

# Winter habitat of selected stream fishes and potential impacts from land-use activity

Richard A. Cunjak

**Abstract:** This paper reviews the habitat characteristics and the behaviour of selected stream fishes during winter in temperate–boreal ecosystems. Emphasis is placed on the salmonid fishes upon which most winter research has been directed. As space is the primary factor regulating stream fish populations in winter, aspects of winter habitat are considered at various spatial scales from microhabitat to stream reach to river basin. Choice of winter habitat is governed by the need to minimize energy expenditure, with the main criterion being protection from adverse physicochemical conditions (e.g., ice, spates, low oxygen). The distance moved to wintering habitats, and the continued activity by many fishes during winter, need to be considered when making management decisions regarding fish habitat. How habitat is affected by land-use activity in stream catchments is discussed with reference to impacts from water withdrawal, varying discharge regimes, and erosion or sedimentation. Even stream “enhancement” practices can deleteriously affect fish habitat if project managers are unaware of winter habitat requirements and stream conditions. Maintenance of habitat complexity, at least at the scale of stream sub-basin, is recommended to ensure the diversity of winter habitats for fish communities.

**Résumé :** Le document fait l'examen des caractéristiques de l'habitat et du comportement de certains poissons de cours d'eau pendant l'hiver en écosystèmes tempérés ou boréaux. L'accent est mis sur les salmonidés qui ont fait l'objet de la plus grande partie des recherches effectuées en hiver. L'espace étant le premier facteur régissant les populations de poissons de cours d'eau en hiver, les aspects de l'habitat d'hiver sont examinés en fonction de diverses échelles spatiales allant du micro-habitat, au segment et au bassin du cours d'eau. Le choix de l'habitat d'hiver est régi par le besoin de minimiser les dépenses énergétiques et a pour critère principal la protection contre les conditions physiques et chimiques adverses (glaces, crues, faible teneur en oxygène). La distance parcourue pour atteindre les habitats d'hivernage et le maintien de l'activité d'un grand nombre de poissons pendant l'hiver doivent être pris en compte au moment de la prise de décisions de gestion touchant l'habitat du poisson. La façon dont l'habitat est affecté par l'utilisation des terres dans le bassin du cours d'eau est traitée dans le contexte des incidences de la captation d'eau, de la variation des régimes d'écoulement, de l'érosion et de la sédimentation. Même les activités de «mise en valeur» des cours d'eau peuvent altérer l'habitat du poisson si les gestionnaires de projet ne tiennent pas compte des besoins en habitats d'hiver et des conditions du cours d'eau. Le maintien de la complexité de l'habitat, du moins à l'échelle du sous-bassin du cours d'eau, est recommandé pour garantir la diversité des habitats d'hiver des communautés de poissons.

[Traduit par la Rédaction]

## Introduction

“We had not thought seriously of winter; we dwelt in fancied security yet”

Henry David Thoreau (circa 1850)

In the past decade, the number of publications focusing on the winter ecology of stream fauna has increased (e.g., Cunjak and Power 1986a; Brown and McMahon 1988; Ultsch 1989; Griffith and Smith 1993; Heggenes et al. 1993; Irons et al. 1993; Scrimgeour et al. 1994). Although these studies have contributed to an improved understanding of habitat use and behaviour of stream fishes during winter, much remains to be learned. The need to understand, identify, and quantify the winter habitat of fishes during all life stages is an obvious prerequisite to successful fisheries management. This requirement is all the more urgent given the potential impacts and

complications imposed by anthropogenic perturbations in stream catchments (see Power et al. 1993) and the demands for land-use activity, which are increasing.

This paper reviews the winter habitat characteristics and the winter behaviour of selected stream fishes, particularly those common to the streams of the Great Lakes drainage. My goal is to identify the critical characteristics of winter habitat to ensure their protection and, hence, conservation. Emphasis is given to salmonid fishes upon which most research has been directed. I will restrict my review to running waters and will only make limited reference to lacustrine environments as wintering areas recognizing, however, their significance for many stream fishes (Cederholm and Scarlett 1982; Peterson 1982; Hutchings 1986). Winter diet, metabolism and energetics, and the habitat of pre-emergent fish (i.e., overwintering eggs, alevins) are also not included in this review. The paper concludes with a section describing potential impacts to winter habitat from land-use activity in stream catchments. Largely speculative given our current ignorance of biotic responses to anthropogenic perturbations in winter, this section suggests that maintenance of habitat complexity, at least at the scale of stream sub-basin, is needed to satisfy the diverse habitat requirements of lotic fish communities in winter.

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**R.A. Cunjak.** Department of Fisheries and Oceans, Science Branch, P.O. Box 5030, Moncton, NB E1C 9B6, Canada.

**Table 1.** Generalized criteria for winter habitat selection by fishes in natural, coldwater streams, listed in order of relative importance (priority).

Relative priority <sup>a</sup>	Habitat criterion	Example(s) of selected habitat
1	Protection from adverse physicochemical conditions (e.g., ice, low oxygen, winter freshets), and access to refugia or alternate winter habitats	Suitable water depth, instream cover, floodplain habitat and side-channels, source of aeration, groundwater discharge zones, subice corridors
2	Protection from predators	Suitable water depth, instream cover
3	Access to food	Low-velocity (micro)habitats and concomitant shift to nocturnal, benthic feeding pattern

<sup>a</sup>Relative priorities can vary among life stages and for different streams depending on availability of food, on water temperature (and metabolic demand), on local predator density, and on the stability of environmental conditions.

Winter is herein described as that period immediately following egg deposition by autumn-spawning salmonids (and coincident with a decline in water temperature) and extending until the loss of all surface ice (often accompanied by a major spate and snowmelt) and prior to any reproductive activity by spring-spawning, non-gadid fishes. This definition, considered to have more biological relevance than one following calendar dates, has been modified from one suggested by Cunjak and Power (1986a). The streams reviewed in this paper are those subject to near-freezing temperatures (<1°C) or ice formation for some portion of the winter period (such that growth over winter is considered negligible). The winter habitat of fishes in warmwater streams is not considered here, although there is a corresponding lack of information from these environments, and for the unique strategies employed by resident species (e.g., *Cyprinodon* spp.; McMahon and Tash 1988).

### Characteristics of preferred winter habitat

Space, specifically suitable physical habitat features (e.g., low-velocity areas, instream cover), is the primary factor regulating stream fish populations in winter because reduced metabolic demands at low water temperatures lessen, or eliminate, time spent feeding and defending territories (see Chapman 1966). Cunjak and Power (1986a) suggested that the specific choice of winter habitat, and the behavioural pattern adopted by stream-dwelling brook trout (*Salvelinus fontinalis*) and brown trout (*Salmo trutta*) in winter, was governed by the basic need to minimize energy expenditure. This was accomplished by selecting positions in low-flow microhabitats with suitable cover and physicochemical attributes, but where predation risk and energy depletion were minimized. The concept that winter habitat selection is based on minimizing energy expenditure has been proposed for other juvenile salmonid species (Bustard and Narver 1975a; Rimmer et al. 1984; Cunjak 1988a; Griffith and Smith 1993; Riehle and Griffith 1993), and for smallmouth bass (*Micropterus dolomieu*; Todd and Rabeni 1989), largemouth bass (*Micropterus salmoides*; Carlson 1992), and blacknose dace (*Rhinichthys atratulus*; Cunjak and Power 1986b).

Assuming that the principal factor governing the choice of winter habitat is to minimize energy expenditure, I have prioritized criteria for winter habitat selection (Table 1). The same criteria could define fish habitat at other times of the year (except the reproductive period when fish also need access to suitable spawning habitat and mates). Rather, the difference in habitat selection criteria is in the relative priorities and particu-

lar environmental conditions inherent to winter compared with other seasons.

### Protection from adverse physicochemical conditions

A variety of adverse conditions can develop in streams during winter. These include midwinter flood events, deoxygenation in ice-covered pools, de-watering of stream sections, ice blockages, and freezing temperatures. To survive, stream fishes have adopted specific habitat preferences where the probability of encountering adverse conditions is minimized. Two of these preferences, instream cover and groundwater discharge, are discussed in some detail.

#### Instream cover

Preferences for a particular type and structure of winter cover (as inferred from frequency of use data from field studies) differ among species (Table 2). Strongly photonegative (winter) species such as juvenile Atlantic salmon (*Salmo salar*), chinook salmon (*Oncorhynchus tshawytscha*), brown trout (Norway, Idaho), brook trout (Newfoundland, northern Quebec), rainbow trout (*Oncorhynchus mykiss*), cutthroat trout (*Salmo clarki*), cottids, some cyprinids, and most centrarchids (and darters?) prefer sheltering beneath rubble-boulder where rock diameter is often directly proportional to the size of the fish beneath (Rimmer et al. 1984; Cunjak 1988a). Some of these fish may move 15–30 cm below the substrate surface (Everest 1969; Erkinaro et al. 1994; J. Thorpe, Freshwater Fisheries Laboratory, Scotland, personal communication). Brook trout and brown trout in the Credit River, Ontario, were rarely observed beneath rocks in winter, preferring instead positions beneath woody debris, undercut banks, and shelf ice, or within macrophyte mats (Table 2). Rocks and boulders were used as winter cover by other Credit River fishes such as mottled sculpin (*Cottus bairdi*), longnose dace (*Rhinichthys cataractae*), and blacknose dace (Table 2). Maciolek and Needham (1952) found that brown and rainbow trout frequently used shelf ice as cover in Convict Creek, California. Hillman et al. (1987) found wintering juvenile chinook salmon under cover of vegetated banks or cobble in an Idaho stream, whereas juvenile coho salmon (*Oncorhynchus kisutch*) were generally found to prefer pools and off-channel habitats with woody debris cover (Hartman 1965; Bustard and Narver 1975a), abundance being positively related to cover complexity (McMahon and Hartman 1989). Cover use can also change during the winter. Recently, Griffith and Smith (1995) observed that the density of young-of-the-year rainbow trout in macrophyte beds steadily declined between November and

**Table 2.** Frequency of use of different types of cover by individual fishes in the Credit River system, Ontario, during winter (November–March) 1982–1985.

Species	Woody debris	Surface (shelf) ice	Cobble-boulders	Surface turbulence	Vegetation	Undercut bank	Depth > 1 m
Brook trout	119	4	3	4	67	60	2
Brown trout	17	6	2	13	9	3	0
Blacknose dace	0	0	81	1	0	0	0
Longnose dace	0	0	7	0	0	0	0
Mottled sculpin	0	0	28	0	0	0	0
White sucker (adults)	2	0	0	0	1	0	41
Bluegill	0	0	0	0	4	0	0
Pumpkinseed	1	0	2	0	3	0	0

Note: Frequencies are based on underwater observations.

January despite continued availability of the vegetation cover; instead, most of the trout overwintered in cobble–boulder substrate, where available.

Large-bodied, adult fish (e.g., salmonids, catostomids, centrarchids), probably because suitably sized rock shelters are scarce in many streams, generally overwinter in deep pools where depth is assumed to provide the requisite cover requirements. Adult white suckers (*Catostomus commersoni*), as solitary fish (Table 2) or in aggregations, overwintered in the deepest pools of the upper Credit River (Cunjak and Power 1986a). Carlson (1992) found that adult largemouth bass aggregated in a few deep, winter refuge areas in the Hudson River estuary where conditions permitted a minimum of energy expenditure. However, deep water does not necessarily imply suitable winter habitat. Cunjak and Caissie (1994) measured the accumulation of frazil ice in a large, main river (Miramichi) pool (55 105 m<sup>3</sup>) in New Brunswick over two winters where it was generally believed post-spawned Atlantic salmon (kelts) overwintered. They found that, on average, frazil ice filled > 75% of the pool volume between December and March, and was often in contact with the pool bottom in the deepest part (8.7 m). The remaining pool space was assumed to be of marginal suitability because of the consequent higher water velocities deflected there by the frazil mass. More recent research in the Miramichi River has found that frazil ice also occurs in other large pools surveyed in the Miramichi River (D. Caissie, Department of Fisheries and Oceans, Moncton, N.B., unpublished data). In such cases, off-channel areas of river (e.g., braids, backwaters) may provide the habitat conditions necessary for overwintering fishes (i.e., free of frazil ice, adequate water depth, low water velocity as suggested from tracking radiotagged kelts, (R.A. Cunjak, unpublished data).

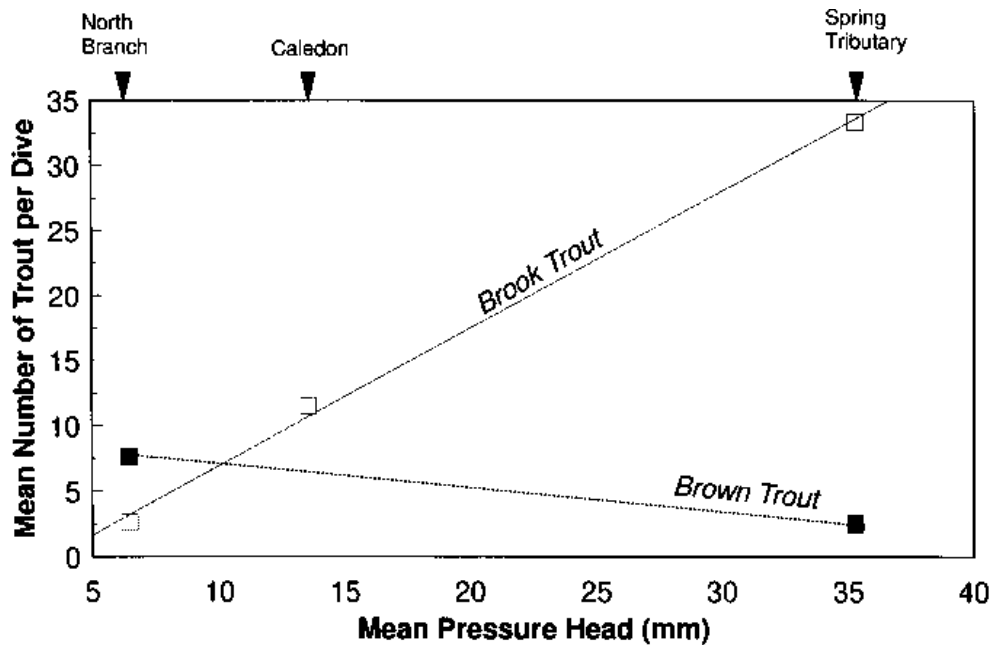
#### Groundwater discharge

Point sources of groundwater discharge which provide “winter-warm” microhabitats may serve as winter refugia (Table 1) from instream problems such as ice and variable streamflow. Cunjak and Power (1986a) found large numbers of brook and brown trout aggregated near such point sources in the headwaters of the Credit River in southern Ontario. Occasionally, pumpkinseed (*Lepomis gibbosus*) and cyprinids (such as blacknose dace) were also observed in such locations, actively swimming (Cunjak 1986a), which is not typical winter behaviour for these species. Known to be important thermal refugia during periods of high-temperature stress in

summer (Gibson 1966; Snucins and Gunn 1995), point sources of groundwater discharge are now recognized for their importance as winter habitat. Swales et al. (1986) found that juvenile coho salmon in an interior British Columbia stream preferred to overwinter in side-channels and ponds where groundwater maintained warmer temperatures than in the main river. Craig and Poulin (1975) found stream populations of grayling (*Thymallus arcticus*) and arctic char (*Salvelinus alpinus*) overwintering in two perennial spring sections of an Alaskan river. In arctic systems, groundwater may be the most important winter habitat criterion (J.B. Reynolds, University of Alaska, Fairbanks, Alaska, personal communication) where, otherwise, streams can freeze completely. In temperate latitudes, the winter-warm conditions of groundwater discharge have been associated with increased winter survival of brook trout in Wisconsin (Hunt 1969); rainbow trout in Idaho (Smith and Griffith 1994); and juvenile steelhead, coho, and chinook salmon in British Columbia (Bustard 1986).

Proximity to the source of groundwater discharge, where water temperature is often warmest in winter, is not preferred by all species, even if cover is abundant. Brook trout, especially young individuals, typically prefer to position themselves close to point sources of groundwater. Brown trout, in contrast, do not and prefer to aggregate downstream from such sources, where water temperatures have cooled but still remain above freezing. Spatial variation between species is illustrated by plotting the abundance of individual (i.e., nonaggregated) trout during winter and the strength of the groundwater discharge (pressure head) as measured at three sites in the Credit River (Fig. 1). Brook trout abundance was positively related to strength of the discharge, whereas brown trout abundance was least at the site with greatest pressure head (Fig. 1) and where winter water temperature was highest (range 1.5–5.5°C). Avoidance by brown trout of such sources of undiluted, warmer groundwater was also noted by Hansen (1975) in a Michigan stream. Recently, R.A. Cunjak (unpublished data) found similar avoidance of spring sources by Atlantic salmon parr in several catchments in Prince Edward Island although brook trout were abundant. It may be that certain salmonid species are not physiologically adapted to effectively use the higher water temperatures in winter. The concomitant increase in metabolic activity at water temperatures between 5 and 7°C (as are often found near sources of groundwater discharge) would necessitate an increased feeding and assimilation efficiency. Not all fishes are metabolically efficient at such low water temperature. Instead, the advantages of the

**Fig. 1.** Abundance of brook and brown trout observed during daytime underwater observations at three sites in the upper Credit River, Ontario (1983–1985), in relation to strength of groundwater discharge. Groundwater pressure (mm) was measured according to the technique outlined by Lee and Cherry (1978). Note that brown trout do not occur in the Caledon site.



groundwater warming may be better realized at a distance from the source, where ice formation is precluded and stream-flow is still relatively stable, but where reduced water temperature (i.e., 2–4°C) would minimize metabolic activity. Alternatively, the local availability of certain physical habitat features (e.g., water depth, instream cover) and the specific habitat preferences of some salmonids may also explain the differential use of groundwater discharge zones. Such species-specific differences in winter habitat preferences may also reduce potential competition for space along a longitudinal gradient.

Hynes (1970, 1983) explained the importance of groundwater to stream ecosystems in general. More specifically, Meisner et al. (1988) hypothesized on the importance of groundwater as thermal refugia and how these may affect salmonid populations under the scenario of climate warming. Point sources of winter-warm water should be conserved. However, the appreciation and identification of groundwater discharge is not always obvious, especially if the discharge is small, diffuse, or in midstream. Detailed monitoring of water temperature at numerous points along a length of stream in midsummer or midwinter is one means of groundwater discharge identification. The location of open water and unfrozen sections of stream bank in midwinter often indicate groundwater, as do certain species of vegetation such as watercress (*Nasturtium officinale*) and eastern white cedar (*Thuja occidentalis*). Finally, if underwater observations are possible, winter (and summer) aggregations of juvenile salmonids are generally good indicators of groundwater discharge (Cunjak and Power 1986a).

#### Predator avoidance

Avoidance of predators and adverse physical conditions in the stream during winter (Table 1) is greatly influenced by a fish's

swimming ability and its critical holding velocity, both of which are markedly reduced at low water temperature (Sandström 1983; Rimmer et al. 1985; Heggenes and Traaen 1988; Veselov and Shustov 1991; Bodensteiner and Lewis 1994). This is especially problematic for fishes trying to avoid endothermic predators (e.g., mink, otter, mergansers), which are known to be effective predators of overwintering fishes (Salyer and Lagler 1940; Alexander 1979; Carss et al. 1990) and which are not subject to the same temperature constraints to metabolism as are ectotherms. The problem may be compounded where suitable overwintering areas (e.g., pools, off-channel backwaters) are few, resulting in large concentrations, or aggregations, of overwintering fishes and may partly explain reports of substantial winter mortality (Bustard 1986; Dolloff 1993; Power and Mitchell 1994).

#### Access to food

Whereas feeding in summer is primarily the means to achieve surplus energy for growth and (or) reproductive maturity, winter feeding is often viewed as the way that fish, particularly young (juvenile) individuals, sustain a minimal level of metabolic activity (Cunjak 1988b) with negligible growth (e.g., Conover 1992; Metcalfe and Thorpe 1992). There are exceptions to this rule. Many spring-spawning fishes complete maturation in late winter (Tartar 1969; Lalancette 1973; Medford and Mackay 1978; Chilton et al. 1984). Atlantic salmon kelts resume feeding (and growth) in late winter (personal observations), and pre-smolt Atlantic salmon were found to continue growing in laboratory experiments (Metcalfe et al. 1988). In general, however, access to food at near-freezing water temperatures is probably a low-priority criterion for selection of winter habitat for most stream species (Table 1). Griffith and Smith (1993) estimated that only 61–66% of the juvenile cutthroat and brown trout overwintering in an Idaho

**Table 3.** Generalized behavioural strategies employed by stream fishes for overwintering in temperate–boreal systems in North America.

Strategy	Tactics	Examples of fish taxa
Emigration to lentic habitats (e.g., lakes, estuaries)	Long-distance movement in late autumn or early winter	Arctic char, some <i>Oncorhynchus</i> spp., some adult Atlantic salmon
Active, stream resident	Shift to low-velocity habitats; behavioural changes (e.g., gregarious, nonterritorial, photonegative); continued feeding activity; substrate-hiding (daytime)	Most salmonids (especially juveniles), pike, cottids, some centrarchids, umbrids, and gadids
Inactive, stream resident	Shift to low-velocity habitats; some substrate-hiding; reduced metabolic activity (semitorpid?); minimal (sustenance) feeding	Catostomids, black-nosed dace, juvenile brook trout (sub-Arctic streams), darters, gasterosteids
Hibernation–torpor	Basal metabolism; fasting; “burrowers”	Many cyprinids, some centrarchids

river (water temperature approximately 7°C) emerged each night from beneath boulder concealment, presumably to feed. They suggested an even less frequent emergence in midwinter at lower water temperatures.

In many of our streams, invertebrate (food) abundance and biomass remain relatively high, particularly where winter-growing insect species (e.g., Plecoptera, some Ephemeroptera) are common (Hynes 1970). Assuming winter food availability and suitability are adequate (which has yet to be rigorously tested), I contend that the selection of winter habitat is primarily driven by the need to avoid adverse instream conditions and predation. Food, however, may become limiting to stream fishes in late winter following loss of potential prey individuals through death, emergence, or pupation–diapause. In this situation, or during a sudden rise in midwinter water temperature that may increase metabolic demand, access to food can become a relatively high priority habitat criterion (Table 1).

### Winter habitat: aspect of scale

In dealing with conservation, or enhancement, of fish habitat, it is important to match habitat requirements to a scale and context appropriate to the range of that animal. Winter habitat data derived from one stream basin may be inappropriate for another area where different hydrologic conditions (Fig. 2) dictate alternate winter behaviour patterns by resident fishes. Stream fishes use different strategies for overwintering, depending on the species, life stage, and the availability of suitable habitats in the system (Table 3). I will consider aspects of winter habitat and behaviour at various spatial scales from the detailed characterization of microhabitats (fine scale) to the ecological conditions inherent to habitat types and stream reaches (medium scale). Large-scale considerations of winter habitat, which include whole river catchments, sub-basins, and landscape relationships, are discussed only with regards to long-distance movement between summer and winter areas.

#### Fine-scale habitat considerations

Focal-point measurements of microhabitat variables are routinely collected by fish ecologists in characterizing the microhabitat preferences of fishes (e.g., Cunjak and Green 1983; Fausch 1993; Cunjak and Power 1986a; Heggnes and Saltveit 1990; Hillman et al. 1987; Gibson 1988). Typical measured variables include focal point water velocity and water depth, mean water velocity (at 0.6 depth), total water depth, proximity to cover, type of cover, and substrate type.

Often these data are subsequently used to construct habitat suitability index (HSI) curves for use in habitat simulation models such as IFIM-PHABSIM (Bovee 1982).

Maximum suitability and availability of winter microhabitats for resident stream fish communities is achieved where complexity of instream structure and form is conserved. Indeed, habitat quality may be more important than quantity in winter, as suggested by Todd and Rabeni (1989) in noting the relative importance to adult smallmouth bass of a few strategically placed boulders in a Missouri stream. Similarly, rubble-boulder shelters were critical winter habitats for stream salmonids and cyprinids (Bustard and Narver 1975b; Cunjak and Power 1986b; Cunjak 1988a; Griffith and Smith 1993; Hillman et al. 1987).

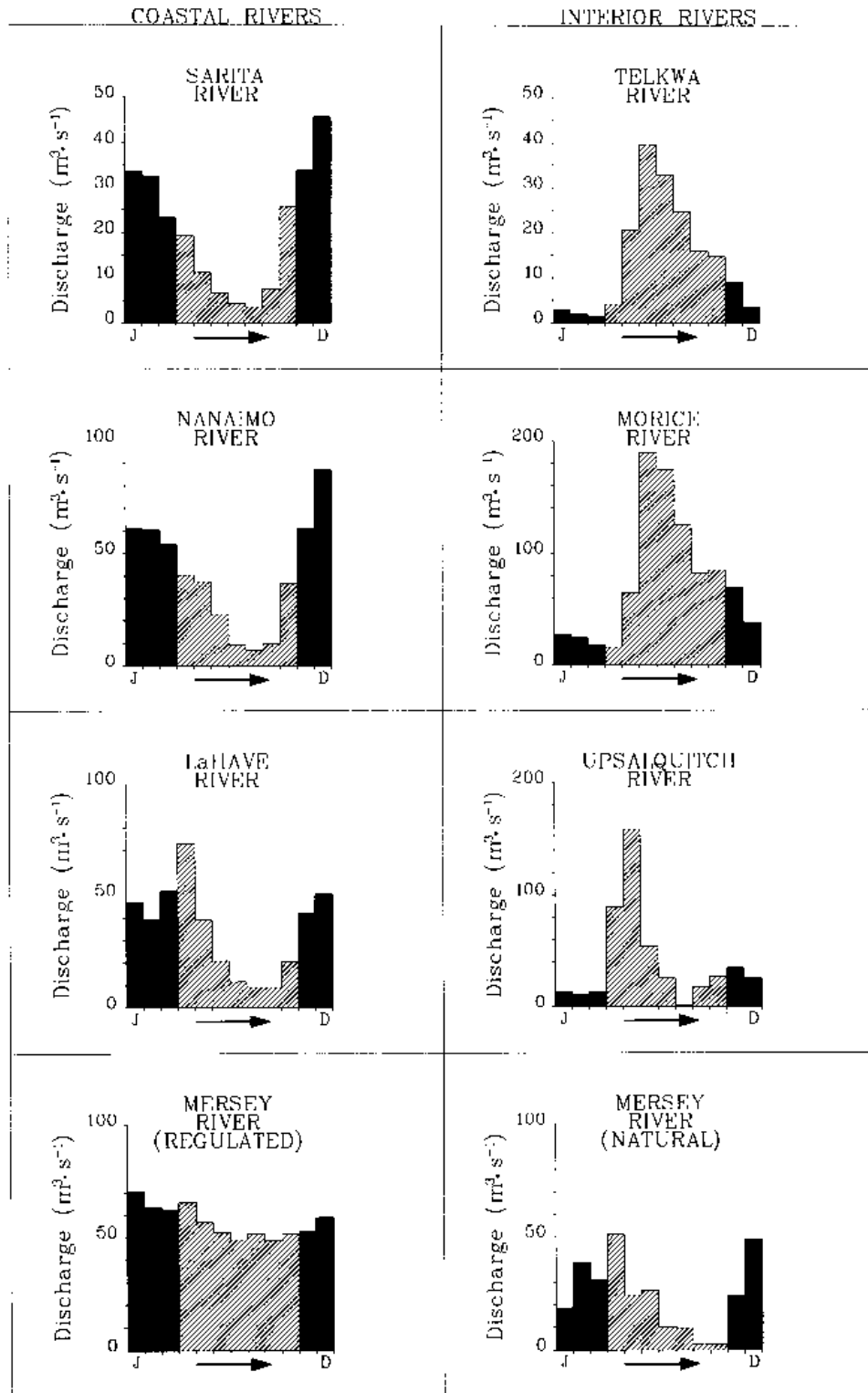
Microhabitat choice in winter may be a function of competition for similar shelters among stream-dwelling fishes (Cunjak and Power 1986a, 1986b), frogs (Cunjak 1986b), and invertebrates (e.g., crayfish). Hartman (1965) hypothesized that vertical partitioning of winter habitat (with steelhead juveniles preferring the stream bottom to the midwater positions preferred by coho salmon) was the result of competition. Heggnes et al. (1993) similarly suggested that intra- and inter-specific competition among stream salmonids in winter may be severe because of more restricted habitat requirements. That winter space (i.e., habitat) may be limiting and the focus of competition among stream organisms seems probable, but still unproven, and deserves further attention.

The lack of information concerning the winter microhabitat requirements of non-salmonid species is an obstacle to effectively managing fish populations as multispecies assemblages or communities. Much of what we know is based on anecdotal evidence (e.g., Table 2). Generally, thick cover in the form of complex woody debris or rubble-boulders, or deep pools for larger adults, is preferred by most centrarchids, catostomids, and cyprinids (Webster 1954; Hasler and Wisby 1958; Paragamian 1981; Tallman and Gee 1982; Cunjak and Power 1986b; Pajak and Neves 1987; Todd and Rabeni 1989). Is there movement over winter; what is the frequency of emergence from winter shelters and do they feed; to what depth into the substrate do these fishes move to overwinter? These basic questions about microhabitat and behaviour remain unresolved for many stream fishes.

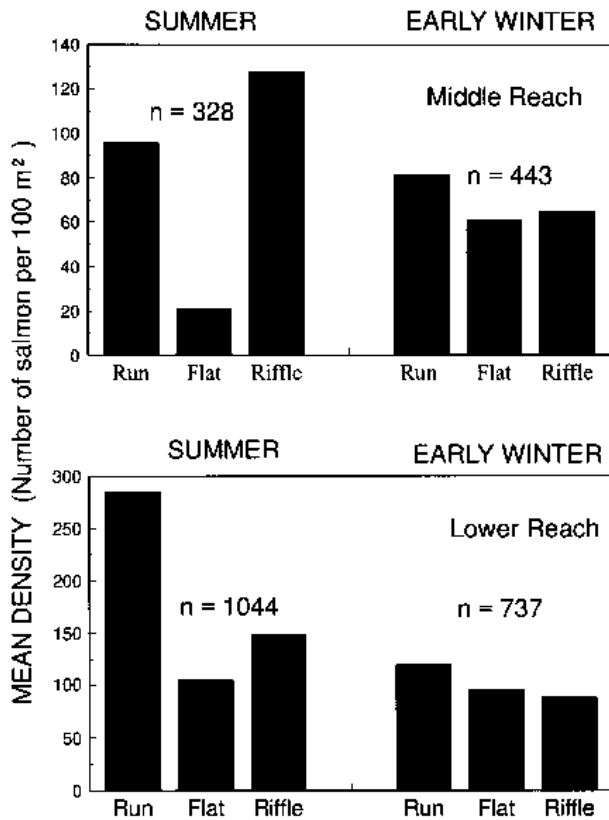
#### Medium-scale habitat considerations

Stream habitat, when viewed at the scale of habitat type (e.g., riffle, run) or stream reach, offers a variety of instream condi-

**Fig. 2.** Differences in mean monthly stream discharge regimes for selected Canadian rivers from contrasting climatological regions. Solid bars represent typical winter months; hatched bars represent the spring–autumn period. Data for British Columbia streams (Sarita, Telkwa, Nanaimo, and Morice) were reproduced, with permission, from Bustard (1986); data for Upsalquitch River (northern New Brunswick) and the LaHave and Mersey rivers (southwestern Nova Scotia) were taken from Environment Canada gauge station records. Note that the Mersey River (natural) flow regime is from a station upstream from the regulated station. J, January; D, December.



**Fig. 3.** Changes in mean density of juvenile Atlantic salmon (ages 0+ to 2+) from summer (July) to early winter (November) among different habitat types in two stream reaches of Catamaran Brook, New Brunswick, in 1991. Densities are averages of two of each habitat type based on three or four electrofishing sweeps. *n*, total number of salmon caught per reach per season. Note that flats were within 100 m of numerous riffles and runs in the Catamaran Brook study area.



tions reflecting the heterogeneity of running waters (Hynes 1970; Hawkins et al. 1993). Boulder-strewn riffles, deep pools, beaver ponds, groundwater seeps, stream edges beneath shelf ice cover, off-channel backwaters, and woody debris jams are examples of some of the habitats used by stream fishes at different times during winter. Accessibility, as well as availability, to these various habitats are important factors in assessing survival of stream fauna because of the dynamic nature of the winter stream environment (Reimers 1963; Mackay 1979; Prowse and Gridley 1993) and increasing evidence of movement by stream fishes in winter (Chisholm et al. 1987; Cunjak and Randall 1993; Jakober 1995). Cunjak and Power (1986a) suggested that the continued activity by brook and brown trout in the Credit River system was adaptive because of periodic flooding, freezing, and thaws common to such temperate latitude streams. A similar explanation was originally used by Reimers (1963) to account for the winter feeding by rainbow trout in a Californian stream.

#### *Instream variability and habitat shifts*

Variability of instream conditions during winter occurs even within habitat types, or across the width of a river. In Idaho streams, Riehle and Griffith (1993) and Griffith and Smith

(1993) have shown that, as water temperatures declined below 8°C, juvenile salmonids concealed themselves during the day primarily amongst boulders with low imbeddedness, vegetation, and undercut banks. In contrast, Cunjak (1988a) found that most juvenile Atlantic salmon sheltering beneath rocks in a Nova Scotian river during the day were closer to midstream than to stream margins. This difference might be explained by the interaction of fine sediments, ice, and associated water flow patterns. Although ice was rare in the Idaho study, shore ice was common in the Nova Scotian stream. Ice tends to deflect and concentrate water current (Prowse 1994a) toward midstream (thalweg), thereby minimizing substrate imbeddedness and sediment deposition, which was more likely beneath shore-bound ice along the stream margin. It is also possible that the salmon parr observed by Cunjak (1988a) during the day may have moved to stream margin microhabitats at night, when they emerge from beneath rock shelters. Heggenes et al. (1993) found juvenile brown trout in ice-covered Norwegian rivers at night, moving to the stream margins and other areas with low water velocities including streambank areas. Diel variation in preference, and modifications imposed by hydraulics and physical structure are, therefore, important when considering habitat use.

As indicated earlier, and suggested by others (Hartman 1965; Cunjak and Power 1986a; Heggenes et al. 1993; Pajak and Neves 1987; Chisholm et al. 1987; Swales et al. 1986; Nickelson et al. 1992a; Griffith and Smith 1993), winter habitat selection often differs from that in summer, generally involving movement to areas with lower water velocity (day and night) and suitable daytime cover. Where adequate wintering conditions are available nearby, the distance moved from summer rearing areas may be relatively short, simply to adjacent habitat types. In Wyoming streams, Chisholm et al. (1987) found that adult brook trout, radiotagged for two winters, moved an average of 86–163 m (mainly downstream) preferring low water velocity areas (i.e., <15 cm·s<sup>-1</sup>). Seasonal electrofishing surveys (summer and early winter) in different habitat types of two stream reaches in Catamaran Brook, New Brunswick (Fig. 3), demonstrated relatively greater use, by juvenile Atlantic salmon in winter, of flats (i.e., slow-flow habitats with gravel-rubble substrate). This was most obvious in the Middle Reach flats, which were deeper than those in the Lower Reach. Riffles and runs, which were preferred by salmon in summer, were used proportionally less than flats in early winter (Fig. 3).

#### *River ice*

During winters with low stream discharge but with an abundance of ice precluding access to adjacent stream habitat types, Cunjak and Randall (1993) suggested that instream movement (to more suitable habitats) was significantly restricted and contributed to substantial mortality. For their three study streams in eastern Canada, estimated mortality of resident juvenile Atlantic salmon over winter was 25–57%, being highest in the stream where winter conditions were most severe and in that year when ice and low streamflow could have restricted instream movement (Cunjak and Randall 1993). Subsequent research in a variety of habitat types in Catamaran Brook corroborated these estimates; winter mortality exceeded 65% of the resident salmonid population during that winter when streamflow was least and ice accumulation substantial (R.A.

Cunjak, unpublished data). In British Columbia, Bustard (1986) estimated similar winter mortalities of 30–60% for juvenile salmonids in side-channel habitats exposed to severe freezing and suggested that the reduced streamflow and ice conditions of interior streams (Fig. 2) were the reason that many juvenile salmonids overwintered in mainstream habitats where suitable water depth was maintained. In coastal rivers, in contrast, winter is a period of high streamflow (Fig. 2) and juvenile salmonids often overwinter in side-channels, floodplain sloughs, and riverine ponds (Bustard and Narver 1975a; Cederholm and Scarlett 1982; Tschaplinski and Hartman 1983; Hartman and Brown 1987).

Chisholm et al. (1987) noted evidence of habitat exclusion by ice for brook trout overwintering in those stream sites (low elevation) where abundant surface ice occurred in the riffles. In contrast, Berg (1994) found little evidence of habitat exclusion (based on a minimum 6 cm depth criterion beneath ice) for rainbow trout in ice-covered pools along an elevational gradient in California's Sierra Nevada during two relatively dry winters. Berg did note limitations in trying to apply his results to geomorphically different streams, particularly wide, shallow, low-gradient streams where ice would more likely limit trout movements. Cunjak and Caissie (1994) suggested that frazil ice accumulations in large river pools (see above) may preclude their use for overwintering Atlantic salmon kelts.

One of the many challenges facing fish biologists and resource managers is to appreciate (quantify) the significance of environmental variability and the subsequent biotic responses. Ice (surface, frazil, and anchor ice) is common in many North American rivers (Brown et al. 1953; Chacho et al. 1986; Brown 1994; White 1994) including the Great Lakes Basin (Barnes 1928; Benson 1955). Ice accumulation in pools can reduce winter habitat space (Fig. 4) and suitability. The environmental aspects of river ice has begun to receive some attention (Prowse and Gridley 1993; Berg 1994; Prowse 1994a, 1994b; Scrimgeour et al. 1994). How ice and its consequent influence on stream hydraulics may impact fish habitat, particularly the dynamics surrounding freeze-up and break-up events (Prowse 1994a), is still a mystery. Calkins (1989) in reviewing the winter habits of four stream salmonids, noted that no fisheries article that he reviewed had calculated the hydraulic properties or flow regime beneath ice cover. Such omissions need to be corrected to quantify availability and suitability of wetted space (habitat) beneath ice cover and how these usable areas change with different ice and streamflow regimes.

#### *Backwater habitats and beaver ponds*

Pool-like habitats and backwaters, because of the deep water and low-velocity conditions that they offer, are the winter habitat of choice for many stream fishes. Such conditions are also available in beaver ponds. That large, deep pools are often the habitat type in least supply in many small streams of today (e.g., Sedell and Luchessa 1982; Cunjak et al. 1993) is further evidence of the potential importance of beaver ponds as winter habitat. In Wyoming, Chisholm et al. (1987) found brook trout moving into a beaver pond in October where they remained active all winter. In Rocky Mountain streams, as autumn water temperatures declined below 7°C, densities of bull trout (*Salvelinus malma*) and cutthroat trout declined in all habitat

types except beaver ponds where large aggregations of both species overwintered (Jakober 1995). The use of beaver ponds for overwintering was also noted for juvenile coho salmon in coastal Oregon streams (Nickelson et al. 1992a) and for coho salmon and Dolly Varden (*Salvelinus malma*) in a southeastern Alaskan stream (Chichagof Island) where survival was considered better relative to other winter stream habitats (A. Dolloff, U.S. Forest Service, Blacksburg, personal communication) although predation by otters was concentrated here in early spring (Dolloff 1993). In a beaver pond in Catamaran Brook, an aggregation of more than 60 brook trout (12–25 cm fork length) was observed (mid-October, water < 8°C), more trout than observed in any other pool in the system in the previous 3 years (R.A. Cunjak, unpublished data). In such shallow streams where ice cover is often in contact with the stream bed, a beaver pond may represent one of the few available wintering sites.

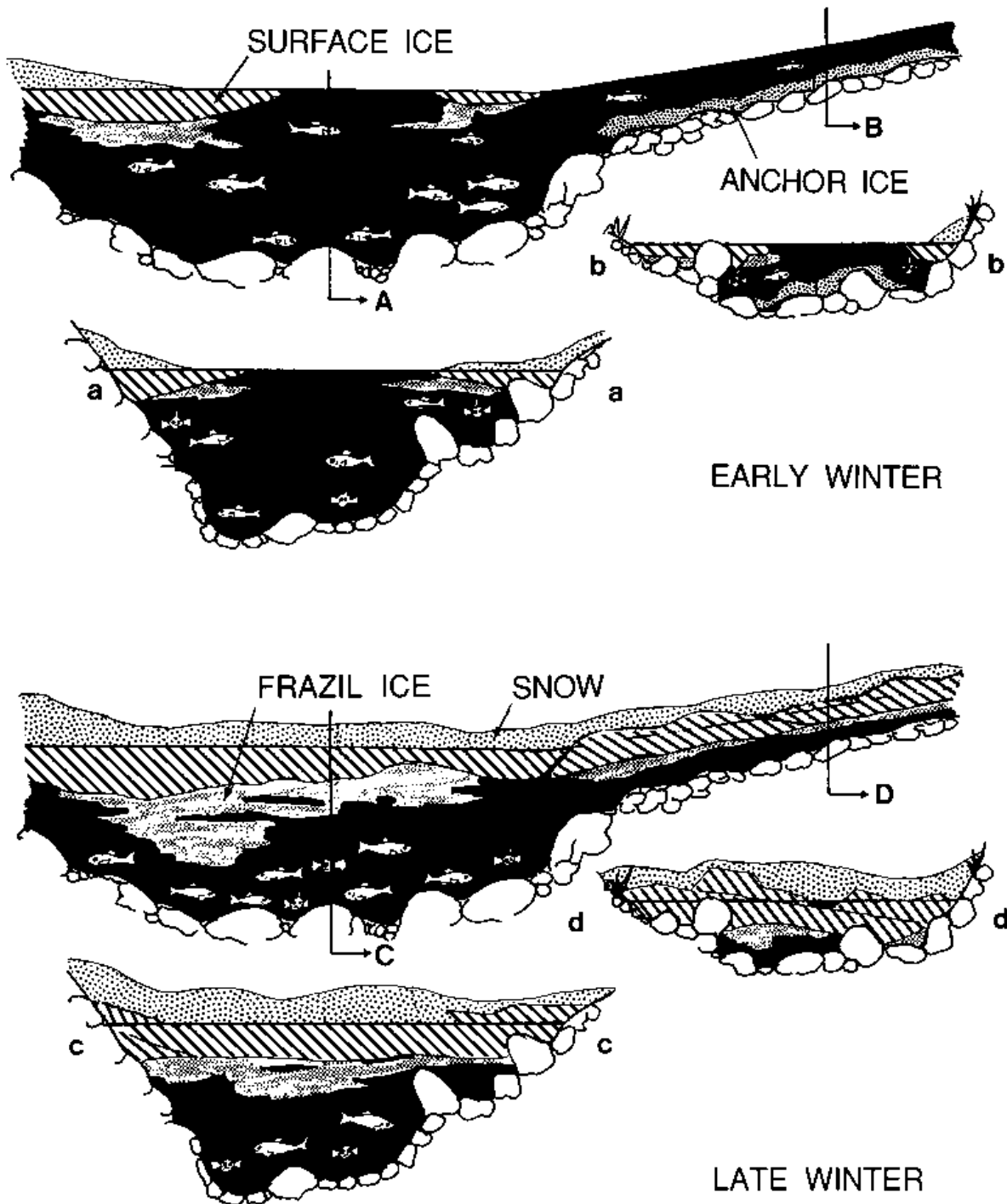
The value of beaver ponds as wintering habitats for fishes is underappreciated. The deeper water in the pond, and in the adjacent flooded backwaters, provide the requisite space where fish can aggregate and swim, even beneath a complete ice cover. Indeed, the frequency of occurrence of large winter aggregations noted in the above-cited research and in other winter studies (e.g., Hartman 1965; Bustard and Narver 1975a; Craig 1978; Paragamian 1981; Cunjak and Power 1986a) may be evidence that adequate winter habitat is limiting in many systems. Aggregations, therefore, may be useful as indicators of important wintering areas.

#### **Large-scale habitat considerations**

Movement to wintering habitats can involve long distances. In the North Ram River, Alberta, Brown (1994) found that radio-tagged, adult cutthroat trout moved upstream and downstream an average of 1–2.4 km, but some moved as far as 7.6 km from the site of release to wintering pools. Apparently these movements were in response to changing subsurface ice conditions in the river, as trout sought suitable pools or “warm” groundwater inputs (Brown et al. 1994). Clapp et al. (1990) found that large (43.7–63.5 cm) brown trout in a Michigan stream had separate summer and winter ranges, with some fish moving approximately 10 km upstream to overwinter in slower, deeper parts of the river. Similar long-range movements were noted in the northwestern Miramichi River, New Brunswick, where some post-spawned Atlantic salmon (kelts) moved 5–10 km downstream to the head of tide (R.A. Cunjak, unpublished data). As in Alberta, kelt movement was likely in response to frazil ice accumulation in the riverine pools (e.g., Cunjak and Caissie 1994); such accumulations were minimal in tidal water because of the flushing action of the tides. Adult largemouth bass in the upper Mississippi River were active in winter, moving 3–14 km to wintering areas (slightly warmer, no-flow backwaters), which may be the limiting habitat for centrarchids (largemouth bass, bluegills, and crappies) in this part of the Mississippi (J. Pitlo, personal communication). In some ice-covered northern Ontario rivers, adult lake sturgeon (*Acipenser fulvescens*) equipped with physiological radiotags (to monitor electromyogram activity) moved at a rate of  $\approx 6 \text{ km} \cdot \text{day}^{-1}$  to overwinter in a deep pool at the confluence of two rivers, where they remained active until the start of the spawning migration in mid-January (S. McKinley, University of Waterloo, Waterloo, Ont., personal communication). In the



**Fig. 4.** Conceptual representation of the change in habitat availability in a temperate stream riffle and pool as winter progresses and ice accumulates. Open sections in riffles may generate anchor ice and frazil ice, which can subsequently restrict habitat available to fish in downstream stream sections and may contribute to ice dam formation and streamflow alteration (modified from Power et al. 1993).



arctic, where winter conditions can be severe and suitable winter habitat is least available, migration distances between summer and winter areas can be  $\approx 100$  km (West et al. 1992). These long-distance movements between summer and winter areas emphasize the need for a seasonal appreciation of habitat requirements and a large-scale river basin approach to fisheries management (Clapp et al. 1990).

Such long-distance winter movements are in marked contrast to some published research on instream movements. For example, Garcia deLeaniz (1989) found that home areas were less than  $8 \text{ m}^2$  for 75% of the marked Atlantic salmon parr that were monitored for 17 months in a Scottish stream. Heggenes et al. (1991) found limited movement by cutthroat trout between January and August in a British Columbia stream where

63.2% of the recaptured individuals moved less than 10 m. In these latter two studies, the absence (British Columbia) or minimal amount of ice (Scotland) in the streams (which could influence winter habitat suitability) may partly explain the differences in movement. Alternatively, where suitable winter habitat is immediately available, and relatively stable throughout the winter, long-distance movement is unnecessary (Bjornn 1971; Dolloff 1987).

The preceding should impress upon habitat managers that river systems must accommodate the range of movement and habitats used by stream fishes in winter. Further, protection of preferred winter habitat(s) is only one consideration for habitat conservation. Just as important are the "corridors," the stream channels that permit access between seasonal habitats. Some fishes move many kilometres to overwinter in relatively few suitable habitats, and many continue to move among different habitats during the course of the winter. Therefore, winter habitats need to be viewed not as discrete units but rather as a dynamic continuum within a population's distributional range. Such a scenario is admittedly daunting in trying to establish guidelines for habitat conservation. The task becomes further complicated when considering the potential impacts to winter environments from anthropogenic activity in stream basins.

### Impacts to winter habitat from land-use activity

Fisheries managers today need to understand and quantify how land-use activity in a stream basin might alter habitat. Ideally, before attempting such a cause-effect linkage, one needs first to understand the natural variability within the stream before attempting to assess man-made impacts (Rinne 1990). This is a difficult ideal to attain because of our limited knowledge of stream conditions and species' habitat requirements in winter. Nevertheless, some general considerations and associations are possible to assist management decisions relating to winter habitat impacts.

#### Loss of habitat complexity

For those fishes that prefer to overwinter beneath medium to large substrate (i.e., cobble-boulders), habitat quality and availability is deleteriously affected by land-use activity that introduces fines into the stream, thereby imbedding potential winter cover. Simulating winter cover conditions in a small stream, Bustard and Narver (1975*b*) demonstrated that juvenile salmonids prefer clean rubble over silted rubble, and the preference was strongest at the lowest water temperatures (i.e., 2–6°C). Winter electrofishing by Griffith and Smith (1993) in portions of the Snake River, Idaho, indicated that boulder sites that were heavily imbedded (25–50% fines) had <30% of the cutthroat trout density of adjacent boulder sites that were moderately or slightly imbedded (<25% fines). In a Nova Scotian river subject to erosion and sedimentation from land-use activity in the catchment, Cunjak (1988*a*) found that 40% of the salmon parr that he observed underwater in winter were located beneath stones in salmon redds, which accounted for only 10% of the study area. He suggested that this disproportionate use of redds for overwintering was a function of high imbeddedness in the stream.

Improper forestry and agricultural activities can introduce fine sediment to streams, especially where suitable riparian

buffer strips are inadequate to prevent erosion and soil runoff (Brown and Krygier 1971; Barton and Taylor 1981; Campbell and Doeg 1989; Hartman and Scrivener 1990). In Prince Edward Island streams, sedimentation from the erosion of agricultural land is a serious problem for aquatic habitats. Recently, 253–305 t (1 t = 1000 kg) of topsoil was excavated from a pit at the base of a 12.2-ha potato field in the West River catchment, in midsummer; after three strong rain events (≈6 weeks), the pit completely filled in with eroded soil, which then overflowed into the river (T. Dupuis, Atlantic Salmon Federation, Charlottetown, P.E.I., personal communication). Similar problems are realized in the sand-plain streams of Norfolk County along the north shore of Lake Erie (personal observation), which resemble Prince Edward Island in geology, topography, and land use. After forestry activity in the Alsea catchment (Oregon), yields of suspended sediments increased from 26–97 to 90–300 t·km<sup>-2</sup>·year<sup>-1</sup> (Beschta 1978, as cited in Hartman and Scrivener 1990). In Carnation Creek, British Columbia, where the most detailed study of fishery-forestry interactions has taken place, deposition of fines increased 4.6–5.7% following logging coincident with a decline in survival to emergence for coho and chum salmon (Scrivener and Brownlee 1989). Winter habitats of most stream fauna (e.g., Campbell and Doeg 1989; Cobb and Flanagan 1990), not only fishes, are deleteriously affected by such sediment loading.

Pools, side-channels, backwaters, large organic debris (LOD) complexes, and some undercut stream margins provide important low water velocity refugia and instream cover, conditions preferred by many stream fishes in winter (see above). However, the nature of these habitats often predisposes them to infilling and damage from improper land-use activities, thereby reducing their suitability as winter habitat (e.g., Bustard and Narver 1975*b*; Tschaplinski and Hartman 1983; Hartman and Brown 1987; Hillman et al. 1987). For example, backwater habitats along the upper Mississippi River act as thermal (and flow) refugia during winter for many centrarchid fishes and are infilling at an average rate of 2.5–6.3 cm·year<sup>-1</sup> (J. Pitlo, DNR, Bellevue, Iowa, personal communication). Sedimentation is one of the major causes of habitat degradation of these backwater refugia (Brietenbach and Peterson 1980, cited in Pitlo 1993) by reducing water depth and oxygen content. Consequently, Pitlo (1993) suggested that winter habitat may be the limiting habitat for many centrarchids of the Upper Mississippi River. Tschaplinski and Hartman (1983) found that juvenile coho populations were better able to resist displacement from autumn-winter flood events in Carnation Creek if instream cover (LOD) remained in the winter habitats (i.e., pools). In those stream sections adjacent to clearcuts, LOD was scarce and coho populations were reduced by 63–74%; in comparison, a section with stream-side buffer strips retained LOD and coho reductions were only 40–45%. Heifetz et al. (1986) estimated that 73% of pools (the preferred winter habitat of juvenile salmonids in Alaskan streams) were formed by LOD and that stream reaches in clearcuts without buffer strips had significantly less area of pool habitat. Loss of stream habitat complexity is common to river catchments where improper land use has occurred.

#### Alteration of streamflow

Winter streamflow contributes a proportionally smaller

amount to the annual hydrograph as one moves away from the moderating influence of a coastal climate to the continental interior (Fig. 2), where winter precipitation is more likely to fall as snow and where freezing conditions prevail. Therefore, the potential impacts to fish habitat from waterflow alteration need to be viewed in the context of the local hydrologic regime. Hydroelectric facilities divert, store, and release water for generating energy largely in response to human demands for power rather than with consideration to natural streamflow patterns. Proposals for water withdrawal from streams during winter for snowmaking for alpine ski operations are increasing in New England (R.A. Cunjak, personal observation) and probably elsewhere. Withdrawals effectively remove a portion of the streamflow with no return until late winter or spring when a larger than normal snowpack melts. Regulation of streamflow, be it for hydroelectricity or for other purposes, can markedly change the natural discharge pattern (Fig. 2) and the seasonal cues to which the resident stream fauna have evolved specific strategies. For example, the suppression of major flood periods in regulated West Coast streams might preclude access to floodplain winter habitats for juvenile salmonids or their return to the main channel in spring.

Barriers to instream migration can deny access to wintering areas. As noted previously, some stream fishes (e.g., salmonids, centrarchids, sturgeon) move long distances prior to and during winter. How well fish can locate alternative wintering areas once dams are built is unknown. The impacts will be deleterious where winter habitats are limited in abundance and where fish demonstrate strong site fidelity for particular wintering areas. Pitlo (1993) found evidence of homing to specific wintering sites in the Upper Mississippi River; several radiotagged largemouth bass were found in the same general area in summer but moved more than 5 km to widely separated backwater habitats in winter, bypassing backwaters used by other wintering bass.

Water withdrawal and its direct influence on reducing available habitat (wetted space) probably impacts stream fish populations more than any other winter alteration of streams. The situation is most pronounced in shallow streams and rivers (often the most productive rearing habitats for juvenile salmonids) and is exacerbated by ice conditions (Power et al. 1993). West et al. (1992) noted the susceptibility of Alaskan grayling to habitat damage from water abstraction (for construction of ice roads, airstrips) because of the shallowness of rivers and the extremely limited winter habitat (i.e., unfrozen water beneath ice). Griffith and Smith (1995) noted that when winter discharge was kept low in a regulated stream, juvenile rainbow trout could not use near-bank concealment habitat that had held a high density of fish throughout a previous winter. Chisholm et al. (1987) suggested that the impact of winter water withdrawal may be more severe at low-elevation sites because of habitat exclusion by surface and subsurface ice accumulation and "... the lack of suitable means for determining winter streamflow needs under these conditions."

A winter reduction in streamflow will generally accelerate ice formation. Land-use activities such as forestry and agriculture often result in wider, shallower stream channels, which in turn are conducive to greater ice accumulation. Together, these effects can markedly reduce available habitat beneath ice cover in rivers. Maciolek and Needham (1952) reported on the mortality of brown and rainbow trout in Convict Creek, Cali-

fornia, when subsurface ice accumulation precluded water flow into side-channels where trout were subsequently stranded. Bams (1987<sup>1</sup>) in his report on potential impacts of hydroelectric development in the Nechako River, British Columbia, suggested that the reduced intragravel flow to chinook salmon redds would affect incubation time, development, and survival of eggs and alevins. Curry et al. (1992) cautioned that streamflow reductions for hydroelectric development in the Nipigon River, Ontario, could alter groundwater flow to brook trout incubation habitat and result in freezing of eggs and alevins.

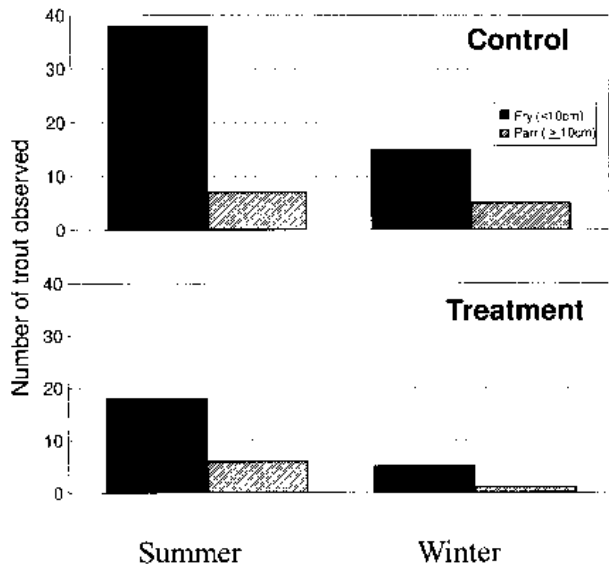
The reduction in accumulated thermal units as a consequence of water withdrawal could severely impact fishes that are poorly adapted for activity at freezing temperatures. The discovery of moribund and dead fish (representing 37 species) in the upper Mississippi River was attributed to their inability to cope with water temperatures below 1°C in the main channel and because warmer off-channel refugia (backwaters) were lacking nearby (Bodensteiner and Lewis 1994), possibly because these habitats had been altered by land-use activity in the catchment (see Pitlo 1993). Similar impacts might be expected for fishes that are near the northern limit of their distributional range. In the Great Lakes drainage, species such as white perch (*Morone americana*), which have a low tolerance for near-freezing winter temperatures (Johnson and Evans 1991), would likely be deleteriously affected by activities that resulted in lower water temperatures.

#### Stream enhancement and winter habitat

In some cases, attempts at "enhancing" stream habitats in summer may have negative consequences for wintering fish. That is, summer gains in production may be nullified by constraints related to winter carrying capacity. Streamside debris-brush removal, particularly of alders, is a popular component of some stream enhancement projects (e.g., OMNR 1986). Improved access (for anglers), increased streamflow, and flushing of fines are often cited to rationalize the habitat alteration. Such changes were made along a section of the Valleyfield River, Prince Edward Island, where stream enhancement was carried out in 1988–1989 (R.A. Cunjak, unpublished data). Alders, still present in a control area upstream, impeded water movement and resulted in the littoral deposition of fines and the formation of a wide channel with shallow stream margins. In the treatment zone, in contrast, alder removal led to faster streamflow through a narrower channel with little depositional area. A seasonal snorkeling census of brook trout abundance in both areas indicated that fewer trout used midstream or margin habitats post-treatment in comparison with the control (Fig. 5). Habitat alteration in the treatment area scoured midstream macrophytes where brook trout often sought cover and eliminated the shallow (<10 cm depth), low-flow, alder margins, which young-of-the-year trout used extensively, particularly in winter. Some trout were able to find suitable habitat in proximity to a few enhancement structures (i.e., deflectors and low-head barriers) placed nearby, but these conditions favoured mainly older trout (R.A. Cunjak, unpublished data).

<sup>1</sup> Bams, R. 1987. "Expert" report. Prepared for court case on environmental assessment of proposed Nechako River hydroelectric project (ALCAN).

**Fig. 5.** Mean number of brook trout observed during underwater observations in two stream reaches of the Valleyfield River, Prince Edward Island, in summer (June–September 1989) and winter (December 1989–March 1990). Both sites were of similar width and length. The treatment site underwent bank-side brush (alder) removal and the installation of stream enhancement structures in 1988; no such changes occurred within the control reach, which was just upstream of the treatment.



Ruggles (1966) carried out comparative experiments in stream channels to increase smolt production of juvenile coho salmon by increasing winter cover (cement blocks). Contrary to expectations, smolt production was markedly higher in channels without cover. In a small stream on Vancouver Island, Mason (1976) attempted to increase winter habitat for juvenile coho salmon by constructing streamside refugia. However, less than 5% of the introduced coho used the refugia as most fish remained in the natural stream habitats and eventually emigrated during winter freshets. Mason indicated that “a 6- to 7-fold increase in potential smolt yield induced by a supplemental feeding strategy during the summer was nullified by the natural carrying capacity of the stream over winter.” Constructed pool habitat (plunge pools and dammed pools) in Oregon streams, which were effective in providing suitable summer habitat for juvenile coho salmon, were used significantly less in winter (Nickelson et al. 1992b) when coho preferred alcove (off-channel) habitats (Nickelson et al. 1992a). Cunjak and Power (1987) studied winter cover use by brook and brown trout in a small spring-fed tributary of the Credit River by comparing frequency of use of submerged versus above-water cover, in riffle and pool habitats. Both species preferred submerged cover, but brown trout frequented only the pool habitat closest to the stream mouth, whereas brook trout used submerged cover with similar frequency in all four habitat types. The use of riffle habitats in winter was in contrast to where brook trout normally were observed in other Credit River sites (Cunjak and Power 1986a) and was explained by the relatively low focal point velocities beneath riffle cover structures caused by accumulation of debris behind which trout frequently positioned themselves (Cunjak and

Power 1987). Obviously, these results underline the complexity of winter habitat requirements of stream fishes and our relative ignorance of what constitutes important habitat in winter and summer.

More consideration needs to be given to the efficacy of habitat enhancement projects in winter. Calkins et al. (1989) found that frazil and anchor ice often accumulated around boulders and deflectors and eventually formed a surface ice sheet. Despite a relatively mild ice break-up in the year of study, a 70-kg boulder was displaced by ice floes and led the authors to recommend that boulders be at least 100 kg for use in such projects. Boulders, which act as cold sinks, also play a major role in the initial freeze-up process (Calkins and Brockett 1988). Where partially exposed above the water, boulders formed air gaps when surface ice perched on them as water levels dropped (Calkins et al. 1989). Sub-ice air gaps can be ecologically significant by inhibiting further ice growth and acting as an insulating layer, an interface for aeration, an “exit” for winter-emerging macroinvertebrates, and a corridor for sub-ice movements by fish-eating mammals (Calkins et al. 1989).

#### Modeling habitat conditions in winter

Habitat simulation models and instream flow methodologies are commonly applied throughout North America (Reiser et al. 1989), often with the objective of assisting biologists and managers in providing adequate habitat protection for aquatic resources subject to proposed streamflow alteration (Shirvell 1989; Armour and Taylor 1991). Most of the habitat-suitability curves used in these models are derived from measurements made during spring–autumn and are not appropriate for winter habitat simulations. In two Virginia streams, Pajak and Neves (1987) found that rock bass (*Ambloplites rupestris*) distribution was most restricted in winter (in deep pools) and led the authors to suggest that winter conditions were probably more appropriate than summer low flows in determining habitat suitability for these populations.

Previously cited evidence of shifts in seasonal habitat preferences of stream fishes and the unique hydrologic characteristics of an ice-covered stream in winter (e.g., Calkins and Brockett 1988; Calkins 1989; Prowse and Gridley 1993; Prowse 1994a), which the hydraulic submodel of PHABSIM cannot properly simulate, should dissuade the use of these instream flow models in winter until more appropriate simulations and validations are carried out (e.g., Berg 1994; Martinson et al. 1994). Similar concerns regarding the use of these models for simulating conditions in ice-covered rivers were made by Petryk et al. (1994). Indeed, surveys of state and federal agencies concerning instream flow practices in North America (Reiser et al. 1989) found that a number of respondents identified the need to develop new methods for determining winter flow requirements of fishes.

#### Conclusions

Stream fishes have adopted many adaptive mechanisms to meet the demands of winter. The complexity and dynamic nature of a stream in winter must be viewed from a spatial, as well as a temporal, aspect. That is, winter habitat suitability can, depending on individual preferences and local environmental conditions, be achieved in any number of habitat types,

stream reaches, and basins. Further, habitat suitability and use can vary with time over the course of winter (e.g., early winter vs. late winter vs. midwinter; day vs. night). Such complexity suggests a fragility in the inter-relationships between animal and habitat in winter. The frequency and prevalence of significant winter mortalities seem to emphasize this fragility.

Assurance of winter habitat protection for the many life stages and species that comprise a fish community will not be an easy task for fisheries managers. Because of the variety of winter habitat preferences and the long distances that some fishes travel between summer and winter sites, the most obvious advice is to maintain habitat complexity. In the case of degraded streams, winter habitat enhancement needs to restore complexity. That each stream is different and unique is known to any field biologist but an unwelcome statement to a manager trying to develop habitat guidelines with broad geographic applicability. However, there are some generic rules regarding winter habitat that apply to all streams. These rules include the understanding that diverse, complex microhabitats and the corridors that allow access between them are essential for overwintering fishes, that summer and winter habitat requirements may be different, that groundwater discharge zones provide winter refugia, that ice can markedly influence habitat suitability, and that land-use activities that increase sediment loading and reduce streamflow can deleteriously alter availability of winter habitat. Quantitative data demonstrating the importance of winter habitats, and contrasting survival under different winter conditions, are largely lacking and can only be obtained by applying the type of effort previously reserved for the spring–autumn period. Not until we consider winter as part of the field season rather than a time to work up summer data, will we be able to effectively conserve and manage fish habitat.

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