THE INFLUENCE OF RIVER ICE ON BIRDS AND MAMMALS

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ABSTRACT

Few publications address the topic of this review directly. The winter ecology of some species has not been studied though there is some data for the more conspicuous and valuable waterfowl and bald eagles and for fur-bearing aquatic mammals. Winter poses special problems for warm blooded vertebrates and most birds migrate to milder regions. A few aquatic mammals modify their winter habitat to enhance survival while others depend on a suitable sub-ice microclimate. Agricultural activities and industrial developments have the potential to modify conditions in ice-covered rivers to the detriment of wildlife. This subject needs more intensive study to properly evaluate the impacts on birds and mammals of changes in winter conditions in rivers.

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INTRODUCTION

This review offers a brief introduction to what appears to be a neglected area of avian and mammalian ecology. The literature is dispersed, the information is often anecdotal and the conclusions speculative. Comments and data on the effects or river ice on birds and mammals may form only a minor part of studies with other primary objectives, making the material hard to find. In this respect, this review is not exhaustive but, by bringing attention to the lack of information, we hope to stimulate more interest in this topic.

Birds and mammals which are associated with ice covered rivers must meet certain requirements to survive. The environment is very different from that found during the open water season. Water temperatures are near 0°C and access to and availability of water is limited by ice and low water levels. There are changes in water quality and sudden, perhaps catastrophic, changes in discharge during freeze-up and break-up events (Prowse and Gridley, 1993). Day length is short and light levels in the water may be very low. This can limit the time during which visual foraging can occur. Birds and mammals require a regular food supply to meet their high metabolic demands. To maintain high core temperatures they are well insulated with water repellant outer coverings of fur or feathers and they exhibit other anatomical and behavioral adaptations to conserve heat (Calder and King, 1974). Aquatic species must have access to water and to air for breathing. This is particularly critical for species living beneath the ice. The dynamic nature of the ice covered riverine environment appears to have selected species of aquatic mammals which remain alert and able to respond appropriately to any sudden changes in their habitat. Birds, on the other hand, have the option of leaving if conditions become too difficult. For both birds and mammals, the level of information available seems to fall into three categories: no information; fortuitous observations; and planned research. Examples of each, for birds and mammals, are described in the sections which follow.

BIRDS

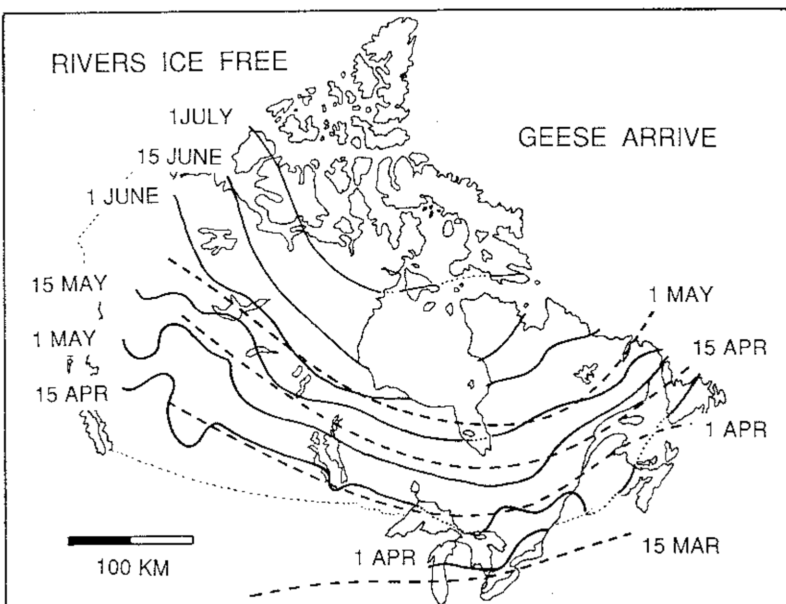
The general response of birds to the onset of winter is to migrate to areas with more suitable climate. The migrations are triggered by shortening day-length, endogenous physiological rhythms as well as a genetic component (Gill, 1989). This is as true for the orders of aquatic birds (loons - Gaviiformes; grebes - *Podicipediformes*; herons, bitterns, storks, etc. - *Ciconiiformes*; swans, geese and ducks - *Anseriformes*) as it is for the migrating song birds and finches (*Passeriformes*). Birds migrate along broad continental flyways which, in North America, are oriented north-south, partly because of the shape of the continents and the orientation of the main mountain chains and river valleys. Aquatic species tend to follow waterways and Bellrose (1976) developed the concept of "migration corridors" to depict the more precise movements of waterfowl, often tangential to the main axis of migration.

The migration corridors of Canada geese (*Branta canadensis*), mapped by Bellrose (1976), are 48-80 km wide. They follow river valleys, lakes and coastal marshes so that the birds have safe resting areas, food and water along the way. Canada geese prefer sleeping on the water, a safe haven from foxes and other predators that could easily attack them at night (Breen, 1990). It is, therefore, important that migration is timed to ensure that rivers offer ice-free refuges for waterfowl. In spring, rivers open up before lakes and geese arrive about two weeks before rivers are ice free, taking advantage of polynia that develop along the water courses (Figure 1).

Robins (*Turdus migratorius*) may also appear along river channels before the snow has disappeared and the ice has broken-up. Observations made along the Roseau River, about 65 km south of Winnipeg, Manitoba, for most years between 1977 and 1982 and occasionally since, revealed that two species of stonefly (*Taeniopteryx nivalis* and *T. parvula*) emerge in March to mid-April. They crawl up through cracks in the ice, metamorphose into adults, move to shore and, because they are black, they quickly "melt" into the snow. At the peak of emergence there were up to 5 stoneflies $.min^{-1}.m^{-1}$ of shore. In most years robins stationed themselves at 2-4 m intervals along the river banks in riffle zones, consuming the stoneflies as they

Figure 1

The mean dates of arrival in spring of Canada geese compared with the dates when rivers are ice free. Based on figures in Dorst (1962) and Allen (1977).



arrived on shore (J.F. Flannagan, personal observations).

The onset and intensity of freeze up and thaw varies from year to year, as does the severity of winter, and birds dependent on access to open water are sometimes trapped. Information on mortalities due to being caught by river ice is hard to find although there are several bird species exposed to risk. The belted kingfisher (*Ceryle alcyon*) may winter in extreme southern Québec and a few individuals may remain in southern Ontario, Nova Scotia, Prince Edward Island and southern Newfoundland. Similarly, the great blue heron (*Ardea herodias*) occasionally winters in the Maritimes and southern Ontario (Godfrey, 1986). The kingfisher frequents smaller rivers because it requires overhanging riparian vegetation to provide perches for surveillance of open water. The heron fishes in the shallows of larger rivers. Although both species may be observed in early winter in places that later freeze over, we found no information on winter mortalities.

Agricultural practices have resulted in some waterfowl either delaying or failing to migrate south as food is provided in the form of spoilings from the grain harvest. Canada geese foraging on corn residues in southern Ontario during the winter of 1992-93 were in poor condition by March. Rivers in Waterloo County had been frozen since January, with virtually no open leads. Access to corn had been made difficult by layers of snow and freezing rain and the geese were reluctant to fly when approached (Power, personal observation). Although no carcasses were observed, the birds must have been easy prey for foxes and coyotes.

Jorde *et al.* (1983) studied the feeding ecology of mallards (*Anas playthynches*) wintering along the Platte River, Nebraska. The mallards foraged in three different habitats: river channels; irrigation drainage canals; and agricultural fields. The availability of food was influenced by ice conditions, water depth and discharge rates, and snow accumulation. Even when high discharge and heated effluent from a power plant prevented an ice cover forming on the Platte River, accumulation and movement of slush ice limited mallard foraging. Approximately 5-25,000 mallards overwintered in the study area in 1979 and 1980, along with Canada geese and other waterfowl. Plant foods made up 97% of the diet of mallards, corn and sorghum accounted for 54%, duckweed and other wild plants accounted for

43% while invertebrates (mostly molluscs) made up only 3% of the food. Corn provided an elevated carbohydrate intake (83%) which helped meet the mallards' high winter energy requirements. Invertebrate foods were scarce and ice cover limited foraging. This component of the diet is believed essential and mallards spent 55% of their time foraging in riverine habitats in 1979, when most of the river was frozen, and 38% in 1980 when it was open, turbulent and at flood levels. High concentrations of mallards depleted natural foods at open water sites and birds overwintering farther south consumed more invertebrates and wild plants.

The mallards usually make one flight in late afternoon (average 3.8 km, max. 20 km) to the corn fields (Jorde *et al.*, 1983). This exposes the birds to raptor predation. Mallards ignore bald eagles (*Haliaeetus leucocephalus*) when they are on the ground and will forage close to them. However, there is a link established between the mallards, duck hawks and bald eagles when the eagles are deprived of their normal fish prey by ice.

The primary prey of bald eagles is fish, particularly spawning salmon and salmon carcasses, but they also scavenge other food, including dead and dying waterfowl. As food becomes scarce they resort to inter- and intraspecific kleptoparasitism, stealing food from other raptors and younger conspecifics. In winter they range widely in search of food and open water with concentrations of ducks and, perhaps, winter-killed fish attracts them (Griffin and Basket, 1985). The winter range in Alaska is restricted to bays and river mouths in the south-central region of the state. They are absent from the north slope because inland waters are nearly completely frozen, as is the sea. Open water on the Tanana River, however, supports some overwintering eagles because of the abundance of salmon,, mallards and common mergansers (*Mergus merganser*) (Ritchie and Ambrose, 1987). In the Chilkat River, Alaska bald eagles left the river when severe ice build-up along the river edge reduced the availability of salmon (Hodges *et al.*, 1987). In Nebraska during the winters of 1978-79 and 1979-80, Jorde and Lingle (1988) studied the diet and behaviour of bald eagles practising kleptoparasitism. Species from which prey were stolen included the ferruginous hawk (*Buteo regalis*), red-tailed hawk (*B. jamaicensis*), rough-legged hawk (*B. lagopus*) and golden eagle (*Aquila chrysaetos*).

During the harsh winter of 1978-79, when heavy ice restricted their access to fish, mallards formed 38% of the diet of bald eagles. Interspecific kleptoparasitism occurred when the mallards were foraging in agricultural fields. Hawks used fence posts, trees and power lines as vantage points. Whenever a hawk immobilized a mallard, the bald eagles moved in and stole its prey. The eagles learned where the mallards were feeding and often acted in groups, stealing prey from each other in the process. During the mild winter of 1979-80, river channels remained open and fish were generally available. Mallards were consumed mainly in March, following an outbreak of disease when many carcasses were available (Lingle and Krapu, 1986, cited in Jorde and Lingle, 1988). Conditions that favour kleptoparasitism include 1) a shortage of primary food, 2) an abundance of secondary foods, 3) predictable primary and secondary food sources, and 4) a concentration of hosts and prey. River ice can affect all these conditions.

An early study of the effect of river ice on overwintering birds was that of Salyer and Lagler (1940) on the American (common) merganser (*Mergus merganser*) in Michigan. Beginning in early October, the ducks gather on Great Lakes bays, river-mouth lakes and the lower reaches of rivers in the northern half of the lower peninsula. Large flocks distribute themselves over available water until freezing weather arrives, when they normally migrate southward. The winter of 1933-34 was exceptional in that the wintering population of mergansers in Michigan was large. Early winter was mild followed by a sudden freeze and one of the coldest late winters recorded. Many of the lingering migrants, and the normal winter population, were forced to the unfrozen middle reaches of trout streams where they were held by the cold from January until March 1934. Salyer and Lagler (1940) provided details of the ducks being forced to move because of heavy flows of pancake ice and releases of anchor ice. They also suggested that heavy concentrations of ducks (up to 300 km^{-1}) could adversely affect the trout populations. Based on examination of stomach contents, they estimated trout consumption at about 0.5 kg per duck day^{-1} and suggested that a concentration of 100 ducks could kill 7,000 trout in two weeks. They made various suggestions to protect the trout, such as organized duck drives to disperse the birds. The problem is there is no direct proof the mergansers deplete the trout populations over the long term, although evidence for at least temporary local depletion is strong.

MAMMALS

Information on the effects of river ice on overwintering mammals is as scanty as it is for birds. Some observations appear trivial but could have genetic implications. For example, very few mountain goats (*Oreamnos americanus*) residing in the canyon of the Stikine River, British Columbia cross the river, but they do so on ice (Foster and Rahs, 1985). Other mammals use ice bridges to cross rivers, gain access to islands and colonize them and this can have an important effect on the mammalian communities found on islands (Lomolino, 1990). Caribou have been reported to be attracted to icings, perhaps because the ground water is mineralized (Edwards and Ritcey, 1960).

Mammals living beneath an ice cover are very difficult to study, accounting for the lack of winter observations. The American water shrew (*Sorex palustris*) is an example. It inhabits swift streams in forested areas north almost to the tree-line and to 2,250 elevation. It is active all year, breeding from January through August and feeding on small fish and aquatic invertebrates. The habitat it occupies lends itself to the formation of a hanging ice cover supported on large woody debris and boulders and the sub-nival under ice microclimate (Calkins and Shanley, this proceedings) protects it from extreme cold.

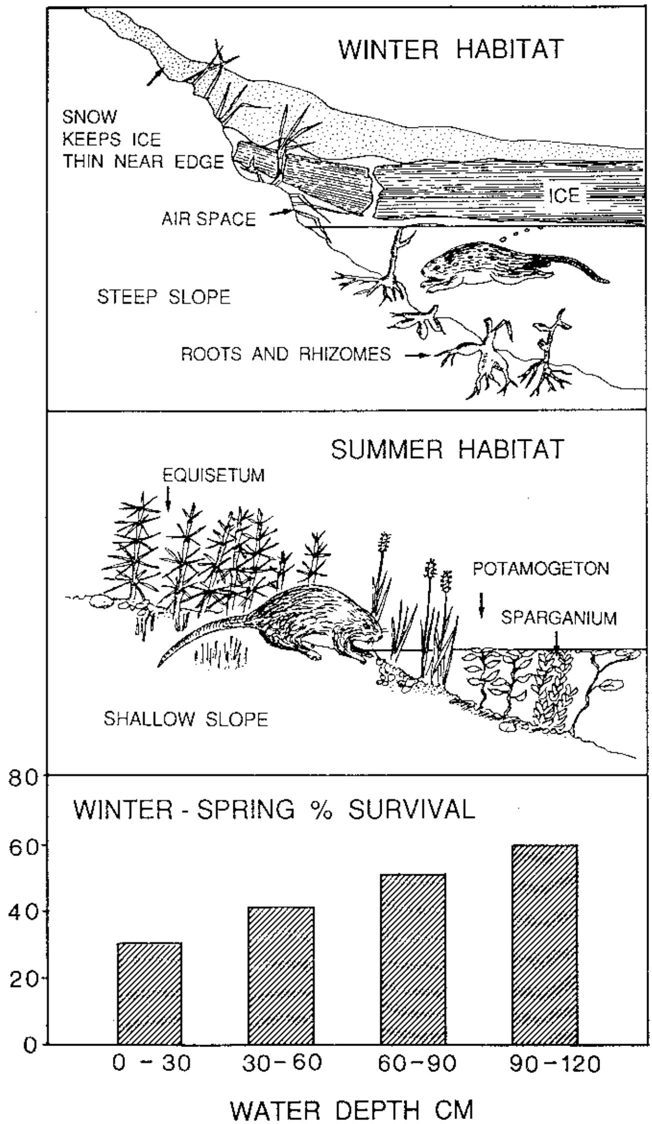
The diets of otter (*Lutra lutra*) and mink (*Mustela vison*) overlap (Chanin, 1981), especially in winter when prey is limited (Erlinge, 1969). The mink is less dependent on fish and takes smaller specimens but, under ice conditions, it likely competes with the otter for this resource. In Loch Park, N.E. Scotland, otters continued to hunt as the ice was forming, breaking the ice after each dive, leaving elliptical holes (Hewson, 1973). Eels were the predominant prey during the winters of 1976-1979, when the lochs were almost completely frozen for three months and the River Dee frozen along the edges and, in places, right over (Jenkins, 1980). Access to the water was restricted and, in the vicinity of open water, eels, which are dormant in winter, may have been depleted. Otters attempting to gain entry to water elsewhere left "wallows" in the ice. Larger, paired otters may prevent juveniles and singles entering the few feeding areas and the extent of ice may be critical for the survival of autumn born young (Jenkins, 1980). In spring, birds are preyed upon (Hewson, 1973). They are probably vulnerable when confined to small areas of open water (Jenkins and Harper, 1980). The mink, if anything, is more terrestrially oriented in its hunting and prey and Jenkins and Harper (1980), when speculating about the relationships between otter and mink, thought that mink will prey on rodents when fish are inaccessible.

Just how many fish can be consumed by a family of otters was revealed by Dolloff (1993), based on the number and shapes of otoliths found in scats. A pair of otters with two kits, living in the Kadashan River, Alaska, ate at least 3,300 juvenile salmonids (*Onchrhynchus kisutch* and *Salvelinus malma*) and about 550 coastrange sculpins (*Cottus aleuticus*) in a six week period in late spring. At such a rate of predation, otters are quite capable of locally depleting fish stocks, especially when their hunting territories are restricted by ice.

Muskrats (*Ondatra zibethicus*) have been fairly extensively studied because of their value as pelts and as native food to subsistence communities across Canada and elsewhere (Errington, 1963; T.P-A.D.P.G., 1973; Geddes, 1980; Jelinski, 1989 and references therein). Aquatic plants are the main food of muskrats. In the MacKenzie Delta during summer they use emergent hydrophytes which colonize shallow sloping shores but these freeze to the substrate in early winter. The muskrats then shift to a diet of roots and rhizomes of submerged hydrophytes which accounts for 96% of the winter food (Jelinski, 1989). To facilitate this change, the animals burrow in higher, steeper banks closer to deep water in winter (Figure 2). In the Slave River Delta the muskrat live in bank burrows in the small distributaries. These channels provide the suspended ice cover and air spaces which allow access to suitable food as water levels fall during winter (Geddes, 1980). In northern areas, shallow bays and lake margins are unsuitable winter habitats. Extensive ice and freezing of wetlands is believed to be a major cause of winter mortalities (Olsen, 1959; Errington, 1963); Ambrock and Allison, 1973 cited in Jelinski, 1989). As well as forming burrows, muskrats build lodges which can be entirely ice supported. Lodge-building may be

Figure 2

A comparison of winter and summer habitats of muskrat in the MacKenzie Delta and the importance of water depth to overwinter survival. **Based on Jelinski (1989) and** T.P-A.D.P.G. (1973).



stimulated by the first hard frosts and the formation of an ice cover. Muskrats, in fact, modify their habitat to enhance survival. They construct 'push-ups", domes of frozen, submerged, aquatic vegetation overlying open cracks or plunge holes in the ice. They are installed and maintained after a persistent ice cover has formed and spaced to allow access to air. They also excavate and maintain channels across shallows.

Muskrats do not shift burrows in winter as movements below the ice are likely to result in intraspecific conflict if they encroach on neighbouring territories. Muskrats are sensitive to cold (MacArthur, 1979) and risk hypothermia and freezing if exposed on the surface to wind and low temperatures. Group occupation of lodges in winter can raise the temperature within to 20°C above ambient (MacArthur and Aleksuik, 1979). Floods in cold weather can cause crises, as in Squaw Creek in central Iowa in 1935. During the high flood stage the temperature fell to about -20°C and the creek valley turned into a freezing lake, almost destroying the muskrat population (Errington, 1963). In the Peace-Athabasca Delta water levels have fallen $>$ 1 m, greatly reducing muskrat numbers. Many habitats are now too shallow and freeze to the bottom, making winter survival impossible (Dirschl, 1971). Penetration of the frost line can limit availability of food and cause drought-like conditions under the ice.

Muskrats take advantage of air spaces in stratified ice to create subsurface living quarters which they plug and reinforce with mud and vegetation. Winter thaws can cause problems as surface waters seep into living spaces and the muskrats are forced to gnaw away more chamber space higher up in the lodges or burrows, repair exposed retreats, rehabilitate abandoned lodges or construct new lodges on the ice (Errington, 1963). Food resources may become unavailable in late winter due to ice thickness and the muskrats are forced to forage on the surface with a higher risk of mortality (Jelinski, 1989). Spring break-up must be a particularly stressful time for muskrats occupying river channels, requiring quick adjustments to living spaces to accommodate flood conditions.

BEAVER

Although the beaver (*Castor canadensis*) is probably the most conspicuous Canadian aquatic mammal and much has been written about its activities and effects on temperate freshwaters, there is need for a focused study on its influence on the ice regime of rivers. It is a striking example of an animal that modifies the ecosystem in which it lives to its own advantage (Naiman *et al.*, 1988). Beavers do not hibernate but remain active all winter beneath the ice and in the living spaces of their lodges which protrude above water level. Lodges attain 2-3 m height and are constructed of interwoven branches glued together by frozen mud. They are strong enough to provide protection from predators yet porous enough for gas exchange. In larger rivers beavers occupy bank burrows, the entrances of which are about 1 m below the water surface (Banfield, 1974). They are best known for their woodcutting and dam building. They also maintain channels from springs and across shallows. It is these activities that change stream drainage patterns, modify riparian vegetation and alter run-off and sediment transport. Impoundments behind dams can be > 2 m deep to ensure sufficient water beneath the thickest ice cover for access to the feeding câches established by the beaver colony the previous year.

Beaver ponds retain sediment, trap carbon, generate methane, modify fish and invertebrate communities, alter nutrient cycling, change groundwater levels and the riparian forest (Naiman and Melillo, 1984; Naiman *et al.*, 1986; McDowell and Naiman, 1986; Ford and Naiman, 1988; Johnston and Naiman, 1990a, 1990b). Just how much they can modify an environment when left undisturbed was documented in the Kabetogama Peninsula, N. Minnesota between 1940 and 1986. The number of dams increased from 71 to 835 and the area impounded increased from < 1% to 13% of the peninsula (Naiman *et al.*, 1988). Along with these habitat alterations are marked shifts in soil redox potential and pH which indicate a change from aerobic (in drained soils) to anaerobic in soils affected by flooding. Exacerbating this change is the accumulation of organic sediments behind the dams and stagnant conditions in the ponds. Naiman and his co-workers have suggested that the functional dynamics of stream ecosystems are very much influenced by the state of beaver populations. Beavers stabilize rivers by retaining large amounts of biomass and nutrients in the tributaries and these are turned over and released slowly into the downstream reaches of the river.

The effects of beaver on river ice dynamics may be considerable. Large woody debris, such as trees which have partly fallen or been dragged into the water, hang-up ice sheets and provide increased under ice air spaces and protected micro-habitats. Increased water area and opening up of the canopy of tributary streams enhances radiative heat losses. More water is locked up in ice and the timing of freeze-up and break-up altered. Where large populations of beaver exist, this could reduce the severity of spring floods and decrease the risk of ice dam formation. Lengthening the period of spring high water would have benefits for fish migration and the success of spring spawning fish.

DISCUSSION

Although the topic of this review has not often been addressed directly in the scientific literature, it is clearly important. Questions arise as to how birds and mammals survive in ice covered rivers when their living space and activities are restricted. What are the risks and benefits of life under these conditions? How do animals modify their environment to increase survival? How does agriculture, urban and industrial development alter this environment? These questions have only been touched on in this review.

The physiological adaptations required of air breathing warm-blooded vertebrates to cope with ice covered rivers creates in us a sense of wonder but we should not forget that the animals found in these conditions are those that normally survive them. Where losses occur, these too are part of a natural cycle. They are most likely to occur at the fringes of the range where conditions are marginal. In periods of favourable climate the range expands only to contract in unfavourable periods. This is the process that determines the distribution of species and, although the range is marked on maps as a static area, it is not. These variations in mortality do not influence the survival of species. Only when alterations are permanent, such as following dam construction or water diversion, will new equilibriums be established and these may lead to drastic declines in species abundance or even local extinctions. The problem in predicting such losses is in being able to identify the critical limitations in the habitats occupied by different species. While the literature has provided some clues, for example slope and water depth for muskrats, we still have scant information on many species that inhabit ice covered rivers.

Of equal interest is the question of whether and to what extent can the ice regime of rivers be altered by birds and particularly by mammals? Should the role of beavers be considered in physical models of the ice dynamics of rivers or is their impact insignificant compared with the physical processes involved? We suspect the latter but feel the question should be asked. Another question that might be asked is can the behaviour of animals be used to forecast events like freeze-up or, more importantly, break-up? Since break-up almost certainly leads to a disruption in the activities of aquatic mammals, do they anticipate this event with any precision? Techniques such as radio-telemetry are now refined enough that monitors can be attached to animals to record their movements and activity patterns so this question can be addressed.

There are many other questions that can be asked about birds and mammals and the role of river ice in their lives. We hope, in time, they will be asked and answered and a future review, or reviews, on this subject will be more comprehensive.

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