APPENDIX H – IMPORTANCE OF FLOW AND STAGE FOR RIVERINE ECOSYSTEMS

Ecological Importance of Flow and Stage in Riverine Systems

The importance of naturally dynamic flow and stage regimes to the long-term maintenance of a river's physical structure, biogeochemistry and ecological integrity is widely recognized (Junk et al. 1989, Poff et al. 1997, Lytle and Poff 2004, Tockner et al. 2008, Arthington 2012). In lotic ecosystems, flow is considered a master variable that drives key physicochemical processes, shapes physical habitat, influences life history strategies and as a result affects the composition, distribution and interactions of biological communities. While water level (i.e., stage) is linked with flow, they are mechanistically distinct, and therefore often influence related but different aspects of riverine form and function. Therefore, the maintenance and long-term integrity of lotic ecosystems is largely determined by the range of both flows and levels that comprise their "natural flow regime" (Hill et al. 1991, Poff et al. 1997, Richter et al. 1997, Poff and Zimmerman 2010, Arthington 2012). The following summary describes the importance of and negative effects of alterations to flows and levels within riverine environments.

Research clearly demonstrates that alterations of high and low flows have profound effects on all aspects of lotic environments, from physical structure, habitat quality, and biogeochemistry to biological community structure and ecological functioning. As such, the long-term persistence and integrity of riverine ecosystems is fundamentally linked to their naturally dynamic flow regime (Poff et al. 1997, Richter et al. 1997, Ward et al. 1999, Poff et al. 2009, Arthington 2012).

The current environmental flows paradigm asserts that flooding and drying events are necessary to maintain an ecosystem's natural characteristics (King and others 2003) and that healthy aquatic and wetland populations and communities require variable flow regimes to protect habitat and life history processes (Poff and others 1997). Multiple MFLs are set in an effort to provide protection to multiple portions of a system's flow and stage regimes.

Hill et al (1991) suggest that the influence of a river's natural flow regime is manifest in four critical ways: 1) flood flows create and maintain floodplain and valley features; 2) overbank flows maintain riparian vegetation, water tables, soil saturation zones and adjacent upland boundaries; 3) in-channel flows determine the structure and function of stream banks and channels; and 4) in-channel flows meet critical life-history needs of aquatic biota. The following sections summarize the importance of maintaining the natural, dynamic flow and stage hydrologic regimes to a river's physical structure, biogeochemistry and ecological integrity.

Geomorphology and Physical Habitat

Channel and floodplain geomorphology are both dependant on flood and drought magnitude, duration, frequency, timing and rate of change. River channel sinuosity and cross section shape are determined by the interplay between flow regime, parent geology, local gradient and sediment character (Chorley et al. 1984, Newbury and Gaboury 1993, Leopold 1995). Natural channel migration and formation of undercut banks is mediated by the frequency and duration of channel forming flows (i.e., bankfull events; Leopold 1995). Flows and levels also influence channel geometry (e.g., width to depth ratio), and the diversity and stability of small patches of habitat within the channel and floodplain (Arthington 2012). Flow influences current velocity and the particle distribution and transport/deposition of fine sediment, thereby influencing streambed structure, topography and complexity (Newbury and Gaboury 1993, Ritter et al. 1995).

In addition to influencing the character of within-channel structure, natural flow and stage variability and magnitude also maintain the long-term geomorphology of floodplains. Floodplains are dynamic environments created and maintained by overbank flows through the processes of erosion, channel migration, point-bar extension, mid-channel bar formation and ultimately floodplain development due to the vertical and lateral accretion of alluvial sediments (Newbury and Gaboury 1993, Leopold 1995). Natural flow variability and within-channel processes control channel migration and, therefore, help maintain valley and floodplain geomorphology, long-term succession of riparian vegetative communities and overall floodplain ecosystem integrity (Wolman and Leopold 1957, Nanson and Beach 1977, Leopold 1995). High-energy flood flows increase the heterogeneity of floodplain habitats, which is linked to increased biodiversity (Salo et al. 1986, Junk et al. 1989). At a given stage, lower flow results in lower stream power and a reduced ability of lotic systems to erode, transport and deposit sediment. Therefore, even if stage is kept constant (e.g., by vegetative damming or some other natural or anthropogenic process) flow reductions can, via reductions in stream power, have a significant negative effect on the long-term maintenance of floodplain structure and function.

Flow regime influences channel migration, which in turn influences the abundance and distribution of two important riverine habitats: undercut banks and large woody debris. Undercut areas caused by channel migration and bank erosion serve as important cover habitat for predatory fish and refugia for both large and small species. Flood induced bank erosion causes riparian tree fall and this input of large woody debris (LWD) in turn provides numerous benefits to lotic systems. These benefits include but are not limited to: increased streambed stability; energy absorption and reduced channel erosion; increased habitat volume and habitat complexity; pool formation; increased carbon input (basal resource for heterotrophic foodweb); increased trapping of fine inorganic sediment; and increased transient storage of fine particulate organic matter (Bilby 1984, Harmon et al. 1986, Abbe and Montgomery 1996, Rosenfeld and Huato 2003, Arthington 2012).

Organic Matter and Nutrient Dynamics

Flow regime also affects the transport and distribution of energy (i.e., organic carbon) and nutrients. Overbank floods flush organic carbon from floodplain to channel, contributing material that ranges in size from large trees to particulate detritus to dissolved organic matter. For large floodplain rivers, lateral contributions of carbon from the floodplain are thought to be much more important to overall river productivity than upstream sources (Junk et al. 1989). Once in the channel, flowing water then moves woody debris downstream, changing the distribution of LWD habitat, fragmenting detritus from coarse to fine and dissolved fractions, and finally transporting and redistributing this basal food resource among different habitats. LWD influences the trapping and storage of fine and coarse particulate organic matter, which allows for increased retention and utilization by microbes, microinvertebrates and macroinvertebrates (see summary in Harmon et al. 1986).

During large floods, previously isolated areas become important food sources for the microbial foodwebs (primarily bacteria and fungi). High flood stages that increase lateral connectivity between the channel and floodplain also increase the transport of higher quality dissolved and fine particulate organic matter to adjacent and lower river reaches (Atkinson et al. 2009). During these two-way exchanges between channel and floodplain, energy and nutrients from highly productive microbial communities is transferred through higher trophic levels, resulting in increased production of microinvertebrates and macroinvertebrates, fish and other vertebrate species (Junk et al. 1989, Bunn et al. 2006, Poff et al. 2009, Arthington 2012).

In addition to being a key driver of carbon cycling, flow also mediates the biogeochemical processing of nutrients (Bernot and Dodds 2005). Flood flows transport nutrients from the channel to the floodplain facilitating nutrient filtration and removal, as well as remineralization and dissimilatory removal (e.g., denitrification). During high flow events nutrients and carbon are transported from the floodplain to the channel (Junk et al. 1989). These physical processes and biogeochemical reactions are key to both autotrophic and heterotrophic productivity within channel and floodplain environments. Biogeochemical processing of nitrogen depends on how water interacts with benthic sediments and organisms within the channel and between channel and floodplain (Cohen et al. 2011). Flow-mediated inputs of LWD increase instream habitat complexity and transient storage of nutrients, thereby shortening nutrient spiraling lengths and ultimately increasing uptake and dissimilation (e.g., denitrification; Webster and Patten 1979, Newbold et al. 1981, Ensign and Doyle 2005, Bukaveckas 2007). Nutrient flux within lotic systems is a function of transport mediated by flood stage and flow, physical storage, biotic retention and remineralization (Newbold et al. 1981). Therefore, nutrient uptake length is strongly influenced by flow. Flow alterations can affect nutrient availability and metabolic waste removal within microbial/biofilm communities, influencing nutrient uptake and transformation. Decreased local velocities can also reduce uptake by decreasing dispersion through biofilms, stimulating increased dependence on internal recycled nutrients (Mulholland et al. 1994). Increased connectivity with the floodplain can also increase system-wide retention of both dissolved and particulate nutrients (Meyer et al. 1988). Decreased flows can reduce denitrification rates in lotic systems by reducing necessary labile organic carbon (e.g., from floodplain, or organic matter fragmentation; Bernot and Dodds 2005). Flood flows and stages can also affect the retention of phosphorus, the uptake of which is related to transport of particulate organic matter and sedimentation rate (Meyer et al. 1988).

River floodplains act as both sources and sinks for sediment and nutrients. The frequency and duration of inundation directly affects nitrogen cycling in floodplains (Arthington 2012). Flood flows mobilize and deposit nutrient rich inorganic and organic sediment. Natural fluctuations between wet and dry phases in turn alternate the duration of aerobic and anaerobic phases within floodplain alluvial soils (Pinay et al. 2002). Aerobic phases are marked by increased nitrification of ammonia, and uptake of nitrate by microbes and plants. During anaerobic phases nitrate is reduced to ammonia, organic material is also reduced to ammonia (ammonification), and dissimilatory removal (i.e., denitrification) occurs. Despite periods of increased denitrification during anaerobic phases, evidence suggests that some floodplain wetlands are overall nitrogen sinks (Brinson et al. 1980). Phosphorus bound to oxidized sediments are deposited, and are taken up by vegetation and microbes. Redox conditions in the surface sediment determines phosphorus release. During long periods of high water level on the floodplain anoxic conditions lead to mobilization and availability of phosphorus. Release and storage of both phosphorus and nitrogen are mediated by hydrology, vegetative cover and growing season (Junk et al. 1989).

During both phases nutrients are incorporated into the microbial loop and vegetative communties. A naturally functioning floodplain is the site of nutrient storage, transformation, uptake and removal. Therefore, flood flow alterations that decrease natural water-table fluctuations and soil saturation, in turn reduce floodplain and whole system fertility and productivity (Arthington 2012). Alteration of the natural flow regime also reduces the ability of floodplains to remove excessive nutrients from the system.

Biological Communities

As a major determinant of geomorphology, physical habitat structure and water chemistry, flows and levels also influence the abundance, diversity and distribution of aquatic and wetland-dependant organisms within riverine channels and floodplains (Poff and Ward 1990, Poff et al. 1997, Bunn and Arthington 2002, Lytle and Poff 2004, Arthington et al. 2006). By redistributing sediment in the channel and floodplain, flow affects habitat suitability and distribution of macroinvertebrates, fishes and other aquatic species (Ward and Stanford 1983, Bain et al. 1988, Ligon et al. 1995, Poff et al. 1997, Marchetti and Moyle 2001). As well as increasing habitat suitability for native fauna and flora, high flows also scour and remove excessive algae and macrophytes, and purge exotic and/or invasive species (e.g. *Hydrilla*) from river and stream channels

(Arthington 2012, King 2014). Reduced variability of river levels can favor exotic fish species that prefer seasonal stability (Moyle and Light 1996, Gehrke et a. 1995).

One of the primary functions/benefits of flow-mediated maintenance of in-channel and floodplain structural heterogeneity and integrity, is the provision of forage, reproductive and refugial habitat for biological communities (Bunn and Arthington 2002). Natural flood flows and levelsincrease habitat heterogeneity and complexity through the scour of pools, increased inputs of LWD and increased undercut banks. Greater habitat complexity provides increased niche diversity, and foraging opportunities. Maintenance of complex habitat increases macroinvertebrate and fish species richness, relative abundance and distribution (Angermeier 1989, Gorman and Karr 1978, Resh et al. 1988, Poff and Allan 1995, Spence et al. 1999, Schneider and Winemiller 2008). Flood induced inputs of LWD provide numerous benefits for lotic communities, including, sediment (organic and inorganic) and nutrient storage; pool formation; provision of substrate for macroinvertebrates, microbial biofilm, periphyton and filamentous algae; basking sites for reptiles; resting sites for birds; and cover for fishes and other vertebrates (Harmon et al. 1986, Piégay et al. 1997, Collins and Montgomery 2002, Pusey and Arthington 2003, Wallerstein and Thorne 2004; Arthington 2012). Fallen trees that have been eroded by floods provide important basking habitat for turtles, snakes and alligators (DonnerWright et al. 1999, Lindeman 1999). In some riverine systems, turtle density, abundance and assemblage structure are positively and strongly related to abundance of downed trees, which serve as basking sites and control water velocity and depth (Gippel 1995, DonnerWright et al. 1999, Lindeman 1999). Exposed trees and logs also provide valuable resting habitat for many species of birds.

The maintenance of river levels sufficient to cover fallen submerged trees is critical for fishes, which rely on LWD in numerous ways (Bilby and Bisson 1998). Submerged LWD is used as spawning substrate (Van Den Avyle and Petering 1988), cover from avian and piscine predators (Angermeier and Karr 1984, Crook and Robertson 1999), protection from high flows (Todd and Rabeni 1989), visual isolation from other fish (Crook and Robertson 1999), thermal refuge (Bilby and Bisson 1998) and especially as foraging habitat (Benke et al. 1985, Van Den Avyle and Petering 1988, Lehtinen et al. 1997, Bilby and Bisson 1998, Schneider and Winemiller 2008). LWD is especially important as a source of invertebrate prey for many sunfishes (*Lepomis* spp.) and other fish species (Wallace and Benke 1984, Benke et al. 1985, Crook and Robertson 1999). LWD input is related to increased habitat complexity and concomitant increases in richness and abundance of fishes and macroinvertebrates (Frothingham et al. 2001, Brooks et al. 2004, Schneider and Winemiller 2008, Lyon et al. 2009, Howell et al. 2012).

In addition to structuring instream habitat through LWD inputs, pool formation and increasing substrate heterogeneity, flood flows also increase the area, diversity and complexity of aquatic habitat by connecting the main channel to temporarily isolated areas (floodplains, sloughs, backwater pools, etc). Flow and stage dynamics also create a diverse mosaic of habitat patches of varying depth, inundation and vegetation successional stage (Ward et al. 1999). This expansion of habitat provides important nursery areas for fish and abundant forage habitat for invertebrates, fish, amphibians, reptiles and birds. Regular flooding increases floodplain fertility, and the abundance of food resources for fishes and other aquatic and wetland-dependent species. Forage for invertebrates and vertebrates may increase to the point where it is not limiting to species abundance or individual growth (Junk et al. 1989).

The natural flow and stage regime of a river is thought to maintain maximum biodiversity at an intermediate level of connectivity between the channel and floodplain (Ward et al. 1999). Low connectivity with the floodplain fragments and reduces habitat, and excessive connectivity homogenizes habitat, thereby reducing biodiversity (Ward et al. 1999). Naturally receding floodplain stage creates ephemeral, heterogeneous and irregularly distributed areas of shallow water with concentrated prey for wading birds and other animals (Battley et al. 2003, Gimenes and Anjos 2011). Reduction of flood levels reduces foraging habitat causing concomitant reductions in diversity and abundance of wading birds (Kushlan 1993, Kingsford and Thomas 1995).

Floodplain inundation enhances dispersal and recruitment and may be important to the population dynamics of many fish species (Copp 1989, Leitman et al. 1991, Hill and Cichra 2005). Prolonged periods of high stage allow fish, invertebrates and other species to migrate from the channel to the floodplain, to foraging and spawning habitats. Seasonal floodplain inundation has also been associated with increased spawning activity and production of riverine fishes (Bayley 1991, Burgess et al. 2012). While some fish species spawn opportunistically within the channel, reproductive cues for some species are tied to timing of rising river stage and floodplain inundation (Bunn and Arthington 2002). Duration of floodplain inundation can influence growth potential and recruitment success for some fish species (see review in Poff et al. 1997, Sommer et al. 2001). Increased stage in the floodplain also provides increased forage opportunities for numerous species of mammals and birds (Postel and Richter 2003). High flood stages that increase lateral connectivity between the main channel and floodplain (and backwater sloughs, etc.) are critical to the many life-history process of aquatic and wetland-dependant species (e.g., invertebrates, fishes, turtles, alligators, wading birds, etc.; Bunn and Arthington 2002, King et al. 2003, Arthington 2012).

Natural instream flow variability and magnitude can also influence macroinvertebrate and fish communities through density-dependent interactions. By changing the relative area (or habitat volume) of different types of habitat within the channel and/or floodplain, as well as accessibility to floodplains, backwaters and off-channel structures, natural flood variability often shifts the competitive advantage of different species over time. Therefore, flow-mediated environmental variation can lead to long-term community stability and increased biodiversity within riverine systems (Grossman et al. 1998, Taylor et al. 2006). Loss of high flows has been shown to impact aquatic communities through reduced diversity, altered assemblages and dominant taxa, reduced abundance and increased exotic species (Poff and Zimmerman 2010). Some research suggests that flood flows may remove exotic fish species while also improving spawning habitat conditions for natives (Marchetti and Moyle 2001).

In addition to creating spatial and temporal habitat patchiness, flow variability also affects aquatic communities through natural selection (Facey and Grossman 1992, Bunn and Arthington 2002, Lytle and Poff 2004). Biota within a given riverine system have evolved life history strategies in response to the natural range of hydrological and hydraulic conditions in that system (Townsend and Hildrew 1994, Poff et al. 1997, Richter et al. 1997). Critical life-history events, for both animals and plants, are tied to short and long-term flow variability. Frequency and timing of high flood stages and flows provide for life-cycle transitions for fish (e.g., movement to floodplain, spawning cues, migration upstream; Poff et al. 1997). Some adaptations are manifest as behavioral responses, such as the flow-induced increase in downstream drift of many macroinvertebrate species. Other types of behavior (e.g., spawning) and emergence from diapause of macroinvertebrates, benthic microorganisms and zooplankton are also linked to rate and magnitude of rising flood waters (Bunn and Arthington 2002). Morphological and behavioral adaptations of some fish species confer a competitive advantage in heterogeneous flow environments (Facey and Grossman 1992, Bunn and Arthington 2002, Lytle and Poff 2004). Therefore, flow regime alterations may reduce the fitness and long-term persistence of some species (e.g., darters, benthic minnows) that are suited to high or variable flow (Carlisle et al. 2010). Reduced maximum and minimum flows has been shown to change fish and macroinvertebrate community composition, favoring those species that can leave unsuitable conditions (e.g., strong swimmers, fast crawlers) or that prefer fine versus coarse substrate (Carlisle et al. 2010). Flow also influences lotic assemblage structure and recruitment by distributing adults and early life stages of fish and invertebrates among different habitats and by aerating fish nests and eggs (see reviews in Poff et al. 1997 and Arthington 2012). For large, low-gradient floodplain rivers, continued connectivity between the channel and floodplain is critical to their diversity, production and long-term ecological integrity (Junk et al. 1989, Sparks 1995, Arthington 2012).

Aquatic macrophyte assemblage structure is, in part, determined by flow. Physical processes mediated by flow include direct scour, substrate stability, micro-scale variability in velocity and shear stress (Wetmore et al. 1990, French and Chambers 1996). Macrophyte location is often patchy within a river. A major driver of this patchy distribution is flow and shear stress variability. Spatial variability in disturbance (i.e., flood flow) frequency and magnitude results in variations in persistence and recolonization (Rea and Ganf 1994, Bunn and Arthington 2002). Reduced flow or flow variability can negatively influence recruitment of floodplain plants, transport of seeds, nutrient availability, and removal of metabolic waste products. Reduction of high flows can impact aquatic macrophyte communities by reducing scour and thereby reducing habitats suitable for recolonization.

Riparian vegetative communities are also structured by flood flows that scour floodplain soils, remove competitors, and saturate soils (Bunn and Arthington 2002). Location and structure of riparian and floodplain vegetative communities are determined, in part, by water table elevation and soil moisture. Frequency and duration of flooding influence distribution, abundance and diversity of plants within floodplains and wetlands adjacent to the river channel (Nilsson and Svedmark 2002). Alterations to flood stage magnitude, duration and frequency can affect plant community succession, boundary location and persistence (Arthington 2012). The natural variability of flooding events is necessary to maintain the native diversity of riparian plant communities, and plants species within a community (Postel and Richter 2003). Natural duration and frequency of de-watering events are also essential, as they allow for soil decomposition, nutrient transformation and recruitment of wetland plant species that need moist, non-inundated soils for natural regeneration (e.g., cypress). Elevated water tables in the floodplain and riparian margin also provide seedlings with prolonged soil moisture, necessary during establishment (Arthington 2012). Flood frequency and timing are also of importance because the life cycles (e.g. seed dispersal, germination etc) of many riparian plant species are adapted to a natural flow regime (Poff et al. 1997).
Note: Literature cited is listed in main MFLs report.