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Ecological effects of river ice break-up: a review and perspective

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SUMMARY

1. Abiotic disturbances strongly modify spatial and temporal patterns of lotic ecosystem community structure and function. Such effects are produced because disturbances alter organic matter, nutrient and contaminant dynamics and the distribution and abundance of bacterial, algal, macroinvertebrate and fish communities.
2. River ice break-up is a seasonal disturbance in rivers at high altitudes and latitudes world-wide and is characterized, in part, by large increases in current velocity, stage, water temperature, concentrations of suspended materials and substrate scouring.
3. These abiotic factors are likely to have important effects on primary producers, consumers, and food-web dynamics of river biota. Despite the potential importance of river ice break-up on community structure and function, detailed information describing the magnitude of their effects and underlying causal mechanisms is scarce.
4. The objective of this paper is to provide a hydrological and ecological review and perspective on the potential effects of ice break-up on lotic ecosystems. Specifically, the potential importance of break-up on water temperature, river sediments and geomorphology, riverine energy sources, contaminants, and its effects on river biota and food-web dynamics are evaluated.

Introduction

It is widely appreciated that disturbances play a major role in determining the structure and function of lotic ecosystems (Fisher *et al.*, 1982; Sousa, 1984; White & Pickett, 1985; Resh *et al.*, 1988). Disturbances such as catastrophic floods are strong modifiers of nutrient, contaminant and organic matter dynamics as well as affecting bacterial, algal, macroinvertebrate and fish community abundance and diversity (Fisher *et al.*, 1982; Grimm, 1987; Erman, Andrews & Yoder-Williams, 1988; Resh *et al.*, 1988; Scrimgeour & Winterbourn, 1989; Poff & Ward, 1990; Reice, Wissmar & Naiman, 1990; Steinman & McIntire, 1990; Mackay, 1992). Although numerous studies have characterized the effects of disturbances such as floods and droughts on lotic ecosystems, little information exists on the effects of the seasonal break-up of river ice.

In the broadest sense, river ice break-up can be defined as the process of ice decay starting from the initiation of thermal degradation of ice cover, to the time of complete clearance of ice from the river (modified from Allen, 1977; Reedyk, 1988; Prowse, 1989). This process is a characteristic feature of those rivers at high latitudes and altitudes that are covered in ice during winter. The physical nature of break-up is governed by a range of hydrothermal and hydromechanical processes, the relative importance of each being largely dependent on hydraulic and meteorological conditions. In general, ice break-up is accompanied by rapid changes in water stage, velocity, temperature and suspended sediment concentrations, and can be associated with intense scouring of the river channel and banks. Despite the physical significance of the ice break-up process, the ecological effects on aquatic ecosystems are poorly understood. Potentially important consequences include alterations to water chemistry, nutrient cycling, the fate and uptake of contaminants, and the effects on primary and secondary producers.

The objective of the present study is to review briefly the physical characteristics of river ice break-up. The potential effects of these physical processes on aquatic ecosystem structure and function are examined. Because there has been a paucity of research in this field, identification of plausible ecological effects were based on knowledge of open-water ecology, and judgements on the probability of impacts resulting from ice-affected physical processes. A discussion of the potential effects of changes in break-up intensity on river systems resulting from climate change concludes the paper.

Hydrological conditions

Break-up

River ice break-up is preceded by a period during which ice cover remains largely intact, although significant thinning may occur at the ice surface and base as a result of atmospheric and hydrothermal heat fluxes (e.g. Prowse, 1984; Prowse & Marsh, 1989). As runoff from the landscape continues, discharge increases and stage rises (Beltaos, 1984; Prowse, 1990;

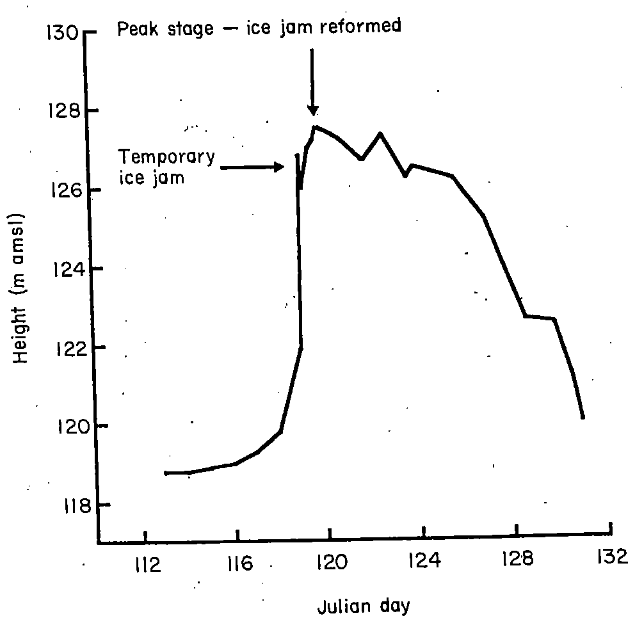

Fig. 1 Spring 1983 stage hydrograph for the Liard River, Northwest Territories, Canada. Redrawn with permission from Prowse (1984). amsl = above mean sea level.

Fig. 1). The magnitude of these events is determined by a variety of hydraulic and meterological conditions (Thompson & Sporns, 1964; Beltaos, 1984; Prowse, 1984) that can produce one of two general types of break-up: (i) dynamic (i.e. pre-mature) and (ii) thermal (i.e. over-mature; Deslauriers, 1968; Beltaos, 1981, 1984; Prowse, 1989). In the over-mature case, which most closely approximates break-up conditions on lakes, spring discharge remains low while the ice sheet thins, detaches from the banks and loses significant strength. In rivers, this is usually associated with low spring runoff following small accumulations of winter snow, and the presence of a thin weak ice cover (Prowse, 1994b). Eventually the ice sheet weakens until it poses low resistance to spring flow. In contrast, dynamic break-up is characterized by the presence of strong, intact ice cover which may still be attached firmly to the shore, and is caused by a large, spring flood wave created by rapid and extensive snowmelt, sometimes augmented by rainfall. With rising discharge, the downstream forces rupture and dislodge the intact ice sheet, driving it downstream.

The severity and pattern of break-up is influenced by the alignment of the river course relative to the local climate. On rivers in which snowmelt, runoff and ice break-up proceed downstream with the seasonal advance of warm weather, the ice jam and flood risk is heightened because the spring flood wave pushes against the intact ice sheet (Beltaos, 1984; Prowse, 1994b). The risk is lower on rivers flowing in a direction opposite to that of regional warming because thermal ablation of the downstream cover prior to spring melt can greatly reduce the probability of ice jamming.

Break-up fronts and ice jams

In a thermal break-up, numerous small-scale break-up fronts can be initiated at sites where the ice has been preferentially weakened, thinned and/or forced by tributaries or localized instream flow. The downstream passage of such thermal break-up fronts is usually characterized by: (i) a small stage increase because of low hydraulic resistance offered by the ice cover; and (ii) minimal scour along the banks because of ice cover separation from the banks, and of the bed, as a result of limited ice shoving and thickening (reviewed by Prowse, 1994b).

Dynamic break-up is usually driven by a rapidly moving front or surge, often produced by the sudden collapse of an ice jam and the release of water in channel storage. Such fronts can increase downstream water levels and velocities dramatically (Beltaos, 1984; Prowse, 1994b). In large rivers, breaking fronts (i.e. transitions between intact and fragmented or fractured ice; Fig. 2) can career downstream through intact ice covers often at speeds exceeding $5\,\mathrm{m\,s^{-1}}$, and can produce rapid increases in water level (e.g. $>1.0\,\mathrm{m\,min^{-1}}$; Doyle & Andres, 1978; Parkinson, 1982; Gerard *et al.*, 1984). The magnitude and rate of surge characteristics represent a more catastrophic flood potential than is typically possible under similar open-water flow conditions.

Resistance of ice to the progression of breaking fronts is offered by channel resistance, as created by downstream hydraulic (e.g. channel slope, roughness, flow depth and velocity) and ice conditions (e.g. bank–bed attachment, mechanical strength and thickness; Calkins, 1983). Arresting of a breaking front can lead to the formation of another ice jam. In fact, break-up over long distances within a river can be viewed as a series of surge–stall processes related to the successive failure and formation of ice jams.

Ice jams are possible under both thermal and dynamic conditions, although the largest backwaters and flooding are generally produced by the latter type. The level of backwater increase created by an ice jam depends on its overall flow resistance, which is determined largely by its thickness relative to water depth. Once formed, ice jams remain in place until there is a sufficient rise in upstream forces, or decrease in downstream resistance, to cause the accumulation to rupture and create another surge or break-up front. Detailed information on break-up, breaking fronts and ice jams is given by Prowse (1994b).

Ecological effects of river ice break-up

Sediments and geomorphology

The abrasive action of rapidly moving break-up fronts can be an important modifier of channel beds and banks, particularly on alluvial rivers (Smith, 1980; Scrimgeour & Prowse, 1993; Prowse, 1994b). Most significance erosion effects should occur during dynamic events where ice strength, velocity and stage are maximized. Distinctive erosional features, such as high-level benches (Smith, 1980), undercut banks (e.g. Marusenko, 1956) and, in permafrost regions, thermo-erosional niches (e.g. Lawson, 1983) are produced in channel cross-sections. Ice scour also enhances erosion of meander banks (e.g. Martinson, 1980).

Despite geomorphological and laboratory studies (e.g. Wuebben, 1988) having been undertaken on the erosional effects of river ice, field data documenting suspended sediment and bed loads during this dy-

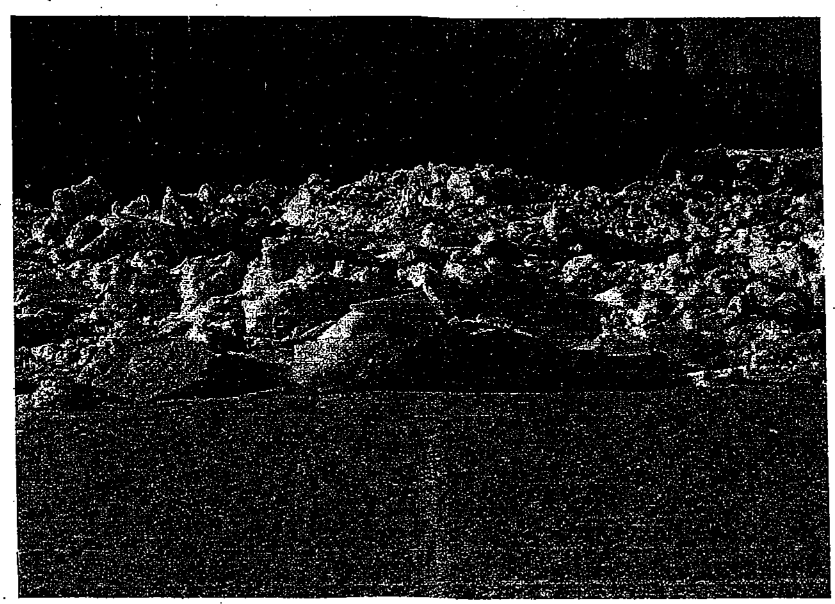

Fig. 2 Dynamic break-up front showing the transition from intact ice to heavily fractured ice in the Liard River, Northwest Territories, Canada. Breaking front was advancing in excess of $5\,\mathrm{m\,s^{-1}}$.

namic period are rare. Prowse (1994a) reported a 30-fold increase in suspended sediment concentrations during break-up in the Liard River, Northwest Territories, Canada (Fig. 3). Comparable data are not available for bed loads, but Beltaos (1993) estimated that sufficient shear stress could be produced by the break-up surges (e.g. $5\,\mathrm{m\,s^{-1}}$) to move bed material particles as large as 20 cm in diameter. Although sediment deposition within channels and in over-bank flood zones is commonly observed after break-up, reports vary about the quantities involved and its potential effects on algae, benthos and fish. Field observations indicate that sediment deposits range from a thin veneer to deep localized accumulations over 1 m deep (Eardley, 1938).

Under open-water conditions, the transport and deposition of sediments can reduce species richness and abundance of stream biota (e.g. Rosenberg & Wiens, 1978; Culp, Wrona & Davies, 1986; Lloyd, Koenings & LaPerriere, 1987; Ryan, 1991), and increased suspended sediment concentrations resulting from mining activities can reduce primary production (Van Nieuwenhuyse & LaPerriere, 1986; Lloyd *et al.*, 1987). Rosenberg & Wiens (1978) documented significant increases in macroinvertebrate drift caused by sediment additions to experimental channels. Reductions in macroinvertebrate abundance associated with sediment addition potentially result from a diversity of factors, including reduced primary production, clogging of food filtering apparatus, and a reduction in the quantity and quality of usable habitat (Gammon, 1970; Ryder, 1989; Ryan, 1991). High concentrations of suspended sediment also affect fish by reducing survival of sac fry, availability of their invertebrate or algal prey, and the ability of some visual feeders to locate prey (see reviews by Alabaster & Lloyd, 1982; Ryan, 1991).

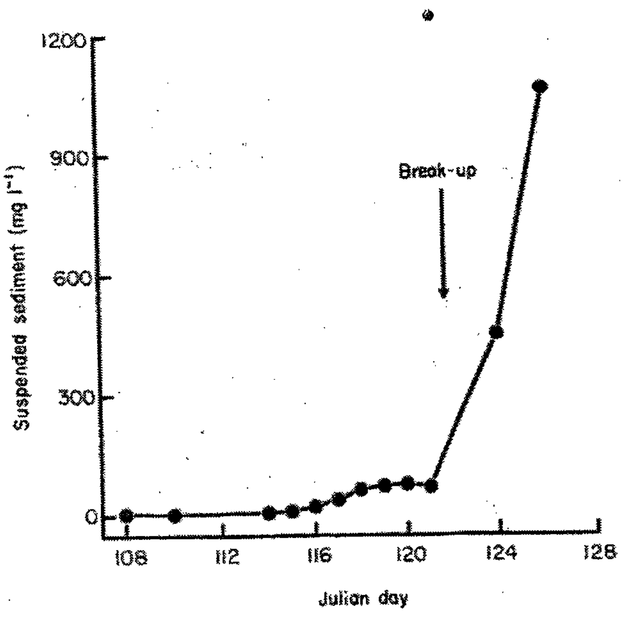

Fig. 3 Suspended sediment concentration ($\mathrm{mg\,l^{-1}}$) before and immediately after river ice break-up on the Liard River, Northwest Territories, Canada, 1987. Redrawn with permission from Prowse (1994a).

More prominent features of break-up include the characteristic ice-push ridges, island buttresses, boulder barricades, ridges, and larger relief forms resembling glacier eskers, boulder pavements, drumlins and roche moutonneé (glacier worn rocks). In general, most information about ice-produced features refers to the riparian zone; little is known about the nature or prevalence of such features within open-water flow channels.

Water temperature

Metabolic processes of many members of the biota in aquatic ecosystems are strongly dependent on water temperature. Microbial, algal, macroinvertebrate and fish activities and growth rates typically increase as water temperature increases, although they may decrease when an upper temperature threshold is exceeded (e.g. Ward & Stanford, 1982; Butler, 1984; Rempel & Carter, 1986; Holtby, 1988). Most information on the effects of water temperature on stream biotic processes originates from studies conducted during the open-water or intact-ice seasons when water temperatures are controlled largely by day-to-day and diurnal changes in meteorological heat fluxes.

In contrast, the large hydrothermal heat flux associated with river ice break-up can produce abrupt changes in temperature that are unrelated to diurnal cycles (e.g. Marsh & Prowse, 1987; Marsh, 1990). Under a stable ice cover, even during periods of pre-break-up warming, river water temperatures are typically low (<0.02°C) and stable, sometimes differing less than 0.01°C between consecutive days (e.g. Marsh & Prowse, 1987; Marsh, 1990; P. Marsh, unpubl. data). In contrast, water temperature can increase abruptly with the passage of break-up fronts (Terroux *et al.*, 1981; Parkinson, 1982). For example, the 13 h transition from intact ice cover to open-water conditions in the lower Mackenzie River, Northwest Territories, Canada, was accompanied by an approximately 9°C increase in water temperature (Parkinson, 1982; Fig. 4). The highest ice-edge water temperatures result from dynamic break-ups; ice cover is completely cleared leaving long reaches of open water in which uninterrupted heating may occur (Prowse & Marsh, 1989). In contrast, the irregular downstream progression of thermal break-ups often leaves alternating reaches of ice and open water, thereby reducing the potential for high temperatures at the ice to open-water interfaces. The biological effects of rapid temperature increases of the scale that can occur during river ice break-up are unknown.

Organic energy sources

Energy sources derived from organic carbon compounds fixed by primary producers, either within (i.e. autochthonous primary production) or outside (i.e. allochthonous primary production) the lotic environment, fuel metabolic processes of food webs in rivers (Vannote *et al.*, 1980). The relative importance of autochthonous and allochthonous inputs and riverine productivity is determined by many environmental factors including channel morphology, turbidity, water temperature and nutrient availability. In large temperate and tropical rivers such as the Mississippi (Grubaugh & Anderson, 1989) and the Amazon (Day & Davies, 1986), high spring or summer flows trigger the annual release of organic material from floodplain to channel and are the principal forces that maintain river productivity (Cummins *et al.*, 1983; Sedell, Richey & Swanson, 1989; Sparks *et al.*, 1990). In contrast, both the size and frequency of flooding of many high latitude rivers are greater during break-up than during the open-water period (Prowse, 1994b). This suggests that an annual organic nutrient pulse may occur during break-up. Moreover, the magnitude of the allochthonous load will be determined by the severity of ice break-up. Under the extreme scenario of dynamic break-up, ice scour by rapidly moving break-up fronts will lead to organic matter input to a river reach. Sources of this input are organic material stored within upstream sediments, channel banks and riparian zones. In rivers that are not strongly incised (i.e. unconstrained with broad valley floors) the formation of ice jams and the resultant inundation of the floodplain will also provide substantial inputs of dissolved and particulate organic matter (Mackenzie River Basin Committee, 1981). Whereas organic matter inputs during dynamic and thermal break-up events have not been quantified, the large amount of recently eroded river bank and riparian material transported during dynamic break-up events suggests that organic matter inputs during dynamic events may exceed those during thermal events (Prowse & Scrimgeour, pers. obs.). Thus, temporal variation in break-up intensity could result in annual variability in the size of allochthonous organic matter inputs, and, depending upon processing rates, the quantity of organic detritus stored along a river reach may decrease following successive years of low-intensity, thermal break-ups.

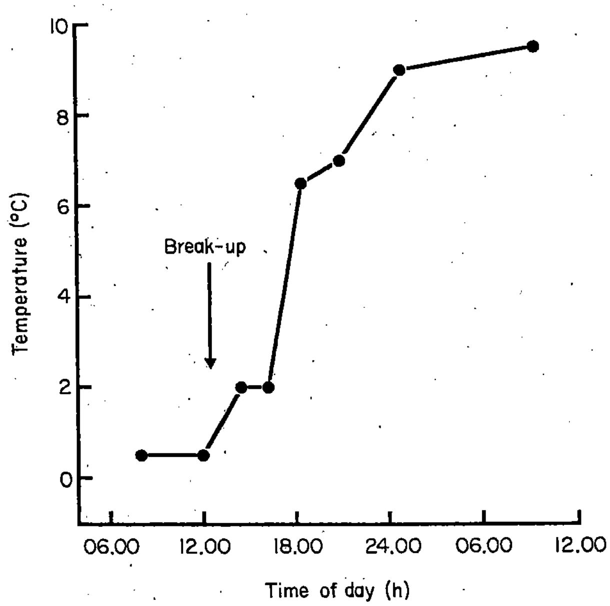

Fig. 4 Water temperature in the lower Mackenzie River, Northwest Territories, 24–25 May 1980. Redrawn with permission from Parkinson (1982).

As Sedell *et al.* (1989) have suggested for temperate and tropical rivers, the relative contributions of autochthonous and allochthonous materials to productivity of rivers at high latitudes or altitudes can be expected to be related to river size, and carbon inputs from upstream and the surrounding terrestrial vegetation. In forested regions at high latitudes, biological productivity of low order (first to third) streams is most likely to be driven by organic carbon inputs triggered by spring ice break-up. Although autochthonous primary production may be of greater importance in mid-order streams (fourth to sixth), limited data suggest that allochthonous inputs commonly serve as the dominant carbon source in these systems (Peterson *et al.*, 1985), again implicating the potential importance of break-up-related organic nutrient pulses.

In addition to their quantity, the quality of organic inputs influences the abundance of detritivores (Culp & Davies, 1985) and river productivity. Terrestrial leaf litter and other non-woody particulate organic matter deposited in riparian zones and floodplains often enters streams in a less decomposed state than material that has been stored in river sediments for an equivalent period of time. Because cold temperatures and permafrost greatly slow decomposition in terrestrial environments of boreal and subarctic forests, the contribution of high quality, undecomposed, detrital material to the total organic load may be greater for high latitude northern rivers than southern, temperate rivers. Thus, inputs of dissolved and particulate organic matter at the time of ice break-up should provide riverine microbes and invertebrate detritivores with a rich allochthonous food source.

Inputs of organic materials to river systems may also display spatial and temporal variability as a result of differences in stream morphology and changes in break-up characteristics. For example, reaches of the Mackenzie River with sharp bends or shallow shoals may regularly receive inputs of organic matter from alluvial, riparian and floodplain sources, because ice jams typically form in these areas (Mackenzie River Basin Committee, 1981). Among-year variations in break-up intensity may result in annual variability in inputs of allochthonous organic matter such that the quality and quantity of organic detritus stored along a river reach may be correlated with break-up intensity. We hypothesize that the quantity of detritus stored in a river bed will decrease during successive years of low intensity, thermal break-up events because processing of detrital carbon by decomposers, and the export of detritus by fluvial transport, will exceed detrital inputs to the river.

Nutrients and contaminants

Primary and secondary productivity in high latitude rivers has been hypothesized to be limited by the availability of nutrients, particularly phosphorus and nitrogen (e.g. Welcomme, Ryder & Sedell, 1989; Bodally *et al.*, 1989; Roy, 1989). Ecosystem responses of high latitude rivers to nutrient additions has been well documented in the Kuparuk River, Alaska, U.S.A. (reviewed by Peterson *et al.*, 1993). Phosphorus enrichment in the Kuparuk River over a 4-year period affected all trophic levels by increasing some microbial processes, algal biomass and productivity, and invertebrate and fish growth rates. Enrichment effects varied among years however. The strong 'bottom-up' effects observed in years 1 and 2 were less apparent in years 3 and 4 when strong 'topdown' feedbacks became prominent (Peterson *et al.*, 1993). Nutrient additions have also been shown to increase periphyton biomass and invertebrate densities in mountain streams (e.g. Winterbourn, 1990); and invertebrate and fish biomass in temperate rivers (e.g. Perrin, Bothwell & Slaney, 1987; Johnston *et al.*, 1990).

Ice break-up should have strong effects on nutrient budgets because dissolved and particulate organic matter inputs to rivers from shoreline and floodplain aggradations contain substantial amounts of phosphorus and nitrogen. Whalen & Cornwell (1985) reported that 30% of the annual input of phosphorus to a small Alaskan stream was transported in the 10 day period following break-up and the commencement of spring flow, whereas only 10% of the total annual volume of water was discharged during the same period. Ice break-up in the Colville River delta, northern Alaska, U.S.A., is a major contributor of mineral and organic matter including nitrogen, the limiting nutrient in arctic coastal waters (Hamilton, Ho & Walker, 1976). Similarly, total phosphorus and nitrogen concentrations in the Athabasca River, at Athabasca, Alberta, Canada, peaked in April during the period of ice break-up (Fig. 5). Extractable metal concentrations also peaked in April and May (Mackenzie River Basin Committee, 1985). It is difficult to separate the effects of ice action and discharge increases on the mobilization of nutrients and metals because they occur simultaneously. However, since total nitrogen and phosphorus did not continue to increase with increasing discharge after break-up in the Athabasca River (Mackenzie River Basin Committee, 1985), it is likely that nutrient mobilization may result predominantly from the erosive action of ice. The importance of discharge to the entrainment and transport of nutrients is consistent with the findings of Brunskill *et al.* (1975) for large rivers in northern Canada. For example, whereas annual

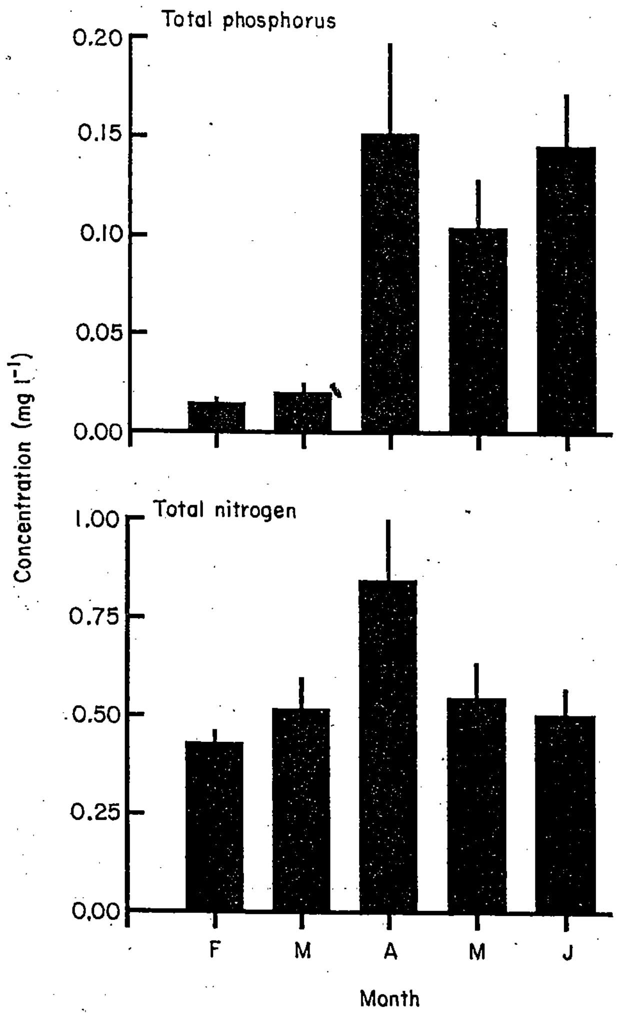

Fig. 5 Monthly nutrient concentrations ($\bar{x} \pm$ SE) in the Athabasca River, Alberta, Canada between February and June, 1963–90. Data provided by Alberta Environmental Protection, Edmonton, Alberta, Canada.

nutrient transport rates in the Arctic Red, Liard, Mackenzie, Peel and South Nahanni Rivers are high (720–4100 and 8400–20 000 mol km^{-2} total phosphorus and total nitrogen, respectively), most of the phosphorus and nitrogen occurs in the particulate form (Brunskill *et al.*, 1975).

Break-up of ice also has important implications for transport pathways of contaminants since exchange rates at the water–sediment interface are affected by flow rates and concentrations of suspended solids in the water column. In the Mackenzie River, Northwest Territories, Canada, downstream transport of polyaromatic hydrocarbons is influenced by flow regime, presumably because of alterations to exchange rates between the water column and the sediments (Nagy *et al.*, 1987). Moreover, since break-up follows a protracted period of ice cover and low flow, the high flows during break-up may be associated with unusually high metal or contaminant concentrations. These may be the result of changes in sediment redox conditions, or the suspension of particulates that have accumulated near point source outfalls or depositional areas during the winter. In the Hudson River, New Jersey, U.S.A., high PCB concentrations in the water column have been associated with discharges sufficiently high to scour and resuspend bottom sediments (Limburg, 1986). Likewise, in the Athabasca River, extractable aluminium, copper, iron, magnesium and zinc concentrations, and pesticide (e.g. 2,4-D and α-BHC) concentrations observed during periods of maximum discharge likely relate to scour and resuspension of sediments and their adsorbed metals and contaminants (Mackenzie River Basin Committee, 1985).

In addition to changes in open-water chemistry, the resuspension of bottom material by break-up surges, and the incorporation of riparian and floodplain sediments into the water column can affect riverbed chemistry. Whereas break-up surges are capable of removing large diameter bed material, fine particulate sediments are most susceptible to removal and resuspension. Since fine sediments have a greater binding capacity for contaminants than coarse sediments (see Buckman & Brady, 1960), their flushing from riverbeds can have significant impacts on both riverbed and open-water chemistry. Thus, the removal, suspension and subsequent deposition of fine sediments along a reach of the Pembina River, Alberta, Canada, was associated with decreases in nutrient concentrations and increases in oxygen penetration of the riverbed in places scoured of fine sediments (Chambers, Prepas & Gibson, 1992). Furthermore, the higher binding capacity of fine sediments for contaminants means that resuspension and deposition of these materials can transport pollutants far downstream from their origin.

Biota

Disturbances are important organizing factors in lotic ecosystems (Resh *et al.*, 1988; Grimm & Fisher, 1989; Reice *et al.*, 1990; Sparks *et al.*, 1990; Mackay, 1992; Poff, 1992). However, defining what constitutes disturbance is a contentious issue in aquatic ecology (e.g. Resh *et al.*, 1988; Poff, 1992) and numerous definitions exist (Sousa, 1984; White & Pickett, 1985; Resh *et al.*, 1988; Grimm & Fisher, 1989; Steinman & McIntire, 1990; Poff, 1992). For our purposes, disturbance is defined as any relatively discrete event that changes the local environmental conditions irrespective of the predictability of the event. In many studies the effects of open-water floods on algae, macroinvertebrates or fish have been investigated, and not surprisingly they have been found to reduce species diversity, biomass, and the density of producers and consumers.

Primary producers. In addition to stimulating primary production through increased nutrient availability, the scouring action of ice and water during break-up is likely to reduce epilithon biomass. Such reductions are likely to be small however, because algae are not abundant under ice where irradiance and water temperatures are growth limiting (e.g. Rosemarin, 1975). Whereas periphyton communities recover rapidly from catastrophic open-water disturbances (e.g. Scrimgeour, Davidson & Davidson, 1988; Steinman & McIntire, 1990; Lohman, Jones & Perkins, 1992), the importance of scouring in determining maximum biomass and species composition is not known. However, it is reasonable to assume that among-year differences in the severity of break-up could affect the timing of peak algal biomass, in addition to abundances of individual species and the taxonomic composition of communities. Whereas dynamic break-up events have the potential to severely deplete algal biomass, thermal break-ups are likely to leave algal communities largely undistributed and ready to grow rapidly during the open-water period. A comparable situation has been documented for open-water conditions, where the absence of seasonal flood disturbances permitted periphyton to increase substantially (e.g. Rounick & Gregory, 1981).

Ice break-up may also play a significant role in determining the distribution and abundance of submerged macrophytes and riparian vegetation (Mackay & Mackay, 1977; Nichols, Schloesser & Hudson, 1989). The effects of break-up on these plants are a function of both its intensity and plant type. For example, shrubs and trees have persistent aboveground parts whereas submerged macrophytes and most annual plants lack these structures. Along the continuum from dynamic to thermal break-up, herbaceous plants will be broken and uprooted at lower forces. In fact, measurements of floristic composition along an exposure gradient on an island in the Rideau River, Ontario, Canada, showed that terrestrial herbaceous plant cover decreased from 77 to 23% with increasing exposure to ice scour and water flow. In contrast, woody plant coverage ranged from an estimated 80% cover at the exposed end of the island to 100% at a more protected downstream location (Cameron & Lambert, 1971). The ability of herbaceous plants to recolonize river beds after break-up and high flows will be determined by the number of surviving underground perennating organs (rhizomes, tubers, stolons) as well as by introductions from undisturbed areas. Nichols *et al.* (1989) noted that whereas the April 1984 development of a 0.4–7.0 m ice jam in the St Clair River between Lakes Michigan and Erie (U.S.A.–Canada) delayed the onset of submerged macrophyte growth, the riverbed was not scoured, and by September, the location, size and shape of plant beds was similar to that in the previous year.

Under dynamic break-up conditions, ice can be pushed up a riverbank above and beyond the highest floodwaters (Fig. 6), uprooting trees and shrubs, and causing bark damage several feet above ground (Cameron & Lambert, 1971; Mackay & Mackay, 1977). The upper limit of ice action determines the lower limit of trees, and is often marked by a chaotic heap of driftwood, uprooted trees and shrubs, and mud and stone heaps (Mackay & Mackay, 1977). The success of both herbaceous and woody plants in establishing and recolonizing the ice-push zone will be determined, in part, by break-up intensity (i.e. dynamic versus thermal break-up events). Severe annual scours may act as reset mechanisms, and result in a return to dominance by highly productive, fast-growing pioneer species (Cameron & Lambert, 1971).

Consumers. Ice break-up may strongly affect the composition, abundance and biomass of invertebrate and fish communities because of the presence of high sediment concentrations, bed scouring and movement, and the erosion of riparian zones. The effect of break-up on consumers is likely to parallel the results of flooding, that is, reduce density, species richness and biomass (e.g. Siegfried & Knight, 1977;

Fig. 6 Ice shove into the bank of the Mackenzie River, Northwest Territories, Canada. Top of ice push is 10 m above water level.

Matthews, 1986; Sagar, 1986; Scrimgeour *et al.*, 1988; Scrimgeour & Winterbourn, 1989). For example, Sagar (1986) and Scrimgeour & Winterbourn (1989) reported reduced macroinvertebrate abundance and diversity immediately following spates in two braided New Zealand rivers. They also reported significant relationships between mean total faunal density and spate intensity (i.e. maximum mean daily discharge in the 30 day period prior to benthic collections; Sagar, 1986), and spate frequency (i.e. length of the low flow period prior to benthic collections; Scrimgeour & Winterbourn, 1989). The magnitude of effects of river ice break-up on benthic invertebrates is likely to be related to the intensity of break-up in a similar way to that observed for the effects of flood events on aquatic communities (e.g. Reice *et al.*, 1990; Mackay, 1992). Hence, it is reasonable to predict that the effects of break-up on consumers will be greatest when dynamic events occur, and lowest for thermal events.

Ice break-up has the potential to affect fish communities by causing mortality of eggs, juveniles and adults, reducing the abundance of their invertebrate prey, and by stranding and displacing fish downstream (e.g. Alabaster & Llyod, 1982; Cunjak & Power, 1986; Matthews, 1986; Scrimgeour & Winterbourn, 1987; Ryan, 1991). Bed disturbance may also kill other aquatic vertebrates, such as northern leopard frogs, *Rana pipens*, which over-winter in the bottoms of streams in Ontario, Canada (Cunjak, 1986).

In general, fish communities of highly disturbed river systems (as in New Zealand braided rivers) and those present immediately following floods have low species richness and low numerical abundance (e.g. Glova, Bonnett & Docherty, 1985; Matthews, 1986). For instance, Glova *et al.* (1985) found that fish standing crop and density were several-fold higher, and species richness greater, in the more benign Ashley River than in the physically harsher Hurunui and Rakaia Rivers. Similarly, Matthews (1986) concluded that total fish fauna was more stable in a benign midwestern (U.S.A.) stream, Piney Creek, than in Brier Creek, a stream subject to greater flow variability. In contrast to floods, the effects of ice break-up on fish communities, and the mechanisms by which they operate, are poorly understood.

Ice break-up: a temporal perspective

The effects of disturbances on ecosystem processes are influenced by the rates at which flora and fauna return to pre-disturbance levels. Whereas disturbances such as open-water floods can have strong short-term effects on the densities of many aquatic species, in the long term many are remarkably persistent (e.g. Grossman, Dowd & Crowford, 1990; Steinman & McIntire, 1990; Wallace, 1990). In freshwater systems, recovery of algal, macrophyte, macroinvertebrate and fish communities following catastrophic disturbances can be rapid, and return to pre-disturbance levels may occur within 3–12 months depending upon the generation times and the colonizing abilities of the taxa concerned (Matthews, 1986; Rushforth, Squires & Cushing, 1986; Scrimgeour *et al.*, 1988; Nichols *et al.*, 1989; Sedell *et al.*, 1990; Mackay, 1992).

In addition to changing ecosystem processes, disturbances affect community structure. The intermediate disturbance hypothesis (Connell, 1978) predicts that species diversity will be lowest in physically harsh environments and in particularly benign conditions, and highest under intermediate frequencies or intensities of disturbance. If the intermediate disturbance hypothesis is applicable to streams (Ward & Stanford, 1983), a shift from intense, dynamic break-ups to less severe, thermal events would be expected to alter community richness. Likewise, rivers at high latitudes and altitudes that differ in break-up intensity may exhibit differences in species richness.

Alterations to flow regimes resulting from the construction of dams or global climate warming, for example, could alter the structure of aquatic and riparian communities in rivers at high altitudes and latitudes by affecting ice break-up intensity. Global circulation models predict that a doubling of atmospheric CO_2 concentration could increase annual air temperatures by 4–7°C in arctic regions depending on latitude (e.g. Manabe & Stouffer, 1980; Washington & Meehl, 1984). Higher winter temperatures can be expected to reduce ice thickness because the latter is related positively to the number of degree days below zero accumulated during winter (e.g. Butyagin, 1972). Similarly, increases in air temperatures are predicted to reduce the length of the ice cover period in the Mackenzie River by 13–19% (Reedyk, 1988).

Although general models predicting the occurrence of thermal and dynamic break-ups are not available, Prowse (1986) was able to distinguish between thermal and dynamic break-up conditions on the Liard River, Northwest Territories, Canada, between 1978 and 1985 using the total number of accumulated degree days (i.e. the sum of mean daily temperatures) from 1 April to the time of break-up. Whereas there was no apparent pattern in break-up date between dynamic and thermal events, the number of accumulated degree days for dynamic break-up events ranged from −32.1 to −174.2°C. In contrast, the accumulated degree day totals for two thermal events were positive (i.e. +70.8 and +149.1°C, respectively; Prowse, 1986). Although the ability to discriminate between dynamic and thermal ice break-up events using accumulated degree days has proven useful at one site in the Liard River, the utility of accumulated degree days at other sites remains to be tested (Prowse, 1994b). We suspect that the use of degree days to predict changes in break-up type will likely be of limited use because high degree day totals can be associated with thermal events because of reduced ice strength and rapid runoff, characteristics of dynamic events. The ability to discriminate between dynamic and thermal events based on other climatological conditions could represent a critical initial step in predicting the effects of flow alteration on community structure of rivers at high latitudes and altitudes.

The ability to distinguish between thermal and dynamic break-ups is further complicated because global circulation models also predict increased winter precipitation in arctic regions (e.g. Manabe & Stouffer, 1980; Washington & Meehl, 1984). The combination of increased winter precipitation and warmer air temperatures could produce sufficiently high spring runoff to rupture and drive an intact ice cover downstream. The ability to determine the effects of break-up on stream community structure and function will depend on our understanding of the relationship between climatic conditions and break-up type (i.e. thermal versus dynamic) and carrying out a baseline monitoring programme in which a variety of community characteristics (e.g. species richness, abundance, energy flow) are considered. Such an approach should assist the development of quantitative models relating the physical characteristics of break-up to ecosystem processes.

In summary, we have briefly described the physical characteristics of river ice break-up, and discussed a variety of known and plausible impacts of break-up on aquatic ecosystems. Our account is not an exhaustive review because many of the predicted effects are yet to be observed, and the state of understanding of the few known impacts and the mechanisms producing them is incomplete. Nevertheless, most evidence suggests that ice break-up should have strong population, community and ecosystem effects as a result of changes to river sediments and geomorphology, temperature, energy sources, nutrient processing, fate and uptake of contaminants, and the quality and quantity of carbon resources available to the biota.

The effects of river ice break-up on stream ecosystems are thought to be mediated through a diversity of pathways. For instance, break-up will directly affect stream herbivores because of increased mortality during break-up. After break-up, the animals remaining are affected indirectly by reductions in the abundance of their algal food resources, and changes in the abundance and distribution of macroinvertebrate and fish predators. The effects of break-up on herbivores may be even more subtle if break-up reduces the rate at which algae recover to predisturbance levels. For example, this might result if nutrient inputs from instream and riparian sources are reduced. The magnitude of such effects will undoubtedly vary temporally and spatially as a result of differences in disturbance type (i.e. dynamic *v* thermal break-ups). If invertebrate abundance, diversity and production are affected by disturbance intensity, then the relative frequency of dynamic and thermal break-ups could result in among-year variations in invertebrate community structure and production. This example further emphasizes the need to understand the effects of disturbance frequency and intensity, necessary prerequisites for the development of predictive ecosystem level models for rivers at high latitudes and altitudes.

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