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 Review Paper

Maintaining and restoring hydrologic habitat connectivity in mediterranean streams: an integrated modeling framework

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Abstract Hydrologic alterations designed to provide a stable water supply and to prevent flooding are commonly used in mediterranean-climate river (med-rivers) basins, and these alterations have led to habitat loss and significant declines in aquatic biodiversity. Often the health of freshwater ecosystems depends on maintaining and recovering hydrologic habitat connectivity, which includes structural components related to the physical landscape, functionality of flow dynamics, and an understanding of species habitat requirements for movement, reproduction, and survival. To advance our understanding of hydrologic habitat connectivity and benefits of habitat restoration alternatives we provide: (1) a review of recent perspectives on hydrologic connectivity, including quantitative methods; and (2) a modeling framework to quantify the effects of restoration on hydrologic habitat connectivity. We then illustrate this approach through a case study on lateral hydrologic habitat connectivity that results from channel restoration scenarios using scenarios with different historic and climate-change flows to restore fish floodplain habitat in a med-river, the San Joaquin River, California. Case study results show that in addition to the channel alterations, higher flows are required to recover significant flooded habitat area, especially given reductions in flows expected under climate change. These types of studies will help the planning for restoration of hydrologic habitat connectivity in med-rivers, a critical step for mediterranean species recovery.

Keywords River restoration · Ecosystem functions model · GIS · Sacramento splittail · Chinook salmon

Introduction

Aristotle considered the Mediterranean basin as the only place suitable for human habitation and, for thousands of years, regions with similar climatic conditions have supported human settlement and intensive agriculture. Mediterranean-climate river systems (med-rivers) are characterized by variable stream flow rates across space and time. Variation in flow regimes experienced in mediterranean regions (med-regions) influences the spatial and temporal dynamics of hydrologic connectivity, water-mediated transport of matter, energy, and organisms present

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(Freeman et al., 2007). Alterations to these flow regimes in turn affect the availability and suitability of aquatic habitat for mediterranean species (med-species). Because few large freshwater lakes occur naturally in med-regions, and groundwater tends to either be far below the land surface or in thin bands along the stream corridor, people rely heavily on rivers for freshwater. In response to the intra-annual seasonality and inter-annual unpredictability of freshwater supply, human communities have generally relied on intensive water management infrastructure to improve water supply reliability, including large dams and conveyance projects. The projects have lowered the variability in stream flow and in some cases greatly reduced the amount of flowing water. This in turn impacts river-floodplain connections throughout med-rivers and has caused a dramatic loss of freshwater habitat connectivity. In this review, we focus on the coupling of hydrologic connectivity with med-species habitat and life history requirements that together influence habitat suitability and organism persistence.

To advance our understanding of these issues, we: (1) review recent perspectives on hydrologic connectivity especially from med-rivers; (2) provide a modeling framework to assess the impacts of climate-change and channel alteration scenarios on hydrologic habitat connectivity; and (3) illustrate this approach through a California med-river case study examining two channel restoration scenarios using historic and forecasted flows under climate change to improve fish recovery. Our case study is from the Sacramento-San Joaquin Bay-Delta, which is at the center of a key water supply linkage for California's agricultural and urban sectors. The Bay-Delta provides drinking water for 25 million Californians, and it supports irrigation supplies for a $27 billion agricultural industry. The Delta also once supported some of the state's largest fisheries, and many people are working to bring back winter- and spring-run Chinook salmon (*Oncorhynchus tshawytscha*), Central Valley steelhead (*Oncorhynchus mykiss irideus*), delta smelt (*Hypomesus transpacificus*), Sacramento splittail (*Pogonichthys macrolepidotus*), and southern green sturgeon (*Acipenser medirostris*) (Sommer et al., 2007). This case study illustrates how useful our general framework is for measuring and modeling the potential ecological benefits that may result from different river restoration options as well as under expected changes to flow as a result of climate change.

Hydrologic habitat connectivity: structural, functional, and ecological

The study of hydrologic habitat connectivity is still an emerging discipline. However, it is widely recognized that maintenance of natural patterns of longitudinal and lateral connectivity is essential to the viability of populations of many riverine species (Bunn & Arthington, 2002). This conclusion stems from the fact that stream flow influences physical habitat as well as the aquatic species that can often only persist under the natural flow regimes in which they evolved (Lytle & Poff, 2004). An understanding of the importance of hydrologic connectivity is particularly relevant given the degree to which such connectivity has been broken or affected by human activities such as roads, dams, and rerouting of water for agriculture and urban uses and its influence on freshwater ecosystems (Pringle, 2003).

Some researchers have recently argued that connectivity science can contribute to a unification of hydrology and ecology, and can advance inter-disciplinary research in ecohydrology and watershed science in general (Tetzlaff et al., 2007). For example, Freeman et al. (2007) point out the fact that application of connectivity science has a longer history in terrestrial ecology and conservation biology than in hydrology or freshwater ecology; yet, the importance of connectivity science has been increasingly adopted in stream ecology and watershed science. The applicability of tools used in terrestrial corridor design for identifying connectivity within freshwater systems has not been widely applied. Hydrologic habitat connectivity, as compared to terrestrial, is complicated by the fact that hydrologic connectivity can be expressed in longitudinal, lateral, vertical, and temporal dimensions. The interface between corridor science and watershed hydrology can provide a unique framework to examine how connectivity can bring the study of hydrology, ecology, and conservation science together (Tetzlaff et al., 2007). The integration of connectivity concepts across hydrology and ecology is well-illustrated by Larsen et al. (2012), who take advantage of a graph theory construct used often by terrestrial landscape ecologists (Minor & Urban, 2008) to measure connectivity for aquatic-dependent species.

Connectivity results from flow paths over time in all directions, including longitudinal (upstream–downstream), lateral (across the channel/floodplain), and vertical (surface–groundwater). Hence, the physical process of stream flow in large part determines levels of hydrologic connectivity and therefore is the focus for measuring and recovering hydrologic connectivity. Equally important is the object for which connectivity is relevant, because hydrologic connectivity is the water-mediated transport of matter, energy, and organisms within or between elements of the hydrologic cycle (Pringle, 2001; Freeman et al., 2007). Therefore, we focus on hydrologic habitat connectivity or how habitat availability and suitability are influenced by hydrologic connectivity that varies greatly in med-rivers depending on flow regimes and channel morphology. In actuality, hydrologic habitat connectivity is the explicit coupling of species habitat requirements with hydrologic connectivity analysis to provide metrics designed to aid the recovery functional freshwater connectivity.

Connectivity theory is increasingly being applied at the watershed-scale and includes sedimentologic as well as hydrologic connectivity studies (Bracken & Croke, 2007). At the landscape scale, connectivity captures the importance of the upland processes such as land use and habitat fragmentation on stream processes including water quality, quantity, and sediment dynamics (Pringle, 2003; Tetzlaff et al., 2007). The importance of longitudinal connections from the headwaters down is also recognized in the River Continuum Concept (Vannote et al., 1980) and river corridor principles (Ward et al., 2002; Gangodagamage et al., 2007). A review of increasing numbers of landscape scale watershed studies revealed that landscape context and heterogeneity can help to predict freshwater ecosystem composition, structure, and function (Johnson & Host, 2010).

It is important to differentiate efforts to quantify structural versus functional connectivity. Some authors distinguish the two as a separation between static influences that do not change over the short-term, such as physical characteristics of the catchment, and they refer to this as "structural connectivity". In contrast, the more dynamic information such as rainfall and runoff patterns is referred to as the basis for "functional connectivity" (Lexartza-Artza & Wainwright, 2009). However, terrestrial ecologists use these terms differently. They assess structural connectivity based on the physical landscape characteristics; whereas, functional connectivity implicitly includes measurements of an organism's movement through the landscape or estimates of habitat suitability required for movement based on species preferences (Rudnick et al., 2012). We argue that hydrologic connectivity, both structural and functional, as well as species habitat requirements at different life stages, needs to be considered to fully understand hydrologic habitat connectivity and to assess potential consequences of hydrologic alterations on species and ecosystem processes. This approach is in line with Geist (2011), who points to the need for qualitative and quantitative integration of abiotic and biotic concepts developed in freshwater ecology with biodiversity conservation approaches.

Emergence of hydrologic connectivity science literature

The increased recognition of the importance of understanding hydrologic connectivity and its utility for research in both physical and ecological watershed science can be seen in the increasing number of articles published that include this subject. Our search of references included in Web of Science in January 2012 reveals that before 1996 there were no records for articles that include the two words, hydrology and connectivity, but by 2005 there were 75 references detected and, more recently, over 30 per year for a total of 249 through the end of 2011 (Fig. 1). The emergence of hydrologic connectivity science and its utility for both physical and ecological watershed research can be seen in the fact that 53% of these papers were published in physical science journals such as *Journal of Hydrology* ($N = 16$) and *Hydrological Processes* (N = 31); 33% in ecological journals such as *Hydrobiologia* ($N = 5$) and *Journal of the North American Benthological Society* ($N = 5$); and 10% in inter-disciplinary journals such as *Wetlands* ($N = 9$). Even with the advent of the journal *Ecohydrology* designed to foster increased scholarship on interactions between the hydrologic cycle and ecosystem processes, there are only a few examples of freshwater community responses to hydrologic alterations (e.g., Cadbury et al., 2010; Arthington & Balcombe, 2011; Arriana Brand et al., 2011).

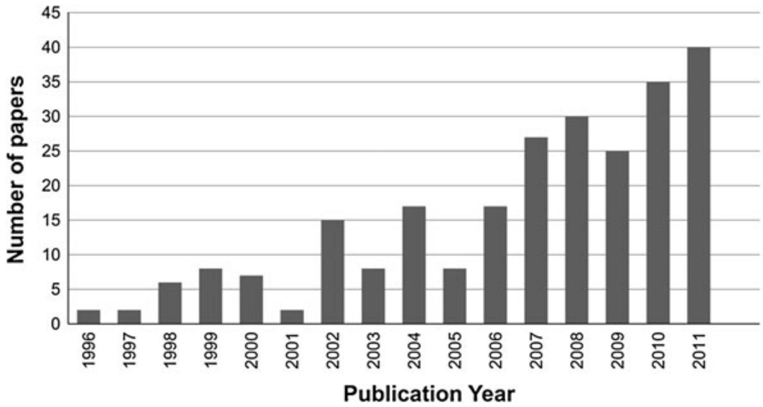

Fig. 1 Numbers of articles containing hydrology and connectivity as key words cataloged in the web of science over time (search updated as of November, 2012)

Hydrologic habitat connectivity loss and recovery in med-rivers

Approximately 10% of the published articles identified above appear to report research done specifically on med-rivers. This research has advanced our understanding of hydrologic habitat connectivity for med-rivers. For example, based on river research done in Spain, Gallardo et al. (2009) emphasized that hydrologic connectivity is one of the main controlling factors of habitats and aquatic assemblages on river floodplains. Because stream biota in med-regions are adapted to characteristic seasonal and inter-annual variability, they can often persist in disconnected pools or the hyporheic zone during the dry season (Bêche et al., 2009). However, these seasonal streams can still be impacted when natural flow variation is reduced both during the wet season when ecosystem processes depend on high flow events and during the dry season when there is little to no rainfall to replenish the system (Resh et al., 1988; Gasith & Resh, 1999).

Hydrologic alterations designed to provide a stable water supply and to prevent flooding in these areas are known to reduce natural flow variability in river systems. Here, we refer to hydrologic alterations as any anthropogenic disruption to the magnitude or timing of natural river-flows over time and space (Rosenberg et al., 2000). In most cases, dams, water abstraction patterns, and flow path alterations support productive human systems yet fail to protect the ecologic functions of rivers (Postel et al., 1996). A thorough review of field studies documenting observed changes to freshwater plants and animals, world-wide, associated with a loss in hydrologic connectivity is provided by Bunn & Arthington (2002).

The loss of natural flow variability and river management simply for minimum flows has led to extensive loss of native species (Moyle & Light, 1996). Biodiversity losses associated with hydrologic abstractions are well-illustrated on the med-climate Iberian Peninsula, where numerous water projects have been implemented to mitigate flood risk along with channel modification to accommodate intensive land use. These alterations, along with polluted water conditions, led to observable changes in the distribution of nine native fishes and the expansion of 18 introduced freshwater fishes across a southeastern Pyrenees watershed (Aparicio et al., 2000).

Recent research in the Central Valley, California, demonstrates the overall importance of hydrologic connectivity, as variable flow regimes influence the functionality of these once vast floodplains (Opperman et al., 2010). They describe the ecologic benefits of reconnecting floodplain along the Sacramento River by removing a degraded levee, creating 600 ha of reconnected habitat and improving flood protection for urban areas downstream as well as adjacent agricultural areas. This research emphasizes that ecologically functional floodplain requires connectivity to a river and variability in flow regimes to activate and maintain floodplains.

Recontouring the landscape can influence hydrologic connectivity and Meerkerk et al. (2009) provide an example of how to measure these impacts using connectivity metrics. The connectivity measure they used for evaluating the influence of agricultural terraces on med-river hydrology in southeast Spain is an integral of a function that quantifies the average distance over which two adjacent locations are connected in any direction. They found that connectivity, as measured by changes in average flow path distance, and total discharge both increased with terrace removal. These spatially explicit modeling efforts demonstrate one way to quantify changes in hydrologic flow paths and provide measures for how inter-annual variation in rainfall, as well as expected changes in climate, will likely influence hydrologic connectivity. Although these methods offer attractive simplification of the hydrologic network and estimates of flow connectivity, we need to expand beyond network geometry to better integrate spatially explicit hydrologic modeling with species functional response models to measure hydrologic connectivity. The merging of species functional response models with spatially explicit hydrologic modeling as described in the framework below will help improve our understanding of the potential consequences of flow alterations and impaired connectivity on freshwater communities.

Grantham (2011) provides an example of how measurements of longitudinal flow connectivity directly link to species requirements. This research took advantage of 2D hydraulic model simulations under different flow conditions and least-cost path analysis to identify the deepest potential migration pathway for salmonids in California's coastal streams. Application of this fish habitat connectivity analysis across multiple stream locations allowed for the range of minimum flow requirements to be estimated for fish passage. In addition, the modeling freshwater habitat connectivity under different flow magnitudes allowed for examination of the impacts of inter- and intra-annual variation in stream flow on an aquatic species.

Impacts of low stream flow on med-river hydrologic habitat connectivity and species persistence

Both drought and water removal can result in a loss of hydrologic habitat connectivity, which in turn impacts stream ecosystem processes and native biota in med-rivers. Habitat loss, reduced productivity, and mortality associated with water removal may be greater in med-rivers that rely on high flows for geomorphic processes and fish migration, and that have little to no rainfall during the dry season to replenish streamflow. In California's med-rivers, changes in macroinvertebrate composition resulted from reduced longitudinal hydrologic connectivity during drought conditions (Bonada et al., 2006). The observed increase in variability with respect to species richness that was observed among disconnected pool communities was attributed to differences in the duration of pool isolation. This demonstrates that loss of hydrologic habitat connectivity can result in changes in the number and size of pools, as well as the time during which they remain isolated and both can increase stress for pool inhabitants.

Another example of where drought can compound the effects of flow alterations on fish community composition is the Iberian Peninsula, where warmer lower flows resulted in elevated numbers of invasive species (Bernardo et al., 2003). These results are consistent with other med-regions where both fish and riparian plant communities show marked changes after periods of drought even without extensive alterations (Bêche et al., 2009). Their long-term field study revealed that native fish abundance was the lowest during the drought period and highest during the wet years. A prolonged period of drought allowed for the establishment and persistence of the invasive green sunfish (Centrarchidae: *Lepomis cyanellus*) despite subsequent large flow events (Bêche et al., 2009). Invertebrate communities in that stream were also influenced by flow levels but recovered from drought more quickly and in a predictable fashion. Because there is little to no rainfall during the summer in med-climate regions, reduction in spring and summer stream flows, whether the result of drought or water extractions, can have more profound impacts on aquatic species in med-regions as compared to more mesic climate regions. For example, field research done in Australian med-climate intermittent streams demonstrates that while some macroinvertebrates possess strategies to survive drying, drought conditions can eliminate or decimate several groups of macroinvertebrates (Boulton, 2003).

It is important to note that increasing hydrologic connectivity in med-rivers is not always desirable if it occurs at time when native species are adapted to fragmented habitat found under low flow conditions. For example, abnormally high flows during what is usually the dry season in med-rivers can result from summertime irrigation practices in agricultural and urban landscapes (de Jalón et al., 1992; de Jalón, 2003; Kondolf & Batalla, 2005). Hence, some streams suffer from higher than normal dry season flows as a result of what some have referred to as "urban drool" or the use of river corridors as conduits to supply downstream water users with water stored upstream. For example, along the Pacific Ocean, young salmon fry survive in low flow and intermittent pools through spring and summer, conditions that are unfriendly for invasive fish predators. When streams are used as conduits to move stored water during the dry season, the resulting abnormally high summer flows can result in marked reductions in salmon populations as was observed in the Russian River, California (Moran, 2012). In these cases, reducing summer flow, and hence decreasing longitudinal hydrologic connectivity, can be essential for native species recovery and invasive species control (Jackson & Pringle, 2010).

Hydrologic habitat connectivity restoration modeling framework

Integrated modeling used in environmental decision support has been gaining popularity as a result of increased recognition of the need to integrate human and environmental issues for policy making (Oxley et al., 2004). Some integrated models focused on land degradation are comprised of sub-models that simulate hydrology, human influences, crops, natural vegetation, and climatic conditions, all differing in spatial and temporal resolution (Oxley et al., 2004; van Delden et al., 2007). The modeling framework we describe below is designed to couple physical and ecologic models to quantify impacts to hydrologic habitat connectivity associated with topographic alterations, flow restoration, or climate-change scenarios. This is the first attempt that we know of to illustrate all the necessary spatially explicit, hydrologic, and ecologic modeling components required to quantify hydrologic habitat connectivity and evaluate the impacts of channel and flow alterations for individual species habitat requirements. Previous research including a good deal of advances in GIS science, hydrologic modeling, and habitat suitability analysis provide the fundamental components incorporated into the framework illustrated in Fig. 2.

Stream flow and channel context: first steps

The integrated modeling framework presented in Fig. 2 can be used to explore hydrologic habitat connectivity for floodplain-dependent species by evaluating different flow and climate scenarios (Step 1) as well as changes in the physical landscape (Step 2). Examination of differences in year-to-year changes in stream flow (Step 1) is particularly important for med-rivers. This is because the amount and timing of precipitation within the wet season is highly variable between years, compared to other regions with similar total annual rainfall. Climate change introduces another source of uncertainly with respect to the amount and timing of rainfall, which will influence the probability of recovering hydrologic habitat connectivity. Therefore, global climate-change models need to be integrated with hydrologic information to be able to examine the influence of likely changes in stream flow patterns that may result from future climate change. These alternative flow scenarios can be incorporated as shown in Step 1 (Fig. 2). Extensive engineered hydrologic rerouting is common in med-regions to increase controls on flooding and water delivery. These alterations have obstructed natural hydrologic processes that control the intensity and frequency of flooding and floodplain interactions (Bunn & Arthington, 2002). Hence, the restoration of med-rivers often requires physical infrastructure alteration such as dam and levee removal which in turn changes the physical landscape (Step 2) and the resulting hydrologic routing of water to improve lateral connectivity between river channels and adjacent floodplains.

Once the relevant hydro-climate and channel or other physical restoration scenarios are selected, the relevant stream flow and topographic representation of the physical alterations proposed must be procured and processed as the gears in Step 3 and 4 suggest (Fig. 2). Stream flow records drive the analysis of hydrologic dynamics (Step 3), and can reflect historic periods, future predictions such as climate changes, or proposed managed flow scenarios. In addition, a physical representation of the channel-floodplain topography (Step 4) must be specified to examine longitudinal, lateral, or vertical hydrologic connectivity under alternative flow scenarios.

Hydraulic modeling (Step 5)

With recent advances in watershed science and increased access to remote sensing data and computing power, many options exist for hydraulic modeling

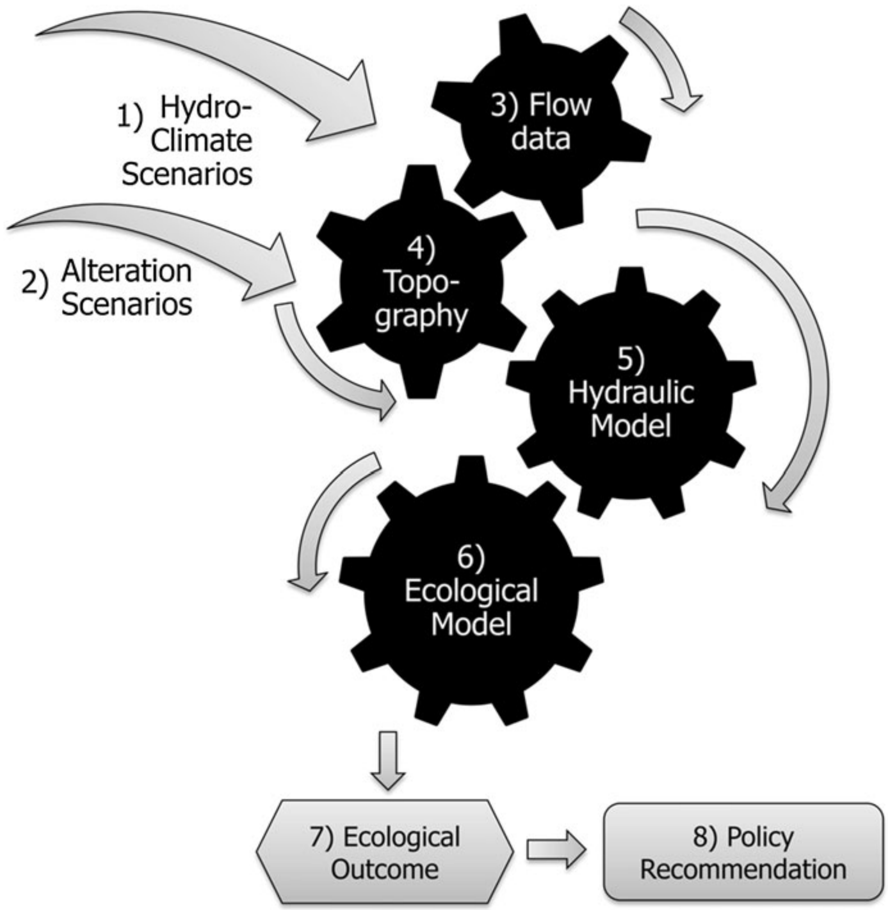

Fig. 2 This integrated Hydrologic Habitat Connectivity Modeling Framework includes: (*1*) incorporation of climate-change models at a fine (daily) temporal scale; (*2*) proposed alterations to the channel morphology at a fine (2 m pixel topography) spatial scale; (*3*) fine-scale empirical hydrology; (*4*) fine-scale empirical topography data; (*5*) spatially explicit hydraulic modeling; (*6*) species and life stage-specific ecological models; (*7*) to produce quantitative ecological outcomes such as changes in habitat availability; and (*8*) decision support for policy and management adoption

(Step 5) (Hunter et al., 2007; Tarekegn et al., 2010). One widely used method for hydraulic modeling uses cross sections perpendicular to the flow direction in a standard riverine numerical model based on one-dimensional (1D) finite difference solutions of the full Saint–Venant equations using programs such as MIKE-11 and HEC-RAS (Bates & De Roo, 2000). Two-dimensional (2D) models using depth-averaged Saint-Venant equations are increasingly used for aquatic biology and geomorphology because they provide finer-scale distributions of velocity vectors with lateral components instead of cross-sectional average downstream speeds that result from a 1D model (Pasternack et al., 2004). 1D storage area models representing floodplain cells can be an appropriate compromise between 1D compound channel and 2D models (Besnard & Goutal, 2011). New, increasingly efficient 2D model formulations of shallow water equations are also available for creating more realistic representations of floodplain flows (Bates et al., 2006). Three-dimensional (3D) models of fluvial dynamics offer a more complex representation of flows, including a vertical component, but require more computational power and sophisticated assumptions to parameterize a model (Lane et al., 1999).

Researchers in med-rivers are applying hydraulic modeling tools to examine flow scenarios. For example, Moussa & Bocquillon (2009) demonstrate how a reduced complexity 2D hydraulic model can be used to represent effects of fourteen scenarios of construction of dams, embankments, or coupling of both dams and embankments in Southern France. Nunes et al. (2009) examined the role of soil moisture in increasing the hydrologic connectivity between hillslopes in two med-watersheds in Portugal using the MEFIDIS storm runoff and erosion model. Ramireddygari et al. (2000) added groundwater to surface water modeling to integrate modeling with a management scenario approach to develop a comprehensive, watershed-scale, continuous simulation model, but like the previously cited studies, they did not attempt to integrate an ecologic model necessary to estimate species' responses to changes in flow.

Ecologic modeling (Step 6)

The connection between hydraulic results and ecologic outcomes requires an ecologic model (Step 6) that specifies relationships between flow regime characteristics and ecologic response. Environmental flow requirements established using generalized flow-ecologic relationships provide the basis for recovering natural flow regimes into river management practice across biogeographic regions (Poff et al., 2010). Unfortunately, very few quantitative ecologic response models are available for freshwater species because they require an in depth understanding of species biology and responses to different hydrologic conditions. Hence there is a need for quantifying ecologic responses across well-defined gradients of flow regime alterations to support the type of ecologic models we propose (Poff & Zimmerman, 2010).

A few studies have quantified ecohydrologic interactions in non-med-regions and may have applicability to future studies in med-rivers. Acreman et al. (2009) present a simple framework for evaluating wetland ecohydrologic response to climate change in the UK, outlining steps similar to our approach, though specific to climate models and static physical landscapes. They emphasize the need to run models to define relevant ecosystem variables to assess the potential impacts of climate on the habitat requirements of the species and communities of interest. Another integrated modeling study linking hydrology and community dynamics in wetlands focuses on evaluation of restoration project sites using habitat function performance measures such as growth rate of key species, habitat suitability analysis, isotope abundance of indicator species, and a bird census (Twilley & Rivera-Monroy, 2005). Focusing on ecohydraulics for stream and river restoration specifically, Bockelmann et al. (2004) implemented a field and numerical modeling study in the UK to predict habitat distributions of macroinvertebrate species using macroinvertebrate suitability relationships to 2D velocity and bed shear stress.

Fortunately, there is an ecosystem functions model (Step 6) relevant to the lowland river-floodplain systems of the med-climate Sacramento-San Joaquin Rivers Basin where we conducted our case study (USACE, 2002). This model was developed to estimate functional responses based on key indicators/taxa of biologic change. Essentially, this ecologic model is a statistical tool that facilitates definition of flows that are useful for particular biota or ecologic processes. For example, Shafroth et al. (2010) used this ecologic modeling approach to estimate riparian tree seedling establishment and to evaluate the response of these seedlings to floods based on a 1D HEC-RAS hydraulic model. In addition, they employed a MODFLOW model to assess groundwater interactions contributing to re-emergence of surface flow downstream.

Final steps of the modeling framework

In summary, the steps of the integrated modeling framework (Fig. 2) currently require the use of an individual model type chosen by a user for each major step. This provides flexibility in choice of hydraulic model (1D or 2D), ecologic model (e.g., EFM), and data management/spatial tools to evaluate model output. Selection of component models must be made wisely, with a clear understanding of project purpose, data availability, and computational limitations (Lane et al., 1999; Bates & De Roo, 2000; Hunter et al., 2007). For example, if one is studying a hydroecologic relationship for salmon spawning, patterns of sediment erosion and fish habitat quality can be better resolved using 2D models of lateral flow variations, as 1D models appear to over-predict habitat quality (Brown & Pasternack, 2009).

The final outcome of this integrated modeling framework quantifies the potential ecologic response to changes in habitat availability under the various hydrologic and/or physical alteration scenarios. The results from these integrated modeling scenarios can inform policy-makers considering options in a given study area (Step 8).

Case study: modeling scenarios for improving hydrologic habitat connectivity

The integrated analysis framework presented above and illustrated in this case study was developed to better quantify flow requirements for the protection of floodplain ecosystems in highly managed med-climate watersheds. The framework comprises the following actions: (1) Acquire high resolution topography and fine-scale empirical flow data; (2) Integrate hydraulic models to account for inter- and intra-annual flow variability; (3) Apply the best available ecologic models to relate flow magnitude, duration, and frequency to species requirements; (4) Examine how ecologic processes may respond to channel restoration options, expected changes to flow under climate change, or that may result from water management modification; and (5) Provide scenario results to inform policy and management decision-making in an effort to reveal trade-offs between water use and essential levels of hydrologic connectivity for ecosystem recovery.

In this case study, we examine lateral hydrologic habitat connectivity for floodplain-dependent taxa. The analysis was done for a small portion of a med-river, the San Joaquin River, that once provided fertile floodplain habitat for freshwater communities across California's San Francisco Bay-Delta. In this system, large inundated flood basins, shallow seasonal lakes, and backwater sloughs were once common during winter and spring when high river flows spilled onto the land (Katibah, 1984; Kelley, 1989). The San Joaquin River once supported one of the most productive in-river fisheries for Chinook salmon (*O. tshawytscha*) in the state of California (CDFG, 1990; Yoshiyama et al., 1998).

The San Joaquin River drains approximately 83,000 km^2, running about 560 km, flowing northward to meet the Sacramento River in the Delta, which exhibits a network of islands and channels that feed into San Francisco Bay. The habitat has been impacted by development and water diversions and constrained by levees that limit riparian and floodplain processes, although these levees sometimes fail under high flows (DWR, 2005; Florsheim & Dettinger, 2007). Over 80 dams on the San Joaquin River and its primary tributaries capture or store more than 135% of the average annual yield of the basin, such that the San Joaquin has experienced a 71% decrease in annual water yield (Cain et al., 2003). In addition, the Lower San Joaquin River is considered by the State as an important area for restoration projects to provide ecosystem benefits as well as flood risk relief for the downstream city of Stockton (DWR, 2010).

This study used the integrated modeling steps outlined in the framework described above (Fig. 2) to evaluate the potential for increased lateral floodplain habitat connectivity for several species of concern. The Sacramento splittail (*P. macrolepidotus*) is a native freshwater minnow that was once very common in the upper San Francisco Estuary and Central Valley of California. Splittail can tolerate moderately salty water and prefer slow-moving water found in marsh and slough habitat along the river and they spawn in the adjacent floodplains. This species has all but been eliminated from most of its former range and is now restricted to the last of the remaining marsh habitats including those primarily found in the lower Delta, Suisun Bay, Suisun Marsh, and Napa Marsh (Moyle, 2002). Similarly, Chinook salmon were once prevalent in the Sacramento-San Joaquin river system, with annual in-river catches reaching 4–10 million pounds prior to large-scale commercial ocean fishing (Yoshiyama et al., 1998). In fact, the Sacramento-San Joaquin river system was responsible for over one half of the annual ocean harvest (PFMC, 1984). Recently, these native populations were extirpated; however, flow and fish recovery efforts are underway. Young fry grow best in areas with lower water velocity and high rates of invertebrate drift such as floodplains (Sommer et al., 2001). We also include phytoplankton in our group of key taxa to demonstrate the broad range of conditions under which lateral hydrologic habitat connectivity can be impacted by differences in flow regimes and channel morphologies. Phytoplankton production is critical for the entire food web; however, it requires the fewest number of inundation days for ecologic benefits to accrue.

We quantified the habitat availability under different hydro-climate regimes (Step 1, Fig. 2) to compare three restoration alternative options (Step 2, Fig. 2). We compared the following land modification scenarios: Scenario (1) the existing channel and associated flow path; Scenario (2) the flow path predicted with the addition of a slough bypass; and Scenario (3) a new flow path predicted after removing the eastern levees (Fig. 3). These alteration options were analyzed using flow regimes including the historic flow record as well as the forecasted hydrologic record from climate-change scenarios based on USGS CASCADE project daily flows at Vernalis (Step 3, Fig. 2) (Cloern et al., 2011). The spatial landscape was modified in the GIS to reflect changes in topography (Step 4, Fig. 2) that allow for increased inundation and then a HEC-RAS hydraulic model (Step 5, Fig. 2) was run to simulate changes in flow paths under different flow magnitudes.

Ecosystem function models (Step 6, Fig. 2) for the study species were employed using hydrologic criteria (including flow frequency, duration, and seasonality) and ecologic criteria (including inundation seasonality, duration, and habitat characteristics) documented in the literature (Sommer et al., 1997; Jassby & Cloern, 2000; Sommer et al., 2001; USACE, 2002; Sommer et al., 2004; Table 1).

The restoration alteration options include Scenario 1, which reflects the current position of levees in the Vernalis to Mossdale Corridor upstream of Stockton, CA. Scenario 2 includes a proposed slough bypass that results from allowing the Walthall Slough to be activated as part of the flow path via a 6.1 m elevation-weir allowing inundation of lands adjacent to the main stem of the San Joaquin River. Scenario 3 represents the removal of the eastern levees of the San Joaquin and some cross-levee removal from nearby agricultural fields. Because the most extreme climate-change model used reflects air temperature increases of 0.42°C per decade (A2GFDL scenario) with a significant precipitation decline (28 mm per decade) (Cloern et al., 2011), the A2GFDL scenario also displays a significant negative trend in unimpaired runoff and a reduced frequency of spring floods.

Case study results

The integrated modeling approach used in this case study reveals the area of inundation and the flow conditions required for each species' functional habitat requirements (flood duration and frequency). The results demonstrate how factors relevant to ecologic function such as the duration and frequency of inundation reduce the availability of functional floodplain habitat for the three taxa examined. Table 1 includes ecologically relevant flow parameters for the selected species and the probability that criteria were met or exceeded under the historic (1929–2010) and A2GFDL climate change (2010–2099) flow regimes, as well as the concurrent flow rate observed or estimated. Hence, we see differences in ecologic outcomes (Step 7, Fig. 2) with respect to the estimated flooded habitat area useable by each species and the associated flow magnitude required between past and forecasted future periods of record. Much of the floodplain is not usable for the taxa of interest, because they require more frequent flows in particular seasons and durations than is regularly observed or forecasted to occur.

Under existing levee-floodplain conditions (Scenario 1), the available floodplain habitat totals to

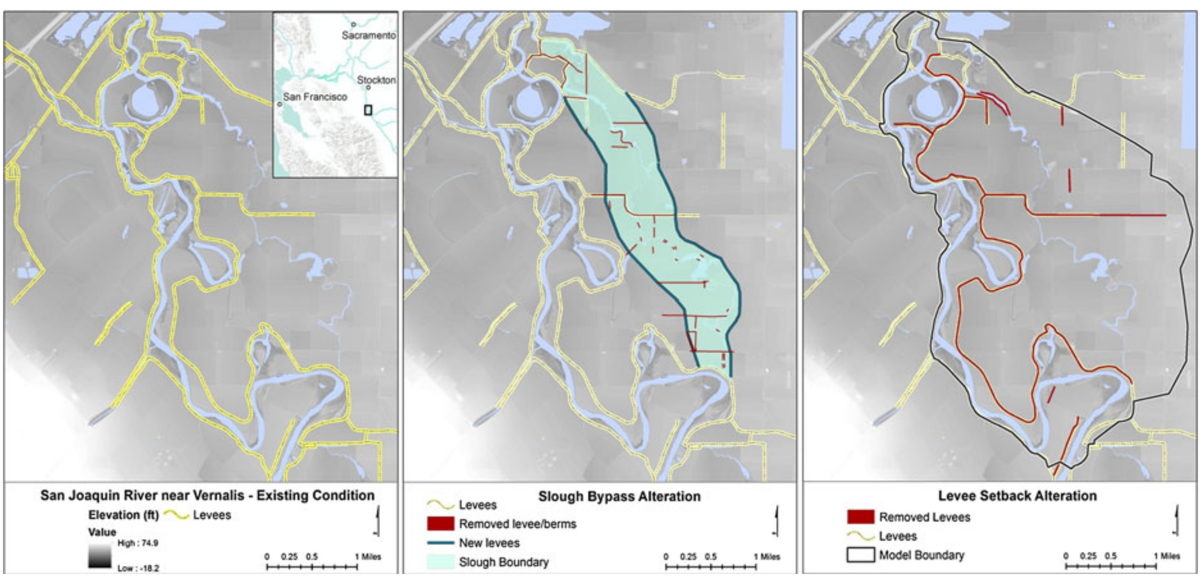

Fig. 3 Schematics of physical topography used to model three scenarios. The *left panel* shows the entire levee system currently in place and the wetted channel (*blue*) for the San Joaquin River between Vernalis and Mossdale, California. The *middle panel* shows the slough bypass (*light green*) that would be inundated periodically if a weir and new levees are installed. The *right panel* shows the area of floodplain that could be hydrologically reconnected to the main channel and flood periodically if the eastern levees were removed (*black line polygon*)

Table 1 Ecologically relevant flow parameters for selected taxa and the probability that criteria were met or exceeded under the historic (1929–2010) and the A2GFDL climate change (2010–2099) flow regimes, as well as the concurrent flow rate observed or estimated

Ecologic relevance	Season	Duration	How often	Exceedance probability	Flow (cms)
Historical Vernalis Flow Regime (1929–2010)					
Splittail spawning and rearing	Feb–May	At least 21 days	At least every 4 years	0.25	435
Chinook salmon rearing	Dec–May	At least 14 days	At least every 2 years	0.5	181
Phytoplankton production	Dec–May	At least 2 days	At least every 1.3 years	0.769	118
Climate-Change Vernalis Flow Regime A2GFDL (2010–2099)					
Splittail spawning and rearing	Feb–May	At least 21 days	At least every 4 years	0.25	203
Chinook salmon rearing	Dec–May	At least 14 days	At least every 2 years	0.5	127
Phytoplankton production	Dec–May	At least 2 days	At least every 1.3 years	0.769	97

216 ha for splittail, 89 ha for Chinook salmon rearing, and 54 ha for phytoplankton production, resulting largely from the differences in the flood frequency requirements for these taxa. The increased benefit of additional functional floodplain habitat for the key taxa of interest afforded by a bypass or levee setback treatment at our site is mapped in Fig. 3. While the bypass (Scenario 2) would open up 1,212 ha to potential flooding and the levee setback treatment (Scenario 3) increases the maximum potentially inundated area from 696 to 2,496 ha, the taxa we examined receive far fewer flood area benefits because of their seasonal, frequency and duration flood requirements (Fig. 4). Splittail gain 51% more potential functional area under a bypass alternative, and 30% more under the levee setback alternative. Chinook salmon increase potential functional area by 9% in the bypass configuration (scenario 2) but the setback configuration (scenario 3) produces no increase in the functional floodplain area. Phytoplankton production increases in functional floodplain habitat area are similar, with increases of 17% for the bypass and no increase for setback configurations. The levee setback configuration only opens up to inundation when flows exceed 400 cms, explaining the paucity of habitat benefits observed under the historic flow regime. Recontouring of the landscape and additional channel restoration could increase the total inundated area associated with these treatments.

The two topographic alterations (Scenarios 2 and 3) add inundation area but drastically fewer flooded benefit acres are achieved when flood frequency requirements are increased for species life history requirements. Thus, our case study results indicate that altering channel configurations to change flow paths can at best result in a 51% increase in habitat acres for the most flexible species requirements and point to the need for increasing stream flow to improve the desired ecologic returns in flooded benefit area for all of these focal taxa. If a policy based on a minimum flow threshold similar to the State Water Resources Control Board recommendation of a 60% unimpaired flow criteria (SWRCB, 2010) were

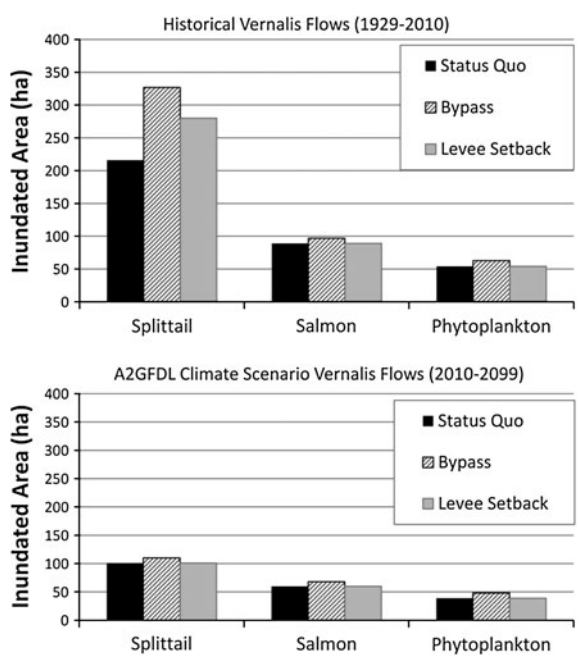

Fig. 4 Inundation areas for three ecosystem benefits under two hydrologic records and three physical configurations of lateral river-floodplain connectivity based on historic and climate-change scenario flows forecasts from the USGS CASCADE project at Vernalis (Cloern et al., 2011)

enacted for the San Joaquin River, results would show approximately threefold increases in splittail area and over fourfold increases in salmon area for both setback and bypass configurations.

The hot and dry climate-change modeled outcomes (A2GFDL) pose even more challenges for restoration of habitat for fish and the food web, as under these conditions the Scenario 3 setback alteration's benefit area for splittail is reduced by 64%, from 280 ha of flooded benefit area to 101 ha. The impact of climate-change flows for our study area is notable, but there is potential for mitigating the magnitude of floodplain benefit decreases by implementing a minimum flow threshold based on water year types and mimicking natural flow regime patterns (SWRCB, 2010).

The results of this case study support policies that would allow for a levee setback over a bypass given larger flows (Step 8, Fig. 2). We suggest employing a minimum flow threshold based on operations of upstream dams to greatly enhance the functional hydrologic habitat connectivity of the proposed restoration scenarios. Increases in flow rates would increase flood frequency and duration during the right time of year to meet the habitat requirements outlined in Table 1 for the study species.

Discussion and conclusions

We concur with King & Caylor (2011) that the fields of hydrology and ecology have yet to be truly combined in a hybrid discipline. Our review of the literature on the theory and application of connectivity science to ecohydrology reveals that hydrologic habitat connectivity offers an important approach to integrating hydrologic and ecologic processes for the study of freshwater ecosystem and species recovery. In fact, understanding patterns of hydrologic habitat connectivity can explain patterns of species richness in med-river systems, help forecast community dynamics and guide conservation of biodiversity (Bornette et al., 1998). In order to effectively assess hydrologic habitat connectivity for med-rivers, we need to examine what has previously been referred to as structural and functional connectivity, including relatively fixed landscape and channel characteristics, dynamic stream flow processes, and aquatic species habitat and movement requirements.

Med-regions face trade-offs between providing water security to meet the human demands for freshwater and the need for dynamic natural flow regimes required to support biodiversity. Many med-river management plans include habitat restoration and floodplain recovery to correct for the loss of riverine wetlands resulting from historic river management for flood control and water security at the expense of environmental protections (Logan & Furse, 2002; DWR, 2011). Our California med-river case study emphasizes the value of modeling floodplain connectivity restoration to quantify potential benefits for aquatic species persistence and recovery.

The modeling framework we present relies on a scenario-based approach to estimate the ecologic returns of different hydrologic alterations including changes to the physical landscape and flow dynamics which influence habitat connectivity for freshwater biota. The utility of this modeling framework is demonstrated with a case study of lateral stream-floodplain hydrologic habitat connectivity, whereby changes in physical flow paths improve the available number of flooded habitat hectares but changes to the hydrologic flow regimes are required for maximum ecologic benefits for freshwater fish, especially to allow for climate-change adaptation.

Scenario planning remains one of the best tools we have for environmental problem solving when a high level of uncertainty about the system exists and manipulation may be difficult (Peterson et al., 2003). Also, given that there are always multiple ecosystem services traded-off for any proposed ecosystem alteration, it is critical that scenarios be developed that take uncertainty into account, and reduce the chances for unintended consequences or perverse results. Trade-offs are often associated when searching for solutions to the demand for water security in mediterranean-climate regions and restoring to the extent possible natural flow regimes. We need to examine the inherent trade-offs associated with various policy options so we can better inform local decision-makers of their consequences and identify the best options for habitat conservation.

Integrated physical and ecologic modeling methodologies for ecologic forecasting are challenging often due to data limitations and a high level of uncertainty in our understanding of the relationship between land use and physical and ecologic responses (Nilsson et al., 2003). However, many researchers argue that evaluating modeled simulations is the best approach to evaluate how freshwater ecosystems respond to non-equilibrium conditions, to identify places that might be prone to failure, and to evaluate system performance under different scenarios such as increased development or climate change (McKinney et al., 1999). While our case study takes advantage of high resolution data, long-term flow records, and several well-established hydroecologic relationships, uncertainty still exists and the results are hard to assess through validation. This uncertainty deems a scenario approach more appropriate than a forecasting approach. The scenarios we use are very different in the area of additional habitat being considered, however, the inherent error in the ecologic functional relationships as well as climate-change flow scenarios is the same between the various scenarios. Thus, the relative changes to habitat connectivity between the scenarios remain highly relevant to the restoration decision-making process.

There remains an urgent need for more studies to link ecologic data with hydrologic modeling and observations (King & Caylor, 2011). This is especially true for med-rivers systems because of their reliance on a high level of variable flows that have often been eliminated in an effort to provide a more consistent year-round water supply to downstream agricultural and urban users. Hence, our ability to integrate hydrologic connectivity into useful restoration ecologic outcomes analysis for med-river systems hinges on comparing flow scenarios that reflect the spectrum of observed inter-annual variability. Integrated human and natural system models are essential to assess the consequences of the large number of hydrologic alterations that have been and continue to be imposed on med-rivers. However, integration of hydrologic and ecologic models is difficult in part because of the high levels of variation associated with med-river systems which require high temporal and spatial resolution data to provide a fully informed picture of the potential range of outcomes. Nonetheless, recent approaches to ecologic habitat connectivity as well as recent advances in integrated physical and ecologic modeling can now be used to estimate the consequences of different river management options on today's biota and inform climate-change adaptation strategies for med-river systems.

The need for validation through physical and ecologic field monitoring cannot be over-stated. This type of monitoring is essential to make necessary revisions to our models and provide an adaptive feedback loop for management decision-making based on the best available science. Developing scenarios and forecasting outcomes is similar to adaptive management in that it takes into account uncertainty (Peterson et al., 2003). Adaptive management is critical to maintaining the utility of environmental modeling through continued improvements in input data, model refinement, and revised scenarios that reflect increased understanding of potential adjustments to the system.

The framework we propose does not explicitly incorporate social context or costs in addition to the ecologic returns that various restoration alterations might result in under different flow scenarios. However, the estimated ecologic benefits can ultimately be compared with costs for restoration, benefits for flood protection, loss of land productivity, and other social factors. Combined hydrologic and economic models exist and are useful for assessing water management and policy issues (McKinney et al., 1999; Newburn et al., 2011). Quantitative agricultural economic models have been used to help stakeholders assess trade-offs for various water planning options based on financial feasibility, economic development, social welfare, environment preservation, and agricultural self-sufficiency (Cai et al., 2004).

The integration of hydrologic habitat connectivity within the existing social context and evaluation of trade-offs is essential to reap the full benefits to management decision-making and improve the way funds are allocated to restoration options. Another advantage of using these models is the visualization of results which is very advantageous to improving the public understanding of likely outcomes and engaging stakeholders in the decision-making process. Most restoration decisions are made without estimating the potential ecologic outcomes of different options or the trade-offs between cost and ecologic benefits. Even more problematic, restoration seldom includes changes to stream flow dynamics because of our dependence on water resources and the economic benefits we draw from access to and control of freshwater for purposes such as food production and flood protection, respectively (Kondolf et al., 2006; Christian-Smith & Merenlender, 2010).

In conclusion, river management institutions need to develop better restoration alternatives to improve hydrologic habitat connectivity before additional med-species go extinct. These restoration actions should be prioritized using a systematic conservation-planning framework that weights both ecologic and economic costs and benefits (Viers & Rheinheimer, 2011). However, the science that should underpin these planning processes is often either unavailable or requires increased attention and support to extend the results to political processes and decision-makers. We recommend using the hydrologic habitat connectivity restoration framework outlined in this paper to quantify freshwater habitat recovery, improve restoration investment decision-making, and to serve as a visualization tool for med-river management. In addition, the protective environmental policies need to be enforced, and new solutions are required to reduce current and future conflicts over water allocation and ecologic flows to maintain freshwater species in med-basins, especially given increased tensions that are likely to arise as our climate changes (Hermoso & Clavero, 2011).

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