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A Primer on Winter, Ice, and Fish: What Fisheries Biologists Should Know about Winter Ice Processes and Stream-Dwelling Fish

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A Primer on Winter, Ice, and Fish: What Fisheries Biologists Should Know about Winter Ice Processes and Stream-dwelling Fish

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ABSTRACT: Stream-dwelling fish face highly-variable environmental conditions from fall to winter due to fluctuations in water temperatures, discharge, and ice conditions. We provide an in-depth description of the interactions between these complex environmental conditions and behaviors of stream-dwelling salmonids during winter. Fisheries managers should be aware of the conditions that fish confront during winter in order to make appropriate management decisions. Diverse habitats, including deep pools with low water velocities, coarse rock substrate, and abundant cover, as well as side channels and backwaters, aid in the survival of overwintering fish. The inflow of relatively warm groundwater into the water column can be an important factor affecting winter habitat. Considering the length of winter and the vulnerability of fish during winter, a broad understanding of winter ice process and their effects on stream dwelling fish can aid in the preservation and improvement of winter habitats.

Introducción a la relación entre el invierno, el hielo y los peces: qué deben saber los biólogos pesqueros acerca de los procesos del hielo y los peces de río

RESUMEN: los peces demersales de río enfrentan condiciones ambientales altamente variables entre otoño e invierno debido a fluctuaciones en la temperatura del agua, descargas fluviales y las condiciones del hielo. En la presente contribución se ofrece una descripción detallada de las interacciones entre estas complejas condiciones ambientales y los comportamientos de los salmónidos en los ríos durante el invierno. Los administradores de pesquerías deben considerar las condiciones que confrontan los peces durante el invierno para tomar decisiones apropiadas de manejo. Diversos hábitats como las piscinas profundas con bajas velocidades de corriente, sustratos rocosos así como ríos tributarios y aguas estancadas, participan en la supervivencia de los peces hibernantes. El influjo de agua relativamente más cálida, proveniente del subsuelo, hacia la columna de agua puede ser un factor importante que afecta el hábitat invernal. Considerando que la duración del invierno y la vulnerabilidad de los peces durante esta estación, el entendimiento de los procesos fluvio-glaciares y sus efectos en los peces demersales de río puede aportar información para la preservación y mejoramiento de los hábitats invernales.

Stream-dwelling fish face many challenges as a result of the highly variable environmental conditions from fall to winter to spring due to fluctuations in water temperatures, discharge, and ice conditions. Our purpose is to create a wider awareness of winter ice processes, habitat conditions, responses of fish to winter conditions, and the challenges that winter conditions pose in the management of many lotic fisheries. The relative

role that groundwater plays in the formation of fish habitat can vary both temporally (i.e., changes among and within seasons) and spatially within a stream network. Thermal conditions and winter habitats for salmonids can be highly variable in some segments of streams and rivers, but relatively stable in others. Winter habitat for fish within a stream or river segment is affected by a complex array of factors includ-

Figure 1. Patchy anchor ice on the North Ram River, Alberta. Photo by R. S. Brown.



ing groundwater input, snowfall, elevation, latitude, channel type, and channel size. Anthropogenic influences, such as hydroelectric dams, groundwater extraction, and construction of instream structures to improve fish habitat are additional factors that affect winter habitat conditions in lotic systems. These complexities make it difficult to understand the winter habitat needs and behaviors of stream-dwelling fish, particularly their responses to river ice dynamics and interactions between groundwater and river ice. This review provides descriptions of the interactions among complex environmental conditions and behaviors of stream-dwelling fish during winter in order for fisheries managers to understand the conditions that salmonids confront. We attempt to link environmental conditions to management needs, describe when salmonid movements occur during winter and why, and examine the instream habitats that may be unstable during winter and why. Concurrently, we describe the instream habitats that are likely to be stable during winter and may be candidates of protective measures or habitat improvements. This review focuses on rivers and streams in temperate regions where it is cold enough for waters to have

Frazil ice crystals suspended in supercooled water have been called “active” because they are growing and have the ability to stick to any and all unheated underwater objects, including rocky substrate, vegetation, woody debris, or man-made structures (Ashton 1986).

ice formations during winter. Within temperate regions, most winter research has been conducted on trout and salmon in rivers and streams. For this reason, the emphasis is on salmonids in flowing waters. This review synthesizes the endeavors of previous authors, such as Cunjak (1996), and complements those of others, such as Huusko et al. (2007), who focused primarily on juvenile salmonids.

For this review, Cunjak’s (1996) definition of winter is used—“the period immediately following egg deposition by autumn-spawning salmonids (and coincident with a decline in water temperature) and extending until the loss of all surface ice (often accompanied by a major spate and snowmelt)

and prior to any reproductive activity by spring-spawning, non-gadid fish.” This definition is more appropriate than the astronomical definition of the period between the winter solstice (December

21) and the spring equinox (March 21) within the Northern Hemisphere, because freezing water temperatures and ice are often present in north-temperate streams well before December and last as long as frigid air temperatures and moderate water discharge persist.

RIVER ICE PROCESSES

In regions where average air temperatures drop below 0°C for periods of days or more, the heat loss from the water surface to the atmosphere causes the water temperature to decrease until it reaches 0°C. The rate of decrease depends on water depth, volume of flow, and exposure of the water surface. The fact that water has its maximum density at 4°C influences the vertical temperature distribution throughout its depth. As the water cools in the range of 4°C to 0°C during the winter season, it becomes less dense and the possibility of stratification arises. In streams and rivers with any appreciable current velocity, turbulent mixing generated by the river current is sufficient to overcome stratification, vertically mix the water column, and produce a uniform water temperature throughout. However, in lakes, ponds, and river reaches where the flow velocity is very low to non-existent, the water column becomes stratified with the coldest, least dense water at the surface. In these cases, ice production is limited to the water surface.

SUPERCOOLING, FRAZIL AND ANCHOR ICE FORMATION

Within vertically-mixed stream or river reaches, the entire water column can cool to below 0°C and become supercooled. Supercooling levels are small, typically less than 0.1°C. While it is not common to think of water being a liquid at temperatures below 0°C, it must be remembered that, as long as the air temperature is below 0°C, the only mechanism limiting the magnitude and duration of supercooling is the latent heat released when liquid water changes to solid ice. Water will remain supercooled until the latent heat warms the water column back to 0°C. However, there is a time lag before enough growing ice is present to overcome the heat loss to the atmosphere and warm the water back to near 0°C.

In practical terms, supercooling occurs when little or no surface ice is present, the air temperature is sub-freezing, and the water flow is sufficiently turbulent to overcome stratification. The genesis of the very first ice crystals is thought to result from seed crystals introduced at the water surface that become suspended in the water column by turbulence. Once introduced, these initial crystals lead to the creation of many new crystals that grow in size in the supercooled water (Daly 1984). This type of ice formation is referred to as frazil ice. Frazil ice crystals suspended in supercooled water have been called "active" because they are growing and have the ability to stick to any and all unheated underwater objects, including rocky substrate, vegetation, woody debris, or man-made structures (Ashton 1986).

Frazil ice deposited on the channel bottom is called anchor ice (Figure 1). Anchor ice in streams and rivers is typically composed of many small ice crystals and often has a milky appearance (Figure 2). In some cases, anchor ice includes sediment deposited along with the ice crystals and takes on a brownish appearance. The actual form of anchor ice is related to the flow conditions (Kerr et al. 2002; Kempema and Ettema 2009). In riffles with fast current, it can become quite thick and create anchor ice dams (Gerard 1989; Figure 3). These dams can temporarily block much

or all of the water discharge in a stream or river leading to large fluctuations in water levels (Maciolek and Needham 1952; Daly 2005, Stickler et al. 2008a). For example, in a small Newfoundland stream, it was observed that anchor ice dams increased water depth by up to 0.7 m, decreased water velocity, and changed riffles to runs upstream from dams (Stickler et al. 2008a).

Anchor ice has been observed to lift from channel beds during early daylight hours following cold nights when frazil ice is formed. Anchor ice can transport large amounts of sediment, gravel, and aquatic invertebrates downstream (Martin et al. 2000; Kempema et al. 2002). It is common to see frazil slush on the surface of streams or rivers after a period of frazil ice production (Figure 4). Frazil slush is composed of anchor ice lifted from the bottom and frazil ice crystals, either singly or flocculated together. Since frazil slush is buoyant, it can consolidate on the water surface and pack or clump together into large floes. Freezing of interstitial water among consolidated ice crystals increases the strength and rigidity of floes.

In stream and river reaches with turbulent flows, frazil crystals at the surface may not consolidate and frazil ice may stay in the form of slush. In less turbulent reaches, circular, pancake floes may form with diameters of a meter or more (Figure 5). In reaches with low current velocities, very large floes can form and their effective diameter can be on the order of the channel width (Osterkamp and Gosink 1983).

ICE COVER FORMATION

Stationary ice cover can have a significant effect on both discharge and stage of streams and rivers (Ashton 1986). Ice moving at or near the velocity of the water surface has little impact on flow conditions. However, when the surface concentration and strength of floating ice increases to the point where significant shear stresses can be transmitted to the channel banks through the surface ice, it can begin to influence water flow. Shear stress causes the velocity of the floating ice to slow relative to the water in the rest of the channel. This slowing exerts resistance on the flowing water, decreasing the rate of discharge and increasing the stage of the river upstream, while decreasing these factors downstream.

The formation of stationary solid surface ice covers generally from where the moving ice motion is arrested by natural obstacles such as intact ice cover, river constrictions, or changes in channel slope. Ice motion can also be arrested by anthropogenic obstructions, such as bridge piers, dams, or ice control structures. Once ice motion is arrested, stationary ice cover can progress upstream with the leading edge of the ice cover advancing due to the arrival of ice floes from upstream (Figure 6).

The ice formation process depends on the form of ice (i.e., slush, pancake floes, or large floes) when it arrives at stationary ice cover, the hydraulic conditions at the leading upstream end of the ice cover, and the heat loss rate to the atmosphere. Initial ice cover, formed of individual ice floes, can thicken abruptly through shoving or consolidation events. These events start immediately after ice cover is formed and continue until ice cover is strong enough to resist the forces acting on it (Beltaos 2008; Hicks 2009). In addition, the strength and thickness of ice cover can increase through heat transfer to the atmosphere as the

Figure 2. An underwater photograph of anchor ice clinging to the bottom of Dutch Creek, Alberta. Photo by R. S. Brown.



interstitial water among the initial ice floes forming the ice cover freezes (Calkins 1979).

HANGING DAMS

The upstream progression of stationary ice cover may slow or stop altogether in reaches with fast-flowing water. Reaches that remain free of ice cover can produce substantial quantities of frazil ice that are transported downstream and deposited under ice cover (Figure 7). When this ice is deposited under ice cover in reaches with low water velocity—such as pools—a significant portion of the channel cross section can be blocked by deposited frazil ice. These depositions, sometimes referred to as hanging dams, can become quite large (e.g., extending across the channel of large rivers and up to a kilometer or more in length), restrict water flow, and increase current velocities through pools, transforming pools into areas with high current velocities (Gold and Williams 1963; Cunjak and Caissie 1994; Komadina-Douthwright et al. 1997; Brown et al. 2000).

Once stationary ice cover has formed on a stream or river reach, it can last throughout the winter as long as air temperatures remain cold and the discharge remains steady or declines. The amount of surface ice cover varies with both latitude and altitude. Streams and rivers in the Arctic may be covered in surface ice for more than half of the year, whereas streams and rivers at low latitudes or at low altitudes in the north temperate region may not have complete surface ice cover (Craig 1989).

ICE COVER BREAKUP AND ICE JAMS

Breakup of stationary ice cover transforms a completely ice-covered stream or river reach into an open system. Two examples illustrate the types of breakup commonly found in north temperate regions of North America (Daly 1995; Beltaos 2008). At one extreme is thermal meltout. During an ideal thermal meltout, ice cover deteriorates through warming and the absorption of solar radiation, and melts in place, with no increase in discharge and little or no movement of ice. At the other extreme is the more complex and less understood mechanical breakup. Mechanical breakup requires no deterioration of ice cover but results from an increase in discharge. The increase in discharge induces stresses in the ice cover, and the stresses cause cracks and fragment the ice cover into pieces that are transported by the current.

Breakups of stationary ice cover take place most often during warming periods when the strength of the ice cover deteriorates to some degree and the flow entering the stream or river reach increases because of snowmelt or precipitation. Therefore, most ice breakups actually fall somewhere between the extremes of thermal meltout and mechanical breakup. As a general rule, the closer a breakup is to being a mechanical breakup, the more dramatic it is because of the increase in flow and the large volume of fragmented ice produced (Daly 1995; Beltaos 2008).

Ice jams can occur at locations where the ice fragments stop moving with the current. Severe and sudden flooding can result upstream of ice jams or downstream of ice jams when they release. Surface ice cover can fill the entire channel with chunks of ice and create ice jams that flood large upstream segments of streams or rivers and leave downstream segments dewatered (Beltaos 1995).

FISH AND WINTER

Water temperature influences feeding, metabolism, and behavior

Water temperature has a substantial effect on fish because they are poikilothermic and their body temperatures vary with the external environment. At a given water temperature, the body temperature of freshwater fish is almost precisely the temperature of the water (Diana 1995). As body temperature changes, so do metabolic processes. When water temperature declines from fall into winter, metabolic processes slow down and the abilities of fish to swim, feed, avoid predators, and defend their locations decline (Beamish 1978; Parsons and Smiley 2003). At winter water temperatures (i.e., about 1°C or less under ice), most freshwater fish have little ability to respond to changes in their environment, such as changes in flow, or to avoid predators, such as mink (*Mustela vison*).

As water temperatures decrease in fall or early winter, defense of feeding positions becomes less important to fish while the search for suitable winter habitat becomes more important (Cunjak and Power 1986; Cunjak 1996; Lindstrom and Hubert 2004a). Adult trout may initiate movements, some of which may be very long distances, in search of suitable winter habitat (Bjornn 1971; Chisholm et al. 1987; Brown and MacKay 1995; Jakober et al. 1998; Lindstrom and Hubert 2004a). Such movements occur as the swimming abilities of fish decrease with declining water temperatures (Contor 1989; Sheppard and Johnson 1985; Simpkins et al. 2000a).

Many fish, such as salmonids, do not cease activity entirely, and feed throughout the winter (Needham and Jones 1959; Cunjak and Power 1987; Kolok 1991, Riehle and Griffith 1993; Pirhonen et al. 1997, Hebdon and Hubert 2001a; Simpkins et al. 2000b), even when water temperatures are less than 5°C (Lyons and Kanehl 2002, Dare and Hubert 2003). However, the ability of salmonids to acquire and assimilate food becomes more limited as water temperatures decline to near 0°C (Chapman and Bjornn 1969; Brett and Glass 1973; Metcalfe and Thorpe 1992). Concomitantly, growth may cease during winter (Cunjak and Power 1986; Metcalfe and Thorpe 1992).

During winter, the production of benthic invertebrates declines, and densities of drifting food items are low, so there can be little food available for sight-feeding insectivores such as trout (Simpkins et al. 2000b; Hebdon and Hubert 2001b). Cold water temperatures depress metabolic rates of fish during winter and prolong the duration that salmonids and other fish can survive with little or no food (Cunjak 1988;

Connolly and Peterson 2003; Simpkins et al. 2003a). Thus, the combination of cold water temperatures and depressed metabolic rates during winter provides a survival mechanism for salmonids and other fish in streams.

Use of energy stores

Because of the physiological constraints on capture and consumption of food at low water temperatures and reduced availability of prey during winter, fish must utilize energy stored in their bodies (Cunjak 1988; Simpkins et al. 2000b, 2004a, 2004b). For example, salmonids are adapted to mobilize energy reserves and survive long periods without food (Toneys and Coble 1980; Navarro and Gatierrez 1995; Simpkins et al. 2003a). A complex three-stage physiological mechanism is involved in the mobilization of energy reserves and the defense of critical body organs (Castellini and Rea 1992; Hervant et al. 2001; Simpkins et al. 2003b). In short, during the first few days of food deprivation, glycogen reserves in the liver are used as an energy source. As starvation continues, the body switches to use of lipids as an energy source while preserving proteins. In later stages of starvation when lipids are depleted, the body begins to use proteins as a source of energy. The use of proteins compromises vital organ functions. Starvation and death occur after lipid reserves are depleted and protein degradation destroys the function of vital organs.

This starvation process has been widely observed among salmonids and has been related to declines in lipids through the course of winter among fish in both the wild (Beckman et al. 2000; Finstad et al. 2004a) and controlled experiments (Simpkins et al. 2003a, 2003b, 2004a, 2004b). Declines in



Figure 3. An ice dam on the Grand River, Ontario. The water level is elevated upstream of the dam. Photo by R. S. Brown.



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body condition using indices of plumpness based on length and weight measurements have also indicated starvation processes among salmonids during winter (Simpkins et al. 2000b; Hebdon and Hubert 2001a), but body condition indices are not an accurate index of lipid reserves, or the extent of starvation experienced by fish (Simpkins et al. 2003a, 2003c). Starvation and associated mortality of fish during winter are related to the size of fish, with higher rates of starvation and mortality among smaller fish, especially age-0 fish in streams (Sogard 1997; Biro et al. 2004; Simpkins et al. 2004a; Borgstrom and Museth 2005). Size-selective mortality is a function of the fact that smaller fish have low levels of stored energy in their bodies (Shultz and Conover 1997; Finstad et al. 2004a) and higher mass-specific metabolic rates (Paloheimo and Dickie 1966; Miranda and Hubbard 1994).

The metabolic limitations that fish experience during winter have a variety of ecological consequences, resulting particularly in less ability to withstand the stresses of forced swimming events and predation by warm-blooded vertebrates (Marshall 1936; Sealander 1943; Gerell 1967; Jakober 1995; Simpkins 1997; Lindstrom and Hubert 2004b). When changes in environment or habitat occur, fish may be forced to swim from their winter refuges to find new refuges (Brown and Mackay 1995; Jakober et al. 1998; Simpkins et al. 2000a; McKinney et al. 2001; Annear et al. 2002; Dare et al. 2002). Forced swimming during winter enhances the rate of lipid depletion and generates size-selective mortality (Simpkins et al. 2003a, 2003b, 2003c, 2004a). If fasted fish are forced to swim to exhaustion, direct mortality may occur or they may be more vulnerable to predation (Simpkins et al. 2004b).

FISH BEHAVIOR AND ONSET OF WINTER

Habitat changes in fall

The slowing of the metabolism of fish with decreasing water temperatures during fall and early winter has implications on behavior and habitat use by fish in streams and rivers. Because their metabolism slows and they feed less, fish are less likely to defend feeding positions (Cunjak and Power 1986; Cunjak 1996). Also, because fish are feeding less, the habitats that were optimal during warmer parts of the year can become less favorable. Larger juvenile and adult fish may abandon feeding territories and aggregate (a type of schooling (i.e., shoaling) behavior) in areas where they can find winter refuges (Hartman 1965; Cunjak and Power 1986; Brown and Mackay 1995; Jakober et al. 1998). While this occurs for larger fish, smaller fish may become nocturnal, move short distances, and hide within interstitial spaces in channel substrate, preferring crevices among larger rock substrates (Hartman 1965; Griffith and Smith 1993; Linnansaari et al. 2008).

As water temperatures decrease in the fall, larger fish often make lesser use of shallow areas with higher water velocities, and greater use of deeper areas with slower water velocities. This behavior has been observed among riverine salmonids (Hartman 1965; Cunjak and Power 1986; Chisholm et al. 1987; Baltz et al. 1991; Heggenes et al. 1993; Brown and Mackay 1995; Jakober et al. 1998) and centrarchids (Lyons and Kanehl 2002). Because areas with these types of habitats are often limited in streams and rivers, it is common for fish to be found in large groups or aggregations within more optimal habitats.

The presence of stationary ice cover influences behavior and habitat use. For example, Atlantic salmon (*Salmo salar*) parr were observed to be nocturnal during winter, but their activity increased during daytime as stationary ice cover became thicker (Linnansaari et al. 2008). Although Atlantic salmon parr prefer larger substrates, they may use smaller substrate when stationary ice cover is present (Linnansaari et al. 2008, 2009).

Aggregations

Aggregation may be a clumping or squeezing effect resulting from limited habitat availability (Cunjak and Power 1986). Habitat can be much more limited in winter than in other seasons due to low discharge and exclusion of previously suitable habitat by stationary ice (Chisholm et al. 1987; Brown et al. 1994; Brown and Mackay 1995; Jakober et al. 1998). Aggregation may also provide advantages to members of the group by decreasing predation risk (Neill and Cullen 1974; Milinski 1979; Tremblay and Fitzgerald 1979; Pitcher 1986).

Occurrence of winter aggregations of fish is linked to the general water temperature of the majority of the stream and the inflow of relatively-warm groundwater into the water column. The tendency of fish to form high-density winter aggregations increases with decreasing overall stream temperature (Cunjak and Power 1986; Brown 1999). Aggregations of cutthroat trout (*Oncorhynchus clarki*), brook trout, and brown trout (Cunjak and



When anchor ice fills a pool, the water then flows through the ice in one or more high-velocity conduits, at water velocities that are often unsuitable for fish to maintain position

Power 1986; Brown 1999) have been observed in small areas of warm groundwater discharge. However, Brown and MacKay (1995) observed that fish aggregations were less common in long stream sections warmed by groundwater than in colder sections without groundwater inputs.

Figure 4. Frazil slush on the surface of the Grand River, Ontario. Photo by R. S. Brown.



NATURAL FACTORS AFFECTING FISH HABITAT AND BEHAVIOR DURING WINTER

Winter habitats of fish can range from very stable to almost consistent change due to variation in ice conditions and water temperatures. In some riverine environments, stationary ice cover forms early in the winter and seals fish under a stable sheet of ice. Deep snow can bridge small streams and also provide stable overwintering habitats (Chisholm et al. 1987; Hubert et al. 2000; Lindstrom and Hubert 2004a). However, among reaches of streams or rivers, habitats without complete surface ice or snow cover are likely to have dynamic ice conditions (Brown 1999; Lindstrom and Hubert 2004a; Barrineau et al. 2005).

From the start of freeze-up, ice can occlude fish habitat and influence fish behavior. Laboratory studies have shown that super-cooled water temperatures and frazil ice can stress fish (Brown et al. 1999). In addition, stationary ice can form in habitat that was available during summer and be very dynamic, making otherwise suitable habitats unusable either temporarily or for most of the winter (Chisholm et al. 1987; Brown and Mackay 1995; Jakober et al. 1998; Brown 1999; Lindstrom and Hubert 2004a; Barrineau et al. 2005). As winter progresses, stationary ice cover can increase in thickness until it excludes large portions of habitats used by wintering fish in streams and rivers (Chisholm et al. 1987; Berg 1994; Scruton et al., 1997). An extreme example occurs in the Arctic where most streams and rivers freeze to the bottom of the channel because surface ice can grow to a thickness of more than 2 m (Mueller et al. 2006). Consequently, fish must reside in the deepest parts of rivers in pockets of unfrozen water or

in areas influenced by groundwater (Craig 1989; West et al. 1992; Reynolds 1996; Brown et al. 2010).

THE EFFECTS OF FRAZIL AND ANCHOR ICE

When stationary ice cover forms and melts frequently during fall and winter, the resulting frazil ice and anchor ice events create harsh conditions that force fish movements and cause mortality (Maciolek and Needham 1952). Anchor ice can build up to the water surface and occlude fish from entire pools or reaches. When anchor ice fills a pool, the water then flows through the ice in one or more high-velocity conduits, at water velocities that are often unsuitable for fish to maintain position (Figure 8; Brown and Mackay 1995; Jakober et al. 1998; Brown 1999; Whalen et al. 1999). Several researchers have observed that fish are forced to make larger numbers of movements when influenced by frazil ice or anchor ice. Fish often shift habitats as the water temperatures decrease in the fall (Brown and Mackay 1995; Jakober et al. 1998) and may spend the entire winter at these new locations. However, if these new habitats are unstable due to the influences of ice, the fish may be forced to make multiple movements as ice occludes these habitats. One study found that cutthroat trout — in reaches influenced by anchor ice — made substantial movements 6 times more often during a winter, and moved 30 times farther than cutthroat trout in reaches free of anchor ice (Brown 1999). Other researchers have found that both bull trout (*Salvelinus confluentus*) and cutthroat trout moved more often in streams affected by anchor ice than in streams with stationary ice cover (Jakober et al. 1998). Cutthroat trout and brook trout overwintering in beaver ponds with stationary ice cover have been observed to move less than those in reaches of the same stream that were influenced by unstable ice conditions (Lindstrom and Hubert 2004a). Forced movements during frazil ice and anchor ice events can be energetically costly to fish and increase the probability of mortality. Because frazil ice and anchor ice form in stream sections that do not have stationary ice cover, fish in moderately cold climates may be forced to make more ice-related movements than fish in colder climates.

While larger juvenile and adult fish are forced from their habitats by anchor ice, small juvenile fish may not be influenced. One study found that although anchor ice completely blanketed a stream, Atlantic salmon (*Salmo salar*) parr were not forced to move (Roussel et al. 2004). Other researchers have found juvenile Atlantic salmon use anchor ice as cover (Stickler et al. 2008b), and redistribute daily as frazil ice and anchor ice form and melt (Whalen and Parrish 1999).

Recent research indicates that the distribution of anchor ice may influence whether stream reaches can be used by juvenile fish. Linnansaari et al. (2009) found that Atlantic salmon parr were able to remain in reaches with patchy, unconsolidated anchor ice. However, in reaches where dense growth of anchor ice extended from the substrate to the stream surface, the fish were not able remain, and did not re-enter over the course of the winter.



THE EFFECTS OF ICE DAMS AND HANGING DAMS

Thick deposits of anchor ice in riffles can create ice dams similar to ice jams (Gerard 1989; Beltaos 1995; Figure 3), causing a stage (i.e., water level) increase upstream from the ice dam, and decrease downstream from the ice dam (Maciolek and Needham 1952). In a high-elevation California stream, researchers found dead brown trout and rainbow trout (*Oncorhynchus mykiss*) stranded on damp rocks in dewatered pools downstream of an ice dam (Maciolek and Needham 1952) and concluded that this type of mortality was common, but others have found that ice dams may have little influence

Figure 5. Pans of frazil slush forming stationary surface ice in a small backwater area along the edge of the Grand River, Ontario. Photo by R. S. Brown.



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on fish. For example, while habitats used by Atlantic salmon parr in a small Newfoundland stream upstream of an ice dam increased in water depth and decreased in water velocity the fish moved little if at all (Stickler et al. 2008a), but the ice dam was short lived, forming at night and disintegrating the next day.

Frazil ice can affect fish habitat by forming hanging dams. Hanging dams can form frequently in cool-temperate and colder climates (Komadina-Douthwright et al. 1997), forcing lotic fish to cope with resultant changes in habitat. Brown et al. (2000) observed that 80% of a pool in an Ontario river was filled by a hanging dam causing much higher water velocities in the pool (Brown et al. 2000). Others have observed more than 80% of the volume of pools filled by hanging dams in

other systems (Cunjak and Caissie 1994; Caissie et al. 1997; Komadina-Douthwright et al. 1997).

Hanging dams can cause major difficulties for fish during winter, but they are often unnoted because they form under ice and are difficult to observe. Increased water velocities coupled with reduced pool volume can change pools from suitable to unsuitable overwintering habitat. This is indicated in studies where radio-tagged fish moved out of pools where hanging dams formed, but often returned to the same pools after the hanging dams were no longer present (Brown et al. 2000; Lindstrom and Hubert 2004a). Hanging dams can remain in place for days or from fall freeze-up to spring break-up (Beltaos and Dean 1981; Komadina-Douthwright et al. 1997; Brown et al. 2000; Barrineau et al. 2005).

THE INFLUENCE OF GROUNDWATER

The inflow of relatively warm groundwater into the water column can play a complex role affecting winter habitat for fish in streams and rivers. Groundwater input to flowing waters can provide stable overwintering habitats for fish and their eggs when they are near the source, but it can also contribute to unstable winter conditions further downstream. Many researchers have found fish dwelling within the main channel or side channels (often in large aggregations) where groundwater maintained ice-free habitat (Craig and Poulin 1975; Cunjak and Power 1986; Brown and Mackay 1995; Brown 1999; Harper and Farag 2004; Lindstrom and Hubert 2004a; Barrineau et al. 2005). However, as air temperatures decrease, or the distance downstream from groundwater sources increases, the thermal effects of groundwater input dissipate and the amount of ice-free habitat decreases. Reaches at the downstream end of groundwater-influenced stream segments are likely to have unstable ice conditions during winter (Brown 1999; Lindstrom and Hubert 2004a). In these reaches, frazil ice may form during colder weather and contribute to anchor ice and hanging dams farther downstream (Brown 1999; Lindstrom and Hubert 2004a; Barrineau et al. 2005). For example, Brown (1999) noted radio-tagged cutthroat trout were forced out of the lower reach of a groundwater-influenced stream segment by anchor ice during cold periods. The fish moved upstream toward the source of warmer groundwater during cold periods and later dispersed back into the lower reach of the groundwater section as air temperatures increased, allowing the length of the groundwater-influenced segment to expand. Lindstrom and Hubert (2004a) also noted that brook trout and cutthroat trout tended to avoid pools affected by groundwater that were greater than 250 m downstream of the sources of influx because winter habitat conditions in these pools were dynamic and unstable.

ICE BREAKUP AND FLOODING

Break-up of stationary ice cover can result in large changes in fish habitat and cause fish movements that commonly lead to mortalities. The occurrence of large volumes of ice moving with the current during break-up and associated flooding can result in remodeling of river channels, moving of small islands, redistribution of alluvial gravel bars (Power et al. 1999), and crushing of riparian vegetation (Gatto 1994; Hicks 1994; Beltaos 1995). Under these conditions, fish may move long distances as their winter habitats are altered (Brown et al. 2001). As discharge increases during stationary ice break-up and flooding, water depth and velocities increase in the main channel. These changes can make main channel habitats more energetically demanding and less preferable for fish, so fish may move downstream, into backwaters, or to the edges of pools or runs. For example, Brown et al. (2001) found more than 10% of a group of radio-tagged white suckers (*Catostomus commersoni*) and common carp (*Cyprinus carpio*) stranded on



a floodplain following stationary ice break-up and associated flooding, and concluded that such stranding may be a major cause of mortality.

Use of stream margins within runs or backwater areas has been found to be one mechanism through which fish avoid being swept downstream during stationary ice break-up and flooding. While many backwater habitats are shallow or dry during low-flow periods, they are commonly used as refuges by fish, too (Brown et al. 2001). Additionally, several species of centrarchids have been observed to move into backwater areas during winter (Knights et al. 1995; Raibley et al. 1997; Karchesky and Bennett 2004). Having backwater habitats

Figure 6. Frazil slush forming stationary surface ice on the North Ram River, Alberta. Photo by R. S. Brown.



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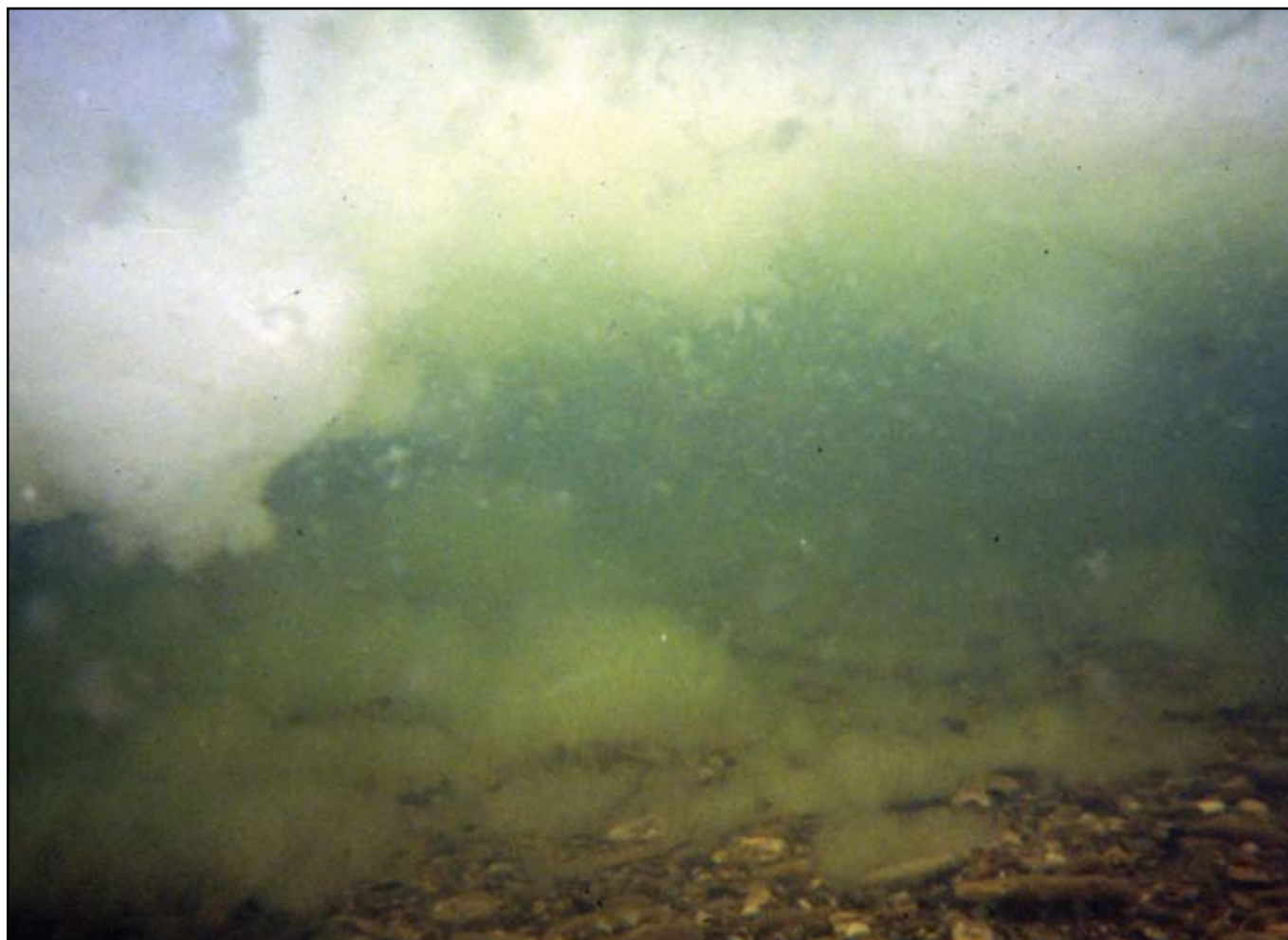
available in streams and rivers may decrease the numbers of fish that are caught in the current and forced to move downstream. Backwaters may also reduce the numbers of fish stranded on the flood plain where they can easily be taken by predators or die as waters recede.

Floods associated with stationary ice break-up can also influence the movements and behaviors of juvenile fish. For example, in an experimental stream, Atlantic salmon parr made more extensive movements during simulated floods, and the proportion of fish homing to their “home stone” after nocturnal movements was lower during these flood events (Linnansaari et al. 2008).

WINTER HABITATS

Suitable winter habitats for fish in streams and rivers are locations that allow fish to minimize energy expenditures while maximizing protection from environmental variation (Cunjak 1996; Bonneau and Scarnecchia 1998; Lindstrom and Hubert 2004a). Complex mixes of habitat features can provide suitable winter habitat for fish (Jakober et al. 1998; Harvey et al. 1999; Ford and Lonzarich 2000; Mitro and Zale 2002). Such habitats are generally the result of natural fluvial processes that maintain connections and create habitat diversity allowing full expression of life

Figure 7. This image shows three kinds of ice. Anchor ice can be seen on the bottom. In mid-column can be seen frazil slush or flocs of frazil ice. At the top of the image, a hanging dam can be seen forming under the stationary surface ice as frazil slush becomes buoyant and gathers under the surface ice. Photo by R. S. Brown.



history traits and processes influencing dispersal and survival of fish (Muhlfeld and Marotz 2005). In general, microhabitat features needed by stream-dwelling fish include low-velocity water and protection from predation (Hiscock et al. 2002; Beechie et al. 2005; Gillette et al. 2006), but specific habitat needs within these general features can vary among species (Dare and Hubert 2003).

Deep pools often provide microhabitat features needed by fish during winter, and their quality as winter habitat for fish can be enhanced by the presence of crevices between rocks, large woody debris, or submergent vegetation (Mitro and Zale 2002; Muhlfeld et al. 2001). Deep pools have been widely described as habitat features needed by stream-dwelling fish during winter, but most of the literature characterizing this generality comes from salmonid studies (Bustard and Narver 1975; Cunjak and Power 1986; Heggenes et al. 1993; Bonneau and Scarnecchia 1998; Jakober et al. 1998; Simpkins et al. 2000a; Dare et al. 2002; Lindstrom and Hubert 2004a). Deep pools in small streams provide low-velocity waters and a stable environment when there is relatively large variation in discharge during ice events. However, in larger streams and rivers, additional habitat features are needed in pools for them to provide suitable winter habitat (Simpkins et al. 2000a). The additional features include unique elements, such as complex bank habi-

tat with large rocks (Mitro and Zale 2002), off-channel pools with groundwater inputs that slightly raise water temperatures (Harper and Farag 2004), large woody debris, or submerged aquatic vegetation. Generally, when juvenile salmonids find pools with low current velocities and instream cover, they move infrequently from these pools during winter (Heggenes et al. 1991; Hilderbrand and Kerschner 2000; Simpkins et al. 2000a; Sanderson and Hubert 2009).

Water velocities suitable to fish during winter vary among species and life stages. Among juvenile salmonids, suitable water velocities during winter have been reported to be less than 1 body length per second (Simpkins et al. 2000a, 2004a; Beechie et al. 2005; Enders et al. 2007). Elements of habitat complexity in pools and runs that create specific locations with little or no current velocity during winter, include rocky substrate with crevices between rocks, large woody debris, and submerged aquatic vegetation. Numerous studies of salmonids have described fish concealing themselves in crevices among rocks during winter (Schrader and Griswold 1992; Griffith and Smith 1993; Riehle and Griffith 1993; Meyer and Gregory 2000, Muhlfeld et al. 2001; Riley et al. 2006). Other authors have described the use of small eddies downstream from large cobbles or boulders as habitat used by salmonids during winter (Simpkins et al. 2000a; Dare and Hubert 2003). Large woody

Figure 8. An underwater photo of a conduit through anchor ice in Dutch Creek Alberta. Most of the stream was covered in anchor ice leaving just a few of these high velocity conduits for water to pass through. Photo by R. S. Brown.



debris has been described as being used to provide protection from current and concealment for salmonids in many systems during winter (Meyer and Gregory 2000; Muhlfield et al. 2001; Harper and Farag 2004; Beechie et al. 2005; Muhlfield and Marotz 2005). Large woody debris and backwater habitats may be particularly important to salmonids during high-flow periods (Harvey et al. 1999, Brown et al. 2001). Many studies have described use of submerged aquatic vegetation as cover by salmonids during winter (Cunjak and Power 1986, 1987; Bendock and Bringham 1988; Heggenes et al. 1993; Griffith and Smith 1995; Mitro and Zale 2002). However, submerged aquatic macrophytes can deteriorate during winter, forcing fish to move and seek new habitat (Simpkins et al. 2000a). Instream cover in the form of rocks, large woody debris, and submerged aquatic vegetation have been shown to be an important winter habitat feature for several species of centrarchids as well (Carlson 1992; Cunjak 1996; Karchesky and Bennett 2004).

Habitats along stream and river banks can be important winter refuges for fish. Juvenile salmonids have been observed to use stream-bank habitats as refuges during anchor-ice events (Griffith and Smith 1993; Riehle and Griffith 1993; Heggenes et al. 1993). Atlantic salmon parr have been observed to be positioned closer to the stream banks during winter in comparison to summer and fall (Mäki-Petäys et al. 2004; Enders et al. 2008). Stream-bank habitats may provide cover from high current velocities and homoiothermic predators (Cunjak 1996; Mäki-Petäys et al. 2004).

Habitat stability during winter is important to fish (Dare et al. 2002). If habitat is stable, fish are not forced to move, seek

new areas of residence, expend more energy, or experience greater predation risk (Brown and Mackay 1995; Brown et al. 2000; Lindstrom and Hubert 2004a). There is substantial natural variation in the stability of stream and river habitat during winter. For example, three classes of winter stream conditions have been described among streams of the Rocky Mountains, with differing extents of stability during winter (Chisholm et al. 1987; Hubert et al. 2000). First are small, high-elevation stream segments with low-to-moderate channel gradients that become entirely bridged by snow with no stationary ice cover during winter. Such streams maintain consistent flows and cold water temperatures during winter to provide stable habitats. Second, there are moderate-sized, mid-elevation stream segments with moderate channel slopes that do not snow bridge and have patches with and without stationary ice cover during winter. These streams experience variation in water temperatures and have dynamic ice conditions throughout winter providing unstable habitats for fish. Third are foothills stream segments that are larger and tend to have lower channel slopes with little snow cover but substantial stationary ice cover. Habitat conditions in these stream segments also tend to vary during winter, but not as severely as in mid-elevation stream segments.

One of the most stable habitats for fish during winter is beaver (*Castor canadensis*) ponds (Collen and Gibson 2001) with consistent water levels, very low current velocities, and stationary ice cover throughout winter. Numerous studies have shown that trout select beaver ponds during winter (Chisholm et al. 1987; Jakober et al. 1998; Lindstrom and Hubert 2004a).

ANTHROPOGENIC INFLUENCES ON WINTER HABITAT

A wide variety of anthropogenic activities can affect winter habitat for fish in streams and rivers. These include construction and operation of reservoirs, placement of barriers to fish movements, thermal effluents from electrical power production facilities and other industries, point sources of contaminants, nonpoint sources of sediments, and instream structures built to enhance habitat for fish.

EFFECTS OF DAMS AND RESERVOIRS

Widespread construction of reservoirs has had substantial effects on downstream fluvial habitats (i.e., tailwaters) during winter. Many reservoirs alter natural temperature regimes downstream due to hypolimnetic releases resulting in warmer-than-natural winter water temperatures. Warmer water temperatures within tailwaters can eliminate stationary ice cover, enhance the dynamics of ice processes, facilitate predation by homoiothermic predators, increase energy demands of fish during a period of low prey availability, and allow the persistence of angling during winter.

Warmer water temperatures in tailwaters can prevent formation of stationary ice cover across the channel for long segments downstream from dams (Simpkins et al. 2001a), and contribute to occurrences of anchor ice and frazil ice in these segments (Ward and Stanford 1979). Frazil ice and anchor ice can fill interstitial spaces among gravel and cobble substrates where juvenile fish have sought cover (Stickler et al. 2007a; Stickler et al. 2007b), remove submerged aquatic macrophytes that are important as sources of cover and protection from predation (Simpkins et al. 2000a; Johnson and Douglass 2009), and force fish to move from normal feeding and resting areas to refuges, such as the bottom of deep pools or under shelf ice in shallow water near shore (Griffith and Smith 1995; Simpkins et al. 2000a; Van Kirk and Martin 2000; Stickler et al. 2008a). The movements and lack of feeding opportunities in tailwaters caused by frazil ice episodes accentuate energy demands on fish, affect starvation processes, and perhaps force fish to move downstream out of managed reaches (Brown and Mackay 1995; Hebdon 1999), and enhance mortality of juvenile salmonids (Simpkins 1997; Simpkins et al. 2000a; Annear et al. 2002).

Together, warmer water temperatures and lack of snow and stationary ice cover enable salmonids to feed throughout the winter in tailwaters (Simpkins and Hubert 2000b; Hebdon and Hubert 2001b). However, availability of prey is limited in tailwaters during winter, as most aquatic invertebrates have life cycles that make them unavailable or inactive during winter (Filbert and Hawkins 1995; Simpkins and Hubert 2000b; Hebdon and Hubert 2001b). Nonetheless, warmer water temperatures lead to higher metabolic

rates, greater swimming ability, and more activity among salmonids in tailwaters, thereby generating a demand on stored energy reserves (Berg and Bemset 1998; Cunjak et al. 1998; Simpkins and Hubert 2000b; Hebdon and Hubert 2001a; Simpkins et al. 2003a, 2004a; Finstad et al. 2004b). Loss of energy reserves can reduce the ability of fish to respond to variation in habitat or threats from predators, thereby enhancing mortality of small fish in tailwaters (Metcalfe and Thorpe 1992; Bull et al. 1996; Cunjak 1996; Finstad et al. 2004b). The lack of stationary ice cover associated with warmer winter water temperatures in tailwaters can enhance predation on fish by homoiothermic predators such as mink and river otter (*Lutra lutra* L.; Fraser et al. 1993; Valdimarsson and Metcalfe 1998).

Channels downstream from reservoirs often change and lose the complexity that existed prior to construction of the dam due to reductions in extremely-high flows and the lack of sediment released from dams (Ward and Stanford 1979). The result is often a loss of deep pools with low current velocities important to overwintering fish (Stickler et al. 2008b). Reservoirs also affect the occurrence of cobble substrate with interstitial spaces important to juvenile salmonids during winter (Rimmer et al. 1984; Heggenes 1996; Mäki-Petäys et al. 1997; Linnansaari et al. 2008; Stickler et al. 2008b). Highly-embedded, armored channels downstream from reservoirs generally lack cobbles with interstitial spaces.

Because dams regulate the flows of rivers for a variety of economic reasons, discharge regimes during winter are often quite different from relatively stable natural conditions. Variable discharges to meet hydro-power, flood control, and water storage functions can lead to variable flows during winter, causing substantial variation in habitat at a time when fish need stable habitat (Dare et al. 2001; Lagarrigue et al. 2002; Enders et al. 2008). Variation in flows during winter downstream from reservoirs can strand fish (Saltveit et al. 2001; Berland et al. 2004; Stickler et al. 2007a; Stickler et al. 2007b; Enders et al. 2008), force

fish to move from previously occupied habitats (Armstrong et al. 1998; Dare et al. 2002; Enders et al. 2008), accentuate mortality due to predation by vertebrates, and cause mortality due to the collapse of shelf ice along the shore onto fish below (Johnson 1994). Although rapid

reductions in flows during winter can negatively affect fish, enhanced flows appear to have less of an effect, causing fish to shift in their habitat use but not stimulating long movements (Heggenes 1988; Simpkins et al. 2000c; Brown et al. 2001). Effects of hydropower peaking during winter on juvenile salmonids have been studied in artificial streams and rivers (Bradford et al. 1995; Saltveit et al. 2001; Scruton et al. 2005; Enders et al. 2008), but there is little information regarding the cumulative effects on incubating embryos or adult fish. In general, slow changes in discharge within the natural range of variation are needed to avoid negative impacts on juvenile salmonids (Bradford et al. 1995; Enders et al. 2008).

Dams, as well as culverts, dewatering of stream reaches, and alteration of stream channels, can also provide barriers to fish movements, impeding movements among habitats needed during winter or summer, or for spawning, or rearing of young across a watershed or river-scape (Northcote 1997; Fausch et al. 2002). For example, Sanderson and Hubert (2009) found that water diversion structures prevented

Diverse habitats, however, including deep pools with low water velocities, coarse rock substrate, and abundant cover, as well as side channels and backwaters, increase the probability of survival of overwintering fish.

adult cutthroat trout who wintered in the mainstem of the Salt River in Wyoming from accessing many tributary streams flowing from surrounding mountains with high-quality spawning and rearing habitat. Reductions in the area of available habitat due to anthropogenic fragmentation may lead to a loss of habitat complexity and decline in life history variations important to stream-dwelling fish (Rieman and McIntyre 1993; Schlosser and Angermeier 1995).

THERMAL DISCHARGE

Thermal discharges from electrical-generating plants and industrial and municipal sources can affect winter habitat in ways similar to reservoirs by preventing surface ice formation and providing opportunities for frazil ice episodes in downstream reaches. Additionally, thermal discharges during winter can cause fish to aggregate in the effluent plume where demands on energy reserves may be greater than in colder waters. The physiological effects of residence in thermally-enhanced areas during winter have not been widely studied, but at least one study suggests that reproduction may be negatively affected by such behavior (Cooke et al. 2004). Aggregation of fish in areas with point sources of both warmer water and contaminants can expose them to higher levels of contaminants than might otherwise be experienced.

SEDIMENTATION

Sedimentation, both from natural and anthropogenic sources, can lead to a decrease in both the quantity and the quality of fish habitat during winter (Cunjak 1996). Fine sediment can fill the interstitial spaces among rocks reducing the amount of habitat for small fish which hide in the substrate (Griffith and Smith 1993; Linnansaari et al. 2009). In addition, fine sedimentation can decrease water flow through redds during winter, reducing the survival of salmonid embryos (Chapman 1988; Levasseur et al. 2006).

INSTREAM IMPROVEMENT STRUCTURES

Instream structures have been widely used to improve or restore habitat for fluvial salmonids (Platts and Rinne 1985; White 1996). Instream structures are generally built to enhance pool habitat, but little is known about habitat associated with such structures during winter (Nickelson et al. 1992). Barrineau et al. (2005) assessed two types of instream structures (i.e., log-plunge and diagonal-boulder weir structures) constructed on a low-gradient reach of a mountain stream and found substantial differences in the quality of winter habitat formed by the two structures. Moreover, they observed that the habitat formed by instream structures in stream segments affected by groundwater sustained serious impacts from frazil ice and anchor ice during winter. Their research indicated that managers need to understand the thermal dynamics of a stream before constructing instream structures intended to benefit salmonids during winter. Groundwater areas may provide stable overwintering habitat in reaches near the source, but contribute to unstable ice conditions downstream and unsuitable overwintering habitat for fish in these reaches. If winter habitat is to be improved, reaches downstream from warm groundwater input need to be identified before such habitats are altered, and calculations or observations should be made to ensure that frazil ice and anchor ice during winter does not occlude habitat formed by instream structures.

SUMMARY

During winter, fish are vulnerable to numerous threats to their survival. Protecting or creating suitable winter habitat in temperate climates is critical because fish spend a large part of the year in these habitats. Both freeze-up and ice break-up are especially dynamic times when ice can cause riverine habitats needed by fish to be unstable and movement routes to be blocked. Diverse habitats, however, including deep pools with low water velocities, coarse rock substrate, and abundant cover, as well as side channels and backwaters, increase the probability of survival of overwintering fish. The inflow of relatively warm groundwater into the water column can be an important factor affecting winter habitat, and can either enhance or diminish winter habitat quality for stream-dwelling fish. Understanding the influences of groundwater, industrial or municipal effluents, or upstream reservoirs on winter water temperatures and ice dynamics in downstream reaches is critical to successful preservation or creation of suitable winter habitat. Research is needed on habitat needs of fish during winter to ensure preservation of these habitats and to ensure that suitable habitats are created when fisheries managers make habitat improvement efforts. To date, most habitat preservation and improvement efforts have focused on habitats used from spring through fall, with little consideration or understanding of the influence of winter on these habitats. Considering the length of winter and the vulnerability of fish during winter, a much broader effort to understand, preserve, and improve winter habitats is warranted. ☞

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