RIVER RESEARCH AND APPLICATIONS

River. Res. Applic. **24**: 197–217 (2008)

Published online in Wiley InterScience
(www.interscience.wiley.com) DOI: 10.1002/rra.1058

FISH RESPONSE TO MODIFIED FLOW REGIMES IN REGULATED RIVERS: RESEARCH METHODS, EFFECTS AND OPPORTUNITIES

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ABSTRACT

Globally, rivers are increasingly being subjected to various levels of physical alteration and river regulation to provide humans with services such as hydropower, freshwater, flood control, irrigation and recreation. Although river regulation plays an important role in modern society, there are potential consequences which may negatively affect fish and fish habitat. While much effort has been expended examining the response of fish to fluctuating flow regimes in different systems, there has been little in the way of a comprehensive synthesis. In an effort to better understand the effects of river regulation on fish and fish habitat, we conducted a systematic review of available literature with three goals: (1) summarize the various research methodologies used by regulated river researchers, (2) summarize the effects found on fish and fish habitat and (3) identify opportunities for future research. The results of the synthesis indicate that a wide variety of methodologies are being employed to study regulated river science, yet there is a gap in incorporating methodologies that examine effects on fish at a cellular level or those techniques that are interdisciplinary (e.g. behaviour and physiology). There is a clear consensus that modified flow regimes in regulated rivers are affecting fish and fish habitat, but the severity and direction of the response varies widely. Future study designs should include methods that target all biological levels of fish response, and in which detailed statistical analyses can be performed. There is also a need for more rigorous study designs including the use of appropriate controls and replicates. Data on physical variables that co-vary with flow should be collected and examined to add explanatory power to the results. Increased multi-stakeholder collaborations provide the greatest promise of balancing ecological concerns with economic needs.

KEY WORDS: river regulation; meta-analysis; management; biological impacts; sampling design; hydroelectric; synthesis; flow modification

Received 13 January 2007; Accepted 13 July 2007

INTRODUCTION

Management of rivers for societal benefits has greatly modified natural flow regimes throughout the world (Vörösmarty *et al*., 2004). Although river regulation practices date back thousands of years, such modifications have increased in the mid-1900s and continue to escalate today. As the demand for services such as hydropower, freshwater, flood control, irrigation and recreation increases both in developed and developing nations, humans around the globe continue to depend heavily upon river modification and regulation practices (World Resources Institute, 2003). In the past two decades alone, hundreds of dams have been constructed in tropical regions of the world to meet the growing demand for hydroelectric generation (Anderson *et al*., 2006a). Estimates suggest that 77% of the largest river systems found in the United States, Canada, Europe and the former Soviet Union are either moderately or strongly affected by regulation (Dynesius and Nilsson, 1994).

Although regarded a necessity in modern society, river management through the regulation of streamflow is in fact considered to be one of the most extensive forms of human disturbances to riverine systems (Petts, 1984; Stanford *et al*., 1996). One important ecological impact of physical manipulations to rivers is the resulting alterations to the natural flow regime (Anderson *et al*., 2006a). River impoundments tend to modify flow patterns often causing dramatic fluctuations in discharge, mainly in direct response to human demand. These changes can

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range from drastic reductions in flow to fill reservoirs, to sudden increases in flow volume to fulfill peak energy demands (Vehanen *et al*., 2005). The alteration of the physical characteristics of a river can lead to changes in the availability and suitability of aquatic habitat, which in turn may result in negative consequences on fish populations (Anderson *et al*., 2006a). Flow variations are known to have both individual and population level effects on riverine fish (Borgestrøm and Løkensgard, 1984). Hydropeaking in particular can affect fish through physical displacement, behavioural changes and loss of habitat (Vehanen *et al*., 2000; Flodmark *et al*., 2002). As such, many studies have been undertaken to assess the ecological consequences associated with altered hydrological regimes (e.g. Bain *et al*., 1988; Bunn and Arthington, 2002; Hauer and Lorang, 2004). However, despite decades of research generating numerous reports, there has been little in the way of a comprehensive synthesis. The existing reviews are limited either by geographic region (e.g. river Don Basin, Russia; Volovik, 1994), specific taxa (i.e. salmonids; Hunter, 1992) or topical focus (e.g. ecological responses; Steele and Smokorowski, 2000).

Prior to initiating this synthesis, a preliminary survey of the literature revealed that the majority of studies have only led to speculation on how fish are in fact responding to modified flows. This level of ambiguity is likely the result of what we have recognized as trends in current research approaches and methodology. Many studies have taken a species specific approach, whereby they assess the impact of flow modification on fish physiology or behaviour throughout various life history stages (e.g. Chanseau and Larinier, 1999; Arnekleiv and Ronning, 2004; Asaeda *et al*., 2005), or on the overall quality or quantity of fish habitat available (e.g. Bowen *et al*., 1998; Slavik and Bartos, 2001; Arthington *et al*., 2003). Traditionally, instream flow incremental methodology (IFIM) has been employed as a way of determining the minimum flow regime necessary to maintain fish resources (KGS *et al*., 1991). Many studies rely upon related modelling approaches such as the physical habitat simulation model (PHABSIM), which simulates the spatial distribution of depth and velocity at varying flows to calculate the availability of useable spawning habitat, cover and feeding area (Sale and Otto, 1991; Van Winkle *et al*., 1998; Yrjana *et al*., 2002). Although widely applied in studies, many of these models have limitations and have been deemed poor predictors of true species requirements (Heggenes, 1996). Still commonly overlooked in other studies is the assumption that rivers exist as a continuous gradient of physical habitat, and that species will respond in a predictable and continuous manner. In reality, these systems are in constant flux and species' responses will vary (Steele and Smokorowski, 2000). As a result, the applicability and reliability of models which rely on physical parameters alone for use in qualifying fish responses has been debated (Castleberry *et al*., 1996; Van Winkle *et al*., 1997) and remains a concern today.

While there is relevance in every study, inconsistency and uncertainty exists regarding the effects of flow modification on fish and fish habitat in regulated rivers. Understanding these effects is essential for improvement of river management practices, especially if a balance is to be met between supporting the economic interests of humans and the ecological requirements of fish (Gibbins and Acornley, 2000). Through a meta-analysis of existing and forthcoming literature, we (1) summarize the various research methodologies for studying such effects, (2) summarize the statistical and apparent effects found on fish and fish habitat and (3) identify opportunities for addressing gaps in the existing knowledge to enhance regulated river science.

METHODS

In light of recent criticisms towards the methodological and reporting rigour of ecological reviews by Pullin and Stewart (2006) and Roberts *et al*. (2006), we have attempted to make our methods as transparent as possible to allow for replication and updating following further advances in the field (see Figure 1).

Primary literature keyword search criteria and electronic database selection

Before a search for primary literature was initiated, a list of keywords was developed for evaluation. From the list of keywords selected, the following search strings were used to locate articles examining fish response to modified flow regimes: (1) fish* + flow* + fluctuat*, (2) fish* + regulat* + river*, (3) fish* + regulat* + flow*, (4) fish* + fluctuat* + river*, (5) fish* + hydro* + river*, (6) fish* + hydro* + flow*, (7) fish* + hydro* + regulat* and (8) fish* + hydro* + fluctuat*.

DOI: 10.1002/rra

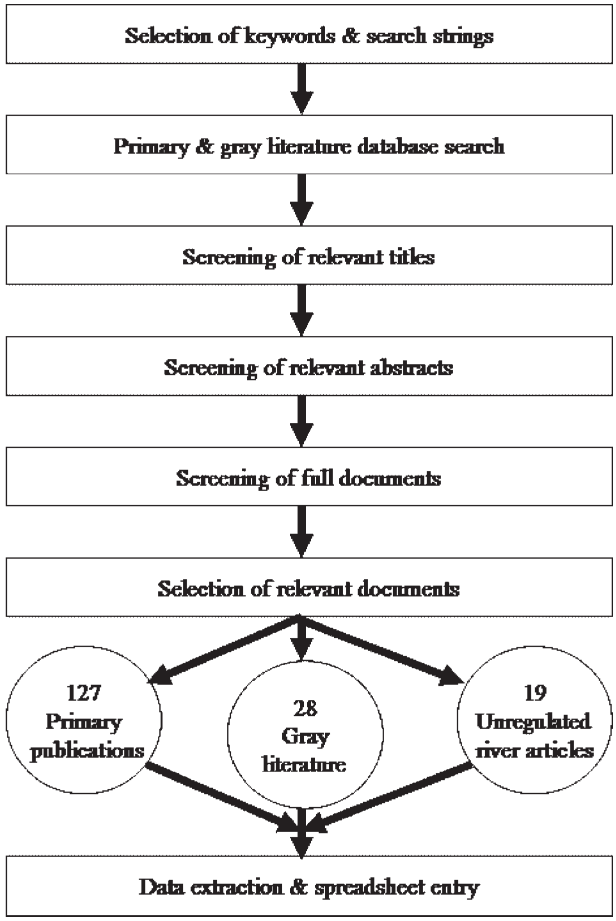

Figure 1. Schematic of literature review methodology outlining the various steps taken from acquiring data to extracting information

To evaluate which academic database would provide the most extensive list of primary literature on the topic of fish responses to modified flow regimes, the search strings were entered into the following library article databases: (1) *Web of Science*, (2) *Aquatic Sciences and Fisheries Abstracts A*, (3) *SCOPUS* and (4) *BIOSIS Previews*. *Web of Science* was selected for use as it covered the greatest range of dates (1945–present), and provided the highest number of hits.

Managing and selecting primary literature for inclusion in the review

Our search was conducted on 5 October 2006 and all search hits were imported into a reference management program (Reference Manager 10.0, ISI ResearchSoft, 2001). All duplicate articles were eliminated, and unique reference numbers were applied to those remaining. A total of 4450 titles were generated by this approach. Titles were screened to eliminate any references that were obviously irrelevant. If any uncertainty existed as to whether a title should be screened or not, it remained in the list for evaluation in the second screening process. A total of 844 tiles remained after the preliminary screening. The second screening process involved evaluation of the remaining title abstracts. To remain on the list, abstracts had to clearly indicate that there was some examination of effects of flow on fish and/or fish habitat. A total of 326 articles were selected for full review.

Gray literature search methods

Potential sources of gray literature were identified through industry and government resources online. An initial list of Canadian utilities was supplied by the Canadian Electricity Association (CEA) and a standard request letter

DOI: 10.1002/rra

for contributions was sent to a designated contact at each organization. Transmission and electrical distribution companies were not contacted for this review. Hydro Quebec was not on the CEA registry, but this utility was also contacted. Canadian federal and provincial government agencies that were deemed to have a direct interest in regulated rivers were also contacted. In addition to electronic requests and direct contacts, available online databases managed by regulatory departments were searched with the previously established primary literature search criteria. The scope of this search was limited to regulatory agencies and utilities from North America due to time constraints and ease of acquiring documents. Box I details the online databases searched for possible relevant literature. Where primary publications were suggested by government or industry contacts, they were screened for inclusion in the study.

Box I: Online databases and websites included in the gray literature search. All websites were accessed between 14 September and 5 October 2006.

- Department of Fisheries and Oceans—WAVES database (http://inter01.dfo-mpo.gc.ca/waves2/index2.html?__LANG=en)
- Gouvernment du Québec—Ressources naturelles et faune (http://www.mrn.gouv.qc.ca/guichet/publications/index.jsp)
- Gouvernment du Québec—Développement Durable, Environnement, et Parcs (http://www.mddep.gouv.qc.ca/ministere/rejoindr/renseign.htm)
- Hydro Québec Publications and Documentation Centre (http://www.hydroquebec.com/sustainable-development/repertoire/liste.html)
- Government of Ontario—Ministry of the Environment (http://www.searchontario.gov.on.ca/)
- Manitoba Conservation Library (http://www.gov.mb.ca/conservation/library/index.html)
- Government of Saskatchewan Publications Centre (http://www.publications.gov.sk.ca/)
- B.C. Ministry of the Environment—EcoCat: The Ecological Reports Catalogue (http://srmapps.gov.bc.ca/apps/acat/)
- U.S. Fish and Wildlife Services Library (http://library.fws.gov/uhtbin/cgisirsi.exe/x/0/49)
- U.S. Geological Survey (http://www.usgs.gov/pubprod/)
- U.S. Army Corps of Engineers Library (http://www.corpslibrary.com/search/um/Express.html)
- Northwest Fisheries Science Center (http://www.nwfsc.noaa.gov/publications/index.cfm)
- Pacific Fisheries Environmental Laboratory (http://www.pfeg.noaa.gov/research/publications)
- StreamNet Library—Pacific Northwest scientific community (http://www.fishlib.org/catalog/local.htm)
- NMFS Scientific Publications Office (http://spo.nmfs.noaa.gov/)
- Alaskan Fisheries Science Centre (http://www.afsc.noaa.gov/Publications/default.htm)
- Washington Department of Fish and Wildlife Publication Archive (http://wdfw.wa.gov/archives/archives.htm)
- DNR Illinois—Illinois State Water Survey (http://www.sws.uiuc.edu/pubs/search.asp)
- DNR Minnesota—Division of Fish and Wildlife http://www.dnr.state.mn.us/fishwildlife/index.html
- DNR Minnesota—Division of Waters http://www.dnr.state.mn.us/water/index.html
- DNR Wisconsin http://www.dnr.state.wi.us/
- Google Scholar http://scholar.google.com

Managing and selecting gray literature for inclusion in the review

A list of potentially relevant gray literature titles was generated via the above search criteria. An identical process to that of the primary literature was used to screen and eliminate articles (i.e. examination of titles first, then abstracts). A total of 133 and 85 gray literature articles were screened by title, and then by abstract, respectively.

DOI: 10.1002/rra

Literature on unregulated rivers

By the nature of our selected keywords and search strings, literature containing fish response to modified flow regimes in unregulated rivers was generated (e.g. fish response to spring freshet). Titles generated through primary and gray literature searches were screened as outlined above so that a comparison of methodologies and effects between both regulated and unregulated rivers experiencing modified flows could be made.

Review of selected primary and gray literature

All selected primary and gray literature documents were scanned fully (beyond the abstract) for relevance to the topic of fish response to modified flow regimes. If the study did not specifically examine the direct response of fish and/or effects on fish habitat as a result of operational effects of flow regulation, the study was excluded. The inclusion/exclusion criteria were agreed upon by all team members prior to review to reduce selection bias. A total of 174 documents were selected for data extraction ($n = 155$ for regulated rivers, $n = 19$ for unregulated rivers).

Data extraction

To achieve the goals of the synthesis (i.e. evaluate the various research methodologies for studying fish response to modified flows, summarize the statistical and apparent effects found on fish and fish habitat, identify opportunities for addressing gaps in the existing knowledge) a spreadsheet (Microsoft Excel, Microsoft Crop., Redmond, Washington) was created with standard fields of entry. In this way, all data were entered in a standardized format for ease of meta-analysis after the literature review was complete.

Acknowledged bias

The authors recognize that the studies included in this synthesis are not an exhaustive list of all of the available and relevant primary and gray literature on the topic. The keyword and database selection, group screening process and limited search of North American gray literature are all acknowledged to have presented some bias in the results of this study. The shortcomings of the article selection however, are outweighed by the benefits of the review.

ANALYSIS AND DISCUSSION

Overview

To be able to put into context the various methodologies used to examine fish response to flow modifications and the results of these studies, it is important to have an overview of the characteristics of the publications included in this review.

Publication information. Of the 155 publications included in our review, the majority (81.9%, $n = 127$) were peer-reviewed primary literature. The high percentage of peer-reviewed publications is not surprising due to the limitations of our gray literature search. Although gray literature accounted for only 18.1% ($n = 28$) of the studies included in the meta-analyses, we feel that these studies contain important results and are highly relevant to the topic of fish response to modified flows. There is, however, an increasing temporal trend in industry participation in producing primary publications. Out of 29 primary publications in which the industrial sector participated, 3 studies were published in the 1980s, compared to 7 studies in the 1990s, compared to 19 in the 2000s. This increasing tend is encouraging as peer-reviewed publications are considered to be more scientifically defensible (National Research Council, 2000).

Contributions to the literature available on fish response to modified flow regimes were examined for the academic, government and industrial research sectors. Documents produced strictly by each research sector were comparable between government (30.1%, $n = 47$) and academic institutions (29.7%, $n = 46$), with the industrial sector responsible for 11.5% ($n = 18$) of publications. A collaborative effort between any combination of research sectors was responsible for the remaining 28.4% ($n = 44$) of the studies. A strong representation of collaborative

DOI: 10.1002/rra

work in the field of regulated river science is integral to the success of determining management strategies that are acceptable to all stakeholders.

The primary literature examined in this review was published in 41 different journals. Of the 128 primary publications, the majority of studies on this topic were published in *River Research and Applications* (21.9%, $n = 28$; note that formerly this journal was known as '*Regulated Rivers*'), *Transactions of the American Fisheries Society* (12.5%, $n = 16$), *Journal of Fish Biology* (7.8%, $n = 10$), *North American Journal of Fisheries Management* (7.8%, $n = 10$) and *Hydrobiologia* (5.5%, $n = 7$). As *River Research and Applications* is an international journal dedicated to the promotion of basic and applied scientific research on rivers, it is not surprising that the majority of primary literature was found within this journal.

Temporal and geographic trends. The first study to be included in our review was published in 1970 (Corning, 1970). Since that time, there has been a steady increasing trend in research until 1995, when the number of studies escalated over twofold (Figure 2). It is expected that the number of studies examining the response of fish to modified flow regimes will continue to increase rapidly over the next few decades as the importance of this issue increasingly becomes the focal point of government agendas (e.g., new Center of Expertise on Hydropower Impacts on Fish and Fish Habitat, Fisheries and Oceans Canada, http://www.osl.gc.ca/chip/en/index.html).

Studies included in this review took place in 28 different countries. Studies were grouped by continent to examine geographic trends in publication of literature on fish response to modified flow regimes (Table I). Of the 155 studies examined, over half of the studies (53.5%, $n = 83$) were conducted in North America, and a large percentage of the remaining studies were conducted in Europe (32.3%, $n = 50$). Given that the number of hydroelectric plants is greatest in these two continents (Dynesius and Nilsson, 1994), it is not surprising that the majority of research has been focused in these two geographical areas. As hydropower production is expanding rapidly in South America (Anderson *et al*., 2006a) and Asia (Dudgeon, 2000), it is expected that more studies will emerge from these regions in the future.

Purpose of river regulation and duration of operation before study occurred. The purpose of river regulation was determined for each study included in the review and categorized under one of four main headings: hydropower, navigation, water diversion (i.e. flood control, irrigation) or mixed usage (which represented any combination of the three). Studies that did not clearly state the purpose of river regulation, or did not apply specifically to any of the categories made up 18.1% ($n = 28$) of the literature. Over half of the rivers studied

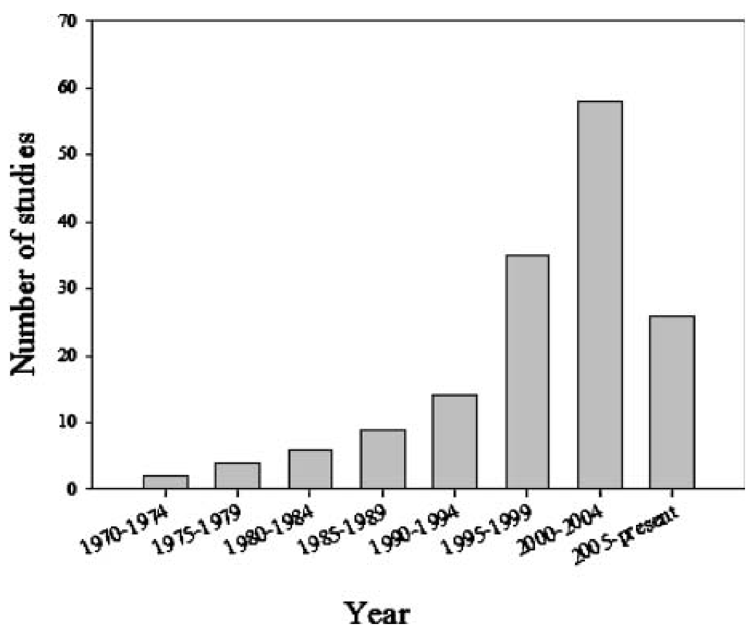

Figure 2. Progression of research examining the response of fish to modified flow regimes evidenced by publication date. Publications indicated as 'present' are those published between 1 January 2006 and 5 October 2006

DOI: 10.1002/rra

Table I. Summary of the geographic locations in which studies examining fish response to modified flows were based

Continent	Percentage of studies reviewed ($n = 155$)
North America	53.5 ($n = 83$)
Europe	32.3 ($n = 50$)
Australia/New Zealand	5.2 ($n = 8$)
South America	4.5 ($n = 7$)
Asia	1.3 ($n = 2$)
Africa	1.3 ($n = 2$)
Not applicable	1.9 ($n = 3$)

Note that '*n*' denotes the sample size. 'Not applicable' studies were those that did not reference their work to any geographic centre.

included in this review were regulated for the purpose of hydropower (55.5%, $n = 86$). Rivers regulated for mixed usage represented 16.8% ($n = 26$) of the studies. Water diversion and navigation were the purpose of river regulation in 9.0% ($n = 14$) and 0.6% ($n = 1$) of studies, respectively. The importance of understanding the purpose of river regulation lies within the degree of flow fluctuations biotic communities experience. For example rivers regulated for hydroelectric generation tend to be subjected to more drastic fluctuations in flow on a daily basis (Berland *et al*., 2004), whereas rivers regulated for irrigation *per se* tend to experience more pulsed flows during the dry season (Cambray *et al*., 1997).

The duration of time for which a river had been regulated before a study occurred was considered an important piece of information to extract from the literature to provide context in which possible effects could be discussed. For example, it has been suggested that biotic interactions are enhanced by more predictable flow regimes (Dudgeon, 1991), and as such a study taking place 1 year after initiation of river regulation may find differing effects than if the study occurred 10 years later. Only non-literature review studies ($n = 135$) were included in this analysis. Surprisingly, nearly half (49.6%, $n = 67$) of the studies did not clearly indicate this information. This particular lack of information will be discussed further in the identification of opportunities for future research.

Characterization of study organisms—study species family and life stage. Out of the 135 non-literature review studies included in our analyses, we extracted information on which fish species were chosen for examination. For ease of summarizing the information, the family in which each species belonged was entered into a separate category. The majority (68.1%, $n = 92$) of publications focused on a single fish family for their study, while 28.9% ($n = 39$) examined multiple families. In some instances the study species was unknown, or a study of just fish habitat was conducted, resulting in the final 3.09% ($n = 4$). We examined the frequency in which each fish family was studied (Table II). Salmonidae were studied more that twofold more than any other fish family (see Crisp *et al*., 1983; Anderson and Nehring, 1985; Underwood and Bennett, 1992). Cyprinidae (e.g. Cambray *et al*., 1997), Percidae (e.g. Mion *et al*., 1998) and Catostomidae (Paukert and Rogers, 2004) were the next most frequently studied fish families. The focus on Salmonidae is not surprising given the geographic focus of the studies included in our review. The family Salmonidae is the dominant family in the northern waters of North America, Europe and Asia (Scott and Crossman, 1998). Salmonids are also known for their intrinsic recreational and commercial value (Scott and Crossman, 1998).

Fish life stages, determined as egg, larval, juvenile, adult or mixed (a combination of two or more of the life stages) were also extracted from the literature surveyed (Table III). Mixed life stages were most frequently examined (38.5%, $n = 52$), followed by juvenile (20.7%, $n = 28$) and adult (17.8%, $n = 24$) life stages. Various life stages will respond to flow modifications in different ways. For example, newly emerged fry appear to be more vulnerable to stranding because of their use of substrate as cover in shallow water habitats, and their limited swimming ability, whereas larger juveniles tend to reside in deeper, higher velocity waters where they are less susceptible to stranding (Jones & Stokes, 2002; California Department of Water Resources, 2004). Studies that do not clearly state the life stage studied present difficulty when interpreting published results.

DOI: 10.1002/rra

Table II. Number of studies examining the various families of fish

Family	Number of studies
Salmonidae	83
Cyprinidae	38
Percidae	21
Catostomidae	14
Centrarchidae	10
Poeciliidae	10
Cottidae	9
Esocidae	8
Balitoridae	8
Ictaluridae	7
Acipenseridae	6
Lotidae	6
Percichthyidae	6
Petromyzontidae	5
Anguillidae	5
Moronidae	5
Characidae	4
Pimelodidae	4
Gasterosteidae	4
Polyodontidae	4
Prochilodontidae	4
Anostomidae	3
Doradidae	3
Atherinidae	3
Galaxiidae	3
Auchenipteridae	3
Curimatidae	3
Loricariidae	3
Fundulidae	2
Terapontidae	2
Melanotaeniidae	2
Cobitidae	2
Bagridae	2
Gobiesocidae	2
Chichlidae	1
Mugilidae	1
Heptapteridae	1
Serrasalmidae	1
Paradontidae	1
Erythrinidae	1
Callichthyidae	1
Clupeidae	1
Sciaenidae	1
Hiodontidae	1
Osmeridae	1
Eleotridae	1
Siluridae	1
Lepisosteidae	1
Aphredoderidae	1
Belonidae	1
Engraulidae	1

DOI: 10.1002/rra

Table III. Summary of the percentage of studies examining the various fish life history stages evaluated in studies of river regulation

Life stage	Percentage of studies reviewed ($n = 135$)	Example references studying the life stage
Egg	0.7 ($n = 1$)	Reiser and White, 1981
Larval	7.4 ($n = 10$)	Veshchev, 1994; Humphries *et al*., 2002; Weyers *et al*., 2003
Juvenile	20.7 ($n = 28$)	Slavik and Bartos, 1997; Cattaneo *et al*., 2001; Saltveit *et al*., 2001
Adult	17.8 ($n = 24$)	Arnekleiv and Kraabol, 1996; Robards and Quinn, 2002; Barrella and Petrere, 2003
Mixed	38.5 ($n = 52$)	Cardwell *et al*., 1996; Dauble *et al*., 1999; Fischer and Kummer, 2000
Unknown	12.6 ($n = 17$)	
Not applicable	2.2 ($n = 3$)	

Note that '*n*' denotes the sample size. Literature reviews/meta-analyses were not included in the data extraction. Studies that did not specify the life stage were considered unknown. Studies related to habitat only or fish passage were considered 'not applicable'.

Summary of research methodologies

Choice of gear type and/or technology. The methodologies used to examine potential effects of flow manipulation on fish and/or fish habitat were extracted from the 155 studies included in the synthesis. From these methodologies, nine general categories emerged from the data. The categories included: (1) active and/or passive gear (e.g. electrofishing, gill netting, seining), (2) hydroacoustics, (3) lab and/or flume studies (e.g. experimental streams with controlled and simulated flows), (4) literature reviews and/or meta-analyses, (5) modelling, (6) stranding (e.g. observations of natural stranding and enclosure experiments), (7) telemetry and/or tagging (e.g. electromyogram telemetry, passive integrated transponders (PIT) tags), (8) visual surveys (i.e. snorkelling, underwater cameras) and (9) any combination of two or more of the mentioned categories. The appropriate method group was assigned to each study for ease in summarizing the data. The number of studies using the various methodologies is outlined in Table IV.

Studies that combined two or more of the methodologies for examining potential impacts of flow manipulation on fish and/or fish habitat were most common in the literature reviewed (32.9%, $n = 51$). The most frequently

Table IV. Percentage of studies using various methodologies for examining potential effects of flow manipulation on fish and/or fish habitat

Methodology group	Percentage of studies reviewed ($n = 155$)	Example references using the methodology
Active/passive gear	23.9 ($n = 37$)	Mion *et al*., 1998; Lagarrigue *et al*., 2002; Humphries *et al*., 2006
Hydroacoustics	0.6 ($n = 1$)	Rakowitz and Zweimuller, 2000
Laboratory/flume	4.5 ($n = 7$)	Reiser and White, 1981; Lupandin, 2005; Vilizzi and Copp, 2005
Literature review/meta-analysis	12.9 ($n = 20$)	Petts, 1990; Hunter, 1992; Irwin and Freeman, 2002
Modelling	8.4 ($n = 13$)	Quiros, 1990; Geist *et al*., 1996; Alexander *et al*., 2006
Stranding	0.6 ($n = 1$)	Saltveit *et al*., 2001
Telemetry/tagging	12.9 ($n = 20$)	Bunt *et al*., 1999; Murchie and Smokorowski, 2004; Robertson *et al*., 2004; Scruton *et al*., 2005
Visual surveys	1.9 ($n = 3$)	Bauersfeld, 1978; Pert and Erman, 1994; Robards and Quinn, 2002
Combination of 2 or more of the above	32.9 ($n = 51$)	Higgins and Bradford, 1996; Paukert and Fisher, 2001; Reyjol *et al*., 2001b
Unclear	0.6 ($n = 1$)	
Not applicable	0.6 ($n = 1$)	

Note that 'unclear' studies were those that did not clearly state their methods, and those 'not applicable' are those which collected only temperature data.

DOI: 10.1002/rra

combined methodologies included active and/or passive gear and modelling (23.1%, $n = 12$), and active and/or passive gear and telemetry (21.2%, $n = 11$). It is not surprising that active and/or passive gear were often combined with other methodologies as they are often required as the capture technique of the fish that are used in such telemetry, laboratory/flume and stranding surveys.

The use of each of these methodologies is discussed in detail outlining the biological level (i.e. cellular, individual, population and ecosystem) to which studies most frequently targeted their endpoints. Cellular endpoints generally included an assessment of biochemical or physiological parameters (e.g. cortisol and glucose levels in the blood). Individual endpoints generally included an assessment of an individual fish's behaviour, spatial ecology, reproductive capacity or survival. Population level endpoints generally included an assessment of demographics, whereas ecosystem level endpoints typically assessed trophic relations/food webs, or habitat impacts. Inherent and specific advantages and disadvantages of each gear type for use of studying the effects of flow regulation on fish and/or fish habitat is also discussed.

Active and/or passive gear used on their own were the second most commonly employed methodology for examining the response of fish to modified flow regimes (23.9%, $n = 37$). Each biological level (cellular, individual, population and ecosystem) was examined using this methodology in one or more studies. Active and/or passive gear types have many inherent advantages and disadvantages. All passive gears are selective to some extent, fish and gear must overlap spatially and temporally and fish must interact with the gear to get caught or trapped until the gear is retrieved. In rivers, passive gears have the advantage of being pseudo active, in that water flows through the stationary gear, increasing the sampled area. Conversely, limitations imposed by access and turbulence may bias results as gear was deployed more as a factor of access rather than systematically. Additional factors that can affect the efficiency of the gear are season, water temperature, water levels, turbidity, and flow (Hubert, 1983). The advantage of active gear is the ability to encircle targets within a habitat or geospatially defined area, although with seines it is often difficult to get an accurate estimate of the area sampled compared to a gear pulled through the water such as a trawl (Hayes, 1983). In addition, fish that encounter active gear could avoid it by swimming over, around or under or be pushed by the pressure wave (seines and dip nets) or electrical field (electrofishing) (Hayes, 1983; Reynolds, 1983). These factors can affect the selectivity of the gear with a given species or size class. The very nature of sampling in flowing riverine environments may reduce the efficiency or effectiveness of an active gear type as external influence may affect performance.

Literature review and meta-analysis were used in 12.9% ($n = 20$) of the studies included in this synthesis (e.g. Zhong and Power, 1996; Svensson, 2000). Literature reviews and meta-analyses examined topics on each biological level, but typically emphasized studies conducted at the population level (e.g. Volovik, 1994; Agostinho *et al*., 2004). Literature reviews and meta-analyses are advantageous in the sense that they provide a synthesis of the data, but can be biased when they are not done in a repeatable manner (Pullin and Stewart, 2006).

Telemetry and/or tagging studies were also used in 12.9% ($n = 20$) of the studies included. Such studies focused very strongly on the individual level, but also included some assessments at the population level. The general advantage of telemetry and biologging is the ability to track individual fish in real-time providing positional and behavioural data not readily attainable using traditional techniques. The cost however is possibly the largest disadvantage of telemetry limiting the number of fish, and thereby the number of samples that can be collected, which in turn reduces the statistical power of the study (Cooke *et al*., 2004b). The majority of telemetry studies used for studies of river regulation use radio technology (e.g. Chanseau and Larinier, 1999; Scruton *et al*., 2002) rather than acoustic telemetry (e.g. Linnik *et al*., 1998; Thorstad *et al*., 2003), as radio telemetry typically has superior performance in riverine systems (Cooke *et al*., 2004b). Most telemetry studies tend to use mobile (manual) tracking techniques (e.g. Bunt *et al*., 1999; Berland *et al*., 2004), however, there is growing application of fixed telemetry arrays (see Scruton *et al*., 2002; Thorstad *et al*., 2003). Fixed telemetry arrays enable real-time continuous monitoring enabling the simultaneous study of multiple tagged fish. Recently, biotelemetry transmitters capable of measuring locomotor activity (i.e. EMG transmitters; Cooke *et al*., 2004a) have been used for the study of regulated rivers (e.g. Murchie and Smokorowski, 2004). Once calibrated, EMG transmitters could be used to estimate the bioenergetic costs of different flow conditions. The use of other tags (PIT tags, jaw tags, floy tags) is less expensive, but often generally relies on the recapture of individuals to attain appropriate data. PIT tagging antenna arrays (e.g. Connor *et al*., 2003) provide promise for studying fish responses to flow, but only in small fluvial systems (e.g. streams) or at infrastructure where fish must past through a confined detection region.

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Studies that focused on using models for determining effects of flow modification on fish and/or fish habitat were used 8.4% of the time ($n = 13$). Models examined in this review focused on every biological level except cellular (e.g. Alexander *et al.*, 2006). While modelling provides an opportunity to test a variety of scenarios not possible in the field, the challenge is developing a robust result that accounts for the multitude of environmental variables that act in concert or independently to affect fish behaviour in a dynamic flowing environment. Links between various numerical models and population parameters such as abundance, growth, survival or recruitment have not been well documented (Korman *et al.*, 2004).

Laboratory or experimental flume studies accounted for 4.5% ($n = 7$) of the studies included in this review. Laboratory/flume studies reviewed focused strictly on effects at the individual or population level. The advantage of laboratory or flume studies is the precise control or manipulation of physical factors providing the opportunity to evaluate the response of fish to specific parameters. There is also opportunity to obtain replicates and to use appropriate controls. However, an artificial flume only mimics conditions that may be found in a natural river, and it is necessary to treat any significant findings with some degree of caution and to verify the effects in a field setting (Vilizzi and Copp, 2005).

Visual surveys alone represented 1.9% ($n = 3$) of the studies included in the review (e.g. Hoffarth, 2004), and focused on individual and population level effects. Visual surveys, both shore-based and in-water provide opportunity for the observer to document behaviour *in situ*; however, the presence of the observer may affect the behaviour of the subject and bias any interpretation, particularly when attempting to quantify a response.

Studies strictly using stranding methodologies alone accounted for only 0.6% ($n = 1$) of the literature reviewed. Stranding studies have the advantage of physically measuring rates of flow decline and habitat exposure in real time under a variety of actual conditions or flow scenarios. Coupled with this is the ability to design experiments using passive gear to trap or retain fish following the receding water. Stranding studies are limited in the amount of habitat that can be evaluated and subtle variations in river bed morphology and substrate type may have significant influence on the ability of a fish to become stranded. This potentially creates bias when attempting to apply the results within a system or across disparate watersheds. In addition, factors such as season, turbidity and temperature can all affect fish behaviour during ramping studies.

The use of hydroacoustics for studying the effects of flow manipulation on fish only occurred once (0.6%) in the literature reviewed, and focused specifically at examining population level effects. The advantages hydroacoustics employed in river systems are the low variance (more samples can be collected on a given time scale) and the potential for absolute population estimation (Thorne, 1983). Disadvantages include poor species discrimination, little or no sampling capability near the surface or the bottom, complex and high start up costs, lack of biological samples and potential bias associated with target strength and calibration (Thorne, 1983).

We surveyed the literature reviewed on non-regulated rivers to determine if there were any methodologies used in examining effects of natural pulsed flow conditions on fish and/or fish habitat. However, no novel technologies were apparent. Out of the 19 studies surveyed, the majority of studies used active and/or passive gear 63.2% ($n = 12$). Literature reviews and/or meta-analyses accounted for 15.8% ($n = 3$) of the studies, compared to modelling-based surveys which represented 5.3% ($n = 1$) of the surveys. Three studies used a combination of methodologies, wherein active and/or passive gear was used in conjunction with literature reviews and/or meta-analyses (10.5%, $n = 2$), or visual surveys were coordinated with modelling techniques (5.3%, $n = 1$).

In general, there was a diversity of methodologies available to regulated river researchers for examining the response of fish to regulated flow regimes. However, methodologies targeting cellular level biological responses of fish were rarely used (only with active/passive gear). This gap in the methodologies will be addressed further in the directions for future research.

Sample size and use of controls. Studies that were based on literature-reviews or meta-analysis of other data ($n = 20$) were excluded from the following analyses as they did not present original field or laboratory data, and therefore remaining observations on the characterization of the study design were conducted on a total of 135 studies. The number of fish and rivers used in each study were examined to determine the range in sample sizes for each parameter.

Fish sample sizes were grouped into various categories for ease of comparison (Table V). The majority of studies (37.0%, $n = 50$) had a sample size of 1000 fish or greater. Surprisingly though, the sample size was not clearly

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Table V. Summary of the percentage of studies using various fish sample sizes for determining effects of flow modification on fish

Fish sample size category	Percentage of studies with sample size fitting in the category ($n = 135$)
1–9 fish	0.7 ($n = 1$)
10–49 fish	16.3 ($n = 22$)
50–99 fish	3.0 ($n = 4$)
100–499 fish	11.9 ($n = 16$)
500–999 fish	3.7 ($n = 5$)
>1000 fish	37.0 ($n = 50$)
Unknown sample size	20.0 ($n = 27$)
Not applicable	7.4 ($n = 10$)

Note that studies that focused on effects of fish habitat or production of general models were considered 'not applicable' in this analysis.

indicated for 20.0% ($n = 27$) of the studies. The lack of information on the fish sample size in a publication results in difficulty when interpreting stated effects and makes quantitative meta-analysis impossible. The omission of this type of data will be discussed further in addressing opportunities for future studies.

A total of 128 of the 135 studies clearly stated the sample size of rivers/streams. Of these studies, the majority (71.9%, $n = 97$) were conducted on only one regulated river. River sample size ranged up to a maximum of 65 rivers (see Cattaneo, 2005). Since the majority of research conducted on regulated rivers included in this review focused on one river, we were interested in evaluating what was used for statistical controls in the 135 studies.

A before-after, control-impact (BACI) study design (i.e. Conquest, 2000) was employed in 17.8% ($n = 25$) of the study designs (e.g. Scheidegger and Bain, 1995; Arthington *et al*., 2003), and 34.1% ($n = 46$) included one or more controls. Of the 46 studies that included controls in their study design, the most frequently used control was using unregulated sections of the study river for comparisons (30.4%, $n = 14$; e.g. Lagarrigue *et al*., 2002; Barrella and Petrere, 2003). Other study controls included comparisons on a separate, unregulated river (28.3%, $n = 13$; e.g. Crisp *et al*., 1983; Bain *et al*., 1988), use of baseline/pre-impoundment data (19.6%, $n = 9$; e.g. Dejalon and Sanchez, 1994; Humphries and Lake, 2000), use of control fish (13%, $n = 6$; e.g. Arnekleiv and Kraabol, 1996; Berland *et al*., 2004) and the use of a controlled flume study (8.7%, $n = 4$; e.g. Flodmark *et al*., 2002; Geist *et al*., 2005). Experimental controls are important because biological systems are prone to variability (Hurlbert, 1984).

Collection of physical environmental parameters. The majority (97.0%, $n = 131$) of the non-literature review/meta-analyses studies included in the synthesis collected data on discharge (e.g. Murchie and Smokorowski, 2004) or some surrogate of flow (e.g. water depth and/or velocity (e.g. Capra *et al*., 2003). Other physical habitat variables studied included water chemistry data (e.g. dissolved oxygen, pH and chemical parameters; 22.2%, $n = 30$), photoperiod (13.3%, $n = 18$), habitat variables (substrate and channel width; 49.6%, $n = 67$) and water temperature (49.6%, $n = 67$).

Since temperature is known to co-vary with flow (Cushman, 1985), and observed effects could be partially attributed to this variable, we were interested in the extent to which the 67 studies that collected water temperature actually examined the influence of this factor on observed or apparent effects. Although almost half (49.6%, $n = 67$) of the studies included in this synthesis collected water temperature data, the majority of authors (56.7%, $n = 38$) failed to examine the potential thermal consequences of the modified flow regimes. For the remaining studies that did examine the thermal consequences, the effects are discussed in the next section. Lack of use of collected physical variables, especially those known to co-vary with flow, may lead to the loss of explanatory power of observed results.

Summary of statistical and apparent effects on fish and/or fish habitat

Only the 135 non-literature review studies included in our review were synthesized to examine effects of modified flow regimes on fish and/or fish habitat.

Statistical and power-analyses. Our examination of the 135 study designs revealed a number of issues that could seriously compromise the results and conclusions of many of the studies. Although a majority of studies surveyed (72.6%, $n = 98$) conducted formal statistical analyses, very few studies (1.5%, $n = 2$; i.e. only Golder Associates,

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2003; Alexander et al., 2006) clearly performed power analyses either *a priori* or *post hoc* to determine whether or not their sample size was large enough to detect a statistically significant effect of flow manipulation on fish and/or fish habitat. Power analyses are an important tool in experimental design as they help to determine an adequate sample size for accurately detecting biologically significant effects (Peterman, 1990). In the cases where sample size is too small, it becomes increasingly likely that statistical tests will fail to yield significant results; consequently, biologically relevant phenomena are more likely to go undetected. As such, statistical power analysis can be considered necessary for relating statistical and biological significance (Thomas and Juanes, 1996).

Synthesis of statistical effects. For each methodology group, the number of studies conducting statistical analyses and finding statistically significant effects is summarized in Table VI. Note that significance was assessed at different levels in the various studies (e.g. 0.10, 0.05), however, 0.05 was by far the most common. Of the 99 studies that conducted statistical analyses, 73.5% ($n = 72$) resulted in statistically significant effects of flow modification on fish and/or fish habitat. We provide more detail for studies using the top three most popular methodology groups (a combination of methods, active/passive gear and telemetry and tagging).

Out of 51 studies using a combination of methods to collect information on effects of flow modification on fish and/or fish habitat, 36 conducted statistical analyses. Out of the 36 studies that conducted statistical analyses, 27 found a statistically significant effect. The most common combination study employed modelling with field data collection either to build the model or conduct *post hoc* validation. For example, Baran *et al*. (1995) used data collected from a number of regulated rivers and controls to build a predictive model to determine fish distribution. They noted significant correlations between abundance, fish assemblage, flow and area of cover. Others related proportion of non-native species (Brown and Ford, 2002) and juveniles (Capra *et al*., 2003) to variations in modelled flow. Although no statistically significant effects were found when telemetry was combined with an active/passive gear, there were still suggestions that fish movement was in response to changes in flow (e.g. Cambray *et al*., 1997; Paukert and Fisher, 2001). Lab/flume studies in combination with an active/passive gear (i.e. electroshocking) were also used in a number of studies. However, the results reported were variable with one study determining that fry densities and growth rates increase under modified flow conditions (Irvine, 1987) while in another growth rate was retarded (Weyers *et al*., 2003).

Out of 37 studies using active/passive gear to collect information on effects of flow modification on fish and/or fish habitat, 30 conducted statistical analyses. Out of the 30 studies that conducted statistical analyses, 24 found a statistically significant effect. Studies that used active/passive gear to collect information typically noted significant affects on abundance and movement of fish in regulated rivers and in some cases related the findings to controls. For example, Freeman *et al*. (2001) noted that fish abundance was significantly higher at their unregulated control site than in the regulated river. In addition they noted a lower abundance of spring spawning species at the regulated sites. Species noted for their sensitivity to flow regulation are often displaced from flow impacted sites and habitats

Table VI. Summary of method groups conducting statistical analyses and finding statistical effects

Methodology group	# of studies ($n = 135$)	# of studies conducting statistical analyses	# of studies finding a statistically significant effect
Active/passive gear	37	30	24
Hydroacoustics	1	1	0
Laboratory/flume	7	7	6
Modelling	13	7	5
Stranding	1	1	1
Telemetry/tagging	20	14	7
Visual surveys	3	1	1
Combination of 2 or more of the above	51	36	27
Unclear	1	1	1
Not applicable	1	0	0

Note that ‘unclear’ studies were those that did not clearly state their methods, and those ‘not applicable’ are those which collected only temperature data.

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most affected by flow regulation immediately downstream of dams contain assemblages dominated by species tolerant to flow regulation (Gehrke *et al*., 1999). Results from other studies suggested that there was a statistically significant increase in growth rate for trout following regulation as well as population densities of trout and bullhead (Crisp *et al*., 1983). When flows are enhanced by establishing a minimum flow after regulation, various studies found that populations responded favourably to the conditions. Travnichek *et al*. (1995) found that an enhanced flow regime (implementing a minimum and consistent flow release) supported more abundant and diverse fish community assemblages, with the abundance of fluvial specialists increasing to over 80%. Also, a number of authors observed an increase in the number of alien species and reduced species diversity in increasingly regulated catchments (Gehrke *et al*., 1995; Marchetti and Moyle, 2001).

Of the 20 telemetry and tagging studies, 14 conducted statistical analyses. Seven of these studies found statistically significant effects. Telemetry studies finding statistically significant effects typically found a significant relation between flow and fish movement (e.g. Linnik et al., 1998; Berland *et al*., 2004, 2006). For example Brenden *et al*. (2006) found that discharge significantly affects both habitat use and selection of muskellunge in the New River, Virginia, USA. Murchie and Smokorowski (2004) and Scruton *et al*. (2005) noted that river regulation could be energetically costly to fish species. Scruton *et al*. (2005) observed Atlantic salmon in a hydro-river had larger home ranges when compared to fish in unregulated rivers. Murchie and Smokorowski (2004) observed brook trout and walleye muscle activity patterns mimicked flow fluctuation patterns but could not statistically correlate the two parameters. The authors suggested that a multi-parameter model which included variables that may co-vary with flow (i.e. water temperature, photoperiod) may have added explanatory power. Telemetry studies also found no effects on fish. For example, Robertson *et al*. (2004) found that flow did not affect Atlantic salmon habitat use or displacement, and had little effect on fish activity within diel periods. Similarly, McMaster *et al*. (1977) found fluctuations in flow did not influence movement patterns of chinook salmon or steelhead. Although Bunt *et al*. (1999) observed that fluctuating river levels did not appear to influence the degree to which brown trout moved within their study site, they did mention that effects may have been moderated by the use of instream cover (i.e. woody debris).

We also conducted a comparison of statistically significant effects found on studies occurring on unregulated rivers subject to variable flows. Out of 19 studies, 100% conducted statistical analyses examining the effects of peak flow on fish and/or fish habitat, and all (i.e. 100%) found statistical effects. In general, studies found peak flow events had an effect on fish community composition (richness, diversity), fish migration, reproduction, foraging, growth, year-class strength, catch-per-unit-effort and overall habitat condition. For example, Grossman *et al*. (2006) found young-of-the-year densities of mottled sculpin were strongly positively correlated with annualized mean daily flows during drought years, and negatively correleated during non-drought years. Intermediate flows produced the highest recruitment of YOY mottled sculpin. Delays in Atlantic salmon migrations were found to be the result of low discharge years by Tetzlaff *et al*. (2005a).

It is not surprising that the meta-analysis revealed that the majority of studies identified that there were statistically significant effects of flow modification on fish and/or fish habitat given the continued attention that this topic generates. However, what was concerning, was the lack of use of controls and power-analyses to support these statistically significant findings. Indeed, there were a number of studies that noted apparent effects but provided no statistical support. Here, we briefly summarize these non-statistical or apparent effects that we observed during our synthesis (i.e. instances where authors noted an effect but did not have formal statistical analysis) Generally it appeared that modified flow regimes in regulated rivers could be responsible for spatial transitions in species assemblages (Mainstream Aquatics Ltd and Gazey Research, 2006), reduced recruitment (Gehrke *et al*., 1995), and alterations to spawning migration timing (Pender and Kwak, 2002). Possible reasons for lack of statistical analyses of the data in many studies may include low sample size (e.g. White and Wade, 1980), and lack of controls (e.g. Slavik and Bartos, 1997). Although apparent effects can point to future research questions, results should be treated as speculative until they are backed by statistical support.

Synthesis of thermal consequences. Overall, thermal consequences were given little attention in studies, as data failed to be collected or was collected without further evaluation or reporting. Temporal shifts were the most commonly stated thermal consequence of pulsed conditions. Dare and Hubert (2003) reported increased winter water temperatures in response to river regulation, resulting in an effect on species distribution, behaviour and

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abundance. Due to hypolimnetic dam releases, yearly fluctuations in water temperatures were observed to differ from neighbouring rivers or up-stream and down-stream reaches (Cambray *et al*., 1997).

Overall, the volume of the pulsed flow appeared to have the greatest impact on downstream systems. A common observation was that high-pulsed flows were correlated with lower than normal downstream water temperatures (Brown and Ford, 2002; Brewer *et al*., 2006). Conversely, some studies found that the downstream thermograph was localized resulting in warming effects in summer (McAdam, 2001). However, in this particular case it was observed that impacts were dampened by the presence of tributaries downstream which served to re-establish more natural conditions.

Future opportunities

A common theme in the conclusion of many of the 155 studies reviewed was the need for future studies examining the response of fish habitat to modified flow regimes. We suggest that future research should consider addressing some of the gaps we have identified in our study. Such gaps or productive research topics are identified in Box II.

Box II: Proposed research directions and a template for elevating regulated rivers science and research.

1. Need for detail on the temporal aspects of the study relative to river regulation: Many of the studies that we examined failed to provide information on the number of years that a river was regulated prior to the initiation of the study. Such information provides context for findings. As noted earlier, some effects of river regulation may be short-lived whereas others may not be apparent for many years. Longer study durations would also be desirable.
2. Greater inclusion of non-salmonid taxa: There is a paucity of information on the effects of river regulation on non-salmonid fish species. There is a need for additional research focused on a diversity of fish models, including those with no direct economic value.
3. Need for greater emphasis on multiple life-stages: Few studies incorporate more than one life history stage into a single study or program. Comprehensive analyses will require analyses that evaluate all life-stages, particularly in long-lived species (e.g. sturgeon).
4. Need for more interdisciplinarity: There is a need for more interdisciplinary studies that integrate researchers with different training and perspectives. Integrating field, laboratory and modelling components would be a productive approach for increasing interdisciplinarity. Closer integration of hydraulic modelling (i.e. engineering) with biological responses is needed to advance regulated rivers science. Inclusion of these non-biological perspectives from early stages of biological research will ensure that findings are relevant to all stakeholders.
5. Need for studies that focus on multiple biological endpoints: We revealed that most studies focus on few biological endpoints. We suggest that there is a need for inclusion of methodologies that focus on assessing the response of fish at all four biological levels (cellular, individual, population and ecosystem) or that cross biological levels (e.g. linking behaviour, physiology and demographics). Particularly under-represented are studies that focus on physiological endpoints or those that assess the bioenergetic consequences of river regulation. There are now a number of well-developed physiological techniques that can be applied to field environments (i.e. field physiology or conservation physiology; Wikelski and Cooke, 2006) that could yield important information on the sublethal consequences of river regulation. As the field of bioenergetics is focused on the currency of life (i.e. energy), it is a logical approach for the assessment of fish responses to fluctuating flow conditions as it incorporates elements of the organism and the ecosystem.
6. Need to study fish responses to rise and fall of river flows, not just the absolute flow level: Most of the research to date has focused on evaluating the consequences of low or high flows on fish. Few studies have actually evaluated the behaviour etc. of fish during dynamic periods such as flow increase or decrease (i.e. during the ramping). As many organisms shift position during the periods of flow alteration, there is a need to understand the cost and consequences of those shifts for the organisms. New technology such as biotelemetry arrays (e.g. Thorstad *et al*., 2003; Cooke *et al*., 2004b) or EMG transmitters (e.g. Cooke *et al*.,

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2004a; Murchie and Smokorowski, 2004) enable the real-time assessment of fish behaviour, activity and position during periods of dynamic flow.

7. Need for increased rigour in experimental design: There are a number of challenges inherent in regulated rivers research that complicates experimental design. In particular, it is often difficult to identify an appropriate control. Essentially, many studies resort to contrasting biological endpoints during high and low flow. These data are autocorrelated and not independent, limiting analysis and often leading to pseudoreplication (Hurlbert, 1984). Careful thought regarding experimental design and proper identification of replicates is needed to develop rigorous experiments, not simply random observations. There is, for example much opportunity for use of adjacent non-regulated systems as controls (e.g. Crisp *et al*., 1983; Bain *et al*., 1988). Ideally, BACI designs could be used (e.g. Scheidegger and Bain, 1995; Arthington *et al*., 2003). However, BACI requires research prior to installation or operation of river regulation infrastructure. Given that many regulated rivers science is used in formal environmental hearing and sometimes courts of law, the studies and their conclusions need to be justified and defensible.
8. Need for increased rigour in statistical analysis: We revealed that there were many studies on regulated rivers where the statistical analysis was incomplete or simply non-existent. The inclusion of rigorous formal statistical tests backed by power analyses (Peterman, 1990) is essential. At present, very few studies in regulated rivers science clearly incorporate power analysis (i.e. report their results). These characteristics are fundamental to the generation of scientifically credible findings.
9. Need for examination of physical variables known to co-vary with flow: Although many studies monitored water temperature (which co-varies with flow in many cases), few included this information in formal statistical analyses. To increase explanatory power of analyses, there is a need to include more data on environmental conditions. Use of multivariate statistical techniques could enhance analyses. Such information would also be useful for integrating with bioenergetic assessments as water temperature is considered the 'master' environmental factor for fish.

The requirement for more and better research is emphasized by the diverse management strategies suggested in the documents. For example, some studies emphasize the need to sustain high flows (Paukert and Fisher, 2001), or to at least provide stable flows that are of sufficient duration and discharge to allow for spawning, larval development and juvenile residence (Freeman *et al*., 2001), whereas others caution against releasing flows that are too high during velocity-sensitive stages such as spawning and growth (Anderson and Nehring, 1985; Cattaneo, 2005). The need to mandate ecologically acceptable minimum flow levels and eliminate or reduce pulsed flow operations is also widely recommended (Dejalon and Sanchez, 1994). To provide managers and regulators with credible information to balance complex and often competing interests, there is a clear need to elevate regulated river research.

Many studies highlight the need to approach the issue of flow regulation from a holistic, ecosystem perspective. For example, by improving land use practices (through minimizing deforestation, agricultural expansion, industrialization and urban growth) it is possible to reduce levels of total suspended solids and enhance larval protection in watersheds (Petts, 1990; Mion *et al*., 1998). A holistic approach would also involve integrating the management of dams on different streams that are within a single watershed (Stanford and Hauer, 1992; Gehrke *et al*., 1995). Any new structural developments on the river should first undergo comprehensive ecological considerations to provide the flows necessary to sustain the downstream river ecosystem post-development (Petts, 1990; Drinkwater and Frank, 1994). Adaptive management was proposed by several authors as an effective tool for involving stakeholders in addressing aquatic needs in regulated rivers (Stanford and Hauer, 1992; Irwin and Freeman, 2002; Anderson *et al*., 2006a).

CONCLUSIONS

In this paper, we have attempted to effectively synthesize a large body of relevant literature regarding the response of fish to modified flow regimes in regulated rivers. The goals of the meta-analysis were met with a synthesis of the

DOI: 10.1002/rra

various research methodologies used to examine fish response, a synthesis of observed statistical and apparent effects of flow modification on fish and/or fish habitat, and by providing direction for future studies to enhance regulated river science (see Box II). The need for further examination of the effects of river regulation on fish and fish habitat is imperative to the successful management of fluvial systems today and in the future. By nature, large river systems are in limited supply, and by process of human exploitation, unaltered large river systems are even scarcer (Benke, 1990). Increased collaboration integrating researchers with different training and perspectives (e.g. Olson and Metzgar, 1987; Higgins and Bradford, 1996; Scruton *et al*., 2002) provides the greatest promise for balancing ecological concerns with economic development in future studies.

ACKNOWLEDGEMENTS

We are grateful to the numerous individuals that helped us obtain industry and government reports. The work presented here was supported by B.C. Hydro through a grant to SJC.

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