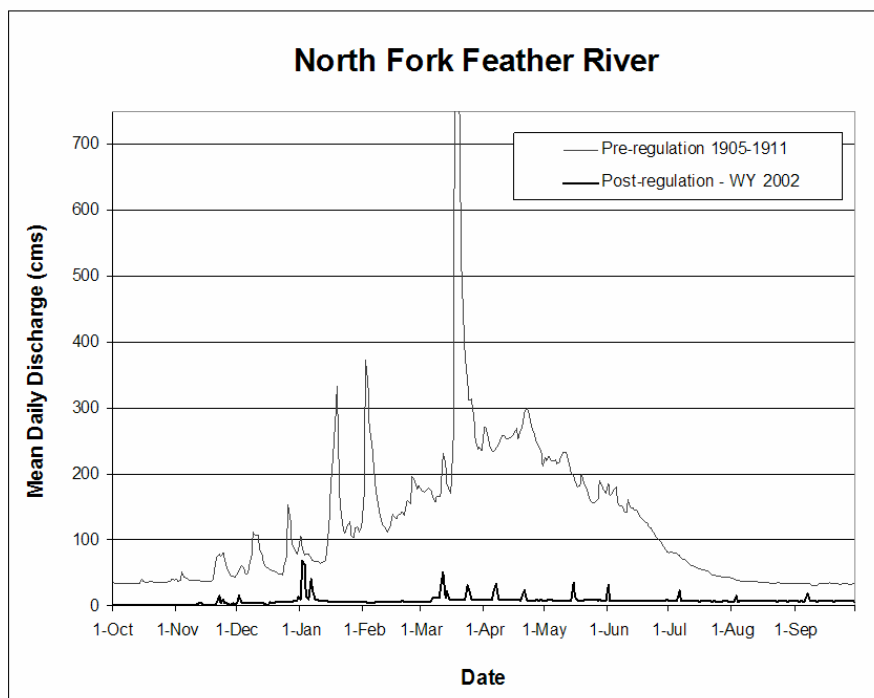


Figure 9. Annual hydrograph of a regulated river in a mixed rain-snow-dominated Mediterranean-montane basin. Data from the North Fork Feather River, California, USGS gage 11404330, elevation 451 m (post-regulation) and USGS gage 11405000, elevation 261 m (pre-regulation). In the northern hemisphere spring typically occurs between March and June.

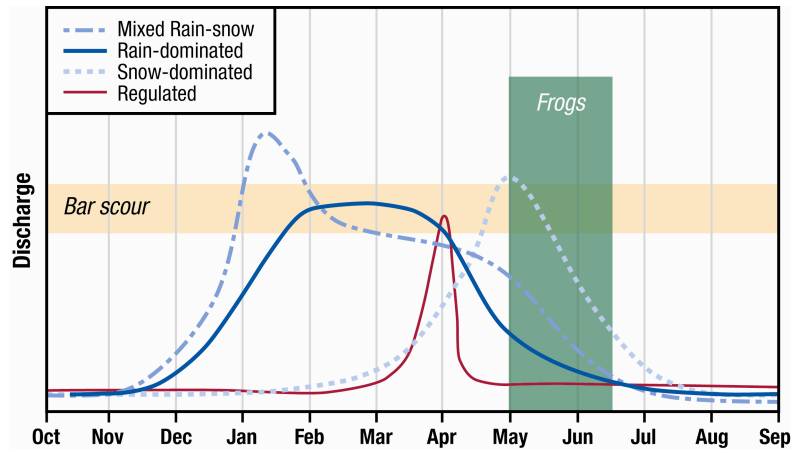


Figure 10. Abiotic and biotic thresholds for Foothill yellow-legged frog (*R. boylii*). Prior to but not during the reproduction window (green box), flows must be high enough to initiate bar scour (pink box). During the breeding window, flows must recede slowly enough to avoid desiccation of eggs.

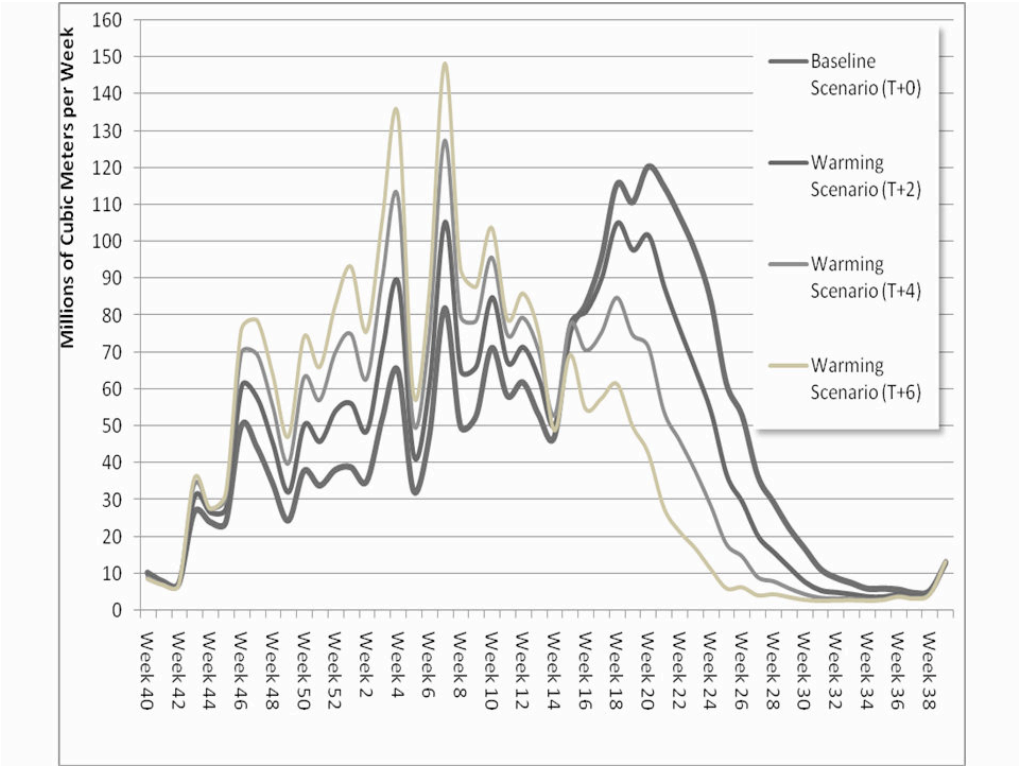


Figure 11. Simulated weekly hydrograph of Tuolumne River under warming scenarios. Snowmelt recession progressively declines in magnitude and slope as air temperature is increased. Weeks refer to California Water Year, beginning October 1 (week 40).