

Validation of the Flow Management Pathway: Effects of Altered Flow on Fish Habitat and Fishes Downstream from a Hydropower Dam.

Keith D. Clarke¹, Thomas C. Pratt², Robert G. Randall³, Dave A. Scruton^{1,4}, Karen E. Smokorowski²

¹ Northwest Atlantic Fisheries Center
Science, Oceans and Environment Branch
Fisheries and Oceans Canada
St. John's, NL

² Great Lakes Laboratory for Fisheries and Aquatic Sciences
Fisheries and Oceans Canada
Sault Ste. Marie, Ontario

³ Great Lakes Laboratory for Fisheries and Aquatic Sciences
Fisheries and Oceans Canada
Burlington, Ontario

⁴ *Sikyumiut* Environmental Management Ltd.
Suite 200, Regatta Plaza, 80 Elizabeth Ave.
St. John's NL

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by

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Smokorowski²

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Suite 200, Regatta Plaza, 80 Elizabeth Ave.
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TABLE OF CONTENTS

ABSTRACT	V
RÉSUMÉ	V
1. BACKGROUND	1
1.1. PATHWAYS OF EFFECTS	1
1.2. SELECTION AND APPROACH TO VALIDATION OF FLOW MANAGEMENT PATHWAY	2
2. INTRODUCTION TO FLOW MANAGEMENT	3
2.1. EFFECT OF ALTERED FLOW ON RIVER DISCHARGE, WIDTH AND WETTED AREA	3
2.2. NATURAL FLOW REGIME	4
2.3. LAND-BASED AND IN-WATER ACTIVITIES THAT AFFECT FLOW	5
2.4. SPATIAL CONTEXT OF FLOW MANAGEMENT	5
3. VALIDATION OF FLOW MANAGEMENT LINKAGES AND END POINTS	5
3.1. CHANGE IN FLOW → CHANGE IN TOTAL GAS PRESSURE	5
3.1.1 <i>Gas Bubble Trauma (Disease)</i>	6
3.1.1.1. Mortality	7
3.1.2 <i>Mitigation of change in total gas pressure</i>	8
3.2. CHANGE IN FLOW → CHANGE IN ACCESS TO HABITATS	8
3.2.1. <i>Effects of Limiting Access to Habitats on Fishes</i>	9
3.2.1.1. Longitudinal Effects	9
3.2.1.2. Vertical Effects	12
3.2.1.3. Lateral Effects	12
3.2.2. <i>Mitigation of Limiting Access to Habitats on Fishes</i>	13
3.3. CHANGE IN FLOW → STRANDING OF FISH	13
3.3.1. <i>Fish Species/Size</i>	14
3.3.2. <i>Fish Behaviour</i>	14
3.3.3. <i>River Morphology/Substrate</i>	15
3.3.4. <i>Rate and Range of Flow Change/Attenuation</i>	16
3.3.5. <i>Temporal/Seasonal Influences</i>	17
3.3.6. <i>Mortality</i>	18
3.3.7. <i>Mitigation of Stranding of Fishes</i>	19
3.4. CHANGE IN FLOW → CHANGE IN FISH BIOENERGETICS	19
3.4.1. <i>Bioenergetics Overview</i>	19
3.4.2. <i>Metabolism/Swimming</i>	20
3.4.3. <i>Feeding and Holding Station</i>	21
3.4.4. <i>Growth and Feeding</i>	22
3.4.5. <i>Behaviour</i>	23
3.4.6. <i>Competition and Behaviour</i>	23
3.4.7. <i>Morphological and Behavioural Adaptations</i>	24
3.4.8. <i>Interactions with Habitat</i>	24
3.4.9. <i>Seasonal Effects</i>	25
3.4.10. <i>Stressors</i>	26
3.5. CHANGE IN FLOW → CHANGE IN WATER TEMPERATURE	26
3.5.1. <i>Temperature Overview</i>	26
3.5.1.1. Increased or steady flow	27
3.5.1.2. Reduced or fluctuating flow	27
3.5.2. <i>Effects of Changing Water Temperature on Biota</i>	28
3.5.2.1. Temperature decreases	28
3.5.2.2. Temperature increases	30
3.5.2.3. Stable Temperature	32
3.5.2.4. Fluctuating Temperature	32
3.5.3. <i>Mitigation of a Change in Temperature</i>	32
3.6. CHANGE IN FLOW → CHANGE IN NUTRIENT CONCENTRATIONS	33

3.6.1.	<i>Nutrients Overview</i>	33
3.6.1.1.	Longitudinal.....	34
3.6.1.2.	River Mouths.....	35
3.6.1.3.	Lateral.....	36
3.6.1.4.	Vertical.....	36
3.6.2.	<i>Effects of Changing Nutrient Concentrations on Fishes</i>	37
3.6.3.	<i>Mitigation of Change in Nutrients</i>	38
3.7.	CHANGE IN FLOW → CHANGE IN FOOD SUPPLY	38
3.7.1.	<i>Food Supply Overview</i>	38
3.7.1.1.	Longitudinal Impacts.....	39
3.7.1.2.	Lateral.....	43
3.7.2.	<i>Effects of Changing Food Supply on Fishes</i>	43
3.7.3.	<i>Mitigation of a Change in Food Supply</i>	45
3.8.	CHANGE IN FLOW→ PHYSICAL EFFECTS (EROSION AND DEPOSITION).....	46
3.8.1.	<i>Introduction to Physical Effects</i>	46
3.8.2.	<i>Erosion – Bed Scouring</i>	47
3.8.2.1.	Increase in Bed Scouring.....	47
3.8.2.2.	Increase in Armouring.....	48
3.8.2.3.	Increase in Aquatic Macrophytes.....	48
3.8.2.4.	Change in Food Supply.....	49
3.8.3.	<i>Erosion – Bank Erosion</i>	49
3.8.3.1.	Change in Suspended Sediment Concentrations.....	50
3.8.3.2.	Increase in Cross-Sectional Width.....	50
3.8.3.3.	Hydropeaking and Bank Erosion.....	50
3.8.3.4.	Delta and Shoreline Erosion.....	51
3.8.4.	<i>Deposition</i>	51
3.8.4.1.	Bench Development and Decrease in Cross-Sectional Width.....	51
3.8.4.2.	Riparian Vegetation.....	52
3.8.4.3.	Reservoir Flushing.....	53
3.8.5.	<i>Ice Formation</i>	53
3.8.6.	<i>Effects of Erosion and Deposition on Fishes</i>	54
3.8.7.	<i>Summary of Physical Effects</i>	55
3.8.8.	<i>Mitigation of Physical Effects</i>	55
4.	INTERACTIONS	56
5.	CONCLUSION AND RECOMMENDATIONS	57
5.1.	POE DIAGRAM.....	57
5.2.	SUMMARY OF EFFECTS.....	58
5.3.	SUMMARY OF MITIGATIONS.....	60
6.	REFERENCES	62
7.	TABLES	100
	TABLE 1.....	100
	TABLE 2.....	102
	TABLE 3.....	106
8.	FIGURES	108
	FIGURE 1.....	108
	FIGURE 2.....	109
	FIGURE 3.....	110
	FIGURE 4.....	111

ABSTRACT

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Validation of the flow management pathway: effects of altered flow on fish habitat and fishes downstream from a hydropower dam. Can. Tech. Rep. Fish. Aquat. Sci. 2784: vi + 111 p.

The Department of Fisheries and Oceans (DFO) Habitat Management Program developed a series of Pathways of Effect diagrams that describe the cause-effect linkages between a development activity and a habitat impact. To ensure that the cause-effect linkages were science-based, DFO Science conducted a review of the science literature to validate the Flow Management Pathway. The review focused on whether flow management practices, including altering the frequency, amplitude, duration, timing and rate of change of flow, affected fishes downstream of barriers. Our review showed that the majority of the cause-effect linkages outlined in original Flow Management Pathway were supported in the literature, though a number of additional effects were identified as missing and subsequently added to a modified Pathway. Flow management practices can have direct (survival) and indirect (growth, reproduction, bioenergetics) impacts on fishes. Specific impacts on fishes resulting from flow alteration included changing total gas pressure, habitat access, stranding, water temperature, nutrient dynamics, bioenergetics and food supply. Flow management also affects physical habitat, altering erosion and deposition patterns resulting in changes in habitat structure and cover. The likely outcomes of flow management on fishes and their habitat were well-documented and fairly consistently represented in the literature, and the potential impacts were significant for many species.

RÉSUMÉ

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Le Programme de gestion de l'habitat du ministère des Pêches et des Océans (MPO) a élaboré une série de diagrammes de séquences des effets qui décrivent les liens de cause à effet entre une activité de développement et l'impact sur l'habitat du poisson. Pour s'assurer que les liens de cause à effet reposaient sur des bases scientifiques, le Secteur des sciences du MPO a examiné la littérature scientifique afin de valider la séquence de la gestion des débits. L'objet de cet examen était de savoir si les pratiques de gestion des débits, notamment dans les modifications de fréquence, d'amplitude, de durée, d'horaire et de taux, influent sur les poissons en aval des obstacles. L'examen a permis de constater que la majorité des liens de cause à effet décrits dans la séquence de gestion des débits originale étaient appuyés par la littérature. D'autres effets dont l'absence a été constatée ont été ajoutés à une séquence modifiée. Les pratiques de gestion des débits ont parfois des répercussions directes (survie) et indirectes (croissance, reproduction, bioénergétique) sur les poissons. Les impacts de la modification des débits sur les poissons incluent les changements dans la pression totale

du mélange gazeux, l'accès à l'habitat, l'échouement, la température de l'eau, la dynamique des nutriments, la bioénergétique et la nourriture disponible. La gestion des débits influe aussi sur l'habitat physique en modifiant les schèmes d'érosion et de dépôt, ce qui entraîne des changements dans la structure et la couverture de l'habitat. La littérature démontre efficacement et avec une certaine constance les conséquences probables de la gestion des débits sur le poisson et son habitat, et fait état d'impacts éventuels importants pour beaucoup d'espèces.

1. BACKGROUND

1.1. Pathways of Effects

Within the Oceans and Habitat Sector of Fisheries and Oceans Canada (DFO), the Habitat Management Program (HMP) is the federal regulatory program mandated to conserve and protect fish habitat under Canada's *Fisheries Act*. In 2004-2005, the Habitat Management Directorate implemented the Environmental Process Modernization Plan (EPMP), which is designed to provide a more modern regulatory system that provides management decisions in a more timely, efficient and consistent manner. The key element of EPMP is the development and implementation of a science-based Risk Management Framework (RMF). This framework sets out a series of principles and practices used to evaluate development projects with the potential to affect fish habitat. The RMF is intended to ensure that project proposals (referrals) are evaluated in a consistent and transparent fashion and HMP resources can then be re-allocated from the review of routine, low risk activities, to the review of projects with the greatest degree of risk to fish habitat.

A significant component of the Risk Management Framework is the development and validation of a series of Pathways of Effect (PoE) diagrams that describe the cause-effect linkages between a development activity and a habitat impact (see Jones *et al.* 1996; 'hypothesis of effects' diagrams). These PoE diagrams are essentially a logical map (flow chart) that begins with a development activity (e.g., river-based hydropower generation), that leads to a series of qualitative changes in fish habitat (e.g. flow alterations, sediment increases) which can be linked to changes in biological productivity (e.g. reduction in food availability). DFO's habitat biologists and proponents are to use these PoEs to assess the potential effects from any given project. The PoE diagrams would also assist the proponents to develop mitigation plans to avoid the negative effects of a given activity, where possible. To date the Habitat Management program has conceptually developed 21 PoE diagrams for land based (10) and in-water (11) activities.

The Habitat Management Program requested that Science Branch conduct a detailed scientific literature review to support and validate the cause-effect relationships within each Pathway of Effect. The first such validation exercise focused on specific end points that comprise 70% of all the linkages in the combined set of Pathway of Effects Diagrams, namely: (1) change in sediment concentrations, (2) change in habitat structure and cover, (3) change in water temperature, and (4) change in dissolved oxygen concentrations. Three working papers were developed, and subsequently presented at a DFO National Workshop Meeting to determine the scientific validity of the four reviewed endpoints. The participants, including both DFO scientists and academic researchers, conducted an impartial and objective scientific peer review of the working documents. The key conclusions (scientific information/advice) from this meeting have been documented in a Canadian Science Advisory Secretariat (CSAS) Proceedings report (DFO 2006). The review on change in habitat structure and cover and the report on change in sediment

concentrations have been published (Smokorowski and Pratt 2006, Robertson *et al.* 2006, respectively).

1.2. Selection and Approach to Validation of Flow Management Pathway

For this second validation exercise, Habitat Management and Science chose to follow a different approach by validating all cause-effect linkages within one Pathway Diagram, through to the validation of endpoints. Linkages and endpoints were distributed among science groups (Newfoundland, Burlington, and Sault Ste. Marie) and then amalgamated into one complete document, to be subject to peer review. The Flow Management pathway (Fig. 1) was chosen as a case study for testing. The specific objectives were to: 1) evaluate the efficacy of the PoE approach, in terms of science support and utility for application; 2) undertake a literature search to provide science support for all pathway linkages and endpoints; 3) suggest modifications to the PoE flow diagram if needed, based on the results of the literature search, and 4) identify general mitigation options for flow management. When possible, impacts to fishes were identified by linking the effects of flow alteration to the specific life history traits that affect production - survival, growth and reproductive potential. The focus was on peer-reviewed literature relevant to Canada (literature from other countries was to be included if deemed relevant to species and ecotypes within Canada).

Inclusions and Exclusions of the Literature Survey

The flow management Pathway of Effect was designed by Habitat Management to address all key in-water or land-based activities that impact on river flow (section 2.3). However, the main focus of this literature review was on hydropower development, more specifically, the impacts of water impoundment and flow regulation on the river ecosystem downstream from the dam. The effects of water level regulation in impoundments (and other lacustrine systems) are to be developed as a separate pathway diagram and review. Also, the effects of water withdrawal are dealt with elsewhere. This literature review deals specifically with the effects of changes in schedule of flow, not changes in the total amount of flow.

The flow management PoE diagram illustrated in Figure 1 shows the original pathway developed by the Habitat Management Program (a), and a somewhat modified pathway (b) based on the results of the literature review. In addition to the direct effects of flow management on the characteristics of water flow (change in magnitude, timing, duration, frequency and rate of change of flow), the key habitat impacts were bank erosion, scouring of channel beds, deposition, and changes in substrate composition, sediment concentrations, and habitat structure and cover (square text boxes). The endpoints addressed were change in gas pressure, change in migration/access to habitats, displacement or stranding of fish, change in water temperature, change in nutrient concentrations, and change in food supply. The remaining two endpoints identified in Figure 1, change in contaminant concentrations and change in salinity, were not addressed in this review, but will be addressed elsewhere.

Additional limitations and exclusions of the literature review included: 1) although reasonably thorough, the literature review was not exhaustive; 2) literature on impacts to fishes sometimes focused on species of salmonines more so than other species; 3) citations often referred to a specific river, taxon, or flow alteration, with no or limited replication, making extrapolation or generalizations about impacts uncertain; 4) literature on models for assessing changes to fish habitat were NOT included in this review (e.g., Physical Habitat Simulation System (PHABSIM), Weighted Useable Area (WUA), Habitat Evaluation Procedures (HEP), Habitat Suitability Indices (HSI), and Instream Flow Incremental Methodology (IFIM)); 5) cumulative effects were not addressed; 6) impacts to estuaries and receiving waters were not addressed comprehensively, but are mentioned briefly for some endpoints (e.g., nutrients, section 3.6.1.2); 7) for each endpoint, some mitigation actions were listed as examples, but the list of mitigations was not exhaustive, nor were different mitigation options evaluated; and finally 8) literature on effects in winter was very limited.

Key conclusions and synthesis from the pathway literature review were peer reviewed and documented as a Canadian Science Advisory Secretariat (CSAS) Proceedings and as this Technical Report.

2. INTRODUCTION TO FLOW MANAGEMENT

2.1. Effect of Altered Flow on River Discharge, Width and Wetted Area

River discharge rate (Q , $\text{m}^3 \text{sec}^{-1}$) is the product of the cross sectional area of flow (width times depth, wd) and average current velocity (v), as described by the equation: $Q = wdv$ (Leopold *et al.* 1964). Accordingly, water velocity is a function of discharge: $v = aQb$, where a and b are regression coefficients. Both equations, sometimes called regime equations, are based on well documented empirical data and are often cited in general summaries of channel flow dynamics (Hynes 1970; Beaumont 1975; Stalnaker *et al.* 1989; Kellerhals and Church 1989). Coefficients a and b are river dependent. Changes in water flow will invariably lead to changes in the cross sectional area (depth and width) of the river channel and average water velocity. These changes can be quantified and predicted with reasonable confidence. For example, if the power coefficient b is 0.54, a reduction in discharge of 33% will decrease the river width by about 20%. The total wetted area available as fish habitat would be reduced as well, although the relationship may not be directly proportional. As an example, the functional relationship between usable physical habitat for rainbow trout and monthly or daily variability in streamflow was discussed and illustrated by Stalnaker *et al.* (1989). Although the physical habitat time series was less variable than the streamflow time series, for certain periods a moderate reduction in flow resulted in a large reduction in physical habitat, and for other periods the converse was true.

Flow management and regulation will invariably modify discharge rates, flow patterns and usable fish habitat. Depending on the type of regulation, discharge can be decreased, increased (flashing, hydropeaking) or made more stable than natural flow patterns. That

is, regulation can affect not only the magnitude of discharge but also the flow characteristics of timing, duration, frequency and rate of change. Terms used to describe flow regime are defined in Table 1.

2.2. Natural Flow Regime

Natural flow regimes vary in the different regions of Canada, depending on regional climate and seasonal precipitation which is expressed as surface water, soil water and groundwater. Regional climate, geology, topography, soils and vegetation determine both the supply of water and the pathways by which precipitation reaches the river channel (Poff *et al.* 1997; Poff and Ward 1989). Where winter precipitation accumulates as snow and ice, river flow is reduced in winter, and this is followed by heavy spring flooding (e.g. Catamaran Brook, NB; Fig 2). Depending on the region, there is often an increase in rainfall and river discharge in autumn as well, but of lower magnitude than the spring flood (Bronte Creek, ON; Fig. 2). The ratio of maximum flood to minimum winter discharge varies considerably among regions, ranging from a 2:1 ratio in the Mackenzie River, to a 125:1 ratio for tributaries in the northern Quebec, and a 100 to > 1000:1 ratio in the coastal watersheds of British Columbia (Northcote and Larkin 1989; Roy 1989). During high discharge, the river edge is inundated (riparian and floodplain; Fig. 3), and the water-land ecotone is extended laterally.

The natural flow regime of each watershed, characterized by the magnitude of discharge, duration, frequency, timing and rate of change, regulates both the physical and the ecological processes of the river ecosystem. Many channel and floodplain habitat features such as river bars and pool-riffle sequences are formed and maintained by dominant seasonal discharges (Poff *et al.* 1997).

The food organisms, nutrients and other aspects of fish habitat that support fish production in rivers are controlled and influenced by these natural seasonal fluctuations in flow (Junk *et al.* 1989; Poff *et al.* 1997). For example, all river life stages of anadromous Atlantic salmon (*Salmo salar*), from spawning and emergence of alevins to out-migration of smolts, are closely tied to fluctuations in river discharge (Scruton *et al.* 2007b). The importance of synchrony between flow regimes and fish survival in freshwater systems is analogous to the long-standing match-mismatch hypothesis in marine systems (Platt *et al.* 2003), whereby key life history processes are closely synchronized with seasonal cycles in environmental conditions and productivity. Disruptions to the natural flow regime in rivers can disrupt life history processes and impact on the survival of rheophilic fishes.

Dams are the most obvious modifiers of river flow, potentially affecting the magnitude, timing and other characteristics of flow. For example, dams designed for hydropower generation or flood control capture both high and low flows. The resulting absence of high flushing flows (magnitude, timing, duration) may lead to the deposition of fine sediments in the streambed, which is detrimental to biota (fishes and their prey) that are sensitive to sedimentation (Stalnaker *et al.* 1989). Peaking hydropower operations are designed to follow variations in electricity demand (load following) resulting in significantly increased frequency and rates of change that differ markedly from the natural flow regime (Fig. 4).

As will be evident in this review, the magnitude of impact to fish habitat and fishes depends on the type of flow management and the extent of departure from the natural flow regime. Impacts to fish habitat range from low for run-of-the-river operations to high for hydropeaking operations.

2.3. Land-based and In-water Activities that Affect Flow

Five large-scale (watershed) anthropogenic activities affect river flow: hydropower generation (impoundment, flow regulation); navigation (impoundment, dredging, levees), forest harvesting in the riparian zone (surface flow and groundwater), agriculture (drainage, irrigation, impoundment, levees), and urban development (channelization, impervious landscaping, levees). For many rivers, land-use activities such as agriculture, forest harvest and urbanization, are the primary cause of altered flow regimes, particularly in headwaters. Often these activities reduce the retention of water in the watersheds; rather, water is routed quickly downstream, increasing the size and frequency of floods and reducing baseflow levels during dry periods. Flood control activities also isolate the floodplains from overbank flows. All five activities can significantly affect the natural flow regime and consequently fish habitat (Ward and Stanford 1989). Human modification of natural flow regimes and the associated hydrologic processes are reviewed by (Poff *et al.* 1997).

However, as noted above, hydropower generation is the primary activity affecting flow and fish habitat that is addressed in this literature review, Nevertheless, the literature will be relevant to the other activities affecting river flow as well.

2.4. Spatial Context of Flow Management

Natural river ecosystems have a strong spatial connection with the surrounding landscape, as the sources of water, nutrient ions, and organic matter come from the watershed, and together determine the river productivity (Hynes 1970; Hynes 1975). The major landscape-river pathways were described by Ward and Stanford (1989) as having four dimensions: a longitudinal dimension from headwaters to the river mouth, a lateral dimension between the river and the riparian and floodplain zones, a vertical dimension which links the river ecosystem with the groundwater (Fig. 3), and a temporal dimension. A change in flow regime will impact connections along all four dimensions. Changes to the flow regime in the river channel will also ultimately and cumulatively impact on the outflow at the river mouth or estuary.

3. VALIDATION OF FLOW MANAGEMENT LINKAGES AND END POINTS

3.1. Change in Flow → Change in total gas pressure

Total Gas Pressure (TGP) refers to the total concentration or additive partial pressures of the atmospheric gases nitrogen, oxygen and argon dissolved in water. An excellent

discussion of the physical laws governing the solubility of gases in a liquid was provided by Harvey (1975). In general, under normal atmospheric pressure the TGP of water would not be expected to exceed 100%; however, there are both natural and anthropogenic situations where TGP can exceed 100% and the water becomes supersaturated with gas (see Weitkamp and Katz 1980). The mechanisms by which TGP can exceed 100% are described by Weitkamp and Katz (1980) and three of these mechanisms are of importance from a flow management perspective and these are the focus of this review.

The most common and by far the most studied situation where TGP can reach supersaturation in flow managed rivers are in the spillways of hydroelectric dams (Ebel *et al.* 1975; Ruggles *et al.* 1981; Ruggles and Murray 1983; Weitkamp and Katz 1980; Antcliffe and Finster 1999; Backman and Evans 2002; Backman *et al.* 2002; Weitkamp *et al.* 2003a). Water and gases are mixed in spillways and if allowed to plunge to depth the hydrostatic pressure of water is increased thus increasing the solubility of gases in water, which can lead to supersaturation (Weitkamp and Katz 1980). This process has the capacity to supersaturate a large volume of water and thus can be of significant importance. This phenomenon first garnered scientific interest during the 1960's and 70's due to observations on the Columbia River (see citations in Weitkamp and Katz 1980) but was also reported previous to this from hydroelectric projects in Scandinavia (Jarnefelt 1948; Lindroth 1957). Although the hydrostatic pressure is usually the cause of increased TGP at hydroelectric projects there has been at least one case where air injected into water from a vent within a turbine was the causative factor (MacDonald and Hyatt 1973). It is important to note that not all spillways are subject to increased TGP as both the height of the water falling and the depth to which it is allowed to plunge will have an effect on the resulting hydrostatic pressure.

The other two situations where elevated TGP can occur in flow managed systems are either caused by a significant and quick increase in water temperature or very high levels of photosynthesis. As temperature increases, the ability of water to hold gas in solution decreases thus causing the supersaturation of water that was previously at or near saturation (Weitkamp and Katz 1980). Increases in water temperature have been shown to lead to supersaturated conditions in the cooling water effluents of steam generating facilities (DeMont and Miller 1972; Adair and Hains 1974; Jensen 1974; Miller 1974) and nuclear power plants (Marcello and Fairbanks 1976). Very high rates of photosynthesis can occur in some reservoirs which can also result in elevated TGP (Schisler and Bergersen 1999). Both of these situations are generally localized in their effect but the photosynthesis within reservoirs can compound the problem at spillways (Schisler and Bergersen 1999).

3.1.1 Gas Bubble Trauma (Disease)

The main ecological consequence of elevated levels of TGP is a condition known as Gas Bubble Trauma or Disease (GBT) which affects a wide variety of aquatic organisms including fishes and invertebrates (MacDonald and Hyatt 1973; Ebel *et al.* 1975; Weitkamp and Katz 1980; Heggberget 1984; Lutz 1995; Weitkamp *et al.* 2003b). Weitkamp and Katz (1980) provided a detailed description of GBT with respect to its

causes and symptoms. In general, GBT is often associated with exophthalmia or 'pop eye' but the most common external sign of GBT is bubbles or blisters under the skin. These bubbles can be located in a variety of places depending on the severity of GBT and species in question (Mesa *et al.* 2000) but common locations include between the fin rays, on the head, along the lateral line and in the lining of the mouth. Haemorrhages frequently accompany these bubbles in chronic GBT (Meekin and Turner 1974). In acute cases of GBT, bubbles in the gills may be the only external sign (Wyatt and Beiningen 1971). There are also internal lesions associated with GBT but these require either necropsy or histological investigations and are thus not compatible with most field investigations (Mesa *et al.* 2000).

Fish that are suffering GBT exhibit abnormal behaviours which are consistent with severe physical stress (Weitkamp and Katz 1980). Under acute conditions fish can lose equilibrium, and other swimming abilities (Wyatt and Beiningen 1971). Under more chronic conditions feeding, growth (Meekin and Turner 1974; Dawley and Ebel 1975), swimming performance (Schiewe 1974) and loss of lateral line sensitivity (Schiewe and Weber 1976; Weber and Schiewe 1976) may be affected. While GBT has been shown to affect larval fish (i.e. yolk sac stage), the egg stage (Weitkamp and Katz 1980; Krise and Meade 1988; Gale *et al.* 2004) and reproductive success (Gale *et al.* 2004) appear to be resilient. Salmonid fry with large gas bubbles in their yolk sac tend to show erratic swimming (Adams and Towle 1974; Weitkamp and Katz 1980) and this condition usually results in death.

3.1.1.1. Mortality

Mortality of juvenile and adult fish in acute cases of GBT is generally attributed to anoxia resulting from stasis of the blood (Weitkamp and Katz 1980). In very severe cases the bubbles in the blood stream can be large enough to block blood movement through the heart, but more commonly the stasis occurs in the gills (Weitkamp and Katz 1980). It was the high rate of mortality in salmonids associated with GBT on the Columbia River during the mid 1960's and early 70's that brought GBT and TGP to the forefront of scientific investigation. One report during this period estimated that 6% to 60% of adult salmonids died in the middle Columbia River during the period from 1965-1970 (Meekin and Allen 1974). There is a large body of literature on mortality trials for pacific salmonids, and this work was summarized in Weitkamp and Katz (1980). Direct mortality can also occur in larval (i.e., yolk sac stage) fish (Weitkamp and Katz 1980). In this situation the bubbles form between the yolk sac and the perivitelline membrane and death occurs when the vitelline membrane ruptures (Weitkamp and Katz 1980).

Many authors have associated the sublethal symptoms of GBT with a higher probability of mortality. Fish with severe bubbles or blisters in the mouth have been observed to refuse food (Dawley and Ebel 1975). Any impairment of the lateral line may affect the fish's ability to sense its environment which may make it more susceptible to predators or injuries (Stroud *et al.* 1975; Schiewe and Weber 1976; Weber and Schiewe 1976). Also, mortality due to a secondary infection in fish that had recovered from GBT was observed by Weitkamp (1976) and Jensen (1974).

3.1.2 Mitigation of change in total gas pressure

The main mitigative measure that resulted from the research in the 1960's and 70's was the use of flow deflectors, which were either designed into new spillways or retrofitted on existing projects (Weitkamp and Katz 1980; Ruggles and Murray 1983). Flow deflectors essentially reduce the plunging action of the water falling over spillways thus reducing the entrainment of atmospheric gases (Ruggles and Murray 1983; Muir *et al.* 2001). The utilization of flow deflectors along with some other operational changes was generally thought to have eliminated high levels of TGP at hydro electric installations (Ruggles and Murray 1983; Mesa *et al.* 2000; Muir *et al.* 2001; Weitkamp *et al.* 2003b). Elevated levels of TGP and the resulting GBT did not resurface as issues until the 1990's when surface spill became one of the preferred options for passing downstream migrating juvenile salmonids (Mesa *et al.* 2000; Ryan *et al.* 2000; Muir *et al.* 2001).

A second mitigating factor related to elevated levels of TGP which has received scientific attention is the idea of hydrostatic compensation. Hydrostatic compensation is a natural phenomenon where deep water reduces the overall TGP (Weitkamp and Katz 1980); for every meter of water depth the TGP is reduced by about 10% (Weitkamp *et al.* 2003 a, b). While the idea of hydrostatic compensation is not new (Weitkamp 1976; Weitkamp and Katz 1980; Heggeberget 1984) it has received much recent attention due to the utilization of spill waters as a method to pass downstream migrating salmonids (Muir *et al.* 2001; Weitkamp *et al.* 2003a; Johnson *et al.* 2005; Beeman and Maule 2006). The artificial increase of spill waters to increase smolt passage has brought into question the effect the extra spill may have on TGP and GBT (Ryan *et al.* 2000; Beeman and Maule 2006). The advent of telemetry techniques has allowed field investigations to characterize the migration depth of a variety of species (Weitkamp *et al.* 2003a; Johnson *et al.* 2005; Beeman and Maule 2006) thus giving a better understanding of the actual TGP that should be experienced by these fish. In general, with the species studied to date, fish utilize deep areas if available and thus for the most part avoid high levels of TGP (Weitkamp *et al.* 2003a; Johnson *et al.* 2005; Beeman and Maule 2006). This observation may explain why the incidence of GBT is often lower than predicted from laboratory experiments or surface TGP measurements (Backman *et al.* 2002; Weitkamp *et al.* 2003b).

3.2. Change in Flow → Change in access to habitats

Flow management can alter a fish's ability to access habitats in a variety of ways. Due to this variety, the following sections have been organized to describe changes in the three physical dimensions that allow ecological connectivity in an intact river (Ward 1989; Ward and Stanford 1995; Cowx and Welcomme 1998; Jungwirth 1998; Calles 2005). The fourth dimension, time, plays an important role in all three physical dimensions through changes induced on periodicity and frequency of hydrological events and will be discussed within each section. The first, and possibly best studied, physical dimension relates the effects flow management may have in a longitudinal direction (i.e., the river corridor). This section covers such things as movement and migration in the up and downstream directions. Vertical effects are discussed next, which relate changes that

may occur in surface water - ground water interactions. These interactions can affect habitat in the hyporheic zone, which is an important area for many species as a spawning habitat. The lateral dimension will cover changes that affect the river's connection to its flood plain, which also includes inundations.

3.2.1. Effects of Limiting Access to Habitats on Fishes

3.2.1.1. Longitudinal Effects

The most obvious effect of placing flow control structures within a river is the resulting fragmentation of the river corridor (Jungwirth 1998). With this fragmentation, the free movement of fish (e.g. papers in Jungwirth *et al.* 1998; Hanrahan *et al.* 2004), and other materials (e.g. Gregory *et al.* 1991), may be impeded or delayed. Dams and weirs can be complete barriers to movement (e.g. EPA 2002; Hanrahan *et al.* 2004) but most recent and future projects can be equipped with fish passage facilities if required, so the potential for changing migration patterns and its resulting effects will be the focus of this review. Migration has been defined by Northcote (1998) as movements involving regular cyclic alteration between habitats used for spawning, feeding or survival. Migratory fishes are often encouraged to move upstream by rising flows and many migrations occur during increasing or seasonally high discharge with little movement occurring when flows are maintained uniformly low (Hynes 1970). Thus, flow operation regimes and the release of water downstream of barriers can play an important role in fish movement.

The habitat requirements of any given species will generally change throughout its life history; inherent with these changes is a need to move from one habitat to another either ontogenetically or on a seasonal basis (Northcote 1998; Thorpe 1999; Armstrong *et al.* 2003). The most pronounced example of this 'need to move' is seen in the diadromous fishes which are known to undergo vast migrations and utilize habitats in both fresh and saltwater. It is not surprising then that fish movement and migration research has been dominated by work on these diadromous forms, which is especially true of the salmonids (see Northcote 1998; Murchie *et al.* 2008). The migration literature is also dominated by observations conducted during the open water season and only recently have winter and under ice observations been conducted (Robertson *et al.* 2003; Enders *et al.* 2007; Hussko *et al.* 2007). While these studies have given us new insight into the movement patterns of salmonids during winter most have been conducted in small streams and have not directly evaluated changes that may occur due to flow management (Hussko *et al.* 2007).

Flow management scenarios can affect fish movement in both the up- and downstream directions, though research has historically focussed on upstream migrating salmonids (Northcote 1998). Migrations are energetically expensive (see Section 3.4.2), environmental conditions are often adverse (e.g., elevated temperatures, high discharge), distances are long and difficult, and significant impediments to migration could affect arrival times on spawning grounds thereby negatively affecting spawning success (Bernatchez and Dodson 1987). Hydroelectric dams are known to cause delay in the upriver migration of migratory species (Thorstad *et al.* 2005) because fish are attracted to

high water velocities and discharge, hydrologic conditions which are associated with hydroelectric plant tailraces (Bernatchez and Dodson 1987). Thus when upstream migrants are presented with channels of differing discharge they are attracted to the channel with highest velocity, which is usually the tailrace and not the opening to a fish passage structure. This can result in “false-attraction” to the tailrace area and cause delay in migration (FERC 1995; Smith *et al.* 1997). Tailrace attraction may result in injury and delay, increased exposure to predators, higher risk of disease, and environmental stress (Winstone *et al.* 1985). Migration may be further delayed by fish exhibiting a wandering behaviour in search of a sustained directional flow (Kynard 1993) or reversing migration direction completely (Rivinoja *et al.* 2001; Thorstad *et al.* 2005).

One of the most studied migrations in flow managed rivers is the ascent of anadromous salmonids to their freshwater spawning grounds. The impact of migration delays on spawning can be context specific and will depend on the location and extent of the delay relative to spawning sites, species, energy consumed, the state of maturity, difficulty of the remaining migration, and environmental conditions. Studies of upstream migration of adult Atlantic salmon on the Exploits River, Newfoundland, have documented tailrace entrainment among migrating fish (Scruton *et al.* 2007a). Salmon were delayed in the tailraces for an average of 33.4 h (2002) and 3-12 days (2004), however, these delays are considerably less than those reported in the literature (e.g., citations within FERC 1995; Thorstad *et al.* 2003; Gowans *et al.* 1999; 2003). Scruton *et al.* (2007a) concluded that despite tailrace attraction, the actual consequence to the timing of migration was relatively small, and most salmon continued to migrate upstream via a bypass channel after leaving the tailrace area. In contrast to the observations in Newfoundland, Rivinoja *et al.* (2001) found that only 26% of wild adult Atlantic salmon and no hatchery fish were able to locate a bypass channel and fishway on the River Umealven, Sweden. This failure was attributed to attraction to the power plant outflow relative to the weaker flow of the bypass channel. Similar trends with respect to Atlantic salmon have been observed in Norway (Thorstad *et al.* 2003) and Scotland (Gowans *et al.* 2003) with maximum delays of 71 and 52 days, respectively.

Migratory delays in relation to tailrace attraction have also been well documented for salmonids in the Pacific Northwest (e.g. Davidson *et al.* 1943; FERC 1995; Williams 1998) and delays as little as 3 days have been shown to have effects on spawning success (Fleming and Reynolds 1991). Tailrace attraction has been observed in other species such as arctic grayling (Fleming & Reynolds 1991) and white sturgeon (Pavlov 1971; Khoroshko 1972). Arctic grayling stopped short of their upstream goals and were displaced to downstream areas, resulting in the use of lower quality spawning habitat (Fleming and Reynolds 1991). Female white sturgeon were attracted to power plant tailraces for extended periods and their eggs lost the capacity for fertilization thus reducing their spawning success (Pavlov 1971; Khoroshko 1972).

Migration patterns can also be altered due to flow management when fish are moving downstream, but this issue has received less attention than upstream migration (Northcote 1998). The travel time for downstream migration is directly related to the velocity of water, as most downstream migrants move passively and during high flow

periods associated with snow melt and runoff (Ruggles 1980; McCormick *et al.* 1998). Giorgi *et al.* (1997) found that the primary determinant of the migration rate of spring sockeye salmon, hatchery steelhead, and wild steelhead in the middle reaches of the Columbia River was flow rate, accounting for 42, 36, and 31% of the migration rate, respectively. Berggren and Filardo (1993) found a similar relationship in downstream migration rate models with flow accounting for 74 and 39% of the variation in models for juvenile Chinook salmon on the Snake and middle Columbia Rivers, and for 90 and 62% of the migration speed for steelhead on the same rivers, respectively.

Regulated rivers typically store spring runoff for future power generation thereby reducing flows during spring, potentially delaying migration (Petts 1984a). These delays can cause de-smoltification in salmonids (i.e., fish may reside in the river for an additional year), possibly resulting in exposure to unfavourable environmental conditions (e.g., temperature, salinity) and may deplete energy reserves (Raymond 1979; Ruggles 1980, McCormick *et al.* 1998). Timing of entry is important because downstream migrants (smolt, kelt) typically have an 'environmental window' whereby their physiology and environmental conditions are optimal for adaptation to salt water and survival (Raymond 1979). Increasing the migration time for downstream migrants can also increase exposure to predators (Rieman *et al.* 1991; Jepson *et al.* 2000; Naughton *et al.* 2005).

On the upper Columbia River, dam construction altered the life history of fall juvenile Chinook salmon by flooding historical spawning areas and forcing them to use cooler headwater streams, thereby changing the annual smolt migration from a late spring, pre-project period, to a summer migration (Connor *et al.* 2002). Summer flow augmentation to increase discharge and decrease temperatures has been used to mitigate the dam caused changes in life history timing by increasing the rate of seaward migration and decreasing the migration time from 1 to 5 days (Raymond 1988; Connor *et al.* 2003a). Construction of dams and regulation of flows has had a significant impact on Chinook salmon in the Central Valley Region including the Sacramento River of California (Yoshiyama *et al.* 1998). Regulation has increased the spring-summer flows while decreasing historically higher flows during the fall, winter and early spring; these low flows impeded migration. Flow regulation of the Sacramento River tributaries has resulted in later spawning and delayed smolt migration, which has contributed to declines in salmon populations.

Anadromous salmonids have dominated the movement literature with respect to flow management issues, but recent advances in telemetry technology have created an increase in movement studies (see references in Spedicato *et al.* 2005). Many of these studies have centered on resident fish and it is now more evident that movement is an important component of many riverine fish populations (Robertson *et al.* 2003; Carlsson *et al.* 2004; Schmetterling and Adams 2004). It is still not entirely clear what effects dams and weirs have on these resident populations but habitat fragmentation has been implicated in both changing community composition (Gehrke *et al.* 2002; Dodd *et al.* 2003; McLaughlin *et al.* 2006) and reducing genetic diversity (Fagan 2002; Meldgaard *et al.* 2003; Alo and Turner 2005; Jager 2006) and thus reducing overall species persistence (Dunham *et al.* 1997; Fischer and Kummer 2000; Jager *et al.* 2001).

3.2.1.2. Vertical Effects

Groundwater is the most important component of the vertical dimension within a river, and the area where groundwater mixes with surface waters is referred to as the hyporheic zone (Jones and Mulholland 2000). The extent of the hyporheic zone is quite variable among rivers and is dependant on other physical factors such as discharge and the permeability of the surrounding soils (Stanford and Ward 1988). Within an individual river (or river reach) the exchange of water that occurs in the hyporheic zone is governed by differences in the hydraulic head (Wondzell and Swanson 1999). Since variability in discharge and hydraulic head are both related to the variability in the hydrograph (Malcolm *et al.* 2004) any management activity that changes the natural hydrograph also has the potential to affect hyporheic water quality and discharge (Calles 2005).

The hyporheic zone is known to be an important incubation habitat for a variety of salmonid species (Curry and Noakes 1995; Geist 2000; Geist *et al.* 2002; Malcolm *et al.* 2003; Groves and Chandler 2005). The hyporheic water can regulate the level of dissolved oxygen and promote the removal of metabolic wastes in the salmonid redds (Curry *et al.* 1995; Crisp 1996; Peterson and Quinn 1996). While there has been very few directed studies on the effect flow regulation has on hyporheic waters (Curry *et al.* 1994), there has recently been a few studies that have investigated the role of seasonal discharge (Dent *et al.* 2000; Ward and Wiens 2001; Malcolm *et al.* 2004; Calles 2005). This remains an important area for future research as changes in hyporheic water quality have been shown to have a significant effect on the survival of salmonid eggs (Malcolm *et al.* 2004; Groves and Chandler 2005; Malcolm *et al.* 2005).

3.2.1.3. Lateral Effects

Regular inundation of the floodplain connects the river with riparian vegetation which can be important for nutrient cycling (Meyer and Likens 1979; Junk *et al.* 1989; section 3.6.1.3.) and habitat formation (Hesse and Sheets 1993; Ward *et al.* 1999; Bowen *et al.* 2003). It also plays a role in large scale river dynamics such as channel migration, (Sheilds *et al.* 2000) which promotes a diversity of habitats and supplies the raw materials for structures such as sand bars. Many of the slow water, off channel habitats that are created during floodplain inundation have been shown to be very important to a number of fish species, especially the younger age classes (Welcomme 1979; Kwak 1988; Copp 1989, 1997; Scheidegger and Bain 1995; Bowen *et al.* 1998; Freeman *et al.* 2001).

Flow management tends to store water thus removing or altering the natural peaks of the hydrograph (Poff *et al.* 1997). This storage of water tends to reduce or eliminate the inundation of the floodplain downstream of an impoundment, which can prevent fish from seasonal use of these areas for spawning and feeding (Petts 1984a). The inability to use these areas can reduce the production of the species with a strong connection to these shoreline habitats and favours species capable of using a wide variety of aquatic habitats (Kinsolving and Bain 1993; Scheidegger and Bain 1995). Thus fish communities become less diverse and less productive. Additionally, irregular flooding of floodplain areas by reservoir releases can allow fish to use these areas for feeding and as refugia from high

flows. Sudden reductions in flow can then cause fish to be stranded in these areas (Petts 1984a). Stranding is a well studied lateral effect which is usually observed during a specific flow management operation (i.e., hydropeaking) and as such is covered by its own section (see below).

The continual expansion and contraction observed under some flow management regimes may also change fish behaviour. Several recent studies have demonstrated juvenile fish to have larger home ranges under hydropeaking flows, as compared to natural flow systems. In a large Norwegian river operated under a peaking hydropower regime, home ranges for salmon parr averaged 2770 m² (Berland *et al.* 2004) while in a Newfoundland hydropeaking study, summer home ranges for salmon parr averaged 700 m². These home ranges are much larger than expected when compared to those reported for smaller naturally flowing rivers, which range from 30 to 50 m² (Saunders and Gee 1964; Hesthagen 1990; Armstrong *et al.* 1997). Large home ranges reported under hydropeaking regimes suggest this type of water fluctuation may be energetically costly and could affect growth, production and survival (Scruton *et al.* 2005).

3.2.2. Mitigation of Limiting Access to Habitats on Fishes

Reconnecting the river to its various dimensions is important if we expect to continue to avail of water and power resources while still retaining ecological integrity (Cowx and Welcomme 1998). Issues in the longitudinal dimension have a long history of research and the main mitigative measure employed to supply upstream movement is engineered fish passage structures (Rivinoja *et al.* 2001; Katopodis 2005). The science and engineering surrounding fish passage is a large field (see Jungwirth *et al.* 1998; Odeh 1999) which will form the subject of an entirely separate review. The survival of fish moving in the downstream direction can also be enhanced by engineered structures (see papers in Odeh 1999) but in recent years surface spill has been one of the more used methods of getting fish over dams (e.g., Muir *et al.* 2001; Williams *et al.* 2001). Inherent to the success of these fish passage facilities is properly timed flow releases that either promote attraction to entrances or move fish to areas known to support high survival. Issues pertaining to the lateral and vertical dimensions are not as well studied but recent efforts have focused on replacing important components of the hydrograph (Poff *et al.* 1997). The 'natural flow' method of water releases will be discussed further in section 5.3.

3.3. Change in Flow → Stranding of Fish

Stranding is considered the separation of an aquatic organism from flowing surface water due the decline in river discharge. This section deals only with stranding as it relates to fish species although stranding can also occur with other species such as benthic invertebrates (see section 3.7). Stranding can result in beaching, when fish are completely out of the water, or trapping, when fish are isolated in small pockets of water completely separate from the flowing river (Hunter 1992). Rate and range of change and duration; time of day (light); season and/or temperature; fish species, life stage (size) and behaviour; and the morphology and substrate character of the stream appear to be the most influential factors determining the potential for stranding (Steele and Smokorowski

2000; Halleraker *et al.* 2003). While season is listed as an important factor determining the potential for stranding, it is important to note most studies have been conducted during the open water season and there is a general lack of knowledge for under ice conditions (Scruton *et al.* 2005). Flow fluctuations associated with hydro production result in reduction of shallow water habitat on river margins, habitat required by many riverine species, as well as dewatering and/or scouring of spawning areas during the incubation period. Hydropeaking is the mode of hydroelectric generation that most dramatically alters quantity and quality of habitat available to fish and resulting effects can be direct (e.g., stranding, mortality or habitat abandonment) or indirect (e.g., downstream displacement, volitional movement, depleted food production, increased physiological stress; Moog 1993; Valentin *et al.* 1996; Bradford 1997).

3.3.1. Fish Species/Size

Most of the available literature on stranding effects from hydroelectric operations has been for salmonids, particularly for *Oncorhynchus* species, including Chinook, chum and pink salmon, steelhead trout, and *Salmo* species, Atlantic salmon and brown trout. Most of the differences between species in potential for stranding have been attributed to habitat preferences, selection and behaviour, and spatial and temporal variability in these attributes, and these aspects are described in more detail in the ensuing sections. For example, Chinook salmon are not as vulnerable to hydropeaking operations as are chum and pink salmon because they tend to use deeper spawning habitats which are less likely to become dewatered by low (minimum) flow conditions (Connor and Pflug 2004). Atlantic salmon juveniles, in comparison to brown trout, demonstrated more pronounced seasonal and diurnal variation in their susceptibility to stranding in response to rapid flow changes on a Norwegian river (Saltveit *et al.* 2001).

Juvenile salmonids have been demonstrated to be more vulnerable to stranding than older age classes as they tend to inhabit the slower water areas along the river margins; areas that are first to be dewatered by rapid flow decreases (citations in Hunter 1992). Berland *et al.* (2004) observed that large Atlantic salmon parr were readily able to avoid stranding during both day and night flow manipulations. Newly emerged salmon fry, however, are extremely susceptible to stranding as they use the shallow, slow river margins after emerging from the redd environment (Bradford 1997). Adult salmonids typically inhabit the deeper and faster areas in the river channel, as well as larger deeper pools, and these areas are less likely to be dewatered during rapid decreases in discharge. Additionally adults are less associated with the substrate and interstices, are stronger swimmers, and are better able to sense and react to changing discharge conditions. Nonetheless stranding of adult salmonids as a result of flow fluctuations related to hydro production has been documented (citations in Hunter 1992).

3.3.2. Fish Behaviour

It has been demonstrated that the potential for fish to become stranded can be strongly tied to behaviour and social hierarchy (Shirvell 1994; Berland *et al.* 2004). Dominant and sub-dominant fish react differentially to flow changes, with less dominant fish responding

more readily than dominant fish that hold territories (Mäki-Petäys *et al.* 1997). This mobility may make them less susceptible to becoming stranded by hydropeaking operations. In an experimental hydropeaking study in Newfoundland, juvenile Atlantic salmon demonstrated two distinct movement patterns in response to flow change; one pattern being strong site fidelity and the second extensive movement, suggesting a possible dominance based behavioural component to observed responses (Scruton *et al.* 2002a, 2003, 2005). Under changing flows, fish experience confinement and discomfort related to inter- and intra-specific competition and potential exposure to predators, and fish will react to this stress by abandoning their station/territory and moving to find more preferred habitat conditions. Bradford (1997), for example, observed that juvenile salmonids in side channels were sensitive to flow changes and emerged from cover moving towards faster flows in the main channel as flows decreased.

A number of juvenile salmonids demonstrate a marked shift in behaviour between summer and winter, and this behavioural shift is considered an adaptation to avoid predation, minimize energy expenditure and avoid harsh environmental conditions (Cunjak *et al.* 1998; Valdimarsson and Metcalf 1998; Hiscock *et al.* 2002). In an experimental hydropeaking study in Newfoundland, differences in movement by juvenile Atlantic salmon between summer and winter suggested fish were sheltering more in the substrate in winter and were therefore not as exposed to flow conditions as in summer, when they would be more actively foraging (Scruton *et al.* 2005). The authors cautioned that while this winter behaviour of sheltering in the substrate may reduce energetic costs associated with hydropeaking related flow changes, it may increase the potential for fish to become trapped and/or stranded during flow reductions. This may particularly be a concern in habitats that are subject to dynamic ice formation and anchor ice production, such as higher gradient, coarse substrate reaches (Stickler *et al.* 2007).

3.3.3. River Morphology/Substrate

Stream morphology and substrate may be the most important considerations in determining propensity of fish to move during hydropeaking operations and hence influencing susceptibility to stranding (Debowksi and Beall 1995; Flodmark *et al.* 2002). Physically and hydraulically complex stream reaches afford better hydraulic and behavioural shelters (refugia) during both low and high flow conditions. Simple stream reaches more commonly experience incremental losses of preferred microhabitats with changing flow, until a threshold is reached and fish passively (through displacement) or actively abandon the reach (Pearson *et al.* 1992; Valentin *et al.* 1996).

Certain types of river morphology and substrate can have a large influence on the incidence of stranding, as a river reach with side channels, deep pools, low gradient gravel bars, or with significant braiding will have a greater potential for stranding than a simple river reach with a single, uniform channel (Hunter 1992). Long side channels, often with intermittent flows, have been shown to be notorious for trapping fish during flow declines as these are valuable rearing habitats for older juvenile salmonids (citations in Hunter 1992). Deep pools or potholes are formed in a river due to scouring during high flow events and are often used by older juveniles as rearing areas and refugia from

environmental conditions (e.g., high velocities or water temperatures), predators and/or competitors. Fish can become trapped in these potholes, which can retain water for hours to months, depending on the character of the pothole and river stage. One study reported that the threat of stranding related mortality was variable between potholes, with the incidence of stranding being unrelated to ramping rate and inversely related to the water depth above the pothole before flow decrease (Beck Associates 1989 as cited in Hunter 1992).

Most documented incidences of stranding of juvenile Pacific salmonids have been for fry on gravel and cobble substrates (citations in Hunter 1992). Monk (1989), in laboratory studies, determined that Chinook salmon and steelhead fry positioned over cobble substrates held station and as flow declined, became trapped in pockets of water between cobbles. Finally, as beaching became imminent they moved into the interstices where they were trapped. Conversely, fry over gravel substrates were more mobile, often in schools, and as flow declined they retreated with the water margin. Juvenile rainbow trout and Pacific salmon species were observed to be stranded on a British Columbia river, with most fish found in the interstitial spaces of the substrate not visible from the surface (unpublished data as reported in Bradford *et al.* 1995). Salmon fry have been shown to become beached on low gradient gravel bars during hydropeaking, with the incidence of beaching occurring on bars with less than 4 - 5% slopes (citations in Hunter 1992). In a Norwegian study, in which the river substratum was predominantly cobble with little interstitial space as refugia from increased velocities, juvenile salmonids held position until their dorsal fin was exposed before moving with the waters edge during receding and increasing flow (Harby *et al.* 2001, Saltveit *et al.* 2001). Several authors have concluded that the relationship of stranding and substrate was related to behaviour, station holding versus schooling, and the directionality of flow during decreases; i.e., over cobbles the water drained into the substrate while over gravels more water flowed off on the surface.

River morphology will also greatly influence the distance downstream of a dam that will be affected by flow change and the time lag for that effect to be realized. Pool and side channels have the capacity to store water which attenuates flow change. Tributaries augment flows with the ability to attenuate flow decreases, ramping rate, and ramping range (Hunter 1992). Large lakes and standing water bodies play a large role in attenuating flow changes, both natural and man made. As well there can be a lag time, the time it takes for a fluctuation to move from one location to another on the river, which is influenced by channel configuration, gradient, discharge, etc. Thus, the maximum change in river stage and resulting impacts may not necessarily occur in the reach immediately below the site of discharge, but can occur some distance downstream.

3.3.4. Rate and Range of Flow Change/Attenuation

Several studies have demonstrated that the rate and range of flow change, the flow conditions prior to the change, the frequency of flow change, and the duration of the flow conditions can all influence the potential for stranding and this has been demonstrated under both operational and experimental conditions. Many studies have concluded that

the ramping rate, or the rate of decline in river discharge and/or river stage, is one of the most important determinants of the propensity for stranding with high ramping rates associated larger numbers of fish being stranded. The ramping 'range', or the difference between the high and low flow limits associated with hydropeaking, also affects the incidence of stranding as this influences the total area of exposed gravel bars, and the number of side channels and pools that become isolated from the main channel flow (citations in Hunter 1992). Several studies have suggested that the stability of the flow regime can influence stranding with a stable flow environment prior to the flow change resulting in an increased incidence of stranding of fry (Phiney 1974, as cited in Hunter 1992).

Saltveit *et al.* (2001) reported stranded juvenile Atlantic salmon and brown trout on river banks after rapid flow reductions. Low densities of juvenile Atlantic salmon in Norwegian rivers below power stations have been assumed to be the consequence of sudden flow reductions (Saltveit 1990). The rate of stranding of juvenile Chinook and coho salmon in side channel habitats on a British Columbia river was related to the rate of flow decrease, and for coho salmon, more fish were trapped at night than during the day. Considerable numbers of juvenile salmonids were trapped in isolated pockets as flows declined, even at relatively slow rates of change (Higgins and Bradford 1996). The rate of change influenced the number of fish becoming trapped in the side channels, with more fish being trapped during rapid ramping (Bradford 1997). Even under slow ramping rates, and under natural flow changes, a significant proportion of fry may become entrapped in side channels. Survival of salmon embryos in side channels probably improves under a regime of higher sustained baseflows as this would improve the lateral hydraulic connectivity between side channels and the main channel (Connor and Pflug 2004).

The effect of ramping rate is attenuated with distance downstream from the flow fluctuation source and river characteristics greatly influence this attenuation. Impacts of flow fluctuations are typically greatest in the reach immediately below the facility and decline with distance downstream (Kinsolving and Bain 1993), although this can depend on river morphology and gradient. Consequently stranding rates have also declined downstream due to flow attenuation and increasing influence of tributary stream inputs with natural flow conditions (Connor and Pflug 2004).

3.3.5. Temporal/Seasonal Influences

Season and time of day has been demonstrated to influence the propensity for fish to respond to flow change and the potential for stranding, and this is linked to fish behaviour and habitat selection (Cushman 1985; Hunter 1992). Atlantic salmon parr, for example, demonstrate marked seasonal changes in habitat use. As temperatures decline in the fall more fish shelter in the interstices of coarse substrates and in winter this behaviour is more pronounced in winter with fish sheltering in substrate during the day and becoming active at night (Cunjak 1996; Heggenes *et al.* 1999). A higher frequency of stranding in relation to hydropeaking was reported for juvenile Atlantic salmon and brown trout at low temperatures (< 4 °C) during winter than at higher temperatures (> 9 °C) during summer and fall (Saltveit *et al.* 2001). In an experimental study Bradford (1997) noted that

temperature influenced stranding as 6 fold more juvenile Chinook salmon were stranded on a gravel bar at 6 °C as compared to 12 °C, regardless of the rate of flow change (ramping). Bradford (1997) suggested a strong seasonal component to susceptibility to stranding of juvenile Pacific salmon on gravel bars related to a tendency for greater use of substrate and interstices in winter.

Several studies have demonstrated that the time of day of the flow change event is important with higher rates of stranding reported for salmonids during daylight hours while concealed in the substrate (Woodin 1984 as cited in Hunter 1992; Saltveit *et al.* 2001; Bradford *et al.* 1995). Connor and Pflug (2004) found that salmon fry stranding rates were seven to eight fold greater during the day as opposed to night at all ramping rates tested on the Skagit River, Washington. Brown trout fry and Atlantic salmon parr demonstrated a tendency for more fish to be stranded during the day than at night in winter with the reverse trend in summer/fall (Saltveit *et al.* 2001). Hvidsten (1985) observed Atlantic salmon parr to become stranded during daytime flow decreases on a Norwegian River and this was attributed to concealment in the cobble substrate during daytime.

3.3.6. Mortality

Direct mortality has been reported as a result of rapid changes in flow, an effect attributed primarily to stranding and beaching (Hunter 1992). Extended periods of trapping in isolated pools can lead to death by asphyxiation, elevated temperatures, starvation, increased predation, and freezing (Cushman 1985). Alternatively, fish and ova can be subject to mortality as a result of flow increases leading to scour and movement of substrate (Stober *et al.* 1982; Pflug and Mobernd 1989). It is also important to note that trapping of fish in the interstices, and resulting mortality, can result in underestimation of mortality associated with hydropeaking as fish are not readily observed (Steele and Smokorowski 2000).

Stober *et al.* (1982) and Pflug and Mobernd (1989) (cited in Connor and Pflug 2004) found that there was high mortality of salmon eggs, alevins, including periodically high levels of fry stranding on gravel bars and in potholes in association with a hydropeaking operations on the Skagit River, Washington. Scruton *et al.* (2005) noted anecdotal evidence of beaching, leading to mortality, and trapping in small pools of juvenile Atlantic salmon in an experimental hydropeaking study in Newfoundland. Mortalities of juvenile Atlantic salmon and brown trout were also noted in a Norwegian river subject to hydropeaking (Hvidsten 1985; Saltveit 1990). Fish trapped in side channels or pools during flow change may be subject to high mortalities, depending on the nature of the hydroelectric operating regime. In regimes where the pools remain isolated for considerable lengths of time, refugia may dry out or become too warm leading to mortalities and increased exposure to predators. In rivers subject to daily hydropeaking, isolated pools will be consistently reconnected to the main river channel thereby reducing mortality risk.

Rochester *et al.* (1984, cited in Hunter 1992) noted that flow increases associated with hydropeaking can result in gravel scour which can kill eggs or alevins in the substrate.

Seiler *et al.* (2001) (cited in Connor and Pflug 2004), suggest that high levels of egg and fry mortality on the Skagit River may be caused by widespread gravel scour caused by peak flow conditions from power plant operations.

3.3.7. Mitigation of Stranding of Fishes

Several studies have made recommendations as to possible ways of mitigating the effects of hydropeaking power production and stranding and a few (e.g. Connor and Pflug 2004) have reported on the effectiveness of mitigations. Some of the recommendations have included reducing peak flows during spawning and increasing minimum flows during incubation, thereby reducing the differences between spawning and incubation flows, only permitting down-ramping at night, and limiting the rate and amplitude of flow change. Unfortunately, few long term studies have been conducted before and after flow management changes directed at reducing stranding and the potential for stranding is very context and species dependant and no one management scenario will fit every situation.

Conner and Pflug (2004) have reported on one long term study that was conducted to evaluate the effects of flow management changes on the stranding of incubation habitats and fry with respect to Pacific salmonids. Significant changes in flow management were implemented in relation to power production on the Skagit River, Washington. This river had a long term dataset on spawner abundance thus allowing for a before-after comparison of the two flow regimes. After the new flow management regime was initiated on the Skagit River significant increases in spawner abundances were observed for the managed reach (Conner and Pflug 2004). These increases were also higher than any observed in nearby rivers providing strong evidence that the new flow management regime was the causative factor.

3.4. Change in Flow → Change in Fish Bioenergetics

3.4.1. Bioenergetics Overview

The bioenergetics of organisms can be described as a simple mass balance between consumption of energy via intake of food, and the output of energy into various metabolic functions (egestion, excretion, respiration, specific dynamic action), growth, and reproduction (Kitchell *et al.* 1977). All metabolic functions are governed by temperature, and the rate of respiration is strongly influenced by the level of activity of the organism, which in the case of fish, includes swimming to either maintain position, feed, or relocate. A decrease in energy consumption or an increase in metabolic costs via a change in temperature or increased activity cost will ultimately have negative effect on the energy available for growth and reproduction. Therefore, any change in the environment that has the potential to affect these functions will have consequences to the fitness of the individual and can influence population health.

The potential bioenergetic impacts of any flow modification will be largely determined by the size and scale of the river system and the scope of the alteration, river

geomorphology, habitats and their distributions. Generally, small streams respond more quickly and extremely to hydrological events and flow modifications than larger rivers and consequently species inhabiting smaller dynamic systems are often considered more resilient to environmental changes (Mathews and Stiron 1981; Gordon et al 1992). Similarly, the timing of the flow changes in relation to the life history of the affected fish species will be an important determinant of any bioenergetic consequences. Overall, the relationship between altered flow and bioenergetics is extremely complex.

3.4.2. Metabolism/Swimming

The total metabolic expenditure for a fish consists of both standard metabolic rate and increased metabolic rate related to activity (swimming). Standard metabolic rate is primarily determined by temperature and fish size, while increased metabolism due to swimming is less sensitive to temperature and related to fish size and swimming speed, which in turn is primarily determined by water velocity and flow conditions (Beamish 1980).

Geist et al. (2005) examined the response of juvenile white sturgeon (*Acipenser transmontanus*) to artificial fluctuating flows on the Snake River, Idaho below a power plant. Using laboratory respirometry studies, coupled to field studies using electromyogram telemetry, they determined that distance moved and area used was similar under all flows, but the swim speed and oxygen consumption was lower at lower discharges. Higher flows, even of short duration, restricted the movement of juvenile sturgeon; however they did not result in an increase in energy expenditure, possibly due to behavioural and morphological adaptations.

Rincon and Lobon-Cervia (1993) determined that metabolic costs for stream dwelling brown trout holding feeding stations were primarily determined by swimming costs, which in turn was primarily determined by water velocity and temperature. They also found that energetic costs at feeding stations varied widely through the year according to a pattern determined by swimming costs. Adult sockeye salmon were shown to adapt their swimming strategy depending on mean current speed of the site, opting to minimize energy expenditure in low or moderate current speeds by finding low current speed pathways, but bursting through sites with high velocity to expedite passage (Stenden et al. 2004).

Upstream migration to spawning grounds is very energetically taxing and many salmon species, both Atlantic and Pacific, do not feed during migration, relying on stored energy reserves (Brett 1995). Environmental extremes such as high water temperature or high discharge can greatly increase metabolic demands further reducing energy reserves with a number of consequences including fish not reaching preferred spawning grounds, increased river mortality due to exhaustion and predations, and poorer gonadal production. Rand et al. (2006) have clearly linked the ability of Fraser River sockeye salmon to migrate and reach preferred spawning habitats (Stuart River) to the hydrological conditions they encounter during migration. Furthermore, they have identified

some critical reaches whereby high and variable flow can greatly increase swimming effort and may critically deplete energy reserves (Rand and Hinch 1998).

Murchie and Smokorowski (2004), using electromyogram telemetry, determined that the relative activity level of brook trout and walleye mimicked the flow patterns in an Ontario river under a peaking flow regime, with peak activity corresponding to peaks in flow. They concluded that this hyperactivity could be a result of moving to seek refugia, increased swimming to hold position, or possibly increased feeding activity due to increased levels of drift at high flows. There was also some indication of increased activity at low flows, possibly linked to the need to avoid habitat loss or the opportunity, due to the lack of velocity barriers, to exploit other habitats.

3.4.3. Feeding and Holding Station

For drift feeding salmonids habitat and food availability are integrally linked with stream flow, and position choice in the water column is often a tradeoff between energy expended holding position versus the potential energy gain from access to food items. Any modification to flow, whether it be natural or human-induced, that will alter that dynamic by increasing the cost of position choice (e.g. flow augmentation) or reduction in drift (e.g. flow reductions) may have a significant effect on the metabolism of that fish. Fish persisting in highly variable systems, such as rivers affected by hydropeaking, may also experience highly variable growth rates. Initially, during the peaking part of the regime, fish may be flushed from their habitats causing them to exert energy to maintain position and/or avoid flushing. Fish will then have to expend additional energy to re-invade the habitat they abandoned and this process will continue as a constant source of increased metabolic cost. The frequency and rate of flow changes can be significantly greater in a river impacted by a hydropeaking facility relative to natural changes.

High flow velocities typically result in a higher supply of drifting food resources (Fausch 1984) but the ability of fish to exploit these resources may be reduced (Hughes and Dill 1990; Nislow et al. 1998). In an experimental flume, consumption of drifting food by a rheophilic cyprinid decreased to zero above a size-dependent critical velocity, and swimming costs increased with water velocity, declining with body weight (Flore and Keckeis 1998). For many species, holding position (station) against flow requires continual expenditure of energy through sustained swimming (Hill and Grosman 1993). Juvenile salmonids also expend energy during a variety of locomotory activities, including foraging and competitive interactions which can involve the use of burst swimming and swimming in turbulent flow conditions, all which may use up anaerobic energy reserves (Kemp et al. 2006; Enders et al. 2003). Highly territorial salmonids such as juvenile Atlantic salmon hold station and establish territories to maximize profitability under one flow condition, and as flows change, these positions become less profitable with likely energetic consequences (Armstrong et al. 1998). Energy expenditure while foraging can be reduced by restricting the distance traveled to reach prey, however even short travel distances can be costly at high velocities (Metcalf et al. 1986). The relationship between

flow velocity and foraging energetics is complex and greatly influences profitability of feeding and growth (Nislow et al. 2004).

3.4.4. Growth and Feeding

The effect of river regulation on fish feeding and growth is a complex interaction of flow, temperature, food availability and resulting effects on fish metabolism. Arndt et al. (2002) examined the effect of floods on growth and feeding of juvenile Atlantic salmon and found the average feeding rates were affected by flow. Natural floods caused short term reductions in growth rates of salmonids, but after the flood peak growth rates recovered, suggesting that juvenile salmon were fairly resistant to floods of magnitude that occur naturally. Letcher and Terrick (1998) found an increase in body size and decreased abundance of age-0 Atlantic salmon following a massive flood in a New England stream. Generally, floods, or flow modifications that significantly increase flows, reduce the growth rates in fish largely through increased activity costs rather than reduction in feeding rate (Arndt et al. 2002). Increased flow can also reduce efficiency in feeding for sight and drift feeders as flow increases are often coupled to increased turbidity and suspended debris which makes it more difficult to detect prey (e.g. Robertson et al. 2007).

Harvey et al. (2006) manipulated flow in an experimental stream to study the effects of reduced summer flows on growth and survival of rainbow trout. Growth was reduced 8.5 fold in the flow reduced sections, as compared to natural controls, while overall survival was unaffected. Growth effects were partially attributed to differences in drifting invertebrates. Lower stream flows can reduce foraging opportunities for drift feeding salmonids (Nislow et al. 2004). Obviously flow rates can have a major influence on the entry of benthic invertebrates into drift and the distance traveled therefore the availability of prey is directly linked to flow velocity (Poff and Ward 1991). Similarly invertebrates may be flushed or removed from the affected reaches, either through catastrophic drift, or over time as their food resources (e.g. periphyton, particulate organic matter, macrophytes) are reduced (Moog 1993). During the low flow part of the cycle (water storage), heating of the water channel may increase oxygen demand and metabolic rates. Food resources (benthos, etc.) may be further reduced due to desiccation.

Regulation may alter the temperature regime, possibly extending periods of preferred temperatures for feeding and growth. Both increased summer flows and improved temperature regime can offset negative effect of variable flows, resulting in average or possibly increased growth. Jensen (2003) reported for the Norwegian River Alta that only minor changes in Atlantic salmon parr growth rates were attributable to river regulation although growth rates initially decreased in early summer but increased correspondingly later in the season.

Paragamian and Wiley (1987) looked at growth of smallmouth bass (*Micropterus dolomieu*) on a Iowa river in relation to stream flow and concluded that growth of juvenile bass was tied to stream flow, and more directly to drift (and its relation to discharge), while growth of older bass, owing to a more varied diet and larger energy reserves, was

less influenced by discharge variations. Deegan et al. (1999), in a 10 year study, related variability in the growth of Arctic grayling to variability in annual flow rates and other parameters.

3.4.5. Behaviour

Kemp et al. (2006) examined the growth and performance of juvenile Atlantic salmon in relation to varying discharge in an experimental stream and found the activity and area used were highest at the lower discharge, consistent with behavioural adjustments to reduce energy costs at high discharge. Despite these behavioural modifications to reduce energy expenditure, the energetic costs of foraging at high discharge caused a substantial reduction in growth. Increased small scale movements as a consequence of flow fluctuation can lead to increased incidents of antagonistic behaviours, with associated energetic costs (Sloman et al. 2001). In a study in Newfoundland juvenile Atlantic salmon demonstrated behavioural modifications to flow increases, demonstrating high site fidelity and exploitation of refuges in interstitial spaces, (Scruton et al. 2002b; 2005).

Sotiropoulos et al. (2006) studied the effect of low summer discharge on feeding, habitat use, and behaviour of age-1 brook trout and found the fish adopted a habitat use strategy of minimizing predation risks and energy costs rather than maximizing forage gain, explaining the low summer growth under these conditions. This type of behavioural response could also limit growth under low flow modified discharge conditions. Gries and Juanes (1998) have reported salmonids to abandon summer foraging under low flow conditions leading to zero or negative growth.

Lake sturgeon responded positively to a change in operating characteristics of a hydro facility, specifically from a hydropeaking to a run-of-river mode. An increased number of heavier sturgeon were in reproductive readiness and spent less time at spawning sites, increasing egg production and lowering energy expenditure (Auer 1996). Lake sturgeon migrate to optimize reproductive success and spend as little time on spawning grounds as necessary where there is little food and protective cover. Sturgeon appeared to be able to detect and exploit areas where bottom velocities remained low and relatively constant across a range of flows (Chandler et al 2001 as reported in Geist et al. 2005). Khoroshko (1972) observed spawning lake sturgeon females have their eggs lose capacity for fertilization after remaining below the Volgograd power station in Russia for an extended length of time during the spawning period.

3.4.6. Competition and Behaviour

Competition among juvenile salmonids has been shown to influence the propensity to move from preferred habitats in response to hydropeaking, and this is in part related to species, size and resulting social hierarchy (Shirvell 1994). Dominant and sub-dominant fish may react differentially to flow changes, with less dominant fish responding more readily than dominant fish that hold territories (Mäki-Petays et al. 1999). Mobile sub-

dominants may be more profitable under long term hydropeaking conditions as there may be a selective advantage for individuals with a mobile habitat selection strategy (Hutchings 1986). Kemp et al. (2003) found that only a fraction of juvenile Atlantic salmon parr redistribute themselves in response to changes in discharge, suggesting parr showed a high degree of site fidelity under both stable and fluctuating flows (e.g., Huntingford et al. 1998; Armstrong et al. 1998). This was in part related to social hierarchy as sub-dominant fish showed stronger site attachment in the presence of competitors, in contrast to the observations of Mäki-Petäys et al. (1999). Regardless, site fidelity could increase the possibility of stranding during hydropeaking power production (Halleraker et al. 2003). In a Newfoundland study of response of juvenile Atlantic salmon to flow changes simulating hydropeaking operations, fish demonstrated two distinct movement patterns. One group demonstrated strong site fidelity while the second group moved considerably, suggesting a possible dominance based behavioural component to the observed responses (Scruton 2002a and b; Scruton et al. 2003).

3.4.7. Morphological and Behavioural Adaptations

Some fish species are better adapted to coping with flow variability; for example, benthic species use morphological and behavioural adaptations to utilize higher or more variable velocity habitats with less energy consumption (Facey and Grossman 1992). Atlantic salmon parr hold station in the current by using enlarged pectoral fins, acting as hydrofoils, to cling to the substrate and generate negative lift as water flows over them, allowing them to avoid swimming while maintaining position adjacent to fast currents (Arnold et al. 1991). Atlantic salmon parr are also less buoyant and have greater swimming ability than other salmonids, allowing them more efficient access to food resources in drift (Sosiak 1982; Peake et al. 1997).

Facey and Grossman (1992) examined the relationship between microhabitat use and energetic costs in relation to water velocity for rainbow trout (*Oncorhynchus mykiss*), rosyside dace (*Clinostomus funduloides*), longnose dace (*Rhinichthys cataractae*), and mottled sculpin (*Cottus bairdii*). Rainbow trout and rosyside dace occupied water column microhabitats and demonstrated the typical energetic cost hypotheses whereby habitat selection is determined by energetic cost and is often a tradeoff between swimming effort and food availability. Conversely the mottled sculpin and longnose dace, two benthic species, used behavioural and morphological adaptations to hold position over increasing water velocities without incurring any significant increase in metabolic demand.

3.4.8. Interactions with Habitat

Substrate provides a number of habitat requirements for stream fishes including velocity refuges. Under changing flows, fish can experience confinement and discomfort, thus substrate characteristics will be important in determining propensity of fish to move (Debowski and Beall 1995; Flodmark et al. 2002). Simple stream reaches experience incremental loss of preferred microhabitats with changing flow, until a threshold is reached and fish passively (through displacement) or actively abandon the reach (Harby et al. 2001; Saltveit et al. 2001). Physically and hydraulically complex stream reaches on

the other hand provide better hydraulic and behavioural shelters during both low and high flow conditions (Pearson et al. 1992; Valentin et al. 1996; Scruton et al. 2003). Changing flows and water levels during hydroelectric production can force fish into sub-optimal habitats where excessive energy can be expended to hold station, forage, compete for mates, or generally compete for other life history requisites (Cushman 1985; Hunter 1992; Steele and Smokorowski 2000).

3.4.9. Seasonal Effects

Many fish species show marked seasonal changes in habitat use, and shifts in behaviour may be adaptations to avoid predation, minimize energy expenditure and avoid harsh environmental conditions (Cunjak et al. 1998; Valdimarsson and Metcalf 1998). Fish maximize energy intake during the growing season to maintain lipid reserves to survive winter; flow-induced activity in winter may be costly in consumption of stored reserves (Cunjak and Power 1987; Cunjak 1988; Cunjak 1996; Valdimarsson and Metcalfe 1998; Metcalfe et al. 1999; Hiscock et al. 2002). Generally, the late summer can be a period of low food availability as it is past the peak in spring aquatic insect emergence and these conditions can be exacerbated by low discharge further reducing the rates of prey flux for drift feeders (Fausch 1984).

In a Newfoundland study of the seasonal movement of juvenile Atlantic salmon, during winter, fish sheltered more in the substrate and were not as exposed to ambient flow conditions as in summer when they would be more actively foraging (Scruton et al. 2005). While this winter behaviour of sheltering in the substrate may reduce energetic costs associated with flow changes, it may increase the potential for fish to become trapped and/or stranded during flow reductions and/or frazil and anchor ice formation (Cunjak 1996; Heggenes et al. 1999; Stickler and Alfredsen 2005).

A number of studies have examined the seasonal differences in habitat use in terms of 'home range' and larger home ranges have been reported for juvenile Atlantic salmon in summer than in winter (Berland et al. 2004; Scruton et al. 2005). These results suggest that in summer, flow alterations could potentially be energetically costly as greater movement under variable flow regimes could affect growth, production and survival. This may be even more important in winter as fish are less active, conserving energy, and stored energy reserves from summer may be critical in determining over-winter survival.

Juvenile striped bass have been shown to be flexible in their behaviour depending on the necessity to actively swim at winter temperatures (Hurst and Conover 2001). When the energetic costs of swimming increased with velocity, fish increased food consumption to meet their metabolic needs so long as sufficient food was available. The laboratory experiments of Hurst and Conover (2001) also demonstrated that swimming speed increased with increasing temperature, thus in winter, physical or behavioural refuges would be required to minimize energy expenditure and maintain position in a river environment where velocities would exceed swimming ability in cold temperatures.

3.4.10. Stressors

Rapid and intermittently fluctuating water levels can act as an acute stressor in fish (Einarsdóttir and Nilssen 1996; Flodmark et al. 2002). Flodmark et al. (2002, 2006) have suggested that long periods of daily fluctuating flow are unlikely to reduce growth or cause a higher incidence of disease related to stress, and suggested that stream salmonids, in the absence of stranding, can rapidly habituate to these conditions.

3.5. Change in Flow → Change in Water Temperature

3.5.1. Temperature Overview

In lotic systems, water temperature is proportional to the heat load divided by the discharge, thus altering either variable will affect temperature (Hockey *et al.* 1982; Poole and Berman 2001). Other drivers of water temperature in riverine environments include climate, stream morphology, groundwater, and riparian canopy. The influence of a dam on water temperature depends on a number of factors including its scale or size, depth, purpose (flood control, irrigation, hydroelectricity production), position in the watershed (and relative to other dams), and operations (Webb 1995; Patera and Votruba 1996). The highly variable discharge resulting from hydropeaking can result in large daily temperature fluctuations due to changes in discharge (Tonello and Nuhfer 2004). Conversely, river regulation can reduce daily temperature fluctuations in streams due to steady release of water from a more thermally stable reservoir (Jaske and Geobel 1967; Smith 1972; Ward and Stanford 1979; Webb and Walling 1988b, 1993). Water temperature can be sensitive even to short-term fluctuations in discharge, so climate or energy demand induced annual variations in dam operations may result in significant inter-annual variability in thermal regimes (Webb and Walling 1996, 1997).

The location of the draw from a reservoir can significantly influence how discharge affects temperature, depending on the level of stratification of the reservoir, temperature differentials between levels, and how reservoir drawdown changes the effective location of the draw (Webb and Walling 1997). Hypolimnetic draws will generally reduce downstream temperatures in summer and delay the onset of warming (Edwards 1978; Edwards and Crisp 1982; Paller and Saul 1996; Preece and Jones 2002; Flodmark *et al.* 2004), and increase temperatures in winter (Ward and Collins 1974; Bolke and Waddell 1975; Pitchford and Visser 1975; Armitage 1984; Jensen 1987). Epilimnetic draw from the reservoir, or draws from shallow isothermal reservoirs, may result in little change in downstream regimes (Zhong and Power 1996; Beznosov and Suzdaleva 2001), or can increase summer maximum temperatures (Moore 1967; Lessard and Hayes 2003; Horne *et al.* 2004) depending on the location of the dam longitudinally along the river, potentially having a greater effect in the upper reaches (Palmer and O'Keefe 1989). Webb (1995) documented how one epilimnetic release dam resulted in increased mean temperatures, eliminated freezing, depressed summer maxima, delayed the annual cycle and reduced diurnal fluctuations relative to pre-dam conditions. The location of the draw may also affect how stratification progresses through the summer, for example when a hypolimnetic draw increases the depth of the epilimnion by pulling warmer water down, which may

eventually reach the level of discharge ports and effectively become an epilimnetic draw in an isothermal system (Ward and Stanford 1979; Mackie *et al.* 1983; Farquhar and Gutreuter 1989). A number of site-specific factors, including dam mechanistics and operational regime (storage, peaking), should be considered when evaluating the effect of flow on temperature.

3.5.1.1. Increased or steady flow

Increases in flow can have a variable effect on water temperature depending on the location of the draw and magnitude of the increase in discharge. In general, higher discharge extends the thermal conditions of the headwaters further downstream as the greater volume will be less responsive to atmospheric effects (Ward and Stanford 1979; Ward 1982) or to groundwater input (Webb 1995). In late summer an epilimnetic draw coupled with high discharge will increase temperatures downstream as the proportion of dam discharge relative to groundwater flow increases (Webb and Walling 1988a; 1997). A hypolimnetic draw can cool a river during summer, warm it during winter, but have no thermal effect during snowmelt when release water is similar to river water (Smith 1972; Baxter 1977; King and Tyler 1982; Byren and Davies 1989; C  r  ghino and Lavandier 1998b). The effects of a hypolimnetic draw can extend for over a hundred kilometres downstream, resulting in a temperature gradient as environmental factors such as solar radiation, groundwater, tributaries and radiant heat gradually warm the water further from the dam (Paller and Saul 1996).

High and stable flows can result in stable temperatures relative to low or fluctuating flows (Sinokrot and Gulliver 2000; Flodmark *et al.* 2004), not only reducing diurnal temperature fluctuations, but also delaying both spring warming and fall cooling (Crisp 1977; Edwards and Crisp 1982; Webb and Walling 1988a; 1993; 1996). Increased winter temperatures below reservoirs will also prevent the formation of ice cover, an effect shown to extend from 5 km (Webb and Walling 1993; 1996), to 9 km (Ward and Collins 1974), to at least 20 miles from the outlet (Lehmkuhl 1972). Irrigation reservoirs are generally operated to provide constant, augmented flow, which can cool summer water temperatures, increase winter temperatures and dampen seasonal patterns (Casado *et al.* 1989; Finlayson *et al.* 1994). Dams used for flood control and minimum summer flow augmentation can raise the summer minimum through the release of warm reservoir water (Collings 1973). Steady release from a shallow warm reservoir increased mean water temperatures and reduced diurnal temperature fluctuations by 80% below the dam, with effects extending as far as 22 km downstream (Fraleay 1979). Peaking hydroelectric operations operate to synchronize with electricity demand which normally means high discharge during the day. If coupled with a hypolimnetic draw, minimum diurnal temperatures often occur with peak daytime discharges (Ward and Stanford 1979).

3.5.1.2. Reduced or fluctuating flow

Reductions in flow affect water temperature by reducing the stream's assimilative capacity for heat (Gu *et al.* 1998; Poole and Berman 2001), potentially significantly elevating peak summer temperatures (Sinokrot and Gulliver 2000; Tonello and Nuhfer

2004) or reducing winter temperatures (Ward and Stanford 1987). Decreased discharge on the Columbia River due to hydroelectric development resulted in a warming of the lower river as much as 30 days earlier, higher peak temperatures, and a delay in fall cooling relative to historical records (Quinn *et al.* 1997). Reducing flow in the winter can result in lower than normal temperatures, increase the formation of anchor ice and thus bottom scouring (Ward and Stanford 1979). When flow is low and temperatures are high, hypolimnetic releases during peaking operations can cause rapid and large changes in downstream temperature multiple times per day (Ward and Stanford 1979). When flow is lower at night, which is typical with hydroelectric dams, water temperatures will be greater than during the day, which is opposite to the diurnal temperature fluctuations of an unregulated system (Flodmark *et al.* 2004).

3.5.2. Effects of Changing Water Temperature on Biota

Water temperature is perhaps one of the most significant variables influencing physiology, metabolism, susceptibility to disease, and life history traits of aquatic organisms (Forseth and Jonsson 1994; Jobling 1996; Sinokrot and Gulliver 2000; Bacon *et al.* 2005), and temperature influences many physiochemical properties of water (Smith 1972; Wetzel 1981). Fishes are well known to have wide ranging temperature preferences depending on the species (Scott and Crossman 1973), so temperature should be considered as one important aspect of fish habitat. Going beyond the optimum temperature range for a species in either direction can have negative consequences, although these can be much more critical when the upper lethal limit is reached, whereas dropping to 0 is usually not lethal (for salmonids) if fish remain free from ice (Elliott 1994). The relationship between water temperature and fish growth rates, for example, is usually asymmetric with the decrease to zero occurring more quickly above the optimum temperature than below (Elliott and Hurley 2003). Temperature was shown to be a significant determinant of year-class strength in river-dwelling cyprinids (Mills and Mann 1985). Temperature and flow are considered the two most important cues to trigger migration and spawning of a number of fish species (Heggberget 1988; Jonsson 1991; Hembre *et al.* 2001). Altering temperature can change community composition as thermal limits are reached, altering predation and competition dynamics (Smith 1972), and potentially facilitating establishment of invasive species (Dunham *et al.* 2002). The intention of this review is not to detail how temperature affects growth, metabolism, consumption or other physiological and life history characteristics of fishes, but to give an overview of how changing temperature due to dam operations has been shown to impact biota.

3.5.2.1. Temperature decreases

A decrease in water temperature due to a hypolimnetic discharge can reduce production of lower trophic levels including bacterioplankton and phytoplankton (Beznosov and Suzdaleva 2001), and intolerant macroinvertebrate taxa (Hilsenhoff 1971; Lehmkuhl 1972; Ward and Collins 1974; Ward and Stanford 1979; Saltveit *et al.* 1994; Camargo and Voelz 1998). The elimination of some taxa could in part be due to temperature moderation from a hypolimnetic release: warming in the winter and cooling in the summer resulted in failure of certain temperature controlled development stages, with the effect

sometimes evident over 100 km downstream from the dam (Lehmkuhl 1972). As well, warmer winter temperatures from a hypolimnetic discharge caused earlier insect emergence and increased mortality in the still-snowy terrestrial environment (Raddum 1985). Cold summer and warm winter conditions has resulted in a reduction in invertebrate diversity, yet overall density can increase with disproportionate increases by some species (Ward 1976; Boles 1981; Boon 1987; Rader and Ward 1988). Some taxa that are resilient to changes in temperature regimes (C  r  ghino and Lavandier 1998b), can thrive in the altered conditions if they are able to adapt (Briggs 1950; Spence and Hynes 1971; Brittain and Saltveit 1989), or recover quickly upon a return to normal thermal conditions (Marchant 1989). However, low diversity and high biomass of invertebrates are characteristic of a stressed ecosystem, and the altered temperature regime is implicated as being largely responsible (Ward and Collins 1974).

Hypolimnetic draws can lower temperatures enough to reduce survival of some warmwater fish species (Edwards 1978; Finlayson *et al.* 1994; Zhong and Power 1996), or fail to provide minimum temperatures for successful reproduction (Cadwallader 1978). Cold temperature exclusion of native fish species works in the favour of introduced species, but may then allow the initiation of a cool or coldwater fishery (King and Tyler 1982; Gippel and Finlayson 1993). Therefore, sometimes the change in temperature regime results in a desirable change which works towards fisheries management objectives. If policy objectives include the establishment of a cold or coolwater fishery, then cooling downstream temperatures from a mixed or bottom draw would be beneficial so long as temperatures are not below the optimum for even a cold water fish community. An extremely cold hypolimnetic draw can impair embryonic development (Marsh 1985), or reduce growth and transformation from the larval to the juvenile stage (Clarkson and Childs 2000). Susceptibility to cold-water diseases (and to warm-water disease if too warm), and thus survival, may be affected (Snieszko 1974). Lower feeding and evacuation rates at lower temperatures will result in a reduced energy budget and associated consequences (Salvatore *et al.* 1987). Augmentation of flows with colder water can reduce the total number of degree days for the year, which can negatively affect growth and year-class strength of some fish species (Grande and Andersen 1990; Cowx 2000). While cold water release and mitigation of summer minimum may favour salmonid populations, the negative effects of peaking flow can outweigh the benefits (Casado *et al.* 1989). On the other hand, in some cases the benefit of reducing diurnal temperature fluctuations can result in increased fish density despite cold temperatures limiting growth (Crisp *et al.* 1983). Winter warming below a hypolimnetic release dam could potentially extend the growth period for some fishes, and hybridization and adaptation can improve adjustment to altered thermal regimes (Ward and Stanford 1987), although hybridization may not be desirable from a management point of view.

Most case studies examining hypolimnetic release demonstrate a negative effect on fish populations. A decrease in water temperature below the Flaming Gorge Reservoir in the upper Colorado River significantly reduced stocked trout production from a maximum of 93 pounds per acre to an eventual net loss within 5 years (Mullan *et al.* 1976). Reduced growth of Atlantic salmon and brown trout due to cold hypolimnetic release caused fish to smoltify one year later than fish in the unregulated section of the river, leading to higher

stream mortality and reduced oceanic success (Saltveit 1990). Similarly, dam construction resulted in lower average water temperatures and a subsequent delay in the timing of fry emergence, growth to smolt size, smolt emigration, and increased the percentage of overwintering Chinook salmon (Connor *et al.* 2002). Reduced survival of Chinook salmon smolts was attributed to delayed migration, which resulted in migrating under conditions of low flows and high temperatures (Connor *et al.* 1998). Colder temperatures caused a delay in spawning by up to 60 days for some fish species below dams in China (Zhong and Power 1996), and a sudden change to hypolimnetic release caused a cyprinid to either cease spawning activity, or if already spawned, was the likely cause of some dead or deformed embryos (King *et al.* 1998). Paller and Saul (1996) found a direct relationship between gizzard shad spawning time and proximity to the dam, with spawning delayed up to four weeks closer to the dam. Immediately below the dam, temperatures remained unsuitable for spawning, potentially eliminating recruitment, with an impact detected over 190 km downstream (Paller and Saul 1996). Cold water effects have been reported to extend as far as 400 km from the dam (Holden and Stalnaker 1975).

At extremely high water velocities, fish can become displaced, limiting their ability to forage or hold station in the water column (Garner 1999; Tetzlaff *et al.* 2005). Critical holding velocities can be reduced at lower temperature (Rimmer *et al.* 1985; Graham *et al.* 1996), which would have implications for fishes below a dam operating at high discharge from a hypolimnetic draw. Using 10 years of discharge data, water temperature, and juvenile fish length, Tetzlaff *et al.* (2005) calculated the critical displacement velocity for Atlantic salmon and found that higher temperatures in the summer allowed fish to withstand higher discharges before displacement, whereas during winter, critical velocities were more variable.

An increase in anchor ice due to low discharge in winter can result in a decrease in suitable habitat for fish, particularly if the anchor ice accumulates in pools, necessitating their movement to less suitable habitat devoid of cover (Brown *et al.* 1993). Formation of surface ice can protect fish habitat from the development of anchor ice, but surface ice formation can be prevented below a reservoir releasing winter warm water (Lehmkuhl 1972). Turbulent water released from a dam at 4 C in the winter can quickly turn to frazil ice as it supercools downstream, which can cause direct mortality of fish through suffocation (Tack 1938 cited in Brown *et al.* 1993). In general however, little information was found on how flow-mitigated changes in temperature affect ice dynamics in rivers, and this topic warrants further exploration.

3.5.2.2. Temperature Increases

Increasing water temperature resulting from a surface release reservoir reduced the abundance of some mayfly species (Brittain and Saltveit 1989). Increased stream temperatures were shown to shift invertebrate communities to warmwater forms, cause earlier emergence and increase total abundance of invertebrates, but decrease diversity (Fraleigh 1979). While surface-release flows can contain large amounts of seston and detritus that can support high densities of collector-gatherer invertebrates, elevated

temperatures can depress the growth rate of some important mayfly species below a surface-release dam (Mundahl and Kraft 1988).

For fish, increasing water temperature will alter the thermal cues governing the timing of migration for migratory species, which can alter thermally driven life history traits (e.g. growth, reproduction, survival), change fish behaviour, and alter fish community composition. Earlier warming of the Columbia River coupled with reduced flows resulted in faster upriver migration and earlier arrival dates for sockeye salmon and American shad (Quinn and Adams 1996; Quinn *et al.* 1997). While it is difficult to separate the relative impacts of flow vs. temperature due to their high correlation, the greater stress due to higher temperatures may be somewhat offset by the lower energy requirement in the reduced flows (Quinn *et al.* 1997) or by finding thermal refugia (Berman and Quinn 1991; Torgersen *et al.* 1999). High water temperature did slow fall Chinook salmon and steelhead migrations on the Columbia River, two species more affected by temperature than discharge, as they sought refuge in coldwater tributaries, held position, or strayed during migration, as assessed through 12,000 PIT tagged fish (Keefer *et al.* 2004). Similarly, Salinger and Anderson (2006) documented decreased swim speeds and increased passage times through in-river structures for both Chinook salmon and steelhead trout as temperature increased. Elevated temperatures on the Willamette Falls and Snake River system can cause migration delay, increased incidence of disease, and potentially direct mortality of migrating salmon (Schreck *et al.* 1994; Dauble and Mueller 2000). Water temperatures greater than 21°C were shown to be a barrier to upstream migration of sockeye salmon, which can reduce survival or ultimate spawning success (Major and Mighell 1967). Streamflow and temperature are considered to act together to influence survival of Chinook salmon smolts, with lower survival at higher temperatures (Raymond 1988; Kjelson and Brandes 1989). Using 12 years of migration data from a Quebec river, Trépanier *et al.* (1996) demonstrated that landlocked Atlantic salmon showed little response to temperature change and initiated their upstream migration with a decrease in water flow and reduced current.

Significantly increased temperatures due to epilimnetic draw have been shown to reduce brook trout and brown trout densities and change macroinvertebrate community composition below the dam (Lessard and Hayes 2003). Increased temperatures resulting from reduced discharge were implicated as the cause of the lack of natural reproduction by brown trout below a dam in Michigan (Tonello and Nuhfer 2004). Using 10 years of hourly water temperature data, earlier brown trout emergence and increased growth were predicted to result from river regulation and warming of water temperatures (Webb and Walling 1993). Both timing and duration of smallmouth bass spawning was impacted directly by flow related temperature changes in the New River drainage basin in Virginia (Graham and Orth 1986). Decreased flows were associated with increasing temperature and initiation of spawning, whereas increased flow was associated with decreased temperatures and the cessation of spawning (Graham and Orth 1986).

3.5.2.3. Stable Temperature

Trout exposed to high and stable flows and temperature had a higher food intake and growth rate than those exposed to low and fluctuating flows (Webb and Walling 1988a; Flodmark *et al.* 2004). Conversely, reducing diurnal temperature fluctuations can negatively affect some species whose body processes require a wide daily temperature range for optimal energetic efficiency (Lehmkuhl 1972; Ward and Stanford 1979). Most biota inhabiting lotic environments are adapted to diurnal fluctuations in water temperature, which naturally occur on a 24 hour basis (Hubbs 1972) usually reaching a minimum in the early morning hours and a maximum in late afternoon (Caissie 2006). Diel temperature fluctuations can be significant, particularly on wide and shallow rivers with little groundwater input (Caissie 2006), and have been observed to range up to 6 degrees Celsius in some Canadian rivers (Smokorowski, pers. obs., Randall, pers. obs.). Artificially stabilizing temperatures could have a negative effect on organisms adapted to variable thermal environments (Sweeney 1978).

3.5.2.4. Fluctuating Temperature

The rapid and frequent changes in flow below a peaking hydroelectric dam are often accompanied by rapid fluctuations in water temperature (Cushman 1985). Sudden and large changes in temperature can cause thermal shock and a loss of equilibrium in the youngest life stages of fishes, which can increase mortality through involuntary drift (Clarkson and Childs 2000). Sudden temperature changes due to hypolimnetic peaking operations below the Hungry Horse dam on the Flathead River are of a magnitude considered highly stressful, if not lethal, to much of the zoobenthos and fish in the river, including organisms in the hyporheic zone (Stanford and Hauer 1992).

3.5.3. Mitigation of a Change in Temperature

Mitigation strategies for flow-induced temperature effects on rivers depend on the identified problem. Some reservoirs have destratification systems (e.g. air lift or bubbling systems) which are set to function when temperature differentials between surface and hypolimnetic waters reach a set threshold (Koberg and Ford 1965; Smith 1972). However, stratification can still occur despite operation of mixing systems (Webb and Walling 1997). As the only alternative to dam removal, suggested mitigation of coldwater release impacts on indigenous fishes in the Colorado River included warming of discharge (Clarkson and Childs 2000).

Adjusting the depth of release from the dam via multiple control structures could allow for temperature manipulation as needed (King *et al.* 1998), but require the installation of multiple release structures upon dam construction, or a dam retrofit (Smith 1972; Stanford and Hauer 1992; Horne *et al.* 2004). Blinn *et al.* (1989) described how a planned change from a cold hypolimnetic release to warmer subsurface water from the epilimnion (to improve habitat for a native chub species) would alter epiphytic diatom communities and therefore affect the invertebrate grazers. On the other hand, a change to a hypolimnetic release was predicted to increase steelhead recruitment by 59-129% in a river currently

subject to warm summer epilimnetic release (Horne *et al.* 2004). Hubbs (1972) advocated the use of adaptable outlets to allow for release of warmer (mostly epilimnetic) water during the day and colder (mostly hypolimnetic) water at night to simulate natural diurnal fluctuation, reducing the probability of thermal shock should a large temperature change occur due to changes in stratification relative to dam intakes. An \$80 million retrofit of a water storage dam in California allowed for adjustable release from multiple elevations which could be operated in a complex manner to meet discharge temperature targets set for Chinook salmon (Hanna *et al.* 1999). While the installation of a multi-level intake structure allowed mean temperatures and total degree days to return to near pre-dam condition at the Flaming Gorge Reservoir, the rate and timing of warming still differed, and invertebrate richness failed to increase as expected (Vinson 2001). It is important that attention be paid to the reservoir when operating multilevel discharge ports to the benefit of downstream temperatures, as their operation can exert an important influence on water quality and biological productivity in large stratified reservoirs (Stroud and Martin 1973).

Since most existing dams will not be equipped with multiple release structures, manipulating the timing of flow release could improve habitat conditions, subject to other potentially conflicting factors influencing dam operation (i.e., demand for hydroelectricity production). For example, a hypolimnetic discharge could be strategically manipulated to cool the river during seasonally hot periods, or could be increased at night to mimic night time cooling (Tonello and Nuhfer 2004). Introducing a minimum flow regime could mitigate against high summer temperature peaks that may result from lower water levels (Gu *et al.* 1998; Sinokrot and Gulliver 2000). Augmenting flow for Chinook salmon smolt migration increased survival through a combination of facilitating passage and lowering temperature, although again augmentation options can be limited by reservoir supply and conflicting demands (Connor *et al.* 1998).

3.6. Change in Flow → Change in Nutrient Concentrations

3.6.1. Nutrients Overview

Nutrients in this section refer not only to the nutrient elements that are important to aquatic ecosystems (carbon, nitrogen, phosphorus, and silicon), but also to organic matter (detritus) that is an important food source for aquatic invertebrates (Hynes 1970; Hynes 1975).

There is unequivocal evidence in the primary science literature that altered flow regimes will have a significant, usually negative, impact on nutrient dynamics and nutrient availability in fluvial systems, as detailed below. Longitudinal, lateral and vertical pathways are affected, by an interruption of the upstream-downstream transport of nutrients, and by a disconnect between the river channel and the river edge, the adjacent riparian zone and floodplains, and the hyporheic zone.

3.6.1.1. Longitudinal

River ecosystem characteristics vary longitudinally from the headwaters to the river mouth. The river continuum concept (RCC; Vannote *et al.* 1980) is a conceptual model of longitudinal variation in primary production. This concept is based on the assumption that geo-physical variables follow a continuous and integrated gradient from source to mouth. In temperate rivers, headwater streams are heavily influenced by riparian vegetation that provides large scale inputs of allochthonous nutrients. As stream size increases, allochthonous inputs become less important, and aquatic communities depend more on autochthonous processing of materials, some of which are imported from upstream. The RCC predicted energy flow in rivers of Oregon (Hawkins and Sedell 1981), the Oldman-South Saskatchewan River system (Culp and Davies 1982) and the Moisie River in Quebec (Sedell *et al.* 1989), but it was not a satisfactory model for the Amazon, where extensive floodplains modified the longitudinal patterns (Sedell *et al.* 1989). Primary productivity and energy processes in the floodplains were analogous to headwater reaches. Also, RCC may not apply to rivers with constricted channels, such as the upper Ohio (Thorp and DeLong 1994). Nevertheless, for temperate rivers, the RCC concept is an important reminder that unidirectional flow functionally links upstream processes with downstream communities (Ward and Stanford 1989).

Flow regulation, particularly impoundments, interrupts the river continuum. The Serial Discontinuity Concept (Ward and Stanford 1983) acknowledges the alteration in the macroinvertebrate community below dams, with the severity of the alteration (discontinuity) depending on the position of the dam along the longitudinal profile, and the distance upstream or downstream from the dam. Key variables such as temperature, substrate and species richness are measured in relation to distance downstream from the dam to evaluate reset or recovery. Changes in nutrient enrichment or depression associated with the reservoir is a key response variable that is measured (Stanford and Ward 2001; Vinson 2001). The discontinuity concept has merit as it has been shown to accurately predict the consequences of regulation (Stanford and Ward 2001).

The creation of reservoirs has a profound affect on biochemical cycles and nutrient transport from upstream to downstream reaches (Friedl and Wuest 2002). Sedimentation of organic particles, both allochthonous and autochthonous, occurs in the reservoirs, and nutrients are withdrawn from the lower river system as a consequence. Reservoirs can act as efficient sinks for phosphorus (Friedl and Wuest 2002) and silica (Conley *et al.* 1993; Conley *et al.* 2000), and to a lesser extent for nitrogen (Friedl and Wuest 2002). In oligotrophic systems, nutrient depletion might cause changes in the food web and thus create problems for fishes downstream of the impoundment. In Kootenay Lake, British Columbia, for example, phosphorous loadings decreased significantly after construction of dams on two of its tributaries (Ashley *et al.* 1999). Declines in phosphorous loading resulted in declines in phytoplankton and zooplankton production, and subsequently to catches in kokanee (landlocked sockeye salmon). The effect of nutrient withdrawal by reservoirs may be different in eutrophic or polluted rivers, where reductions in nutrient elements may be beneficial (Friedl and Wuest 2002). The loss of nutrients can be

spatially extensive, and significantly affect the productivity in receiving waters such as estuaries (Rosenberg *et al.* 1997) (see river mouths below).

Changes in nutrient concentrations below impoundments, however, depends on the depth of the released water. If tailwaters receive water from the hypolimnion, Wetzel (1981) predicted that C/N ratios can increase significantly. Consequently, fauna associated with high alkalinity water would be favoured (e.g., gastropods; Petts 1984a). Impacts of impoundments on nutrient distribution and dynamics are complex. Petts (1984a) summarized the impact of epilimnial versus hypolimnial releases: 'during summer, a stratified surface-release reservoir will discharge well-oxygenated, warm and nutrient-depleted, water whilst low-level outlets will produce relatively cold, oxygen-depleted and nutrient rich releases'. Further generalizations and details about the interaction of factors (depth of release, water temperature and chemistry, nutrients and seston export) and impacts to nutrient dynamics, invertebrate food supply and fishes in tailwaters are beyond the scope of this review. A comprehensive introduction to the quality of reservoir releases and impacts to downstream fauna are provided by Petts (1984a).

Dams obviously have a direct effect on fish migration (fish passage is discussed in a separate Pathway of Effect), but migration barriers also indirectly affect upstream nutrient transport. Migrating anadromous fishes transport nutrients with their bodies from the ocean into the river system. The natural fertilization from this process is a significant source of nutrients (Bilby *et al.* 1996; Larkin and Slaney 1997; Helfield and Naiman 2001). Blocking fish passage will lead to the oligotrophication of upstream reaches. Similarly, the transport of nutrients from downstream to upstream areas likely affects inland watersheds as well.

3.6.1.2. River Mouths

Changes to natural hydrological flows can have large scale and long term effects on downstream areas. River mouths, receiving embayments and estuaries are 'cradles of biological productivity' because of the delivery of nutrients to them by freshwater runoff (Ward and Stanford 1987; Rosenberg *et al.* 1997). Nearshore biological processes such as primary productivity and fish spawning, feeding, growth and migration are synchronized with the seasonal dynamics of flow, as is the case in the river proper. Altered flow regimes will impact on both the nutrients and food supply of fishes in receiving waters. In the Danube River for example, because of reductions in the riverine delivery of dissolved silicate in the riverine delivery, average silicate concentrations decreased significantly in the Black Sea, offshore of the Danube Delta, after hydroelectric dams were constructed. The resulting phytoplankton community and food chain shifts led to a decline in fisheries. Similar effects were described for other major river deltas, including the Nile and Mississippi (Friedl and Wuest 2002). After completion of the Aswan Dam, fewer nutrients were transported to coastal waters of the Mediterranean, phytoplankton blooms ceased, and fish catches (*Sardinella*) declined (Aleem 1972). Changes in nutrient ratios in coastal areas were also responsible for the growth of toxic algae, although other factors (changes in nutrient balance, habitat, and temperature

regimes) were also important. Impacts of regulated flow regimes on estuaries will be addressed in detail in another Pathway of Effect.

3.6.1.3. Lateral

Flow regulation affects floodplain connectivity and therefore nutrient cycling. The moving littoral, a dynamic zone of high activity, is the nearshore zone from the water's edge to a few meters depth (Junk *et al.* 1989). This zone traverses the floodplain as seasonal flooding and drawdown takes place. During flooding, nutrients previously mineralized during the preceding dry season are dissolved, and transported laterally (Bayley 1995; Glazebrook and Robertson 1999; Tockner *et al.* 1999; Baldwin and Mitchell 2000). The flood-pulse concept (Junk *et al.* 1989) and the moving littoral zone functionally supports high biodiversity and productivity. Bowen *et al.* (2003) found that regulated flows resulted in 3 to 3.5 times less area of inundated woody vegetation during normal and dry years in the Missouri River compared with the unregulated Yellowstone River. Bowen *et al.* (2003) emphasized that the smaller area of inundation would mean that nutrient cycling and the ecological benefits of a moving littoral zone would be significantly reduced in the regulated system.

In British Columbia, off channel habitats are an important holding and conditioning location for leaf litter (Brown 2002). Numerous aquatic taxa feed on the decomposing litter, and invertebrate densities in the off channel sites are equal to main channel sites. Off channel sites are an important feeding area for certain salmonid species (e.g., coho salmon), particularly during winter (Brown 2002). Hydromodification has isolated or reduced more than 70% of the wetland habitats in the lower Fraser River (Brown 2002).

The lateral transfer of nutrients occurs not only from land to river, but also from the river to adjacent aquatic and floodplain habitats during flooding. In the Mackenzie Delta, flooding from river channels plays a dominant role in the annual flushing, nutrient replenishment and reinitialization of lacustrine ecosystems connected to the floodplain (Lesack *et al.* 1998). In alluvial floodplains of western North America, cottonwoods are a dominant riparian tree species. Scour by flooding creates the substrate needed for cottonwood seed generation, and importantly, hyporheic flow mediates the hydration and fertilization of these riparian trees (Harner and Stanford 2003). In alluvial rivers, hyporheic zones are large (measured in km³), and aquifer upwellings exert proximal controls on production and biodiversity both directly in the river channel and laterally in the floodplain and riparian zone (Stanford and Ward 1993). Changes in flow patterns and flooding regimes will result in changes to this lateral transport of nutrients to and from river channels and floodplains.

3.6.1.4. Vertical

As noted above, rivers are in contact with groundwater aquifers which have a water volume greater than the river channel itself, and have a significant influence on habitat conditions in the river ecosystem (Hynes 1983). This vertical hyporheic zone serves as a sink for organic matter and is important for carbon cycling in running waters (Hynes 1983;

Stanford and Ward 1993; Brunke and Gonser 1997). Microbial transformation and transport of solutes in groundwaters is an important source of nutrients for channel floras in streams and rivers (Stanford and Ward 1993; Valett *et al.* 1997); for example, nitrate levels are often higher in aquifers (Stanford and Ward 1993). Benthic animals can survive drought (and other disturbance events) in these hyporheic refugia, providing a reservoir for recolonization after drought (Brunke and Gonser 1997). Various anthropogenic activities that affect flow (reservoirs, aggradation, forest harvest, degradation of the river bed, water extraction) can change the height of the groundwater table and have ecological consequences (Ward and Stanford 1989).

3.6.2. Effects of Changing Nutrient Concentrations on Fishes

To test the hypothesis that the productivity of the benthic food web was limited by nutrient elements, phosphorus and nitrogen were added to stream mesocosms in the flow-controlled Nechako River, British Columbia. Periphyton and macroinvertebrate densities, especially midges and mayflies, increased significantly after phosphorous additions. Benthic invertebrates that increased during the experiment were the predominant prey in Chinook salmon fry diets (Perrin and Richardson 1997).

As a result of impoundments, and partially related to nutrients, the planktivorous species of alewife and blueback herring increased in the Saint John River, New Brunswick, while salmon and shad populations declined (Ruggles and Watt 1975). Supersaturation of nitrogen below the Mactaquac dam caused direct mortality to Atlantic salmon in the Saint John River.

Maintaining floodplain connectivity contributes significantly to river productivity, as the increase in the area of water during the floods transfers nutrients from the terrestrial into the aquatic components of the ecosystem, and vice versa (Welcomme 1979; Hesse *et al.* 1989.; Ward and Stanford 1989; Stanford and Ward 1993; Bayley 1995; Ward *et al.* 1999). Welcomme (1979) emphasized the importance of floodplains to fisheries production, and noted that annual fluctuations in fish catches could be traced to the history of flooding in previous years. More recently, Bayley (1995) found that yields of fishes per unit water area were higher in river floodplains than in equivalent water bodies without floodplains. That is, flood pulses provided a bonus in production above that which would be expected merely from the increase in surface area.

Much of the above information on the influence of lateral connectivity on fishes is from tropical systems because many floodplain rivers in temperate regions have been perturbed (Welcomme 1979). However, the importance of floodplains to river productivity is equally important in temperate regions (Halyk and Balon 1983; Ward and Stanford 1989; Bayley 1995). Additionally, light and temperature regimes in temperate latitudes may modify the biological effects of natural discharge pulses, making the timing of the pulse important (Junk *et al.* 1989).

In Canada, much research has been done on the growth and production of anadromous Pacific salmon in coastal floodplain habitats. In his comprehensive literature review,

Brown (2002) documented that juvenile salmon continued to grow during winter in off-channel habitats, because of the available nutrients and food supply. Significantly, floodplain habitats in the Pacific northwest were important to coho production (Brown and Hartman 1988; Sharma and Hilborn 2001; Sommer *et al.* 2001), and produced 20-25% of a watershed's total smolt production (Brown 2002). Anecdotal observations of interior British Columbia rivers indicated that temporarily flooded lands were important to juvenile salmonids as well, but these habitats were less well studied.

3.6.3. Mitigation of Change in Nutrients

Maintaining a natural flow regime to the extent possible is the primary mitigation tool for ensuring that nutrient distribution and dynamics in rivers are not disrupted.

To compensate for the loss of phosphorus loading to Kootenay Lake, British Columbia, due to upstream impoundment, lake fertilization was initiated. As a result, phosphorus concentrations increased, phytoplankton and zooplankton productivity increased and kokanee populations responded as well (Ashley *et al.* 1997; Ashley *et al.* 1999; Friedl and Wuest 2002).

Forest harvesting can change the hydrologic system, peak flow magnitudes and water levels at sites (Brown 2002). Maintenance of forest buffer strips adjacent to the stream and river channels are important for conserving fish habitat, as they protect the nutrient dynamics between the riparian and river zone, and the hyporheic habitat. Details of mitigation activities associated with forest harvest that are designed to protect natural flow regimes are, however, beyond the scope of this review.

The Serial Discontinuity Concept (SDC) can be used as a conceptual tool for predicting the consequences of the placement of dams along the longitudinal axis on upstream-downstream habitat conditions, including nutrient levels and availability (Stanford and Ward 2001; Ward and Stanford 1989).

To be effective tools for mitigation, hydrological models need to incorporate connectivity of the floodplain for future water resource management (Heiler *et al.* 1995; Galat *et al.* 1998; Kingsford 2000). Because many river-floodplain systems in temperate regions have been perturbed, Bayley (1995) recommended that experimental restoration should take priority over research in these severely impaired river-floodplain systems. Poff *et al.* (1997) cite two restoration projects that targeted improving nutrient dynamics in floodplain habitat (Toth 1995; Stanford *et al.* 1996). Floodplain restoration for biodiversity is a particularly promising area for research (Bayley 1995; Sparks 1995; Power *et al.* 1996).

3.7. Change in Flow → Change in Food Supply

3.7.1. Food Supply Overview

Food supply, and nutrients by implication, are included in the definition of fish habitat in the *Fisheries Act*: 'Spawning grounds and nursery, rearing, food supply and migration

areas on which fish depend directly or indirectly in order to carry out their life processes' (section 34). Fish taxa inhabiting rivers utilize all trophic levels in their diet, depending on the species, life stage, locality and season (Hynes 1970; Welcomme 1985). Sources of food include detritus, algae, plants, plankton, macro-invertebrates from the benthos or river drift, and other fishes. Food for fishes can originate from within the aquatic system itself (autochthonous) or from outside (allochthonous). Autochthonous invertebrates are the most widespread and important food source for fishes, particularly invertebrates that enter the river drift. Both allochthonous and autochthonous food sources are affected by altered flow regimes.

Food items of 207 species of fishes that inhabit freshwater habitats in Canada, most of which occur or prefer running water, were summarized by Coker *et al.* (2001). Insects and crustaceans were the most frequent items in the diet of fishes, although molluscs, fish, and macrophytes (associated epibiota) also occur quite frequently. For the purpose of this report, impacts of altered flow regime on the food supply of fishes are discussed under the diet categories of 1) algae, plankton and macrophytes, 2) invertebrate benthos and drift; and 3) fishes.

Invertebrates affect the cycling of nutrients and carbon as they are an intermediate link between primary producers, detritus pools, primary consumers and predators higher up in the trophic web, including fishes (Malmqvist 2002). Thus there is a strong link between nutrient dynamics (section 3.6) and food supply.

3.7.1.1. Longitudinal Impacts

Algae, Plankton and Macrophytes (and associated epibiota): The presence of impoundments affects the biota of downstream reaches by influencing the structure and function of the lower food web. The plankton content of the water can be increased below dams (Hynes 1970; Perry and Sheldon 1986; Layzer *et al.* 1989), depending on nutrient limitations (Petts 1984a), and plankton in reservoirs may improve conditions for the development of plankton below the dams (Talling and Rzoska 1967). Depending on the source of the reservoir discharge (epi- or hypolimnetic), growth of filamentous algae sometimes occurs below dams, and the thermal habitat may be affected. Impoundments change the primary food source from allochthonous to autochthonous carbon in tailwaters. Autochthonous energy includes filamentous algae and associated epiphyton (Angradi and Kubly 1993; Blinn *et al.* 1995, 1998). This change in food resource modifies the trophic structure of the tailwater reaches, favouring invertebrate grazers, rather than shredders, collectors and detritivores, resulting in reduced invertebrate diversity in tailwaters (Ward and Stanford 1989; Valentin *et al.* 1995). More stable patterns of discharge may encourage plant growth (Hynes 1970).

Because of the link between primary production and the associated invertebrate fauna, changes in algae, plankton and macrophytes will lead to changes in the composition of biota in the tailwater reaches and therefore the food supply of fishes. Discontinuity in the river continuum, as discussed above for nutrients, also affects the food supply of fishes (Ward and Stanford 1989; Imbert and Stanford 1996; Osmundson *et al.* 2002) .

Benthos and Drift: Discharge rate and the associated water velocity are key factors affecting the quantity and composition of invertebrate benthos and drift in running waters (Hynes 1970; Brittain and Eikeland 1988; Clausen and Biggs 1997). Natural high discharge events (spates) lead to increased drift. Rheophilic invertebrates are adapted in terms of their morphology, physiology, and life history to withstand large fluctuations in flow rate and water currents (Bunn and Arthington 2002). Natural diel and seasonal variability in drift rates are high (Hynes 1970; Rempel *et al.* 2000). Drift rate also depends on mesoscale habitats, with riffles producing more drifting invertebrates than pools. Drifting invertebrates represent surplus production and contribute to secondary productivity as a key food source for rheophilic fishes. Regulation of water flow affects the quantity and composition of invertebrate drift and, in turn, the food supply of fishes.

Responses of benthic invertebrate communities to flow regulation were summarized in a number of reviews (Brooker 1981; Armitage 1984; Petts 1984a; Cushman 1985; Ward and Stanford 1987; Malmqvist and Englund 1996; Ward and Wiens 2001). Generally, reductions in species diversity, alterations of community composition and trophic guilds, and increases or decreases in abundance are characteristic responses. However, specific impacts on the invertebrate taxa depend on the altered flow regime. Reduced flow results in a loss of wetted area, and allows silt to fill interstitial spaces, thus reducing the area for macrobenthos to reside (Armitage 1984; Moog 1993). To avoid stranding, invertebrates can migrate with the receding water level, or seek refuge in the substrate. In an experimental stream, Corrarino and Brusven (1983) observed catastrophic increases in drift following flow reduction. The timing of the response in drift rate and vulnerability to stranding and desiccation was taxa-dependent. Similarly, Poff and Ward (1991) found significant increases in drift following experimental flow decreases in an otherwise stable flow stream. Constant seasonal flow and stable substrate conditions are favourable to sessile invertebrates (often filter feeders), such as Simuliidae and net-spinning Trichoptera. Invertebrate grazers may also increase if algae and macrophytes increase in regulated tailwaters. Invertebrate detritivores may decrease because reservoirs interfere with upstream-downstream detrital transport; allochthonous material along the river edge may not be transported downstream (Saltveit *et al.* 1987; Cortes *et al.* 2002). The elimination of flushing action, resulting in siltation, may have deleterious effects on certain stream invertebrates. However, Ward and Stanford (1987) also concluded that although many species of benthic invertebrates are eliminated or reduced in abundance, a few taxa flourish under the altered flow regime. The net effect of seasonal flow constancy and its effect on physical habitat, as is the case with reduced flow, is the alteration of the structure and composition of the benthic invertebrate community.

Short-term fluctuations in flow adversely affect benthic communities, by reducing biomass, diversity, and taxa richness (Ward and Stanford 1979; Armitage 1984; Cushman 1985; Saltveit *et al.* 1987; Casado *et al.* 1989; Munn and Brusven 1991; Moog 1993). For example, the benthic community below a dam in an Idaho river was severely altered and simplified, with high abundance of a few species but low overall diversity: the majority of the benthos was chironomids, which are known to be tolerant of rapid changes in discharge (Munn and Brusven 1991). Short-term fluctuations also induce drift, and may result in stranding of invertebrates along shallow river edges. Recolonization may be

ineffective for restoring losses because impoundments disconnect the upstream reaches from the downstream tailwaters. Efforts to reduce the extremes in fluctuations by establishing minimum flows were partially successful, as Trichoptera larvae and other taxa were provided with protection from exposure and desiccation, and their resulting densities were higher than pre-mitigation (Weisberg *et al.* 1990).

Large increases in flow lead to the scouring of the river bottom, thereby reducing epilithic algae attached to the substrate (Armitage 1984). In an artificial stream, Bond and Downes (2003) observed that the increased drift rate they recorded was caused by the increased flow, rather than by the increased suspended sediments associated with the flow. Sustained high flow can reduce benthic invertebrate abundance by increasing the drift rate of certain taxa (Armitage 1984), as was found to be the case in an experimental channel in the upper Colorado River (Poff and Ward 1991).

If fluctuations in discharge are extreme in regulated rivers, as during hydropeaking, some taxa are reduced or eliminated (Céréghino and Lavandier 1998b), and productivity is decreased (Cushman 1985). A comprehensive review of the effects of pulse type flows on benthic macroinvertebrates was provided by (Reiser *et al.* 2005). These authors noted that in order to avoid stranding and desiccation, benthic invertebrates react to flow modification in one of three ways: by entering downstream drift, by following the retreating shoreline as waters recede, or by finding suitable refugia. Perry and Perry (1986) found that insect stranding occurred when the rate of change of discharge was high. Vulnerability to stranding was taxa and season dependent (Corrarino and Brusven 1983; Perry and Perry 1986): chironomids, simuliids and trichoptera were vulnerable, and stranding was more a factor in autumn than in the spring. The varial zone is the shoreline area that is repeatedly dewatered and inundated because of pulse flows (Fisher and LaVoy 1972). Frequent water level fluctuations are responsible for the periodic exposure of the varial zone. For several reasons, the varial zone has low productivity: the flood/dry period is irregular but usually diel, the degree of exposure is related to season, and most pronounced during summer, and not enough time has elapsed to allow the evolution of well-adapted indigenous fauna in this constantly changing habitat. Consequently the varial zone is characterized by reduced invertebrate density and diversity. Vulnerability of specific taxa, stranding and the effects of the varial zone on algal, invertebrate and fish communities has been well studied (Benenati *et al.* 1998; Blinn *et al.* 1995, 1998; Jourdonnais and Hauer 1993; Stevens *et al.* 1997; Shaver *et al.* 1998; McKinney *et al.* 1999; Paragamian 2002). Although insects can escape to the hyporheic zone if the substrate is porous enough, this escape mechanism would not be effective if the periods of daily flow fluctuation are extended (Gislason 1985; Stanford and Ward 1993).

Periods of drought are a natural extreme in the flow continuum, and plants, invertebrates and fishes can recover quickly from drought (Humphries and Baldwin 2003). For artificial flow alteration, the amount of time it takes invertebrates to recolonize substrate is uncertain, but it is dependent on the flow regime, taxon, and site specific factors (Beckett and Miller 1982; Wood and Petts 1994). Based on an observation period of 28 days, (Gersich and Brusven 1981) projected that 66 days would be needed to reach equilibrium at a flow regulated site. Swink and Novotny (1985) found chironomid densities stabilized

after 2 weeks, but oligochaetes failed to reach equilibrium after 95 days. Troelstrup and Hergenrader (1990) assumed that colonization time to reach equilibrium was at least 5 weeks.

Irvine (1987) emphasized that to properly address the effect of regulated flows on stream biota, an experimental approach is needed with proper controls in space and time. In a small experimental stream, Irvine and Henriques (1984) and Irvine (1985) compared the effects of successive flow perturbations to constant flow on stream invertebrates; the experimental flows were designed to simulate the conditions below a hydroelectric peaking plant. Initial increases in flow after a period of constant flow resulted in significant increases in drift density. Many of the invertebrates displaced by flow changes were resident on sloughed off filamentous algae. The experiment was continued for three weeks, and the increase in drift was less on each successive change. No increases in drift were observed at the end of the experiment due to depletion of the benthic invertebrate density. Perry and Perry (1986) found that drift densities initially increased with increased discharge, but then decreased after the first hour. In more recent experiments, Céréghino and Lavandier (1998a, b) found that Plecoptera and Ephemeroptera responded to peak flow releases with catastrophic drift. Trichoptera benthic densities and biomass were reduced by hydropeaking (Céréghino *et al.* 1997), but the effects of flow *per se* were confounded with temperature changes (hypolimnetic release). Céréghino *et al.* (2002) found that peaking affected the longitudinal zonation of several species; low abundance of several taxa was observed below the impoundment. The amplitude of the disturbance (peaking) may be important for determining drift rate and impact on benthic density (Céréghino *et al.* 2004; Petts and Armitage 1993). Also, Imbert and Perry (1999; 2000) found that abrupt increases in flow increased the drift rate (33X relative to the control) than stepwise increases (10X). Although reductions in benthos density were not observed, Imbert and Perry (2000) suggested that several high flow events may cause significant losses of benthic populations to the drift.

Fishes: Significant flow alteration has resulted in changes to the fish community in rivers (Petts 1984a; Bain *et al.* 1988; Ward and Stanford 1989; Marchetti and Moyle 2001; Paragamian 2002). Non-native fish species sometimes become more prevalent in regulated rivers (Martinez *et al.* 1994; Marchetti and Moyle 2001). Changes to the fish community were caused by changes in habitat (temperature, substrate, access to lateral habitat) and, directly or indirectly, to the resulting changes in the food supply of fishes. Piscivores in rivers would be affected by these changes in the fish community.

Natural flow variation provides piscivores with periodic access to prey but also prevents overharvesting (Meffe 1984; Power *et al.* 1996). Altered flow regimes may upset the balance in predator-prey dynamics and result in loss of biodiversity (Power *et al.* 1996). Bain *et al.* (1988) found that fish species adapted to shallow slow-water habitats decreased in abundance after river regulation. They hypothesized that these fishes were exposed to large piscivores because of changes in water depth (loss of refugia). In the Colorado River, rainbow trout replaced squawfish as the top carnivore, because of the reduction of flood extremes and the resulting changes to the food web dynamics (Ward and Stanford 1989). Marchetti and Moyle (2001) observed that the restoration of natural

flow regimes increased habitat for native fishes but decreased habitat for non-native fish species, which possibly limited native fishes through competition or predation.

3.7.1.2. Lateral

Connected floodplains and ecotone habitats have higher biodiversity, including benthic invertebrates that are prey for fishes, than disconnected floodplains and ecotone habitats (Bayley 1995; Ward *et al.* 1999; Schiemer *et al.* 2001b; Sommer *et al.* 2001), largely because of the influence of the flood pulse, shallow water, and nutrient dynamics (Junk *et al.* 1989). Much of the lateral interchange of water and biota between the river proper and the lateral habitats discussed under nutrients (section 3.6) applies directly to food supply as well, as the nutrients provide the resource base for the productivity of the invertebrate prey species.

3.7.2. Effects of Changing Food Supply on Fishes

The life cycles and feeding patterns of riverine fishes are adapted to synchronize with diel and seasonal variations in their drift and benthos as a food supply (Hynes 1970). A continuing theme in the literature on impacts of food supply to fishes was that the flow-related changes to the invertebrate community resulted, in turn, to changes to the species composition and diversity of the fish community that inhabited the rivers.

Short term pulses of increased turbidity, sometimes associated with short-term flow fluctuation can impact the bioenergetics of fish foraging. Berg and Northcote (1985) found that experimental short term pulses of suspended sediment decreased foraging efficiency of salmonids and probably affected fitness. Lagarrigue *et al.* (2002) found that brown trout consumed prey in the hours immediately following the flow peaking cycle because of the high drift density of invertebrates. Despite the increased drift in the regulated section of the river, juvenile brown trout were adversely affected (30% reduction in biomass) by hydropeaking conditions, possibly because high current velocities affected position maintenance and ability to capture prey. No significant differences were found for adult trout. Movements of salmonids may also be altered because of pulse conditions for reasons unrelated to foraging, such as seeking refuge from turbidity or high flow (Berg and Northcote 1985; Bunt *et al.* 1999), and have potential negative impacts to bioenergetic costs. In the latter study, Bunt *et al.* (1999) found that woody debris in pools provided refugia for brown trout in the Kananaskis River, Alberta, during periods of high flow. The impact of altered flow on fish bioenergetics is discussed in more detail in the section Bioenergetic Costs of Flow Modification (section 3.4).

Flow management effects are not always negative. In a field experiment, the growth of the rainbow trout fry was significantly greater in the altered-flow stream, possibly because of the increased drift and food supply (Irvine 1987). The difference between base and increased flow was significant (5-fold, two times daily). Irvine (1987) cautioned that the experiments were relatively short duration, and the effects may have been different in the longer term or in larger streams. Increases in fish growth and condition that were related

to increased food supply and consumption because of mitigated minimum flow was also observed by Weisberg and Burton (1993) and McKinney *et al.* (2001).

Reservoirs can discharge zooplankton thereby providing a source of food for fishes in tailwaters (Petts 1984a; Hesse *et al.* 1989; Jackson *et al.* 1991; Weisberg and Burton 1993). Often, however, the plankton is rapidly eliminated from the river (Hynes 1970; Petts 1984a), although there are exceptions where the plankton originating from reservoirs may persist for long distances (Hynes 1970). Zooplankton were consumed by several species of juvenile fishes downstream from reservoirs in the Missouri River (Hesse *et al.* 1989).

Channelization due to flood control and dredging often lowers the amount of wood debris in a system (Ward and Stanford 1989). Wood debris and snag habitat supported 60% of the invertebrate biomass and 78% of the drift in a Georgia river (Benke *et al.* 1985; Benke 2001). Removal of wood would likely change the fish community composition, reducing sunfish but favouring catostomids that feed on the benthic mud and sand fauna. Karr and Schlosser (1978) noted that the biomass of fishes may be reduced by greater than 90% by channelization. Similarly, Hesse *et al.* (1989) concluded that changes in the basin and floodplain physiography and channel morphology reduced the commercial fish harvest by more than 80% in the Missouri River. Hesse *et al.* observed that changes to the river channel interrupted the energy flow into the river from allochthonous sources and to higher trophic levels. Additional impacts on fishes of flow management by altering food supply by channelization, dredging, levees and dikes are reviewed by (Ward and Stanford 1989).

In a river in Idaho, the observed change in the fish community from one equally represented by mountain whitefish and largescale sucker to one dominated by largescale sucker, may be related to a reduction in insect prey items due to substrate armouring and the subsequent loss in habitat heterogeneity for Plecoptera and Tricoptera (Paragamian 2002). In the Colorado River, after flow regulation stabilized the river bottom, the major energy pathway changed to a simple food web consisting of dense growths of *Cladophora* algae, and *Gammarus*. The change in food web structure and changes in the thermal regime (to colder water) resulted in a change in the fish community from warmwater endemic cyprinids including the top carnivore squawfish (*Prychoceilus lucius*) to rainbow trout (*Oncorhynchus mykiss*) (Stanford and Ward 1986). In this case, the change in fish assemblage was viewed as being positive, as a new trout fishery was provided.

Development of a varial zone may result in impacts to fish food supply because of the depletion in invertebrate densities (Blinn *et al.* 1998; Blinn *et al.* 1995). Juvenile Pacific salmonids (Chinook salmon, coho salmon, and rainbow trout) were vulnerable to the effects of diel flow fluctuation because they live in the margins of streams and feed on the insects affected by flow fluctuation (Gislason 1985). Growth and condition of the salmonids was reduced in the presence of a varial zone.

Shallow water habitat is most affected (degraded) by water regulation, and these habitats are particularly important for larval fishes (Scheidegger and Bain 1995). Use of these microhabitats is related in part to food supply. Maintaining floodplain connectivity contributes significantly to river productivity and provides refugia and feeding habitat for fishes (Hesse *et al.* 1989; Ward and Stanford 1989; Hesse 1995; Bayley 1995; Bowen *et al.* 2003). Yields of fishes were shown to be statistically higher in river floodplains, after correction for wetted area (Bayley 1995); that is, fish production is strongly related to the extent of accessible floodplain (Welcomme 1979; Junk *et al.* 1989), and the high productivity of these seasonally inundated habitats. Much of the information on the influence of lateral connectivity on fishes is from tropical systems, largely because many floodplain rivers in temperate regions have been perturbed (Welcomme 1979). However, floodplain habitats are extremely important feeding areas for fishes in temperate rivers as well (Power *et al.* 1996). Channel incision and the reduction or elimination of access for biota to lateral floodplain habitats may diminish the resilience, productivity and biodiversity of river ecosystems. Food chain length, an indicator of biodiversity, may be shortened in regulated rivers (Power *et al.* 1996). Floodplains, either natural or restored, provide increased food resources and rearing habitat for juvenile Oncorhynchids (Sommer *et al.* 2001), although these habitats may expose the young fish to increased mortality because of stranding or predation (Sommer *et al.* 2005; Koed *et al.* 2006). The role of floodplain habitats to Pacific salmon and trout in British Columbia is comprehensively reviewed by Brown (2002).

3.7.3. Mitigation of a Change in Food Supply

After documenting the significant reduction in benthic biomass due to hydropeaking Moog (1993) recommended three operational strategies: 1) limit the operations of new peaking hydropower plants to protect the last sensitive reaches of a river; 2) avoid pulse release operations; and 3) determine and mandate acceptable minimum flows to protect downstream areas from dewatering. In his review of the ecological effects of rapidly varying flows, Cushman (1985) noted that management options are available in three main areas: operational changes (specify an upper limit to the amount of variability allowed); structural changes (re-regulating dams); and habitat modification (channel modification).

Recent science literature emphasizes the need to maintain the dynamic flow regimes that maintain the habitat pre-alteration geomorphology, including lateral connectivity (Junk *et al.* 1989; Bayley 1995; Imbert and Stanford 1996; Power *et al.* 1996; Stanford *et al.* 1996; Poff *et al.* 1997; Ward *et al.* 1999; Koel and Sparks 2002; Sommer *et al.* 2005). That is, natural flow regimes, which are region and river-dependent, need to be maintained to the extent possible. Even rare discharge events may be critical for generating habitat diversity that is essential to biota (Power *et al.* 1996), including the prey for fishes. Avoiding large and rapid flow changes can increase the habitable area, production and the diversity of invertebrates (Englund and Malmqvist 1996). Reduction in the amplitude and duration of power peaking flow fluctuations can be a highly effective management strategy for enhancing aquatic insect biomass with the potential for increasing the survival and growth

of fishes dependent on these insects (Gislason 1985). Complete removal of dams is sometimes an option (Benarik 2001).

The determination of minimum flows for rivers, although clearly beneficial (Travnicek *et al.* 1995), often focuses on one or a few target species of interest (e.g., salmonids) that utilize the river channel, and the models assume similarity among rivers (Poff *et al.* 1997). Instream Flow Incremental Methodology (IFIM; Bovee and Milhous 1978) or other models are becoming more sophisticated, but field tests for validation have been mixed (Gore and Judy 1981; Englund *et al.* 1997; Poff *et al.* 1997). Food supply needs for the fishes are sometimes included in habitat suitability models (Bovee 1985). The determination and duration of base flow are important factors affecting the trophic composition of regulated streams; mean velocities in lentic units should not decrease below 8-10cm/s to prevent the growth of nuisance algae (Valentin *et al.* 1995). To manage toward a natural flow regime, new policies are needed to avoid single species or individual component management, but rather to adopt an ecosystem approach to management (Poff *et al.* 1997; Stanford *et al.* 1996).

Many impacts of flow alteration on fish food supply are known, but the impacts are often river-dependent (Rutherford and Kelso 1995), or are inadequately understood or unknown. Further scientific research, including modelling, is needed to better understand the impacts (Bayley 1995; Rosenberg *et al.* 1997; Friedl and Wuest 2002; Halls and Welcomme 2004). For example, Schiemer *et al.* (2001a; 2001b) argued that hydraulic retentivity should become a main research focus for aiding the development of restoration concepts.

3.8. Change in Flow → Physical Effects (Erosion and Deposition)

3.8.1. Introduction to Physical Effects

At a broad spatial scale, flowing water transports eroded material from upland areas downstream to depositional areas. Fine materials, such as silt, clay and sand are transported as sediment as a suspended load, while larger materials such as gravel, cobble and boulders are transported as bedload (Leopold *et al.* 1964; Kondolf 1997). The proportion of sediment and bedload carried in a stream can vary, with steeper sloped and arid systems containing higher amounts of bedload (Schick and Lekach 1993).

Any structure that retains water and alters the natural flow regime will reduce the amount of sediment and bedload carried by a stream. Dams are extremely effective sediment traps, removing up to 99% of the upstream sediment load (Grimshaw and Lewin 1980; Petts 1984a; Williams and Wolman 1984). Trap efficacy and sediment storage can be quite variable, and may depend on the water volume stored, sediment input, release rate, bottom topography, type and location of outlet gates and sediment grain size (Williams and Wolman 1984). In general, larger reservoirs result in increasing sediment trap efficiency. The efficacy of reservoir trap efficiency reduces over time, as there is a 1% reduction in sediment storage capacity per annum in reservoirs (Gvelesiani and

Shmalkmzel 1971). In addition to a reduction in sediment load, a decrease in grain size is observed for the remaining sediment that escapes the reservoir (Brandt 2000).

Water released downstream from the dam has little sediment load, thus it possesses excess kinetic energy that is expended on erosion of the channel bed and banks. The resulting water is sediment-starved (termed 'hungry water'), and the excess energy in this water can manifest itself a number of ways on the streams' physical architecture (Kondolf 1997). Conversely, flow management practices can result in excess sediment being pulsed into a stream. This is less commonly observed, but can have considerable effects on fish habitat.

In addition to altering sediment and bedload transport, flow management results in an alteration of the natural flow regime. While the operation of each dam is unique, in general flow patterns are stabilized under a flow management regime, with fewer high and low flow events observed (Poff *et al.* 1997; Brandt 2000; Bunn and Arthington 2002). Regardless of how flow is managed, there will be physical manifestations of the altered flow due to changes in flow regime and sediment and bedload transport (Petts 1984a). The key physical pathways by which flow management influence fish habitat are outlined below.

3.8.2. Erosion – Bed Scouring

Fluvial processes will ensure a reduction in excess sediment transport capacity by increasing erosion. This can be achieved by eroding bank material, increased scouring of the bed, and/or armouring of the bed substrate. One of the most common outcomes of flow management is erosion and bed scouring immediately downstream of the dam (Petts 1979).

3.8.2.1. Increase in Bed Scouring

The release of hungry water typically results in significant bed scouring immediately downstream of dams. Scouring has been observed in streams dominated by erodible substrates (e.g. Leopold *et al.* 1964; Baxter 1977; Williams and Wolman 1984; McConchie *et al.* 2005), but some harder substrates can resist scouring (Kondolf 1997). Bed scouring, and the associated narrowing and deepening of the channel, is a common outcome due to the sediment-starved water (Petts 1979; Chien 1985). Scouring results in a disappearance of bed differentiation, and the loss of riffle/pool sequences (Assani and Petit 2004). Williams and Wolman (1984) hypothesize that the earliest and most straightforward erosion is the loss of instream bars, followed by bed scouring. Flow regulation resulting in reductions in discharge can significantly reduce wetted areas immediately below dams when scouring occurs due to the excess sediment transport capacity (Petts 1984a; Williams and Wolman 1984).

The rate of degradation generally decreases relatively quickly, as increases in depth usually occur relatively rapidly, i.e. within 7 years, shortly after flow management is implemented (Williams and Wolman 1984; Brandt 2000). However, scouring can take as

long as hundreds of years to appear in some instances (Petts 1979; Williams and Wolman 1984). Scouring will move progressively downstream from the dam until a new equilibrium is reached (Petts 1979); in one river, scouring was evident 150 km downstream of the dam (Lawson 1924). As with all physical effects to flow management, the rate and magnitude of scouring will vary depending on the physical and flow characteristics of the managed river.

3.8.2.2. Increase in Armouring

A second common result of sediment-starved water when bank materials are less erodable, particularly when discharge is reduced, is a loss of finer particles resulting in an armouring of the substrate. These coarser substrates are less easily mobilized by the hungry water, and over time can result in the inability of the bedload to move (Harrison 1950; Petts 1979; Brandt 2000). Armouring can occur even if the flow is capable of moving all the available particles once the fine sediments are removed. This results in an increase in bed roughness, which decreases flows further (Chien 1985; Brandt 2000). One important result of this activity on fish habitat is that riffles are extensively scoured, and deposition in pools is greatly reduced (Brandt 2000). For example, reduced flows result in increasingly stable riffles that gradually enlarge through tributary contributions to the point that they could not be removed by reduced mainstream floods (Graf 1980; Howard and Dolan 1981). Armouring is a common outcome of flow management practices, and is apparent in medium and large rivers (e.g. Livesey 1965; Chien 1985; Pohl 2004). As with scouring, the extent and significance of armouring is difficult to predict *a priori* as each river responds differently to flow management (Hales *et al.* 1970; Petts 1979).

3.8.2.3. Increase in Aquatic Macrophytes

Armouring and bed stabilization also can increase the distribution of aquatic macrophytes in managed systems. The distribution of aquatic macrophytes is limited by light availability, sediment and substrate characteristics (including nutrient concentrations), temperature, flow extremes and velocity (Nichols 1997). The increase in bed stability downstream from dams compared to an unregulated river, results in aquatic macrophytes experiencing lower discharge and reduced scouring stress (Bergkamp *et al.* 2000). North temperate rivers under natural flow regimes also typically experience low winter flows that expose aquatic macrophytes to frost and ice scouring, but these low flow events are often tempered under flow management regimes (Rørslett 1988; Rørslett *et al.* 1989). In addition, the cross-sectional width of regulated rivers often increases, so that the area available for the development of aquatic macrophytes increases (Williams and Wolman 1984). The resulting increase in available area, bed stability and stable flows can result in the development of extensive monotypic aquatic macrophyte communities in regulated systems (Jackson and Davies 1976; Rørslett 1988; Rørslett *et al.* 1989; Walker *et al.* 1994; Blanch *et al.* 2000).

3.8.2.4. Change in Food Supply

In reviewing her own research and that of others, (Power *et al.* 1996) emphasized that bed-scouring floods are significant ecological disturbances because they result in mortality of substrate-bound biota. Rather than having a negative effect, however, these natural scouring events actually lengthen functionally important food chains, by promoting the natural succession of species and by positively affecting predator-prey interactions. The corollary to this is that the *absence* of bed-scouring floods because of altered flow regimes (reduced flow) will result in shorter food chains and hence reduced food supplies for fishes. Periodic natural bed scouring flows are needed to rejuvenate the food web which supports fish and other higher trophic levels ((Power 1995; Power *et al.* 1996; Power *et al.* 1995); Power 1995; Power and Stewart 1987). Céréghino *et al.* (2002) observed that peak flows increased the intensity of bed scour below a hydroplant outlet which led to catastrophic drift. Large numbers of invertebrates were flushed downstream during hydropeaking, particularly in the autumn when the greatest difference existed between natural and peak flows.

3.8.3. Erosion – Bank Erosion

Water released downstream from the dam has little sediment load, thus it possesses excess kinetic energy that is expended on erosion of the channel bed and banks (Kondolf 1997). Hungry water can erode banks if the bank material is more erodable than the channel bed material (Williams and Wolman 1984; Brandt 2000). Stream banks, which are ecologically and environmentally diverse because they represent a dynamic boundary between the river and associated riparian zone, are dependent on inputs of sediment and nutrients from upstream, and reductions in sediment availability alter these habitats (Bergkamp *et al.* 2000).

Bank undercutting and caving are frequently observed in managed rivers when sediments are trapped in upstream reservoirs (Williams and Wolman 1984; Chien 1985). Bank erosion is a normal process in rivers, but the reduction in sediment load means that the material that is normally deposited to compensate for that which is eroded is not available, resulting in excessive bank erosion and increases in cross-sectional width. In addition, flow management can lead to banks being more regularly inundated, leading to greater bank instability (Simon and Collison 2002). Bank erosion is thought to occur only after the loss of bars and enough scouring that the remaining bed is not easily eroded (Williams and Wolman 1984); at this point, bank erosion and the associated channel widening occur rapidly. Lawler (1992) identified three types of bank erosion processes: sub-aerial preparation, which primarily occurs in the upper most stream reaches, fluvial entrainment, which occurs in the mid-river reaches, and the mass failure of stream banks, which occurs furthest downstream. This premise was supported by the observations of Williams and Wolman (1984), who found that bank erosion contributed relatively more sediment to the flow in downstream areas. In some instances large areas of bank erosion have been observed; alluvial sites with non-cohesive banks are most susceptible (Guy 1981; Abdelbary *et al.* 1991; Simon and Collison 2002). This problem also affects beach

development in semi-arid rivers, as the opening of the Glen Canyon Dam on the Colorado River resulted in the loss of bank beaches (Dolan *et al.* 1974).

3.8.3.1. Change in Suspended Sediment Concentrations

Our review found only limited evidence that sediment characteristics of the bank can influence suspended sediment concentrations, particularly at high flows. While it has been shown that water near banks with high proportions of fine sediments usually have greater concentrations of suspended sediment than water near well-armoured banks, the effect is not universal, as factors such as particle shape, the amount and type of fine material and the degree of packing will influence suspended sediment concentrations (McConchie *et al.* 2005). The fact that sediment concentrations in this study were so low that they could not have harmed fish ($0.5 - 20 \text{ m}\cdot\text{L}^{-1}$), coupled with the fact that no other reference could be found supporting this linkage, led us to determine that increasing sediment concentrations were likely not a concern to habitat managers.

Conversely, the reduction in sediment concentration below dams due to the sediment trapping of reservoirs can negatively affect biota. Many formerly turbid rivers demonstrate reductions in turbidity immediately downstream of dams (Gore 1977; Hesse *et al.* 1989; Galat and Lipkin 2000). The loss of suspended sediment is reflected in changes to macroinvertebrate (Gore 1977; 1980) and fish (Minckley *et al.* 2003; Dieterman and Galat 2004) communities downstream of impoundments.

3.8.3.2. Increase in Cross-Sectional Width

Flow management practices that promote bank erosion can lead to enlarged channel widths when bank materials are more readily erodable than channel materials below dams. While an increase in cross-sectional width appears less commonly than channel narrowing in the literature, it was observed in 10 of the 21 rivers examined by Williams and Wolman (1984), and is commonly seen in gravel-bed and formerly meandering rivers (Kellerhals *et al.* 1979; Petts and Pratt 1983; Thoms and Walker 1993; Friedman *et al.* 1998; Assani and Petit 2004). Thoms and Walker (1993) noted both decreases and increases in cross-sectional width in successive dam segments on the same river, and attributed the different responses to different bank composition. Whether scouring or erosion occurs ultimately depends on the relative location of the dam, flow intensity, bank height and the makeup of bed and bank materials (Chien 1985).

3.8.3.3. Hydropeaking and Bank Erosion

Bank erosion has been observed to be much less predictable in streams below hydropeaking plants than for other flow management scenarios (Williams and Wolman 1984; Assani and Petit 2004). Williams and Wolman (1984) found that hydropeaking led to stream channels moving indiscriminately from side-to-side, resulting in repeated bank erosion without any associated deposition. This, in combination with banks being wet on a daily basis, particularly in winter, produced greater bank erosion (Williams and Wolman 1984; Assani and Petit 2004). Increased bank erosion may be only an initial response,

however, as both Williams and Wolman (1984) and Church (1995) noticed an initial increase in bank erosion (and channel widening) followed by a period of deposition (and channel narrowing) after the building of a hydropeaking facility.

3.8.3.4. Delta and Shoreline Erosion

The reduction in sediment load due to flow management invariably reduces the amount of sediment available downstream, altering channel patterns, deltas and beach formation in receiving waterbodies (Bergkamp *et al.* 2000). Flow regulation has markedly reduced the size of deltas of some of the world's largest rivers (Nyman *et al.* 1990; McCully 1996; English *et al.* 1997), and the lost sediments that formerly supplied depositional areas in receiving waterbodies have resulted in extensive shoreline erosion (Inman 1985; Jenkins *et al.* 1988; Mee 1992; Nilsson and Berggren 2000). The loss of sediments and reduction in peak flows has altered channel patterns in many regulated rivers, reducing braided channels to scoured single-thread channels (Kondolf and Swanson 1993; Friedman *et al.* 1998; Surian 1999).

3.8.4. Deposition

The overall reduction in peak flows as a result of flow management will have effects on the pattern of downstream sediment deposition. While flow management frequently results in substrate scouring and armouring near the dam, downstream substrates typically face increased deposition, particularly downstream of unregulated tributary confluences (Petts 1979). The processes that lead to deposition generally take much longer to appear than those that result in erosion (Petts 1979). In addition, reservoir operation can result in the periodic flushing of sediments that lead to deposition, a scenario most commonly observed at dams used as flood control structures (Chien 1985; Qian *et al.* 1993).

3.8.4.1. Bench Development and Decrease in Cross-Sectional Width

Flow management can result in increased deposition in lower river reaches because the reduced flows typically associated with flow management result in the eventual deposition of material mobilised below dams, banks, and material entrained from unimpounded tributaries (Wolman 1967; Petts 1979; Petts 1984a; Mürle *et al.* 2003). The deposition of sediment in low floodplain depositional areas is known as bench development (Petts 1984b). The result of bench development is a two-stage channel in which a narrow baseflow channel lies within the larger channel (Petts 1984b; Sherrard and Erskine 1991; Shi *et al.* 1999; Gilvear 2004). These two-stage channels may reduce extremes in erosion and deposition if the presence of benches limit toe scour and provide areas for the deposition and storage of fine sediment (Petts 1984b). Rivers that traditionally meandered may not undergo significant bench development, but the scope of movement becomes greatly reduced under flow management scenarios (Chien 1985; Church 1995; Friedman *et al.* 1998)

Bench development results in changes in the cross-sectional width of rivers downstream of dams. Channel width can be reduced by >80%, depending on the composition of bed material (Gregory and Park 1974). A decrease in cross-sectional width is becoming increasingly recognized as a common response to regulated rivers around the globe (Williams and Wolman 1984; Petts and Thoms 1986; Sherrard and Erskine 1991; Benn and Erskine 1994; Fergus 1997; Johnson 1997; Shi *et al.* 1999; Surian 1999; Elliott and Hammack 2000). Reaches with the most extensive bench development and channel narrowing occur in close proximity to tributary sediment sources (Petts and Thoms 1986; Gilvear 2004). In addition, the decrease in cross-sectional width is greatest in reaches that historically moved extensively, versus those that were historically stable (Shi *et al.* 1999; Gilvear 2004).

Degradation patterns are not always simple and temporally stable, however, as rivers can initially widen or narrow, but then reverse over time as sediment transport mechanisms and bed and bank material return to equilibrium (Williams and Wolman 1984). Cross-sectional changes occur relatively rapidly after flow management regimes are implemented, as greater than half the changes in cross-sectional width observed by Williams and Wolman (1984) were within months of a flow management regime being implemented.

3.8.4.2. Riparian Vegetation

The development of riparian vegetation communities are influenced by the regime of flooding and sedimentation. Riparian zones are highly fluctuating, non-equilibrium ecozones that provide a variety of benefits to fishes including cover from predation, shade for reducing temperature fluctuations, and woody habitat inputs (Schlosser 1991; Jones III *et al.* 1999). Reduced floodplain inundation and the resulting alteration of hydrology downstream of dams can reduce groundwater recharge in the riparian zone, resulting in lowering of the groundwater table, with consequent impacts on riparian vegetation (English *et al.* 1997; Nilsson and Berggren 2000; Nilsson and Svedmark 2002). Many riparian species rely on floodplain aquifers that are recharged during regular flood events. Species adapted to these conditions are often adversely affected by flow-regulation, as riparian species richness was reduced in rivers subject to flow modification (Johnson 1992; Malanson 1993; Nilsson *et al.* 1997).

The reduction in the frequency of flood flows and the provision of stable low flows may encourage vegetation encroachment on banks and benches which will tend to stabilise new deposits, trap further sediments and reduce floodplain erosion (Smith 1976,; Richards and Wood 1977; Friedman *et al.* 1998; Bergkamp *et al.* 2000). The influx of riparian vegetation is observed on a number of streams and across a wide range of flow management scenarios (Richards and Wood 1977; Williams and Wolman 1984; Sherrard and Erskine 1991; Benn and Erskine 1994; Fergus 1997; Johnson 1997; Elliott and Hammack 2000; Gilvear 2004). These vegetation encroachments can become well-established and difficult to remove as flow management typically results in reduced floods (Sherrard and Erskine 1991; Johnson 1997; Friedman *et al.* 1998), thus stabilizing the channel at its decreased cross sectional width. The ultimate outcome of this scenario is a

decrease in the establishment of riparian species and their replacement with more shade-tolerant species, as reduced meandering limits sites for riparian pioneers to establish (Johnson *et al.* 1976, Friedman *et al.* 1998).

3.8.4.3. Reservoir Flushing

The operation of some dams involves the periodic flushing of reservoirs to reduce the build up of sediment loads. Depending on the frequency and magnitude of these episodic flushing events, sedimentation effects due to flow management may have important habitat implications (Dudgeon 1995). The overloading of water with sediment results in material being deposited in the river bed, usually in the form of bar deposition and braided channels (Chien 1985; Hoey and Sutherland 1991). The end result is a loss of channel area, either by increased bank formation if the sediments are fine, or by a reduction in the depth of the stream bed if the sediments are coarser. While deposition primarily occurs at the stream margins and in pools, fine sediment may be deposited in riffle and run areas where substrates are coarser (Einstein 1968; Beschta *et al.* 1981; Petts 1988; Brandt and Swenning 1999). These effects are generally restricted to areas near the dam (Chien 1985; Brandt and Swenning 1999). There are, however, examples where flows with excess sediments pass without deposition (Long and Qian 1986). In most streams, prior to the sediment release, there were no fine sediments in the bed and the inundation of sediments results in a rapid change in habitat structure (Brandt *et al.* 1995; Brandt and Swenning 1999; Dudgeon 1995). The stream bed is also temporarily raised which increases the probability of flooding (Collier *et al.* 1996; Brandt and Swenning 1999), though in most instances these effects are temporary as sediment-starved water re-enters the stream (Brandt 2000).

3.8.5. Ice Formation

One potentially important aspect of flow management that has received little attention to date is how flow management may influence winter conditions. Overwinter survival is believed to be critical in determining the population dynamics of fishes in temperate rivers (e.g. Cunjak *et al.* 1998; Scruton *et al.* 2005; Stickler *et al.* 2007), and any change in the physical environment during winter could negatively affect fish production. For example, higher winter flows reduce ice formation thereby limiting ice scouring, resulting in changes to substrate composition and aquatic macrophyte proliferation (Rørslett 1988; Rørslett *et al.* 1989) and generally physically unstable winter conditions for fishes (e.g. Jakober *et al.* 1998; Yrjänä *et al.* 2002), while lower winter flows can lead to greater anchor ice formation reducing fish habitat availability (Scruton and LeDrew 1997) and changing fish behaviour (see section 3.3.2). Winter flow regulation can also affect littoral habitats as increased winter flows in the Peace River delta reduce ice-jam induced flooding, and consequently aquatic habitat availability on the floodplain (Peters and Prowse 2001; Beltaos *et al.* 2006). It is apparent from the literature, however, that the effects of flow management on fishes during the winter months require more study.

3.8.6. *Effects of Erosion and Deposition on Fishes*

The temporal distribution, abundance and diversity of in-stream fishes are highly dependent on the interaction of flow and physical habitat (Schlosser 1982; Poff and Allan 1995). Erosion of both the bed and bank or the deposition of sediment on coarser substrates affects the physical structure and cover of fish habitat, which ultimately affects the biomass and productivity of fishes (Smokorowski and Pratt 2007). Thus, flow modifications that result in a change in physical habitat can be expected to have an influence on fish diversity and productivity.

The diversity of fishes can decrease with flow regulation, with many researchers observing communities dominated by generalist or invasive fishes after fish with specialized feeding strategies are lost with flow regulation (Cadwallader 1978; Petts 1984a; Copp 1990; Gehrke and Harris 2001; Gehrke *et al.* 2002). Change in habitat due to flow regulation is identified as a cause for this loss of biodiversity, through the loss of specialist species from regulated rivers due to decreased channel-widths from deposition (Copp 1990) and erratic flows limiting access to nearshore areas (Nelson *et al.* 1987; Freeman *et al.* 2001) that resulted in the loss of unique microhabitats. Restoration of a natural flow regime can improve fish species richness and diversity, as restoring more natural flows (Travnicek *et al.* 1995; Brown and Ford 2002) and dam removal (Hill *et al.* 1993; Kanehl *et al.* 1997) quickly improved downstream biodiversity.

The physical changes fashioned by flow management can influence spawning fishes. For example, armouring can result in a loss of spawning substrate (Parfitt and Buer 1980; Kondolf and Wolman 1993), and bed scouring can reduce gravel recruitment for spawning areas by allowing vegetation encroachment on banks and reducing bank cutting (Brandt 2000). The deposition of sediments from flow management practices has also resulted in the loss of spawning habitats for salmonids in many streams (Chevalier *et al.* 1984; Nelson *et al.* 1987; Reiser *et al.* 1989). Flow management can increase fine sediment infiltration into spawning gravel, negatively influencing spawning success (Sear 1993). It has been further suggested that the depth of bed scour constrains salmonid distributions (Montgomery *et al.* 1999). Thus, this widely distributed and economically important family will be affected as flow modifications alter geomorphological processes by armouring or scouring substrate. Since many valued species use gravel for spawning, the loss of spawning substrate may negatively affect fish biomass and productivity in managed rivers (Nelson *et al.* 1987; Sear 1993; Kondolf 1997). Conversely, bed scouring may help establish spawning areas in highly turbid, low flow situations where rock substrates are generally absent (Milhous 1998). Experimental manipulations of salmonid spawning habitat have demonstrated that fish will use created habitat, and there is some evidence for significant improvements in fish biomass and productivity with habitat enhancement (e.g. Scruton *et al.* 1997; Merz and Setka 2004; Smokorowski and Pratt 2007). Thus, the consideration of flow regimes to mitigate potentially negative consequences may be required to ensure spawning success downstream of flow management structures.

3.8.7. Summary of Physical Effects

The relationship between river channel form and the processes that result in the shaping of that form are complex. In most instances, the frequency of flood discharges and the magnitude and particle-size distribution of the sediment load determine the channel and floodplain morphology. Flow management alters the processes operating in the downstream river system by isolating upstream sediment sources, reducing the frequency of floods and regulating the flow regime (Petts 1979; Williams and Wolman 1984; Brandt 2000; Bergkamp *et al.* 2000). A unique combination of climate, geology, vegetation, size of impoundment and operational procedures produce the effect of any individual dam upon the fluvial processes downstream. Therefore, a range of physical effects are commonly observed under a wide variety of flow management scenarios. Whether the result is increased bank erosion, bed scouring or armouring depends on the relative erosive potential of the bed and bank materials, and the sediment deficiency in the water (Bergkamp *et al.* 2000; Brandt 2000). The effects of flow management are influenced by the distance from the flow management structure. Far enough downstream, surface erosion may provide ample alluvium to the channel even if the reservoir traps 100% of incoming sediment (Phillips 2003). Initial physical effects occur near the dam, progressively shifting downstream over time (Williams and Wolman 1984; Brandt 2000). Finally, it is important to note that there are instances where bed materials are coarse and banks are well vegetated and thus both are relatively immobile, and the complete range of possible physical effects of flow management are not realized. In such cases, managed flows are incapable of moving material in that part of the system and the only effect of flow management is a reduction in frequency of bankfull flows (Petts 1979; Kellerhals 1982; Williams and Wolman 1984; Benn and Erskine 1994; Gilvear 2004). Ultimately, channel degradation below a dam persists until the channel slope reduces, reducing the flow velocity below the threshold for sediment transport, at which point the system stabilizes.

3.8.8. Mitigation of Physical Effects

There are numerous options for mitigating many of the physical impacts that occur with the onset of flow regulation. The most common mitigation measure is the release of compensation flows for the maintenance of ecosystems downstream of a dam (Bergkamp *et al.* 2000). These compensation flows were traditionally a continuous minimum flow release that had to be maintained throughout the year, but in recent years regulators have begun to require that operators vary flow seasonally to mimic the natural seasonal variation in flow (Bergkamp *et al.* 2000). The consideration of large, ecosystem-level requirements have led to suggestions that flow management needs to follow the natural hydrological cycle; to assess the amount, timing, and conditions under which water should be released by dams (Scruton and LeDrew 1997; Bergkamp *et al.* 2000). The acceptance of a natural flow regime has resulted in the release of high flows to maintain floodplain and deltaic ecosystems (Acreman *et al.* 2000), and would help improve overwinter ice conditions for salmonids.

The restoration of diverse macrophyte communities in managed rivers is dependent on reinstating fluctuating water levels, resulting in more frequent shallow and flood conditions (Rørslett *et al.* 1989; Blanch *et al.* 2000). Similarly, Sherrard and Erskine (1991) suggest that large spills are required to remove vegetation that has become established on benches and the benches themselves. Experimental, controlled floods are somewhat successful in restoring habitats alternately degraded by armouring and deposition, but vegetation on bench deposits is not readily removed (Kearsley and Ayers 1999; Schmidt *et al.* 2001, Mürle *et al.* 2003). After five years, many of the habitat improvements were much reduced or lost with the re-establishment of flow management (Kearsley and Ayers 1999; Schmidt *et al.* 2001). Other controlled floods have successfully removed aggraded sediment from bench deposits that were not heavily vegetated (Elliott and Hammack 2000).

The periodic flushing of fine sediments is recommended when managed flows are so low that spawning areas are filled by aggregated materials (Nelson *et al.* 1987; Reiser *et al.* 1989), and controlled floods can be successful in removing fine sediment (Mürle *et al.* 2003). Each managed system will be required to determine its own flow rate and the duration that flow is required to clean the gravel beds though, as the requirements will vary on a case-by-case basis. As well, the addition of spawning gravels to replace those that are lost through deposition or erosion will only be successful if geomorphic principles are adhered to (Kondolf *et al.* 1996).

4. Interactions

Changes in downstream discharge resulting from flow management would not result in the manifestation of a single effect in isolation of the others on the pathway. Flow changes result in the simultaneous occurrence of many effects which would likely not increase risk to the system in a linear or additive fashion. The inclusion of more than one factor should instead be considered as a multiplicative risk due to interactions among factors. This section will highlight some examples of likely interactive effects, but since the ultimate risk would be site specific and often unpredictable, it is not the purpose of this section to thoroughly exhaust potential interactive effects resulting from flow management.

Temperature is the one factor that would interact with most of the other factors in the pathway, potentially the most strongly. For example, the amount of gas that can dissolve in water increases as temperature decreases, meaning that a hypolimnetic draw could exacerbate gas bubble trauma if coupled with physical supersaturation from hydrostatic pressure (Weitkamp and Katz 1980). However, when the water is already at 100% saturation, a sudden increase in temperature (e.g. from cooling effluent) results in the water losing its ability to dissolve the same amount of gas as at the cooler temperature, leading to a supersaturated state. Given time to equilibrate the gas will come out of solution thus reducing the total gas pressure to 100% (Weitkamp and Katz 1980).

Temperature is one of the strongest cues triggering fish migration hence altering temperature will alter timing of migration and potentially access to habitat (Quinn *et al.*

1997). Temperature could also become a migration barrier if river reaches become too warm for efficient swimming (Major and Mighell 1967), again altering the timing of arrival at spawning grounds adversely affecting spawning success (Bernatchez and Dodson 1987). Temperature changes have been shown to alter timing of smolt outmigration, potentially resulting in a mismatch between movement and availability of food resources, or exposure to less than optimal conditions for adaptation to salt water (Raymond 1979). Colder temperatures induce cover-seeking behaviour (Taylor 1988) and as a result have been shown to affect stranding (Bradford et al. 1995; Scruton et al. 2005). Temperature is a moderator of all components of fish bioenergetics, affecting consumption, respiration, egestion, excretion, and growth rates of fishes (Elliott 1979). If a change in temperature changes the amount of anchor ice it may affect erosion processes (e.g. Rørslett 1988; Rørslett *et al.* 1989). Conversely, a change in sediment characteristics will alter the thermal gradient found in the hyporheic zone (Evans et al. 1995).

Non-temperature related interactions are also possible. For example, reductions in nutrient levels will reduce primary productivity affecting food web dynamics. To better understand the effects of disturbance on food web dynamics, ecologists should consider the interaction of multiple causal factors; for example, Wootton et al. (1996) showed that removing scouring floods would result in increases in predator-resistant grazing insects, which would divert energy away from the food chain leading to predatory fish (food web collapse). A change in sediment characteristics would alter the composition and density of aquatic invertebrates (Newcombe and MacDonald 1991) and thus the potential food supply for fishes. Increased incidences of invertebrate stranding (Perry and Perry 1986) plus changes in the timing of drift will both affect the food supply and the bioenergetics of fish foraging (Lagarrigue et al. 2002). In fact, most stressors associated with change in flow will have a bioenergetic cost. Sediment characteristics (interstitial porosity) affect the ability of invertebrates to escape to the hyporheic zone and survive a stranding incident (Gislason 1985; Stanford and Ward 1988) which may be an additional negative consequence of armouring or deposition. Changes in sediment characteristics may also affect the potential for fish stranding (Halleraker et al. 2003) with greater incidences in cobble vs. gravel substrates (Monk 1989). Cumulative effects are also not well addressed by this literature review; however, the inability to address cumulative effects is not a function of the pathway framework as it existed to the same degree before this exercise. Thus, interactions and cumulative effects should be considered when reviewing proposals to alter flow management, potentially requiring greater safety margins for precaution in light of greater uncertainty.

5. Conclusion and Recommendations

5.1. PoE Diagram

This review has highlighted that flow management is a complex issue with many interactions between individual effects (section 4) that can lead to a variety of ecological ramifications. The literature reviewed was generally probabilistic in nature with a limited ability to predict effects with certainty, although some generalizations with respect to both effects and mitigations can be described (section 5.2 and 5.3). The literature was also

heavily biased towards salmonid populations and care should be exercised when extrapolating to non-salmonid communities. In general, the effects and linkages within the PoE diagram (Figure 1) were supported by the literature but we have also suggested a number of modifications to the PoE diagram for Flow Management based on our findings (see Figure 1). The first change of note was to ensure that 'Flow Management' captured all 5 aspects of flow alteration characterized by managed flow regimes by adding 'amplitude and rate of change' to the original descriptors 'change in timing, duration and frequency of flow'. The original diagram had 'De-watering' as a habitat impact which was subsequently removed and its end points, 'change in migration / access to habitats' and 'displacement or stranding of fish', were given a direct link to the flow management operation. Other direct endpoints, namely 'changes in total gas pressure' and 'changes in salinity' were added. The direct endpoint named 'change in contaminant concentrations' was moved under its resultant physical impacts, namely 'bank erosion and erosion of channel beds'. It is important to note that 'changes in salinity' and 'changes in contaminant concentrations' were not reviewed in this document and that these endpoints still require validation.

The physical habitat impacts of 'bank erosion' and 'erosion of channel beds' were left as primary effects of flow management but a second level of habitat impact, namely 'deposition', was added to the Pathway (Figure 1). Deposition was viewed as one of the primary factors that could result in a 'change in substrate composition'. All these substrate based habitat impacts then lead to the endpoint 'change in habitat structure and cover'. The endpoint 'change in sediment concentration', which was linked to the habitat impacts of 'bank erosion' and 'erosion of channel beds', was not strongly supported by the literature (see section 3.8.3.1) but it is acknowledged that this may be a bias in the literature which did not have many examples from naturally sediment laden rivers. An alternative reference for practitioners related to sediment effects was developed during the previous PoE meeting (DFO, 2006; Robertson *et al.* 2006).

The last major change that we have suggested for a revised pathway is the positioning of the 'change in food supply' endpoint. In the original pathway this endpoint was linked to the habitat impact 'change in substrate composition' (Figure 1). During this review it became evident that food supply changes were much more complex and that a number of other endpoints (nutrients, migration / access and habitat structure) as well as habitat impacts (erosion, deposition and scouring) had a role to play in overall effect of flow management on food supply (see section 3.7). Thus, the food supply endpoint was given a central position within our revised pathway (Figure 1). Finally, it is important to note that this review dealt with issues resulting from flow management downstream of a water control structure. The resulting impoundments can also have significant effects on fish and fish habitat (see Smokorowski *et al.* 2005), and a PoE for reservoir creation and operation should be developed and linked to this Pathway much the same way as fish passage is currently referenced.

5.2. Summary of Effects

A summary of the effects on fish and fish habitat that are documented in this review for each of the major linkages and endpoints within the Flow Management PoE is presented in Table 2. Flow management has generally been shown to have a negative impact on fish populations (Richter *et al.* 2003), but there have been a few examples where benefits have occurred (Cooke and Leach 2004). The effects documented by this review generally occurred at the population or community level due to the significant changes in habitat that occurs with flow modification (see Table 2 and text). There were, however, a few instances where direct mortality of fishes was observed. These situations occurred with elevated levels of total gas pressure (section 3.1), stranding of fishes due to dramatic reductions in flow (section 3.3) and during the downstream passage of fish over dams (section 3.2). The mortality observed during downstream passage may be due to direct injury due to blunt force trauma, gas bubble trauma and/or a combination of these and other factors (Muir *et al.* 2001).

Population level effects that were observed as a result of flow management included reduced spawning success, delayed mortality and reduced growth and production potential. Reduced spawning success was observed when fish were delayed in their migration to spawning habitats (section 3.2), where ground water reductions affected spawning habitats (section 3.2) and where reservoir flushing inundated spawning habitats with fine sediment (section 3.8). Delayed mortality was observed when downstream migrating salmonids were delayed in their passage to the sea (section 3.2). This migration delay is associated with both physical barriers and changes in water temperature induced by impoundments (section 3.5). Mortality occurs when fish reach saltwater at a time when they are physiologically unable to make this transition, and this effect can be cumulative and additive with other stressors in large rivers with multiple dams (see Budy *et al.* 2002).

The most commonly reported and possibly most complex population effect of flow management on fishes is the reduction of growth and production potential. Nutrient levels are generally reduced downstream of an impoundment due to the reservoir acting as a sink within the system and disconnecting the river from its floodplain habitat and groundwater sources (section 3.6). Coupled with this reduction in nutrients, changes in water temperature (section 3.5), reductions in micro-habitats (section 3.8) and changes in drift patterns (section 3.7) all can lead to a reduction in benthic invertebrate densities and diversity. These benthic invertebrates generally form the basis of the food web in river systems. Growth and production effects have also been cited when fish are highly active due to hydropeaking regimes (section 3.4), which may also be coincident with changes in benthic drift patterns (section 3.7). Finally, fish production can be reduced by disconnecting the river from its floodplain habitat (section 3.2). This area is both highly productive for detritus based invertebrates (section 3.7) and many younger stages of fish (section 3.2).

Community level responses that are associated with habitat changes induced by flow management include an overall reduction in fish diversity and changes in dominance hierarchy. Reductions in fish diversity have been associated with a reduced cross sectional area and its resultant loss of micro-habitats (section 3.8). These reductions are also strongly correlated to disconnecting the river from its floodplain and longitudinal

corridor (sections 3.2 and 3.6). The relative abundance of species has also been observed to change after flow management due to shifts in the thermal regime (section 3.5). It is important to note that some of these changes may be viewed as positive by managers and user groups (e.g. rainbow trout replacing squawfish on the Columbia River see section 3.5).

5.3. Summary of Mitigations

The human needs for the services supplied by rivers, i.e. hydroelectricity, irrigation, flood defence, drinking water etc., are not abating (Richter *et al.* 2003) and thus a number of mitigations to the ecological effects cited above have been developed. A summary of these mitigations as they relate to fish and fish habitat is presented in Table 3. Mitigation options generally fall into one of two categories, they are either 'engineering fixes' associated with a specific problem or they are 'operational' in nature and may be directed at a specific problem or be more holistic.

Engineered mitigations can include the installation of flow deflectors to reduce total gas pressure (section 3.1) or destratification systems aimed at moderating temperature extremes (section 3.5). Fish passage is an important mitigation to reconnect the river corridor and appropriate fish passage devices for both upstream and downstream migrants are now a requirement at most dam sites (section 3.2). Fish passage is a large area of study onto itself and it will be the subject of a PoE linked to flow management (see Figure 1). The current status and gaps in knowledge with regard to fish passage in Canada was recently reviewed by Katopodis *et al.* (2005). Proper planning can also be important in mitigating ecological effects. Dams can be placed in areas which would be expected to have the least impact on nutrient supplies (section 3.6), supply deep areas downstream of spillways to allow for hydrostatic compensation (section 3.1) and be designed with multiple release structures to moderate temperature changes (section 3.5).

Operational mitigations include the concept of minimum flows downstream of a dam and more recently the concept of 'natural flow releases' which are designed to mimic the natural hydrograph. In their most simplistic form, minimum flows are required to ensure the river bed downstream of a dam does not completely dry out. There may be some seasonal requirements to ensure fish passage (section 3.2), flushing flows for habitat processes (sections 3.6 and 3.8) or increased/decreased flows to moderate water temperature (section 3.5). The methods for assessing minimum flows, including knowledge gaps, have been recently reviewed in a Canadian context by Scruton and Katopodis (2005).

Natural flow releases or the 'Natural Flow Paradigm' is becoming an important first principle in the setting of managed flow regimes throughout the world, including Canada. This principle simply states that managed flow regimes should include elements of natural hydrological variability, both seasonally and inter-annually, in prescribed flow regimes to maintain the ecological integrity of the river system. This approach is designed to reconnect the various dimensions of an ecologically intact river system to allow for the free flow of nutrients (section 3.6), sediment (section 3.8) and fish (section 3.2). This

approach was originally proposed as a method for restoration of severely impacted rivers (Poff *et al.* 1997; Richter *et al.* 2003) and its use as a planning tool for flow management is still the subject of research (e.g. Scruton *et al.* 2007b). One of the current knowledge gaps that may limit its use is identifying the key elements of hydrological variability and at what level they become critical to maintaining the ecological health of the river (Richter *et al.* 2003). Richter *et al.* (2003) have proposed a six step process to move towards ecologically sustainable water management based on natural flow regimes which incorporates existing knowledge, scientific research and adaptive management. This type of process holds much promise for the future.

Knowledge gaps and research needs have been highlighted throughout this review. As discussed above, many of the most promising areas for research deal with the natural flow paradigm and developing quantitative linkages between fish, their habitat and the natural hydrograph. Suggested approaches to move this agenda forward include modeling, adaptive management experiments and directed research, but a combination of these approaches may be needed. Recently, DFO has consulted with industry representatives through the Canadian Electricity Association to discuss the state of knowledge and research priorities with respect to hydroelectric development in Canada (Stoneman 2005; CHIF 2007). While the hydroelectric industry is not the only group involved with flow modification in Canada, the reviews and recommendations within these documents are broad enough to supply a good basis for any project where flow management will be an issue.

6. References

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7. Tables

Table 1. Definition of terms related to flow management.

Term	Definition	Units if applicable	Reference
Discharge rate, flow rate, or magnitude (of discharge)	Volume of flow per unit of time flowing past a fixed point	$\text{m}^3 \cdot \text{s}^{-1}$	
Velocity	Water current	$\text{m} \cdot \text{s}^{-1}$	
Ramping rate	Rate at which turbine water discharge is increased or decreased	$\text{m}^3 \cdot \text{s}^{-1} \cdot \text{h}^{-1}$	
Frequency of occurrence	How often a flow above a given magnitude recurs over a specified time interval. Inversely related to magnitude.		(Poff <i>et al.</i> 1997)
Duration	Time period associated with a specific flow condition. E.g., number of days in a year when flow exceeds some value.	days yr^{-1}	(Poff <i>et al.</i> 1997)
Timing (predictability)	Regularity of flows of a defined magnitude.		(Poff <i>et al.</i> 1997)
Rate of change (flashiness)	How quickly flow changes from one magnitude to another.		(Poff <i>et al.</i> 1997)
Decrease flow; dewatering	Significant artificial reduction in discharge resulting in a decreased river width and wetted production area, and decreased lateral connectivity to the riparian zone and floodplain	m^2 or ha	
Hydropeaking, peaking or pulse release	Rapid increase in discharge (ramping) to meet an increase in power demand (diel). See also ramping rate	$\text{m}^3 \cdot \text{s}^{-1}$	(Moog 1993; Morrison and Smokorowski)

			2000)
Flushing flow	Increased flow designed to remove accumulated sediments	$m^3 \cdot s^{-1}$	(Reiser <i>et al.</i> 1987)
Stable flow			
Natural flow regime	River flow (magnitude, timing, duration, frequency, rate of change) governed by natural diel and seasonal cycles (rainfall and snow melt) and regional geography.		(Poff <i>et al.</i> 1997; Poff 1996)
Flow management	Regulated river flow, usually involving impoundment and tailwater		
Floodplain	Areas that are periodically inundated by the lateral overflow of rivers or lakes and/or by direct precipitation or groundwater; aquatic/terrestrial transition zone (ATTZ).	m^2 or ha	(Junk <i>et al.</i> 1989)
Catastrophic drift	Invertebrate drift associated with flood conditions during which the substrate is physically disturbed by high discharge.		(Brittain and Eikeland 1988)

Table 2. Summary of impacts of flow regulation.

TGP

- Major ecological impact is Gas Bubble Trauma (Disease); this can lead to direct mortality.
- GBT causes stress that may lead to the onset of other diseases or contribute to delayed mortality.

Access

- Migration delays may lead to decreased spawning success.
- Migration delays of downstream migrants can lead to delayed mortality.
- Migration delays of downstream migrants can lead to de-smoltification.
- Direct mortality can result in passage through spillways.
- Disconnecting the hyporheic zone can lead to reduced spawning success.
- Disconnecting the floodplain habitat can impact many young age classes of fishes that rely on this habitat for growth.

Stranding

- Direct mortality can occur with the stranding of fishes.
- Reduced growth/production due to increased activity patterns observed downstream of peaking operations.

Bioenergetics

- Bioenergetics of organisms entails a mass balance between consumption of energy and output via growth, reproduction, and metabolism, the latter being largely a function of temperature and activity levels.
- Increasing energy spent on metabolism via an increased activity cost due to a change in flow will impact growth and reproduction.
- Changing food availability through a change in flow will affect energy available, and since metabolic costs may not change (depending on any change in foraging costs), that will also ultimately impact energy available for growth and reproduction.
- Changing the temperature regime will affect fishes' metabolic functions, potentially increasing energetic costs.
- Many fish species have morphological or behavioural adaptations that can mitigate

against the bioenergetic effects of a change in discharge.

Temperature

- Water temperature is proportional to the heat load divided by the discharge, so altering either variable will affect temperature
- Location of the draw from a reservoir (i.e. epilimnetic or hypolimnetic) will influence how discharge affects temperature.
- Higher discharge extends the thermal conditions of the headwaters further downstream.
- High and stable flows can result in stable temperatures relative to low or fluctuating flows, can cool summer water temperatures, increase winter temperatures and dampen seasonal patterns.
- Reductions in flow affect water temperature by reducing the stream's assimilative capacity for heat, potentially elevating peak summer temperatures or reducing winter temperatures.
- Cold summer and warm winter conditions can reduce invertebrate diversity, yet overall density can increase with disproportionate increases by some species.
- Altering temperature can change fish community composition as thermal limits are reached
- Most case studies examining hypolimnetic release demonstrate a negative effect on fish populations.
- Increasing water temperature will alter the timing of migration for migratory fish species, can alter thermally driven life history traits (e.g. growth, reproduction, survival), and change fish behaviour.

Nutrients and Food Supply

- Dams act as a discontinuity in the river continuum, interrupting nutrient exchange between upstream and downstream reaches
- Reservoirs act as a nutrient sink, reducing the availability of nutrient elements (e.g., phosphorous) to downstream reaches
- Flow regulation reduces the area of inundated shoreline and floodplain habitats, where detritus based productivity is high
- Disconnect between the river and the lateral habitats decreases nutrient exchange

between the terrestrial and aquatic zones

- Regulation may lower the aquifer level, affecting the interaction between the aquifer and the river (nutrient exchange)
- Natural variation of invertebrate drift rates is high and discharge-dependent. Impacts of altered flow on drift must be evaluated in the context of this high background natural variability
- Artificial increases in river discharge will lead to increases in invertebrate drift and hence available food for drift feeders. However, the duration of increased drift is uncertain but finite
- Artificial decreases in river discharge will lead to increases or decreases in drift, depending on the taxa and flow regime
- Aquatic invertebrates can recolonize areas if fluctuations in discharge are short term. Invertebrates seek refuge in the hyporheic zone, or by entering the drift. However, disconnect from upstream reaches because of reservoirs may impede recolonization.
- With altered flow, the rank of sensitivity of impacts to aquatic invertebrates from high to low, is drift rate > species composition and diversity > benthos density
- Significant and extended reductions in flow will cause stranding and desiccation of aquatic invertebrates at river edges. Survival is species-dependent.
- Of the different regulated flow regimes, hydropeaking is the most disruptive to the food supply of fishes.
- Depending on the flow regime, an unstable varial zone may be created. Invertebrate density, diversity and productivity is lower in the varial zone.

Physical Habitat

- Flow regulation will result in physical changes because of alterations in flow regime and sediment and bedload transport
- Reservoirs are highly effective sediment traps, and the release of sediment-starved water usually results in 1) bed scouring immediately below dams, 2) armouring of substrate and 3) bank erosion further downstream of dam, and 4) erosion of delta and shorelines in receiving waterbodies
- More stable flow and substrate conditions can cause the proliferation of aquatic macrophytes
- The dampening of peak flows typically increases deposition further downstream of dams, reducing cross-sectional widths and fostering the development of stable

riparian vegetation communities

- Reservoir flushing can inundate spawning areas with fine sediments
- Fish diversity decreases with the onset of flow regulation, likely due to the loss of microhabitats

Table 3. Flow regulation mitigation

TGP

- Installation of flow deflectors at spillways to reduce TGP.
- Providing deep plunge pools in spillways to allow for hydrostatic compensation.
- **Access**
- Provision of fish passage facilities both for upstream and downstream migrates.
- Reconnect the river to the floodplain and hyporheic zone via flow releases at the appropriate time of year (natural flow).
- Minimum flows and augmented flows during important period for fish passage.
- **Stranding**
- Minimum flows downstream of hydropeaking facilities
- Try and match magnitude of peaking to peaks in the natural hydrograph
- Timing of peaking operations on a diurnal schedule to reduce impacts.

Temperature

- Install destratification systems (e.g. air lift or bubbling systems) to minimize drastic temperature differences.
- Install or retrofit multiple release structures to allow the adjustment of the depth of release at the dam.
- Manipulate the magnitude and timing of flow release to improve thermal habitat conditions.

Food Supply and Nutrients

- Position dam in longitudinal profile at 'least impact' location (SDC)
- Maintain a minimum flow
- Mimic the natural flow regime
 - reduce the amplitude and duration of power peaking flow fluctuations
 - stepwise increases or decreases in flow

- Avoid extreme fluctuations in daily flow and the development of an unproductive varial zone
- Artificial lake fertilization
- Riparian buffer strips and forestry management
- Avoid activities that may affect aquifer levels (aggradation, modification of the river channel, unmanaged forest harvest)
- Allow lateral access for water, nutrient and biota migration and exchange
- Experimental restoration of lateral habitat and adaptive management
- Research

Physical Habitat

- Release of compensation (minimum) flows
- Release of flow to more mimic the natural hydrograph

8. Figures

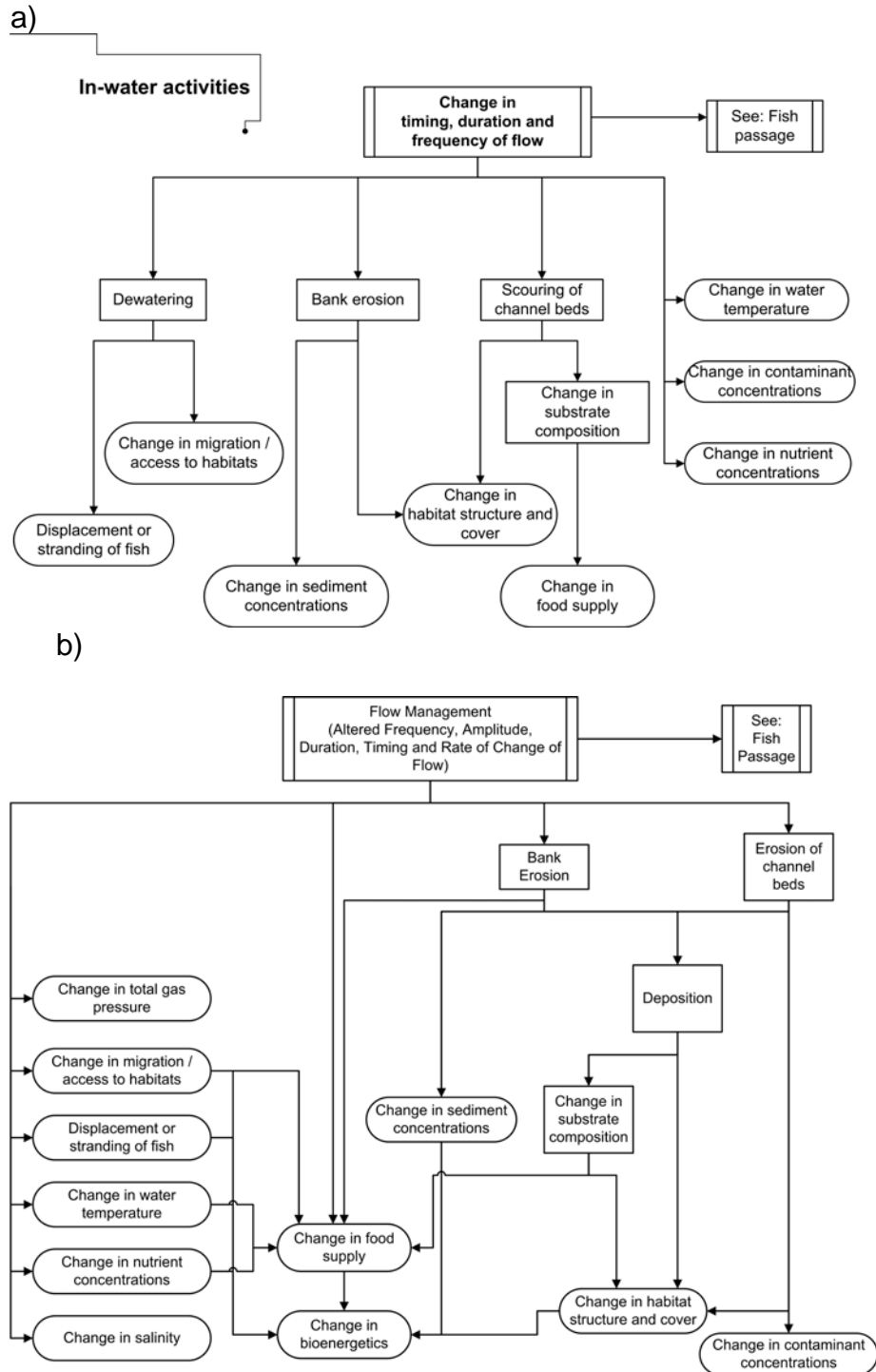
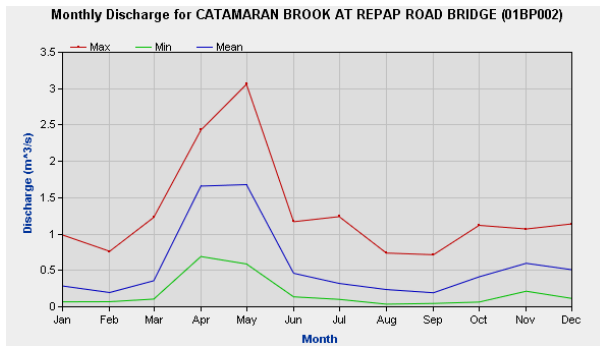
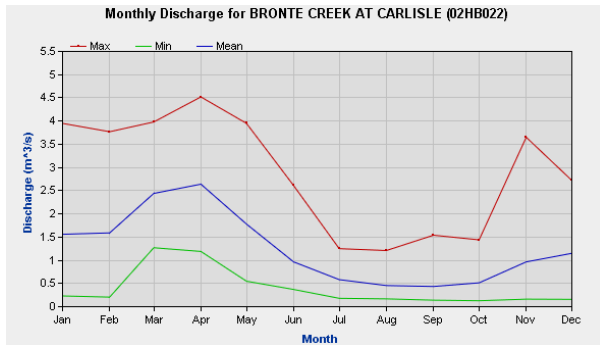


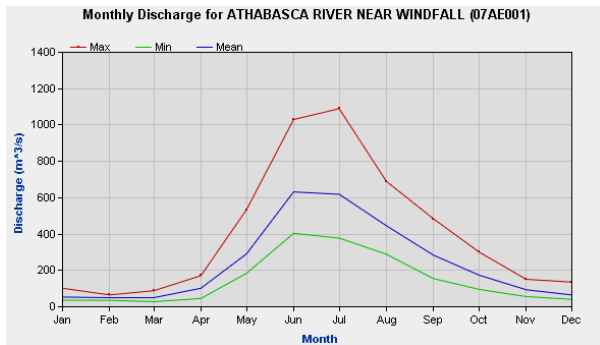
Figure 1. Pathway of Effect diagrams for Flow Management, a) original version (upper) and b) as revised during the literature review process. In-water linkages affecting fish habitat are shown in boxes and endpoints of concern to fish are in bubbles.



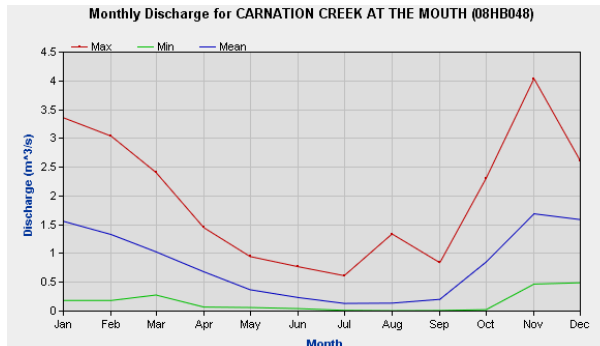
Catamaran Brook, New Brunswick
 Drainage area: 28.7 km²
 Record length: 16 yrs



Bronte Creek, Ontario
 Drainage area: 117 km²
 Record length: 17 yrs



Athabasca River, Alberta
 Drainage area: 19600 km²
 Record length: 46 yrs



Carnation Creek (Vancouver Island)
 Drainage area: 10.1 km²
 Record length: 34 yrs

Figure 2. Examples of natural (unregulated) flow regimes to show seasonal patterns of flow in rivers of Canada. Figures and data are from the Water Survey of Canada (<http://www.wsc.ec.gc.ca/staflo/>). Note that the magnitude of discharge (y-axis), drainage area and data record length (number of years) varies among rivers. Each graph shows the monthly maximum, minimum and average flow in cubic metres per second, averaged for the number of years indicated (record length).

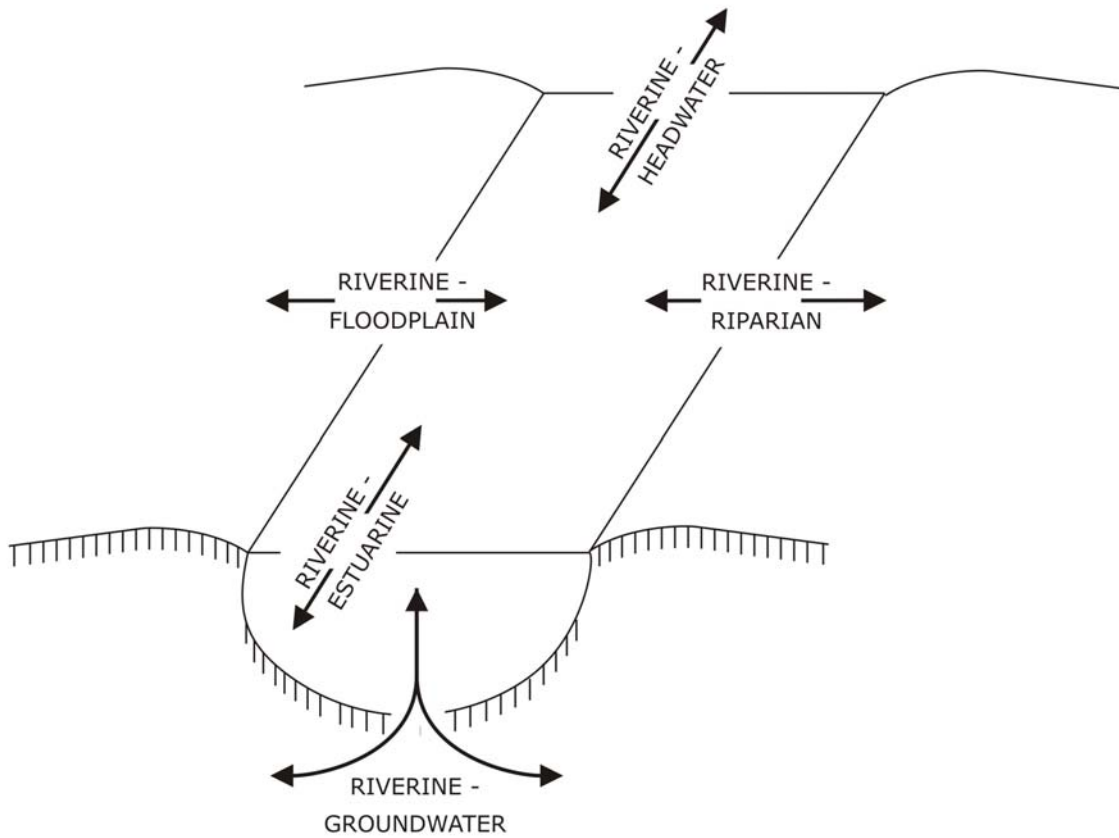


Figure 3. Spatial linkage of riverine ecosystems with headwater, riparian, floodplain, receiving waters, and groundwater areas (reproduced, with permission, from Ward and Stanford, 1989).

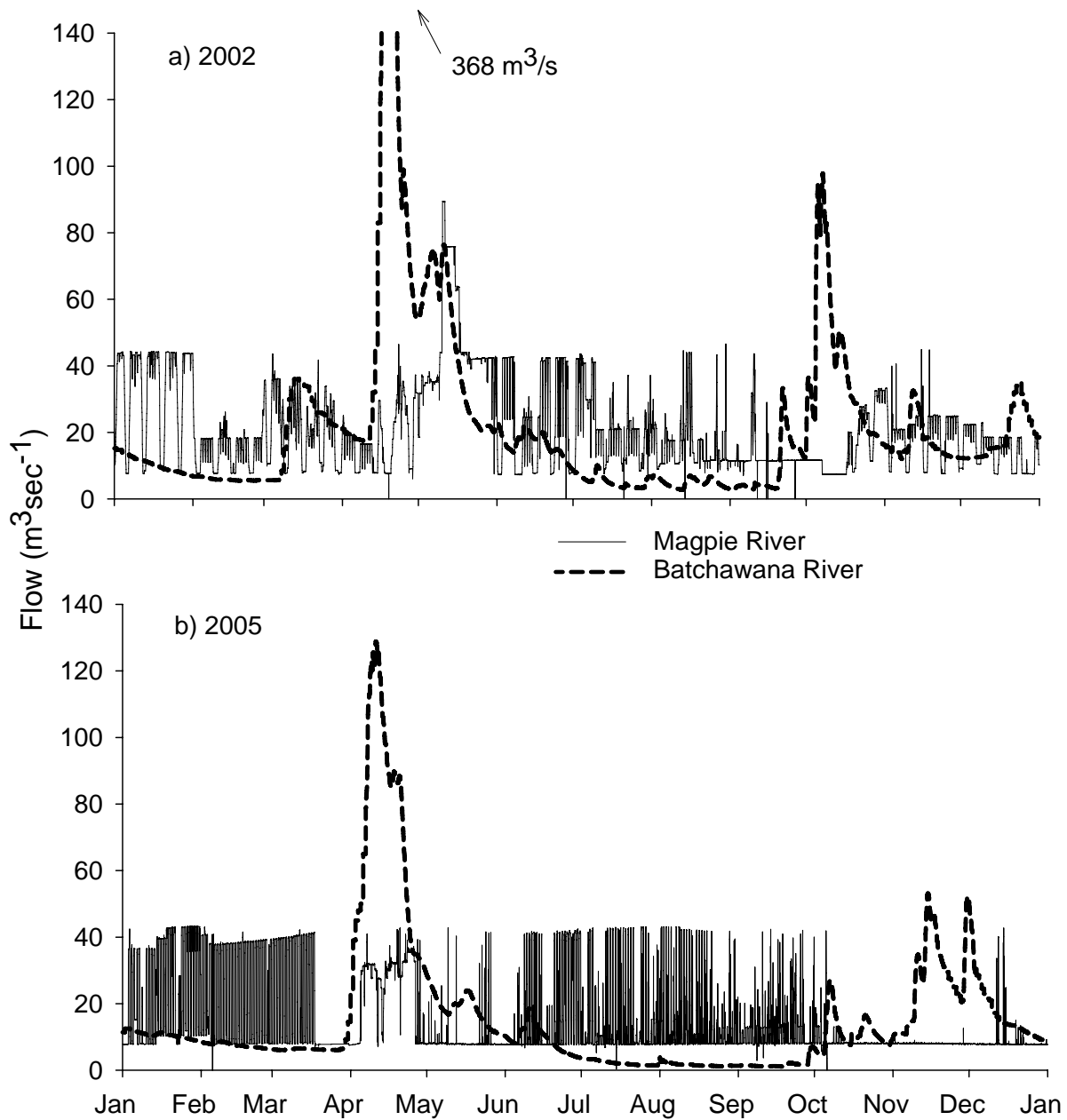


Figure 4. – Regulated hourly stream flow time series at the Steephill Falls Water Power Facility, Magpie River, Ontario, a) 2002 with ramping restrictions, and b) 2005 without ramping restrictions. Also shown are the unregulated stream flow time series for the Batchawana River, Ontario, during the corresponding years.