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Winter Disturbances and Riverine Fish in Temperate and Cold Regions

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Winter is a critical period for aquatic organisms; however, little is known about the ecological significance of its extreme events. Here, we link winter ecology and disturbance research by synthesizing the impacts of extreme winter conditions on riverine habitats and fish assemblages in temperate and cold regions. We characterize winter disturbances by their temporal pattern and abiotic effects, explore how various drivers influence fish, and discuss human alterations of winter disturbances and future research needs. We conclude that (a) more data on winter dynamics are needed to identify extreme events, (b) winter ecology and disturbance research should test assumptions of practical relevance for both disciplines, (c) hydraulic and population models should incorporate winter- and disturbance-specific aspects, and (d) management for sustainability requires that river managers work proactively by including anticipated future alterations in the design of restoration and conservation activities.

Keywords: climate change, refugia, ice, persistence, rehabilitation

Disturbances, which include physical extremes such as floods and droughts, shape riverine habitats and regulate their communities (box 1; Resh et al. 1988). How organisms respond to a disturbance depends on their susceptibility and on the characteristics of the disturbance (figure 1). In high-latitude and high-altitude rivers, disturbance characteristics and organisms' susceptibility undergo pronounced seasonal fluctuations. During the winter, low temperatures, snow, and different types of river ice can fundamentally alter discharge, hydraulics, or gaseous exchange, producing unique high-intensity disturbances (Prowse 2001a). From a biotic perspective, winter is generally regarded as a period of increased susceptibility and mortality (Power et al. 1993, Brown RS et al. 2001). In cold water, ectothermic animals such as fish have reduced swimming abilities (Brown RS et al. 2011), their energy reserves continuously deplete, and their physical condition declines (Cunjak 1996).

Over the past 25 years, disturbance has become a key topic in river ecology, with important implications for management and restoration (Kiernan and Moyle 2012). Most concepts in riverine disturbance research are based on the spring–fall seasons in temperate and subtropical rivers. The ecological role of winter disturbances, however, has received little attention (Prowse 2001b). For example, the breakup of river ice has largely been ignored in basic ecological theories, such as the flood pulse concept and

its extensions (Prowse 2001b), and disturbance theories, such as the intermediate disturbance hypothesis, are rarely tested in winter. The functioning of refugia for fish during droughts has been reviewed with a focus on warm seasons and regions (Magoulick and Kobza 2003), whereas winter low flows remain unexplored.

Understanding the link between the seasonal timing of a disturbance and the organisms' responses is a prerequisite for future management. With global climate change, extreme events in the temperate and cold regions are expected to become more frequent and intense, particularly during winter (Kundzewicz et al. 2007, Durand et al. 2011). Precipitation will more frequently fall as rain instead of as snow, leading to higher winter discharges, lower spring flood peaks, and more rain-on-snow events (Kundzewicz et al. 2007). The ice regime will become more dynamic because of more frequent shifts between freezing and thawing (Beltaos and Prowse 2009).

We link winter ecology and disturbance research by synthesizing the impacts of extreme winter conditions on riverine habitats and the persistence of fish assemblages in temperate and cold regions. First, we characterize winter disturbances by their drivers, temporal patterns, and abiotic effects. Second, we explore the fish response from the individual to the community level and identify intrinsic and extrinsic drivers governing the susceptibility of fish. In this context, we provide an in-depth analysis of the structure and

function of refugia where fish can escape from disturbance (Lake 2000). Third, we discuss human alterations of winter disturbances and their implications for the persistence of fish assemblages. We conclude with a summary and an outline of research needs. We include studies on riverine

fish in temperate and cold regions in which any exceptional winter phenomena—whether they are abiotic, such as catastrophic floods, or biotic, such as mass kills—are reported. We concentrate on natural events but consider selected anthropogenic disturbances where that is relevant for the

discussion. The present study adds to five earlier reviews on the winter ecology of riverine fish (Power et al. 1993, Cunjak 1996, Hurst 2007, Huusko et al. 2007, Brown RS et al. 2011) by placing the existing knowledge in a broader context of disturbance research.

Climatic and geomorphic drivers

A variety of winter disturbances can develop in river ecosystems, including breakup floods, rapid temperature fluctuations, and droughts (figure 1). Disturbance characteristics are governed by climatic and geomorphic drivers that operate at multiple spatio-temporal scales. Climatic drivers, mainly temperature and precipitation, vary

Box 1. Defining winter disturbances and refugia.

Disturbance is a contentious term in aquatic ecology, with definitions focused either on the physical characteristics of an event (Resh et al. 1988, Lake 2000) or on the organisms' responses (Pickett and White 1985). All of its definitions describe exceptional natural or anthropogenic phenomena (Power et al. 1993). In winter studies on riverine fish, the use of the term *disturbance* has been limited. Rather, specific abiotic conditions or, more rarely, fish responses are called *unusual* (Doyle et al. 1994), *atypical* (Cunjak et al. 1998), or *extreme* (Maciolek and Needham 1952).

The intensity of a given disturbance varies between habitats (see figure 2; Resh et al. 1988, Swanson et al. 1998). *Refugia* are habitats within or outside a disturbed area in which a disturbance is absent or reduced in intensity and in which fish can escape from a disturbance (Lake 2000). In winter studies on riverine fish, the term *refuge* is of ambiguous use, often referring to residential habitats (*sensu* Bond and Lake 2005) in which fish spend most of their time throughout winter.

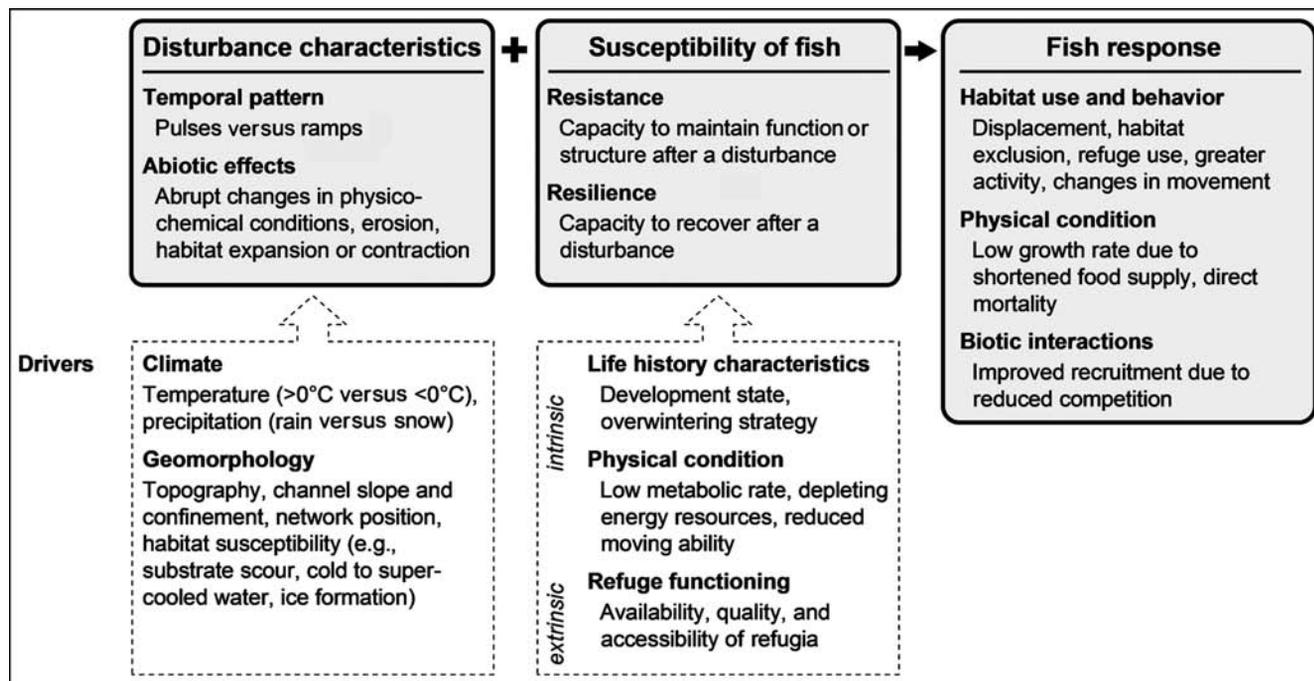


Figure 1. Riverine fish respond to winter disturbances in different ways, ranging from the elimination of entire age classes to recruitment peaks. The response is governed by the disturbance characteristics and fish susceptibility. Disturbance characteristics reflect climatic and geomorphic drivers that interact across local to continental scales. An individual's susceptibility to a disturbance is determined by intrinsic drivers, such as life-history characteristics and the physical condition of the fish, and extrinsic drivers, such as the availability of refugia. Pulses refers to events such as open-water floods, ice breakup floods, debris flows, excessive formation of subsurface ice, and rapid temperature fluctuations. Ramps refers to events such as droughts and excessive ice formation. Abbreviations: °C, degrees Celsius. Source: Adapted from Swanson and colleagues (1998).

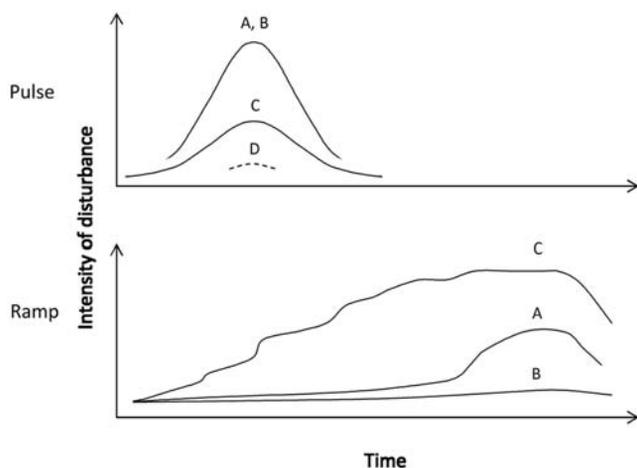


Figure 2. The spatiotemporal pattern of two major types of disturbance. The different lines (A–D) represent different habitats in a river reach. Pulse disturbances arise suddenly, reach their maximum intensity within a short time, and generally last for hours or days, whereas ramps steadily increase in strength and extent over weeks to months. The intensity of any disturbance varies between different habitats, depending on their specific susceptibility (figure 1). Low-intensity habitats provide valuable refugia (box 1). Refugia are disturbance specific; for instance, habitat B is severely affected by a particular pulse disturbance, whereas it constitutes a refuge during a ramp disturbance. Some refugia form only during the disturbance (habitat D, the dashed line). The quality of refugia can decrease over time, such as for habitat A during a ramp disturbance. Source: Adapted from Lake (2000).

Box 2. River ice and its relevance for winter disturbances and refugia.

Two major types of river ice are relevant for winter disturbances and fish refugia: subsurface and surface ice.

Subsurface ice

In turbulent, super-cooled water (water temperature <0 degrees Celsius), tiny ice crystals, collectively called *frazil ice*, are formed. Frazil ice may accumulate in slow-flowing areas (hanging dam) or may adhere to the stream bottom, producing anchor ice (figure 3; Stickler and Alfredsen 2009). In steeper reaches (i.e., with a gradient of more than 0.2%), anchor ice dams can temporarily block streamflow, can change riffles into a stepwise series of pools, and can finally initiate freeze-up of the entire channel. Subsurface ice formation is most pronounced in early winter (Stickler and Alfredsen 2009), but hanging dams may persist throughout winter (Komadina-Douthwright et al. 1997).

Surface ice

A partial or complete surface ice cover is formed in low-gradient rivers or in steeper streams after an extended period of dynamic subsurface ice formation (see above). Surface ice formation often starts in low-current areas, such as pools, and as border ice along the riverbanks or around protruding in-stream structures. Depending on the local climate, surface ice can persist up to several months or can form intermittently, such as in temperate maritime regions (Cunjak et al. 1998). The breakup of surface ice can range from being dynamic, as when an intact ice sheet is destroyed by rapidly increasing water levels (figure 4), to thermal, with the ice sheet deteriorating thermally (Prowse 2001a).

with latitude, altitude, and distance to the sea, which leads to pronounced regional differences in the occurrence and predictability of winter disturbances (Swanson et al. 1998). For instance, rain-induced winter floods are characteristic of winter-wet coastal systems, whereas continental rivers have decreased winter flows, low water temperatures, and excessive ice formation (box 2; McMahon and Hartman 1989, Cunjak 1996, Bradford and Heinonen 2008). Ice-covered temperate streams are subject to periodic thaws and floods, whereas higher-latitude streams rarely experience rain-on-snow events or warming periods long enough to trigger midwinter breakup (Cunjak et al. 1998). Permafrost in arctic catchments reinforces river channels, thereby limiting bed and bank erosion and channel migration (Durand et al. 2011).

Climatic drivers interact with geomorphic characteristics from the catchment to the reach scale. Catchment topography, especially valley confinement and channel slope, are major determinants of flashiness of floods, dynamic ice formation, and snow accumulation (Jakober et al. 1998, Battin et al. 2007). For instance, because of a quick delivery of water, steep, confined channels respond more rapidly to rain-on-snow events. Flashiness is further influenced by the water storage capacity of the snow, which is a function of temperature (Swanson et al. 1998): Warm and wet snow layers melt more quickly, whereas cold and dry snow stores rainwater in the early phase of a rain-on-snow event, attenuating the rise in discharge. In systems with steep hillslopes, winter rainstorms can trigger debris flows, which can deliver masses of soil, sediment, and wood to nearby streams (Lamberti et al. 1991). Furthermore, across

an altitudinal gradient, dynamic ice formation such as excessive anchor ice growth is found only in midelevation reaches (e.g., 2550–2900 meters [m] above sea level [asl] in Wyoming streams, 41 degrees, 2 minutes north latitude) with an incomplete snow and surface ice layer (Chisholm et al. 1987). The accumulation of snow, creating snow bridges in steep, narrow headwaters (more than 2900 m asl) and surface ice in tranquil, lower-gradient reaches at lower elevations (less than 2550 m asl), leads to more stable hydraulic conditions. Besides topographic factors, major differences in stream order control the disturbance intensity across the river network. Flow velocity, turbulence, and shear stress during winter floods were reduced in both perennial and intermittent tributaries compared with the receiving stream (Wigington et al. 2006) and their confluence zones (Harvey et al. 1999). However, because of their high surface-to-volume ratio,

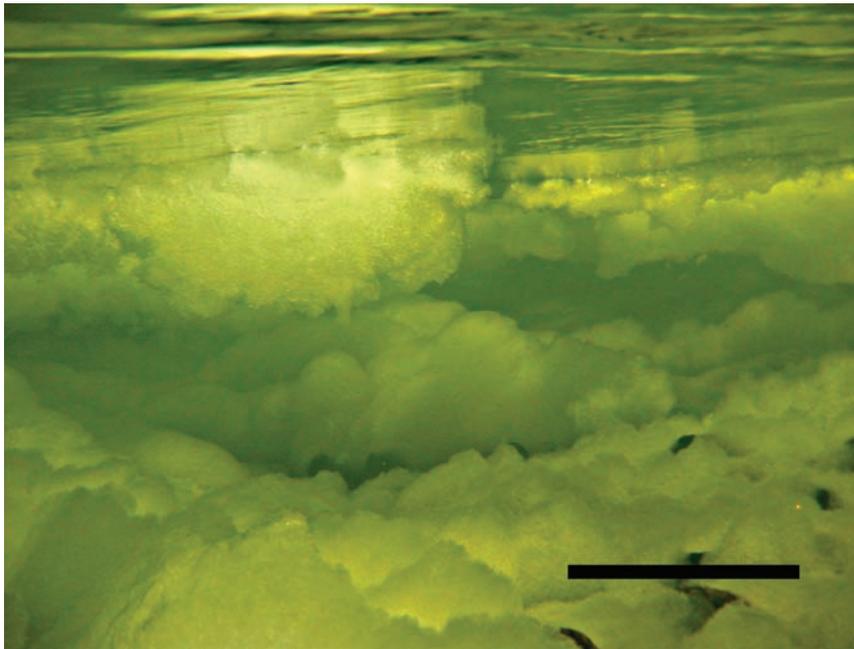


Figure 3. Anchor ice covering bed sediment and penetrating into the interstitial spaces in the Orkla River, Norway. The scale bar represents 50 centimeters. Photograph: Knut T. Alfredsen.



Figure 4. Dynamic ice breakup on the Gaula River, Norway. Photograph: Knut T. Alfredsen.

low-order streams are generally more prone to temperature extremes (Heino et al. 2009), which can trigger, for instance, abrupt temperature fluctuations (Reimers 1963) or bottom-fast freezing (McNeil 1966).

Temporal pattern and abiotic effects

Nested in a climatic and geomorphic context, winter disturbances develop either as clearly delineated, short-term pulses

or as ramps that steadily increase in intensity (figure 2; Lake 2000). Aquatic habitats with their specific substrate or position in the channel differ considerably in their susceptibility to pulses or ramps, which results in the spatial heterogeneity of disturbance intensity. Floods, excessive formations of sub-surface ice, debris flows, and temperature fluctuations all represent pulses (figure 1). Floods are most thoroughly documented in the literature, and two major abiotic effects from open-water events and breakup flooding have been reported. First, high discharges can lead to an expansion of habitat space. Overbank flows result in a reconnection of nutrient-rich floodplain habitats, such as flooded fields or drainage ditches (Masters et al. 2002, Durand et al. 2011), and intermittent tributaries (Brown TG and Hartman 1988). Second, the high discharges cause higher velocities and shear stresses that can cause streambed scour (Seegrist and Gard 1972); bank erosion (Brown RS et al. 2001); and in-stream structures, such as beaver dams, to wash out (Tschaplinski and Hartman 1983). The abiotic effects of flooding, and especially the corresponding erosive forces, are exacerbated in the presence of different types of river ice that confine and divert the flow and constitute direct scouring agents themselves. In particular, the dynamic breakup of a structurally intact ice sheet (figure 4) results in the most pronounced changes of the physical habitat (Doyle et al. 1994), with breakup severity being a function of ice strength and thickness (Cunjak et al. 1998). A thin ice cover is easily broken and removed by a flood peak and results in only minor scour, comparable to an open-water flood. In contrast, a thick ice cover that adheres to the streambed and banks can result in substantial geomorphic disruption during floods (Cunjak et al. 1998). Breakup floods can carry sediment loads two to five times higher than those observed under equivalent open-water floods (Beltaos and Prowse 2009). Ice jams and subsequent surges can divert the floodwater onto the floodplain (Brown RS et al. 2001), causing channel shifts and major erosion over many kilometers, and are able to transport boulders up to 2 m in diameter (Doyle et al. 1994). Conversely, a heavy snowpack

on the river margins constrains the discharge within the channel during rain-on-snow events (snow-constrained flood; Erman et al. 1988). Exceptionally high shear stress and substrate scour occur and exceed the intensity of snowmelt floods of the same or even higher discharge.

Rapid formation of excessive volumes of subsurface ice has been observed in both particularly mild winters in otherwise frozen-over systems (Bisaillon et al. 2007) and comparatively cold winters in otherwise ice-free systems (Chadwick 1982). Furthermore, extraordinary low snowfall results in limited insulation, which promotes the excessive formation of anchor ice (Reiser and Wesche 1979). The excessive formation of subsurface ice affects aquatic habitats in various dimensions. It affects them in a longitudinal-vertical dimension, such that pool habitats are filled by large volumes of floating frazil ice formed in turbulent reaches farther upstream in the channel network. Such hanging dams drastically decrease pool depth and increase flow velocity (Brown RS et al. 2000). It affects aquatic habitats vertically: Anchor ice fills interstitial spaces in the substrate (figure 3; Reiser and Wesche 1979). Finally, it affects them laterally-longitudinally: The buildup and release of anchor ice dams leads to short-term cycles of upstream flooding of the riparian area and downstream drying (Maciolek and Needham 1952, Stickler et al. 2007).

Debris flows, which can be triggered by extreme winter rainstorms, can result in fundamental alterations of riverine habitats through the modification of pool-riffle sequences through scour, which can lower the stream gradient through the deposition of sediment and wood behind a debris dam and can increase irradiance through the removal of riparian vegetation (Swanson et al. 1998, Lamberti et al. 1991). Snow avalanches can represent a pulse disturbance (Resh et al. 1988), locally depositing large amounts of snow and trees, which could temporarily evoke similar effects on aquatic habitats as debris flows. However, to our knowledge, there is no study documenting avalanche effects on riverine fish.

We found only one fish study in which unusually high water temperatures were reported (Reimers 1963). In a high-altitude Californian stream, warm spells in late winter allowed water temperatures to repeatedly rise above a threshold of 4.4 degrees Celsius (°C), which was the long-term average temperature associated with the onset of spring conditions later in the year (higher activity of fish, algae growth, higher availability of mayfly larvae).

In only a handful of articles have ramp disturbances, such as extreme low flows (*droughts*) and excessive ice formation, been discussed. The two events are often interrelated, particularly in smaller streams. Flow reduction increases the surface-to-volume ratio, which boosts water cooling and ice formation (Bradford and Heinonen 2008). In return, the storage of large volumes of water in ice may lower the discharge (Prowse 2001a). Both types of ramp disturbance exhibit two characteristics known from summer droughts (Lake 2000, Magoulick and Kobza 2003). First, the wetted area and water volume contract, which causes shallower

habitats to dry out (Cunjak et al. 1998). Hydrologic connectivity decreases (Bradford and Heinonen 2008), which can cause complete habitat isolation (Schmidt et al. 1989). Second, physicochemical conditions in the contracted habitat space deteriorate, as is demonstrated by interrupted hyporheic flows (Bradford and Heinonen 2008) or hypoxia in isolated, densely populated pools (Schmidt et al. 1989).

Fish response to winter disturbances

Winter disturbances can affect fish directly by physically harming them or by altering their habitat, which necessitates behavioral changes (figure 1). In addition, winter disturbances can operate indirectly by changing biotic interactions, such as competition. Direct and indirect responses to winter disturbances have been described for various fish species, with an emphasis on salmonids, the predominant fish family in high-altitude and high-latitude regions. Responses to disturbances are determined for individual fish, fish populations, and fish communities by *in situ* observations of either radio-tagged individuals (Jakober et al. 1998) or dead fish or eggs (Reiser and Wesche 1979, Erman et al. 1988), or they are derived from postdisturbance measurements, such as spring abundance estimates (Bisaillon et al. 2007). In the latter case, direct mortality can usually not be distinguished from emigration (Elwood and Waters 1969).

During floods without major geomorphic effects, fish show minor to pronounced changes in movement and habitat use but no mortality or physical harm. Habitat shifts represent both passive displacement and active emigration. For instance, after multiple winter floods, adult barbel (*Barbus barbus* L.) were found several kilometers downstream from their wintering habitats, where they had been largely physically inactive (Lucas and Batley 1996). The fish responded with compensatory upstream movement but did not reach the predisturbance position, possibly because of their seasonally reduced metabolism.

Fish responses become much more detrimental after major, erosive floods, which are often observed in the presence of river ice (e.g., breakup floods). The washout of overwintering habitat, such as woody debris or beaver ponds, can evoke a considerable to complete reduction in the densities of juvenile and adult fish in small streams (Seegrist and Gard 1972, Tschaplinski and Hartman 1983), either because of a decrease in carrying capacity or because of displacement or direct kills. Substrate scour leads directly to a mechanical grinding and crushing of substrate-bound species and life stages. For instance, substrate-buried eggs of fall-spawning salmonids experience near to complete elimination (Elwood and Waters 1969), and dead Paiute sculpin (*Cottus beldingi*) of all age classes were found in substrate samples during a snow-constrained flood with major bedload transport (Erman et al. 1988). Such scouring events can reduce sculpin populations by up to 70% (Swanson et al. 1998). Scour-induced mortality can result in long-term population and community responses, such as low-standing crops, an atypical age distribution, or changes in dominance structure.

For instance, reduced fry densities by fall-spawning brook trout lead to an increased survival of spring-spawned rainbow trout fry because of reduced interspecific competition (Seegrism and Gard 1972). After a major midwinter flood, cutthroat trout fry (*Oncorhynchus clarkii* [Richardson]) biomass was on average 43% higher than in the year before, which represents the peak value in the 24-year study period (Swanson et al. 1998). The fry were not exposed to the flood but were descendants from adult survivors. Apart from improved rearing conditions due to the flushing of fine sediment from the substrate, the recruitment peak was explained by reduced interspecific competition (Swanson et al. 1998). The number of distinct winter floods and the maximum winter discharge explained a significant portion of the annual variability in the structure of a fish assemblage sampled over 30 years (Kiernan and Moyle 2012). Elwood and Waters (1969) attributed the low growth rates in adult brook trout in the next summer to the shortage of invertebrate food supply after severe substrate scouring.

Habitat expansion usually results in beneficial responses of fish when high-quality off-channel habitats are reconnected. For instance, the use of flooded fields and ditches by foraging adult pike (*Esox lucius* L.) is positively correlated with discharge (Masters et al. 2002). Many arctic fish species rely on feeding areas that are reconnected by flood pulses during ice breakup in the spring (Reist et al. 2006). Floodwaters lead to a reconnection of intermittent tributaries where juvenile coho salmon (*Oncorhynchus kisutch*) experience higher survival than their conspecifics that stayed in the mainstem (Wigington et al. 2006). However, speed and duration of the expansion matter; abrupt, high-intensity surges after an ice dam break can sweep fish to the floodplain, where they become stranded and suffocate (Doyle et al. 1994).

Habitat contraction produces exclusively detrimental responses because of a loss in habitat and connectivity. The reduction in habitat space resulting from *in situ* ice formation or frazil ice inflow from farther upstream causes habitat exclusion and energy-intensive migrations of fish, as is illustrated by higher-frequency and longer-distance movements (Brown RS and Mackay 1995, Cunjak et al. 1998). Furthermore, Simpkins and colleagues (2000a) hypothesized that 15 of their 40 radio-tagged rainbow trout were directly killed by frazil ice crystals plugging their mouths and gills. Anchor ice and solid ice penetrating into the substrate directly kill the buried eggs of salmonids (McNeil 1966, Reiser and Wesche 1979) and reduce fry abundance in the coming spring (Bisaillon et al. 2007). Localized kills of round whitefish (*Prosopium cylindraceum*) in densely populated habitats were attributed to overcrowding and hypoxia following a loss in connectivity (Schmidt et al. 1989). Fish are stranded and suffocate if habitats dewater completely, such as when anchor ice dams completely block streamflow (Maciolek and Needham 1952). The subsequent drying and freezing of redds lead to considerable mortality of eggs (Chadwick 1982, Bisaillon et al. 2007).

Intrinsic drivers of fish response

The susceptibility of fish to a given disturbance is not constant over time but depends on life-history characteristics, such as the development stage or overwintering strategy, and the physical condition of the fish (figure 1). In general, older age classes seem to be more resistant to winter disturbances than are juvenile fish or larvae and eggs (Harvey et al. 1999). For instance, responses to winter floods were more pronounced and more predictable for young than for adult brook trout (*Salvelinus fontinalis*) and rainbow trout (*Oncorhynchus mykiss* [Walbaum]; Seegrism and Gard 1972). Although the substrate-bound, immobile early life stages were killed by scour of the streambed, the older individuals were affected only by the harshest floods that damaged or destroyed beaver dams. Flood resistance can vary within an age class on the basis of the species' overwintering strategy. Passive integrated transponder (PIT)-tagged juvenile coho salmon that entered intermittent tributaries during early winter floods were recaptured at higher proportions at smolt traps in the following spring than were their conspecifics that stayed in the mainstem (Wigington et al. 2006). Such partial refuge seeking may result from a variety of individual differences, including physical condition, with only the strongest individuals deciding to emigrate. Susceptibility may also vary during winter as a function of ongoing ontogenic processes. For instance, mass kills of burbot larvae (*Lota lota*) in a Finnish river did not occur in years during which the soil-borne acidification peak was highest but only when it occasionally overlapped with the burbot's most vulnerable development stages—the hatching stage and the free-swimming larval stage (Hudd and Kjellman 2002). There is some empirical evidence of a negative synergism for fish in an impaired physical condition that experience winter disturbances. For instance, summer-stocked adult rainbow trout had higher mortality than their wild conspecifics during unusual fluctuations in late winter water temperature (Reimers 1963). The hatchery-reared fish had continuously lost energy since they were stocked, and their comparatively poor prewinter condition had decreased further. The rapid warming increased their metabolic demands, whereas their depleted energy reserves prevented them from readily exploiting the improved food availability of invertebrates.

Species differ in their susceptibility to and recovery from winter disturbances. As was described above, sculpin populations were reduced by up to 70% from a midwinter flood with severe substrate scour (compared with 30% inter-annual variation; Swanson et al. 1998). Conversely, adult cutthroat trout suffered only minimal density reductions (–8%), which were explained by their ability to temporarily move to off-channel refugia. In contrast, the benthic sculpins took refuge in substrate interstices in which they got caught by the scour. The population recovery was estimated to last more than 5 years for the sculpins, but only 1–3 years for the trout.

Refuge functioning as an extrinsic driver of fish response

A variety of habitats serve as refugia from winter disturbances (tables 1–3). All of these examples deal with pulse disturbances, mostly high flows and excessive ice formation. These refugia are current protected and are little affected by dynamic ice, such as frazil ice deposition or floating ice sheets, because of either their position in the channel or their structural richness. For instance, mean flow velocities in pools and runs of the Grand River in Ontario increased in the course of a midwinter flood, forcing overwintering white sucker (*Catostomus commersonii*) and common carp (*Cyprinus carpio* L.) to emigrate (Brown RS et al. 2001). The fish found refuge from floods in backwaters that had consistently lower current velocities (Brown RS et al. 2001). Off-channel habitats are also less affected by ice dynamics, such as the downstream transport of frazil ice in early winter or moving ice during breakup (Komadina-Douthwright et al. 1997). Refuge from excessive subsurface-ice formation is furthermore found in regions of groundwater influx,

as has been demonstrated for cutthroat trout that were excluded from overwintering pools by extensive anchor ice growth (Brown RS and Mackay 1995).

Similar to off-channel habitats, in-stream structures locally reduce harsh hydraulic conditions. The more complex the structure is, the more pronounced its modulating effect is. McMahon and Hartman (1989) reported a series of experiments in which highly branched root material provided a preferred refuge from floods for juvenile coho salmon in artificial outdoor flumes by deflecting flows and creating current-protected, turbulence-free pockets. These experiments corroborate findings from the field, in which structurally rich accumulations of woody debris provided crucial refugia from floods for juvenile coho salmon (Tschaplinski and Hartman 1983).

Refugia from winter disturbances are found over various spatial scales, overlapping with residential habitats (Simpkins et al. 2000a) or representing distinct habitats (Brown RS et al. 2000). The proximity of refugia has been shown to mitigate detrimental responses by reducing disturbance-

induced losses of individuals or energy and by enabling recolonization of disturbed areas. For instance, brown trout populations were wiped out completely during an extremely cold and dry winter in five boreal stream reaches that lacked nearby refugia (Hoffsten 2003). No recolonization was observed by the following fall, but predisturbance densities were achieved or exceeded after 3 years, which suggests immigration from beyond the reach scale. The responses were much less pronounced in two other, arguably more heterogeneous, streams. Interannual variability in coho salmon recruitment was reduced by the presence of high-quality refugia (Brown TG and Hartman 1988). The availability of nearby refugia also prevents fish from long, energy-consuming migrations, during which they could face displacement or stranding (Brown RS et al. 2001).

The longitudinal arrangement of refugia is particularly relevant in the presence of disturbances with a directional pattern, such as floods (Lake 2000). For instance, juvenile coho salmon densities increased by a factor of four following multiple winter freshets in a river section offering stable refugia (Tschaplinski and Hartman 1983). The fish probably washed in from less-structured river sections, located in a large clearcut area farther upstream. In turn, the upstream reaches experienced

Table 1. Physicochemical characteristics of refugia from a winter pulse disturbance—an open-water flood—as a function of species and age class.

Taxon	Age class	Refuge	Duration of use	References
<i>Oncorhynchus kisutch</i>	Juvenile	(Intermittent) tributaries, hatchery streams; ephemeral swamps, riverine ponds; stable accumulations of woody debris and tree roots in deep pools and under undercut banks	Until spring emigration	Skeesick 1970, Peterson 1982, Tschaplinski and Hartman 1983, Brown TG and Hartman 1988, Wigington et al. 2006
<i>Oncorhynchus clarkii</i>	Adult	Downstream of woody debris (tributaries, secondary channels); upstream of large woody debris (main channel); along the banks in pools formed by woody debris; flooded alders along the edges of straight reaches; below a tributary confluence in a pool formed adjacent to bedrock	Flood event	Swanson et al. 1998, Harvey et al. 1999
<i>Cottus beldingi</i> , <i>Cottus bairdi</i>	Juvenile and adult	Within substrate	Flood event	Swanson et al. 1998

Table 2. Physicochemical characteristics of refugia from a winter pulse disturbance—a breakup flood—as a function of species and age class.

Taxon	Age class	Refuge	Duration of use	Reference
<i>Catostomus commersoni</i> , <i>Cyprinus carpio</i>	Adult	Backwaters; low-velocity, backwater-like habitats along at the margins of deep pools	Until water levels drop (<i>C. commersoni</i>); remaining winter months (<i>C. carpio</i>)	Brown RS et al. 2001
<i>Salmo trutta</i>	Adult	Depending on the habitat availability (runs, backwaters)	Flood event	Brown RS et al. 2001
<i>Salmo salar</i>	Adult	Upstream of confluences to small brooks, upstream point sources of major spring runoff, backwaters	Prior to and during breakup	Komadina-Douthwright et al. 1997

Table 3. Physicochemical characteristics of refugia from a winter pulse disturbance—the excessive formation of subsurface ice—as a function of species and age class.

Taxon	Age class	Refuge	Duration of use	Reference
<i>Cyprinus carpio</i>	Adult	Edge of a run 30–50 meters upstream covered by border ice; small, shallow pool 200 meters upstream; lower end of the pool at the ice edge	Duration of the dam (2 weeks)	Brown RS et al. 2000
<i>Oncorhynchus mykiss</i>	Juvenile	At the bottom of deep pools, shallow stream-margin habitats under border ice, at the mouths of intermittent tributaries with no flowing water	Several days	Simpkins et al. 2000a
<i>Oncorhynchus clarkii</i>	Adult	Regions of groundwater influx (up to 4 degrees Celsius warmer than the surrounding stream), deep ice-covered pools	Remaining winter months	Brown RS and Mackay 1995

considerable to complete reductions in densities but were recolonized by small numbers of coho salmon by mid- to late winter. Following a series of winter freshets, Peterson (1982) found the majority of marked juvenile coho salmon sheltering in riverine ponds as far as 33 kilometers downstream from their residential habitats.

Fish use refugia from winter disturbances over various periods of time, ranging from the duration of the disturbance event (Harvey et al. 1999) to the remaining winter months (Brown RS and Mackay 1995). The duration of use depends on at least two factors: refuge connectivity and refuge persistence. Because both factors usually vary over the course of a winter disturbance, the movement into or out of the refugia has to be optimally timed. Trapping in flood refugia has been reported for white sucker and common carp, more than 10% of which died in isolated backwater pools and drainage ditches that they had entered during dynamic ice breakup (Brown RS et al. 2001). If a refuge is hydrologically connected to the residential habitats of the fish, its quality, which is always relative to the quality of the residential habitats, will determine the duration of refuge use. For instance, cutthroat trout were permanently excluded by excessive anchor ice growth from cover-rich pools that they had occupied in the fall (Brown RS and Mackay 1995). The fish retreated to habitats that are less likely to be affected by subsurface ice, such as groundwater-influenced areas and deep, ice-covered pools, where they stayed until spring. These refugia were considered less-preferred winter habitats, because the fish had moved past them in the fall (Brown RS and Mackay 1995). The duration of refuge use also reflects species-specific habitat preferences. Following a midwinter flood, white sucker left backwaters soon after discharge reduction, whereas common carp stayed even after the pre-flood level was reached (Brown RS et al. 2001).

Environmental cues that trigger the behavioral response are necessary to achieve the optimal timing to initiate movement into or out of refugia. Given the potential severity of winter

disturbance effects on fish, such cues have to function as an early-warning system of high reliability (Cunjak et al. 1998). The environmental cues that trigger movement into or out of refugia from winter disturbances have been largely unexplored. The only insights come from laboratory studies in which simulated winter floods indicated that increasing flow velocity may represent an environmental cue. Juvenile coho salmon initiated active downstream movement at velocities as low as 3.2 centimeters per second (Giannico and Healey 1998). In the presence of structurally complex cover, coho salmon resided in the main channel but shifted to the lowest-velocity habitats within these structures as soon

as velocities increased (McMahon and Hartman 1989). Such early responses are difficult to determine in the field, because telemetry studies, for example, would require very frequent positioning and abiotic measurements (Brown RS et al. 2001).

Human alterations of winter disturbances and refugia

Flow regulation, channelization, logging, and agriculture directly and indirectly affect flowing waters, which, as a result, are among the most heavily impaired ecosystems worldwide (Heino et al. 2009). The impacts often function as press disturbances of long-term persistence that influence the natural disturbance regime of a river (Lake 2000). Abundant evidence of human alterations of winter disturbances is found in ice-dominated river systems with hydropower production, in which increased and more variable winter flows due to production releases can result in recurrent breakups (Stickler et al. 2007), incomplete freeze-up (Stickler and Alfredsen 2009), and excessive subsurface ice formation following prolonged periods of supercooling (Alfredsen and Tesaker 2002). Repeated thawing and refreezing of border ice (box 2) can result in bottomfast freezing of shallow, slow-flowing edge waters and in the cutting off of important fish refugia (Alfredsen and Tesaker 2002). During flushing flows without major geomorphic effects, fish generally show either none or only minor changes in movement and habitat use. For example, juvenile rainbow trout demonstrated higher site fidelity and moved below-average distances during an eightfold flow increase (Simpkins et al. 2000b). In contrast, the boost in anchor ice formation led to increased movement in Atlantic salmon parr (Stickler et al. 2007).

Anthropogenic impacts have modified stream morphology, both directly (e.g., channel straightening) and indirectly (e.g., increased input of fines). Human activities result in simplification and homogenization of aquatic habitats and reduction in the availability of refugia from winter disturbances (Brown RS et al. 2001). Logging activities lower the

input of in-stream wood, and the remaining debris accumulations provide less resistance at high discharges; such structures are easily washed away by winter floods and lose their function as important refugia from floods (Tschaplinski and Hartman 1983). In logging and agricultural areas, channels are often wider and shallower and are therefore more prone to excessive formation and accumulation of river ice (Cunjak 1996).

Global climate change is expected to alter the frequency and intensity of extreme winter events in temperate and cold regions (Kundzewicz et al. 2007). In high-elevation catchments that span the current snowline, midwinter flooding will become more common because of a higher proportion of precipitation falling as rain instead of snow, whereas spring peaks will be smaller (Battin et al. 2007). In both high-altitude and high-latitude catchments, major changes in ice-related disturbances can be expected (Beltaos and Prowse 2009). Because river ice thickness is positively correlated with the accumulated degree-days below 0 degrees Celsius (Cunjak et al. 1998), increasing temperatures imply later freeze-ups, thinner ice layers, and earlier breakups, which are associated with a transition from dynamic to more thermal events (Prowse 2001b). Erosion caused by the breakup of river ice directly affects stream morphology and mobilizes nutrients (Prowse 2001b). Any reduction in breakup intensity will have major consequences for the composition, structure, and function of aquatic and riparian communities, such as a reduced biological diversity and productivity (Reist et al. 2006, Durand et al. 2011, Prowse et al. 2011). Small streams in boreal catchments may face particularly pronounced changes in their thermal and hydrological regimes because of their large surface-to-volume ratio (Heino et al. 2009). An increased proportion of precipitation falling as rain could negatively affect fall-spawning brook trout (and benthic Paiute sculpins; Erman et al. 1988) in California headwater streams, whereas spring-spawning rainbow trout could benefit from reduced levels of both flood scouring of redds and interspecific competition (Meyers et al. 2010). Permafrost melt in arctic catchments can reduce bank stability and increase erosion, which could lead to profound geomorphic and water quality changes that affect productivity and habitat availability (Durand et al. 2011).

Summarizing the state of the art

Most of the literature on winter disturbances and riverine fish deals with pulse disturbances (mainly floods), and, despite their widespread occurrence, ramps are understudied (Bradford and Heinonen 2008). There is a particular focus on ice-induced disturbances, which possibly indicates an awareness of winter disturbances in systems in which the major hydrologic events are driven by river ice rather than by surface runoff in other seasons (Prowse 2001a). The literature shows a bias in describing physical disturbances to fish and their habitats and neglects the idea that riverine fish communities could also be subject to purely biological

disturbance during winter, such as an exceptionally high predation by birds or mammals. The geographic focus on high-latitude and high-altitude rivers entails that salmonids, the predominant fish family in this region, are over-represented in the literature.

Overall, we found that complex disturbances, involving geomorphic and physicochemical alterations, are particularly detrimental for all age classes of fish. In only a few studies have indirect, longer-term responses of fish to winter disturbances been discussed, and all of these dealt with pulses. Several studies attributed the resistance of fish to winter disturbance to their mobility, with the least mobile species or life stages being the most vulnerable. Mobility enables the fish to exploit spatial heterogeneity and move into habitats in which the disturbance has a lower intensity. These examples demonstrate that species persistence is very much a question of the spatiotemporal scale of observation.

Water depth and cover availability are of minor importance for refuge quality in winter; adult fish retreat to either open areas during midwinter floods (Harvey et al. 1999) or to shallow habitats during frazil ice events (Brown RS et al. 2000). However, this finding may be biased by the fact that mainly short-term pulses, requiring only limited periods of refuge use, have been documented in the literature. Cover-rich, deep habitats, which are less susceptible to dewatering and which provide protection from predation, might be more relevant during long-lasting ramp disturbances, such as winter droughts (Huusko et al. 2007). For example, cutthroat and brown trout preferred cover-rich pools in a field experiment in which discharge had been successively reduced by a total of 400% over a 3-month period from December to February (Dare et al. 2002). Similarly, we assume that groundwater services in refugia (e.g., provision of baseflow, ice-free areas and migration corridors, and dissolved oxygen; Brown RS et al. 2011) are generally underestimated in the literature that is focused only on pulse disturbances; however, groundwater services may prove more important during longer-lasting ramp disturbances.

Linking winter ecology and disturbance research

The ecological effects of winter disturbances have been studied much less frequently than those in other seasons. The limited consideration of winter disturbances biases our understanding of riverine dynamics in temperate and cold regions toward that of spring–summer disturbances. Disturbance data provide the basis to disentangle anthropogenic impacts from natural variability (Cunjak 1996), which is of special relevance, given the expected climate-change-induced increase in the frequency and intensity of extreme winter events (Kundzewicz et al. 2007). We believe that four gaps need to be filled. First, biotic and abiotic baseline data on winter dynamics are needed in order to identify extreme events. Time series from long-term monitoring are of particular value, because the probability of capturing a disturbance rises with the duration of the study and because the long-term responses can be identified,

Box 3. Questions for future research.

Below, we outline questions to be addressed by future research for improving the understanding of winter disturbances and fish response.

Disturbance characteristics

How do different types of aquatic habitats respond to winter droughts (e.g., sediment transport, flow velocities, oxygen supply)? What is the role of groundwater in ice-induced disturbances (e.g., excessive formation of subsurface ice)? How do riverine fish respond physiologically and behaviorally to particularly early or rapid fall cooling? Can supercooled water represent a disturbance to riverine fish? Can predation pressure by birds or mammals act as a biological winter disturbance? Can biological disturbances lead to disturbance intensification if they coincide with or result from physical disturbance?

Refuge functioning

How is species persistence affected in systems with anthropogenically impaired habitat heterogeneity or connectivity (and, therefore, a lower availability or accessibility) of refugia? What refugia do fish use during ramp disturbances, such as winter droughts or the excessive formation of ice? What factors trigger refuge use during pulse and ramp disturbances? How are these environmental cues influenced by recent and future human activities? Can individual differences in energy resources or physical conditions explain partial movement to refugia?

Fish susceptibility

How do species that overwinter in an immobile to torpid state, such as many cyprinids (Cunjak 1996), respond to winter disturbances? Are fish in frequently disturbed rivers more resistant to winter disturbances than fish at rarely disturbed sites? What are the costs and benefits of winter disturbances to different overwintering guilds? Is vulnerability to a winter disturbance highest when energy reserves are low (e.g., late winter, after major disturbances in the summer months)?

including indirect responses to biotic interactions (Kiernan and Moyle 2012). Technical improvements enable longer studies with different species and age classes, including the increased capacities and smaller size of batteries in radio telemetry and larger reading ranges in PIT technology. Second, winter ecology and disturbance research should be more closely linked by testing assumptions of practical relevance for both disciplines. As a prerequisite, it is worthwhile to clarify terms and definitions (box 1) in order to prevent confusion or duplication. We list questions to be addressed by future research in box 3. Third, hydraulic and population models—crucial tools for prediction and ecosystem understanding—should increasingly incorporate winter- and disturbance-specific aspects, such as various causes of winter mortality (Hurst 2007, Huusko et al. 2007) or dynamic ice formation and its effects on the residential and refugial habitats of riverine fish (Alfredsen and Tesaker 2002). Fourth, management for sustainability requires that river managers and conservationists work proactively by including anticipated future alterations in the design of restoration and conservation activities. Special emphasis should be given to near-natural systems, such as the high-elevation catchments that are often priority areas in present-day conservation efforts and may be particularly susceptible to climate change (Battin et al. 2007). In order to determine management actions for arctic freshwater systems and to advance our understanding of climate-induced changes, increased and standardized monitoring activities are required (Prowse et al. 2011). Furthermore, it is crucial not only to focus on residential habitats but

to conserve the remaining refugia, to restore those that have been lost, and to reestablish the connectivity between residential habitats and refugia (Skeesick 1970, Bond and Lake 2005). A catchmentwide perspective has to be applied, given the large-scale significance of refugia (Peterson 1982). Because many important refugia from winter disturbances form only temporarily (Tschaplinski and Hartman 1983, Brown RS et al. 2001), they are often underappreciated and are therefore neglected in management and legislation. For instance, the jurisdictional status of intermittent streams—key refugia for juvenile coho salmon from winter floods—remains to be made clear in the US Clean Water Act (Wigington et al. 2006).

The importance of disturbance research has increasingly been recognized in the management of river environments for fish, but because winter disturbances have not been as widely studied, management of fish in high-altitude and high-latitude environments lacks an understanding of nearly half of the intra-annual variation in the physical environment. A broader understanding of fish response to winter disturbances will allow for more accurate management and conservation efforts, especially with the uncertainties associated with a changing climate.

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