CHAPTER

4 ENVIRONMENTAL AND ECOLOGICAL EFFECTS OF FLOW ALTERATION IN SURFACE WATER ECOSYSTEMS

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4.1 INTRODUCTION

Flow regime change caused by human alterations to the water cycle is evident in all permanently inhabited continents of the Earth (Chapter 3) and these impacts to hydrological regimes have affected freshwater and estuarine ecosystems worldwide. The hydrological regimes of 172 out of 292 of the world's largest rivers are altered by large dams (Nilsson et al., 2005). Analyses based on data at regional and global spatial extents have identified that 77% and 65%, respectively, of the total volume of water discharged in rivers is impacted by dams, dam operations, and water diversion (Dynesius and Nilsson, 1994; Vörösmarty et al., 2010). Freshwater ecosystems support a disproportionately high contribution to global biodiversity and ecosystem services (e.g., food and water), given the small proportion of the Earth covered by freshwater (Carrete Vega and Wiens, 2012). Freshwater biodiversity and ecosystem services are under multiple threats (stressors), with the alteration of hydrological regimes by dams, weirs, and water extraction being the most globally prevalent (Collares-Pereira and Cowx, 2004; Dudgeon et al., 2006; Strayer and Dudgeon, 2010).

Flow alteration resulting from these various forms of disturbances has impacted the ecological functioning and biodiversity of rivers, wetlands, floodplains, and estuaries worldwide (Poff and Zimmerman, 2010). These collective impacts arise from a variety of direct and indirect causes such as habitat loss and fragmentation, altered water quality and thermal regimes, the loss of important life-history cues, changes to food webs and patterns of energy production, and modification of environments in ways that promote ecological invasion (Bunn and Arthington, 2002). Ecological effects of flow regime alteration have been the topic of research and regular synthesis in aquatic ecology since the 1970s, with this research spanning a broad range of taxa, including algae and biofilms, aquatic and riparian plants, benthic invertebrates, fishes, amphibians, and waterbirds. Such studies have further considered multiple levels of ecological organization (individual, population, community, and ecosystem; Box 4.1). Research has also long considered the effects of flow regime change on physical, chemical, and ecosystem processes such as sediment dynamics, nutrient cycling, and energy fluxes, although ecosystem perspectives have perhaps been less well studied.

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BOX 4.1 PROCESSES AND PRINCIPLES OF RIVER ECOLOGY RELEVANT TO UNDERSTANDING ECOLOGICAL CONSEQUENCES OF FLOW REGIME CHANGE

Ecology is defined as the study of how the physical, chemical, and biological features of the environment interact to determine the distribution and abundance of living organisms (Begon et al., 2006). Freshwater ecology applies the study of ecology to freshwater environments such as rivers, lakes, and wetlands. Conceptualizing the fundamental and unique features of river ecosystems is essential to understanding how human activities such as flow regime change modify the ecological processes that influence the distribution and abundance of species (Boulton et al., 2014).

Spatial scaling: By combining physical geography and biology, ecology requires a clear understanding of spatial scaling (Ward, 1989; Wiens, 1989). Spatial scaling is critical in ecology to understand how ecological processes vary in space across global, continental, regional, and local spatial extents. Freshwater environments are viewed as being organized in a nested hierarchy, whereby microhabitats (e.g., the spaces in between rocks in the river bed) are nested within slow-flowing pools and fast-flowing turbulent riffles. In turn, pool—riffle sequences are nested within reaches, which form separate segments (tributaries) of an entire river system (Fausch et al., 2002; Frissell et al., 1986).

Linkages across scales: A hierarchical view emphasizes the dimensions relevant to spatial scaling in freshwater ecology (Ward, 1989): the lateral dimension (the linkages between stream channels, the riparian zone, and floodplains), the longitudinal dimension (linking between headwater, lowland, and terminal zones), and the vertical dimension (depth of habitats, linkages between surface waters and groundwaters). The temporal dimension describes how interactions along these three spatial dimensions vary in time (Ward, 1989). The presence and movement of water is the strongest determinant of the connections and linkages across spatial dimensions.

Mechanistic roles of water: Within freshwater environments, it is the presence and movement of water that mediates the extent to which physical, chemical, and biological processes determine the distribution and abundance of organisms. Sponseller et al. (2013) classify the ecological roles of water into three distinct mechanisms whereby water acts as: (1) a resource or habitat for organisms; (2) a vector for the exchange and movement of organisms, nutrients, and material by controlling hydrological connectivity (Fullerton et al., 2010); and (3) a driver of disturbance and geomorphology.

Levels of ecological organization: Finally, ecological processes influence different levels of ecological organization. Organisms live as individuals, independently sourcing energy and occupying space. All individuals within a habitat are a population, which vary in abundance, biomass, and structure (size, sex, age). Communities are formed by the co-occurrence and interaction of multiple species populations. These interactions are best known as predation, competition, and parasitism (Begon et al., 2006). At the ecosystem level, communities and their nonliving environment are linked by the exchange of material between living and nonliving components. Separate groups of organism (e.g., birds, viruses, bacteria, phytoplankton, macroinvertebrates, fish, amphibians, mammals, plants, and reptiles) all occupy or interact with freshwater environments.

Bringing these concepts together: Ecological impacts of flow regime change are mediated by the effect of anthropogenic drivers (see Chapter 3) on hydrological components of the flow regime, which have consequences across different levels of ecological organization via distinct ecohydrological mechanisms.

Increasingly, the restoration of both the structure and function of aquatic ecosystems degraded by flow alteration is being sought through the delivery of environmental water (Naiman et al., 2012). Although there are presently few published studies evaluating the success of such efforts (Olden et al., 2014), it is clear that flow restoration will be an essential component in restoring many degraded river systems worldwide affected by flow alteration.

As well as there being a strong conceptual basis for why flow alteration can impact aquatic ecosystems (see e.g., Bunn and Arthington, 2002), numerous more systematic reviews have found strong evidence of the effects of flow regulation on ecosystems (Dewson et al., 2007; Gillespie et al., 2015b; Poff and Zimmerman, 2010). For example, 92% of the studies examined by Poff and Zimmerman (2010) reported ecological effects associated with flow regulation. There is thus a compelling evidence base from which to consider the need for environmental water in hydrologically altered river systems, and to minimize the degree of harmful hydrological change in rivers with low levels of water demand and/or water infrastructure.

Ecological effects of flow regime change are not caused by the driver of hydrological alteration per se (e.g., dams, weirs, and urbanization), but rather by the way in which these drivers alter specific hydrological attributes. The purpose of this chapter is to introduce and illustrate the broad range of ecological responses to changes in specific hydrological components that are often altered by anthropogenic flow regime change (Chapter 3). A clear understanding of the impacts of change in specific hydrological attributes is both essential and beneficial to predicting the ecological consequences of flow regime restoration using environmental water regimes (Box 4.1). We first identify how the drivers of flow regime change (sensu Chapter 3) alter specific components of the flow regime, and then summarize the subsequent ecological responses, building on existing reviews and conceptual papers (e.g., Bunn and Arthington, 2002; Dewson et al., 2007; Poff and Zimmerman, 2010). We also give consideration to the local factors that might influence the degree to which hydrological impacts translate into ecological changes such as channel size and morphology and local species traits, and the implications this has for efforts to synthesize impacts across broad geographic settings. We recognize and discuss briefly the capacity for dams and weirs to alter rivers' temperature regimes (Olden and Naiman, 2010) and disrupt habitat and hydrological connectivity (Fullerton et al., 2010). However, this chapter primarily focuses on the effects of changes to the hydrological regime. Our goal is to emphasize the variety of ecological consequences that arise from different types of flow alteration in different contexts, which in turn contribute to decisions and solutions for effective management of environmental water.

4.2 HYDROLOGICAL COMPONENTS: LINKING DRIVERS OF CHANGE WITH ECOLOGICAL RESPONSES

The most pervasive and widespread cause of flow regime change is the storage and regulation of water by dams for the reliable supply of water for human use (Nilsson et al., 2005; see Chapter 3). Storages can be managed to meet a range of human needs, including flood mitigation, hydroelectric power generation, irrigation, and domestic water supply. Many reservoirs are managed in a way that spans multiple uses, often varying across different seasons (Ahmad et al., 2014; see Chapter 3). For example, many storages used for water supply during dry periods, or for hydropower generation, are also used for flood control following high rainfall. Each of these human needs tends to be associated with a distinctive hydrological fingerprint in terms of downstream river flow alterations, for example by reducing flood magnitude and frequency, reducing winter baseflow(s), and increasing summer flows. Describing these patterns of hydrological change has been an active area of research in its own right. There are a large number of hydrological indices used to describe these different elements of hydrological regimes, and much work has gone into trying to identify small sets of indices that characterize the regime as a whole as efficiently as possible (Olden and Poff, 2003). In assessing hydrological change, Richter et al. (1996) proposed a set of 64 indicators of hydrologic alteration statistics that could be used to quantify the degree of flow regime change on the basis of ecologically meaningful metrics. A number of other similar approaches have been proposed. Common to each of these methods is the focus on distinctive *components* of the flow regime (defined in terms of magnitude, timing, duration, frequency, and rate of change). Although the important and distinctive flow components within any given river will likely vary with geography and climate, common elements include the characteristics of in-channel and overbank floods, seasonal low and high flows, and cease-to-flow periods (Bunn and Arthington, 2002). By understanding the natural patterns of these distinctive hydrological components of the natural flow regime (i.e., the flow regime occurring in the absence of water extraction and/or storage), one can begin to consider the various biophysical processes that might be linked to each flow component, and hence to conceive of which components might need restoring as part of an environmental water regime.

Here we begin by summarizing some of the distinctive impacts of different forms of river regulation on major flow components (baseflow(s), high flows, etc.), before moving on to discuss the consequences arising when each of those flow components is altered in the context of our conceptual understanding of freshwater ecosystems (Box 4.1). It is worth noting as an aside that although recognizing distinctive flow components has proven useful in assessing hydrological impacts and environmental water requirements, rarely are flow components impacted in complete isolation from one another, nor do ecosystems respond in that way. Such complexities present distinctive challenges for scientists seeking to understand flow−ecology linkages and isolate particular events from the broader flow regime (Konrad et al., 2011; Stewart-Koster et al., 2014). Nevertheless, we regard the concept of flow components as a useful construct for organizing research into the biophysical impacts of hydrological change.

4.2.1 REDUCED BASEFLOW(S)

Water extraction for human consumption is a major cause of reduced baseflow(s) (i.e., flows occurring in the absence of overland runoff). Water extraction can occur directly from dams, in river reaches downstream of dams, or from groundwater storages that are connected to surface water ecosystems. Many older storages have no capacity to deliver water downstream except from water overtopping a dam wall or a spillway, and thus it is not uncommon for rivers to receive no base flow immediately downstream of large dams, with some baseflow(s) only being restored by tributary inflows. When water is extracted directly either from dams or unregulated rivers, flow volume is reduced and can lead to much lower flows than expected under natural conditions (Brown and Bauer, 2010; White et al., 2012), or even the complete cessation of flow in what would normally be perennially flowing streams (Ibanez et al., 1996; Martinez et al., 2013). Where river channels are used as conduits to transport water between storages and downstream users, baseflow(s) may increase and/or become more stable, although this may progressively decline downstream via extraction and tributary inflows (e.g., Humphries et al., 2008; Reich et al., 2010). Removal of water from groundwater also reduces streamflow in connected surface water systems (Falke et al., 2011; Kustu et al., 2010). Therefore, the process and location of water extraction has variable impacts on flow magnitude, which in turn determines aquatic ecosystem size and driving ecological effects.

4.2.2 REDUCED FLOODS

Perhaps one of the most pervasive impacts of dam construction is the storage and capture of flood waters, which results in increased constancy (reduced variability) of flow from daily to inter-annual time scales. Across the continental United States, flow regulation has reduced the size of maximum floods (Magilligan and Nislow, 2005; Mims and Olden, 2013). In an analysis of river regulation impacts across Canada, Assani et al. (2006) found that reservoirs altered all aspects of the flooding regime, including the size and frequency of spring flooding peaks, and a loss of most flow events with a recurrence interval of more than 10 years. It is also common for dams to remove moderately sized floods from the regime (e.g., Aristi et al., 2014; Sammut and Erskine, 1995), as these are insufficient to fill storages (Table 4.1). Another important but sometimes overlooked impact of river regulation is a reduction in the duration and size of floods and other high-flow events such as in-channel freshes (Maheshwari et al., 1995; Fig. 4.1). As discussed in the next section, this has important implications for river—floodplain connections and a range of ecological processes.

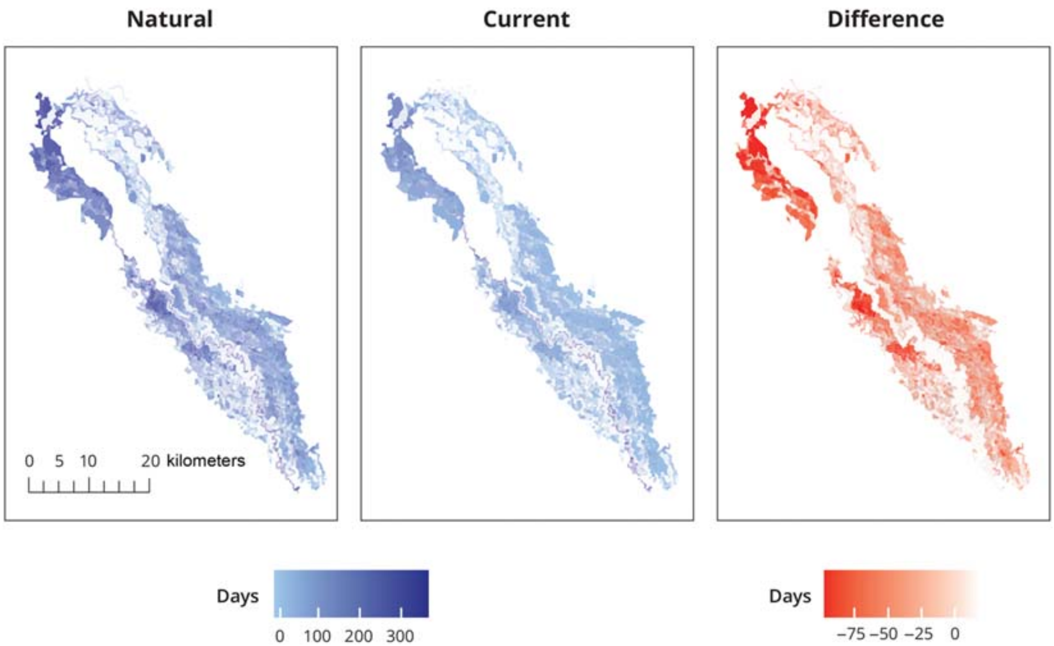

FIGURE 4.1

Plot showing the natural, current, and change in the number of days of floodplain inundation at Koondrook—Perricoota Forest on the Murray River in southeastern Australia. Changes in flood duration as well as magnitude is an important driver of river—floodplain ecology.

Source: Data from CSIRO, Overton et al. (2006)

Table 4.1 Summary of the Effects of Flow Regime Change Caused by Alteration to Specific Components of the Hydrological Regime and Underlying Ecological Mechanism

Hydrological Component	Ecological Mechanism	Ecological Responses
Reduced base flow magnitude	Reduced or complete loss of fast-flowing, turbulent habitats (riffles); reduced wetted area	Increased density and richness of organisms during initial habitat loss (crowding; Dewson et al., 2007) and decline in population size or local extinction of species (Kupferberg et al., 2012) and reduced species richness (Benejam et al., 2010; Boulton, 2003) and encroachment of terrestrial organisms into the riparian and channel zone (Stromberg et al., 2007)
Reduced flood frequency and size	Decline in life-history cues stimulating reproduction (Bunn and Arthington, 2002); reduced disturbance frequency and severity; loss of nutrient inputs and productivity from floodplains	Reduced species richness due to the loss of organisms requiring flowing habitats for feeding or reproduction (Alexandre et al., 2013; Growns and Growns, 2001; Meador and Carlisle, 2012) and reduced cover of bryophytes and macroalgae due to desiccation and invasion of nonnative aquatic and terrestrial species into the riparian and channel zone (Catford et al., 2011, 2014; Dolores Bejarano et al., 2011; Greet et al., 2011; Reynolds et al., 2014; Stromberg et al., 2007) and decline in species richness and functional diversity (Kingsford et al., 2004; Nielsen et al., 2013) and lower ecosystem productivity such as fisheries (Bonvechio and Allen, 2005; Gillson et al., 2009)
Reduced floodplain inundation	Decline in wetland area used for feeding, reproduction, and rearing	Reduced size and density of populations of floodplain-dependent organisms, lower species richness (Kingsford and Thomas, 1995)
Increased base flow (artificial *perennialization*)	Absence of nonflowing habitats and loss of drying events	Altered composition of species to reflect permanently flowing reaches or rivers (Alexandre et al., 2013; Chessman et al., 2010; Reich et al., 2010; Rolls and Arthington, 2014) and increased metabolic activity and productivity of chlorophyll a (Ponsatí et al., 2015) and increased biomass of consumers (Miserendino, 2009)
Increased discharge variability	Frequent drying and flooding of stream channel as disturbances	Population declines (Schmutz et al., 2015) due to increased mortality of eggs, larvae, and adults (Bishop and Bell, 1978; Casas-Mulet et al., 2015; Freeman et al., 2001; Miller and Judson, 2014; Nagrodski et al., 2012) and reduced species richness and altered species composition (Paetzold et al., 2008; Perkin and Bonner, 2011)

4.2.3 INCREASED BASEFLOW(S) (ANTIDROUGHT)

Storage and use of water for dry-season irrigation typically leads to increased discharge downstream of dams during the normal low-flow season (termed *antidrought*; McMahon and Finlayson, 2003). These heightened dry-season flows are often also associated with cold-water pollution (Lugg and Copeland, 2014; Table 4.1). Seasonal flow reversal and reduced flooding is now evident across many of the world's climate regions, including humid tropical, humid continental, and Mediterranean temperate regions (e.g., Assani et al., 2006; Batalla et al., 2004; Li et al., 2015). These changes often mean that rivers that normally cease to flow (termed *intermittent*) are managed so that flows are now permanent (e.g., Bunn et al., 2006; Reich et al., 2010). As low flows and cease-to-flow periods play an important role in the ecology of these systems (Rolls et al., 2012), antidrought can have major ecological consequences, and is an important aspect of environmental flow restoration.

4.2.4 INCREASED SHORT-TERM VARIABILITY (HYDROPEAKING)

Another pervasive impact of hydroelectric dams is increased short-term (diel) flow variability due to hydropeaking, in which flows are increased to coincide with daily periods of heightened electricity demand (Meile et al., 2011; Table 4.1). Hydropeaking can be avoided by operating generation facilities as a run-of-river, but this is typically associated with reduced economic value (due to the short-term spikes in electricity price) and decreased peak-production capacity, which are two of the primary drivers for hydroelectric generation (see Chapter 3). Even when managed as run-of-river (i.e., with minimal impacts on the overall hydrograph), dams disrupt longitudinal connectivity and can convert large sections of river from lotic to lentic habitats, both of which have strong negative ecological effects (Bunn and Arthington, 2002). Although not considered further here, these impacts must be taken into account when setting objectives and assessing the feasibility of using environmental water releases to offset the impacts of dam construction.

4.3 ECOLOGICAL EFFECTS OF FLOW ALTERATION

A fundamental tenet of river ecology is that the flow regime is a *master variable* (Power et al., 1995) and that organisms have adapted to the natural flow regime (Lytle and Poff, 2004). Therefore, anthropogenic changes to the natural flow regime by dams, weirs, diversion, and extraction of water can be expected to cause ecological change (Bunn and Arthington, 2002; Dewson et al., 2007; Poff et al., 1997). These impacts occur via a number of potential mechanisms, however, are all driven by the fundamental ecological roles of water within freshwaters; its role as a habitat and resource, a vector for connectivity and transport of material and organisms, and an agent for disturbance and geomorphic change (Sponseller et al., 2013).

4.3.1 REDUCED BASEFLOW(S) AND INCREASED INTERMITTENCY

Low-flow (base-flow) periods are an important component of the hydrological regime for freshwater ecosystems because the area and depth of aquatic habitats is often compared with higher discharge periods, and both physical and chemical conditions within those habitats can change rapidly as flow declines (Rolls et al., 2012). Reduced discharge can thus have substantial ecological consequences. Declines in discharge volume disproportionately affect habitats that exhibit large elevational gradients and therefore experience fast flows such as riffles, specifically due to changes in area, depth, and velocity (Boulton, 2003). By reducing base-flow discharge due to flow regulation, loss of flowing habitats causes impacts to population size and extinctions of organisms that require flowing habitats such as the foothill yellow-legged frog (*Rana boylii*) in western North American rivers (Kupferberg et al., 2012). Increased densities of organisms occur during flow recession, leading to initial crowding and competition for resources (Dewson et al., 2007). Differences in the composition of communities between regulated and unregulated rivers are reported worldwide (e.g., Grubbs and Taylor, 2004), and are driven by the loss or decline of organisms that have a strong preference to specific hydraulic habitats that are altered by flow regulation (e.g., Gillespie et al., 2015a). For terrestrial organisms, effects of flow regulation on reduced aquatic habitat size contribute to encroachment of riparian plant species such as the invasive *Tamarix* spp. (Stromberg et al., 2007), emphasizing that effects can occur in both the aquatic and riparian terrestrial zone.

Reduced baseflow(s) due to flow regulation also increases flow intermittency that is the frequency and duration of zero flow. Intermittency can be increased in rivers downstream of locations where water is extracted or diverted and also causes marked ecological changes. Such effects are most apparent in *perennial* rivers that naturally flow permanently. For example, water abstraction converted naturally perennial-flowing rivers to intermittently flowing rivers in Spain, leading to a decline in fish species richness by 35% (Benejam et al., 2010). Therefore, ecological effects of flow regime change on altered discharge occur via changes in discharge magnitude and the duration and frequency of flow intermittency, and depend highly on the geomorphologic characteristics of the river channel.

4.3.2 REDUCED FLOOD MAGNITUDE AND FREQUENCY

Alterations to the magnitude and frequency of flood events are widely reported effects of flow regulation (Assani et al., 2006), and are a primary driver of ecological effects of altered flow regimes. Floods influence aquatic ecosystems as a disturbance (where organisms and material are removed and transported from locations), determine habitat structure, and facilitate connectivity and therefore movement (Sponseller et al., 2013). Reduced flood frequency and magnitude by flow regulation causes reduced abundance and richness of flowing specialist taxa (Alexandre et al., 2013) or those that spawn during flood events (Perkin and Bonner, 2011). For example, the decline of flow variability by flooding in regulated rivers of the eastern United States is attributed to have caused the overall decline in 35% of native fish species, and a loss of over 50% of riffle-dwelling taxa (Meador and Carlisle, 2012). Species richness of macroinvertebrates, periphyton, and macrophytes has also been found to be lower in regulated rivers with reduced flood magnitude (e.g., Growns and Growns, 2001).

Loss of temporal variation in flow and reduced flood disturbance frequency with regulation both influence the persistence and establishment of organisms in aquatic and riparian habitats. Percentage cover of bryophytes and macroalgae on rocks was found to be lower in regulated upland rivers when compared with unregulated reaches, and these differences were attributed to reduced temporal variability in flow over fine temporal scales (daily, weekly; Downes et al., 2003).

Reduced flow variability also facilitates the invasion of (often) nonnative species. By reducing flow velocity and flooding disturbances, flow regulation promotes the invasion of nonnative fish in the regulated Ebre River (Spain; Caiola et al., 2014). In the riparian zone, reduced scouring frequency increases richness of terrestrial vegetation due to the increased prevalence of *dry* species intolerant of flooding (Dolores Bejarano et al., 2011; Greet et al., 2011; Reynolds et al., 2014; Stromberg et al., 2007), particularly when flooding seasonality is altered and synchronized with the release of seeds by invasive species (Mortenson et al., 2012). In floodplain wetlands, reduced flooding frequency increases the invasion and dominance of nonnative vegetation (e.g., Catford et al., 2011, 2014). Additionally, increased water level stability in floodplain wetlands in regulated river systems reduces taxonomic and functional diversity of birds, aquatic plants, and microfauna (Kingsford et al., 2004; Nielsen et al., 2013), emphasizing that effects of altered flood disturbance regimes affect ecosystems across aquatic, bankside, and floodplain habitats.

In lowland rivers and their estuaries, floods act less as a disturbance and more as a driver of ecological productivity by linking resources between riverine and floodplain habitats. Termed the *flood pulse advantage* (Bayley, 1991), the productivity of rivers is driven by the size of floods. In turn, reduced flooding size and frequency by regulation drives declines in productivity, mostly reported in estuarine fishery productivity. For example, catch per unit effort of commercial and recreational fish species is positively linked with freshwater discharge to estuaries (e.g., Gillson et al., 2009), or flow volume at the time of spawning (Bonvechio and Allen, 2005; Growns and James, 2005). On the Barmah–Milewa floodplain of the Murray River in Australia, Robertson et al. (2001) found controlled flooding during spring–summer or summer to result in higher net primary productivity of woody trees when compared with spring flooding only or no flooding, yet spring flooding promoted the highest primary production of algae and macrophytes. These findings suggest that both the magnitude *and* seasonal timing of flooding are strong determinants of ecosystem productivity, and alterations to floodplain inundation dynamics by flow regulation could influence levels of primary production for lowland river ecosystems.

4.3.3 REDUCED OVERBANK FLOODING

The decline in area inundated during flood events is a clear consequence of reduced flood magnitude and frequency imposed by flow regulation. In the Murrumbidgee River, Southern Australia, flow regulation has permanently inundated some low-level floodplain wetlands (particularly those associated with weir pools), yet has reduced the duration and frequency of inundation by 40% overall (Frazier and Page, 2006). Floodplain wetland size (spatial extent or area) is often reduced in terminal floodplain wetlands due to upstream extraction of water for irrigation (Kingsford and Thomas, 1995) or because of altered channel morphology due to constant regulated discharge (Gorski et al., 2012). This loss of inundated habitat has substantial impacts for organisms that rely on floodplain wetlands for nesting, recruitment, or feeding (e.g., Kingsford and Thomas, 1995).

4.3.4 INCREASED BASEFLOW(S) (ANTIDROUGHT)

In contrast to flooding impacts, the storage and release of water for dry-season irrigation leads to increased discharge downstream of dams. Unregulated flows can either decline to very low levels or cease completely during dry seasons, but constant elevated discharge under regulated conditions prevents natural low flows from occurring (antidroughts; McMahon and Finlayson, 2003). Flow regulation can consequently cause streams that naturally cease to flow (intermittent rivers; Leigh et al., 2016) permanently (Bunn et al., 2006; Reich et al., 2010). Constant flow releases from large dams in the Mekong River have increased inundation of lowland floodplains in Cambodia (Arias et al., 2014). As low flows play an important ecological role in all rivers (Rolls et al., 2012), anti-drought can have significant ecological consequences and is a novel aspect of environmental water regimes (Lake et al., in prep.).

Ecological effects of increased baseflow(s) due to flow regulation are best understood by changes in community composition to reflect those typical of permanently flowing rivers. Comparisons between regulated and unregulated rivers in southeast Queensland, Australia, identified that the largest shifts in fish assemblage composition occurred in streams that were originally intermittent but had become perennial under current regulated conditions (Rolls and Arthington, 2014). Artificially perennial flow in rivers in Portugal caused an increase in the abundance of taxa with broad environmental tolerances, including nonnative taxa (Alexandre et al., 2013). Across multiple dryland rivers of Australia, changes from intermittent to permanent flow regimes have caused biotic communities to change substantially in composition (e.g., Chessman et al., 2010; Reich et al., 2010). In addition, artificial flow permanence can increase metabolic activity of biofilms and productivity of chlorophyll a (Ponsatí et al., 2015), which in turn can increase density and biomass of consumers such as macroinvertebrates (Miserendino, 2009).

4.3.5 INCREASED SHORT-TERM FLOW VARIABILITY (HYDROPEAKING)

Hydropeaking, pulsing releases of water downstream of hydroelectric dams, causes rapid changes in flow that impact freshwater ecosystems by frequent partial or entire drying of the stream channel and unstable, persistent habitats. Rapid dewatering regimes by hydropeaking causes fish population declines (Schmutz et al., 2015), resulting in changes in community composition (Perkin and Bonner, 2011). These declines occur due to the rapid and frequent dewatering of riffles that severely increase egg mortality of riffle-spawning fish such as Atlantic salmon (*Salmo salar*; Casas-Mulet et al., 2015), stranding, and death of adult individuals (e.g., Bishop and Bell, 1978; Miller and Judson 2014; Nagrodski et al., 2012), or lack of persistent shallow habitats for juvenile fish recruitment (e.g., Freeman et al., 2001). Increased flow variability due to hydropeaking also alters species richness, in both the stream channel and riparian zone. Reduced species richness of riparian arthropod assemblages has been linked with flow regime change due to intradaily hydropeaking (Paetzold et al., 2008). These examples suggest that the combination of habitat loss and disturbance frequency determine the extent to which species richness is altered by flow regime change.

4.3.6 NONHYDROLOGICAL IMPACTS OF FLOW REGULATION REQUIRING CONSIDERATION FOR HOLISTIC MANAGEMENT OF ENVIRONMENTAL WATER

The impoundment and storage of water in dams, weirs, and reservoirs alters aquatic ecosystems due to the process of habitat loss and fragmentation (sensu Fahrig, 2003). Such effects of habitat loss and fragmentation by barriers are not due to changes in the flow regime itself (and therefore unable to be readily addressed by environmental water releases). However, these effects are an important component of the broader consequences of water resource development and therefore necessary to consider simultaneously with flow regime management. Lentic-adapted organisms are better suited to regulated, stable environments, and respond positively to water impoundment (e.g., Taylor et al., 2008). Conversion of lotic to lentic habitats by dams and weirs also alters ecosystem functioning such as reduced wood decomposition due to reduced physical movement and abrasion of detritus in regulated Mediterranean climate streams (Abril et al., 2015). Here, differences in decomposition between river and impoundment habitats were most apparent during winter when hydrological differences between regulated and unregulated rivers were largest (Abril et al., 2015).

Rivers have constrained (narrow) connections linking channel habitats, and are therefore vulnerable to habitat fragmentation by barriers such as dams (Beger et al., 2010). However, depending on catchment topography, dam characteristics (e.g., size), and position in the stream network, the ecological effects of dams can be contradictory. A widely observed effect of large dams is the occurrence of distinct communities of species, primarily fish, between reaches fragmented by dams. For example, fish communities have become fragmented by the effects of the Tallowa Dam (Shoalhaven River, Australia) on restricting movement, particularly for diadromous species (Gehrke et al., 2002). The construction of 1356 dams between 1634 and 1860 reduced connectivity to almost the entire stream network in coastal Maine, United States (Hall et al., 2011). However, natural barriers such as waterfalls also cause significant discontinuities in freshwater fish communities such as in the Madeira River, Brazil (Torrente-Vilara et al., 2011). Inundation and subsequent removal of natural barriers by reservoir impoundments can promote the dispersal of species among previously fragmented reaches (Vitule et al., 2012).

In addition to hydrological effects of flow regime change, the design and operation of dams alters the physicochemical characteristics of water downstream of dams. Altered temperature regimes (the daily and seasonal fluctuations in water temperature) are a global consequence of large dams (Olden and Naiman, 2010). Selective removal and transport of unnatural or unseasonal cold or warm water from large, stratified reservoirs can be the cause of ecological responses to flow regime change (Olden and Naiman, 2010). For example, hypolimnetic releases of water from large dams can reduce water temperatures by up to 15°C for hundreds of kilometers downstream (Casado et al., 2013; Dickson et al., 2012; Lugg and Copeland, 2014; Olden and Naiman, 2010; Preece and Jones, 2002). Additionally, under regulated conditions, stratification of lotic habitats (e.g., temperature and salinity) can be more pronounced when compared with unregulated systems due to reduced turbulence contributing to vertical mixing of the water column (Frota et al., 2012).

4.4 THE IMPORTANCE OF LOCAL FACTORS

The preceding sections of this chapter summarize some of the more consistent impacts that can arise from modifying particular aspects of the flow regime. Yet, perhaps surprisingly, efforts to distill these patterns into simple statistical relationships that would support rules of thumb around the limits to hydrological alteration (Poff et al., 2010) have proven difficult. For example, Poff and

Zimmerman (2010) found that, despite consistent reporting of impacts on the indictors they examined, there was little consistency in response when examined in terms of the relative degree of hydrological alteration (as measured, e.g., by a relative change in high- or low-flow magnitudes). Although this reflects a range of factors, including differences in measurement and analytical approaches, it is likely that *real* differences also arise in different rivers. This has important implications for practitioners involved in providing environmental water recommendations.

To provide several examples, in the first instance, because environmental water regimes will often have to be defined in quite specific terms (e.g., a flow of 1500 per day for 10 days during spring) to a river operator, there is a need to go beyond hydrology alone to consider the hydraulic relationships that link hydrology with biophysical processes. This could be in terms of whether high flows are sufficiently high to dislodge organisms from the streambed or provide access to the floodplain, or whether low flows are causing silt to smother cobbled habitats. Ultimately, it is these interactions between runoff variability and the slope and morphology of the river channel, and the size and shape of the substrate that determines the environment experienced by the biota. Such interactions cannot be discerned from hydrological data alone, which is why most environmental flows assessment depend heavily on hydraulic models. In fact we contend that some information on hydraulics is critical in interpreting or predicting the effects of hydrological alteration.

A second issue is that both life-history characteristics and ecological characteristics (*traits*) play a significant role in determining how individual taxa respond to flow regime change in rivers and streams. The ways in which individual taxa respond to flow regime change culminates in how patterns of biodiversity are linked with flow alteration. For example, fish species that have *opportunistic* life-history traits (e.g., small body size and early maturation) are better adapted to rivers with high interannual runoff variability. Conversely, those with *equilibrium* life histories (e.g., intermediate maturation and high juvenile survivorship) appear to be better adapted to rivers with more stable flow regimes. As a result, the general seasonal stabilization of runoff by river regulation tends to favor equilibrium fauna (Mims and Olden, 2013). However, species and ecological traits also play a large part in explaining why flow regime change facilitates invasion and establishment of nonnative species, and simultaneous decline of native species adapted to historical conditions (Gido et al., 2013). Understanding the broader evolutionary context and biology of organisms within the regional species pool (both of which vary spatially) may be helpful in trying to understand likely impacts arising from particular patterns of hydrological change.

4.5 CONCLUSION

Understanding the effects of flow regime change is essential for the planning, implementation, delivery, and evaluation of the outcomes of environmental water regimes. As shown in this synthesis, flow regulation alters multiple components of the hydrological regime in both consistent but sometimes idiosyncratic ways. Idiosyncracies may arise because dams and weirs are rarely operated in the same way, and local variation in topography, geomorphology, and evolutionary history of the biota may lead to differences in the way that changes in hydrology manifest themselves both physically and biologically. However, in spite of such variation, there are numerous consistencies in impact that occur as particular flow components are modified in particular ways. Many of these are predictable if one considers biotic adaptations to the natural flow regime. By understanding the effects of flow regime change on the desirable structural and functional attributes of ecosystems, the relevant specific hydrological components can be manipulated and restored. For example, recruitment of some riverine fish is facilitated by the access to the resources available in prolonged inundated floodplain habitats—providing the combination of energy-rich and slow-flowing, warm habitats beneficial to growth of newly hatched individuals (King et al., 2003). In this example, fundamental knowledge of the importance of floodplain inundation timing, extent, and duration has helped inform the delivery and evaluation of artificially extended floodplain inundation using environmental water allocations (King et al., 2009). Combining evidence of the effects of flow regime change and the responses of environmental water releases will only improve further development in prediction, monitoring, and evaluation of environmental water requirements (Konrad et al., 2011; Olden et al., 2014). Such evidence is especially central to the application of environmental water regimes as a tool for climate change adaptation (Poff and Matthews, 2013).

The provision of environmental water will typically have large financial costs, either in terms of the need to purchase water and manage it specifically for environmental benefits or the lost opportunities for economic revenue arising particularly from industrial and agricultural water use (see Chapters 18 and 23). It is therefore essential the environmental water is delivered in ways that either maximize ecological benefits while minimizing economic costs, or provide simultaneous benefits for both environmental and economic outcomes. Such outcomes will likely be improved if there is clear knowledge of the context-specific effects of flow regulation on ecosystems, so that the limits of extrapolation and transferability of evidence across local, regional, continental, and global scales are sufficiently understood.

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