Freshwater Biology

Freshwater Biology (2010) **55,** 86–107 doi:10.1111/j.1365-2427.2009.02179.x

Incorporating thermal regimes into environmental flows assessments: modifying dam operations to restore freshwater ecosystem integrity

JULIAN D. OLDEN AND ROBERT J. NAIMAN
School of Aquatic and Fishery Sciences, University of Washington, Seattle, WA, U.S.A.

SUMMARY

1. Despite escalating conflict over fresh water, recent years have witnessed a growing realisation that human society must modify its behaviour to ensure long-term ecological vitality of riverine ecosystems. In response, ecologists have been increasingly asked to guide instream flow management by providing 'environmental flow' prescriptions for sustaining the ecological integrity of riverine systems.
2. Environmental flows are typically discussed in the context of water releases from dams and water allocation for extraction (such as for urban use or irrigation), where there is general agreement that rivers need to exhibit some resemblance of natural flow variability necessary to support a functioning ecosystem. Although productive dialogue continues on how best to define environmental flows, these discussions have been focused primarily on water quantity without explicit consideration of many components of water quality, including water temperature – a fundamental ecological variable.
3. Many human activities on the landscape have modified riverine thermal regimes. In particular, many dams have modified thermal regimes by selectively releasing hypolimnetic (cold) or epilimnetic (warm) water from thermally stratified reservoirs to the detriment of entire assemblages of native organisms. Despite the global scope of thermal alteration by dams, the prevention or mitigation of thermal degradation has not entered the conversation when environmental flows are discussed.
4. Here, we propose that a river's thermal regime is a key, yet poorly acknowledged, component of environmental flows. This study explores the concept of the natural thermal regime, reviews how dam operations modify thermal regimes, and discusses the ecological implications of thermal alteration for freshwater ecosystems. We identify five major challenges for incorporating water temperatures into environmental flow assessments, and describe future research opportunities and some alternative approaches for confronting those challenges.
5. We encourage ecologists and water managers to broaden their perspective on environmental flows to include both water quantity and quality with respect to restoring natural thermal regimes. We suggest that scientific research should focus on the comprehensive characterisation of seasonality and variability in stream temperatures, quantification of the temporal and spatial impacts of dam operations on thermal regimes and clearer elucidation of the relative roles of altered flow and temperature in shaping ecological patterns and processes in riverine ecosystems. Future investigations should also concentrate on using this acquired knowledge to identify the 'manageable' components of the thermal regime, and develop optimisation models that evaluate management

Correspondence: Julian Olden, School of Aquatic and Fishery Sciences, Box 355020, University of Washington, Seattle, WA 98195, U.S.A. E-mail: olden@u.washington.edu

trade-offs and provide a range of optimal environmental flows that meet both ecosystem and human needs for fresh water.

Keywords: coldwater pollution, hypolimnetic release, water quality, water temperature

Introduction

The availability of fresh water to simultaneously meet the demands of a growing human population and ensure freshwater ecosystem integrity has emerged as one of the world's primary resource issues (Alcamo *et al.*, 2008). As world water demand has more than tripled over the last half-century, signs of water scarcity have now become commonplace. Given the realities of human dependency on freshwater ecosystems in the future, ecological thought has evolved from a focus on humans as exploiters of riverine ecosystem services to a world where humans and freshwater systems must coexist to ensure long-term ecological sustainability (Palmer *et al.*, 2004). This represents a formidable challenge in the coming decades, which will only get more difficult with projected growth in the human population, intensified land use and a changing climate (Poff *et al.*, 2003; Palmer *et al.*, 2008).

Achieving compatibility between human and natural ecosystem needs is the ultimate challenge of ecologically sustainable water management (*sensu* Richter *et al.*, 2003), in which scientists are becoming increasingly engaged. One of the most promising approaches to integrating human uses into the larger scope of ecological sustainability is the concept of environmental flows, or the provision of water within rivers to conserve freshwater biodiversity while maintaining the water needs of human society (Acreman & Dunbar, 2004). Environmental flows are typically discussed in the context of water releases from dams and catchment abstraction management (i.e. water allocation strategies for urban use or irrigation), where there is general agreement that they need to exhibit patterns of natural variability to support a functioning riverine ecosystem (Dunbar, Acreman & Kirk, 2004; Richter & Thomas, 2007). Recent dialogue has emerged among scientists on how best to define and prescribe environmental flows in a managerial context (e.g. Acreman & Dunbar, 2004; Arthington *et al.*, 2006; Richter *et al.*, 2006; Poff *et al.*, 2010), yet these discussions have focused primarily on water quantity without the explicit consideration of water quality, such as water temperature, pollutants, nutrients, organic matter and sediments and dissolved oxygen.

Hydrologic alteration is a major consequence of river regulation associated with significant impacts on aquatic biodiversity (Bunn & Arthington, 2002); however, dams and diversions have also greatly modified riverine thermal regimes depending on their mode of operation and specific mechanism and depth of water release (Ward, 1985). For example, a substantial number of large dams throughout the world have intentionally managed thermal regimes by selectively releasing cold water from deep reservoirs to establish highly desirable fishing opportunities for trout, salmon or walleye. Similarly, fluctuating releases by hydroelectric dams from beneath the reservoir's thermocline can result in highly variable and frequently depressed summer water temperatures. Smaller dams and diversions, in contrast, can cause increases in downstream temperatures by releasing warm water directly from the reservoir surface. Dam-induced modifications to a river's thermal regime (also termed thermal pollution) can have both direct and indirect consequences for freshwater ecosystems, yet it has been relatively unappreciated in discussions of in-stream flow management.

While the ecological significance of water temperature in riverine ecosystems is widely acknowledged (reviewed in Magnuson, Crowder & Medvick, 1979; Poole & Berman, 2001; Caissie, 2006), the prevention or mitigation of thermal pollution below dams has received little attention when environmental flow assessments are conducted. This is despite the highly recognised impact of dams on thermal regimes and the inherent relationship between discharge, temperature and a host of other water quality variables (Nilsson & Renöfält, 2008). Clearly, both discharge and temperature must be simultaneously considered for the successful implementation of environmental flow management below dams. We perceive this as a major gap in environmental flow assessments that needs to be both elaborated upon and addressed in the future. Our article aims to narrow this knowledge gap by exploring the concept of the natural thermal regime, reviewing how river regulation by dams modify thermal regimes, and discussing the ecological implications of thermal alteration for freshwater ecosystems. We focus on the thermal effects of dams, although we readily acknowledge that many other human activities such as the direct extraction of water for consumption, sanitation and irrigation influence riverine thermal regimes and are highly relevant in environmental flow assessments. Next, we discuss five major challenges for incorporating water temperatures into environmental flow assessments and highlight research opportunities and some alternative approaches for confronting those challenges. The perspectives developed in this study are that by viewing environmental flows in a holistic manner, in which both water quantity and quality are considered in flow recommendations, we will increase the chances of long-term success in achieving ecologically sustainable water management.

The natural thermal regime and its importance for riverine ecosystems

Stream temperature depends on the amount of heat energy added or lost to the channel (i.e. energy budget) and the volume of water to be heated or cooled (i.e. thermal capacity) (Poole & Berman, 2001; Caissie, 2006). Heat energy is exchanged both at the air⁄surface water interface and at the streambed⁄water interface through a number of physical processes, which are mediated by a multitude of external drivers that control heat and water delivery to the stream (Fig. 1). Heat flux at the air⁄surface water interface occurs primarily through solar or short-wave radiation, long-wave radiation, evaporative processes and convective transfer resulting from temperature differences between the stream and the atmosphere. Heat exchange at the streambed⁄water interface is mainly a function of geothermal heating through conduction and advective heat transfer through groundwater inputs and hyporheic exchange. The rates of these processes are controlled by a number of factors related to atmospheric conditions, topography, streambed and stream discharge (Webb, 1996; Caissie, 2006).

Water temperatures show marked annual and diurnal fluctuations in response to seasonal and daily rhythms in the amount and type of heat energy gained and lost by a stream and the volume and source of runoff contributing to discharge (Ward, 1985; Webb, 1996). A stream's thermal regime describes the distribution of the magnitude of water temperatures, the frequency with which a given temperature occurs, the time of the day or year when a certain temperature occurs, and the duration of time

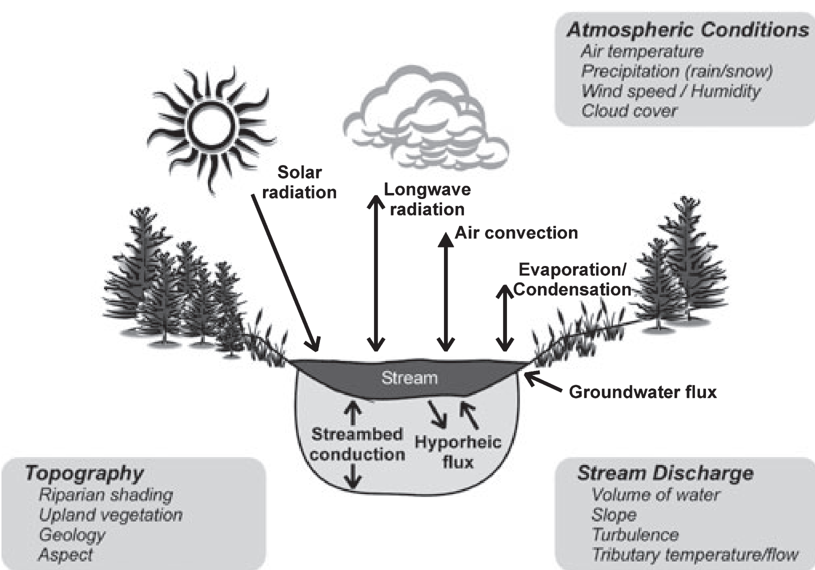

Fig. 1 Heat exchange processes responsible for variability in water temperatures (bold font) and the physical drivers that control the rate of heat and water delivery to stream and river ecosystems (italic font).

for which a stream is above or below a given temperature. We propose that the *natural thermal regime* can be discomposed into its components of magnitude, frequency, duration, timing and rate of change. Therefore, much like the natural flow regime (Poff *et al.*, 1997) and the quantification of its characteristic properties (Olden & Poff, 2003), thermal regimes can be summarised using statistics that describe the central tendency and variability in distributions of temperature conditions (Fig. 2a). For example, Jackson, Gibbins & Soulsby (2007) calculated a suite of metrics describing what they deemed as critical attributes of the thermal regime for invertebrate communities in the Lyon River (Scotland). Such analyses could also include the characterisation of thermal regimes at multiple temporal scales (Steel & Lange, 2007). In addition, the physiological tolerances of freshwater species to particular temperatures (see below for further discussion) and the influence of temperature on other aspects of water quality, such as solute and pollutant fluxes, nutrient concentrations, organic matter and sediments and dissolved oxygen (Webb, 1996; Caissie, 2006), allow for the quantification of more targeted metrics describing thermal characteristics of streams and rivers. For example, development schedules for freshwater fish and insects respond to the summation of thermal units (i.e. the accumulation of daily temperatures above some threshold) as well as absolute temperatures, and fish species have both chronic and acute temperature

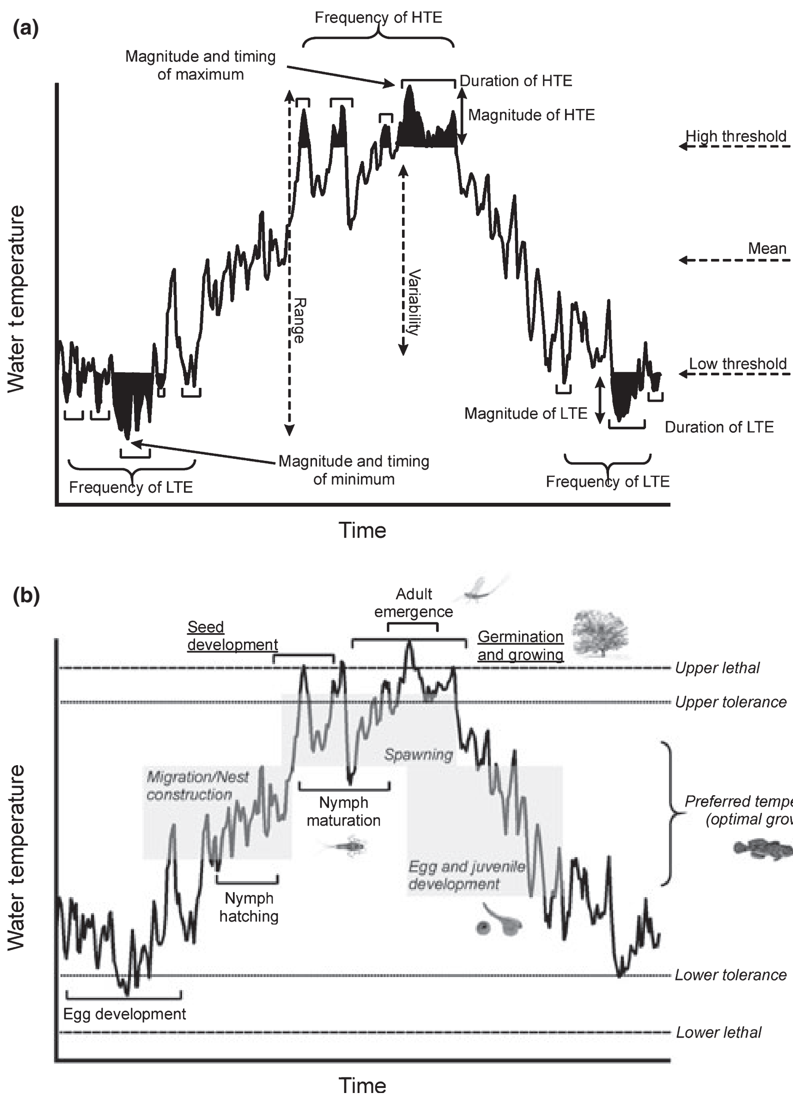

Fig. 2 (a) A stream's thermal regime describes the magnitude, frequency, duration, timing and variability in water temperatures at different spatial and temporal scales. Shown are a number of quantitative metrics that describe different components of the thermal regime, including high thermal events (HTE) and low thermal events (LTE) based on a defined upper and lower threshold, respectively. The threshold could be ecologically derived (e.g. upper and lower lethal temperature, threshold temperature for cueing spawning or positive growth) or based on the statistical distribution of annual temperatures (e.g. 90th and 10th percentile). Other metrics not illustrated here could be appropriate for describing thermal regimes for various objectives. (b) A stream's natural thermal regime influences freshwater biodiversity via multiple mechanisms that operate at different spatial and temporal scales. Shown are a number of examples in which temperature influences the bioenergetic and life-histories of fish (italic font), insects (normal font) and riparian plants (underlined font). Overall, the native biotas of riverine ecosystems have evolved in response to the natural thermal regime.

thresholds for survival, growth and reproduction (Vannote & Sweeney, 1980; Coutant, 1987). This provides the opportunity to derive synthetic metrics that are ecologically relevant for the species or community of interest.

The ecological integrity of lotic ecosystems depends on the natural dynamics of the thermal regime. Water temperature directly influences the metabolic rates, physiology and life-history traits of aquatic species and helps determine rates of important ecological processes such as nutrient cycling and productivity, and indirectly mediates biotic interactions (Magnuson *et al.*, 1979; Petts, 1986; Poole & Berman, 2001; Caissie, 2006; Webb *et al.*, 2008). As ectotherms, freshwater fishes and insects use a diverse array of thermal habitats to meet their specific temperature requirements for survival, growth and reproduction (Coutant, 1987; Vinson & Hawkins, 1998). Consequently, specific components of the thermal regime have specific ecological relevance for freshwater organisms throughout their life history. We highlight a few examples in Fig. 2b.

Water temperatures directly influence growth rates of aquatic organisms and interacts with the lower and upper incipient lethal temperatures to shape species distributions. The availability of thermal heterogeneity also provides ecothermic organisms the opportunity to select habitats that optimise their energy intake relative to physiological costs and thus affecting growth and survival. For example, species of salmon (*Oncorhynchus* spp.) thermoregulate behaviourally by occupying cooler areas, such as seeps and confluences with cold streams, when surrounding temperatures exceed their upper tolerances (e.g. Berman & Quinn, 1991). Similarly, temperate fishes actively seek warm thermal refugia provided by small streams and springs to escape cold waters and take advantage of warmer conditions needed for optimal feeding efficiency and growth (e.g. Peterson & Rabeni, 1996). Development and life-history events of locally adapted populations of aquatic insects and fishes are closely timed to prevailing thermal regimes (Vannote & Sweeney, 1980; Vinson & Hawkins, 1998; Huryn & Wallace, 2000). For example, the natural temperature regime of a river provides thermal cues that stimulate fish migration, spawning and egg hatching, and directly influences egg survivorship and developmental time (Wootton, 1990; Fig. 2b). Changes in temperature can also influence the type and prevalence of diseases affecting fish. Lastly, the accumulation of daily maximum temperatures above a critical threshold has been shown to be a fundamental parameter in shaping the distribution and condition of many aquatic species (Armour, 1991).

Dam-induced modifications to riverine thermal regimes

Spatial and temporal patterns in stream temperatures are influenced by modifications to the energy budget and/or the thermal capacity of the fluvial ecosystem (Poole & Berman, 2001). Any natural process or human activity that alters the external drivers of heat load or stream discharge in a system will influence spatiotemporal patterns of water temperature (Fig. 1). For example, the discharge of heated industrial effluents, such as cooling water from power generating stations, can result in unnaturally elevated water temperatures (Langford, 1990). A reduction in stream discharge resulting from water extraction for human consumption or irrigation practices can also directly affect water temperatures by decreasing thermal capacity and thus increasing the likelihood of high temperature events (Sinokrot & Gulliver, 2000). In an indirect manner, stream temperatures may be modified through changes in catchment land use and channelisation, both of which alter the energy budget and thermal capacity of the water course (Moore, Spittlehouse & Story, 2005; Nelson & Palmer, 2007).

Here, we focus on dams and diversions that have both direct and indirect effects on riverine thermal regimes. In general, the extent to which a dam affects downstream thermal regimes depends on their mode of operation and specific mechanism of water release. Dams directly modify a river's thermal regimes by releasing water that differs greatly in temperature to that occurring naturally in the river. The magnitude of thermal alteration depends largely on stratification behaviour of the reservoir (i.e. depth profile of the thermocline), and the depth at which water is released from the dam. Dams also modify water temperatures indirectly by influencing processes controlling the delivery, distribution and retention of heat within the river channel. Changes to discharge and the volume of water in a river, for example, affect the rate at which water heats and cools in response to natural diurnal heat exchange both at the air⁄surface water and streambed⁄water interface (Petts, 1986; Palmer & O'Keeffe, 1989; Poole & Berman, 2001).

Many large dams throughout the world cause downstream modifications to riverine thermal regimes by altering flow regimes and releasing cold water from below the thermocline of the reservoir (i.e. the hypolimnetic layer). Coldwater thermal regimes are established by releasing water from a single deep portal (often associated with hydroelectric generation) or selectively withdrawing water from different reservoir depths. In many instances, hypolimnetic releases of cold water provide unique and highly desirable fishing opportunities for trout or salmon in geographic regions that could otherwise not support coldwater species (e.g. Brooker, 1981; Horne, Rutherford & Wehrly, 2004; Krause, Newcomb & Orth, 2005). Although dam operations provide optimal coldwater conditions for tailwater fisheries, this is often at the detriment of entire warmwater assemblages of native fishes and other aquatic organisms (see discussion below). Consequently, many ecologists consider this a form of thermal depression or *coldwater pollution* because water temperatures are typically much lower during the spring and summer months compared to free-flowing rivers (although during the winter months, dam operations typically elevate water temperatures in relation to natural conditions). Many other dams (typically smaller in size and located in cooler summer climates) release water from above the thermocline of the reservoir (i.e. the epilimnetic layer) resulting in elevated spring–summer water temperatures (e.g. Lessard & Hayes, 2003).

The thermal impacts associated with dam operations in riverine ecosystems are well recognised (Ward & Stanford, 1982; Ward, 1985; Petts, 1986; Webb & Walling, 1996); although they are examined much less often than river hydrology. A reservoir acts as a buffer that reduces both the annual amplitude of, and daily fluctuations in, downstream temperatures because the reservoir's mass warms and cools more slowly than the free-flowing river. Thermal effects of river regulation by dams vary depending on the landscape position of the dam, mode of dam operation, release depth and environmental and geomorphologic setting. Despite these many factors, an examination of rivers regulated by large, hypolimnetic-release dams from different regions of the world reveals a relatively consistent pattern (Fig. 3). In general terms, reservoirs moderate downstream thermal regimes where temperatures are lower in the spring and summer months, higher in the winter months, fluctuate less seasonally, and exhibit delayed timing of maxima compared to natural conditions. Finer-scale investigations also show that water temperatures downstream from dams often have muted diurnal variation because of the stable temperatures of hypolimnetic waters (Lowney, 2000; Steel & Lange, 2007).

There are many similar examples to that presented in Fig. 3 that could be cited (see references listed above). In Australia, river regulation by hypolimnetic dams has caused the annual thermal maxima of numerous systems to be both reduced and displaced in time; for example, downstream of Burrendong Dam on the Macquarie River (8–12 °C depression and 1–3 month delay) and downstream of Dartmouth Dam on the Mitta Mitta River (8–10 °C depression) (reviewed in Lugg, 1999; Ryan *et al.*, 2001; Preece, 2004). Jackson *et al.* (2007) found that summer water temperatures in the regulated Lyon River were 5–6 °C cooler than the adjacent unregulated Lochay River, Scotland. Similarly, Angilletta *et al.* (2008) reported a decrease in summer water temperature from 17.5 to 14.5 °C after the construction of Hills Creek Dam on the Willamette River, Oregon (U.S.A.). These examples highlight a general pattern toward summer cooling and winter warming resulting from hypolimnetic release operation below large dams. Not surprisingly, a contrasting pattern emerges when we examine epilimnetic-release dams. Lessard & Hayes (2003) examined 10 small dams on Michigan streams (U.S.A.) and found that summer temperature below dams increased an average of 2.7 °C, ranging from a 1.0 °C cooling to a 5.5 °C warming.

Scientists have also provided a wealth of information concerning the extent to which the thermal effects persist downstream beyond the immediate vicinity of the dam. Thermal impacts can encompass relatively short or extremely long distances below their respective dams depending on heat exchange with the atmosphere, hydrologic inputs from tributaries and groundwater recharge, and dam discharge (Palmer & O'Keeffe, 1989). In the Murray-Darling River Basin (Australia), depressed summer temperatures extend up to several hundred kilometres downstream of dams on a number of major rivers, including Murrumbidgee, Marquarie, Mitta Mitta, Namoi and

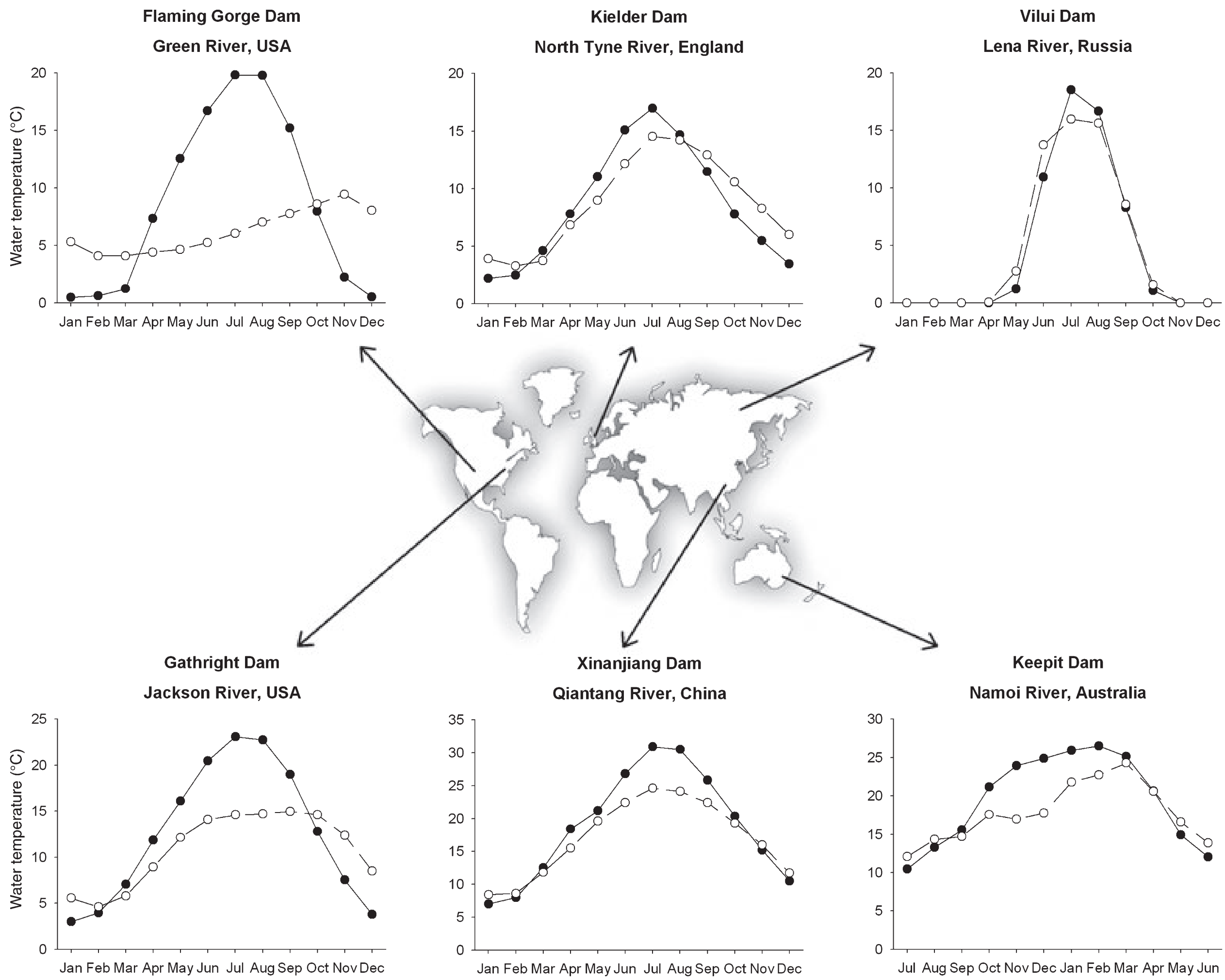

Fig. 3 Annual thermographs from regulated rivers across the world illustrating summer cooling and winter warming caused by hypolimnetic-release dams. Mean monthly temperatures are presented for the unregulated record (filled symbols and solid line) and the regulated record (open symbols and dashed line). The unregulated record includes data recorded either in pre-dam years (i.e. prior to construction), immediately upstream from the dam, or from an unregulated tributary, and the regulated record includes data recorded in post-dam years. Details regarding the temperature data are as follows. Flaming Gorge Dam: unregulated (1958–62), regulated (1963–77), data source (US Geological Survey); Kielder Dam: unregulated (1993–95), regulated (1993–95, River Rede), data source (David Archer); Vilui Dam: unregulated (1950–65), regulated (1966–97), data source (Daqing Yang); Gathright Dam: unregulated (1991–2006, upstream from dam), regulated (1991–2006, downstream from dam), data source (US Geological Survey); Xinanjiang Dam: unregulated (1957–59), regulated (1960–68), data source (Zhong & Power, 1996); Keepit Dam: unregulated (1976–2003, upstream from dam), regulated (1976–2003), data source (Australian Department of Natural Resources).

Murray (Ryan *et al*., 2001; Preece, 2004; Todd *et al*., 2005). The thermal recovery of the River Svratka, Czech Republic, required over 40 km (Ward, 1985), and using rates of maximum summer warming, Stevens, Shannon & Blinn (1997) estimated that a mainstem distance of 930 km would be required for water temperatures to fully recover (increase to pre-dam conditions) below Glen Canyon Dam in the Colorado River, U.S.A. (a distance that is currently prevented by other downstream dams). In coolwater systems affected by epilimnetic-release dams, streams may not be able to shed added heat during the summer and downstream water temperatures may continue to warm due to normal stream processes. Fraley (1979) found significant summer temperature increases in the Madison River, Montana (U.S.A.) that never returned to upstream temperatures even 56 km downstream of a surface-release dam, although diurnal temperature fluctuations did recover with increasing distance.

Ecological consequences of modified thermal regimes

Extensive dam construction throughout the world has raised long overdue concerns regarding the potential impacts of altered thermal regimes on biodiversity and ecological processes. Empirical evidence suggests that dam-induced thermal alteration by dams has significant implications for stream productivity and the reproduction, growth, distribution and assemblage structure of organisms (Haxton & Findlay, 2008). Despite this, our current level of understanding continues to be much less than our knowledge of the ecological implications of altered hydrology (Murchie *et al.*, 2008). Below we illustrate the ecological consequences of modified thermal regimes through a series of case studies.

In Australia, the ecological consequences of coldwater pollution have been more widely recognised compared to other countries. A number of empirical and modelling studies have explored the relationship between dam-induced thermal changes and fish populations in rivers. Cooling and delayed timing of maximum temperatures in the Namoi River below Keepit Dam had significant consequences for the spawning success of several native fish species (Preece & Jones, 2002). Based on the percentage of time in the spawning period that the mean daily water temperature exceeded the temperature threshold for spawning, spawning opportunities for silver perch (*Bidyanus bidyanus* Mitchell, 1838) and golden perch (*Macquaria ambigua* Richardson, 1845) were reduced to 25–70% and 44–87% of pre-dam years, respectively. Using a stochastic population model, Todd *et al.* (2005) explored the impact of altered thermal regimes on the population viability of Murray cod (*Maccullochella peelii peelii* Mitchell, 1838) in the Mitta Mitta River downstream of the fourth largest dam in Australia, Dartmouth Dam. Model predictions showed that cold water releases significantly threaten the post-spawning survival of Murray cod by reducing the average minimum female population size by 76% and increasing population variability by 137%.

In the Qiantang River Basin of China, the construction of Xinanjiang Dam caused mean temperatures to decrease from 19.0 to 13.5 °C, and the annual sum of degree days >15 °C (considered the positive-growth threshold temperature for warmwater fish species) dropped 37% (Zhong & Power, 1996). As a result, the majority of warmwater fishes were extirpated from large sections of river below the dam. In the Hanjiang River below the Danjiangkou Dam, China, the postponed timing of spring–summer warming caused by dam operations resulted in fish spawning times that were delayed by 20–30 days. Late hatching and lower water temperatures reduced the first year growth compared to an unregulated river (Zhou, Liang & Huang, 1980). Similarly, significant declines of native fishes in the Colorado River Basin (U.S.A.) have been attributed, in part, to the depression of spring–summer tailwater temperatures caused by hypolimnial-release dams. For example, the operation of Flaming Gorge Dam on the Green River, lowered spring–summer tailwater temperatures to nearly 6 °C from a previous range of 7–21 °C, which contributed to the extirpation of several native species including the endangered Colorado pikeminnow (*Ptychicheilus lucius* Girard, 1856), humpback chub (*Gila cypha* Miller, 1946) and bonytail chub (*G. elegans* Baird & Girard, 1853) (Clarkson & Childs, 2000). Similarly, Olden (2004) found that depressed summer temperatures below Gathright Dam on the Jackson River, Virginia (U.S.A.), resulted in complete species turnover from a warmwater fish assemblage to a river dominated by cool- and coldwater fish species.

Modified temperature regimes also strongly influence invertebrate communities by eliminating key developmental cues and influencing the rate of egg development and juvenile growth. Consequently, changes in temperature can cause the asynchrony of the life cycle to seasonal patterns in resource and mate availability (Vannote & Sweeney, 1980). Individual species responses can generate significant changes in assemblage structure by shifting the composition from warm stenothermic species to cold-tolerant eurytherms (Ward, 1974). For example, when a hypolimnetic dam was constructed on the Saskatchewan River (Canada), the cue to end egg diapause was eliminated because winter temperatures were maintained near 4 °C and the insect biota no longer experienced a prolonged period near freezing followed by a rapid temperature increase (Lehmkuhl, 1974). This resulted in the complete loss of an insect fauna, switching from a river containing 12 orders, 30 families and 75 species to one that comprised only the midge family Chironomidae. Another potential consequence of warmer winter temperatures is an increase in the growth of aquatic insects, resulting in winter rather than spring or early summer emergence (Ward & Stanford, 1982). Emergence during the winter is either lethal or impedes mating of aquatic insects. In another example, Stevens *et al.* (1997) found that the macroinvertebrate fauna of the Colorado River (U.S.A.) below Glen Canyon Dam was highly depauperate compared with other unregulated rivers of the basin. They collected virtually no species from the Ephemeroptera (mayfly), Plecoptera (stonefly) or Trichoptera (caddisfly) families in the mainstream in 1991, suggesting that cold-stenothermic releases may not permit these taxa to complete their life cycle. Voelz & Ward (1991) observed increasing insect species richness with distance downstream from Granby reservoir dam (Colorado River, U.S.A.) in response to a gradual recovery (increasing) in maximum summer stream temperatures. Additional examples of the effects of hypolimnetic release on macroinvertebrate communities are discussed by Haxton & Findlay (2008).

Dam-induced changes in thermal regimes may also have long-term evolutionary consequences for riverine biota by inducing a mismatch between a species' life-history and other critical environmental conditions. For example, Angilletta *et al.* (2008) hypothesised that warmer temperatures during the autumn and winter below Lost Creek Dam (Rogue River, U.S.A.) may indirectly influence the fitness of Chinook salmon (*Oncorhynchus tshawytscha* Walbaum, 1792) by accelerating the development of embryos, leading to earlier timing of emergence. Shifts to earlier emergence could lead to mortality from high flow events, elevated predation or insufficient resources. Using an age-based population model the authors predicted a decrease in mean fitness of Chinook salmon after dam construction. Although the likelihood for these impacts is unknown (i.e. temperature changes may also result in strong compensatory strategies, such as delayed spawning by adults or slowed development by embryos), the potential evolutionary consequences of thermal alteration should not be overlooked.

Challenges and prospects for incorporating thermal criteria into environmental flow assessments

We propose that a river's thermal regime is a key, yet poorly acknowledged, component of environmental flows. The efficacy of environmental flows to advance ecologically sustainable water management is predicated upon a greater appreciation of the influence of human activities on riverine thermal regimes and other critical water quality variables, and requires new research and tools that help define management options that maintain key hydrologic and thermal processes for the benefit of aquatic ecosystems. Below, we discuss five overarching challenges for incorporating thermal criteria into environmental flow assessments, and lay out some alternative approaches for confronting those challenges. Some challenges are deceptively simple, while others will require new avenues of research. In the sections that follow we use the Flaming Gorge Dam – a 91 m dam constructed in 1962 on Green River, U.S.A. (the largest tributary of the Colorado River) for hydroelectricity generation and flow control – as a working example. Although our discussion, in part, focuses on the role of river regulation by dams and diversions, we believe that many of the challenges are equally pertinent for our ability to incorporate water temperature targets into environmental flows standards for water abstraction practices.

Challenge #1: Advance our understanding of dam-induced impacts to riverine thermal regimes

Continuing research has emphasised the complexity of thermal responses to dams as a result of processes occurring within reservoirs and downstream. Significant inter-annual variation in the impact of dam operations on downstream temperatures has been illustrated and attributed to year-to-year changes in climate conditions, reservoir operation and behaviour, and tributary inflows (Webb & Walling, 1993, 1996; Preece & Jones, 2002; Todd *et al.*, 2005). We highlighted a number of river systems around the world with qualitatively very different annual thermographs between pre- and post-dam time periods (Fig. 3). Similarly, the majority of published studies reporting the thermal impacts effects of dams have focused almost exclusively on simple comparisons of annual or monthly temperatures before and after dam construction, often without supporting statistical analyses. While such comparisons are informative for descriptive purposes, we argue that ecologists must better formalise how dams are altering the various components of the thermal regimes, including the magnitude, frequency, duration, timing and rate of change in temperature events. Each component of the thermal regime has distinct ecological relevance for freshwater organisms, communities and riverine processes (Fig. 2b), which should ultimately guide the appropriate characterisation of the thermal regime and the selection of relevant descriptors (Fig. 2a).

Characterizing thermal regimes and assessing the downstream impacts of dams will be challenging for many of the same reasons that assessing hydrologic variability and alteration continues to be difficult – perhaps even more so. In the United States, water temperature data are collected by a variety of federal, state and local agencies, although the primary source for long-term daily records is the U.S. Geological Survey (also the main source for daily discharge data). As of June 2008, the U.S. Geological Survey has collected data from 24 856 gauges across the country, yet only 7.4% of these gauges contain records of daily water temperature for at least 1 year, and less than 1% of all gauges contain temperature data for at least 15 years. Moreover, most temperature records begin after the construction of a dam or diversion. Given the paucity and appropriateness of long-term water temperature data (a problem common to most other regions of the world), investigators may be forced to rely more heavily on temperature models based on unregulated systems to predict riverine thermal conditions. These will include empirical models that use statistical analyses (e.g. regression, neural networks) to make temperature predictions from meteorological data or catchment characteristics, physically based modelling that involves solving the heat budget equation and hydrodynamic models relating discharge to water temperatures (Gu, McCutcheon & Chen, 1999; Caissie, 2006; Webb *et al*., 2008). Scientists will also benefit greatly from recent technological developments that have facilitated the measurement and monitoring of water temperature using programmable (and remotely downloadable) digital loggers and remotely sensed thermal infrared imagery (Webb *et al*., 2008), in addition to the creation of central depositories or information systems containing water temperature data.

In some cases, long-term daily water temperatures will be available (or modelled) to quantify the impact of river regulation on thermal regimes. As an example, we quantitatively compared the thermal regimes of the Green River (U.S.A.) before and after the construction of Flaming Gorge Dam with respect to metrics describing the magnitude, frequency, duration and timing of water temperatures. These thermal metrics were selected *a priori* based on previous empirical demonstrations of their ecological importance for species occurrence and community structure in the Green River, or more broadly the Upper Colorado River Basin (Clarkson & Childs, 2000; Vinson, 2001). Flaming Gorge Dam uses a hypolimnetic release schedule that has increased predictability and substantially reduced annual variability in water temperatures (Fig. 4). Average late spring and summer temperatures (May–August) are 66% lower in post-dam years decreasing from 17.2 to 5.7 °C, whereas winter temperatures (December–March) showed a marked increase of 802% from 0.7 to 5.4 °C (Fig. 4). Magnitude of 1-, 7- and 30-day minimum temperatures increased from 0–0.2 to 3.4–3.9 °C after dam construction, whereas the magnitude of maximum temperatures for the same duration decreased 56% from 21.1–24.0 °C (pre-dam) to 9.6–10.0 °C (post-dam) (Fig. 4). Dam operations have resulted in significantly lower frequency and duration of low and high temperature events (Fig. 4), and shifted the timing of average minimum temperatures forward 3 weeks (12th February–4th March) and average maximum temperatures ahead over 15 weeks from the summer (24th July) to the autumn (7th November) (Fig. 4). We recommend that future research should focus on the quantitative assessment of thermal alteration associated with dam operations, including the statistical analysis of pre- and post-dam time periods to better elucidate how different components of the riverine thermal regime are modified by dam operations and recovery downstream.

Without detailed and long-term temperature data (either recorded or modelled), it is unlikely that comprehensive evaluations of dam-induced thermal alteration at the landscape scale will be possible. However, in lieu of these data it is possible to qualitatively forecast the thermal impacts of river regulation according to dam/reservoir characteristics (e.g. dam height, reservoir depth and bathymetry), operation schedule (e.g. intake depth, discharge), and geomorphic attributes of the receiving river system (channel form, groundwater influences, position and characteristics of tributaries). In Australia, the states of Victoria, Queensland and New South Wales have completed comprehensive reviews of large dams to

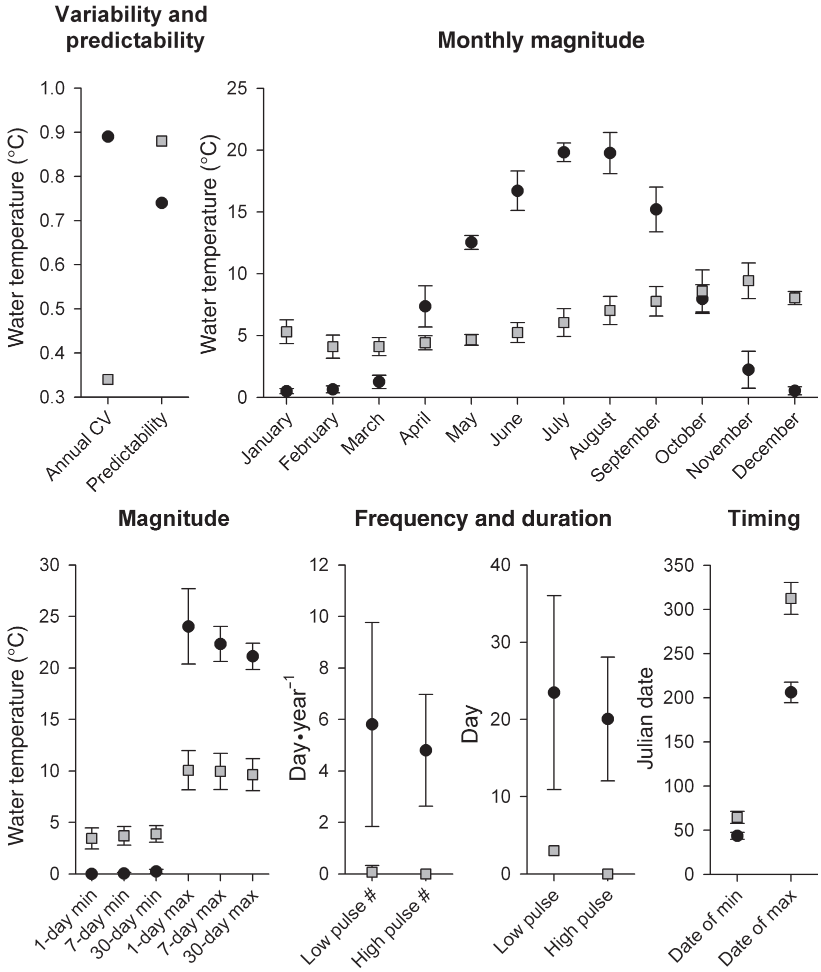

Fig. 4 Hypolimnetic release operations of Flaming Gorge Dam have significantly altered the thermal regime of the Green River (U.S.A.). Comparisons of thermal metrics computed for the pre-dam (1958–62, circles) and post-dam records (1963–77, squares) show considerable effects on the thermal regime, including variability and predictability of annual temperatures, monthly temperatures, magnitude, frequency and duration and timing of thermal events. Low and high pulses (and durations) are based on mean daily temperatures below the 25th percentile and above the 75th percentile of unregulated temperatures, respectively. Bars represent ±1 SD and 'CV' refers to the coefficient of variation.

identify and rank structures based on potential to cause coldwater pollution. Ryan *et al.* (2001) ranked dams in Victoria based on depth and frequency (regular versus occasional) of release, and identified 24 top priority dams for which further assessment and continuous temperature monitoring was recommended. The New South Wales review used intake depth and summer discharge to develop a short list of nine dams (out of 93 in total) predicted to cause severe coldwater pollution (Preece, 2004). With the exception of Australia, the potential for coldwater pollution associated with dams has not been systematically assessed. These so-called 'desktop assessments' may be particularly valuable for identifying those rivers where thermal pollution may be prevalent, thus helping guide future temperature surveillance efforts and prioritizing the possible retrofitting of current gauges to record water temperatures. Moreover, in combination with additional modelling, this information would enable the mapping of spatial patterns in dam-induced thermal alteration across entire riverine landscapes.

Challenge #2: Advance our understanding of the ecological consequences of altered thermal regimes

Hydro-ecological studies are becoming increasingly interdisciplinary, with research focusing on, among other things, the relationships between water quantity and quality, and their importance for riverine biota. However, despite broad recognition of the importance of flow and thermal regimes for river systems, there are relatively few studies that have explicitly linked dam-induced changes in *both* flow and thermal factors to ecological structure and function. In a revealing study, Murchie *et al.* (2008) conducted a systematic review of the literature to identify studies that examined the response of fish to modified flow regimes in regulated rivers. Of the 131 studies identified in their review, they found that although almost half of the studies included the collection of water temperature, the majority of these studies (57%) failed to examine the potential consequences of thermal alteration. Moreover, an extremely small number of studies included temperature data in formal statistical analysis to explore the potential individual and interactive effects of flow and thermal modification on fish assemblages. We cannot emphasise enough the need for this research for supporting a truly holistic approach to environmental flow assessments that incorporates both flow and temperature targets.

The limited literature examining both thermal and flow effects on freshwater organisms suggests that both the direct and interactive influence of these factors are critical. In the Jackson River (U.S.A.) below Gathright Dam, Olden (2004) found that no one single component of the flow or thermal regime explained fish population- and community-level responses to river regulation. Overall, species showed patterns of numerical recovery below the dam that were largely congruent with their ecological requirements; for example, fluvial-specialist species responded positively to decreasing flow alteration and warmwater species responded positively to decreasing thermal alteration. Jackson *et al.* (2007) explored the relative roles of discharge and temperature variation in determining invertebrate community structure in a regulated river in Scotland. The authors found that no one flow or thermal metric exerted an overriding influence on community structure suggesting that whole regime changes, rather than alterations to one particular aspect of the regime, were responsible for the impoverishment of invertebrate communities observed below the dam.

Although some additional examples do exist, in general it remains extremely difficult to ascertain the relative contributions of flow versus temperature (and a number of other water quality variables influenced by dams and human activities) to observed biotic responses in riverine ecosystems (Bednarek & Hart, 2005). This is supported by Haxton & Findlay (2008) who, after conducting a comprehensive review of the literature, lamented the paucity of studies that quantified the effects of particular drivers of dam-induced change on downstream species responses. We view this as a significant challenge that currently precludes our ability to formally incorporate thermal criteria into environmental flow assessments. Confronting this challenge may be facilitated by the simple fact that levels of hydrologic and thermal alteration and rates of downstream recovery vary substantially within and among regulated rivers. By synthesizing and collecting data along these spatial gradients of alteration, greater insight into the relative roles of hydrologic and thermal factors in shaping stream communities will be possible.

Challenge #3: Demonstrate the availability and success of temperature management strategies

A number of management options exist for mitigating the thermal impacts of dams. The indirect management of water temperatures is possible by targeting those drivers of thermal regimes that can be directly manipulated, such as the appropriate management of riparian zones and the maintenance of natural flow variability (Poole & Berman, 2001; Fig. 1). The management of riverine landscapes for thermal integrity will require a broad perspective that recognises the heterogeneous nature in which the topology of the drainage network controls the physical processes shaping spatial and temporal variability in stream temperatures. For example, the ecological importance of tributaries for promoting physical heterogeneity is well recognised (e.g. Rice, Ferguson & Hoey, 2006), and we believe that understanding the dynamics of confluence zones is an integral part of understanding the role of tributaries in mediating the downstream impacts of dams on thermal regimes (in addition to hydrologic regimes and sediment processes). The degree to which unregulated tributaries lessen the thermal influences of dams will depend on the size of the stream and its distance from the dam, and characteristics of the tributary with respect to discharge, sediment and water temperature (Petts, 1986).

The influence of tributaries on mainstem thermal and biological recovery has been illustrated in a number of studies (e.g. Ward, 1985; Stevens *et al.*, 1997; Vinson, 2001). Preece & Jones (2002) showed that the pattern of thermal recovery downstream from Keepit Dam on the Namoi River (Australia) was significantly influenced by the contribution of two unregulated tributaries; the magnitude of this effect was greater in the spring and early summer when tributary discharge was 50% of that from Keepit

Dam, compared to the summer when the relative contribution of the tributaries was small (<10% of Keepit Dam). Sato *et al*. (2005) found that the reproductive success of an important fisheries species, *Prochilodus argenteus* Spix & Agassiz, 1829 in the cold tailwaters below the Tres Marias Dam on the Sao Francisco River, Brazil, was achievable only below the confluence with a medium-sized, unregulated tributary. Vinson (2001) recorded greater insect richness downstream from a tributary confluence on the Green River below Flaming Gorge Dam, and Olden (2004) found elevated richness of warmwater fish species in the Jackson River below Gathright Dam in reaches immediately downstream from incoming warmwater tributaries. Understanding the role in which tributaries contribute to achieving prescribed thermal benchmarks in environmental flow assessments is a key challenge that requires additional exploration.

In highly regulated systems, the management of mainstem channel vegetation and tributary contributions may be insufficient to meet thermal regime standards. In such cases, our ability to incorporate temperature requirements in environmental flows assessments will require suitable technologies for directly modifying water temperature released from dams. Current management options for mitigating thermal impacts from dams divided into two general categories: exploit the temperature stratification of the reservoir by selective withdrawal of water of the desired temperature, or artificially break up the stratification prior to discharging water from the dam. Sherman (2000) provided a review of seven general strategies for mitigating thermal pollution; we briefly summarise these below:

1 Multi-level intake structures make use of the stratification within the reservoir by permitting water with desirable thermal attributes to be withdrawn from defined regions within the water column (Fig. 5a). We discuss the details of this method in subsequent paragraphs.

2 Trunnions (floating intakes) are a variation on the theme of selective withdrawal that involves the intake of epilimnetic and hypolimnetic water through two pipes hinged at the dam wall (Fig. 5b).

3 A variety of destratification approaches exist that induce mixing of the water column to raise the water temperatures of the hypolimnion immediate above the dam prior to release. Local destratification is

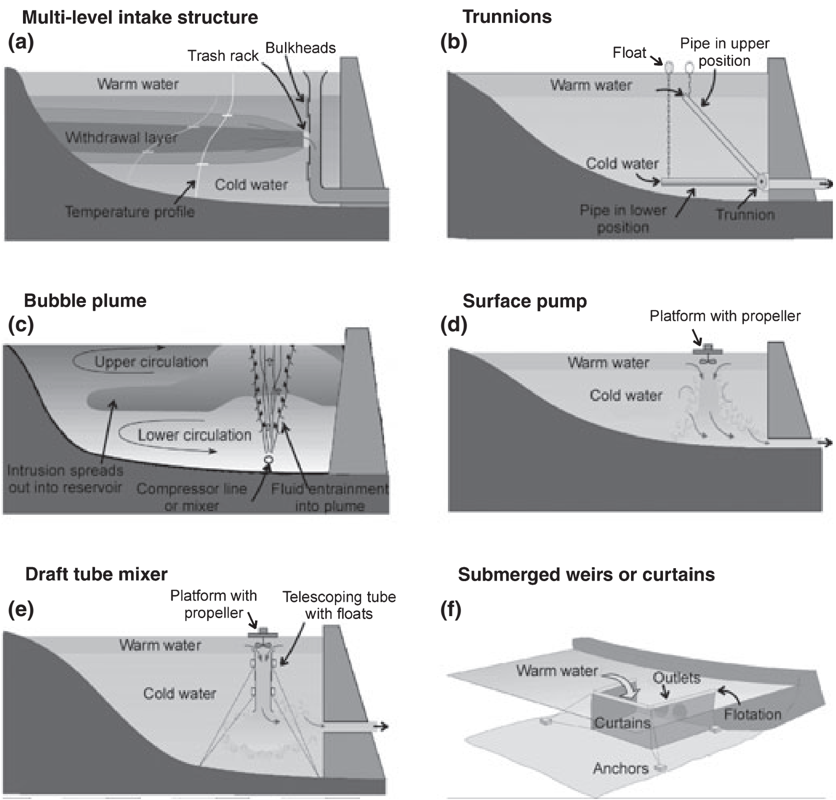

Fig. 5 Current management options for mitigating thermal impacts from dams include: (a) selective withdrawal using multi-level intake structures or (b) trunnions, (c) local destratification using aeration systems, (d) surface pumps or (e) draft tubes and (f) submerged weirs or curtains to redirect either hypolimnetic or epilimnetic water. Figures were provided by Brad Sherman (Australia's Commonwealth Scientific and Industrial Research Organisation: CSIRO).

accomplished by pushing cold water up to the surface using aeration systems that introduce bubble plumes or directly mixing using pumps (Fig. 5c). Bubble plume destratification systems have been typically applied in eutrophic reservoirs to improve overall water quality, particularly to increase dissolved oxygen content and decrease the potential for cyanobacterial blooms, however this approach can also greatly increase hypolimnetic temperature water adjacent to the intake structure.

4 Similarly, surface pumps on floating platforms are also used to locally destratify reservoirs by sending surface water downwards into the withdrawal zone of the intake structure (Fig. 5d).

5 Draft tubes can be anchored in the water column to increase the distance travelled by the plume of water from the propeller (Fig. 5e).

6 Submerged weirs or curtains suspended at various depths can be used to provide a barrier to the passage of water and force warm or cold water above or below the curtain, respectively (Fig. 5f). Modifying the topography of the channel feeding into the dam can also result in a similar effect.

7 Lastly, stilling basins (i.e. large shallow ponds) have been used to delay the downstream release of water so thermal equilibrium may be reached with the atmosphere.

An insightful comparison of these technologies for the Burrendong Dam (Australia) is provided by Sherman (2000).

Selective withdrawal using a multi-level intake structure is the most common and most effective means of controlling the water temperature of dam releases. A selective withdrawal system (also called a temperature control device) can extract water from selected depths of a thermally stratified reservoir to produce a release with desired characteristics (Price & Meyer, 1992). This technology provides the flexibility to increase water temperatures by preferentially selecting warm epilimnetic water from the surface, or decrease water temperature by drawing cold hypolimnetic water from below the thermocline. For example, Flaming Gorge Dam (Green River, U.S.A.) was installed with a multi-level intake structure in 1978 with the goal of increasing summer water temperatures for native species in the trout-dominated tailwaters. The partial success of this thermal restoration is evident by examining the annual thermographs below the dam during different time periods (Fig. 6). After the installation of the intake structure (1978–2007), average stream temperatures during the summer months of May to August almost doubled from a pre-installation (1963–77) temperature of 5.7 to 11.0 °C. Pre-dam temperatures (1958–62) in the Green River during the summer averaged 17.2 °C, but restoring the tailwater to historical temperatures was not the management goal (Fig. 6). This translates to a dramatic decline in per cent thermal alteration during the summer from −66% (pre-dam versus pre-installation: Fig. 4b) to −36% (pre-dam versus

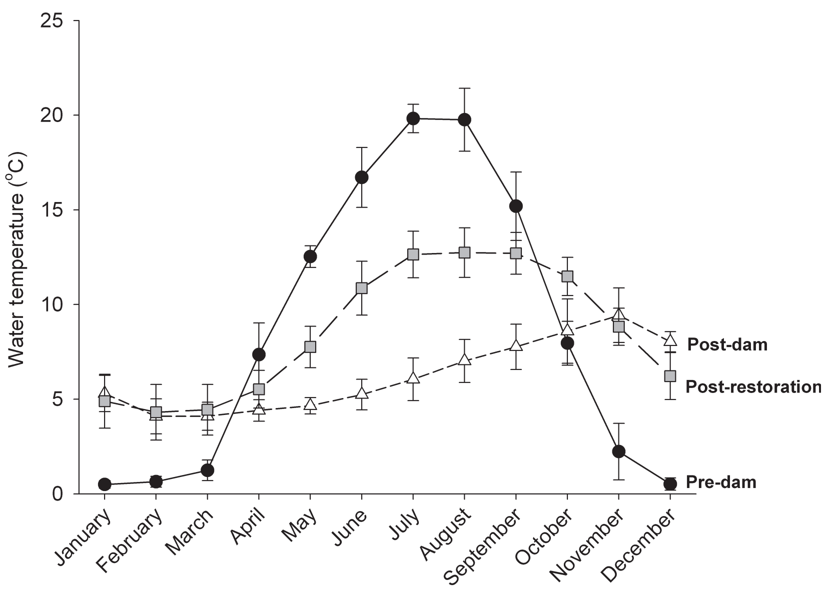

Fig. 6 Selective discharge below Flaming Gorge Dam using a multi-level intake structure has markedly decreased the degree of thermal alteration in the Green River (U.S.A.). Comparisons of monthly water temperature during pre-dam (1958–62, circles), post-dam (1963–77, squares) and post-thermal restoration years (1978–2007, triangles) shows significant increases in spring–summer temperatures toward unregulated conditions. Notably, current operations of the temperature-control device have not decreased the degree of thermal alteration during the winter months.

post-installation). Reasonable improvements were also observed for the frequency and duration of thermal events, and the timing of extreme temperatures. Minimum temperature after thermal restoration occurred, on average, on 8th February (only 4 days earlier than the pre-dam average date of 12th February), and mean day of year of maximum temperatures recovered by moving 10 weeks earlier from 7th November (pre-installment) to 18th August (post-installation); now representing a 5-week delayed timing compared to pre-dam years (24th July). The biological implications of these thermal improvements are discussed later. With another management goal in mind, Shasta Dam (Sacramento River, U.S.A.) was retrofitted with a multi-level intake structure in 1997 to improve downstream temperatures for endangered coldwater salmonids. Dam management is focused on releasing warmer surface waters in the winter⁄spring and colder deep waters in the summer⁄autumn. These two examples illustrate the flexibility of multi-level intake structures for controlling downstream temperatures for a defined ecological goal.

Although most selective withdrawal intake structures are built during initial reservoir construction (ironically, most were originally designed to support tailwater trout fisheries), release structures can also be successfully modified for selective withdrawal later following initial construction (see both example above). However, the capital costs of refitting dams with a multi-level intake structure may be prohibitive. For example, the installation cost for several large dams in Australia was estimated to range between 3 and 30 million AUD (Sherman, 2000), and the actual cost for retrofitting Shasta Dam was 80 million USD. Estimated installation costs for modifying eight intake portals of Glen Canyon Dam (Colorado River, U.S.A.) is 15 million USD. Assuming operations occur during the months of June through August and all releases are surface withdrawals, the economic value of the additional increases in head loss (resulting from the modified intake) are estimated to be 228 000 USD $year^{-1}$ (Vermeyen, 1999). Economic costs aside, there are also a host of other operational, physical⁄chemical and biological considerations that must be assessed when decided whether to refit a dam with a temperature control device.

Despite the capital costs of installing multi-level intakes, recent investigations suggest that these structures provide the most flexible means of modifying downstream water temperatures, even at low to medium release volumes (Sherman, 2000), and may represent the best opportunities for ecological restoration. Sherman *et al.* (2007) predicted that the installation of a multi-level intake structure in Hume Dam, Australia, would increase discharge temperatures by 4–6 °C during the spring–early summer post-spawning period for Murray cod. These temperature increases were forecasted to increase minimum female population abundance in the Murray River by 30–300% depending on the assumed spawning behaviour. Research continues on how epilimnetic versus hypolimnetic withdrawal affects reservoir water quality (e.g. vertical distribution of temperature, dissolved oxygen and nutrients) throughout the year (Johnson *et al.*, 2004), which will help determine the optimal selective withdrawal release strategy. Future research is required to compare the ability of different mitigation strategies (Fig. 5) to meet required temperature standards defined in environmental flow prescriptions.

There is also opportunity to manage reservoir operations to directly affect average daily downstream temperatures through adjustments in the magnitude and timing of discharge releases. Polehn & Kinsel (1997) examined this analytically and suggested that changes in flow may be used to adjust the diurnal temperature cycle at specific locations downstream of a reservoir. However, Lowney (2000) showed that an interesting pattern of 'nodes' and 'antinodes' in the extent of diel variation may develop at different distances downstream from large dams if any particular flow is sustained for more than a few days. Consequently, the control of nodes and antinodes through flow change may require continuous flow adjustment, possibly in conflict with project objectives. In large systems where constant flow is desired and a temperature control system may already be in place, it is possible that a well designed temperature release pattern could restore diurnal variation to that expected under pre-dam conditions (McMahon & Finlayson, 1995). However, meeting diel thermal targets using modified release schedules will be complicated in regulated systems because it will not be possible to mimic the diel temperature variations of a natural system if patterns in discharge are not also mimicked. Quite simply, variation in diel temperatures decreases with increasing discharge due to the increase in thermal mass of the river. Typically, flows released during the summer, either for irrigation or recreation, exceed the natural flow for a river. While it may be possible to modify the mean temperature of the release using a particular mitigation technique, it is unlikely that the nature temperature range will also be restored. In general, the feasibility of controlling river temperature through streamflow management has been recognised for some time, yet the quantitative temperature : flow relationships required for implementing instream flow requirements based on this principle have not be successfully developed (Gu *et al*., 1999).

Challenge #4: Incorporate thermal-criteria into environmental flow assessments

Defining environmental flows with respect to either flow or temperature in isolation is highly unlikely to support ecologically sustainable water management. Consequently, the benefits of environmental flows will be realised only if riverine thermal regimes are also considered. One example supporting this notion is the study of King, Cambray & Impson (1998) who examined patterns of temperature and discharge resulting from an experimental dam release, and their relative importance in triggering successful spawning of a threatened large cyprinid endemic, the Clanwilliam yellowfish *Barbus capensis* Smith, 1841, downstream of Clanwilliam Dam (Olifants River, Africa). A critical flow component for many rivers in the winter-rainfall region of South Africa, including the Olifants River, is the small pulses of higher flow that occur in the dry season (called freshes). Experimental freshes released from Clanwilliam Dam in the early 1990s were strongly correlated with the suspected spawning success of *B. capensis* (Cambray, King & Bruwer, 1997); however, in subsequent years freshes delivered during the species' breeding season failed to induce spawning. King *et al*. (1998) found that differences in the temperatures of the water release were the key factor related to spawning success. Specifically, warm epilimnetic freshes (19–21 °C) triggered fish spawning behaviour and the movement of individuals onto spawning beds, whereas cool hypolimnetic baseflows (16–18 °C) released immediately after the experimental freshets caused fish to abort spawning activities. Moreover, the occurrence of dead and deformed young suggested that the cold water may have had a detrimental effect on offspring of those individuals who spawned during the warmwater events. This research showed that freshets released from Clamwilliam Dam at the appropriate time should be able to induce spawning and support early life stages of *B. capensis* only if water temperatures at the spawning sites exceeded 19 °C. Furthermore, King *et al*. (1998) suggest that successful spawning will lead to high recruitment only if water temperatures are maintained at these levels for an extended period after spawning to provide for the development of the embryos and larvae.

Similar examples exist in the lower Mississippi River (U.S.A.) where research has shown that growth and abundance of juvenile fishes are only linked to floodplain inundation when water temperatures are greater than a particular threshold. Schramm & Eggleton (2006) reported that the growth of catfishes (Ictaluridae spp.) was significantly related to the extent of floodplain inundation only when water temperature exceeded 15 °C; a threshold temperature for active feeding and growth by catfishes. Under the current hydrographic conditions in the lower Mississippi River, the authors report that the duration of floodplain inundation when water temperature exceeds the threshold is only about 1 month year^{-1} on average. Such a brief period of time is believed to be insufficient for floodplain-foraging catfishes to achieve a detectable energetic benefit (Schramm & Eggleton, 2006). These results are consistent with the 'thermal coupling' hypothesis offered by Junk, Bayley & Sparks (1989) whereby the concordance of both hydrologic and thermal cycles is required for maximum ecological benefit.

Similarly, the advantages of thermal restoration may be realised only if flow is also actively managed to mimic natural regimes. As previously discussed, the operation of Flaming Gorge Dam after installation of a multi-level intake structure resulted in significant warming of summer temperatures (Fig. 6) and increased the number of annual degree days from 2340 to 3200 (Vinson, 2001). While these improvements in thermal regimes were predicted to increase invertebrate richness, Vinson (2001) found that the number of taxa collected after partial thermal restoration was similar to or lower than that observed before temperature manipulations. The lack of appreciable increase in richness can be attributed, in part, to the remaining differences in the thermal and hydrologic (and associated sedimentation processes) regimes of the Green

River below Flaming Gorge Dam. In summary, the studies discussed in the previous paragraphs provide striking examples emphasizing that both flow and thermal regimes must be managed simultaneously to have the desired effects on riverine biota.

A key challenge in environmental flow assessments is to determine the critical flow and thermal requirements of riverine ecosystems, while continuing to provide the goods and services expected by human society. Will there be conflicts between flow and thermal targets in environmental flow prescriptions? In the absence of a temperature control device, we expect the answer to this question will be yes, quite simply because stream temperature co-varies with flow. For example, Krause *et al.* (2005) found that proposed modifications to a regulated discharge regime below Philpott Dam (Smith River, U.S.A.) designed to improve physical habitat for brown trout (*Salmo trutta* Linnaeus, 1758) would concurrently reduce the frequency of optimal growth temperatures. This study illustrated that the best management option for improving flow regimes (e.g. for providing critical fish habitat) was not necessarily the best for improving thermal regimes (e.g. for providing optimal growth conditions). Consequently, different aspects of the temperature regime for any stream would require careful analysis before any environmental flow requirements could be safely prescribed. Empirical data and predictive models are needed to help identify and incorporate the potential interactive effects of discharge and temperature recommendations in environmental flow assessments.

Synchronised management efforts are needed to meet both flow and temperature requirements of entire ecosystems by recoupling the natural hydrologic and thermal cycles. Given the complexities and trade-offs regarding alternative dam strategies for meeting both downstream flow and thermal standards, particularly in the absence of a temperature control device, we believe the environmental flow assessments would benefit from the use of formal optimisation frameworks incorporated into adaptive management strategies. Pareto efficiency (or Pareto optimality), for example, is a central concept in economics that is defined as the efficiency of a market which is unable to produce more from the same level of inputs without reducing the output of another product. Recent efforts have developed Pareto-optimal solutions for environmental flow schemes that incorporate variability in flow regimes and provide for human needs (e.g. Suen & Eheart, 2006; Shiau & Wu, 2007), and we believe that the application of Pareto optimality holds promise for incorporating thermal criteria into environmental flow assessments. For example, this multi-objective optimisation approach could be applied to identify a set of flow schemes (i.e. those contained in the Pareto frontier) that are considered efficient with respect to meeting both the temperature and flow needs of a riverine ecosystem while also ensuring the water requirements of human users.

Pareto optimisation could account for the fact that particular flow events that may be deemed critical for riverine ecosystems (i.e. high discharge events for mobilizing sediment and shaping channel forming processes) may not be optimal for restoring critical components of the thermal regime (i.e. high discharge events can increase the magnitude and spatial extent of coldwater pollution). To illustrate this, we examine the Coosa River tailwater below Jordan Dam (U.S.A.), where dam influences on tailwater temperatures extend approximately 4 km downstream under low flow regimes and nearly 15 km downstream under high flow regimes (Jackson & Davies, 1988). In this instance, environmental flow assessments that are considered important for environmental flows are detrimental with respect to thermal targets. By identifying a set of efficient and acceptable environmental flows, an optimal solution could be selected to represent what would be considered the optimal environmental flow prescription for a given river system. Relationships between the conflicting flow and thermal objectives would offer decision makers with the marginal trade-offs useful for the selection of the preferred solutions. In summary, there is continued need for the collection of more empirical data and development of pragmatic models that will provide the basis for adaptive management schemes involving both riverine flow and thermal regimes (Rivers-Moore & Jewitt, 2007).

Challenge #5: Designing temperature-enlightened environmental flow assessments in a changing climate

The prospect of dramatic climate change over the next century underscores the need for adaptive management strategies for effectively designing and implementing environmental flows (Palmer *et al.*, 2008). Projected increases in air temperatures, combined with lower accumulation in winter snowpack, earlier onset of spring peak flows, and lower summer baseflows, will have direct implications for the thermal regimes of streams and rivers (Poff, Brinson & Day, 2002). Equally relevant is the increasingly large and thirsty human population which is rapidly changing the geography of water demand and dramatically shifting current land use practices (Poff *et al.*, 2003; Fitzhugh & Richter, 2004), both of which have direct and indirect implications for water temperatures. By failing to account for projected climate change, ecologists run the risk of making flow recommendations based on the characteristics of past thermal regimes that are not favoured by present-day or future environments.

Future climate change will significantly influence how dams are operated to achieve environmental flows that incorporate water temperatures. For example, Sinokrot *et al.* (1995) found that the predicted impact of climate change on stream temperatures below dams is more pronounced when water is released from the reservoir surface compared to deeper depths. Results from studies like this have been used by some to advocate that management agencies could use dams with deep, coldwater releases to control thermal regimes in a manner that offsets climate warming effects. We do not question that innovative mitigation strategies are needed to prepare for a rapidly changing climate; however, we have a number of concerns with this proposed management approach. First, climate-induced changes in stream discharge are expected to have direct (i.e. thermal capacity) and indirect (i.e. changes to channel geomorphology and riparian vegetation) consequences for seasonal and annual patterns in water temperature, which will be very difficult to predict. Secondly, as previously discussed, hypolimnetic releases by dams from thermally stratified reservoirs often result in abnormally warmer water temperatures during the winter. This warming effect is likely to be compounded in those regions predicted to experience higher air temperatures during the winter season; a trend already observed for some rivers (Durance & Ormerod, 2009). Taken together, we believe that our ability to mitigate the thermal consequences of climate change through the management of dam operations is likely to be unsuccessful. In summary, we urge ecologists to ground their knowledge in the past, but to look to the future in their scientific endeavours. There is no doubt that environmental flow assessments will benefit greatly from directly incorporating the predicted response of freshwater ecosystems to projected changes in flow and thermal regimes from climate change.

Prospectus

Recent decades have witnessed an increasing recognition of the importance of variability of ecosystem drivers, such as river flow and water temperature in maintaining river integrity. Even though there has been tremendous progress in environmental flow research and implementation, what remains unknown is formidable. Is more water alone sufficient without restoring other essential water quality variables, such as recoupling the natural flow and thermal regimes? As we continue to learn about these issues, clear and complete answers remain elusive because of the complexity of the scientific questions and management options. Clearly, new strategies are needed that account for the natural dynamics in temperature-related ecosystem processes by using the *natural thermal regime* as one template for environmental flow management.

From its name, the concept of 'environmental flows' would seem to offer the features of ecologically sustainable water management, but in its current form it has evolved to include only water quantity and it is not comprehensive enough to solve the broad water resource problems that will challenge us in the future. We firmly believe that the benefit of using environmental flows as a paradigm in water management will be its focus on the blending of both water quantity and quality. For this reason, many additional aspects of water quality must be recognised, including pollutants, nutrients, organic matter and sediments and dissolved oxygen (Nilsson & Renöfält, 2008), which can interact with water temperature and discharge in complex ways.

Our objective was to add clarity to the increasing popular but still poorly understood concept of an environmental flow. The issue is not that ecologists do not recognise the importance of water temperature for riverine ecosystems; rather to date we have not formally integrated it into environmental flow assessments. This study began with an overview of the natural thermal regime and its ecological importance, and ended with a discussion of some overarching research opportunities and challenges to incorporating thermal criteria into the prescription of environmental flows.

Based on our assessment, we suggest that scientific research should focus on the ongoing collection of long-term temperature records, comprehensive characterisation of seasonality and variability in stream temperatures, quantification of the temporal and spatial impacts of dam operations on thermal regimes, and clearer elucidation of the relative roles of altered flow and temperature in shaping ecological patterns and processes in riverine ecosystems. Future investigations should also concentrate on using this acquired knowledge to identify the 'manageable' components of the thermal regime, and develop optimisation models that evaluate management trade-offs and provide a range of optimal environmental flows that meet both ecosystem and human needs for fresh water. Lastly, ecologists and water managers must maintain a nimble capacity to incorporate results from ongoing climate change research into adaptive management strategies involving environmental flows.

Acknowledgments

We thank participants of the 3rd International Symposium on Riverine Landscapes (South Stradbroke Island, Queensland, Australia) for insightful conversations, and Mark Kennard, Angela Arthington and Stuart Bunn for their kind hospitality during our visit. We gratefully acknowledge Steve Ormerod and Christer Nilsson for comments on the manuscript, Bruce Webb for discussions regarding the thermal impacts of dam operation, David Archer, Mark Vinson and Daqing Yang for providing temperature data, and Brad Sherman for generously providing the drawings in Fig. 5. J. D. Olden thanks Land and Water Australia and the Tropical Rivers and Coastal Knowledge (TRaCK) research consortium for partial funding support, and R. J. Naiman acknowledges the Freshwater Committee of DIVERSITAS and the Global Water System Project. J. D. Olden conceived and developed the idea for the manuscript and conducted the data analysis, and J. D. Olden and R. J. Naiman wrote the manuscript.

References

Acreman M. & Dunbar M.J. (2004) Defining environmental river flow requirements: a review. *Hydrology and Earth System Sciences*, **8**, 861–876.

Alcamo J., Vörösmarty C., Naiman R.J., Lettenmaier D. & Pahl-Wostl C. (2008) A grand challenge for freshwater research: understanding the global water system. *Environmental Research Letters*, **3**, 1–6.

Angilletta M.J., Steel E.A., Bartz K.K., Kingsolver J.G., Scheurell M.D., Beckman B.R. & Crozier L.G. (2008) Big dams and salmon evolution: changes in thermal regimes and their potential evolutionary consequences. *Evolutionary Applications*, **1**, 286–299.

Armour C.L. (1991) Guidance for evaluating and recommending temperature regimes to protect fish. *U.S. Fish and Wildlife Service Biological Report*, **90**, 1–13.

Arthington A.H., Bunn S.E., Poff N.L. & Naiman R.J. (2006) The challenge of providing environmental flow rules to sustain river ecosystems. *Ecological Applications*, **16**, 1311–1318.

Bednarek A.T. & Hart D.D. (2005) Modifying dam operations to restore rivers: ecological responses to Tennessee River dam mitigation. *Ecological Applications*, **15**, 997–1008.

Berman C.H. & Quinn T.P. (1991) Behavioral thermoregulation and homing by spring Chinook salmon, *Oncorhynchus tshawytscha* (Walbaum), in the Yakima River. *Journal of Fish Biology*, **39**, 301–312.

Brooker M.P. (1981) The impact of impoundments on the downstream fisheries and general ecology of rivers. *Advances in Applied Biology*, **6**, 91–152.

Bunn S.E. & Arthington A.H. (2002) Basic principles and ecological consequences of altered flow regimes for aquatic biodiversity. *Environmental Management*, **30**, 492–507.

Caissie D. (2006) The thermal regime of rivers: a review. *Freshwater Biology*, **51**, 1389–1406.

Cambray J.A., King J. & Bruwer C. (1997) Spawning behaviour and early development of the Clanwilliam yellowfish (*Barbus capensis*; Cyprinidae), linked to experimental dam releases in the Olifants River, South Africa. *Regulated Rivers: Research and Management*, **13**, 579–602.

Clarkson R.W. & Childs M.R. (2000) Temperature effects of hypolimnial-release dams on early life stages of Colorado River Basin big-river fishes. *Copeia*, **2000**, 402–412.

Coutant C.C. (1987) Thermal preference: when does an asset become a liability? *Environmental Biology of Fishes*, **18**, 161–172.

Dunbar M.J., Acreman M. & Kirk S. (2004) Environmental flow setting in England and Wales: strategies for managing abstraction in catchments. *Water and Environment Journal*, **18**, 5–10.

Durance I. & Ormerod S.J. (2009) Trends in water quality and discharge offset long-term warming effects on river macroinvertebrates. *Freshwater Biology*, **54**, 388–405.

Fitzhugh T.W. & Richter B.D. (2004) Quenching urban thirst: growing cities and their impacts on freshwater ecosystems. *BioScience*, **54**, 741–754.

Fraley J.J. (1979) Effects of elevated stream temperatures below a shallow reservoir on cold-water macroinvertebrate fauna. In: *The Ecology of Regulated Streams* (Eds J.V. Ward & J.A. Stanford), pp. 257–272. Plenum, New York.

Gu R., McCutcheon S. & Chen C.-J. (1999) Development of water-dependent flow requirements for river temperature control. *Environmental Management*, **24**, 529–540.

Haxton T.J. & Findlay C.S. (2008) Meta-analysis of the impacts of water management on aquatic communities. *Canadian Journal of Fisheries and Aquatic Sciences*, **65**, 437–447.

Horne B.D., Rutherford E.S. & Wehrly K.E. (2004) Simulating effects of hydro-dam alteration on thermal regime and wild steelhead recruitment in a stable-flow Lake Michigan tributary. *River Research and Applications*, **20**, 185–203.

Huryn A.D. & Wallace J.B. (2000) Life history and production of stream insects. *Annual Review of Entomology*, **45**, 83–110.

Jackson D.C. & Davies W.D. (1988) Environmental factors influencing summer angler effort on the Jordan Dam tailwater. *North American Journal of Fisheries Management*, **8**, 305–309.

Jackson H.M., Gibbins C.N. & Soulsby C. (2007) Role of discharge and temperature variation in determining invertebrate community structure in a regulated river. *River Research and Applications*, **23**, 651–669.

Johnson B.M., Saito L., Anderson M.A., Weiss P., Andre M. & Fontane D.G. (2004) Effects of climate and dam operations on reservoir thermal structure. *Journal of Water Resources Planning and Management*, **130**, 112–122.

Junk W.J., Bayley P.B. & Sparks R.E. (1989) The flood pulse concept in river–floodplain systems. In: *Proceedings of the International Large River Symposium* (Ed. D.P. Dodge), pp. 110–127. Canadian Special Publications in Fisheries and Aquatic Sciences 106. Toronto, Canada.

King J., Cambray J.A. & Impson N.D. (1998) Linked effects of dam-released floods and water temperature on spawning of the Clanwilliam yellowfish *Barbus capensis*. *Hydrobiologia*, **384**, 245–265.

Krause C.W., Newcomb T.J. & Orth D.J. (2005) Thermal habitat assessment of alternative flow scenarios in a tailwater fishery. *River Research and Applications*, **21**, 581–593.

Langford T.E.L. (1990) *Ecological Effects of Thermal Discharges*. Elsevier, London.

Lehmkuhl D.M. (1974) Thermal regime alterations and vital environmental physiological signals in aquatic systems. In: *Thermal Ecology* (Eds J.W. Gibbons & R.R. Sharitz), pp. 216–222. AEC Symposium Series, Springfield, Virginia.

Lessard J.L. & Hayes D.B. (2003) Effects of elevated water temperature on fish and macroinvertebrate communities below small dams. *River Research and Applications*, **19**, 721–732.

Lowney C.L. (2000) Stream temperature variation in regulated rivers: evidence for a spatial pattern in daily minimum and maximum magnitudes. *Water Resource Research*, **36**, 2947–2955.

Lugg A. (1999) *Eternal Winter in our Rivers: Addressing the Issue of Water Pollution*. New South Wales Fisheries, Nowra, NSWa.

Magnuson J.J., Crowder L.B. & Medvick P.A. (1979) Temperature as an ecological resource. *American Zoologist*, **19**, 331–343.

McMahon T.A. & Finlayson B.L. (1995) Reservoir system management and environmental flows. *Lakes and Reservoirs: Research and Management*, **1**, 65–76.

Moore R.D., Spittlehouse D.L. & Story A. (2005) Riparian microclimate and stream temperature response to forest harvesting: a review. *Journal of the American Water Resources Association*, **41**, 813–834.

Murchie K.J., Hair K.P.E., Pullen C.E., Redpath T.D., Stephens H.R. & Cooke S.J. (2008) Fish response to modified flow regimes in regulated rivers: research methods, effects and opportunities. *River Research and Applications*, **24**, 197–217.

Nelson K.C. & Palmer M.A. (2007) Stream temperature surges under urbanization and climate change: data, models, and responses. *Journal of the American Water Resources Association*, **43**, 440–452.

Nilsson C. & Renöfält B.M. (2008) Linking flow regime and water quality in rivers: a challenge to adaptive catchment management. *Ecology and Society*, **13**. Available at: http://www.ecologyandsociety.org/vol13/iss2/art18/.

Olden J.D. (2004) *Fish Fauna Homogenization of the United States, Life-History Correlates of Native Extinction and Nonnative Invasions in the American Southwest, and the Bidirectional Impacts of Dams in the American Southeast. Dissertation*. Colorado State University, Fort Collins, CO.

Olden J.D. & Poff N.L. (2003) Redundancy and the choice of hydrologic indices for characterizing streamflow regimes. *River Research and Applications*, **19**, 101–121.

Palmer R.W. & O'Keeffe J.H. (1989) Temperature characteristics of an impounded river. *Archiv für Hydrobiologie*, **116**, 471–485.

Palmer M.A., Bernhardt E., Chornesky E. *et al.* (2004) Ecology for a crowded planet. *Science*, **304**, 1251–1252.

Palmer M.A., Reidy Liermann C., Nilsson C., Flörke M., Alcamo J., Lake P.S. & Bond N. (2008) Climate change and world's river basins: anticipating management options. *Frontiers in Ecology and the Environment*, **6**, 81–89.

Peterson J.T. & Rabeni C.F. (1996) Natural thermal refugia for temperate warmwater stream fishes. *North American Journal of Fisheries Management*, **16**, 738–746.

Petts G.E. (1986) Water quality characteristics of regulated rivers. *Progress in Physical Geography*, **10**, 492–516.

Poff N.L., Allan J.D., Bain M.B., Karr J.R., Prestegaard K.L., Richter B.D., Sparks R.E. & Stromberg J.C. (1997) The natural flow regime: a paradigm for river conservation and restoration. *BioScience*, **47**, 769–784.

Poff N.L., Brinson M.M. & Day J.W. Jr (2002) *Aquatic Ecosystems and Global Climate Change*. Pew Center on Global Climate Change. Arlington, VA.

Poff N.L., Allan J.D., Palmer M.A., Hart D.D., Richter B.D., Arthington A.H., Rogers K.H., Meyer J.L. & Stanford J.A. (2003) River flows and water wars? Emerging science for environmental decision-making. *Frontiers in Ecology and the Environment*, **1**, 298–306.

Poff N.L., Richter B.D., Arthington A.H. *et al.* (2010) The ecological limits of hydrologic alteration (ELOHA): a new framework for developing regional environmental flow standards. *Freshwater Biology*, **55**, 147–170.

Polehn R.A. & Kinsel W.C. (1997) Transient temperature solution for stream flow from a controlled temperature source. *Water Resource Research*, **33**, 261–265.

Poole G.C. & Berman C.H. (2001) An ecological perspective on in-stream temperature: natural heat dynamics and mechanisms of human-caused thermal degradation. *Environmental Management*, **27**, 787–802.

Preece R.M. (2004) *Cold Water Pollution Below Dams in New South Wales: A Desktop Assessment*. NSW Department of Infrastructure, Planning and Natural Resources, Sydney, NSW.

Preece R.M. & Jones H.A. (2002) The effect of Keepit Dam on the temperature regime of the Namoi River, Australia. *River Research and Applications*, **18**, 397–414.

Price R.E. & Meyer E.B. (1992) *Water Quality Management for Reservoirs and Tailwaters: Operational and Structural Water Quality Techniques*. Technical Report E-89-1. US Army Engineer Waterways Experimental Station, Vicksburg, MS.

Rice S.P., Ferguson R.L. & Hoey T.B. (2006) Tributary control of physical heterogeneity and biological diversity at river confluence. *Canadian Journal of Fisheries and Aquatic Sciences*, **63**, 2553–2566.

Richter B.D. & Thomas G.A. (2007) Restoring environmental flows by modifying dam operations. *Ecology and Society*, **12**. Available at: http://www.ecologyandsociety.org/vol12/iss1/art12/.

Richter B.D., Matthews R.A., Harrison D.L. & Wigington R. (2003) Ecologically sustainable water management: managing river flows for river integrity. *Ecological Applications*, **13**, 206–224.

Richter B.D., Warner A.T., Meyer J.L. & Lutz K. (2006) A collaborative and adaptive process for developing environmental flow recommendations. *River Research and Applications*, **22**, 297–318.

Rivers-Moore N.A. & Jewitt G.P.W. (2007) Adaptive management and water temperature variability within a South Africa river system: what are the management options? *Journal of Environmental Management*, **82**, 39–50.

Ryan T., Webb A., Lennie R. & Lyon J. (2001) *Status of Cold Water Releases from Victorian Dams*. Victorian Department of Natural Resources and Environment, Heidelberg.

Sato Y., Bazzoli N., Rizzo E., Boschi M.B. & Miranda M.O.T. (2005) Influence of the Abaete River on the reproductive success of the neotropical migratory teleost *Prochilodus argenteus* in the Sao Francisco River, downstream from the Tres Marias Dam, southeastern Brazil. *River Research and Applications*, **21**, 939–950.

Schramm H.L. & Eggleton M.A. (2006) Applicability of the flood-pulse concept in a temperate floodplain river ecosystem: thermal and temporal components. *River Research and Applications*, **22**, 543–553.

Sherman B. (2000) *Scoping Options for Mitigating Cold Water Discharges from Dams*. CSIRO Land and Water, Canberra.

Sherman B., Todd C.R., Koehn J.D. & Ryan T. (2007) Modelling the impact and potential mitigation of cold water pollution on Murray cod populations downstream of Hume Dam, Australia. *River Research and Applications*, **23**, 377–389.

Shiau J.-T. & Wu F.-C. (2007) Pareto-optimal solutions for environmental flow schemes incorporating the intra-annual and interannual variability of the natural flow regime. *Water Resource Research*, **43**, W06433.

Sinokrot B.A. & Gulliver J.S. (2000) In-stream flow impact on river water temperatures. *Journal of Hydraulic Research*, **38**, 339–349.

Sinokrot B.A., Stefan H.G., McCormick J.H. & Eaton J.G. (1995) Modeling of climate change effects on stream temperatures and fish habitats below dams and near groundwater inputs. *Climatic Change*, **30**, 181–200.

Steel E.A. & Lange I.A. (2007) Using wavelet analysis to detect changes in water temperature regimes at multiple scales: effects of multi-purpose dams in the Willamette River basin. *River Research and Applications*, **23**, 351–359.

Stevens L.E., Shannon J.P. & Blinn D.W. (1997) Colorado River benthic ecology in Grand Canyon, Arizona, USA: dam, tributary and geomorphological influences. *Regulated Rivers: Research and Management*, **13**, 129–149.

Suen J.-P. & Eheart J.W. (2006) Reservoir management to balance ecosystem and human needs: incorporating the paradigm of the ecological flow regime. *Water Resource Research*, **42**, W03417.

Todd C.R., Ryan T., Nicol S.J. & Bearlin A.R. (2005) The impact of cold water releases on the critical period of post-spawning survival and its implications for Murray cod (*Maccullochella peelii peelii*): a case study of the Mitta Mitta River, southeastern Australia. *River Research and Applications*, **21**, 1035–1052.

Vannote R.L. & Sweeney B.W. (1980) Geographic analysis of thermal equilibria: a conceptual model for evaluating the effect of natural and modified thermal regimes on aquatic insect communities. *American Naturalist*, **115**, 667–695.

Vermeyen T.B. (1999) *An Overview of the Design Concept and Hydraulic Modeling of the Glen Canyon Dam Multi-Level Intake Structure*. ASCE's Waterpower '99 Conference Proceedings, July 6–9, 1999, Las Vegas, NV.

Vinson M.R. (2001) Long-term dynamics of an invertebrate assemblage downstream from a large dam. *Ecological Applications*, **11**, 711–730.

Vinson M.R. & Hawkins C.P. (1998) Biodiversity of stream insects: variation at local, basin, and regional scales. *Annual Review of Entomology*, **43**, 271–293.

Voelz N.J. & Ward J.V. (1991) Biotic responses along the recovery gradient of a regulated stream. *Canadian Journal of Fisheries and Aquatic Sciences*, **48**, 2477–2490.

Ward J.V. (1974) A temperature-stressed stream ecosystem below a hypolimnial release mountain reservoir. *Archive für Hydrobiologie*, **74**, 247–275.

Ward J.V. (1985) Thermal-characteristics of running waters. *Hydrobiologia*, **125**, 31–46.

Ward J.V. & Stanford J.A. (1982) Thermal responses in the evolutionary ecology of aquatic insects. *Annual Review of Entomology*, **27**, 97–117.

Webb B.W. (1996) Trends in stream and river temperature. *Hydrological Processes*, **10**, 205–226.

Webb B.W. & Walling D.E. (1993) Temporal variability in the impact of river regulation on thermal regime and some biological implications. *Freshwater Biology*, **29**, 167–182.

Webb B.W. & Walling D.E. (1996) Long-term variability in the thermal impact of river impoundment and regulation. *Applied Geography*, **16**, 211–223.

Webb B.W., Hannah D.W., Moore R.D., Brown L.E. & Nobilis F. (2008) Recent advances in stream and river temperature research. *Hydrologic Processes*, **22**, 902–918.

Wootton R.J. (1990) *Ecology of Teleost Fishes*. Chapman and Hall, London.

Zhong Y. & Power G. (1996) Environmental impacts of hydroelectric projects on fish resources in China. *Regulated Rivers: Research and Management*, **12**, 81–98.

Zhou C., Liang Z. & Huang H. (1980) Ecological features of the spawning of certain fishes in the Hanjiang River after the construction of dams. *Acta Hydrobiologia Sinica*, **7**, 175–188 [in Chinese with English abstract].

(Manuscript accepted 9 January 2009)