Basic Principles and Ecological Consequences of Altered Flow Regimes for Aquatic Biodiversity[1]

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ABSTRACT / The flow regime is regarded by many aquatic ecologists to be the key driver of river and floodplain wetland ecosystems. We have focused this literature review around four key principles to highlight the important mechanisms that link hydrology and aquatic biodiversity and to illustrate the consequent impacts of altered flow regimes: Firstly, flow is a major determinant of physical habitat in streams, which in turn is a major determinant of biotic composition; Secondly, aquatic species have evolved life history strategies primarily in direct response to the natural flow regimes; Thirdly, maintenance of natural patterns of longitudinal and lateral connectivity is essential to the viability of populations of many riverine species; Finally, the invasion and success of exotic and introduced species in rivers is facilitated by the alteration of flow regimes. The impacts of flow change are manifest across broad taxonomic groups including riverine plants, invertebrates, and fish. Despite growing recognition of these relationships, ecologists still struggle to predict and quantify biotic responses to altered flow regimes. One obvious difficulty is the ability to distinguish the direct effects of modified flow regimes from impacts associated with land-use change that often accompanies water resource development. Currently, evidence about how rivers function in relation to flow regime and the flows that aquatic organisms need exists largely as a series of untested hypotheses. To overcome these problems, aquatic science needs to move quickly into a manipulative or experimental phase, preferably with the aims of restoration and measuring ecosystem response.

The alteration of flow regimes is often claimed to be the most serious and continuing threat to ecological sustainability of rivers and their associated floodplain wetlands (Naiman and others 1995, Sparks 1995, Lundqvist 1998, Ward and others 1999). While the obvious and often irreversible impacts of large impoundments are now well recognized, there is also growing awareness of the pivotal role of the flow regime as a key driver of the ecology of rivers and their associated floodplain wetlands (Junk and others 1989, Poff and others 1997, Richter and others 1997, Puckridge and others 1998, Hart and Finelli 1999).

The primary goal of this review is to illustrate how altering flow regimes affects aquatic biodiversity in streams and rivers. To do so, we pose four guiding principles about the influence of flow regimes on aquatic biodiversity (Figure 1) and examine the consequences of changing flow regimes in light of each of these. The principles are:

Principle 1: Flow is a major determinant of physical habitat in streams, which in turn is a major determinant of biotic composition. We outline the influence of flow on stream habitats at the catchment scale (e.g., channel dimensions), reach scale (e.g., riffle-pool distribution), and patch scale (e.g., hydraulic conditions on individual stones) and discuss how habitat in turn influences the distribution and abundance of aquatic organisms. We then examine how modified flow regimes alter habitat at varying spatial scales and the influence of this on species distributions and abundance, as well as the composition and diversity of aquatic communities.

Principle 2: Aquatic species have evolved life history strategies primarily in direct response to the natural flow regimes. We discuss the degree to which flow pattern has a major influence on shaping life history patterns of aquatic species. We then consider how alteration of flow regimes can lead to recruitment failure and loss of biodiversity of native species.

Principle 3: Maintenance of natural patterns of longitudinal and lateral connectivity is essential to the viability of populations of many riverine species.

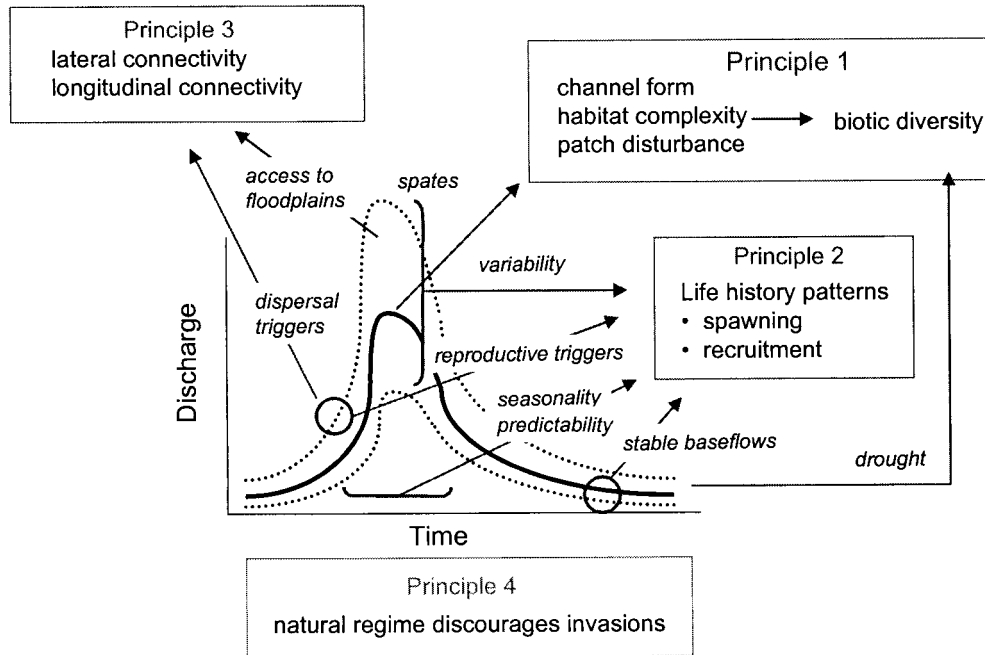## Aquatic biodiversity and natural flow regimes

Figure 1. The natural flow regime of a river influences aquatic biodiversity via several interrelated mechanisms that operate over different spatial and temporal scales. The relationship between biodiversity and the physical nature of the aquatic habitat is likely to be driven primarily by large events that influence channel form and shape (principle 1). However, droughts and low-flow events are also likely to play a role by limiting overall habitat availability. Many features of the flow regime influence life history patterns, especially the seasonality and predictability of the overall pattern, but also the timing of particular flow events (principle 2). Some flow events trigger longitudinal dispersal of migratory aquatic organisms and other large events allow access to otherwise disconnected floodplain habitats (principle 3). The native biota have evolved in response to the overall flow regime. Catchment land-use change and associated water resource development inevitably lead to changes in one or more aspects of the flow regime resulting in declines in aquatic biodiversity via these mechanisms. Invasions by introduced or exotic species are more likely to succeed at the expense of native biota if the former are adapted to the modified flow regime (principle 4).

We discuss how the viability of populations of many species of fully aquatic organisms depends on their ability to freely move through the stream hierarchy, or between the river and floodplain wetlands. Loss of longitudinal and lateral connectivity through construction of barriers can lead to isolation of populations, failed recruitment and local extinction.

Principle 4: The invasion and success of exotic and introduced species in rivers is facilitated by the alteration of flow regimes. Here, we briefly discuss the overall impact of modifying flow regimes on the establishment, spread, and persistence of exotic and introduced species. We also consider interbasin transfers of water as a major mechanism for the spread of exotic and introduced species, as well as disease.

Principle 1: Flow Is a Major Determinant of Physical Habitat in Streams, Which in Turn Is a Major Determinant of Biotic Composition

Flow Influences on Habitat

The movement of water across the landscape influences the ecology of rivers across a broad range of spatial and temporal scales (Vannote and others 1980, Junk and others 1989, Poff and Ward 1990, Poff and others 1997, Sparks 1995). The shape and size of river channels, the distribution of riffle and pool habitats, and the stability of the substrate are all largely determined by the interaction between the flow regime and local geology and landform (Frissel and others 1986, Cobb and others 1992, Newbury and Gaboury 1993). In turn this complex interaction between flows and phys-

Table 1.   Summary of biotic responses to altered flow regimes in relation to flow induced changes in habitat (principle 1)[a]

Flow variables affected	Biotic responses	Sources
Increased stability of baseflow and reduction of flow variability	Excessive growths of aquatic macrophytes	Rørslett 1988, Røslett and others 1989, Walker and others 1994, French and Chambers 1996, Blanch and others 2000
	Proliferation of nuisance larval blackflies	De Moor 1986
	Reduction in fish populations	Converse and others 1998
	Increased standing crop and reduced diversity of macroinvertebrates	*Armitage 1977, Ward and Short 1978, Lillehammer and Saltveit 1979, Williams and Winget 1979*
Erratic (diurnal) patterns in flow below hydroelectric dams	Reduction in species richness of benthic macroinvertebrates	Munn and Brusven 1991, *Mullan and others 1976, Trotzky and Gregory 1974*
	Reduction in standing crop of benthic macroinvertebrates	Layzer and others 1989, *Mullan and others 1976, Trotzky and Gregory 1974, Radford and Hartland-Rowe 1971*
	Stranding of macroinvertebrates	*Kroger 1973*
	Stranding of fish	Bradford 1997, Bradford and others 1995
Conversion of lotic habitat to lentic	Decline of populations of riverine crayfish and snails	Walker and others 1992
	Elimination of salmonids and pelagic spawning fishes and dominance of generalist fish species	Copp 1990
	Loss of fishes adapted to turbid river habitats	Stanford and Ward 1986a
	Loss of fishes due to inundation of spawning grounds	*Hubbs and Pigg 1976*

[a]Additional examples (in italics) to those included in this review are from Petts (1984).

ical habitat is a major determinant of the distribution, abundance, and diversity of stream and river organisms (Schlosser 1982, Poff and Allan 1995, Ward and others 1999, Nilsson and Svedmark 2002). This is evident at even the smallest spatial scales, where subtle variations in flow and near-bed velocities can dictate the distribution and abundance of particular species of plants and animals (e.g., Wetmore and others 1990). Close associations with physical habitat can be found in many stream organisms ranging from algae and aquatic plants to invertebrates and fish.

Influence of Flow and Habitat on Aquatic Plants

The most commonly cited abiotic determinants of aquatic macrophyte assemblage structure are all flow-related factors (e.g., flow extremes, flow regime, hydraulics, substrate composition, and stability). Spatial and temporal variation in plant assemblage structure is influenced by flooding and scouring, desiccation, substrate stability and localized variations in water velocity, turbulence and shear stress (Chambers and others 1991, Biggs 1996, French and Chambers 1996). Aquatic macrophytes typically have patchy distributions as a result of spatial variations in disturbance frequency and intensity, colonization success and growth rates (Sand-Jensen and Madsen 1992, Rea and Ganf 1994).

Flow modifications to Scandinavian rivers (Rørslett and others 1989) and many rivers in the United States, Britain, France, southern Africa, India, Canada, and Australia are responsible for increases in macrophyte abundance (Table 1). For example, reduced summer floods and increased winter flows (i.e., a relatively stable flow throughout the year) cause excessive growths of submerged aquatic macrophytes in Norwegian rivers regulated by hydropower stations. Up to 55% of tailwater surface area and slow-flowing reaches further downstream in the River Otra were covered with prolific growths of the submerged phenotype of *Juncus bulbosus* L. (Rørslett 1988). In its pristine state, the flow regime of the Otra featured low winter flows and spring/summer floods, conditions that exposed plants to extreme stress caused by frost and ice scouring followed by the deleterious scouring effects of spring floods. The regulated regime ameliorates all of these conditions, allow-

ing plants to accumulate massive biomass in regulated reaches.

Numerous species of aquatic plants from permanent backwaters and wetlands on the floodplain of the highly regulated lower Murray River in southeastern Australia have colonized the main channel, where the year-round baseflow in weir pools now provides ideal conditions (Walker and others 1994). Blanch and others (2000) suggest that reinstating a greater amplitude of weir pool water levels, more frequent shallow flooding, and longer periods of inundation would be beneficial for many plant species, promoting diversity by restoring a wider range of water regimes (Table 1).

Influence of Flow and Habitat on Aquatic Invertebrates

Physical disturbance from floods (and droughts) is thought to be a major determinant of the spatial and temporal dynamics of benthic communities in streams (e.g., Resh and others 1988). Rivers with unstable substrates tend to be characterized by low species diversity, and the biota present often have life history or behavioral characteristics of frequently disturbed environments (Sagar 1986, Cobb and Flannagan 1990, Cobb and others 1992).

Macroinvertebrates are vulnerable to rapid diurnal changes in flow, and regulated river reaches below hydroelectric dams, with erratic flow patterns, are typically characterized by species-poor macroinvertebrate communities (Munn and Brusven 1991) (Table 1). Sudden increases in flow can cause catastrophic downstream drift to the extent that as much as 14% of the standing crop of benthic biota can be eliminated each month in some hydropower operations due simply to drift resulting from increased shear stress (Layzer and others 1989). The impact of high flow water releases below hydropower dams can be very selective. Small insect nymphs and invertebrates, which cannot tolerate high velocities, are often underrepresented in downstream reaches (De Jalon and others 1994).

In some cases, flow regulation may favor the proliferation of specific taxa (e.g., orthoclad chironomids) (Munn and Brusven 1991) (Table 1). Since the construction of impoundments on the Lower Vaal River, South Africa, regulation of the once sporadic winter flow regime has allowed large populations of blackfly (Simuliidae) larvae to survive the winter and led to periodic plague outbreaks of adults in spring (De Moor 1986). It has been suggested that this pest species, which poses a health risk in the region, can be controlled to some extent by careful water level manipulations (De Moor 1986).

Influence of Flow and Habitat on Fish

Many fish species display a preference for particular types of habitat such as pools, riffles, or backwater areas (Matthews 1985, Angermeier 1987, Pusey and others 1993). The richness of the fauna often increases as habitat complexity increases, with depth, velocity, and cover being the most important variables governing this relationship (Gorman and Karr 1978, Schlosser 1982, Felley and Felley 1987, Pusey and others 1995). Fish assemblage structure (i.e., taxonomic composition and relative abundance pattern) is also strongly related to habitat structure (Meffe and Sheldon 1988, Pusey and others 1993, 1998, 2000).

Associations between fish and their habitat are influenced by flow variability at a range of spatial scales. Poff and Allan (1995) demonstrated regional differences in fish assemblage structure and functional organization in streams of differing flow variability in the northern midwestern United States. Hydrologically variable streams (i.e., those with a high coefficient of variation of daily flows, moderate frequency of spates) were characterized by species with generalized feeding strategies and preference for low water velocity, silt, and general substrata. In more stable streams, with high predictability of daily flows and stable baseflows, fish assemblages contained more silt-intolerant trophic specialists (Poff and Allan 1995).

Flow variability and habitat structure at smaller spatial scales within the drainage network can also influence fish assemblages. Pusey and others (1993) showed that stream discharge regime varied spatially in the Mary River, southeast Queensland, Australia, with some small tributaries prone to frequent periods of extended zero flows, whereas others have very constant base flows. Tributaries with extended periods of low flow were dominated by small, physiologically tolerant and generalist species (Pusey and others 1993).

Given the often-cited relationships between flow, habitat structure, and fish, it is not surprising that modifications to flow regimes affect fish diversity and the functional organization of fish communities in regulated rivers (Table 1). Impacts may involve any life history stage and have been observed at all spatial scales. For example, pulsed reservoir discharges associated with on-demand hydroelectric power generation limit the quality and quantity of habitat available (Reiser and others 1989, Valentin and others 1994, 1995). Stream fish can become stranded on gravel bars or trapped in off-channel habitats during rapid flow decreases. Susceptibility to stranding is a function of behavioral response to changing flows, and this varies with species, body size, water temperature, time of year and

day, substrate characteristics, and the rate of flow reductions (Bradford 1997). For example, newly emerging salmon larvae, and juvenile salmonids hiding in the stream substrates during winter, are extremely susceptible to being stranded in the substrate during flow reductions (Bradford and others 1995, Bradford 1997). However, mature fish may be able to shift into temporarily suitable habitats to compensate for periodic reductions in the quality or availability of habitat (Kraft 1972, Bunt and others 1999).

The humpback chub (*Gila cypha*) historically ranged throughout the Colorado River system in the arid American southwest, living in swift canyon reaches now inundated or decimated by water development projects (Converse and others 1998). Operations of the Glen Canyon Dam directly affect the Colorado River through changes in flow, temperature, sediment transport and vegetation dynamics. Peak flows are considered important to the chub for habitat maintenance (via sediment transport) and perhaps as spawning cues, but base flows, which occur through the Grand Canyon for 7 to 10 months of the year, are also important. Elevated base flows now occur a greater proportion of the time in the regulated flow regime, and reduce habitat quality to the extent that subadult humpback chub are now much more numerous in the modified shoreline habitat provided by the exotic tamarisk (*Tamarix chinensis*) than in natural habitats (Converse and others 1998). In addition, the dam has altered the thermal regime such that the growth, reproduction and survival of native fishes have almost certainly been affected (e.g., Bulkley and others 1981).

Conversion of Lotic to Lentic Waterbodies

It is often argued that the loss of riverine habitat associated with impoundments is balanced by the creation of lake habitat. This is somewhat misleading, however, as natural lakes and wetlands often function in a very different way than river storages. In lakes and wetlands, much of the carbon and nutrient fluxes occur in the littoral margins (Bunn and Boon 1993, Wetzel 1990). Large impoundments are generally not operated at a constant water level, and productive littoral areas are rarely sustained. In addition, water levels are usually significantly elevated above natural stream levels, flooding part of the terrestrial–aquatic interface and creating a new littoral zone with steeper banks, less complex aquatic habitat, and different physicochemical conditions for aquatic plants and animals (Walker and others 1992).

The effects of weirs on river flow regimes and aquatic habitat can be complex and difficult to separate from the effects of exotic species, which often prolifer-

ate in the newly created lake habitat (see principle 4). In the Lower Murray River in southeastern Australia weirs have transformed the river into a chain of cascading pools, supplanting most of the riverine environment with pool habitats (Walker and others 1992). This has affected the distribution of the Murray crayfish (*Euastacus armatus*), now close to extinction, and several species of riverine and wetland snails have declined (Table 1).

Regulation of the lowland river Great Ouse, UK by weirs, embankments, navigation locks, and dredging has converted it into a series of relatively deep reservoirlike channels, separated by short, shallow lotic stretches. Impacts on fish include the absence of localized salmonids and pelagic spawning fishes (i.e., burbot), historically reported to be abundant; reduction in the range and abundance of rheophilic and limnophilic cyprinids; and the extreme dominance of generalist species (roach and minnows) throughout most of the system (Copp 1990).

The Colorado River is regulated by hundreds of reservoirs varying in area from <1 ha in high-altitude headwaters to >650 km^2 in lowland mainstem segments (Stanford and Ward 1986a). Conversion of one quarter of the river to lentic habitat has resulted in the loss of fishes adapted to turbid riverine habitats. In addition, numerous introductions of highly competitive exotic fishes (over 50 species), many thriving in impoundments and regulated river reaches, have contributed to the extirpation of native fishes in the Colorado River fauna (Stanford and Ward 1986b). Most of the native big-river fish face extinction (Stanford and Ward 1986b). In the headwaters of the upper basin, the range of the Colorado River cutthroat trout (*Salmo clarki pleuriticus*) is limited to a few isolated populations, and nearly all of the endemic desert stream fish are in severe decline.

Principle 2: Aquatic Species Have Evolved Life History Strategies Primarily in Direct Response to the Natural Flow Regimes

Influence of Flow Regime on Life History Patterns

The influence of river flows and wetland water regimes on recruitment and growth of aquatic plants is well established (Table 2). Changes in rates of water level fluctuation and disturbance frequency (floods and spates) and intensity (velocity and shear stress) can affect seedling survival, as well as plant growth rates (Blanch and others 1999, 2000, Froend and McComb 1994, Rea and Ganf 1994, Sand-Jensen and Madsen 1992). Rea and Ganf (1994) suggest that changes in

Table 2. Summary of life history responses to altered flow regimes (principle 2)[a]

Flow variables affected	Biotic responses	Sources
Rates of water level fluctuation	Aquatic macrophyte growth rates and seedling survival	Blanch and others 1999, 2000, Froend and McComb 1994, Rea and Ganf 1994
Timing of spates	Reduced survivorship of larval atyid shrimps following early summer spates	Hancock and Bunn 1997[b]
	Stable low flows required for spawning and recruitment of riverine fish	Milton and Arthington 1983[b], 1984, 1985, Humphries and Lake 2000
Reduced seasonality	Reduced synchrony of breeding in gammarid shrimps	Bunn 1988[b]
Timing of rising flows	Loss of cues for fish spawning and migration	Lowe-McConnell 1985, Nesler and others 1988, King and others 1998
Short-term fluctuations in flows	Adverse effect on species of stoneflies with long larval development times (autumn/winter)	*Henricson and Müller 1979*
Modified temperature regimes below dams	Delayed spawning in fish	Zhong and Power 1996
	Disrupted insect emergence patterns	*Lehmkuhl 1972, Gore 1977*, Ward and Stanford 1982
	Reduced benthic standing crop	*Lehmkuhl 1972*
	Elimination of temperature-specific species of fish	*Trautman and Gartman 1974*

[a]Additional examples (in italics) to those included in this review are from Petts (1984).

[b]Some examples are based on studies of responses to variation in natural flow regimes.

water regime have a profound effect on the establishment and survival of many aquatic plant species owing to their narrow range of tolerances and inability to regenerate under modified conditions. Conversely, the proliferation of species such as *Typha* in numerous artificial and altered aquatic habitats throughout southern Australia (Rea and Ganf 1994, Blanch and others 1999, 2000) is a function of several life history traits. These include high dispersal capabilities (production of large numbers of small seeds dispersed by wind over long distances), a high capacity to germinate while submerged (Finlayson and others 1983), high seedling density and, once established, rapid growth rates and vegetative reproduction (Froend and McComb 1994).

Although temperature regimes influence the life history patterns of many stream and river animals, the timing of particular flow or inundation events is also important (Sweeney 1984, Resh and others 1988) (Table 2). For example, temperature is a major factor influencing breeding in atyid shrimps (Atyidae) (e.g., de Silva 1988a,b). However, life history patterns are also strongly modified by the prevailing hydrology (see Hancock and Bunn 1997). Many Australian and New Zealand stream invertebrates have flexible life history patterns, which are thought to be a direct response to highly variable and unpredictable discharge regimes (Winterbourn and others 1981, Marchant and others 1984, Lake and others 1985). Evidence of greater syn-

chrony of development is found only in regions with a more predictable flow regime (e.g., Bunn 1988). A spectacular example of the influence of flow on aquatic biota is the "boom or bust" dynamics of Australian arid-zone rivers and wetlands in response to unpredictable and episodic flood events (Walker and others 1995).

Flow plays a profound role in the lives of fish with critical life events linked to flow regime (e.g., phenology of reproduction, spawning behavior, larval survival, growth patterns and recruitment) (Welcomme 1985, Junk and others 1989, Copp 1989, 1990, Sparks 1995, Humphries and others 1999). Many of these life events are synchronized with temperature and day length, such that changes in flow regime that are not in natural harmony with these seasonal cycles may have a negative impact on aquatic biota.

Many species in streams with highly variable flow regimes have evolved life history strategies that ensure strong recruitment despite the disturbances wrought by spates (Table 2). Humphries and Lake (2000) proposed the "low flow recruitment hypothesis" to explain patterns of spawning in southeastern Australian fishes in response to seasonal pattern of river flow. Milton and Arthington (1983, 1984, 1985) suggested that small subtropical stream fishes recruit successfully by spawning in the months of low and relatively stable stream flows when their spawning habitats are least likely to be

Table 3.   Summary of biotic responses to loss of longitudinal or lateral connectivity (principle 3)[a]

Flow variables affected	Biotic responses	Sources
Water abstraction	Reduction in migrating shrimp larvae	Pringle and Scatena 1999
Presence of in-stream barriers	Increased predation on juvenile migrating shrimp	Pringle and Scatena 1999
	Loss of migratory fish species	*Hubbs and Pigg 1976, Welcomme 1979*, Harris 1984a,b, Dauble and Geist 2000, Kareiva and others 2000, Reyes-Gavilan and others 1996, Joy and Death 2001
Reduced frequency, duration and area of inundation of floodplain wetlands	Reduced spawning areas and/or recruitment success of lowland river fish	*Jubb 1972, Whitley and Campbell 1974, Lake 1975, Welcomme 1979*, Geddes and Puckridge 1989, Cadwallader and Lawrence 1990
	Decline in waterbird species richness and abundance	Kingsford and Thomas 1995
	Decline in wetland vegetation	Kingsford 2000

[a]Additional examples (in italics) to those included in this review are from Petts (1984).

scoured out or stranded. Similar seasonal patterns of reproductive activity are emerging in many subtropical and tropical fish species (Arthington and Pullar 1990, Pusey and others 2001) and have also been recorded in freshwater turtles (Cann 1998) and the platypus, *Ornithorhynchus anatinus* (Grant 1984).

In contrast to low flow spawning, other aquatic species are cued to increases in flow or the timing of large floods (Lowe-McConnell 1985, Welcomme 1985). In southeastern Alaska, coho salmon (*Oncorhynchus kisutch*) enter many rivers for reproduction at the onset of autumn rains in September and October, whereas in Washington and Oregon rivers entry is delayed until the rains start in November (Naiman and others 2002). The timing of rising flows may also serve as a cue or trigger to the spawning of certain fish species. Examples are the Colorado River squawfish (*Ptychocheilus lucius*) in the Yampa River (Nesler and others 1988), and the Clanwilliam yellowfish (*Barbus capensis*) in South Africa (King and others 1998). In large floodplain rivers, many aquatic species ranging from benthic microorganisms, phytoplankton, zooplankton, and fish are cued to rising flood levels, emerging from resting stages or spawning in response to the cue of rising water levels and inundation.

Influence of Modified Temperature Regimes on Life History Patterns

In many regulated river systems modified flow regimes are accompanied by major shifts in the thermal regime, especially where dams have hypolimnetic water releases (Crisp and others 1983, Travnichek and others 1993) leading to the release of cold oxygen-deficient water downstream. Since aquatic insects and fish use the combined cue of day length and the summation of day-degrees to synchronize emergence as adults, the

release of cooler water downstream of impoundments can influence the spawning behavior of fish and life history processes of invertebrates (Penaz and Jurajda 1995) (Table 2). In the long-term, hypolimnetic releases can cause selective disappearance of susceptible species from downstream reaches. Modified thermal patterns and day-length cues have been shown not only to disrupt insect emergence patterns but also to reduce population success (Ward and Stanford 1982). Coldwater releases have been found to delay spawning by up to 30 days in some fish species (Zhong and Power 1996).

Principle 3: Maintenance of Natural Patterns of Longitudinal and Lateral Connectivity Is Essential to the Viability of Populations of Many Riverine Species

Longitudinal Connectivity

The viability of populations of many species of fully aquatic organisms depends on their ability to move freely through the stream network. Large migratory macroinvertebrates such as shrimps and crabs are an important component of the biota of tropical and subtropical streams because of their direct influence on ecosystem level processes, such as primary production, organic matter processing, sedimentation, and the composition of benthic algal and invertebrate communities (Pringle and others 1993, Pringle and Blake 1994, Pringle 1996). Water abstraction and the construction of dams can have a major impact on the migration of large shrimp (Pringle and Scatena 1999) (Table 3). For example, damming of the lower reaches of one of the main drainages of the Caribbean National Forest in Puerto Rico has had a major impact on shrimp recruitment. More than 50% of migrating lar-

vae were drawn into water intakes for municipal supplies and juvenile shrimps returning upstream faced severe predation below the dam (Pringle and Scatena 1999). Cessation of water abstraction during evening periods of peak nocturnal larval drift, upkeep of a functional fish ladder, and maintenance of a minimum flow could significantly reduce impacts of the dam and its operations.

Diadromous fishes, which migrate long distances within the main channels and larger tributaries of rivers, are particularly sensitive to barriers to longitudinal passage because obstruction of their migratory pathways may interfere with the completion of their life cycles (Table 3). The disappearance or decline of the major migratory fish species often follows river impoundment and the blocking of passage in the system (Bonetto and others 1989, Cadwallader 1986, Harris 1984a,b; Joy and Death 2001, Welcomme 1985, 1992). For example, an extensive network of hydroelectric dams, constructed between 1939 and 1975, has blocked access to or inundated most riverine habitat suitable for spawning by fall chinook salmon (*Oncorhynchus tshawytscha*) in the Columbia River Basin (Dauble and Geist 2000). More that 75% of the original 2500 km of mainstem spawning and rearing habitats has been eliminated. Although dam passage requirements have dramatically mitigated direct mortality, Snake River spring/summer populations are expected to decline toward extinction unless there are modest reductions in first-year mortality or estuarine mortality (Kareiva and others 2000). Migratory species such as shad, lamprey, and eels have disappeared from the Rhone River in France and the Guadalquivir River in Spain (Reyes-Gavilan and others 1996). In New Zealand, Joy and Death (2001) found that fish species richness in Taranaki Ring Plain streams was significantly reduced above dams due to their influence on movements of diadromous species.

In-stream barriers have contributed to the decline of populations of migratory fish species in southern Australia, such as Australian bass, Macquarie perch, and golden perch (Lake and Marchant 1990, Barmuta and others 1992). Barriers have affected 30%–50% of the potential habitat for migratory fish in 22 coastal drainages in southeastern Australia (Harris 1984a). Less than 10% of these barriers had fishways and, of these, only six of the 29 provided suitable conditions for fish migration at the time surveyed (Harris 1984b). River impoundment and the blocking of fish passage are often followed by the disappearance or decline of the major migratory species in river reaches upstream of barriers; this has been observed for Australian bass in east coast river systems (Harris 1984a,b).

It is important to note that the impact of barriers on mobile organisms is not confined to very large structures. Even small in-stream barriers, such as v-notch gauging weirs, can impede the movement of fish [e.g., western minnows (*Galaxias occidentalis*) in southwestern Australian forest streams (Pusey and others 1989)].

Lateral Connectivity

Hydrological connectivity between the river channel, floodplain, and groundwater structures the spatiotemporal heterogeneity of floodplain habitats (Ward and Stanford 1995), leading to characteristic high biodiversity (Ward and others 1999). The lateral expansion of floodplain habitats during flooding creates important spawning, nursery and foraging areas for many fish species and a variety of other vertebrates (Lowe-McConnell 1985, Welcomme 1985, Cadwallader 1986, Junk and others 1989, Ward and others 1999). The extent and duration of river flooding during the wet season can determine whether and for how long fish can gain access to nursery habitats and food (Bayley 1991, Heiler and others 1995), and whether fish will remain trapped in isolated floodplain waterbodies or are released back into the river system (Lowe-McConnell 1985). Mortality of fish trapped in dry season refuges may be very high due to deteriorating physico-chemical conditions, reductions in food availability, and lack of refuge from predators (Kushlan 1976, Lowe-McConnell 1985, Woodland and Ward 1990). In turn, the duration and frequency of connection during periods of high flow (Halyk and Balon 1983, Hillman 1986), periodic isolation of floodplain waterbodies, and the proximity of such habitats to the main river channel are important in determining the composition of fish assemblages (Kushlan 1976, Hickley and Baley 1986, Lloyd and Walker 1986).

Flow regulation by dams, often compounded by other structural modifications such as channelization and levee banks, normally results in reduced connectivity and altered successional trajectories in floodplain rivers (Ward and Stanford 1995). Dams typically dampen flood peaks, reducing the frequency, extent, and often the duration of floodplain inundation. Smaller channel-forming flows modify patterns of channel migration, lowering habitat diversification on the floodplain. These changes ultimately reduce the biological diversity and ecological integrity of floodplain rivers (Ward and Stanford 1995) (Table 3).

Prior to river regulation, many species of fish in Australian rivers were thought to have used inundated floodplain wetlands of lowland rivers for breeding and juvenile habitat (Geddes and Puckridge 1989). River regulation to prevent flooding has seriously affected

Table 4.   Summary of biotic responses to altered flow regimes in relation to invasion and success of exotic and introduced species (principle 4)[a]

Flow variables affected	Biotic responses	Sources
Loss of wet-dry cycles and increased stability of water levels	Reduced growth and survival of native aquatic macrophytes and increased invasion of exotics	Kingsford 2000, Mitchell and Gopal 1991
Reduced flow variability and increased seasonal stability	Favor populations of exotic fish species (carp, mosquitofish)	*Edwards 1978*, Faragher and Harris 1994, Walker and others 1995, Gehrke and others 1999
Conversion of lotic to lentic habitat	Proliferation of exotic fish species	Arthington and Bluhdorn 1994, Davies and Day 1998
Interbasin transfers of water	Transfer of schistosomiasis; translocation of fish species	Pitchford and Visser 1975, Skelton 1986, Cambray and others 1986

[a]Additional examples (in italics) to those included in this review are from Petts (1984).

such recruitment (Cadwallader and Lawrence 1990), and there is an obvious trend of reduced native species abundance with increasingly regulated catchments (e.g., Gehrke and others 1995). On the Macquarie River in eastern Australia, the Macquarie Marshes, a hemispheric wetland reserve for water birds have been reduced to 40%–50% of their original size by flow diversions and weirs (Kingsford and Thomas 1995). Low flows have eroded river channels, further reducing flows onto the floodplain, and a water diversion channel and levee banks have alienated parts of the floodplain from the river and retained floodwater on other parts for periods of more than 12 months. The area with river red gums halved between 1934 and 1981, as did the area of reed beds between 1963 and 1972 (Brander 1987). Over several hundreds of hectares of coolibahs (*Eucalyptus coolibah*) flooded behind levee banks have died since the 1970s. Abundance and species richness of water birds in the northern part of the Macquarie Marshes has declined over an 11-year period (Kingsford and Thomas 1995).

Principle 4: The Invasion and Success of Exotic and Introduced Species in Rivers Is Facilitated by the Alteration of Flow Regimes

For the purposes of this review, the term exotic (i.e., nonnative) species is defined as those that are not indigenous to a country. The term introduced is used more generally to refer to any species intentionally or accidentally released into an environment outside its natural range (Welcomme 1988). Exotic species are favored by many changes to flow regime, and the first three principles help to explain why some exotic plants and animals are so successful under modified flow conditions.

Influence of Altered Flow Regimes on Invasions

The loss of wet–dry cycles in floodplain wetlands often has major ecological impacts that favor exotic species. In Australia stable water levels may reduce the growth and survival of native aquatic macrophytes and encourage the invasion of *Typha* spp. and introduced water hyacinth (*Eichhornia crassipes*) (Kingsford 2000).

Although fish species have been introduced into a wide variety of environments, the greatest success has been achieved in waters which have been dammed, diverted, and otherwise modified, creating permanent standing water (reservoirs) and more constant flow regimes than previously existed (e.g., Moyle 1986, Arthington and others 1990) (Table 4). Long-term success (integration) of an invading fish species is much more likely in an aquatic system permanently altered by human activity than in a lightly disturbed system (Moyle and Light 1996a). The most successful invaders will be those adapted to the modified flow regime (Moyle and Light 1996b).

Moyle and Light (1996a,b) argue that failure of exotic fish species to establish populations in Californian (USA) streams is best attributed to their inability to adapt to abiotic conditions (rather than as a result of the biotic resistance of the recipient community). Invasions of nonnative fishes into Deer Creek, an unmodified tributary of the Sacramento River, have failed, prevented primarily by the natural flow regime (Baltz and Moyle 1993).

Regulation of flows in some Australian rivers is thought to favor exotic fish species such as carp (*Cyprinus carpio*) and mosquitofish (*Gambusia affinis*) (Pusey and others 1989, Faragher and Harris 1994, Walker and others 1995, Gehrke and others 1999). These species appear to benefit from seasonally stable, low flows and may displace native species adapted to more variable

flows and heterogeneous habitat conditions. Common carp, tench (*Tinca tinca*), and European perch (*Perca fluviatilis*) have remained relatively insignificant in some Australian rivers for decades, whereas they have been favored by the increased stability of river flows in the Murray-Darling system (Cadwallader 1986). Gehrke and others (1999) have shown that regulated rivers in the Murray-Darling system have a lower diversity than relatively undisturbed rivers further inland, with the reduction in diversity largely due to greatly increased numbers of carp in regulated reaches.

Influence of Conversion of Lotic to Lentic Habitat on Biological Invasions

Long-term success (integration) of an invading species is much more likely in an aquatic system permanently altered by human activity than in a lightly disturbed system (Moyle and Light 1996a). Most prominently, this is due to the fact that human disturbed systems (e.g., reservoirs) resemble one another over broad geographic areas and favor species that are also favored by humans (Gido and Brown 1999). Creating permanent standing waterbodies and/or more constant flow regimes by damming or diverting river flows favors introduced species, many of which are most abundant in lakes and river backwaters in their native range (Moyle 1986).

Dominance of aquatic macrophyte communities in slow flowing and impounded river reaches by exotic species, such as the water hyacinth (*Eichhornia crassipes*) is a common occurrence. With its free-floating habit and rapid growth rate, the hyacinth can form dense surface growths covering large areas of open water, interfering with flow and water transport, disrupting recreation, impeding the access of stock to water, and blocking light penetration (Mitchell and Gopal 1991).

Conversion of rivers to lentic habitat can lead to the proliferation of exotic species of fish, for example tilapia (*Oreochromis mossambicus*) in large dams in Africa, Sri Lanka, and Australia (Arthington and Blühdorn 1994). However, conversion to lake habitat is not always perceived to be bad. For example, the Lake Tanganyika sardine ("kapenta," *Limnothrissa miodon*) was introduced to Lake Kariba. Between the first introduction in the 1960s and late 1990s, it has developed into a thriving fishery producing 25,000 t/yr, with a piscivore *Hydrocynon vittatus*, feeding on the sardine and forming another important fishery (Davies and Day 1998). Although once thought too small and puny to survive turbulent passage through hydroelectric turbines and sluice gates of Kariba Dam, the sardine has successfully invaded Lake Cahora Bassa (a reservoir) in Mozam-

bique, more than 200 km downstream (Davies and Day 1998).

Interbasin Transfers of Water

Although accidental or deliberate movement of propagules (e.g., stocking) are likely to be the most important mechanisms, alteration of flow regimes and the infrastructure associated with it are also major contributors to the spread of introduced and exotic aquatic species. Historical patterns of species distributions, local endemicity, and metapopulation structure of aquatic organisms are largely determined by catchment boundaries and the presence of natural in-stream barriers (e.g., waterfalls) (Meffe and Vrijenhoek 1988, Bunn and Hughes 1997, Pusey and others 1998). Interbasin water transfers can alter natural distribution patterns of aquatic biota and enhance the spread of pests and diseases (as well as presenting serious problems in terms of water balance, water quality and the disruption of significant ecological processes). Such schemes are increasing in popularity as the number of sites suitable for dam construction and the scale of individual decline (Boon 1992).

The South African Orange-Vaal River Project, the Orange-Fish-Sundays River Inter-catchment Transfer Scheme, and the Tugela-Vaal Water Transfer Scheme provide examples of the impacts of interbasin transfers on biological invasions (Cambray and others 1986) (Table 4). The transfer of endemic flora and fauna between catchments has occurred with a variety of consequences (Skelton 1986). Interbasin transfers of schistosomes in the Orange-Vaal Project into rivers previously free of schistosomiasis have been enhanced by temperature changes below large dams that affect the dynamics of both the snail host and parasite populations (Pitchford and Visser 1975). The catfish *Clarias gariepinnus* has invaded the Great Fish River through the intercatchment transfer tunnel from Lake Verwoerd and has become established in the Sundays River system (Skelton 1986), and there has also been some spread of aquatic macrophytes. Four species of fish have been introduced from the Orange River drainage to the Great Fish River drainage via interbasin water transfers, presumably transferred as eggs or larvae.

Uncertainty and the Role of Science

There can be no question that the natural flow regime has a profound influence on the biodiversity of streams, rivers, and their floodplain wetlands (Poff and others 1997, Hart and Finelli 1999). There are clearly several interrelated causal mechanisms operating over different temporal and spatial scales, and no one char-

acteristic of the flow is responsible (Figure. 1). As a consequence, it is often difficult to determine which attributes of the altered flow regime are directly responsible for observed impacts (e.g., is the decline of a fish species due to reduced capacity to migrate under altered peak flows or because of a change in substrate composition of spawning areas, or both?). An obvious constraint to resolving this is the potential lag effect in biological response to flow alteration. In particular, impacts to aquatic biota caused by changes in physical habitat (principle 1) may not directly coincide with actual changes in flow regime because of longer time scales for channel adjustment.

Despite this, there is growing recognition that certain aspects of the flow regime are important for particular ecological processes (e.g., to trigger fish migration and spawning, and rejuvenate floodplains). However, river managers now wish to predict how far these attributes can be altered from their natural state, before an impact occurs. For example, "what will be the impact of reducing a particular flow attribute from a current level of 10% less than natural to 20% less?" Similarly, managers need to be convinced that providing additional environmental flows (e.g., by reducing irrigation allocations at considerable cost) can produce some demonstrable environmental benefit. Our limited ability to predict and quantify the biotic response to flow regulation is a major constraint to achieving ecological sustainability (Bunn 1999, Naiman and others 1995, Richter and others 1997).

Perhaps a greater challenge to resolving this problem is the separation of direct effects of the modified flow regime from impacts associated with land-use changes that often accompany water resource development (e.g., conversion of forest to irrigated agriculture). In writing this review, we often encountered reports of river systems affected by multiple stressors and were unable to definitively separate the impacts of altered flow regimes from those of the myriad of other factors and interactions. How much of an observed decline in species diversity can be attributed directly to modified flow compared with diffuse inputs of nutrients and other contaminants? A similar problem occurs in our attempts to unravel the cause and effect of exotic species on aquatic biodiversity. Is an observed decline in native fish species the result of a modified flow regime or the direct impact of an introduced species (or both)? Alternatively, is the proliferation of exotic species a direct response to the modified flow or the decline in native species (or both)? Ecological science is not yet able to answer these questions, important as they are.

Ecologists still have much to learn about the ecolog-ical significance of individual flow events and sequences of events, and descriptive science can take us only so far in unraveling these linkages. The advice from aquatic ecologists on environmental flows might be regarded at this point in time as a series of largely untested hypotheses about the flows that aquatic organisms need and how rivers function in relation to flow regime. To overcome these problems, aquatic science needs to move into a manipulative or experimental phase, either by restoring flows, or taking away flows, and measuring ecosystem response. It is hoped, flow restoration experiments will dominate over flow regulation experiments!

Acknowledgments

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