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**On fish in rivers during winter:
The challenges posed by ice and a warming climate**

NRC-OCRE-2024-TR-036

Prepared for:
Arctic and Northern Challenge Program (ANCP)

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Summary

This report is meant to raise general awareness of what is faced by fish in rivers during the winter. As the water temperature drops in the fall, rivers begin to freeze. This occurs at the surface, initially along the shorelines, then away from them. Where the water currents are low enough, a uniform ice cover develops. Higher currents, especially in areas where the water is not deep, will lead to a broken ice cover, which can accumulate in places and form an ice jam. There can also be open water all winter long. Ice can form below the water surface as well, either within the water column or along the riverbed. River ice causes an increase in water levels upstream because of the friction that exists between the flowing water and the bottom surface of the ice cover. A rough bottom surface and thick ice cover can cause significant flooding upstream. The break-up of ice jams may induce a sudden increase in water levels *downstream*.

There are approximately 180 fish species inhabiting Canadian rivers. Some of the most common ones are part of the salmon and trout Family, the minnow and carp Family, and the perch Family. Winter is a difficult time of the year for fish. Depending on geographical location, cold water conditions may last four to eight months. The challenges begin as the water temperature goes down to the freezing point. Fish are cold-blooded animals, and their body temperature is near that of the surrounding water. This causes a reduction in their metabolism. They are then less able to move, and seeking low-energy environments becomes a priority. Ice action is detrimental to fish in a number of ways. It can obstruct the channel and prevent them from seeking a suitable environment, or it can occupy those environments. Underwater ice poses several challenges for fish. For example, if it forms over egg nests, it can inhibit overwinter development of eggs. Surface ice can damage these and other critical habitats if it reaches the river bed or via gouging by drifting pieces. The changes in water levels and water currents during winter are also a liability for fish. Drastic events, such as an ice jam break-up, can have dire consequences for fish. Winter conditions, however, can also favor fish. An ice cover is a solid surface that does not exist in the summer and promotes calm environments when fish need it. It also constitutes a refuge against land-based predators because it is both a visual and a physical barrier.

Human activities can *directly* impact fish ecology – this is briefly reviewed also. The salient concern is the presence of structures built across river channels, such as hydroelectric dams. These are a significant barrier to fish mobility; they are also responsible for modifying the waterway, with a loss in the complexity and natural variability it had before dam construction. The cyclic nature of water releases from hydroelectric dams, which is meant to meet energy demands, is utterly unnatural from an ecological perspective.

Human activities can also *indirectly* impact fish ecology via climate change, primarily through an increase in air temperature, which has an important influence on the formation of ice and river dynamics during winter. In general, a reduction in the length of the ice season is expected, with later freeze-ups and earlier break-ups. Fish ecology will be affected by two concurrent sets of circumstances: water temperatures and ice action. Water temperatures are generally expected to rise, and fish adapted to cool or cold water are vulnerable to climate conditions that lead to warmer waters. Overall, an increase in water temperature will impact the entire food web which the fish depend on. Foreseeing the climate impact on fish in rivers is the subject of ongoing investigations by scientists from several fields of expertise.

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1. Introduction

1.1. Objective

Because of factors such as low water temperatures, currents, and the presence of ice, river habitats in winter have always been a harsh environment for fish. Compounded on that challenge are human-made structures such as dams, as well as a changing climate. This report is meant to raise general awareness of what this implies for fish.

1.2. Target audience

The report was written for an audience with little or no expertise in river ice or fish ecology. It may appeal to shoreline community members and decision-makers at various governmental levels overseeing initiatives and projects of ecological relevance throughout Canada. It could also be of interest to Indigenous communities for whom fish is a subsistence-based commodity, notwithstanding the fact that they already have an extensive knowledge base of their own on these environments.

1.3. Structure and illustrations

The report addresses the following themes:

- *What river ice is*: A summary of salient features related to freezing rivers.
- *Fish ecology in the winter*: A review of fish in rivers and how winter temperatures and river ice affect their lives.
- *The effects of dams*: A look at how these structures influence the ice regime and fish ecology.
- *Climate change*: A brief assessment of how climate evolution is expected to affect river ice and fish ecology.

A fair amount of visual material in the form of drawings and photographs has been incorporated into the text to help facilitate understanding of the various processes and phenomena at play. The author made the drawings with InkScape, an open-source vector graphics editor. Some of the pictures are NRC's; others were obtained from Wikimedia Commons, a well-known open-access image database.

1.4. Method

The information provided herein is the outcome of literature searches that were conducted on NRC's in-house ice engineering database as well as on Scopus¹. Information was also extracted from less well-curated compendia accessed via Internet search engines (Google, Bing). The search, which spanned the last four decades, generated a total of 50 to 80 documents of various relevance levels. Most were books, book chapters, articles published in scientific journals or papers included in the proceedings for conferences on river ice or fish ecology. That material was sorted, examined and distilled into this document. A listing of some of the key sources is provided in Section 8 for additional information.

2. River ice

2.1. A word on rivers

A river is a channel of flowing freshwater (non-saline water). Figure 1 shows a few examples. The width of a river, known as channel width, can range from several meters to kilometers. River flow is directed by gravity, moving from high ground to low ground. Typically, a river starts in the mountains or hills and flows towards lower areas, eventually reaching larger bodies of water such as lakes, larger rivers or the sea and

¹ Scopus is one of two large interdisciplinary abstract and citation databases of peer-reviewed documents – the other is Web of Science. Academic and some governmental institutions typically subscribe to one or both.

ocean. This flow, also known as discharge, increases in the direction the river is flowing. The increase in discharge is caused by the addition of tributaries (smaller streams and rivers that join it), and contribution from groundwater (subterranean flows). River discharge also varies with time because of factors like rainfall, evaporation, snow and ice cover in the winter and snowmelt in the spring. A river differs from a lake, in which currents are much lower, or with a bay or sea expanse, where water is saline and could flow, for instance, during tides.

Note that there is a difference between ‘flow’ (or discharge) and ‘current’. Flow applies to the river’s bulk volume over unit time (typically cubic meters per second). A current, on the other hand, is length over time (typically meters per second) – it is generally in the same direction as the flow but varies locally in both velocity and direction. For instance, currents are usually lower close to the shorelines or the river bed than it is toward the center of the channel. As will be seen later, the presence of ice exerts a strong influence on currents.

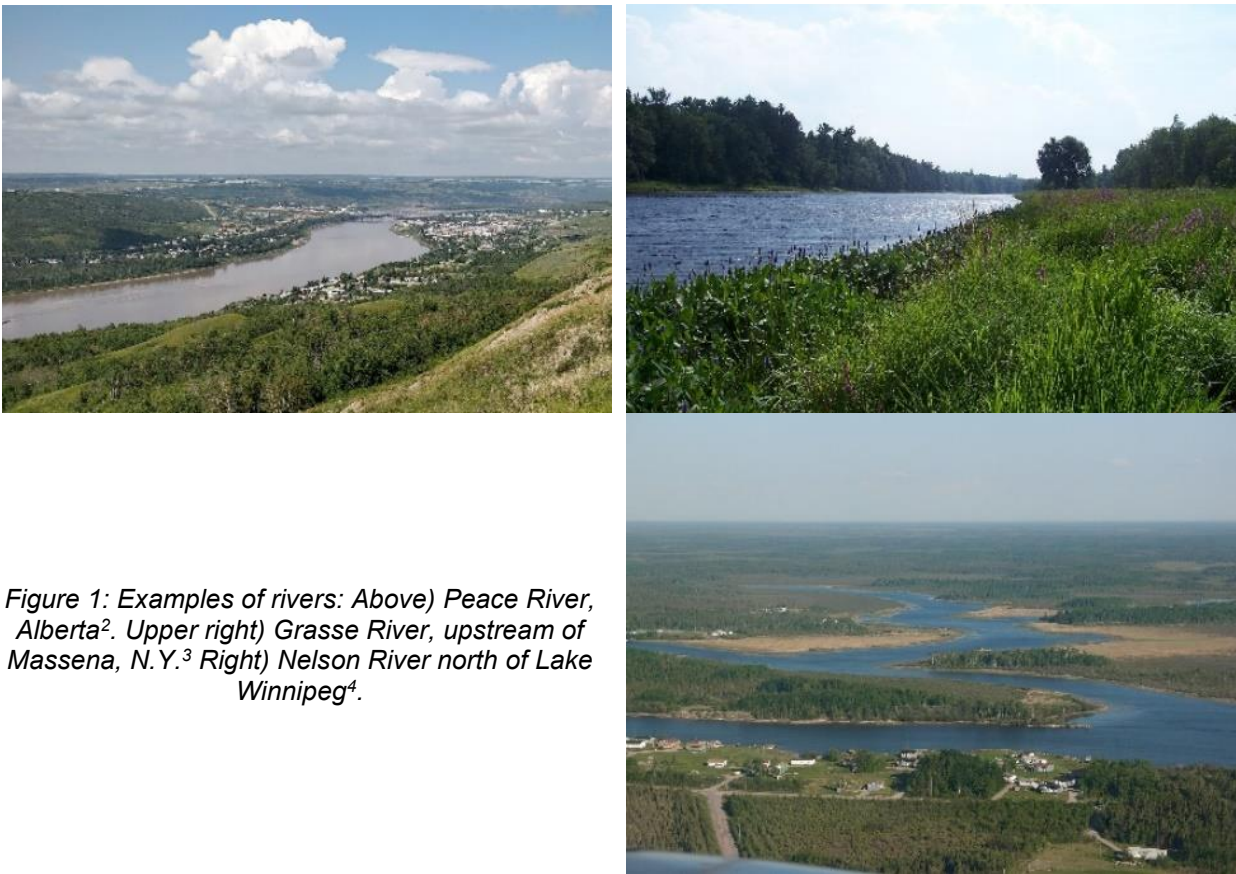


Figure 1: Examples of rivers: Above) Peace River, Alberta². Upper right) Grasse River, upstream of Massena, N.Y.³ Right) Nelson River north of Lake Winnipeg⁴.

² https://commons.wikimedia.org/wiki/File:Sagitawa_Lookout,_Peace_River,_Alberta.jpg, awmcphoe, CC BY-SA 4.0 <<https://creativecommons.org/licenses/by-sa/4.0/>>, via Wikimedia Commons
³ https://en.wikipedia.org/wiki/File:Grasse_massena.JPG
 CC BY 2.5, <https://en.wikipedia.org/w/index.php?curid=7439267>
⁴ [File:Nelson River near Norway House, from the air.jpg](https://commons.wikimedia.org/wiki/File:Nelson_River_near_Norway_House,_from_the_air.jpg) - Wikimedia Commons
 By US Mission Canada - Nelson River near Norway House, from the air, CC BY 2.0, <https://commons.wikimedia.org/w/index.php?curid=25675250>

Following are several aspects pertaining to rivers that are relevant to fish ecology:

- The ultimate destination of water flowing in a river is the sea – at that transition (the estuary), it becomes saline. Fish known as ‘anadromous’ are born in freshwater, migrate to the ocean to mature and grow, then return to the river to reproduce.
- A river provides fish with food and shelter and represents a pathway for travel between habitats, which may vary depending on the stages of their life.
- In shallower areas where the currents are strong enough, turbulent conditions are generated – rapids (white waters) are an example.
- Along the way, the water carries inorganic material in suspension – the stronger the current, the coarser the particles. Silt and clay are more common in calmer, low-turbulence waters.
- A river channel comprises different environments. Riffles (shallow and faster waters) and pools (deeper and slower waters) are more typical of steeper and narrower streams, while further downstream, where they widen and deepen, some river reaches may be more akin to a lake.
- Fallen trees, other forms of vegetation and boulders add to the complexity of habitats available to fish, as do variations in channel shape (straight, meandering) and morphology of the river bed (steep, shallow).

These characteristics locally translate into different habitats that are used by fish at different life stages. Habitat use also varies among species, e.g., some fish have a flat belly and modified fin shapes that allow for more bottom-dwelling, while others’ hydrodynamic profile allows them to move through high-current, turbulent sections.

2.2. Rivers in the winter

In a river, water freezes at the surface but also, under certain circumstances, below it. This section summarizes both cases because both affect fish in their own way. An explanation will also be offered as to why and how river ice leads to an increase in water levels, which is also a phenomenon that affects fish.

2.2.1. What happens at the surface

As air temperatures go down in the Fall, rivers begin to freeze, most commonly along the shorelines (known as *border ice* – an example is shown in Figure 2 and Figure 3). The reason that ice forms first along shorelines is that the water is in contact with the solid matter (soil, rocks, vegetation), which is as cold as the air temperature (below 0°C). Border ice may then extend out toward the river center and that ice may merge with the ice grown from the other shoreline (Figure 3). This scenario applies to many narrow streams and rivers. Just as in lakes, the ice cover then increases in thickness at a rate that mostly depends on air temperature but also on the snow cover, which acts as an insulator. Groundwater⁵ may also play a role because it is generally warmer, thus increasing stream temperature – this can affect open-water habitats throughout winter.

Along river segments where the currents are higher, especially when the water is not deep, open water can persist during the winter (Figure 4).

A summary of river ice formation is presented in Figure 5 – it captures what needs to be known in the context of the present report about what happens in rivers during the winter. It should be borne in mind, however, that there is an infinite number of scenarios, the details of which can vary greatly in complexity.

2.2.1. What happens *below* the surface

From a fish biology perspective, two classes of phenomena below the ice surface are influential: the generation of underwater ice and the thickening of the ice cover.

⁵ *Groundwater is water that naturally exists all year long below the surface, be it land or water, at depths ranging from less than a meter to a hundred meters or more. It is stored in aquifers – layers of soil, gravel or fractured rock formations – and moves through them. It is an important source of drinking water, especially in rural areas.*



Figure 2: Ottawa River, Ottawa. Formation of border ice along the shoreline. Photo: NRC



Figure 3: Rideau River, Ottawa. Slow currents (toward the camera) lead to a uniform ice cover. Border ice is seen on the left side. Photo: NRC



Figure 4: Petite Nation River, Quebec. Fast currents (toward the camera) lead to a broken ice cover and zones of open water. Photo: NRC

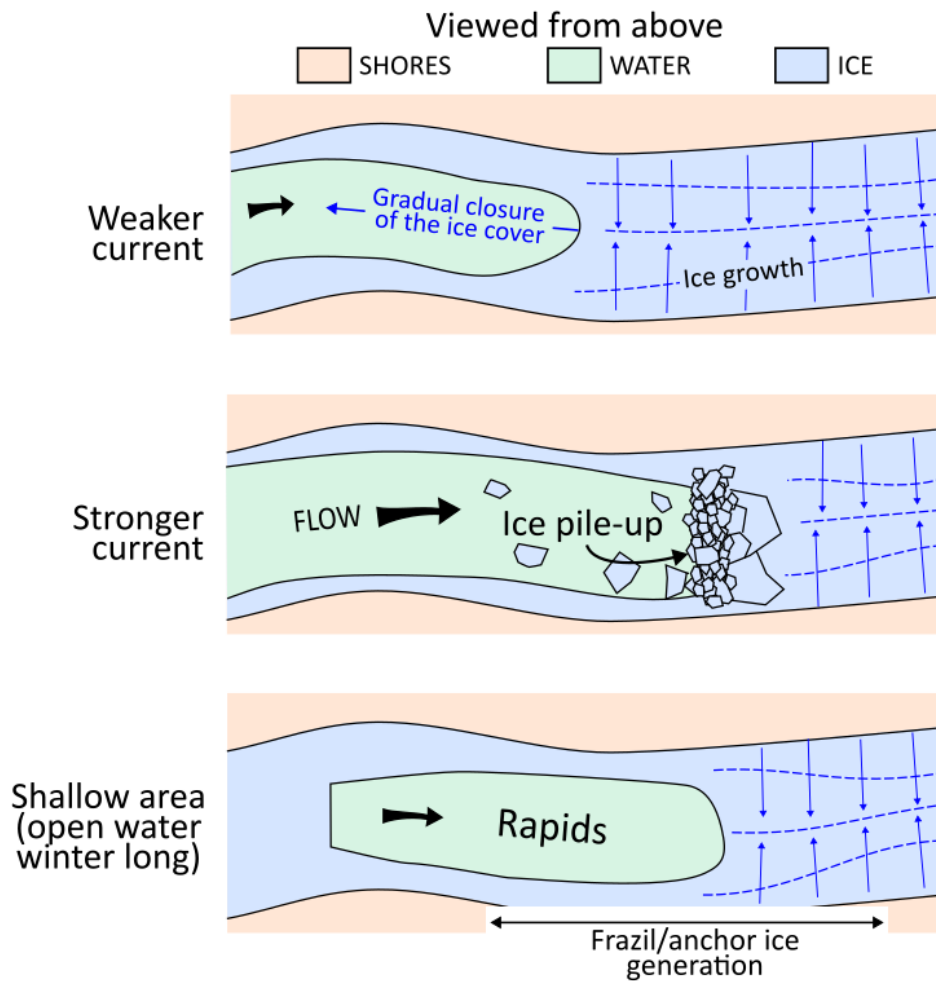


Figure 5: Three idealized scenarios for river ice, viewed from above. Top) Weaker currents lead to an ice cover of uniform ice thickness. Middle) Stronger currents can lead to an irregular ice cover where drifting ice may pile up at a given location, or the currents are strong enough to break the ice cover. Bottom) Where there are rapids, open water can exist all winter long.

Underwater ice

In open water conditions, such as where there are rapids and when the air temperature is very low (typically a clear winter night), a very large amount of ice crystals is generated in the water. This is known as *frazil ice* (Figure 6). That ice then coagulates into clusters, which then float to the surface, appearing as slush pans (Figure 7). Ice can also grow from the river bed and cover it like a blanket – it is then called *anchor ice* (Figure 8). As will be seen later, both affect fish.

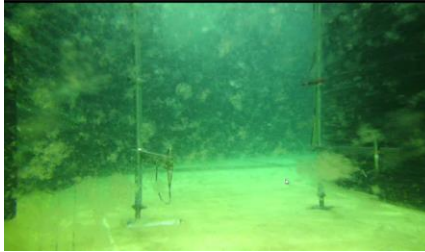


Figure 6: Frazil ice crystals and clusters below the water surface inside an experimental setup. The rods are about 1m in height.
Photo: NRC



Figure 7: Ottawa River, Ottawa. An assemblage of ‘ice pans’ made from frazil ice that has risen to the surface – here, it is seen attached to border ice. Glove on the branch for scale.
Photo: NRC



Figure 8: Rideau River, Ottawa. Ice growth along the river bed, known as anchor ice, is barely seen here through slightly turbulent water (flowing toward the camera). The river width is about 100 m. Photo: NRC

Thickening of the ice cover

In rivers, the ice cover can either be smooth or it may thicken when it is under pressure. In the latter case, the currents are strong enough to cause drifting ice pieces to jam⁶ and pile up (Figure 9). As will be seen in the next section, ice cover thickening has important implications for water levels, which, in turn, affect fish.

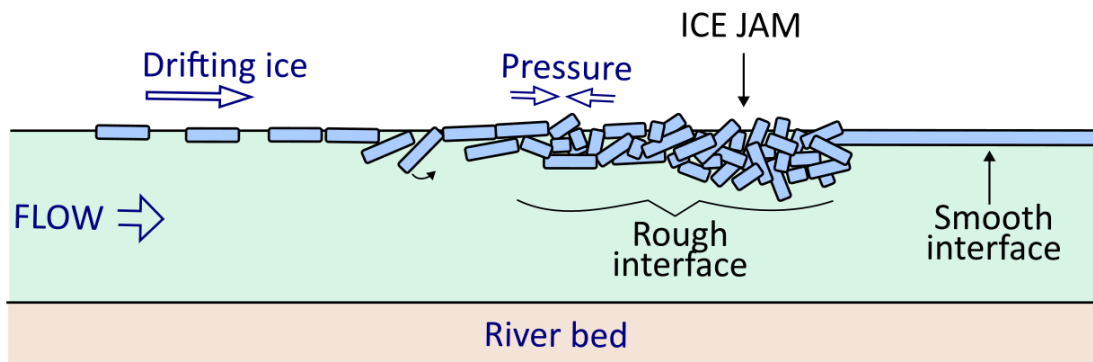


Figure 9: Simplified scenario (in a cross-section) of drifting ice pieces jamming at a given location against a uniform ice cover. It piles up due to strong currents. This increases the roughness of the interface between the ice and the water.

⁶ An ice jam occurs when drifting pieces of ice come to a stop at a given location.

2.2.2. Why and how ice affects water levels in a river

While water flows down a river under the action of gravity, it is counteracted by friction against the shorelines and the river bed. This limits current speed, especially near these interfaces. In the winter, the ice cover is *another* source of friction that does not exist in the summer. As a consequence, the water slows down more, *and the water level upstream increases* – this is known as ‘backwater’. The rougher the interface between the ice’s under-surface and the water, the higher the friction and the higher the water level upstream. This can happen throughout the winter.

At times and in places, the jammed ice can achieve considerable thicknesses, as shown schematically in Figure 10. In addition to the roughness, the ice accumulation also constricts the flow, which increases water levels upstream of the jam to an even larger extent, concomitant to an overall decrease in current velocity. Under some circumstances, the jam can abruptly break up with the release of the ice accumulation (Figure 11). This leads to an increase in water levels *downstream*, preceded by a wave of significant height (known as a ‘jave’) and an overall increase in current velocity.

2.3. Summary

A river is a body of water that is, as a whole, in constant motion. At the local scale, that motion is complex, as it depends on the channel morphology and the intricacies of the shorelines and river bed, including the presence and types of sediments, rocks and vegetation present. In the winter, ice adds another layer of complexity. Firstly, because it is another source of friction against flow, and secondly, because the ice itself, in its various forms, participates in and influences water dynamics. The intent of the foregoing was to capture the salient aspects of those dynamics as they bear on fish ecology.

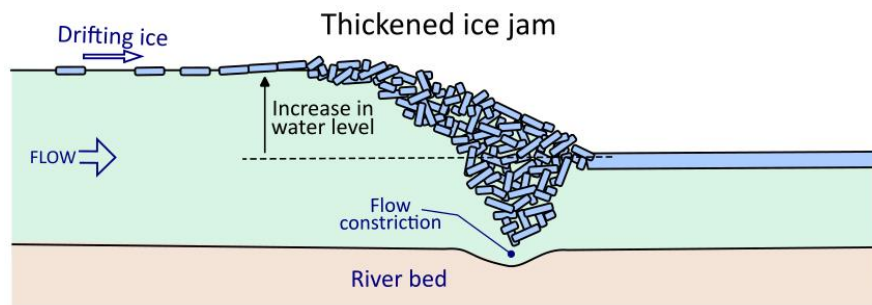


Figure 10: A thick ice accumulation causes a large increase in water levels upstream of it (exaggerated for the purpose of illustration).

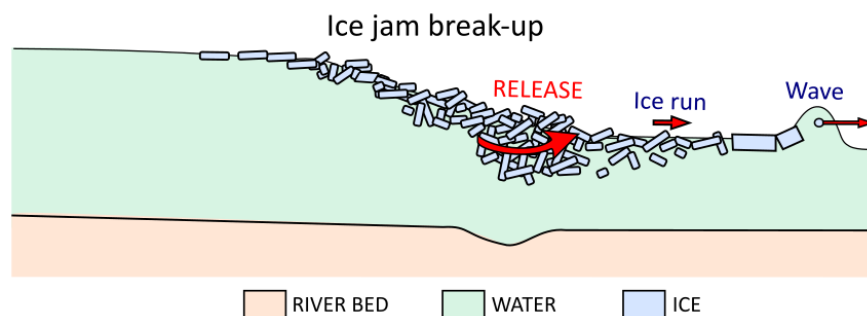


Figure 11: Ice jams can collapse, leading to an ice run and the formation of a large wave ahead of it.







3. River ecology and fish

Out of a multitude of life forms residing in rivers, fish may be among the best known, mostly because they are more visible and have always been a source of subsistence for humans. They play an important role in river ecology, as prey and predators, grazers of vegetation, reshapers of sediments, and overall contributors

to the microbiological ecosystem. Rivers provide fish with a wide variety of habitats: bed sediments, logs and wood debris, boulders and sub-aqueous vegetation can all be components of these habitats, with each one meeting requirements for food availability, shelter and energy management. This also includes anatomic adaptation – for instance, some have a flatter body shape for bottom-dwelling (e.g., sculpins), while the hydrodynamic profile of others allows them to move through high-current, turbulent sections (salmonids – e.g., trouts, salmon).

A total of about 180 fish species, divided into twenty-four families, have been reported in Canadian rivers⁷. Some of the most common ones represent the salmon and trout (salmonids) Family, the minnow and carp Family, and the perch Family (Table 1). Many of the sources that were consulted for this report were primarily concerned with the salmonids, while others dealt with fish in general. The intent herein is to attempt to bring together commonalities in the way that fish, in general, cope with winter conditions.

Table 1: Examples of fish species known to exist in Canadian inland waters. For comparison purposes, the images were processed so that the fish all face in the same direction and dimensions are roughly to scale (indicated by the hand).

| | | |
|--------------------------------|--|--|
| <p>Salmon and trout Family</p> |  <p>Arctic char – <i>Salvelinus alpinus</i> (Source)</p> |  <p>Brook trout – <i>Salvelinus fontinalis</i> (Source)</p> |
| <p>Minnow and carp Family</p> |  <p>Hand for scale</p> <p>Lake chub – <i>Couesius plumbeus</i> (Source)</p> |  <p>Longnose dace – <i>Rhinichthys cataractae</i> (Source)</p> |
| <p>Perch Family</p> |  <p>Yellow perch – <i>Perca flavescens</i> (Source)</p> |  <p>Walleye – <i>Sander vitreus</i> (Source)</p> |

⁷ Scott and Crossman (1973) – See reference section.

The long-term persistence of fish populations is strongly influenced by reproduction and the ability of young fish to survive. For most freshwater fish, reproduction is external, which means the eggs are fertilized outside the body of the female. For river-spawning fish species, the female first lays a large number of eggs on the river bed, a process known as 'spawning'; the male then spreads his sperm over them. In the case of salmon, the female may first carve a depression in the bed with her tail before laying the eggs, then cover them back and watch over the spawning area (also called 'redd') for some time afterward. A male may create and guard a redd site, then wait for a female to 'pick' that site. During the incubation time, the eggs hatch into baby fish, called alevins, which, depending on the species, can remain in the river bed for a while (Figure 12). The availability of running water and a permeable bed at that site is important because it provides adequate oxygenation and also facilitates the removal of metabolic waste (e.g., excrement) generated during their growth.

As will be seen, winter conditions in rivers can be detrimental to the nests in the case of fish species that spawn in rivers prior to the winter.

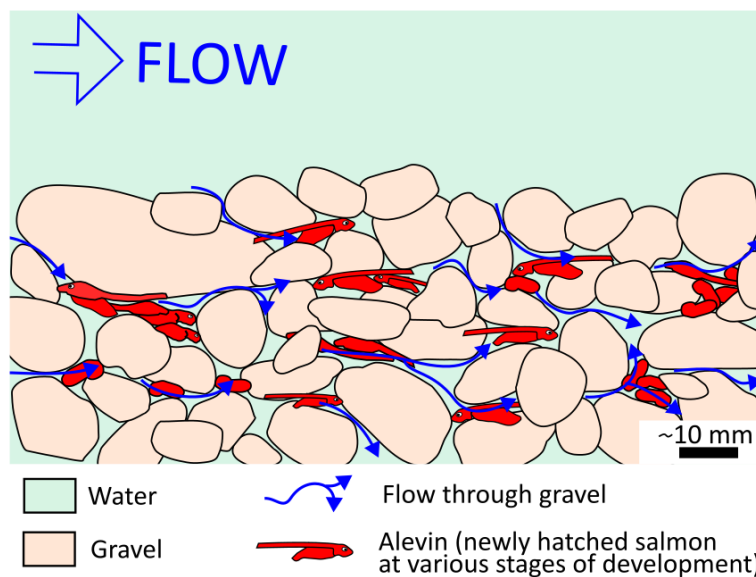


Figure 12: After hatching, the alevins remain in the river bed for some time. Flow through the bed is important for oxygenation and waste removal.

4. Effects of river ice on fish

Winter is a difficult time of the year for fish. Depending on geographical location, cold water conditions may last between four and eight months. In general, it is defined as the period that starts with a reduction in water temperatures in the fall and ends in the spring when all ice has disappeared from the river channel. In addition to the low temperature of the water, the mere presence of ice influences fish populations and behavior. Ice reconfigures the physical space in a river compared to what it is in the summer and in places that can vary from one winter to the next, depending on ice dynamics.

4.1. Water temperature

Water temperature in rivers is important for fish because they are cold-blooded animals, and their body temperature is about that of the surrounding water. Different species react differently to water temperatures, with some having a narrow range of temperature tolerance. This may also depend on age – for instance, fish are often most vulnerable to changes in temperature at the beginning of their lifespan. During the fall, the water temperature decreases progressively. Low temperatures generally translate into low metabolism,

as the fish uses its stored energy more than it is processing food. This induces lower activity levels, so less time is spent feeding and defending territory. During this time, fish are also less able to move or work against currents. Hence, the choice of river habitat can be governed by the need to minimize energy. Factors such as depth and low current velocities, as well as the presence of features such as stones, vegetation, log jams and crevasses, are instrumental for sheltering purposes. So are off-channel areas, such as side channels, swamps and ponds (including beaver ponds). Where groundwater is seeping into the river, since it is usually warmer, it can be favorable to fish.

Fish in low-energy mode are vulnerable when forced to move in the water (examples are provided below) because they then have to consume more energy. This can lead to mortality, depending on factors such as size and predator action.

Under some circumstances, such as during a mid-winter warm spell, the water temperature increases, which may result in a sudden increase in fish metabolism – this could then lead to a need for a different habitat, where food availability becomes a priority.

4.2. Influence of ice

River ice has several implications for fish ecology – Table 2 presents a general summary. Some are an advantage to the fish, i.e., an asset favoring survival. Most others represent a liability.

4.2.1. Detriments

Below is a summary of the main adverse effects caused by winter conditions.

Channel obstruction

What was an open channel during the ice-free season can be occupied or completely blocked off by ice, especially along the shorelines, where the currents are lower (Figure 13). This limits fish mobility, for instance, if they seek water masses with better temperature conditions, better shelter or deeper waters. It entails a reduction of available habitat that can lead to overcrowding of the fish population. This forces fish to migrate to other suitable habitats, and even this may be difficult if the channel is cluttered with ice.

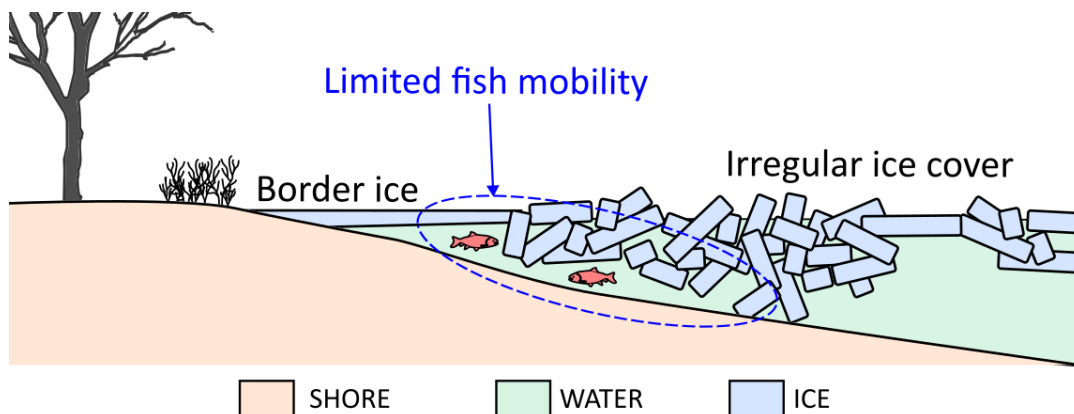


Figure 13: The presence of ice limits fish mobility.

Open water areas

As mentioned earlier, unfrozen water areas during the winter are typically found along rivers where year-long rapids exist. They favor the generation of frazil ice, which fish have been shown to avoid. Frazil ice can also accumulate in very large quantities below the ice cover further downstream or below the border ice, filling in available space where fish can no longer find refuge; that ice also contributes to channel constriction. Open water areas in the winter favor the formation of anchor ice if it fills in pools; this can

deprive fish of otherwise suitable habitats or cause an increase in water currents (because of flow constriction).

Disturbance of the river bed

Under some circumstances, ice can reach down to the river bed, which presents a risk to spawning areas. This can happen as follows:

- *Scenario A:* Near the shorelines and in shallow areas, the downward growth of an ice cover reaches the river bed (Figure 14). That space is thus no longer available for refuge, and the ice may freeze up a spawning area if there is one at that location.
- *Scenario B:* Drifting ice pieces, driven by currents, reach down to the river bed and gouge through these areas, thereby damaging or destroying egg nests (Figure 15). Ice can also disturb or even remove vegetation below the water line, which is an important part of fish habitat.
- *Scenario C:* When anchor ice forms over spawning areas, it can block off access to substrate interstices for sheltering, thereby reducing the intra-gravel flow needed to oxygenate the buried embryos and remove their waste (Figure 16). The damage is more considerable if the freeze-up extends deeper into the river bed.

Changes in water levels

We have seen earlier that the presence of an ice cover can cause an increase in water levels. This also means the levels are lower elsewhere. Such a reduction in water level reduces fish habitat along the shorelines. If the level declines below that where there are spawning areas, the eggs will freeze because they are exposed to cold air temperatures (Figure 17).

Changes in currents

Partial blockage of the river channel unavoidably engenders local increases in current velocity. Fish may not handle higher currents well because their body, at these near-zero temperatures, has a low metabolic rate. This limits their swimming capacity. The presence of ice at some locations will also alter flow in a complex manner (compared to what it was under open water conditions) – this may also be challenging for fish. For instance, an adequate flow that carries oxygen and nutrients (Figure 12) may not always be available at the river bed, adversely affecting spawning areas and juvenile populations.

Ice jam break-ups

When a large ice jam breaks up (Figure 11), the release of the ice that accumulated at that location can gouge its way through gravel bars and remove small islands, thus permanently changing the habitat. It can disturb aquatic vegetation and displace immersed tree trunks, rocks and other features used as substrate or refugia. The outcome could also be favorable if it increases habitat. The rising water levels downstream from the jam as it breaks up can be drastic and very fast. Fish may be carried into floodplains and then get stranded, leading to mortality from predators or suffocation.

Unstable environment

Fish need a stable environment to survive, particularly in the winter, i.e., one that minimizes their energy expenditures. The variations in time and space of ice distribution, water levels, current velocities, temperatures and substrate that occur throughout the cold season are not conducive to habitat stability. This would be the case for the two bottom scenarios in Figure 5.

4.2.1. Benefits

Winter conditions can favor fish in a number of ways. An ice cover is a solid surface that does not exist in the summer. It constitutes a refuge against land-based predators because it is both a visual and a physical barrier. Border ice, which starts to form early in the winter, can assume that role already at that time. It may also favor a more stable environment than under open water conditions.

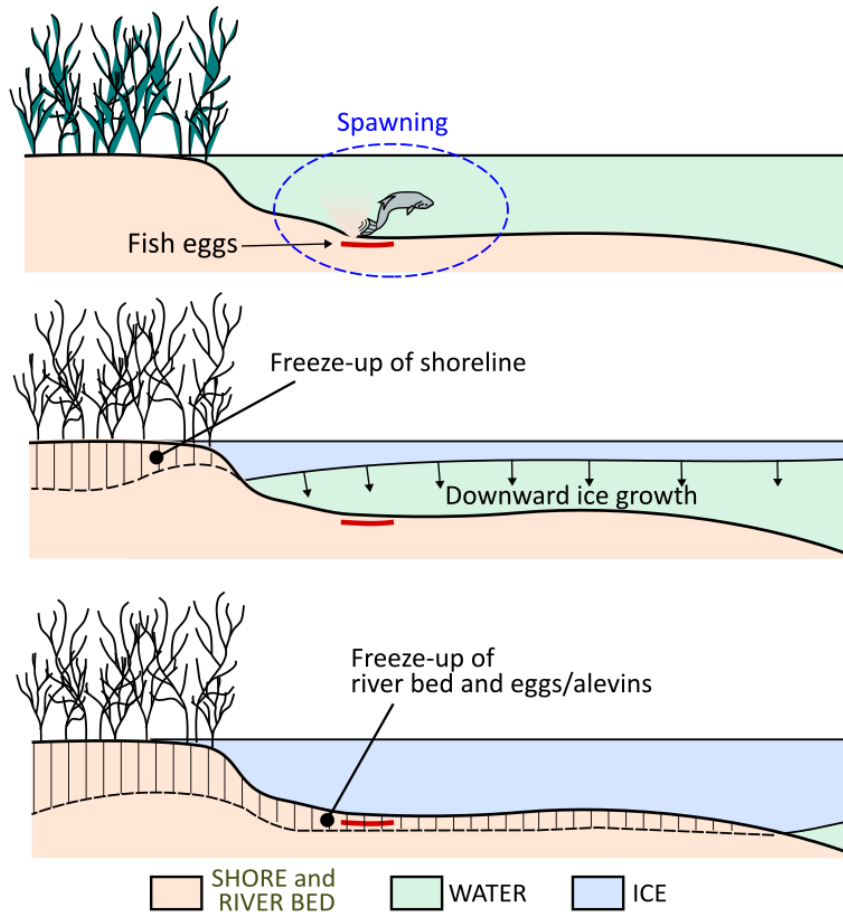


Figure 14: Downward growth of an ice cover that reaches the river bed – this will freeze up a spawning/incubation area.

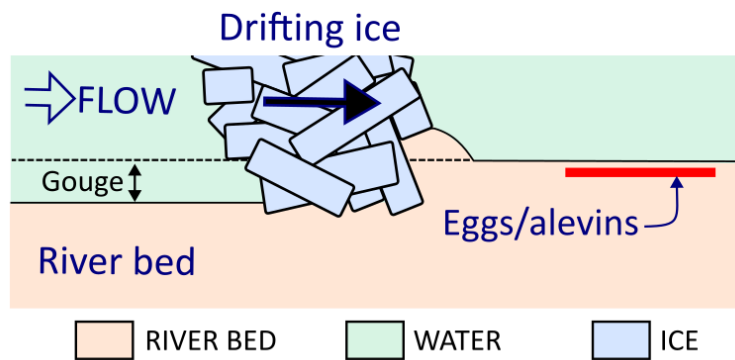


Figure 15: When the ice reaches the river bed, it can plow its way through the sediment and destroy spawning/incubation areas.

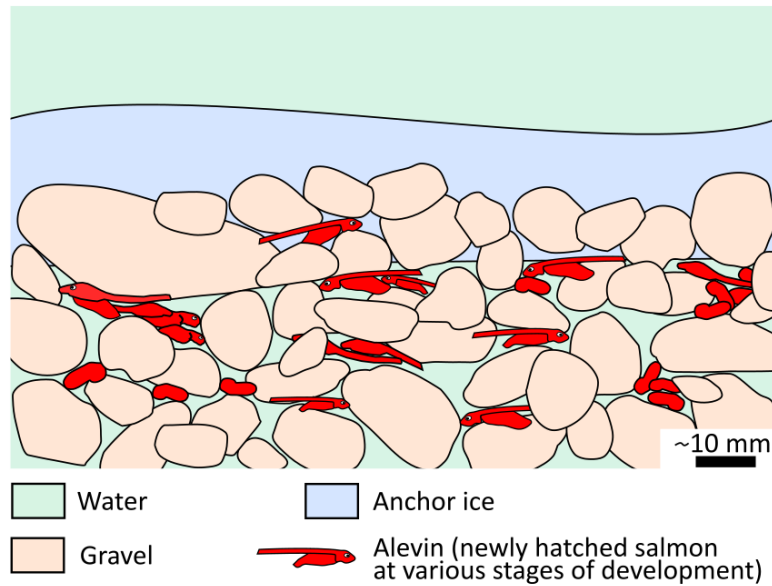


Figure 16: When anchor ice forms above a redd, it prevents the circulation of water through the pores spaces (as shown in Figure 12), thereby presenting a threat to fish survival.

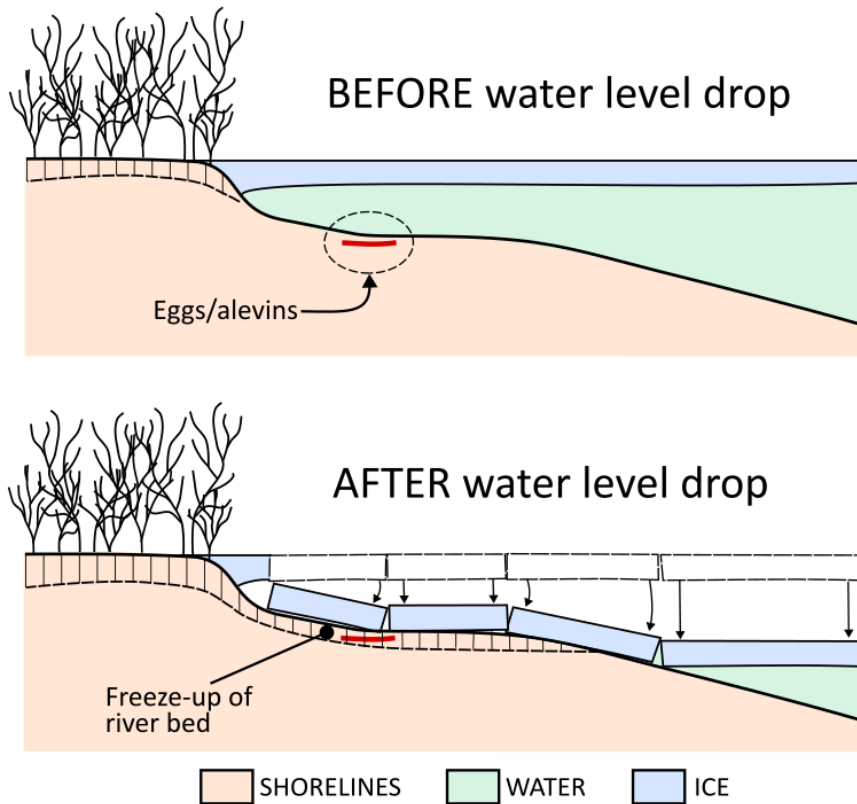


Figure 17: A reduction in water level that allows the river bed to be exposed to cold winter air will cause it to freeze. This represents another liability to spawning/incubating areas.

4.2.2. Benefits

Winter conditions can favor fish in a number of ways. An ice cover is a solid surface that does not exist in the summer. It constitutes a refuge against land-based predators because it is both a visual and a physical barrier. Border ice, which starts to form early in the winter, can assume that role already at that time. It may also favor a more stable environment than under open water conditions.

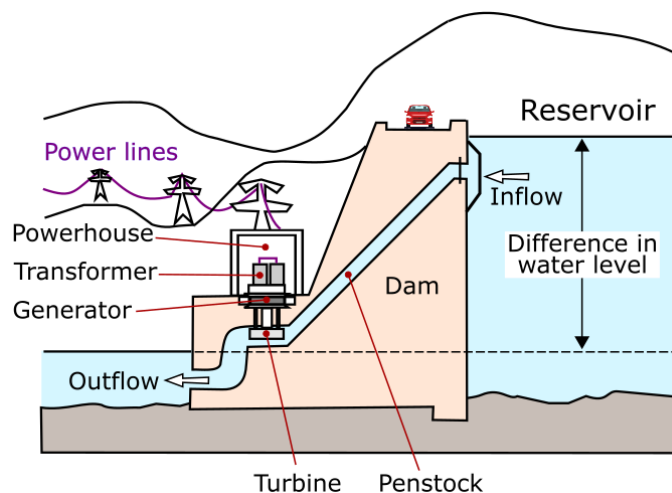
Because the ice cover is a source of friction at the water-ice interface, it slows down the flow. The outcome is an increase in water levels upstream. From the perspective of human communities and shoreline facilities, these can lead to severe floods. A considerable amount of research has been performed over the past several decades and is ongoing to enable the prediction of these flooding events. From the perspective of fish, however, the implications of deeper waters are much more complex. They cause an increase in habitat extent along the shorelines, partly because of the concurrent reduction in current velocity in those waters. This is favorable to fish because it helps them minimize their energy expenditure at a time of the year when they need it most.

Low water temperatures and low light conditions (due to the presence of an ice cover) can also contribute to reducing competition between species or individuals. Overall, if fish have access to a suitable environment and since they function at low metabolic rates, they are able to withstand river conditions in the winter relatively well.

4.3. Influence of dams

Humankind exerts additional pressure on fish populations. It does so directly – one notable example are dams, but there are many others (e.g., channel reconfigurations, shoreline vegetation, pollution, over-fishing, thermal discharges). The term ‘dam’ is used here to mean a generic structure built across a river channel and able to impound water (Figure 18). These structures are typically designed to generate electricity, but they may have other purposes. The implications, summarized in Table 3, compound some of the issues raised in Table 2.

Figure 18: Generic example of a hydroelectric dam.



While some dams accommodate fish migration, in general, they are a significant barrier to mobility. The erection of a new dam permanently modifies the waterway. What may have been a narrow river is converted into a lake-type water expanse upstream of the structure. Fish adapted to a river environment move away from that location. Those adapted to a lake environment move into it. Downstream, the channel may lose the complexity and natural variability it had before the dam construction. This may translate into the removal of favorable habitat and the substrate that was there before is no longer available.

The dam’s normal operations have a major bearing on river ice and fish ecology. In the case of a larger dam with a sizeable water impoundment, water released from a deeper level behind the dam can be warmer than the river downstream from it. The reason is that the temperature at the bottom of the water upstream may be as high as +4°C, while the water temperature downstream is very close to 0°C. This difference is

significant. Instead of a solid ice cover downstream, there may be open water areas, promoting the formation of frazil ice and anchor ice. In some circumstances, the warm water may remove anchor ice that was already there, a positive outcome. An increase in water temperature will increase the fish's metabolic rate, which will promote its activity, but at a time when its food may not be available – the overall outcome in this scenario is a loss of energy reserve.

The cyclic nature of water releases from hydroelectric dams, which is usually more concerned with meeting energy demands than with biology, is utterly unnatural from an ecological perspective. Such variations are inconsistent with any natural processes and occur at a time when fish need a stable environment:

- Sudden short-term increases in *water levels* may increase the probability of fish stranding on dewatered channel margins during low flows. High flows, on the contrary, increase available habitat.
- Random short-term changes in the *amount* of water discharge fed to the river downstream of the dam are also detrimental. For instance, low discharge can lead in places to sedimentation of fine material, which will cover the spawning/incubation areas and deprive them of the oxygenation they require.
- If not managed appropriately, water discharges could lead to repeated ice jam break-up events, keeping the channel in perpetual freeze-up conditions and inducing fish mortality.

5. Climate impact

Global warming is a term used to designate an average increase in temperature of the Earth's atmospheric system since the pre-industrial age in the mid-19th century. The burning of fossil fuels has increased the amount of greenhouse gases in the atmosphere, with carbon dioxide (CO₂) being the most abundant, alongside others, such as methane (CH₄) and nitrous oxide (N₂O). These elements belonged to another geological age – which is why they are called 'fossil' – and were artificially brought into ours. The outcome is a rise in the overall temperature of the Earth's atmosphere by about 1°C. While this appears to be negligible in our day-to-day living, it has important consequences on the temperature distribution over the planet's surface, air circulation, precipitations and other phenomena. These consequences are collectively referred to as 'climate change'⁸ (Figure 19). From the planet's perspective, this is not new – in its geological history, there is evidence of various warming and cooling events, some more dramatic than the current one. The difference is that humans' activities are causing today's warming, with various consequences on our infrastructures and on other lifeforms.

Some of the deleterious impacts are an increase in the frequency, intensity, and duration of climate and weather extremes, notably temperature, precipitation and wind. These changes are highly inhomogeneous and location-dependent. Powerful computer models, known as Global Climate Models (GCMs), are downscaled to Regional Climate Models (RCMs), which are used to assess these phenomena at a local scale. River ice is one of many natural phenomena that is being affected by climate change. Following is a brief summary of what may be expected from rivers and their action on the fish that live in them.

5.1. Impact of climate on river ice

Being able to predict how river ice will evolve at a given location relies on our ability to simulate many variables at that location using RCMs. Air temperature is the most influential one; others include precipitations (rain or snow), solar radiation, and cloud coverage. A changing climate will affect these hydro-climatic conditions, which will, in turn, have an impact on river flow and river ice dynamics. The following are currently believed to be some of the consequences:

- With time, the ice may become intermittent or not form at all, or the ice covers will be thinner. In general, there is a reduction in ice season length, with later freeze-ups and earlier break-ups.

⁸ This term is defined as “[a] persistent, long-term change in the state of the climate, measured by changes in the mean state and/or its variability.” Bush and Lemmen (2019, p. 32)

Table 2: Main implications of river ice on fish ecology.

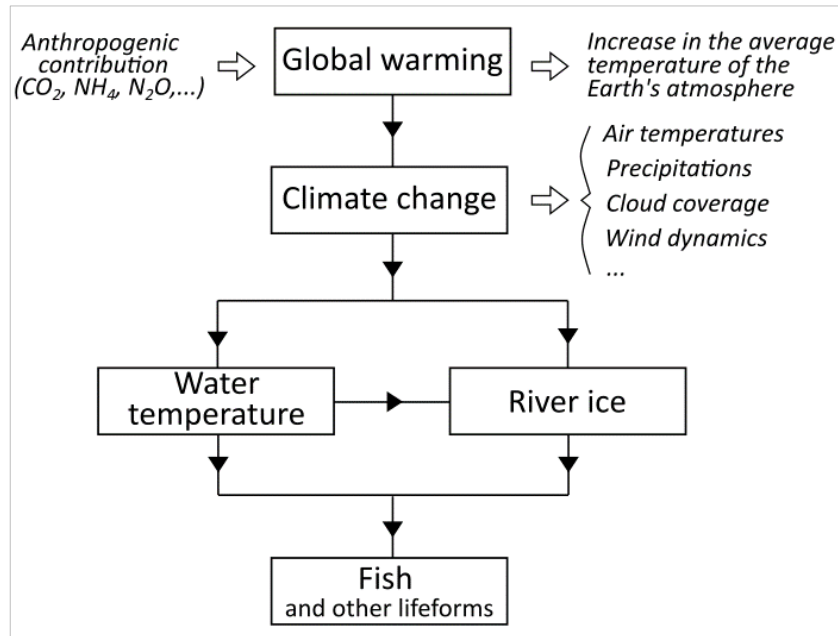
| Factors | What it means | How it affects fish |
|-------------------------------------|---|---|
| Continuous ice cover | A hard surface that was not there in the summer | <i>An ice cover affords some protection against land predators, including below the border ice, where water velocities are low.</i> |
| | Increase in the water level upstream, especially when the ice undercover is rough | <i>New habitat becomes available along the flooded shorelines.</i> |
| | | <i>A reduction in flow velocity helps fish to minimize their energy expenditure.</i> |
| Channel obstruction | Reduction in the channel's cross-sectional area through ice cover thickening, rubble accumulation, etc., along the shorelines or by thick anchor ice accumulation | <i>This limits fish mobility, for instance, if they seek water masses with better temperature conditions, better shelter or deeper waters.</i> |
| | | <i>Crowding of fish population may occur due to the reduction of available habitat, thus forcing fish migration.</i> |
| Open water areas | Generation of frazil ice | <i>That ice contributes to channel obstruction – fish tend to avoid these areas.</i> |
| | Generation of anchor ice | <i>That ice blocks off access to substrate interstices for sheltering and reduces the intra-gravel flow needed to oxygenate the buried embryos and remove their waste. Anchor ice can also fill in pools and deprive fish of an otherwise suitable habitat or cause an increase in water currents.</i> |
| Disturbance of the river bed | Freeze-up of the river bed in shallow areas as the ice reaches down to that level | <i>Freeze-up of spawning/incubating areas.</i> |
| | Gouging by drifting ice as it reaches down to the river bed | <i>By digging into the river bed, the ice can destroy the spawning/incubating areas.</i> |
| | Removal of aquatic plants below the waterline | <i>Vegetation is used as cover and for protection from predators in open water conditions.</i> |
| Changes in water levels | Increase in water levels upstream of an ice cover or an ice jam | <i>Increase in available fish habitat as the water floods the shorelines.</i> |
| | Decrease in water levels due to the action of ice | <i>Reduction in available fish habitat as the water recedes away from the shorelines.</i> |
| | | <i>If the level declines below that where there are eggs or alevins, they will freeze.</i> |
| Changes in currents | Increases in velocities due to a decrease in the channel's cross-sectional area and during ice jam break-up | <i>Fish may not swim against high currents well because their body, at these near-zero temperatures, has a low metabolic rate, thereby limiting their ability to swim.</i> |
| | Locally complex patterns caused by the ice distribution where it is close to the river bed | <i>Adequate flow that carries oxygen and nutrients may not always be available at the river bed, adversely affecting spawning areas and juvenile populations.</i> |
| Ice jam break-ups | A large amount of ice is released and carried downstream by the currents | <i>Removal of gravel bars, small islands and extensive disturbance to aquatic vegetation, permanently changing sub-aqueous environment (wood, pebbles and others used as substrate or refugia), with negative (e.g., disrupting spawning/incubating areas) and positive (increasing habitat) outcomes on fish life.</i> |
| | Sudden increase in water level downstream of an ice jam due to the passage of a wave upon break up of the jam | <i>Fish may be forced or carried into floodplains and then get stranded, leading to mortality from predators or suffocation.</i> |
| Unstable environment | Variations in time and space of ice distribution, water levels, current velocities, temperatures and substrate | <i>This leads to an abrupt increase in water level quickly followed by a decrease, potentially resulting in a wash-out, where the fish is pushed out of the channel and left stranded on land, exposed to predators and suffocation.</i> |
| | | <i>This deprives fish of a stable environment, which they need to survive, i.e., one that minimizes their energy expenditures.</i> |

Table 3: Main implications of a dam on river ice and fish ecology.

| Factors | What it means | How it affects river ice and fish |
|--------------------------------|---|---|
| River crossing | Significant barrier across the channel | <i>It impedes fish mobility, either local or long-range (for the species that migrate).</i> |
| Changes in the waterway | What may have been a narrow channel before dam construction is converted into a lake-type water expanse | <i>Fish adapted to a river environment move away from that location. Those adapted to a lake environment move into it.</i> |
| | Downstream, the channel may lose the complexity and natural variability it had before the dam construction | <i>Favorable habitat and substrate are no longer available for the fish.</i> |
| Release of water | If the water is released from a deeper level in the impoundment behind the dam, it will be a few degrees warmer than the river downstream from it | <i>Instead of a solid ice cover downstream, there will be open water areas, promoting the formation of frazil ice and anchor ice.</i> |
| | Random, short-term changes in <i>water levels</i> downstream of the dam | <i>In some circumstances, the warm water may benefit the fish by reducing or removing anchor ice.</i> |
| | | <i>This increase in temperature will increase the fish's metabolic rate, which will promote its activity, but at a time when prey is not available – the overall outcome is a loss of energy reserve.</i> |
| | Random short-term changes in the <i>amount of water discharge</i> fed to the river downstream of the dam | <i>This may increase the probability of fish stranding on dewatered channel margins.</i> |
| | | <i>Such variations are inconsistent with any natural processes and occur at a time when fish need a stable environment.</i> |
| | | <i>Low discharge can lead in places to sedimentation of fine material, which will cover the spawning areas and deprive them of the oxygenation they require.</i> |
| | | <i>This could lead to repeated ice jam break-up events, keeping the channel in perpetual freeze-up conditions.</i> |
| | | <i>Such variations are inconsistent with any natural processes and occur at a time when fish need a stable environment.</i> |

- Thinner ice covers are expected, as well as a reduced ice cover strength.
- Warmer water temperatures in the fall and an increasing amount of precipitation would delay river freeze-up initiation.
- Increased flow in the fall, on the other hand, may promote thicker ice (because of rubble piling up) and water levels, altogether increasing the level of heterogeneity of a given river.
- The number of mid-winter break-ups can be expected to rise, mainly due to warm spells and winter rain.
- Disruptive break-ups may start to occur more frequently on rivers that normally do not experience these events.

Figure 19: A simplified representation of the relationships between the overarching concepts described in this report. Arrows point in the direction of impact.



5.2. Impact of climate on fish ecology

Fish ecology will be influenced by two concurrent sets of circumstances subjected to climate change: water temperatures and ice action.

- As water temperatures are generally expected to rise, fish adapted to cool water are vulnerable to climate conditions that lead to warmer waters. A northward shift, or to higher altitudes in mountainous areas, in the range of some species should be expected.
- Species with little tolerance to changes in water temperatures will likely suffer the consequences.
- Under these circumstances, an environment that has deeper water pools would be favorable to fish.
- An increase in water temperature will impact the entire food web which the fish depend on. This begins with the rate at which solar energy is converted to organic substances, which will shift or expand. The availability and distribution of winter insects will also change.
- Shorter winter seasons will cause migrating (anadromous) fish to shorten their stay in freshwater environments and travel earlier toward seawater.
- The timing of ice break-up may have a negative influence on the growth and survival of some fish species.
- Multiple break-ups in a given winter will increase the disturbance level of river sections where they occur.

6. Conclusion

Winter is a challenging time of the year for fish. Because they live in water and are cold-blooded animals, the temperature of the water controls their metabolic rate. Low water temperatures translate into a low metabolic rate, which means they cannot swim against a current if it is too high and will thus seek a calm environment. The physical presence of ice is mostly, but not entirely, detrimental to fish. It provides them with a stable environment in places; it also affords protection from land-based predators. However, unlike in lakes, ice in rivers can be very dynamic. Depending on factors such as channel morphology, discharge and climate parameters (namely air temperature and precipitation), an ice cover may never form, leading to the growth of ice throughout the water column and along the river bed. This represents a liability for fish and their spawning grounds. An ice cover can also be converted into a pile of rubble, reaching down to the river bed and blocking off available space. River ice can be unstable. When an ice jam suddenly breaks up, a large amount of ice will be entrained by the flow, with potentially dire consequences on fish microenvironments downstream.

The winter regimes described herein have existed for thousands of years. From an ecological and environmental perspective, therefore, these events are part of what has been happening irrespective of human presence. Humankind now exerts additional pressure on fish populations. It does so directly – one notable example are dams, but there are many others (e.g., channel reconfigurations, shoreline vegetation, pollution, over-fishing, thermal discharges). Human action also affects fish indirectly via climate change. This has several consequences, including warmer water, which has a negative impact on cold water fish, as well as a number of river ice processes. Assessing climate impact is fraught with uncertainties. Firstly, we do not know the amount of greenhouse gases that will be released into the atmosphere by our societies in years to come. Secondly, converting that parameter to climate behavior globally, then regionally, is very challenging. Thirdly, how does that affect rivers, river ice and the biological realm that fish depend on for their survival? This is the subject of ongoing investigations by scientists from several fields of expertise.

7. Acknowledgements

This review was produced in support of the Arctic and Northern Challenge Program (ANCP) of the National Research Council. The ANCP is addressing factors that are affecting the quality of life of Northerners, namely the Indigenous people. This includes access to traditional and country foods, which remain an important source of nutrition for those communities. Comments from H. Swanson, D. Sudom and I. Vouk on a draft version of this report are gratefully acknowledged.

8. Further reading

Following is a selection of documents that provide additional information on the various aspects covered in this report, along with other topics.

Beltaos (2013): This monograph is an extensive account of river ice and related aspects dealt with in separate chapters. These include border ice, underwater ice, ice cover growth and ice jamming.

Jasek and Beltaos (2008): This paper focuses on ice jam break-ups and the consequence of releasing that ice and the water that had accumulated upstream of it.

Huusko et al. (2007): This article is an overview of fish ecology in cold rivers with in-line citations pointing to specific sources of information. It focuses on salmonids, and topics include winter survival and mortality, feeding habits and energetic needs, mobility as well as habitat usage and fish behavior.

Brown et al. (2011): This article is also a review with a focus on salmonids. It captures the main river ice processes (supercooling, ice cover formation, hanging dams, break-up, jams), then moves on to the effects of low temperature, habitat change, effects of underwater ice, groundwater, break-up and flooding. It ends with anthropomorphic effects. There are several informative photographs on river ice.

Bergeron and Enders (2013): This article is dedicated to the effects of the river freeze-up period on fish behavior and mobility in response to low water temperatures and ice formation. Anthropogenic influence is also discussed. The article encloses informative underwater photographs of fish and anchor ice.

Heggenes et al. (2018): This article looks at how hydropower dams affect river flow and what that means for river ice dynamics. It speaks to how salmon and trout react to control flow. The associated changes in ice conditions and low and high flows and their impact on the fish, including at the embryonic stages, is discussed.

Smith et al. (2022): This article is an example of a field study that documents fish behavior in a river during the winter. The Arctic Char is the species that was investigated, the location is the Coppermine River in Northern Canada and the focus is mobility. The authors were able to track fish under-ice migration in the river and in the gulf downstream using acoustic telemetry and link disturbances in expected migration patterns to ice action.

Burrell et al. (2022): This article provides an overview of the various factors that characterize climate change (air temperature, precipitation, cloud cover, wind,...) and of river ice and heat exchange processes. The focus is the protection of infrastructures (not biology). It explains the impact of climate change on the ice cover (reduction in coverage and thickness, ice jams and break-ups) and expected impacts in the future.

Svenning et al. (2024): This article investigates the growth rate of juvenile Arctic Char in lakes in Svalbard, Northern Atlantic Ocean, over five decades. An increase in annual growth rate is correlated with higher water temperatures. In the winter, that increase is tied with thinner ice formed during mild winters, while a slower growth rate is related to higher levels of snow precipitation.

9. References

- Beltaos, S. (2013). River ice formation. Proceedings of the 17th Workshop of the Committee on River Ice Processes and the Environment (CRIPE), Edmonton.
- Bergeron, N. E., & Enders, E. C. (2013). Fish response to freezeup. In S. Beltaos (Ed.), *River ice formation* (pp. 411-432). Canadian Geophysical Union (CGU).
- Brown, R. S., Hubert, W. A., & Daly, S. F. (2011). A primer on Winter, Ice, and Fish: What fisheries biologists should know about winter ice processes and stream-dwelling fish. *Fisheries*, 36(1), 8-26. <https://doi.org/10.1577/03632415.2011.10389052>
- Burrell, B. C., Beltaos, S., & Turcotte, B. (2022). Effects of climate change on river-ice processes and ice jams. *International Journal of River Basin Management*, 1-78. <https://doi.org/10.1080/15715124.2021.2007936>
- Bush, E., & Lemmen, D. S. (2019). *Canada's Changing Climate Report*. <https://changingclimate.ca/CCCR2019/>
- Heggenes, J., Alfredsen, K., Bustos, A. A., Huusko, A., & Stickler, M. (2018). Be cool: A review of hydro-physical changes and fish responses in winter in hydropower-regulated northern streams. *Environmental Biology of Fishes*, 101(1). <https://doi.org/10.1007/s10641-017-0677-z>
- Huusko, A., Greenberg, L., Stickler, M., Linnansaari, T., Nykänen, M., Vehanen, T., Koljonen, S., Louhi, P., & Alfredsen, K. (2007). Life in the ice lane: the winter ecology of stream salmonids. *River Research and Applications*, 23(5), 469-491. <https://doi.org/10.1002/rra.999>
- Jasek, M., & Beltaos, S. (2008). Ice-jam release: Javes, ice runs and breaking fronts. In S. Beltaos (Ed.), *River ice breakup* (pp. 462). Water Resources Publications.
- Scott, W. B., & Crossman, E. J. (1973). *Freshwater fishes of Canada*. Fisheries Research Board of Canada.
- Smith, R., Hitkolok, E., Loewen, T., Dumond, A., Kristensen, K., & Swanson, H. (2022). Overwintering ecology and movement of anadromous Arctic char (*Salvelinus alpinus*) in a large, ice-covered river in the Canadian Arctic. *Journal of Fish Biology*, 100(6), 1432-1446. <https://doi.org/10.1111/jfb.15054>
- Svenning, M. A., Bjørnvik, E. T., Godiksen, J. A., Hammar, J., Kohler, J., Borgstrøm, R., & Yoccoz, N. G. (2024). Expected Climate Change in the High Arctic—Good or Bad for Arctic Charr? *Fishes*, 9(1), Article 8. <https://doi.org/10.3390/fishes9010008>