Winter Ecology of Brown Trout, White Sucker and Common Carp in the Grand River, Ontario

by

Richard S. Brown

A thesis
presented to the University of Waterloo
in fulfillment of the
thesis requirement for the degree of
Doctor of Philosophy

in

Biology

Waterloo, Ontario, Canada, 1999

0-612-51182-0

Abstract

The movement, habitat use, and swimming activity of adult river dwelling brown trout, white sucker and common carp were studied during winter. Movement was quite limited during the winter except during periods of high water discharge or the break-up of river ice. Both white sucker and common carp moved the longest distances during flooding and ice break-up. Brown trout movements were less affected. Both white sucker and common carp had positive relationships between mean weekly movements and water discharge. This relationship was also positive for brown trout, but not significant. During periods of high water discharge and ice break-up, white sucker and common carp used backwater habitats more and main channel habitats less. During high flows, brown trout tended to use runs more and pools less.

None of the three species of fish studied displayed a conspicuous daily rhythm of activity. About one third of the riverine brown trout studied were arrhythmic, and twilight was the only period which usually had the highest activity rates or was not significantly lower than any other period of the day. Diel swimming activity patterns of white sucker were generally arrhythmic or showed the least activity during night. Most common carp which were not arrhythmic were less active during the day than either twilight or night. After surface ice cover formed, the amount of activity at night, relative to day and twilight, decreased in brown trout. The swimming activity levels of most brown trout were changed by the presence of a solid surface ice cover. Water discharge appeared to have little influence on swimming activity of brown trout. Most white sucker and common carp showed a negative relationship between mean daily swimming activity and water discharge. Common carp were much more active than brown trout and white sucker.

Formation of a hanging dam filled over 80% of an overwintering pool with frazil ice and increased mean and bottom water velocities dramatically. Fish left the pool in which the dam developed but activity levels of fish leaving the pool were not affected in a consistent way.

Adult rainbow trout swam less when exposed to frazil and anchor ice in a refrigerated hydraulic flume. Fish appeared more sluggish during the ice events' and were not frightened when approached by observers (showed a reduce escape response).

Acknowledgements

I wish to thank my supervisor Geoff Power for scientific advise. Assistance was provided by Gary Anderson, Al Arthur, Toni Beddow, Julie Brodeur, Ken Chandler, Steve Cooke, Dave Cote, Rick Cunjak, Jason Darisi, Rick Doucett, Anders Koed, Melanie Martin, Dan Thompson, Ian Welch, and Roy Wilhelm. I would like to thank Dave Barton, Spyros Beltaos, and Jeanette O'Hara Hines for scientific advice. I also thank Steve Daly, Kate White, John Gagnon, Jon Zufelt, Charles Clark, and Charles Schelewa of CRREL.

I am grateful for logistical support provided by the Ontario Ministry of Natural Resources, the Grand River Conservation Authority, and the Friends of the Grand River. I specifically thank Art Timmerman, Jack Imhoff, and Darryl Coulson, and Doug Ratz.

This research was supported by a grant from NSERC to R. S. McKinley, G. Power, and G. Dixon and by a grant from the Ontario Ministry of Natural Resources.

Table of Contents

List of Tables

List of Illustrations

Chapter 2

Chapter 3

Chapter 4

Chapter 5

Chapter 1

General Introduction

General Introduction

The winter ecology of fish has long been a neglected area of fish ecology. This is at least in part due to the difficulty in observing and sampling fish during this season. Field conditions are cold and most equipment (which is designed to work at warmer temperatures) is chronically problematic. Surface ice cover instability and break-up also make field work dangerous as well as difficult. Surface ice also makes many techniques for observing fish impossible.

Considering all these difficulties it is easy to understand why research into the winter ecology of fish is so neglected and why there are so many misconceptions about fish behaviour during this season. Many scientists often disregard the need for study during this season thinking that fish are simply in a state of near hibernation, slowed down by their poikilothermic nature. However, winter is a very dangerous time for fish, especially riverine fish.

In cold regions, rivers have highly variable ice and flow conditions. The formation of river ice in the fall often begins with the formation of frazil ice which forms when water temperatures drop below freezing in turbulent areas by losing further heat to the atmosphere (Ettema et al. 1982). When the temperatures drop below freezing the water is called "supercooled" (Tsang 1982). While the water is supercooled, small (0.1-5.0 mm), usually disc shaped, ice crystals form in the water column, called frazil ice (Osterkamp and Gosink 1982). These ice crystals can stick to each other and to underwater objects forming anchor ice (Osterkamp and Gosink 1982; Tsang 1982). Anchor ice can grow to form thick deposits and fill much of the water column over large sections of river and even dam rivers and streams which can cause large fluctuations in water levels or completely dewater stream sections (Maciolek and Needham 1952; Tsang 1982; Brown and Mackay 1995a; Jakober et al. 1998; Brown 1999).

In rivers, surface ice usually forms first along the river margins where border ice grows from the bank out into the main river (Prowse 1995). However, frazil ice is a key proponent to the formation of surface ice on rivers. Frazil ice clusters float to the surface and are exposed to the cold air at the water surface. This cold air freezes the water in the interstitial spaces increasing bouyancy of the frazil slush (Prowse 1995). This frazil slush can form into large sheets or floes. Eventually these floes bridge the entire channel forming an ice cover (Prowse 1995).

Frazil ice can also form thick sub-surface accumulations called hanging dams (Michel 1975). They form in low velocity reaches of rivers below surface ice, typically located downstream of more turbulent faster water sections that retard ice cover formation. Here, in freezing weather, conditions are ideal for generation of frazil ice since in open water there is continuous heat loss to the atmosphere and maintenance of a slight amount of supercooling of the river water (Tsang 1982). There is usually sufficient turbulence to entrain particles, from the surface where they first form, into the main flow. When these are carried into the section downstream, buoyancy causes the frazil particles to deposit underneath the existing ice cover. As the deposit thickens, a hanging dam is formed, blocking the river flow, which produces an increase in the local flow velocity (Cunjak and Caissie 1994; Komadina-Douthwright et al. 1997). The deposition continues until either the upstream supply of frazil ceases, or until the local velocity increases to the point that it is sufficient to suppress the effects of buoyancy and carry the frazil past the hanging dam (Beltaos and Dean 1981). Hanging dams can fill much of the water column for long periods of time making habitats unavailable for fish (Gold and Williams 1963; Cunjak and Caissie 1994; Caissie et al. 1997; Komadina-Douthwright et al. 1997)

The duration of ice formations on rivers, and the frequency of river ice break-up depend on climate. Freshwater ice cover in Canada is highly variable, from periodic skims in southerly temperature regions to mean thicknesses over 2 m on high-latitude rivers (Prowse 1990). Mean freeze-over dates, mean ice thickness, and mean ice-free dates are provided by Allen (1977) and reviewed by Prowse (1990). Many of the colder parts of Canada will only have a single spring ice break-up. This occurs in the northern part of the country, and much of the prairie provinces (Beltaos 1997). In more moderate areas of Canada, such as the southern parts of Ontario, Quebec, and British Columbia, and the Atlantic provinces, ice covers remain for a shorter period of time and both spring and mid-winter ice break-ups are common (Beltaos 1997). The Grand River, is representative of the winter environments expected in moderate areas of Canada. Thus, frequent ice break-up and flooding is observed. These winter floods can produce sudden increases in water velocities at a time when the ability of fish to swim against these currents is at their lowest (Videler 1993).

Surface ice break-up is a dangerous time for fish. During ice break-up, thick ice layers can fill the entire water column with huge grinding masses, scouring both the bottoms and the banks of rivers (Beltaos 1995). At the same time as the fish are coping with ice and flow conditions, these sluggish poikilotherms must avoid predation by mammalian and avian predators, not slowed by the cold temperature. All of these factors combine to make winter a critical period for riverine fish, and a time when mortality rates are probably at their peak.

The feeding rates, digestion rates and growth of fish are drastically reduced during cold temperatures (Cunjak and Power 1986; Cunjak and Power 1987). Thus fish must allocate their limited resources judiciously during winter to avoid starvation. This makes it critical to understand fish activity patterns and how they are influenced by both natural events and by man-induced effects. Any extra increases in the energy consumption of fish brought about by human activities could mean the difference between life and death. Despite the importance of this season, there are relatively few thorough studies of the winter behaviour of riverine fish.

The objective of this study was to expand our knowledge of winter ecology of three species of fish (selected to represent a cool water species, the brown trout (*Salmo trutta*) a somewhat warmer water species, the white sucker (*Catostomus commersoni*) and an exotic species, the common carp (*Cyprinus carpio*)). These species provide a good representation of fish which are influenced by winter conditions. While brown trout and common carp are both exotic species, they are found in both moderate and colder parts of Canada, and can withstand harsh winter conditions. White sucker have a large range throughout both the United States and Canada, ranging almost all the way up to the Arctic Ocean in the Mackenzie River (Scott and Crossman (1998)). While these three species represent fish species found in cold regions, they are just a few of the numerous species which are influenced by cold winter conditions found in temperature and Arctic environments.

One area where information is needed is fish behaviour and activity in winter. Are fish truly very inactive during the winter, or do they remain in some kind of active state to avoid all of the chaotic environmental conditions to which they are exposed? How do they partition limited energy reserves? The numerous studies dedicated to examining the behaviour and activity of fish in coral reef systems (see Helfman (1986) for a review) may not be applicable to temperate rivers which are subject to much more dynamic changes in habitat than coral reef systems which are rather stable.

No study of fish activity during winter would be complete without determining what habitats fish use and how general movements are patterned. Also a thorough examination of winter behaviour of fish should include information about how fish respond to changing ice, temperature, and flow conditions.

To present this material, this thesis has been divided into four chapters:

(1) Habitat use and movements – an analysis of the habitats used by three species of riverine fish over three winters, movements between habitats and how these are influenced by environmental conditions.

(2) Swimming activity and diel patterns – results from two winters of examining swimming activity of riverine fish and how this activity is partitioned among different periods of the day and the winter, and how this activity is influenced by fluctuating riverine conditions.

(3) Effects of hanging dams on fish – the movements and activity of a sample of the fish which had their overwintering areas excluded by a subsurface ice formation, known as a hanging dam.

(4) Effects of frazil and anchor ice on fish – results from a laboratory experiment aimed at determining how swimming activity and behaviour are influenced by frazil and anchor ice.

These chapters follow a logical order, determining how some of the basic behaviours of fish relate to environmental conditions, then examining how some of the more complex activity patterns are affected. Following this, some more specific details of the relationships between swimming activity and behaviour and some of the specific environmental factors which influence fish (i. e. frazil ice, anchor ice, and hanging dams) are considered. Inter-relationships between important aspects of each of these chapters is addressed in the general discussion.

Chapter 2

Winter movements and habitat use of three species of riverine fish

Introduction

Little is known about the movements and habitats used by riverine fish during the winter in temperate climates, or how these are affected by fluctuations in environmental conditions. There have been a few studies of riverine trout during the winter, but none on species such as white sucker and common carp. During winter, riverine trout are often quite sedentary. Chisholm et al. (1987) found that in Wyoming streams, after moving to overwintering areas, brook trout (*Salvelinus fontinalis*) stayed in the same areas all winter. Cutthroat (*Oncorhynchus clarki*) and bull trout (*Salvelinus confluentus*) in Montana, British Columbia and Alberta rivers and streams also move little during winter (Heggenes et al. 1991; Brown and Mackay 1995a; Jakober et al. 1998; Brown 1999). Movements of riverine salmonids occur, however, when riverine habitats are substantially modified by thick, wide-spread anchor ice formations (Brown and Mackay 1995a; Jakober et al. 1998; Brown 1999). Mid and late winter floods and river ice break-up also change riverine habitats substantially, however, little is known about how these changes influence fish. Clapp et al. (1990) noted that radiotagged brown trout tracked throughout the year in a Michigan stream tended to move more during periods of high water. However, since these authors did not provide any water discharge values and only tracked 4 fish every 2 weeks during the winter, more intensive follow up work is desirable.

As water temperatures decrease in fall, riverine salmonids often make less use of shallower areas with higher water velocities and instead use deeper, slower habitats (Hartman 1965; Cunjak and Power 1986; Chisholm et al. 1987; Heggenes et al. 1993; Baltz et al. 1991; Brown and Mackay 1995a; Jakober et al. 1998). While all macrohabitat types are commonly used by adult riverine salmonids during the rest of the year, several researchers have found that pools, beaver ponds, or slow reaches of runs are predominantly used during winter (Cunjak and Power 1986; Chisholm et al. 1987; Brown and Mackay 1995a; Bunnel et al. 1998; Jakober et al. 1998). However, it is unclear what types of habitats fish use during winter when they need to take refuge from winter floods and ice cover break-up.

Although a few studies have addressed movements and habitat use during winter, none have been found which describe how fluctuating water discharges and river ice break-up influence adult fish. Winter floods and the break-up of surface ice on rivers are likely to have a great impact on fish populations and alter fish movement and habitat use patterns. Floods can alter the abundance and distribution of fish in streams (Pearsons and Li 1992). Flooding can also cause fish to move into the riparian zone along stream margins during high flows (Matheney and Rabeni 1995). To determine how natural environmental fluctuations influence riverine fish, brown trout, white sucker, and common carp in the Grand River, Ontario, were implanted with radiotransmitters and tracked during three winters through these changing conditions such as flooding, surface ice break-up, and variations in water temperature.

Study Area

The study was carried out along an 18 km reach of the Grand River between the town of Elora and the town of West Montrose (43°35'-43°41'N, 80°26'-80°29'W), Ontario. There is a barrier to upstream movement of fish at the town of Elora. The study area provides a variety of habitat types. The upper section runs through Elora Gorge, which is a high gradient (mean 5.3 m/km) F1 type channel (Rosgen 1996) cut through the limestone gorge with abundant bedrock substrate. This part of the river has few backwaters or islands. The middle and lower sections are lower gradient (mean 1.4 m/km) C type channel (Rosgen 1996), the channel is less confined and the river flows in a wide open valley. This section has many islands and backwaters. Most of the study area is representative of rivers in southern Ontario. While gorges are not common, high gradient channels, as seen in the gorge are typical of headwater streams.

There are numerous fish species in the Grand River and white sucker are native. Although common carp are not native, they are naturally reproducing. Brown trout are not thought to commonly reproduce in the Grand River and are stocked annually. Brown trout have been stocked in the Grand River since at least 1933. Although brook trout are native to the river, few occur in the study area.

Methods

Four adult brown trout were implanted with radiotransmitters between Dec 12, 1996 and Jan. 2, 1997. Their mean length (FL) was 433 mm (range 351 – 487; SD = 65) and their mean weight was 876 g (range 480 - 1261; SD = 358). Eight adult white suckers, were implanted between Nov. 28 and Dec. 5, 1996. Their mean length was 380 mm (range 310 – 440; SD = 41) and their mean weight was 607 g (range 400 – 940; SD = 206). Eight adult common carp were implanted with radio transmitters between Oct. 21, 1996 and Jan. 2, 1997. Their mean length was 558 mm (range 455 – 620; SD = 50) and their mean weight was 3419 g (range 1749 – 4785; SD = 916). Fish were tracked until April 2, 1997.

Sixteen brown trout were tracked during the 1997-98 season. They were implanted with radiotransmitters (9 with electromyogram (EMG) and 7 with locational transmitters) between Oct. 22 and Dec. 29. Brown trout had a mean fork length of 440 mm (range 365 – 540; SD = 54) and a mean weight of 1071 g (range 628 – 1700; SD = 360). Twelve white suckers were implanted with radiotransmitters (9 EMG, 3 locational) between Oct. 21 and Dec. 30. White sucker had a mean fork length of 420 mm (range 355 – 450; SD = 26) and a mean weight of 933 g (range 612 – 1095; SD = 128). Thirteen common carp were implanted with radiotransmitters (9 EMG, 4 locational) between Oct. 21 and Nov. 6 and tracked until Mar. 30. Common carp had a mean fork length of 580 mm (range 505 – 630; SD = 36) and a mean weight of 3712 g (range 2473 – 4800; SD = 869). Fish were tracked until April 3, 1998.

Five adult brown trout were implanted with EMG transmitters between Dec. 3 and 10, 1998 and tracked until Feb. 26, 1999. These fish had a mean fork length of 511 mm (range 430-570; SD = 57) and a mean weight of 1446 g (range 976–2007; SD = 421).

Transmitters were surgically inserted into the body cavity using methods similar to Brown and Mackay (1995b) or Beddow and McKinley (1999). Either simple locational transmitters or electromyogram (EMG) transmitters (for a description see Beddow and McKinley (1999)), were implanted into fish. After implantation, fish were released at their capture point. Locational radiotransmitters weighed 8.1 g in air and had a predicted lifetime of 425 days. EMG transmitters (Lotek Engineering Inc.) weighed 18 g in air, 8 g in water, and were 5 cm long by 1.6 cm in diameter. They had an estimated lifetime of 90 days. Although EMG transmitters can be used to examine swimming activity of fish, locations of fish can also be attained from implanted fish just the same as with a standard radiotransmitter. Results of swimming activity data collected from EMG transmitters are described in Chapter 3. Transmitters were always less than 2% of the weight of implanted fish in air. After implantation, fish were released at the site of capture. Fish were tracked at least every fifth day from January 1 to April 2, 1997, from Jan. 1 to Feb. 15, 1998, or from Dec. 3 1998 to Feb. 26, 1999. Tracking was done on the ground and fish locations were fixed with a three element YAGI antenna and recorded on aerial photographs (scale 1:20,000).

To determine how available habitats change with fluctuating water discharge, water depths and velocities were measured along 9 transects in 3 different macrohabitat types (pools, runs and backwaters). Surveys were done under several different water discharges between Dec. 18, 1997 and Mar. 11, 1998. Water depth and mean water velocities were estimated every 2-4 m along each transect. Mean water velocity was estimated by averaging point measurements taken at 20 and 80% of the water column. Water velocity was measured using a Sigma Doppler flow meter. Transects were marked so that measurements could be taken at the same spots on subsequent occasions. Water discharge data was provided by Environment Canada from the gauging station at West Montrose which is at the lower end of the study area.

Similar to Bisson et al. (1982), riffles were considered as shallow, turbulent stream segments with higher gradient than pools or runs. Habitats which were moderately shallow, with laminar flow, and which lacked pronounced turbulence were considered runs, and deeper habitats with slower current velocities were considered pools.

Backwaters were considered any large off-channel habitats where water velocities were very low.

Regression analysis was used to determine if there was a relationship between mean weekly movements or habitat use of fish and mean weekly water discharge or water temperature. Regression analysis was also used to determine if there was a relationship between mean weekly water discharge and mean weekly water temperature. Parametric regression analysis was preformed instead of non-parametric correlation analysis since the variance of the data did not appear to differ or be non-normal, and since parametric tests are more robust and fairly immune from even moderate departures from the inference assumptions for the method (Bowerman and O'Connell 1990).

Since fish locations were only acquired every fifth day, daily fluctuations in environmental conditions could not be related to movements and habitat use. Instead, data were averaged over weekly periods for movement and habitat use, and related to the mean weekly water discharge and water temperature. The negative result of averaging flow and temperature data, however, is that short term extremes in water discharge or temperature are obscured. These events, however, still show up as large variations above the baseline temperature or discharge.

Results

Movement was quite limited during the winter with most fish of all three species having small mean weekly movements (always less than 250 m, usually less than 100 m) throughout the winter, except during periods of high water discharge or the break-up of river ice (Fig. 2-1 – 2-3). Both white sucker and common carp moved the longest distances during the break-up of the river ice in mid-February, 1997 and during various discharge increases during both winters they were tracked. These movements usually resulted in net downstream movement.

Brown trout movements were not elevated by the mid-February, 1997 ice break-up, and often were not elevated during periods of high water discharge. Movements of brown trout did not appear affected by water discharge during either the winter of 1996-97 or the winter of 1998-99. During the winter of 1997-98, however, a large peak in movement was noted during discharge increases in early January and late February and March (Figure 2-2). The result of most of these movements was a net downstream displacement of fish. During this winter brown trout resided throughout the study area, while in the winters of 1996-97 and 1998-99 they were only located in the upper portion of the study area. However, brown trout in both the upper and lower part of the study area showed large displacements.

The relationship between movement of riverine fish and water discharge is illustrated well by the results of regression analysis (Figure 2-4). Both white sucker and common carp had significant ($P < 0.05$) positive relationships between mean weekly movements and water discharge, although the relationship for carp was heavily influenced by two data points showing large movements during high flows. This relationship was also positive for brown trout, but not significant ($P > 0.05$). When only the data from the 1997-98 winter are analyzed, however, there is a significant ($P < 0.05$) positive relationship between weekly mean distance moved and water discharge ($r^2 = 0.28$).

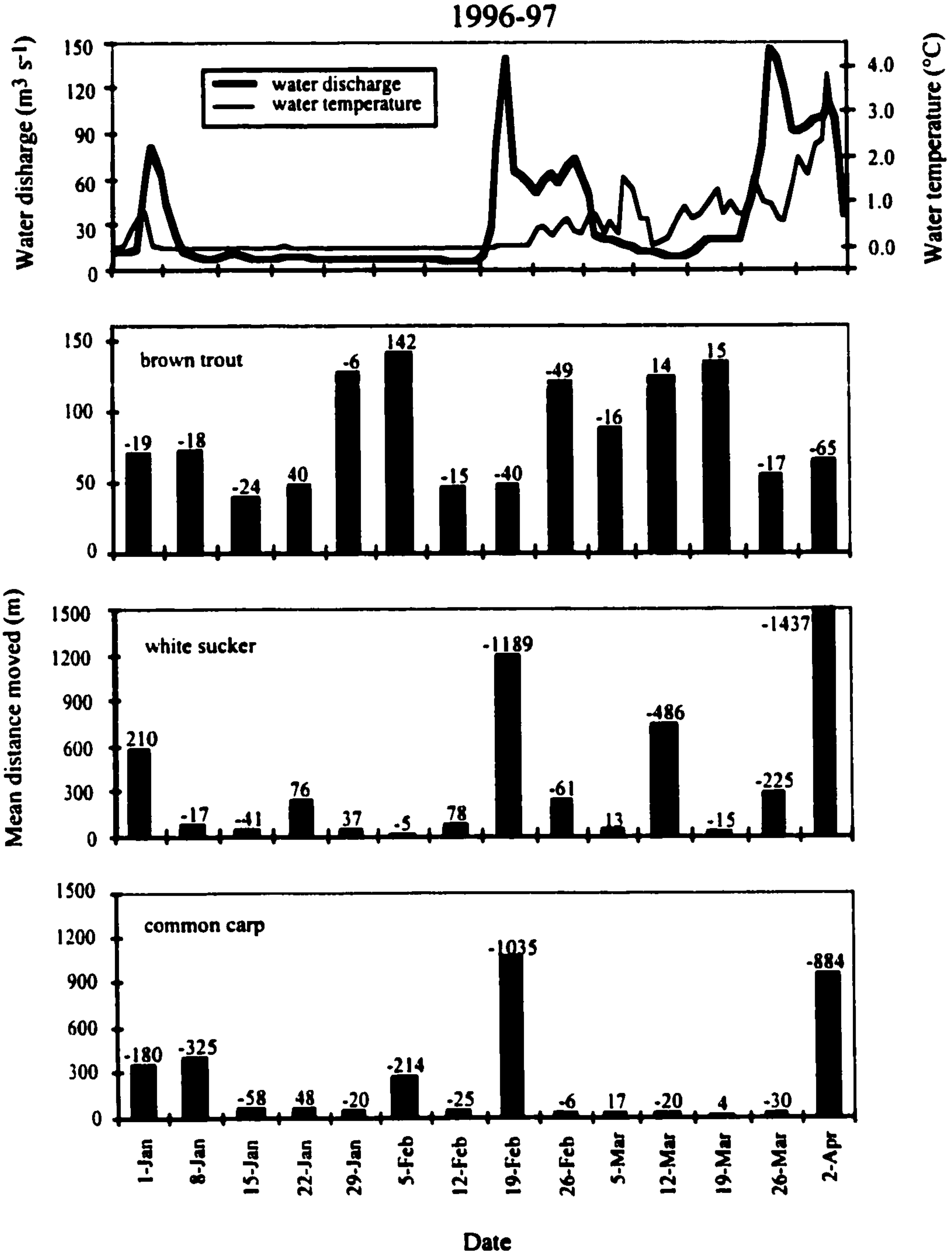

Figure 2-1. Mean weekly movements of radiotagged fish and water discharge and temperature during the winter of 1996-97. Mean net weekly distances moved are shown above bars. Negative numbers depict net downstream movement.

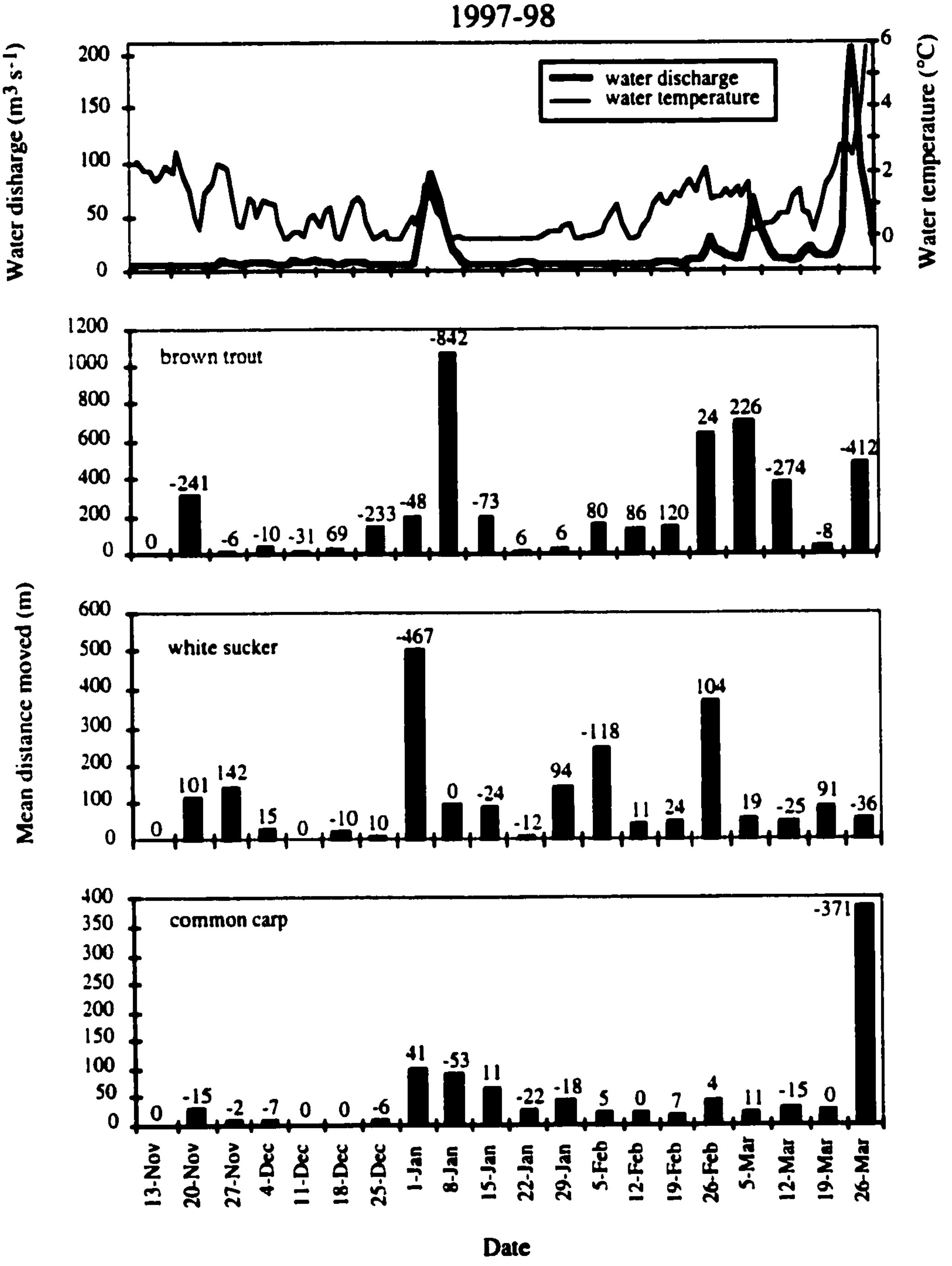

Figure 2-2. Mean weekly movements of radiotagged fish and water discharge and temperature during the winter of 1997-98. Mean net weekly distances moved are shown above bars. Negative numbers depict net downstream movement.

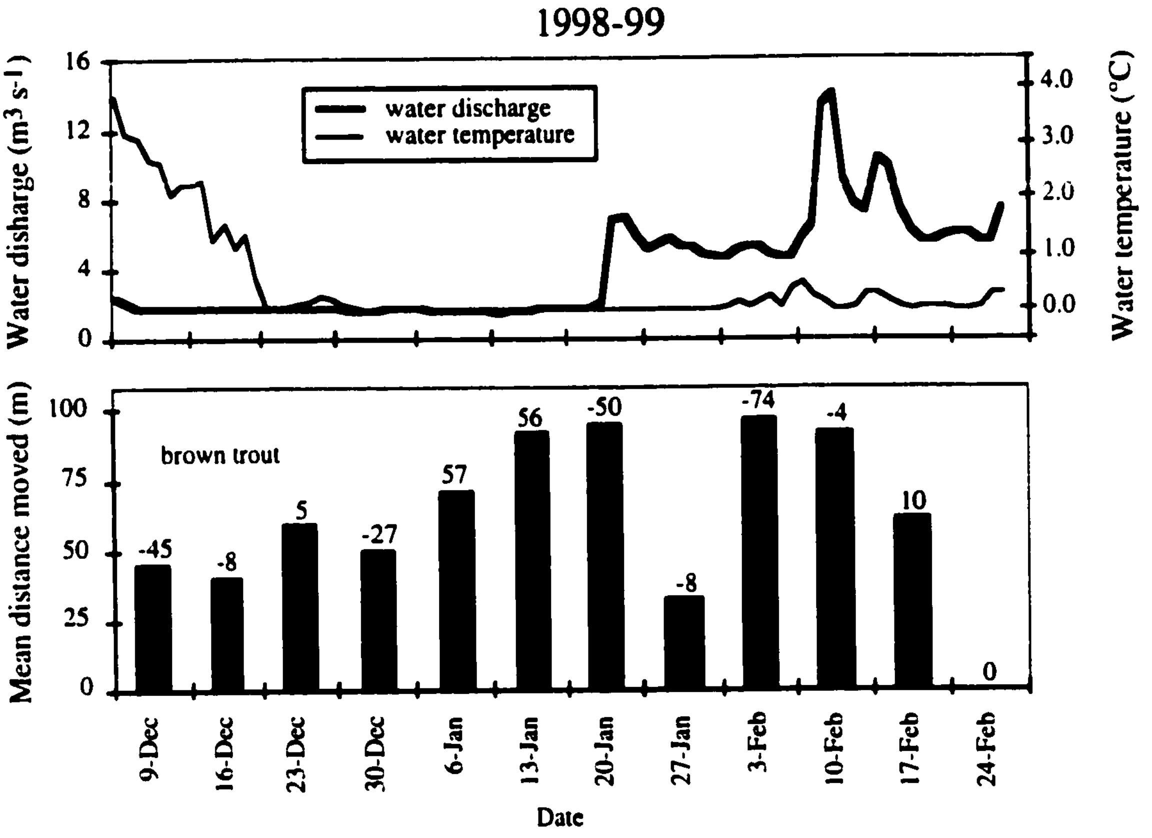

Figure 2-3. Mean weekly movements of radiotagged brown trout and water discharge and temperature during the winter of 1998-99. Mean net weekly distances moved are shown above bars. Negative numbers depict net downstream movement.

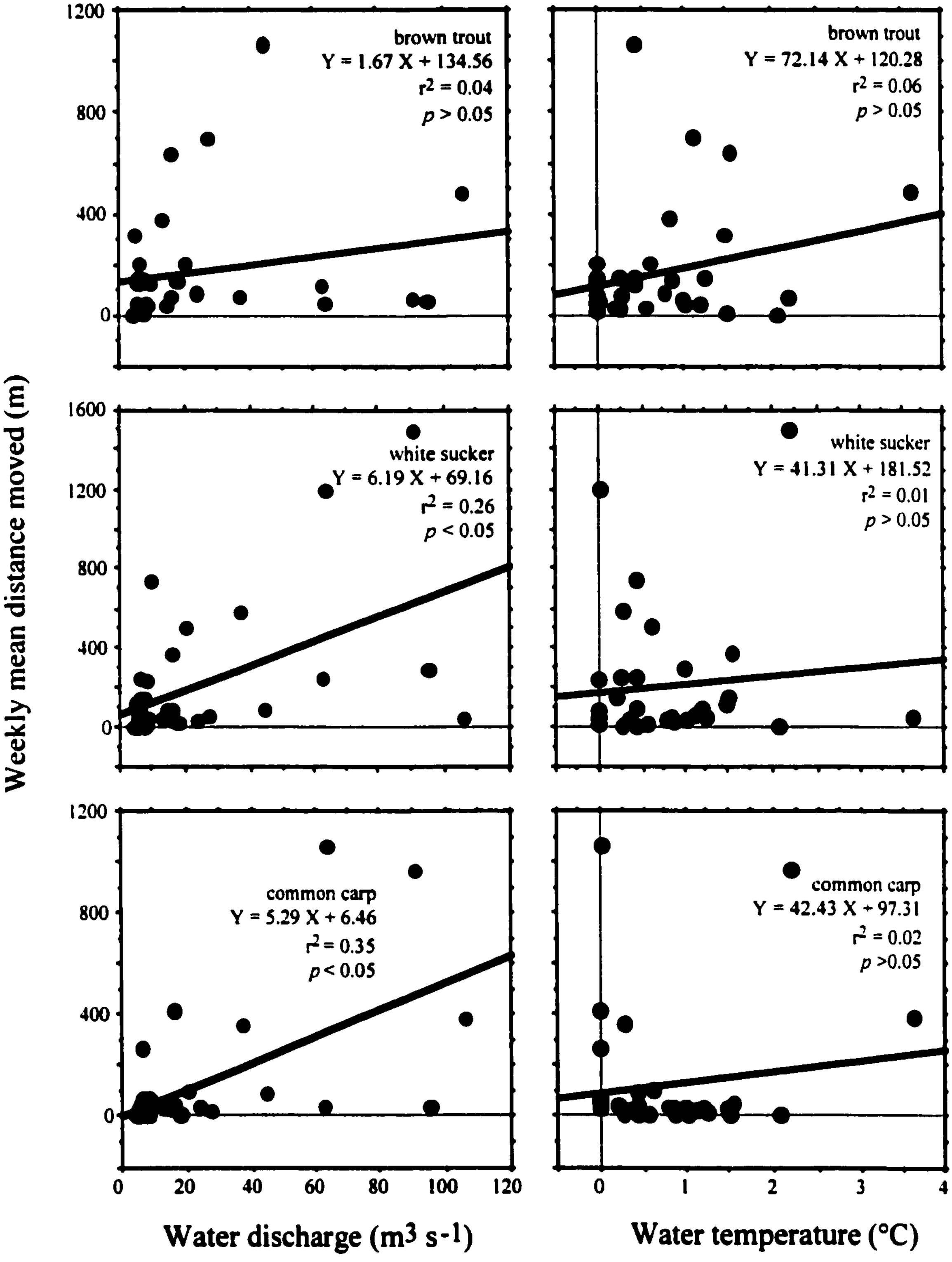

Figure 2-4. Regression plots of the mean weekly distance moved by radiotagged fish at different water discharges and temperatures during three winters.

Water temperature did not appear to have a large influence on movement of riverine fish (Figure 2-4). While all three species had positive relationships between weekly mean distances moved and water temperature, none of these relationships were significant ($P > 0.05$). The trend of positive relationships between movement and temperature is likely a result or a consequence of the significant ($P < 0.05$) positive relationship between water temperature and water discharge.

Fish changed their habitat when flooding occurred and when the river ice cover broke-up (Figure 2-5 – 2-7). During periods of high water discharge and ice break-up, white sucker and common carp used backwater habitats more and main channel habitats (pools and runs) less. For both species, there was a significant ($P < 0.05$) positive relationship between mean weekly water discharge and use of backwater habitat (Figure 2-8). There was also a significant ($P < 0.05$) negative relationship between use of runs and water discharge for both species. The relationship between use of pools and water discharge was also negative for both white sucker and common carp, but only significant ($P < 0.05$) for common carp. Common carp tended to move between runs and backwaters less than white sucker. When water discharge increased, they moved from runs into backwaters but they tended to stay in the backwaters after water levels dropped, while white sucker moved back into runs soon after water levels dropped.

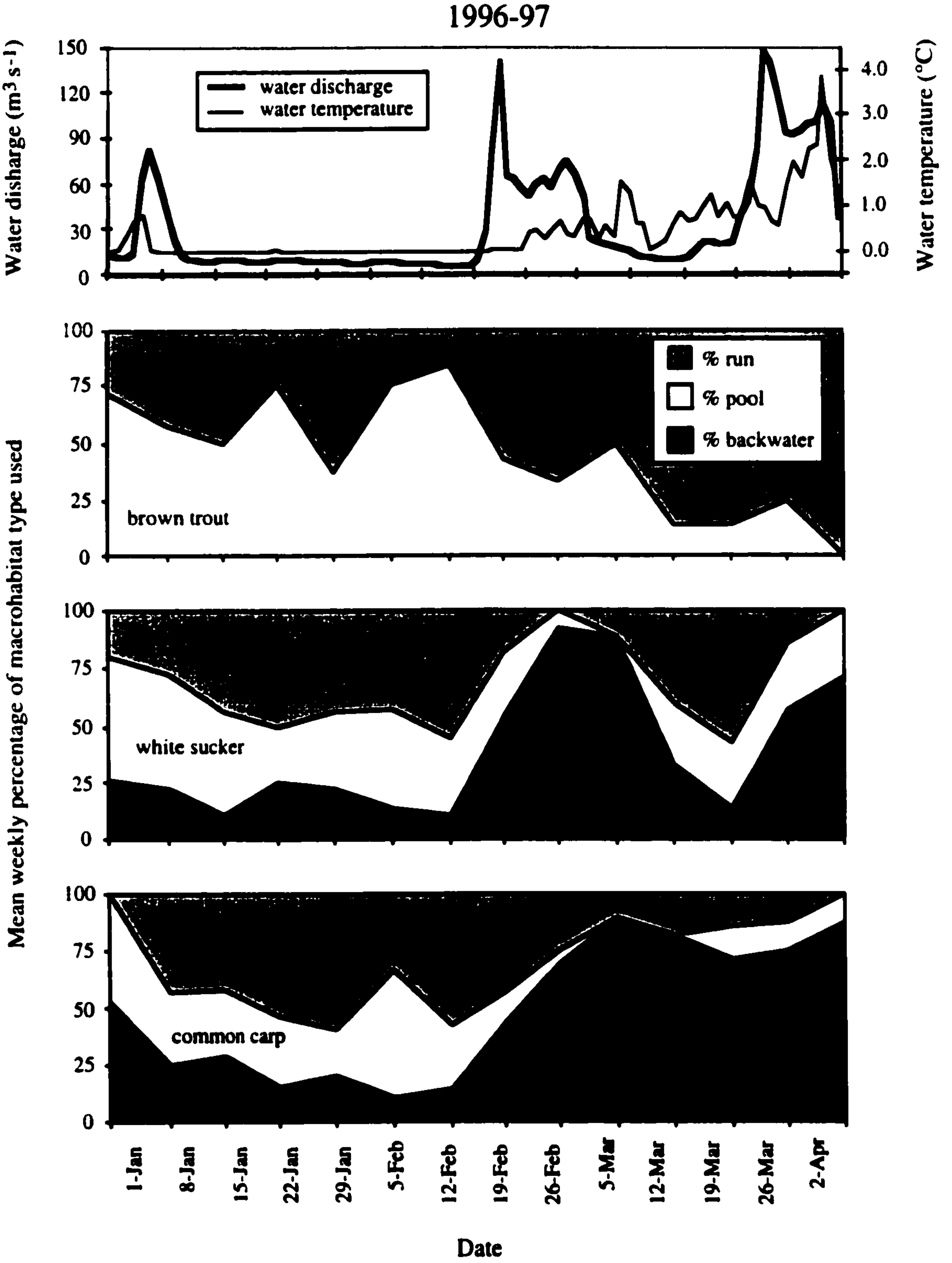

Figure 2-5. Mean weekly use of habitats by radiotagged fish and water discharge and temperature during the winter of 1996-97.

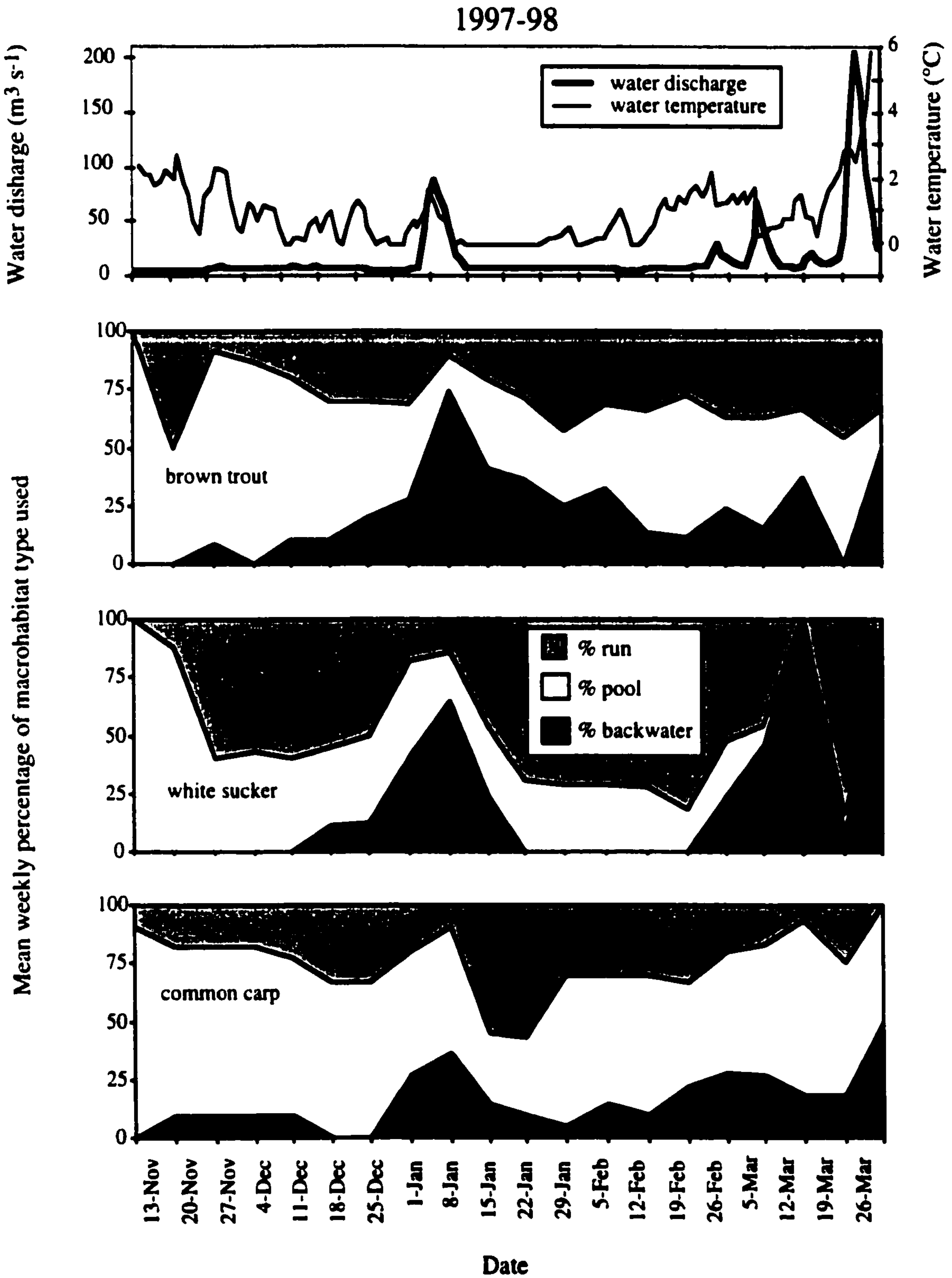

Figure 2-6. Mean weekly use of habitats by radiotagged fish and water discharge and temperature during the winter of 1997-98.

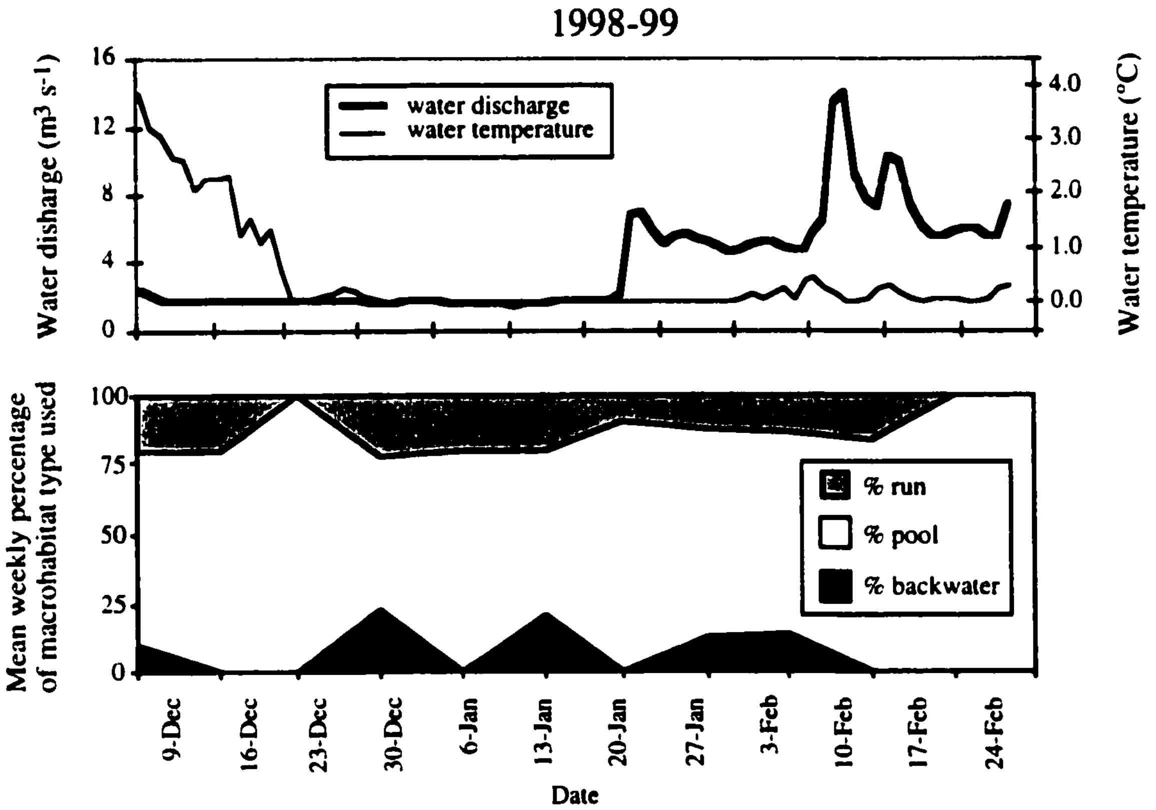

Figure 2-7. Mean weekly use of habitats by radiotagged brown trout and water discharge and temperature during the winter of 1998-99.

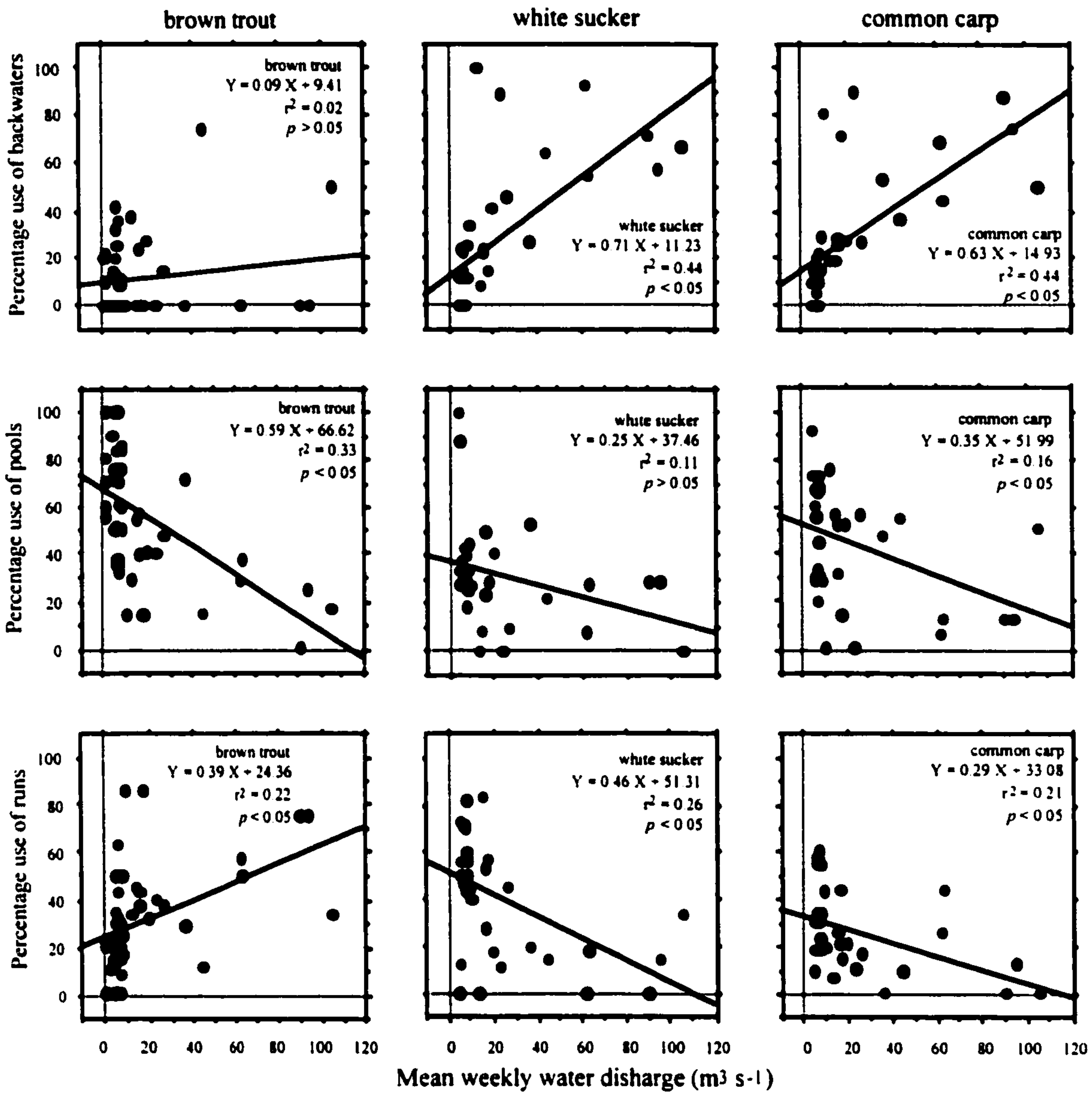

Figure 2-8. Regression plots of the mean weekly use of three habitat types by radiotagged brown trout, white sucker, and common carp at different water discharges during three winters.

The shifts in habitat by brown trout which corresponded to river ice break up and flooding were usually different than those of white sucker and common carp. During high flows, brown trout tended to use runs more and pools less (Figure 2-5 – 2-7). This trend is illustrated in a significant ($P < 0.05$) negative relationship between mean weekly use of pools and mean weekly water discharge, while the opposite relationship was found for runs (Figure 2-8). During the winter of 1997-98, brown trout used backwaters during periods of high water discharge, especially during mid-winter (Figure 2-6). Despite this, there is still not a significant ($P > 0.05$) positive relationship between mean weekly use of backwaters and water discharge when data for all years were combined (Figure 2-8). During the winter of 1997-98, brown trout resided throughout the study area, but during the other two winters they were only tracked in the upper part of the study area. There are few backwater areas available in the upper part of the study area, but they are common in its lower 2/3. When the data for 1997-98 alone are analyzed, there is a significant ($P < 0.05$) positive relationship between mean weekly use of backwaters by brown trout and water discharge ($r^2 = 0.30$).

As fish shifted habitats during periods of high water discharge, the characteristics of riverine habitats also changed (Figure 2-9). Surveys of available habitat showed that, with increasing water discharge, both the water depth and the mean water column velocities of runs and pools increased. The water depth also increased in backwaters, but the mean water column velocities remained low.

The break-up of river ice and accompanying flooding during the winter of 1996-97 resulted in several fish being stranded on the floodplain. On Feb. 25, 1997, one of the

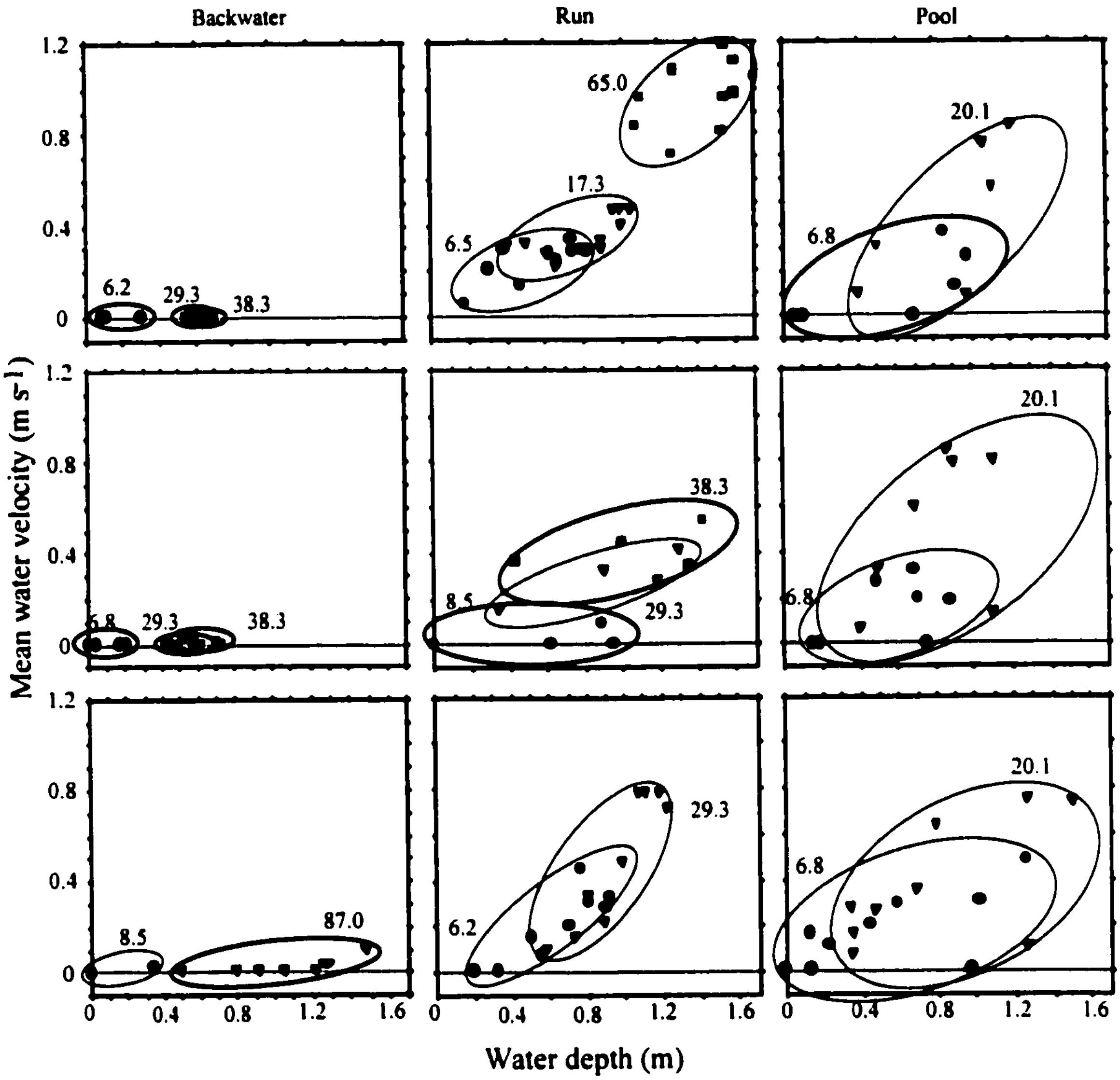

Figure 2-9. Plots of water depths and velocities at different water discharges in three different habitat types. Three separate runs, pools, and backwaters were each sampled at identical spots at 2-3 water discharges. Circles encompass the velocities and depths at a certain water discharge which is labeled next to the circle. Different discharges are also plotted with different symbols; circles, squares, or triangles.

eight radiotagged (12.5%) white suckers was found stranded in a drainage ditch approximately 100 m from the river. Three adult common carp and one adult white sucker (near death) were also within 10 m of the radiotagged fish in the drainage ditch. One of eight (12.5%) radiotagged common carp was also stranded in a backwater pool when floodwaters receded. The fish moved into the backwater during ice break-up (Feb. 24) and remained there until flood waters subsided and the entrance to the backwater dried up. No radiotagged fish were found stranded during years when river ice did not have a dynamic break-up (1997-98 and 1998-99).

Discussion

This study found that many adult riverine fish (brown trout, white sucker, and common carp) made longer movements as habitats were altered by increased water discharge and the break-up of river ice. Juvenile salmon are also known to be displaced during floods in British Columbia coastal streams. The numbers of juvenile coho salmon (*Oncorhynchus kisutch*) that Tschaplinski and Hartman (1983) and Brown and Hartman (1988) found in streams was reduced when fall flooding occurred. Similarly, juvenile coho salmon in laboratory troughs emigrated when water velocities were increased from 3.5 to 38 cm s^{-1} or from 0.64 to 3.2 cm s^{-1} (McMahon and Hartman 1989; Giannico and Healey 1998). Since the fish move out of laboratory channels at velocities as low as 3.2 cm s^{-1}, Giannico and Healey (1998) speculate that fish may be moving in anticipation of worsening conditions. Locations of radiotagged fish would have to be done more frequently than was done during this study to determine if this type of behaviour is also seen in adult fish.

While floods and ice break-up drastically change riverine habitats there are also other factors that make winter habitats unpredictable, much more unpredictable than summer habitats. Subsurface river ice is a natural phenomenon that can create sudden and drastic changes to the riverine environment. Several researchers have noted that when large anchor ice deposits or hanging dams form, fish move more (Brown and Mackay 1995a; Jakober et al. 1998; Brown et al. 1998; Brown 1999).

The amount of movement fish exhibited due to flooding and ice break-up depended on the species of fish. Brown trout were usually less influenced than white sucker and common carp. This is likely due to differences in swimming capabilities, making it harder for some fish to maneuver their way to lateral or backwater habitats if caught in the current. The swimming capabilities of all fish decrease under cold temperatures (Videler 1993), and the presence of unpredictable flow fluctuations during winter likely makes this time of the year much more dangerous and critical than summer.

Fish made few long range movements under low flow conditions. This finding is not surprising since several other authors have found that river dwelling trout usually move little during winter. This study found that fish usually had mean weekly movements of less than 100 m. Brown (1999) found that radiotagged cutthroat trout stayed within a 120 m length of stream when their habitats were stable. When their habitats were influenced by anchor ice, however, they moved 30 times farther and 6 times more often than those in stable habitats. Brown and Mackay (1995a) found that radiotagged cutthroat trout in Alberta rivers and streams did not move 84 - 87% of the time and Jakober et al. (1998) stated that both cutthroat and bull trout moved little during the winter once they were in overwintering areas. Meyers et al. (1992), found that four radiotagged large adult brown trout tracked every two weeks during the winter stayed within a two mile segment of a Wisconsin River. Radiotagged brook trout Chisholm et al. (1987) tracked made mean winter movements of less than 200 m in Wyoming streams and Heggenes et al. (1991) noted that cutthroat trout had small home ranges during winter in coastal British Columbia streams.

The longer movements that fish made during periods of higher water discharge coincided with general changes in available habitat. As water discharges increased the depth of riverine habitats increased, but so did the water velocities in the main channel. These changes likely made main channel habitats less preferable so fish moved into backwaters or the edges of slow runs. While many of the backwater habitats have shallow water, or are even dry during low flow periods, they are commonly used as refuge during ice break-up and flooding.

Many of the fish apparently avoided making long movements by taking shelter in backwaters or the edges of runs. Having these types of habitats readily available in rivers may decrease the numbers of fish that are caught in the current and washed downstream, making them highly susceptible to physical damage. It may also reduce the numbers of fish stranded on the flood plain in shallow water where they can easily be taken by predators, or die as waters completely recede.

Similar to results from the Grand River, during flooding conditions, many juvenile coho salmon in British Columbia streams move to off-channel habitats to seek low velocity shelter (Tschaplinski and Hartman 1983; Brown and Hartman 1988). Also as in the Grand River, many of the off-channel habitats used during these periods are dry in other seasons (Brown and Hartman 1988).

An alternative strategy used by some fish in the Grand River, was to remain in very large deep pools during floods. These pools may provide refuge by having high velocity laminar flow on the top but low water velocities on or near the bottom. Or, as was observed in some cases, pools may contain large backwater-like eddies along their sides which provide low water velocities while other parts of the pools have high velocities. Streams and experimental channels have also been found to retain higher numbers of fish (in these studies, juvenile coho salmon) during floods when cover is available (Tschaplinski and Hartman 1983; McMahon and Hartman 1989).

The influence of ice break-up is difficult to separate from flooding since they occur simultaneously and a dynamic ice break-up only occurred in one of the three years in which this study was done. Some effects on fish were unique to this single break-up period. It was the only time that radiotagged fish were found stranded on the floodplain. Although fish could be washed onto the floodplain during floods, the addition of large ice floes may make remaining in the main channel much more difficult and dangerous. River ice break-up can scour the bottom of the river and damage or remove riparian vegetation (Beltaos 1995). Stranding is likely a major cause of mortality for fish in years with violent ice breakup. In this study, over 10% of radiotagged white sucker and common carp were stranded on the floodplain. Many more fish would likely have been stranded if an ice jam had formed on the river, since release of ice jams can result in a very rapid drop in water levels, and the stranding of many fish (Beltaos, unpublished data 1984).

Unlike open water flooding, floods produced by ice jams that occur during the breakup of river ice can have sudden and often catastrophic impacts on fish populations. When a jam lets go, a surge of water travels down the river, a phenomenon akin to a dam break. Downstream of the site where the jamming occurred water levels can rise very rapidly and flow velocities attain extreme values (e.g. 5 m s^{-1} or more (Beltaos 1995)) capable of wide spread scour of the river bed and erosion of the river banks. The surge is accompanied by a pulse of suspended sediment resulting in very high concentrations for a short time (e.g. a few hours) which can be detrimental to certain fish species. The most extreme impact on fish of an ice-jam surge, however, is the stranding that may occur upstream of the initial jamming site. Here, the water level drops precipitously. If there was floodplain inundation while the jam was in place, as is often the case, many fish would find their way over that (new) area of the watercourse. The quick water level drop gives them little time to find their way back to the main river, and strands them. This type of event occurred during the February 1984 breakup on the lower Thames River, Ontario, when a major ice jam near the community of Prairie Siding released, leaving large numbers of fish stranded (Beltaos, unpublished data 1984).

Conclusions

The observed changes in habitat use seen in this study stress the importance of backwater habitats as areas of refuge for riverine fish during periods of flooding and ice break-up. This is one reason channelization, diking and similar land use activities, which remove these habitats, should be avoided. The shifts in habitat and the increased fish movements during high flows may have implications for the hydroelectric industry. Daily fluctuations in flow under peaking regimes may cause fish to constantly change their habitat and drastically increase their energy use during winter. Further research should be done to determine the influence of hydropeaking on fish during winter. The results of this study also emphasize the mobility of riverine fish during winter. Winter cannot be viewed as a season of quiescence for these animals which must respond appropriately to survive.

Chapter 3

Winter activity and diel activity patterns of three species of riverine fish

Introduction

Although several studies have described the activity and diel rhythms of salmonids in laboratory settings or in small experimental ponds, little is known about the activity of salmonids or other species in natural settings, especially in rivers. It would be valuable to be able to relate fish activity to attributes of their environment such as the availability of habitat types and changes in habitat brought about by ice formation or variations in water discharge and temperature. This information is important for determining ways of either maintaining habitats or optimally managing river reaches influenced by anthropogenic activities, such as those downstream of hydroelectric facilities.

Several laboratory studies have been done to estimate the diel activity rhythms of fish. The diel activity rhythms of brown trout exhibit marked seasonal changes and vary both within and between life stages (Eriksson 1978). One study attempted to determine the diel activity of fish using light beam interrupters in laboratory settings (Reynolds and Casterlin 1978). They found that eighty-nine percent of white sucker activity occurred during the dark at water temperatures ranging from 22°C to 27°C. Unfortunately, Reynolds and Casterlin (1978) did not provide the sizes of the white sucker studied. There is a problem basing conclusions about activity patterns on laboratory studies or on fish confined in cages in natural habitats. The fish cannot forage freely and they are not exposed to, and cannot respond to, the full range of natural stimuli which could alter their behaviour. This emphasizes the need for, and value of, observations in the wild.

Some researchers have used visual observations or inferences from catches in nets to examine activity and diel patterns. Emery (1973) made visual observations of white sucker in Ontario lakes. He noted that they fed during dusk and at night, but during the day swam in schools and did not feed. Spoor and Schloemer (1938) and Carlander and Cleary (1949) monitored gill net catches of white sucker over the diel period in two lakes. Spoor and Schloemer (1938) found that white sucker were netted most from 3-5 a.m. and 7-9 p.m. Carlander and Cleary (1949) found that white sucker were caught more often in deeper water during the day but were caught more often in shallower water during the night, suggesting a daily movement between the two habitats. Both studies draw deductions from gill net catches which may be biased if the fish can see and avoid the nets better by daylight in shallow water. Similarly, if gill nets intercept daily movements between deep and shallow water, inferred higher activity levels at dawn and dusk may be exaggerated.

The lack of data on fish activity in the wild is partially due to the difficulty in observing fish in their natural environments. Attempts have been made to quantify fish activity using conventional radiotelemetry by simply following the locations of fish. However, fish can maintain one location and still be actively swimming (Demers et al. 1996) so this method is inadequate for quantifying swimming activity. Using this technique, Clapp et al. (1990) found that adult brown trout living in a Michigan stream had a mean total range of 11,902 m during autumn-winter. They also found that brown trout had a mean displacement (the distance between successive telemetry observations done about once every 2 weeks) of 3,103 m during autumn-winter.

Attempts to quantify relative activity of fish have also been made by examining the fluctuations in the strength of signals emitted by conventional radiotelemetry transmitters as measured by an ammeter on a radio receiver. However, these fluctuations in signal strength are not calibrated to any certain swimming speed and can only be used as a rough estimate of when activity is occurring, not how much activity is occurring. Using this method Clapp et al. (1990) found that most foraging activity of riverine adult brown trout from June though August occurred under low light conditions between sunset and sunrise. In June, maximum daily activity occurred near 2200 hours, and corresponded to a time of high food abundance. These authors reported that activity seemed to vary with water temperature, being higher during colder periods of hot days. Young (1999) also used this method to study stream dwelling adult brown trout during the summer. He found that light intensity was negatively correlated with brown trout activity and that brown trout were primarily nocturnal. They were relatively quiescent during the day, surging in activity immediately after sunset and remaining relatively active during the night with a sharp decline at sunrise.

In the past ten years, electromyogram (EMG) transmitters have become available for quantifying field metabolic rates and the swimming activity of fish. This technique is especially valuable since it allows comparisons of the energetic demands of various conditions (Hinch et al. 1996) and it overcomes many of the difficulties involved with other techniques. However, relatively few studies have used this technique under natural field settings. Hinch et al. (1996) studied the swimming activity of sockeye salmon (*Oncorhynchus nerka*) at difficult passages of the Fraser River during upstream migrations, and Briggs and Post (1997a; 1997b) studied the swimming activity of EMG transmitter implanted rainbow trout (*Oncorhynchus mykiss*) in a small experimental pond during the summer and fall. They found that fish were primarily crepuscular and that changes in the metabolic cost of activity was strongly correlated with changes in mean water temperature. Although there are a few field studies done using EMG telemetry on fish (lake sturgeon (*Acipenser fulvescens*), McKinley and Power 1992; smallmouth bass (*Micropterus dolomieu*) and largemouth bass (*Micropterus salmoides*), Demers et al. 1996; lake trout (*Salvelinus namaycush*) Weatherley et al. 1996), no studies were found which used EMG transmitters to quantify the swimming activity of riverine fish during the winter or during non-migratory periods. Thus it was the goal of this study to quantify swimming activity and examine diel patterns of activity in a variety riverine species (brown trout, white sucker, and common carp) and determine how they are influenced by environmental fluctuations during winter.

I hypothesized that swimming activity would be positively correlated with water temperature and increases in water discharge. I also hypothesized that swimming activity would decrease when a solid surface ice cover formed on the river, and that diel patterns would vary among species with brown trout being nocturnal and white sucker and common carp being diurnal.

Study Area

The study was carried out along an 18 km reach of the Grand River between the town of Elora and the town of West Montrose (43°35'-43°41'N, 80°26'-80°29'W), Ontario. There is a barrier to upstream movement of fish at the town of Elora. The study area provides a variety of habitat types. The upper three kilometers runs through Elora Gorge, which is a high gradient (mean 5.3 m km^{-1}) channel cut through the limestone gorge with abundant bedrock substrate. The lower section is lower gradient (mean 1.4 m km^{-1}), the channel is less confined, and the river flows in a wide open valley.

During the 1997-98 season, weather was relatively mild as is indicated by water temperatures, (Fig. 3-1) and a solid surface ice only formed over a few small parts of the river for a week or two. During the 1998-99 season, air and water temperatures were lower (Fig. 3-1) and a solid surface ice cover formed on much of the river in late December and remained until early February. In the upper part of the study site, in the Elora Gorge, large quantities of anchor ice were commonly seen in the last half of December and the first week of January. A solid ice cover was present in the gorge for only about two weeks during January. Groundwater is not abundant in the study area, with only a few small springs being present.

There is a large diversity of fish species in the Grand River and white sucker and common carp naturally reproduce in the river. Brown trout are stocked yearly but very little if any natural reproduction is thought to occur. Although brook trout are native to the drainage they are rare in the study area.

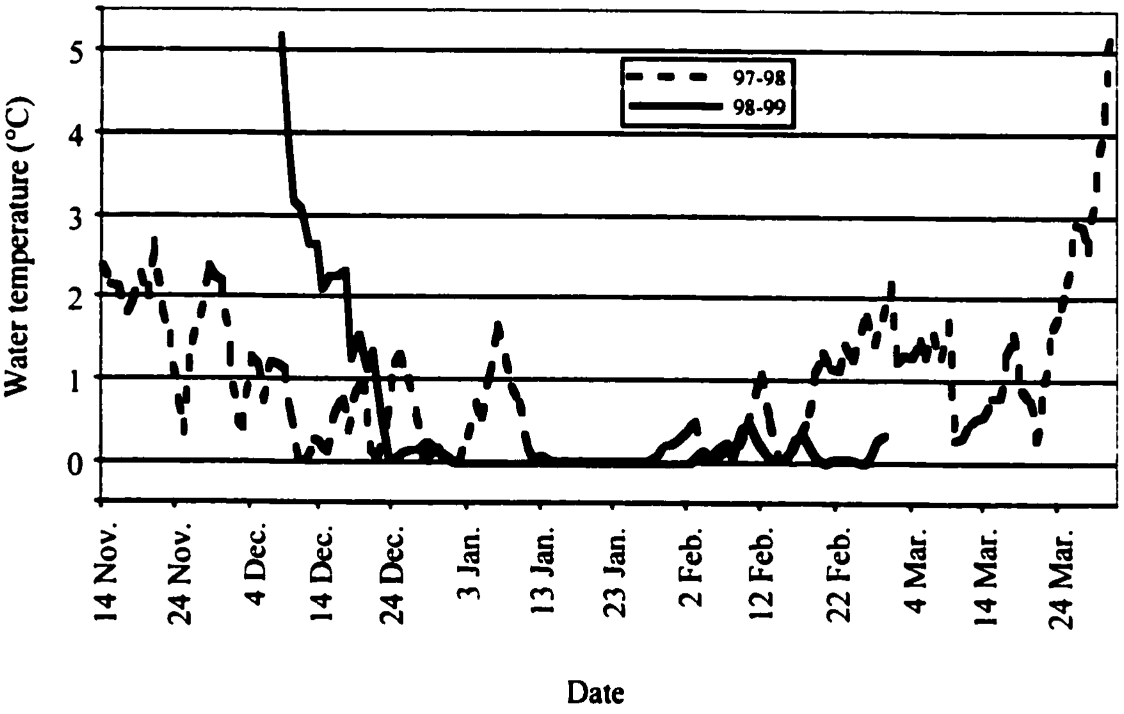

Figure 3-1. Water temperatures (°C) in the Grand River Ontario during the winters of 1997-98 and 1998-99.

Methods

Fish were implanted with electromyogram (EMG) radiotransmitters and monitored over two field seasons from fall 1997 to late winter 1999. During the first field season, nine adult brown trout were implanted between Nov. 17 and Dec. 29, 1997 (Table 3-1). These fish had a mean fork length of 480 mm (range 420-540) and a mean weight of 1291 g (range 881-1700). Nine adult common carp were implanted between Oct. 22 and Dec. 29, 1997 (Table 3-2). These fish had a mean fork length of 574 mm (range 505-630) and a mean weight of 3606 g (range 2473–4785). Nine adult white sucker were implanted between Oct. 21 and Dec. 30, 1997 (Table 3-2). These fish had a mean fork length of 430 mm (range 405-450) and a mean weight of 957 g (range 790–1095). Fish were monitored until the end of March 1998.

During the second field season, five adult brown trout were captured by electrofishing and implanted with transmitters Dec. 3-10, 1998 (Table 3-1). These fish had a mean fork length of 511 mm (range 430-570) and a mean weight of 1446 g (range 976–2007). Signals from these fish were logged until the end of February 1999.

Fish were collected by electrofishing and surgery was performed on the river bank near the site of capture. Implantation techniques were similar to Beddow and McKinley (1999) with the EMG transmitter surgically implanted into the intraperitoneal cavity. Fish were released at their capture point. The transmitters (Lotek Engineering Inc.) weighed 18 g in air, 8 g in water, and were 5cm long by 1.6 cm in diameter. They had two Teflon coated electrode wires which were anchored in the red muscle band and held in place by small (1 mm diameter, 5 mm long) 9 K gold rods, through which the end of the

Table 3-1. Fork length, weight, date of implantation with EMG radiotransmitters, and last day data were logged for brown trout from the Grand River, Ontario. Since EMG signals from fish were not constantly logged, the number of days that data were logged is also shown.

Fish	Length (mm)	Weight (g)	Implantation date	Last logged	Days of data
brown trout 1	450	930	11 Nov. 1997	19 Mar. 1998	44
brown trout 2	445	881	29 Dec. 1997	26 Mar. 1998	12
brown trout 3	455	1250	24 Dec. 1997	23 Mar. 1998	18
brown trout 4	500	1682	4 Dec. 1997	23 Mar. 1998	26
brown trout 5	501	1280	17 Nov. 1997	13 Mar. 1998	45
brown trout 6	505	1490	17 Nov. 1997	27 Dec. 1997	7
brown trout 7	540	1700	29 Dec. 1997	26 Mar. 1998	45
brown trout 8	420	956	29 Dec. 1997	22 Mar. 1998	39
brown trout 9	500	1449	4 Dec. 1997	26 Mar. 1998	32
brown trout 10	570	2007	8 Dec. 1998	6 Feb. 1999	56
brown trout 11	430	976	8 Dec. 1998	17 Feb. 1999	58
brown trout 12	490	1203	8 Dec. 1998	26 Feb. 1999	75
brown trout 13	560	1748	10 Dec. 1998	4 Feb. 1999	51
brown trout 14	505	1296	3 Dec. 1998	22 Feb. 1999	28

Table 3-2. Fork length, weight, date of implantation with EMG radiotransmitters, and last day data were logged for fish from the Grand River, Ontario. Since EMG signals from fish were not constantly logged, the number of days that data were logged is also shown.

Fish	Length (mm)	Weight (g)	Implantation date	Last logged	Days of data
white sucker 1	440	935	Nov. 5, 1997	Jan. 24, 1998	29
white sucker 2	430	967	Nov. 11, 1997	Mar. 23, 1998	46
white sucker 3	420	986	Dec. 30, 1997	Mar. 8, 1998	18
white sucker 4	450	1095	Dec. 30, 1997	Mar. 27, 1998	14
white sucker 5	410	935	Dec. 17, 1997	Jan. 11, 1998	11
white sucker 6	440	950	Dec. 30, 1997	Mar. 27, 1998	14
white sucker 7	435	996	Nov. 5, 1997	Jan. 2, 1998	20
white sucker 8	405	790	Oct. 21, 1997	Dec. 21, 1997	11
white sucker 9	440	963	Oct. 23, 1997	Mar. 4, 1998	42
common carp 1	560	2670	Oct. 26, 1997	Mar. 23, 1998	51
common carp 2	620	4785	Oct. 26, 1997	Mar. 30, 1998	40
common carp 3	505	2473	Dec. 29, 1997	Mar. 30, 1998	20
common carp 4	560	3060	Oct. 26, 1997	Mar. 30, 1998	40
common carp 5	570	3734	Dec. 23, 1997	Apr. 3, 1998	33
common carp 6	595	4580	Oct. 26, 1997	Mar. 30, 1998	34
common carp 7	565	3430	Oct. 26, 1997	Mar. 23, 1998	52
common carp 8	630	4560	Oct. 26, 1997	Mar. 2, 1998	37
common carp 9	565	3160	Oct. 22, 1997	Dec. 11, 1997	10

electrode was threaded. The electrodes feed electrical impulses into the transmitter which are emitted when the fish perform non-burst swimming. Since the electrodes were not placed in the white muscle, burst swimming was not quantified with these experiments. The radiotransmitter stores the electrical impulses in a capacitor and when this was full, the transmitter emitted a signal. Thus, when fish swam faster, signals were emitted more frequently by the transmitter (see Beddow and McKinley (1999) for further details). A datalogging radio receiver (Lotek Model SRX-400 with W20 firmware, Lotek Engineering Inc.) was used to receive and store radio signals, and the receiver software recorded the amount of time between sequential signals, the time each signal is emitted and the strength of the signal.

There are several limitations to the use of EMG telemetry. Transmitters and receivers are expensive, thus sample sizes are often low. Radio receivers can only pick up transmitter signals within a limited range, usually 400 – 800 m. These reception ranges can vary with depth and conductivity of water, the topography of the study area, and with different types of surface ice. If implanted fish are in widespread areas, either more radio receivers are needed to log signals, or fish can only be monitored occasionally. To have a long term, detailed record of fish activity in a field situation where fish can and do move freely, either samples sizes must be limited, or many receivers are needed. This is why only five brown trout were observed during the 1998-99 field season.

Also, batteries which power the transmitters are often undependable. Several of the radiotransmitters failed prematurely. This was preceded by the failure of the transmitter to emit pulsed signals and instead it emitted a constant squeal. The failure of several transmitters is one of the reasons that the number of days that data were recorded from fish was not constant among implanted fish (see Table 3-1 and 3-2).

Although signals emitted from EMG radiotransmitters are correlated with swimming activity (Beddow and McKinley 1999), EMG signals alone can only provide a relative index of swimming activity. Since each EMG radiotransmitter has different specifications (different pulse rates at resting and at a given swimming speed) and the same radiotransmitter will even have different pulse characteristics in different fish (R. Brown and T. Beddow unpublished data) EMG data cannot accurately be grouped among fish unless the pulse rates of the transmitters are known at resting and at several swimming speeds. When individual fish implanted with EMG transmitters are swum at known speeds, however, EMG signal frequencies can be calibrated against speed and used to determine swimming speed of the fish in a field setting.

EMG signals were correlated to swimming speed for three brown trout, one white sucker and two common carp following the 1997-98 season and for two brown trout following the 1998-99 season. Fish were recaptured by electroshocking at the end of March 1998 or the end of February 1999 before the batteries expired in the radiotransmitters. These fish were transported to the laboratory and swum in a Blaska respirometer (described by Smith and Newcomb (1970)) at several known speeds. EMG signals were logged while fish were swimming steadily at each speed increment. Regression analysis was used to calibrate the EMG signals from each transmitter to swimming speed and used to estimate the swimming speeds of the fish while in the wild.

Oxygen consumption was also quantified for two brown trout recaptured from the field in February 1999. Fish were not fed for at least 24 h before experiments were done or for the entire time they were held in the laboratory. Water temperatures were maintained between 1.7 and 2.7°C and fish were acclimated to the swim chamber for at least 30 min before tests were done. These fish were swum at several increasing speed increments in a 120 liter Blazka type swim chamber while oxygen consumption was quantified and EMG signals were logged. Dissolved oxygen concentrations in the respirometer were measured in a parallel external circuit where water was pumped out of the respirometer and returned to it after flowing over the electrode of a YSI oxygen meter (Yellow Springs, OH). Oxygen consumption was adjusted to a standard body mass of 1 kg using the mass exponent of 0.8 (Saunders 1963). A mean of the EMG signals for the trial period was related to oxygen consumption using regression analysis. Every attempt was made to avoid stressing the fish during these experiments to avoid overestimation of the oxygen consumption.

Field EMG signals were transformed into field metabolic rate (FMR) as did Briggs and Post (1997a). The laboratory derived regression equations for oxygen consumption were used to determine the FMR from EMG signals collected in the field over the winter. Results were expressed in mg O_2 kg^{-1} h^{-1} for data averaged over each half hour period.

Swimming activity was also averaged over 0.5 h increments as did Briggs and Post (1997a; 1997b), since fish may have daily activity patterns. This was done for the entire winter. To determine if swimming activity differed when different ice conditions existed, data for each individual fish under different conditions were compared using a repeated measures ANOVA. If there was an overall difference among groups, differences between groups were compared using a paired *t*-test. A repeated measures test was used since activity data for each individual fish was compared within individual under different ice conditions.

To determine when swimming activity was highest, the mean activity rate for all 0.5 h periods was averaged for day, night, and twilight. Twilight was considered to be the first two and the last two hours of the day when light could be measured on a light intensity datalogger similar to Young (1999). Data for each fish were compared using an ANOVA to establish whether swimming activity differed significantly under different light conditions (day, twilight, night).

Since only the mean of the data over the whole season, or over periods with similar ice cover, was used for each 0.5 h period, much of the short term variability was unavoidably excluded from these analyses. For this reason, statistical test results were used principally as a guide for interpretation.

For the fish that had EMG signals calibrated to swimming speed in the laboratory, the total distances swum could be compared among day, night, and twilight. This was accomplished by multiplying the mean swimming speed (in m s^{-1}) for each 0.5 h period by 1800 (the number of seconds in each 0.5 h period) to determine the actual distance swum during each 0.5 h. The sums of the distances swum in each 0.5 h period were compared among day, night and twilight.

Simple linear regression was used to determine if daily mean swimming activity was related to daily mean water temperature or water discharge. EMG data were only used if at least six hours of data were collected during a day. If fish showed a diel pattern in swimming activity, data from all periods which showed a significant ($P<0.05$)

difference from another period were used. To determine an overall response of fish activity to changing water temperatures or discharge, an attempt was made to group the data across individuals within a species. Activity for each individual was placed on a scale from 1(least active day of the winter) to 100 (most active day) and regression analysis was performed with these values for all individuals combined versus daily water discharge or temperature.

Results

Diel Patterns

None of the three species of fish studied displayed a conspicuous daily rhythm of activity (Fig. 3-2 – 3-5). About one third (36%) of the riverine brown trout (5 of 14) studied were arrhythmic, showing no significant ($P>0.05$) difference in mean swimming activity among day, twilight, or night (Table 3-3). Twilight was the only period which usually had the highest activity rates or was not significantly ($P>0.05$) lower than any other period of the day. Four of the nine brown trout which were not arrhythmic (29% of all brown trout) had significantly ($P<0.05$) lower mean swimming activity rates at night than during day or twilight. Two brown trout (14% of all brown trout) had significantly ($P<0.05$) lower mean swimming activity rates during day than during night or twilight. The three remaining brown trout either had highest rates at night, and/or twilight.

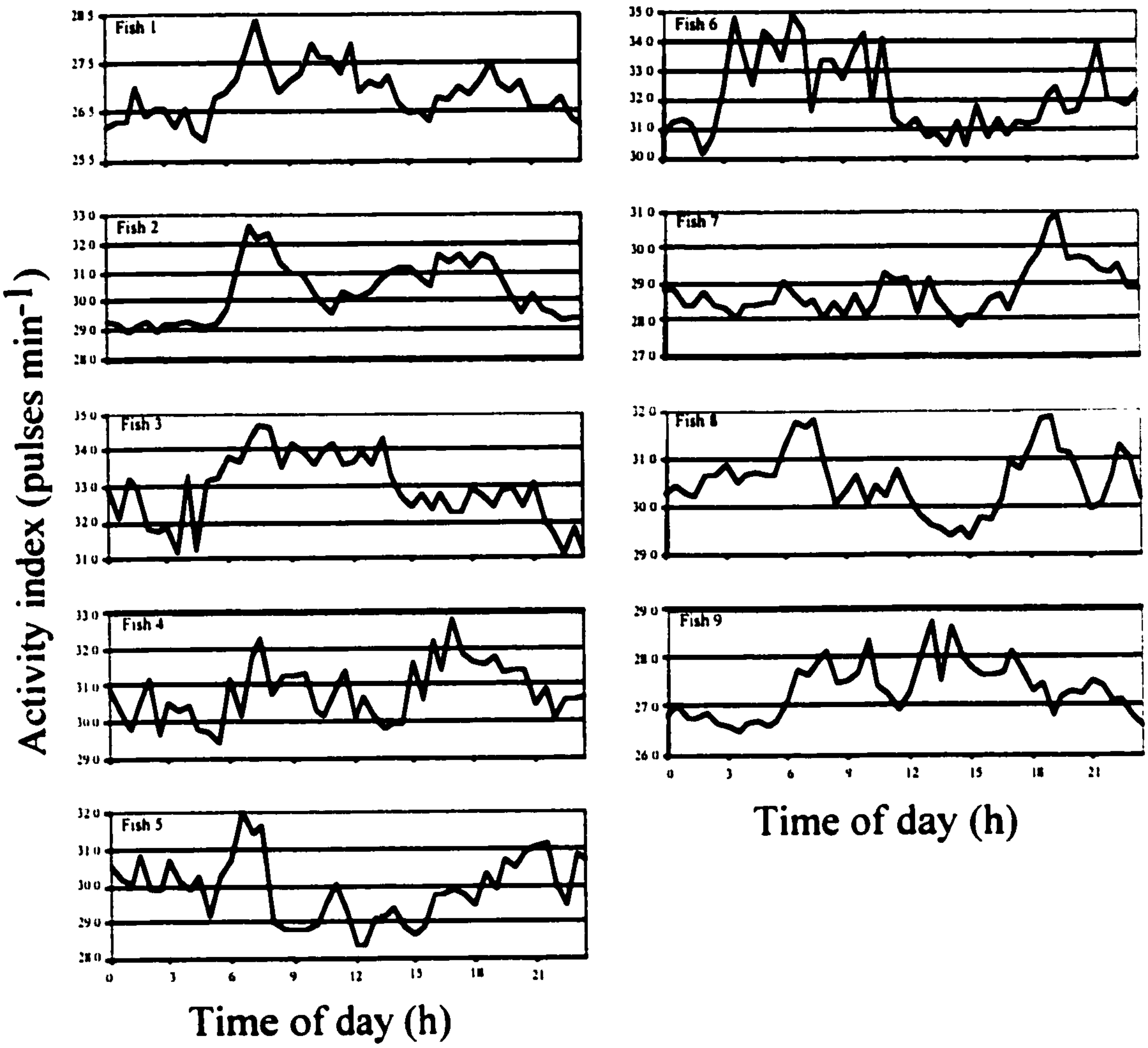

Figure 3-2. Diel activity patterns (expressed as an activity index) of nine brown trout implanted with EMG radiotransmitters during the winter of 1997-98 in the Grand River, Ontario. Periods lower on the activity index indicate lower swimming activity.

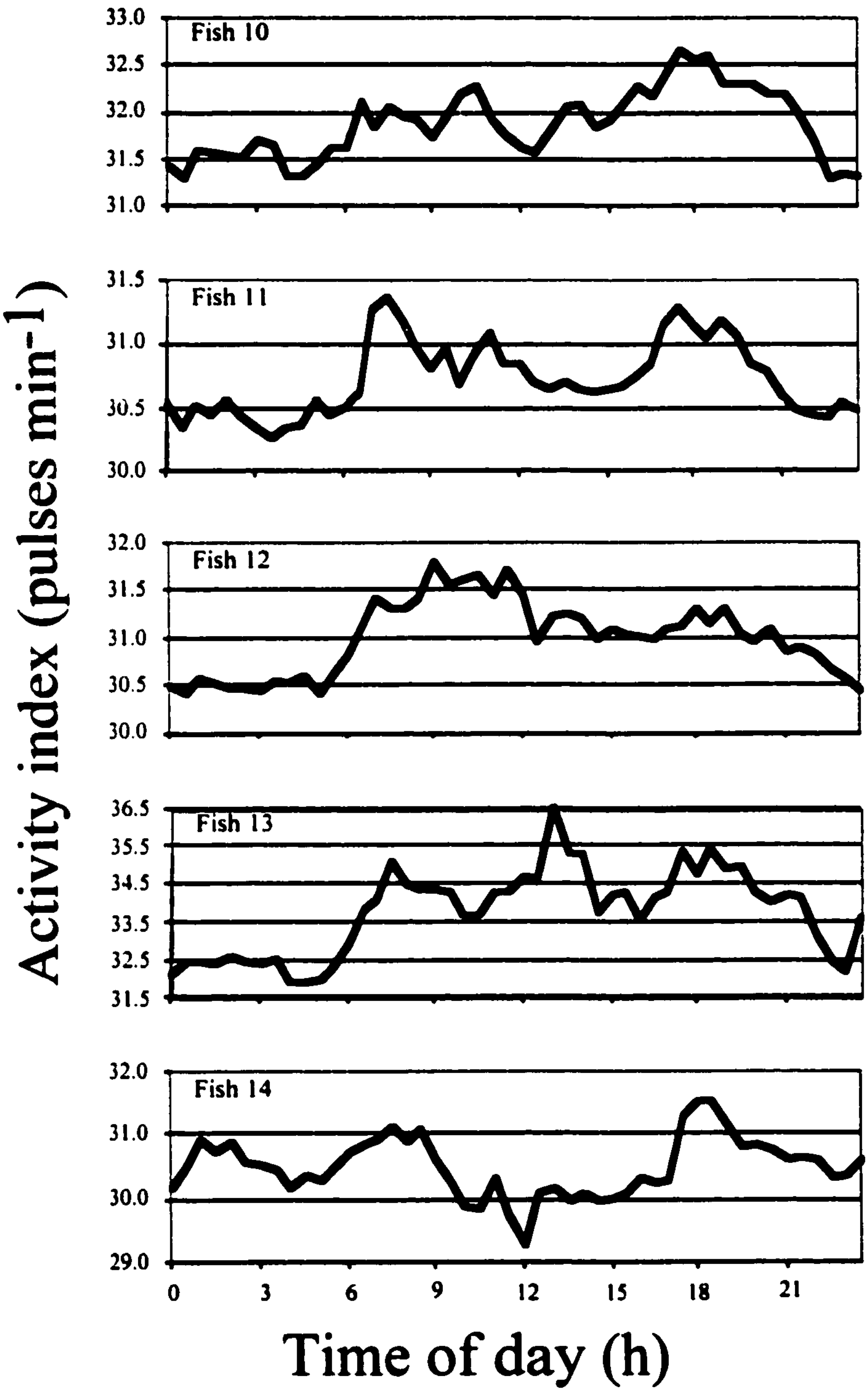

Figure 3-3. Diel activity patterns (expressed as an activity index) of five brown trout implanted with EMG radiotransmitters during the winter of 1998-99 in the Grand River, Ontario. Periods lower on the activity index indicate lower swimming activity.

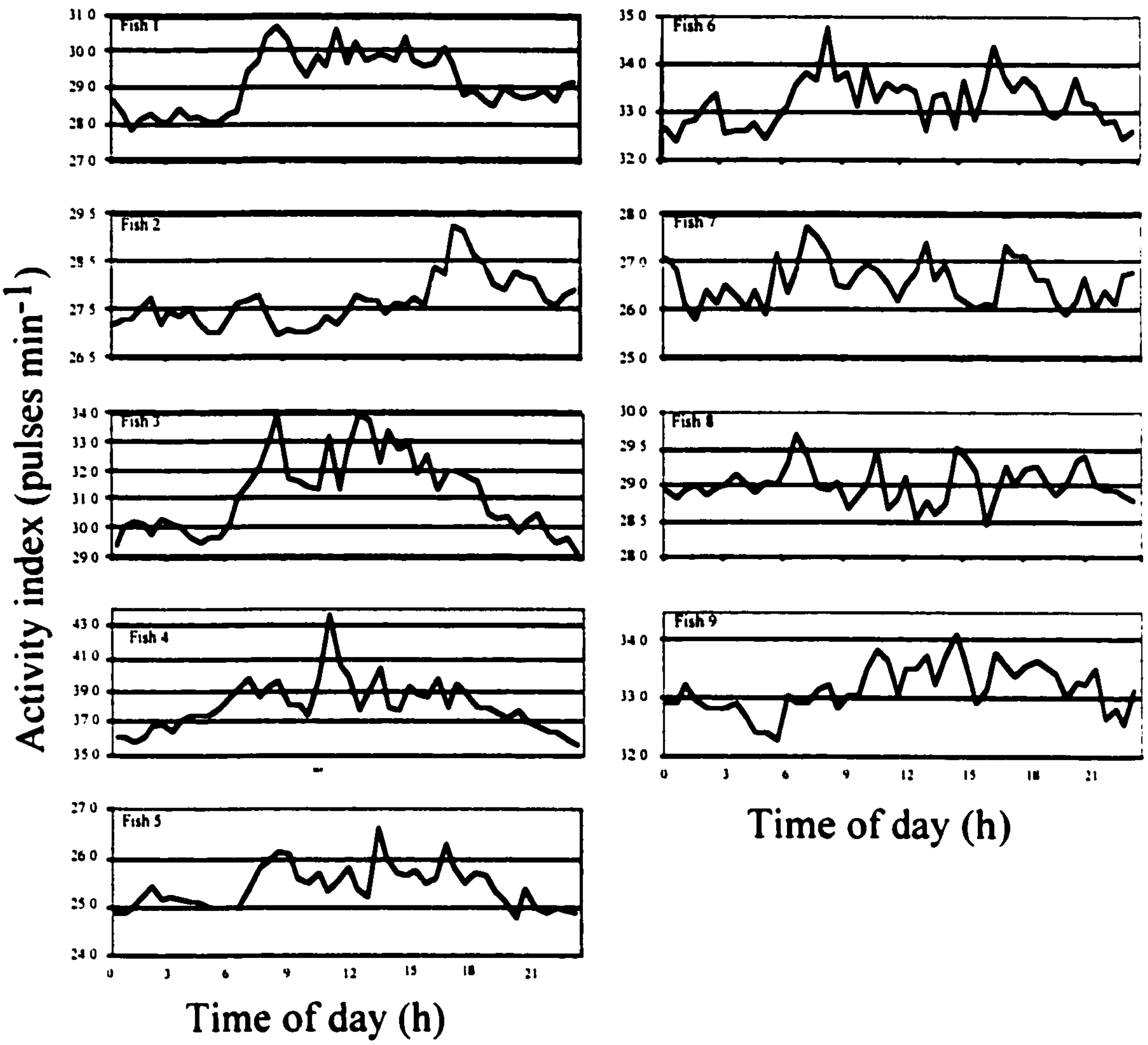

Figure 3-4. Diel activity patterns (expressed as an activity index) of nine white sucker implanted with EMG radiotransmitters during the winter of 1997-98 in the Grand River, Ontario. Periods lower on the activity index indicate lower swimming activity.

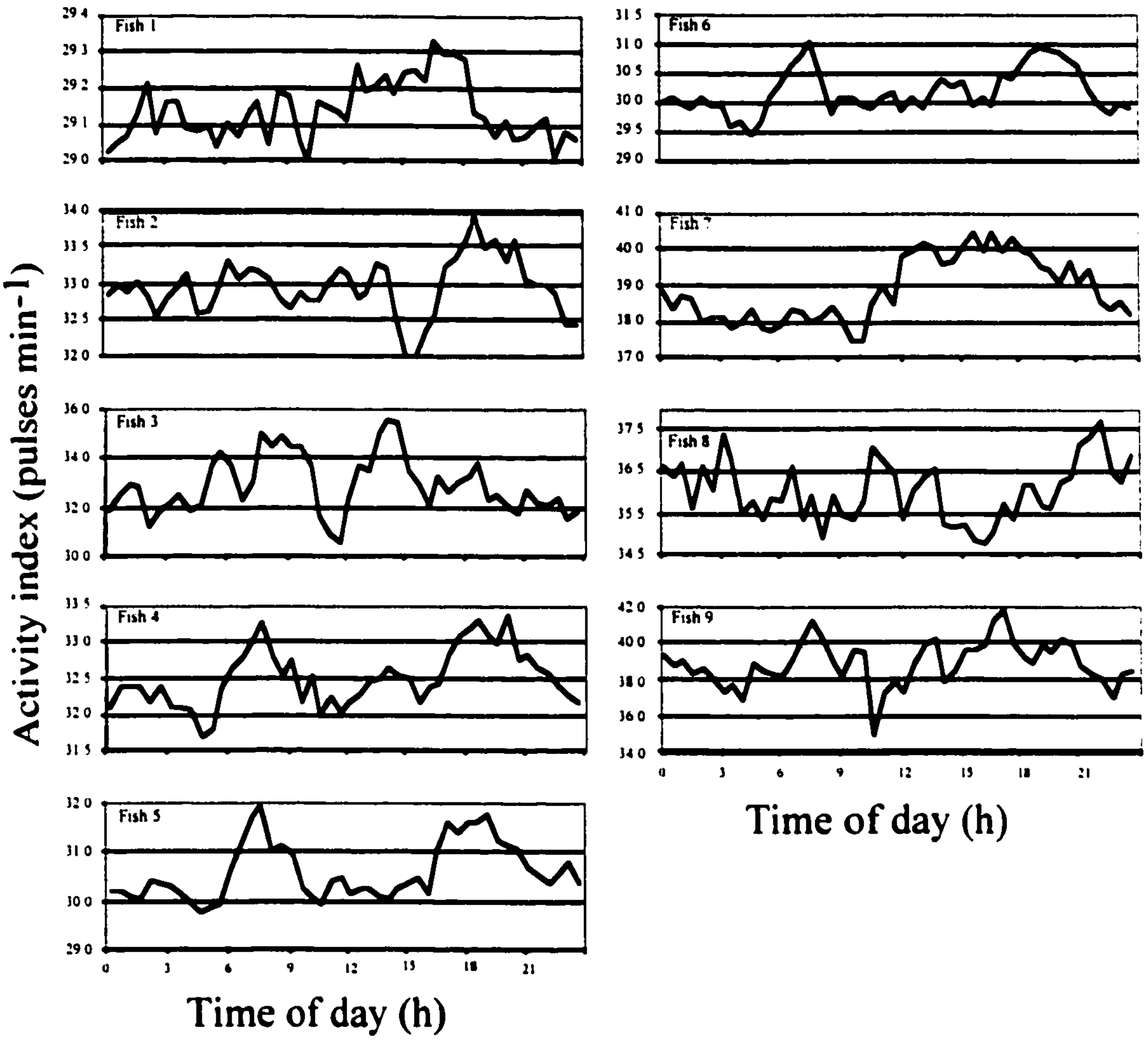

Figure 3-5. Diel activity patterns (expressed as an activity index) of nine common carp implanted with EMG radiotransmitters during the winter of 1997-98 in the Grand River, Ontario. Periods lower on the activity index indicate lower swimming activity.

Table 3-3. Mean swimming activity (expressed as an activity index (pulses min^{-1}) ± SD) of brown trout during day, twilight, and night during the winters of 1997-98 and 1998-99. Periods lower on the activity index indicate less swimming activity. When EMG signals were calibrated to swimming speed, the percentage of total activity was calculated and is shown in brackets. Values along a row with a letter in common are not significantly different (alpha = 0.05).

Fish	Day	Twilight	Night
		1997-98 season	
1	26.4 ± 1.2 z	26.9 ± 0.5 z	26.7 ± 0.7 z
2	30.0 ± 0.9 z	31.3 ± 0.6 y	29.7 ± 1.0 z
3	33.4 ± 0.6 z	33.3 ± 1.2 z	32.2 ± 0.9 y
4	30.9 ± 1.3 z	31.3 ± 0.5 z	30.5 ± 0.9 z
5	28.7 ± 0.6 z	29.4 ± 0.7 zy	30.0 ± 0.8 y
6	31.9 ± 1.4 z	32.0 ± 1.2 z	32.0 ± 1.1 z
7	28.3 ± 0.5 z (26)	28.5 ± 0.4 z (13)	29.1 ± 0.8 y (60)
8	29.8 ± 0.5 z (23)	30.7 ± 0.9 y (16)	30.8 ± 0.7 y (61)
9	27.4 ± 0.6 z (33)	27.9 ± 0.3 z (21)	27.0 ± 0.4 y (46)
		1998-99 season	
10	31.8 ± 0.4 z	32.1 ± 0.2 z	32.0 ± 0.7 z
11	30.9 ± 0.3 z (34)	31.0 ± 0.3 z (18)	30.6 ± 0.3 y (49)
12	31.2 ± 0.4 z	31.3 ± 0.2 z	30.8 ± 0.3 y
13	34.2 ± 1.5 z	34.3 ± 0.5 z	33.4 ± 1.2 z
14	30.0 ± 0.3 z (26)	30.6 ± 0.4 y (16)	30.8 ± 0.5 y (58)

For the fish which had EMG signals calibrated to swimming speed, quantification of the total amount of swimming activity during day, twilight and night was possible. Although all three species exhibited no consistent diel pattern; the length of the winter night meant that the largest amount of activity occurred during the night (Table 3-3, 3-4 and 3-5). The lowest percentage of total activity occurred during the brief four hour twilight period, followed by the relatively short winter daylight period. The proportion of activity in each of these periods was fairly consistent among brown trout and common carp.

Diel swimming activity patterns of white sucker were generally arrhythmic or showed the least activity during night (Fig. 3-4). Four of the nine white suckers (fish 6-9) were arrhythmic, showing no significant ($P>0.05$) difference in activity among day, night or twilight (Table 3-4). Another four of the nine white suckers (fish 1, 3, 4, 5) had significantly lower ($P<0.05$) activity during night than either day or twilight, or both. Three of these white suckers (fish 1, 3, 4) had similar patterns, being significantly ($P<0.05$) more active during both day and twilight as compared to night, while not having significant ($P>0.05$) differences between day and twilight. The fourth of these white sucker (fish 5) had higher activity rates during both day and twilight than night, but the difference between day and night was not significant ($P>0.05$). Only one white sucker (fish 2) had significantly ($P<0.05$) higher swimming activity during night than day.

Table 3-4. Mean swimming activity (expressed as an activity index (pulses min^{-1}) ± SD) of white sucker during day, twilight, and night in the winter of 1997-98. Periods lower on the activity index indicate less swimming activity. When EMG signals were calibrated to swimming speed, the percentage of total activity was calculated and is shown in brackets. Values along a row with a letter in common are not significantly different (alpha = 0.05).

Fish	Day	Twilight	Night
		1997-98 season	
1	29.7 ± 0.6 z	30.1 ± 0.4 z	28.6 ± 0.6 y
2	27.1 ± 0.7 z	27.8 ± 0.6 zy	27.9 ± 0.8 y
3	32.1 ± 1.2 z	32.3 ± 0.7 z	30.5 ± 1.0 y
4	39.2 ± 1.5 z (38)	39.0 ± 0.5 z (18)	36.9 ± 0.8 y (44)
5	25.5 ± 0.5 zy	25.8 ± 0.2 z	25.2 ± 0.5 y
6	33.2 ± 0.4 z	33.7 ± 0.3 z	33.3 ± 1.3 z
7	26.7 ± 0.3 z	26.6 ± 0.7 z	26.5 ± 0.4 z
8	28.9 ± 0.3 z	29.0 ± 0.3 z	29.1 ± 0.3 z
9	32.6 ± 1.6 z	33.3 ± 0.3 z	33.2 ± 0.7 z

Table 3-5. Mean swimming activity (expressed as an activity index (pulses min^{-1}) ± SD) of common carp during day, twilight, and night in the winter of 1997-98. Periods lower on the activity index indicate less swimming activity. When EMG signals were calibrated to swimming speed, the percentage of total activity was calculated and is shown in brackets. Values along a row with a letter in common are not significantly different (alpha = 0.05).

Fish	Day	Twilight	Night
		1997-98 season	
1	29.0 ± 0.2 z (27)	29.2 ± 0.5 zy (18)	29.2 ± 0.2 y (55)
2	32.2 ± 0.8 z (28)	32.4 ± 0.4 z (17)	32.8 ± 0.9 z (56)
3	33.1 ± 1.6 z	33.6 ± 0.9 z	32.6 ± 1.7 z
4	32.3 ± 0.3 z	32.7 ± 0.3 z	32.6 ± 0.5 z
5	29.4 ± 1.1 z	31.1 ± 0.6 zy	31.6 ± 2.7 y
6	29.7 ± 0.7 z	30.3 ± 0.3 zy	30.3 ± 0.6 y
7	37.3 ± 2.8 z	38.8 ± 1.0 zy	39.7 ± 2.6 y
8	35.2 ± 1.9 z	35.2 ± 0.5 zy	36.3 ± 0.7 y
9	38.3 ± 1.5 z	40.1 ± 0.8 y	38.7 ± 1.0 z

Similar to brown trout and white sucker, about a third (3 of 9, 33%) of the common carp studied were arrhythmic (Fig. 3-5). Most common carp which showed a significant ($P<0.05$) difference among day, twilight, and night (6 of 9, 67%), were less active during the day than either twilight or night (Table 3-5). Five common carp (56%; Number 1, 5, 6, 7, and 8) had significantly ($P<0.05$) lower activity rates during day than during night. None of these five common carp had significant ($P<0.05$) differences in activity rates between day and twilight or twilight and night. One common carp (Number 9) had significantly ($P<0.05$) lower activity rates during both the day and night than during twilight. Three common carp (Number 2, 3,and 4) had no significant ($P>0.05$) differences among diel periods.

Several common carp had two distinct peaks in swimming activity during the 24 hours which occurred during both the twilight and night periods. Common carp 4, 5, 6, and 9, had peaks in activity during both the morning and evening, while being less active during the late night, early morning, and afternoon. Two common carp (number 1 and 7) had higher levels of activity in the afternoon and early evening than during the rest of the 24 hour period. Three common carp (Number 2, 3 and 9) had large decreases in activity during the day, with activity dipping below any other point in the 24 hours.

Swimming activity related to ice conditions

Since there was a period of solid surface ice cover on the river during the 1998-99 season, a comparison could be made between diel activity during the ice free and ice covered periods. Only brown trout, however, were studied during this field season. Diel patterns appeared to change in response to surface ice cover in three (brown trout 10, 11, and 14) out of five brown trout (Figure 3-6). Before a solid surface ice cover formed, two of these three brown trout had significantly (*P*<0.05) higher activity rates during night than day or twilight, while the other showed no significant (*P*>0.05) differences among time periods. After surface ice cover formed, the amount of activity at night, relative to day and twilight, decreased in all three of these brown trout. After the surface ice cover was gone, activity became more randomly distributed among day, night, and twilight with no clear trend present. Of the two brown trout that did not show changes in diel patterns with changing ice conditions, one consistently had lower activity at night than during day and twilight (fish 12). The other showed no significant (*P*>0.05) differences in activity among day, night or twilight throughout the entire winter (fish 13).

In addition to changes in diel patterns, the general activity levels of brown trout also varied with the types of river ice present. All five brown trout tracked during the 98-99 season showed a significant (*P*<0.05) difference in swimming activity between different ice conditions (Table 3-6). As freeze up occurred, most brown trout were in fairly low gradient sections of the river and were exposed to little if any anchor ice. One brown trout, however was exposed to about a two week period of multiple anchor ice events. This fish had a significantly (*P*<0.05) higher level of swimming activity during the period when anchor ice was present than before anchor ice formed, or than at any other period during winter.

The swimming activity levels of most (4 of 5; 80%) brown trout were significantly (*P*<0.05) changed by the presence of a solid surface ice cover (Table 3-5).

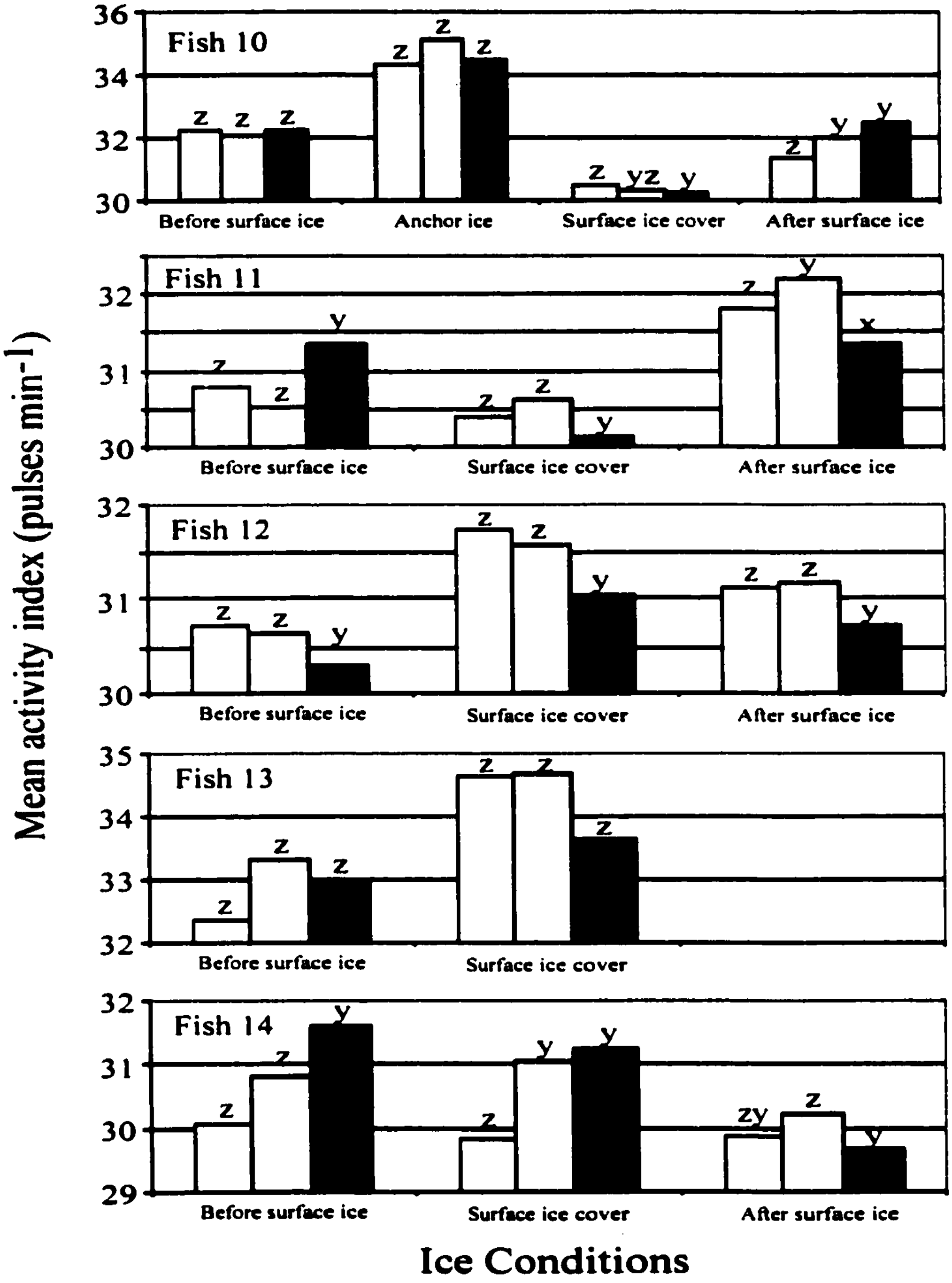

Figure 3-6. Mean activity levels (expressed as an activity index) of five brown trout implanted with EMG radiotransmitters during the winter of 1998-99 under varying ice conditions and daylight periods. Day is signified as light bars, twilight as gray, and night as dark. Periods lower on the activity index indicate lower swimming activity. Values within a group with a letter in common are not significantly different (alpha = 0.05).

Table 3-6. Mean swimming activity (expressed as an activity index (pulses min^{-1}) ± SE) of brown trout before a solid surface ice cover formed, during a period of multiple anchor ice events, while there was a solid surface ice cover, and after the surface ice cover was gone during the winter of 1998-99. Periods lower on the activity index indicate less swimming activity. Values along a row with a letter in common are not significantly different (alpha = 0.05).

Fish	Before ice cover	anchor ice	ice covered	after ice cover
10	31.8 ± 0.1 z w	34.5 ± 0.1 y	30.3 ± 0.03 x	31.8 ± 0.1 w
11	31.0 ± 0.1 z		30.2 ± 0.04 y	31.6 ± 0.1 x
12	30.4 ± 0.1 z		30.8 ± 0.1 y	31.2 ± 0.1 x
13	32.6 ± 0.2 z		33.6 ± 0.1 y	NA
14	31.1 ± 0.1 z		30.8 ± 0.1 z	29.7 ± 0.1 y

However, there was no consistent trend in the direction of this change. Half of the fish which showed a difference were more active when under a solid surface ice cover and the other half were less active. One brown trout was lost near the time the surface ice melted; the remainder had significantly ($P < 0.05$) different swimming activity levels after surface ice melted or broke up as compared to the period of solid surface ice cover. Most brown trout (3 of 4; 75%) became more active.

There was no consistent difference in swimming activity before ice cover as compared to after ice cover was gone. Two (50%) of the brown trout had higher, and one had lower activity post ice cover, while one showed no significant ($P > 0.05$) difference between pre and post ice cover swimming activity levels.

Swimming activity related to water discharge and temperature

The influence of water discharge and temperature on fish activity varied by fish species (Tables 3-7 - 3-10). Water discharge appeared to have little influence on swimming activity of brown trout. Although 4 of 14 (29%) brown trout had a significant ($P < 0.05$) relationship between mean daily water discharge and mean daily swimming activity, there was no consistency in the type of relationship (Figure 3-7). About half (8 of 14; 57%) of the brown trout had a negative relationship between water discharge and activity, while the remainder had a positive relationship. When data were normalized and grouped, however, there was a significant ($P < 0.05$) positive relationship between water discharge and swimming activity, but this was a very weak relationship ($R^2 = 0.03$; Fig. 3-8).

Table 3-7. Range of water discharge and characteristics of the relationship (determined by simple linear regression) between mean daily swimming activity and mean daily water discharge for brown trout implanted with EMG radiotransmitters from the Grand River, Ontario.

Fish	discharge range	Slope	R^2	P	N
brown trout 1	4.4 – 65.4	Negative	0.01	0.53	39
brown trout 2	5.8 – 76.2	Negative	0.07	0.46	9
brown trout 3	5.1 – 65.4	Positive	0.00	0.85	18
brown trout 4	4.7 – 65.4	Negative	0.01	0.67	22
brown trout 5	4.7 – 44.8	Positive	0.06	0.24	25
brown trout 6	5.6 – 9.0	Positive	0.02	0.75	7
brown trout 7	4.7 – 87.4	Positive	0.11	0.08	29
brown trout 8	4.7 – 67.4	Positive	0.05	0.35	21
brown trout 9	4.4 – 87.4	Positive	0.12	0.08	27
brown trout 10	1.5 – 6.9	Negative	0.02	0.31	56
brown trout 11	1.4 – 14.0	Positive	0.40	0.01	56
brown trout 12	1.5 – 13.3	Positive	0.01	0.53	65
brown trout 13	1.5 – 6.9	Negative	0.08	0.05	47
brown trout 14	1.5 – 13.3	Negative	0.18	0.06	20

Table 3-8. Range of water discharge and characteristics of the relationship (determined by simple linear regression) between mean daily swimming activity and mean daily water discharge for white sucker and common carp implanted with EMG radiotransmitters from the Grand River, Ontario.

Fish	discharge range	Slope	R^2	P	N
white sucker 1	4.7 – 87.4	Negative	0.10	0.12	23
white sucker 2	4.7 – 87.4	Negative	0.02	0.46	33
white sucker 3	6.2 – 87.4	Positive	0.00	0.88	15
white sucker 4	6.2 – 151.0	Negative	0.00	0.90	11
white sucker 5	4.4 – 87.4	Negative	0.89	0.01	8
white sucker 6	5.2 – 151.0	Negative	0.14	0.19	14
white sucker 7	4.7 – 9.2	Negative	0.11	0.25	14
white sucker 8	4.9 – 8.9	Positive	0.49	0.02	10
white sucker 9	4.7 – 87.4	Negative	0.02	0.37	36
common carp 1	4.7 – 87.4	Negative	0.02	0.44	38
common carp 2	4.9 - 205.0	Negative	0.13	0.04	33
common carp 3	5.1 – 87.4	Negative	0.13	0.12	19
common carp 4	4.9 – 205.0	Negative	0.20	0.01	35
common carp 5	4.7 – 67.4	Negative	0.06	0.24	24
common carp 6	4.9 – 205.0	Negative	0.30	0.01	25
common carp 7	4.7 – 87.4	Negative	0.03	0.33	35
common carp 8	4.7 – 87.4	Negative	0.01	0.69	18
common carp 9	4.9 – 8.9	Negative	0.00	0.98	5

Table 3-9. Range of water temperature and characteristics of the relationship (determined by simple linear regression) between mean daily swimming activity and mean daily water temperature for brown trout implanted with EMG radiotransmitters from the Grand River, Ontario.

Fish	Temperature range	Relationship	R^2	P	N
brown trout 1	0.0 – 1.6	Negative	0.23	0.00	39
brown trout 2	0.0 – 1.8	Negative	0.35	0.09	9
brown trout 3	0.0 – 1.8	Positive	0.04	0.42	18
brown trout 4	0.0 – 1.6	Positive	0.33	0.01	22
brown trout 5	0.0 – 1.5	Negative	0.23	0.02	25
brown trout 6	0.3 – 1.2	Positive	0.07	0.55	7
brown trout 7	0.0 – 2.9	Negative	0.12	0.06	29
brown trout 8	0.0 – 2.4	Negative	0.03	0.47	21
brown trout 9	0.0 – 2.2	Positive	0.08	0.15	27
brown trout 10	0.0 – 3.1	Negative	0.00	0.84	56
brown trout 11	0.0 – 3.9	Positive	0.06	0.06	56
brown trout 12	0.0 – 3.2	Negative	0.14	0.01	65
brown trout 13	0.0 – 3.2	Negative	0.05	0.14	47
brown trout 14	0.0 – 3.2	Positive	0.06	0.29	20

Table 3-10. Range of water temperature and characteristics of the relationship (determined by simple linear regression) between mean daily swimming activity and mean daily water temperature for white sucker and common carp implanted with EMG radiotransmitters from the Grand River, Ontario.

Fish	Temperature range	Relationship	R^2	P	N
white sucker 1	0.0 – 2.4	Negative	0.00	0.80	23
white sucker 2	0.0 – 2.7	Positive	0.00	0.78	33
white sucker 3	0.0 – 1.6	Negative	0.56	0.01	15
white sucker 4	0.4 – 2.9	Negative	0.06	0.47	8
white sucker 5	0.0 – 1.2	Negative	0.43	0.08	24
white sucker 6	0.0 – 2.9	Negative	0.67	0.01	14
white sucker 7	0.0 – 2.4	Positive	0.10	0.26	14
white sucker 8	0.1 – 2.4	Negative	0.08	0.43	10
white sucker 9	0.0 – 2.4	Negative	0.09	0.08	36
common carp 1	0.0 – 2.4	Negative	0.13	0.03	38
common carp 2	0.0 – 2.6	Positive	0.08	0.12	33
common carp 3	0.0 – 2.9	Negative	0.31	0.01	19
common carp 4	0.0 – 2.8	Negative	0.02	0.44	35
common carp 5	0.0 – 1.6	Negative	0.33	0.01	24
common carp 6	0.0 – 2.8	Negative	0.19	0.03	25
common carp 7	0.0 – 2.4	Negative	0.05	0.18	35
common carp 8	0.0 – 2.4	Negative	0.03	0.52	18
common carp 9	1.2 – 2.4	Positive	0.50	0.18	5

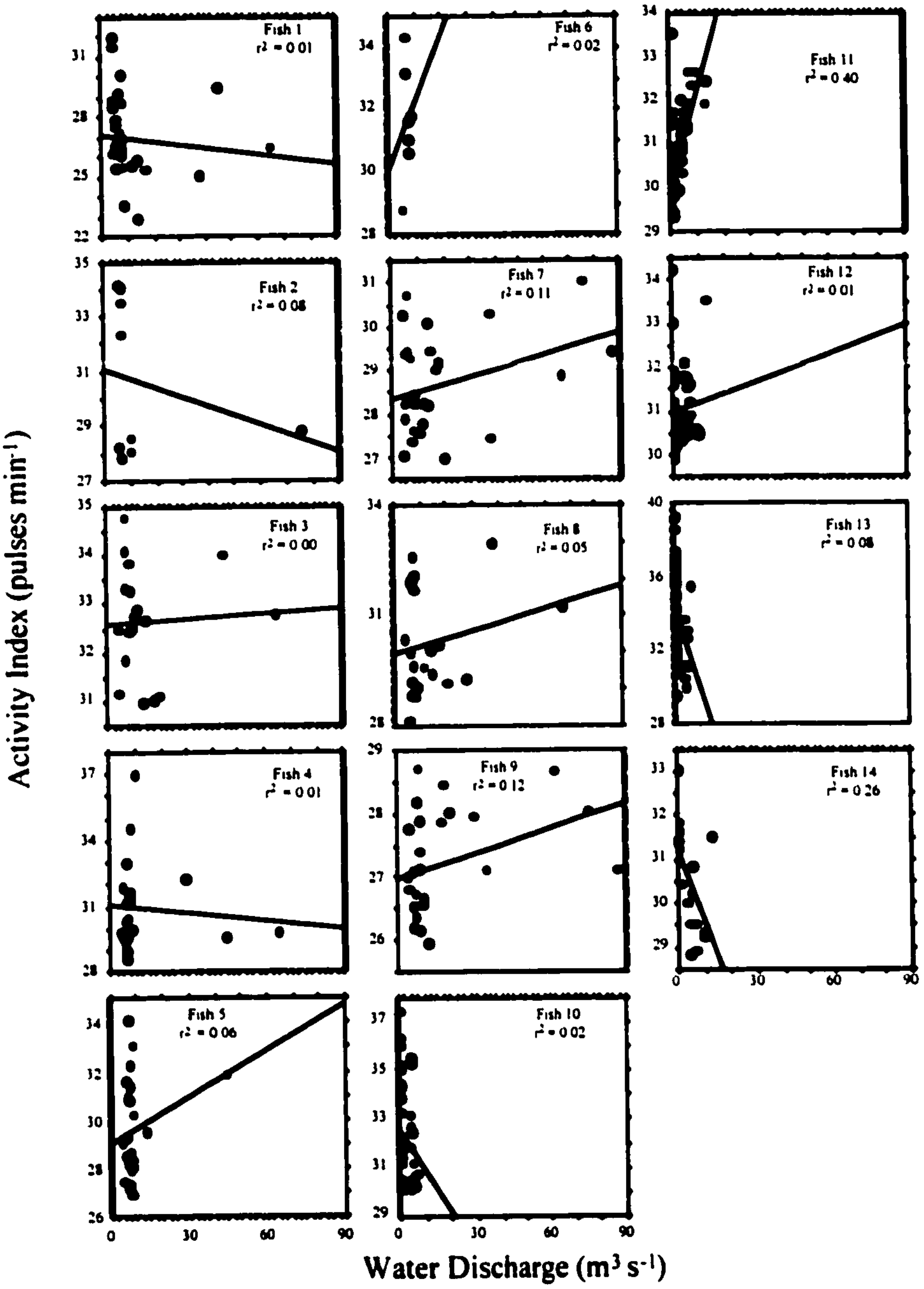

Figure 3-7. Regression plot of the range of daily swimming activity at different water discharges for each of 14 brown trout implanted with EMG transmitters in the Grand River, Ontario. The activity range symbolizes a range from the least active (0) to the most active (100) day that each individual brown trout exhibited over the winter.

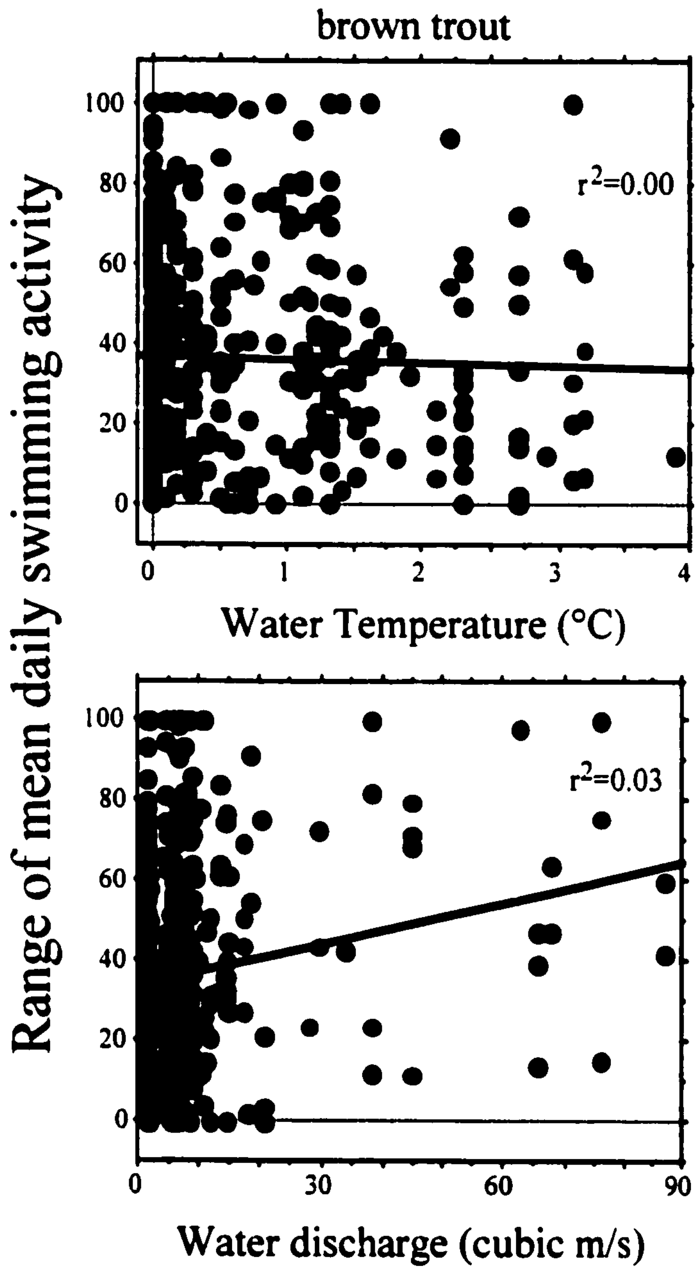

Figure 3-8. A regression plot of the range of daily swimming activity at different mean daily water temperatures (top panel) and mean daily water discharge (bottom panel) for brown trout radiotagged with EMG transmitters in the Grand River, Ontario. The activity range symbolizes a range from the least active (0) to the most active (100) day that each individual brown trout exhibited over the winter.

White sucker, however, tended to have a more consistent relationship between water discharge and swimming activity (Table 3-9). Flooding occurred several times during the winter of 1997-98 (Figure 2-2) and the time of monitoring for most white sucker (7 of 9) included high water discharge. Two white suckers, however, were only monitored when water discharge was under 10 $m^3 s^{-1}$. Of the white sucker which were monitored under a large range of flow (5 to 160 $m^3 s^{-1}$), all but one showed a negative relationship between mean daily swimming activity and water discharge. This relationship was only significant ($P<0.05$) for one of these white suckers. When data were normalized and grouped over all white sucker, there was a significant ($P<0.05$) negative relationship between water discharge and swimming activity (Figure 3-9). This relationship is still significant ($P<0.05$) if the two white suckers which were monitored over a small range of water discharge (4.7 – 9.2 $m^3 s^{-1}$) are omitted from analysis. During lower flows, swimming activity was highly variable, but during higher water discharge, the mean daily swimming activity was usually in the lower 60% of those observed (Figure 3-9).

Common carp had a very consistent negative relationship between water discharge and swimming activity. All 9 fish exhibited this relationship, although it was only significant ($P<0.05$) for 3. Most of the common carp were exposed to a large degree of variation in river flow; only one common carp (Number 9) was monitored over a discharge range of less than 60 $m^3 s^{-1}$. When data were normalized and grouped, there was an overall significant ($P<0.05$) negative relationship between swimming activity and water

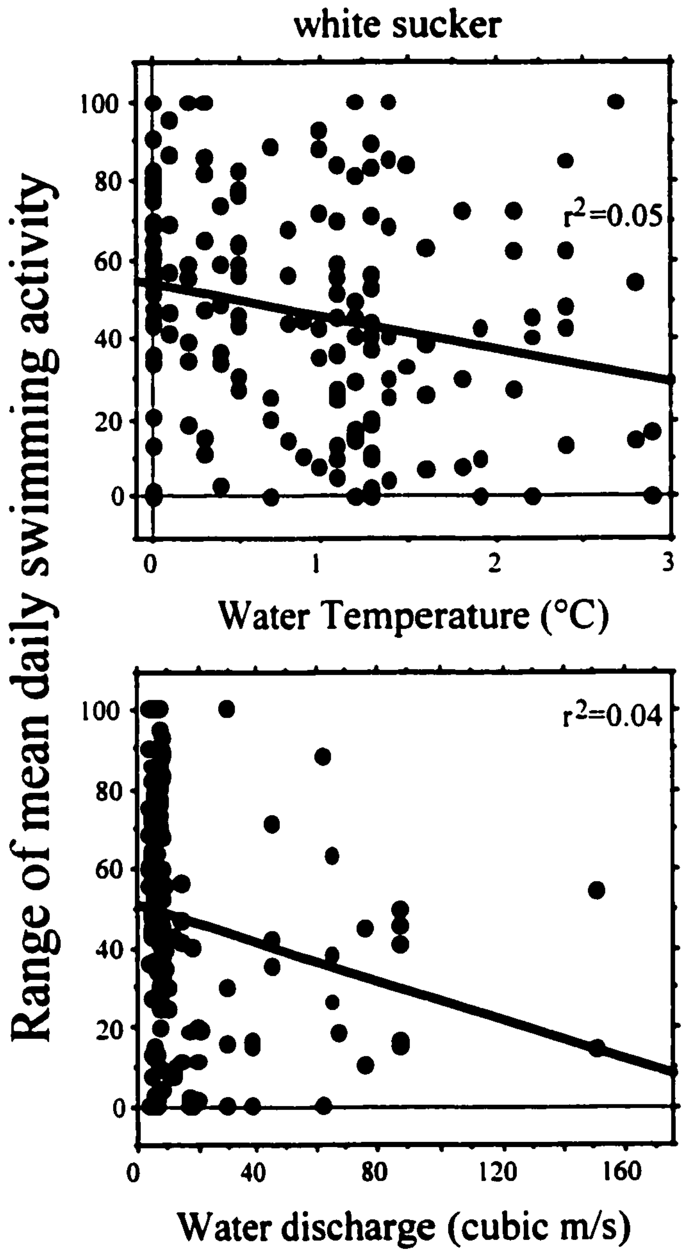

Figure 3-9. A regression plot of the range of daily swimming activity at different water temperatures (top panel) and water discharge (bottom panel) for white sucker radiotagged with EMG transmitters in the Grand River, Ontario. The activity range symbolizes a range from the least active (0) to the most active (100) day that each individual white sucker exhibited over the winter.

discharge. Similar to white sucker, during lower flows swimming activity was highly variable, but during higher water discharge, the mean daily swimming activity was more consistently low (Figure 3-10).

The relationship between water temperature and swimming activity also varied between species, but showed similar trends to the relationship between activity and water discharge. There was no consistent relationship between water temperature and swimming activity in brown trout (Table 3-9). About half of the brown trout (8 of 14; 57%) had a negative relationship (only 3 were significant ($P < 0.05$)) between swimming activity and water temperature, while the remainder had positive relationships (only 1 being significant ($P < 0.05$)). When data were normalized and grouped among all brown trout, there was no significant ($P > 0.05$) relationship between swimming activity and water temperature.

Similar to their relationship with water discharge, most (7 of 9; 78%) white sucker had a negative relationship between swimming activity and water temperature (Table 3-10). However, only two of the nine white suckers showed a significant ($P < 0.05$) negative relationship. When data were normalized and grouped among all white sucker, there was a significant ($P < 0.05$) negative relationship between water temperature and mean daily swimming activity.

Most (8 of 9; 89%) common carp showed a negative relationship between swimming activity and water temperature (Table 3-10). This relationship was significant ($P < 0.05$) in half (4 of 8) of these fish. When data were normalized and grouped among all

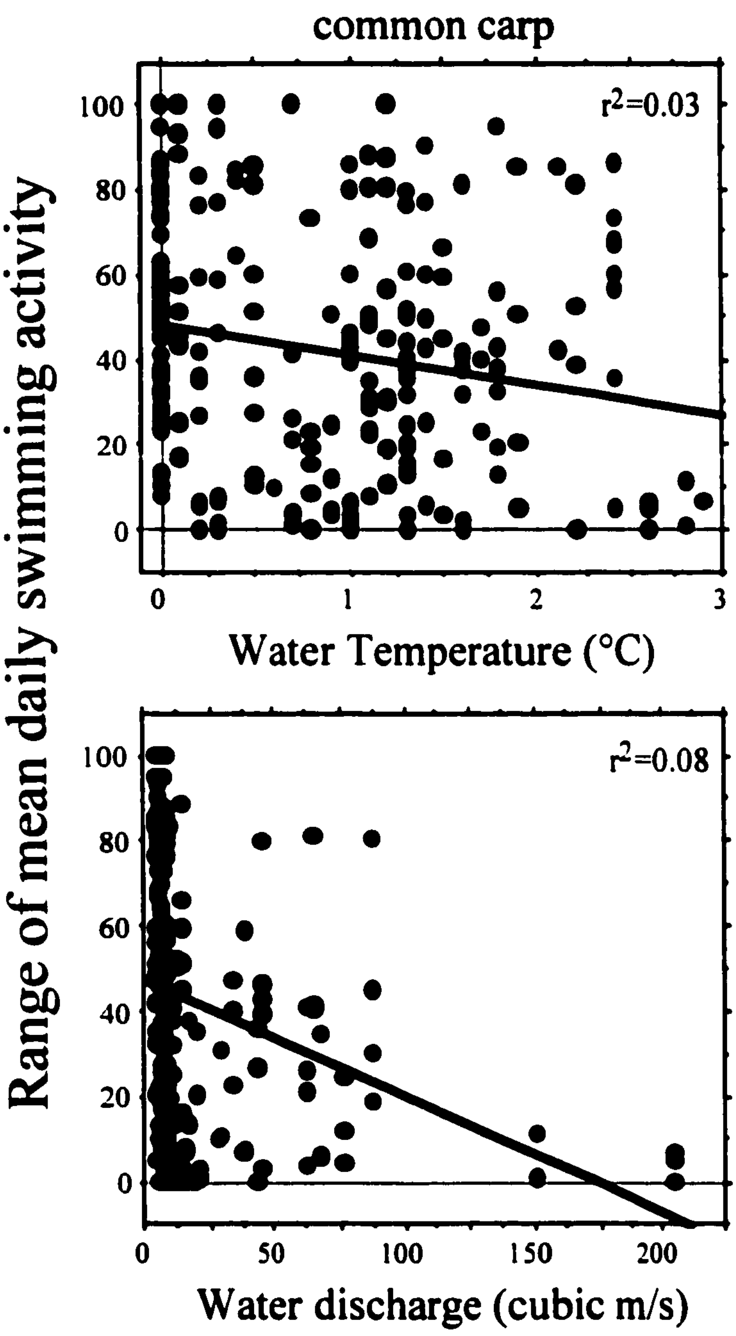

Figure 3-10. A regression plot of the range of daily swimming activity at different water temperatures (top panel) and water discharge (bottom panel) for common carp radiotagged with EMG transmitters in the Grand River, Ontario. The activity range symbolizes a range from the least active (0) to the most active (100) day that each individual common carp exhibited over the winter.

common carp, there was an overall significant ($P<0.05$) negative relationship between swimming activity and water temperature (Figure 3-10).

Since there was a significant ($P<0.05$) positive relationship between water discharge and water temperature, these results may not be independent. In two of the three species, the relationship between activity and water discharge had a higher correlation coefficient than the relationship between activity and water temperature. In the third it was almost identical.

Daily distances swum

For the eight fish whose EMG signals were calibrated to swimming speed, the mean daily distance swum through the water could be calculated. The amount that fish swam per day varied by species (Table 3-11). Mean daily distances swum were similar between white sucker and brown trout, having a mean of 14.9 and 18.0 km respectively. They also had similar mean minimum daily distances moved, but brown trout had almost double the maximum mean daily distance swum. Common carp, however, were much more active than brown trout and white sucker, having swum a mean of 32.6 km through the water per day.

Most (4 of 5) brown trout had fairly similar mean daily distances swum (10.9-15.4), while one was much more active than the others (Table 3-11). There was also a large amount of variance among distances swum per day by brown trout, from a low of only 1.8 km to a high of 45.8 km. There was similarly considerable difference between the mean amount swum by the two calibrated common carp. One fish swam almost twice

Table 3-11. Mean, minimum, and maximum daily distances (km d^{-1}) swum through the water by fish calibrated with EMG transmitters during the winters of 1997-98 and 1998-99. These distance equivalents represent the sum of all swimming activity over an average 24 h period.

Fish	Mean	Minimum	Maximum
brown trout 7	13.6	8.0	21.9
brown trout 8	15.4	8.2	28.4
brown trout 9	14.5	8.9	22.7
brown trout 11	10.9	1.8	20.6
brown trout 14	35.7	24.2	45.8
mean brown trout	18.0	10.2	27.9
white sucker 4	14.9	11.4	16.9
common carp 1	25.0	11.8	29.8
common carp 2	40.1	30.3	49.4
mean common carp	32.6	21.1	39.6

as much as the other.

Metabolic rate

The two brown trout that were tested in the laboratory had similar shaped significant ($P<0.05$) polynomial relationships between their activity indices and their oxygen consumption (Figure 3-11) and between swimming speed and oxygen consumption as quantified by the EMG signals (Figure 3-12). These predictive relationships were applied to field acquired EMG data on these two fish to determine their field metabolic rates (FMR) (Figure 3-12 and 3-13). Since fish showed variability in FMR depending on the time of day, FMR is expressed as a mean for the entire day over the whole season. On days when data were collected over the entire 24 hours, data collected in each half hour interval can be used to show the range and variability in FMR. Brown trout 11 had a daily mean 30 min FMR of 61.4 mg O_2 kg^{-1} hr^{-1} ranging from 51.4–85.3 mg O_2 kg^{-1} hr^{-1} (SD = 11.1; $N = 28$). Brown trout 14 had a daily mean 30 min FMR of 36.0 mg O_2 kg^{-1} hr^{-1} ranging from 15.0–61.4 mg O_2 kg^{-1} hr^{-1} (SD = 16.4; $N = 7$). Brown trout 14 had a more efficient use of oxygen as can be seen from Figure 3-13. Brown trout 14 (which had the higher efficiency) was about twice as active as all of the other calibrated brown trout (Table 3-12). Despite the fact that both of these fish were active, after approximately three months of winter one of them weighed the same (brown trout 11; the less active fish) and the other (brown trout 14; the more active fish) had lost only 22 g.

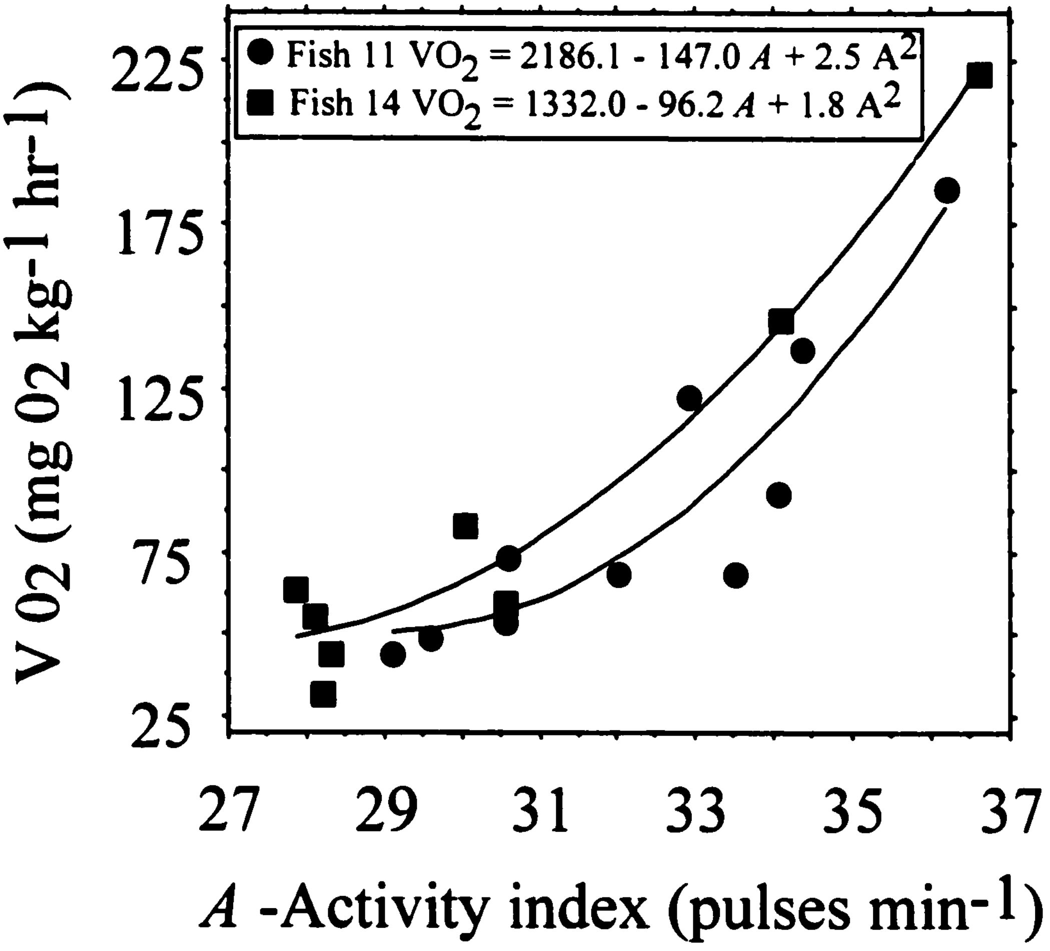

Figure 3-11. The relationship between VO_2 and an activity index (*A*) (at 1.7 - 2.7°C) for two brown trout radiotagged with EMG radiotransmitters. Periods lower on the activity index indicate lower swimming activity.

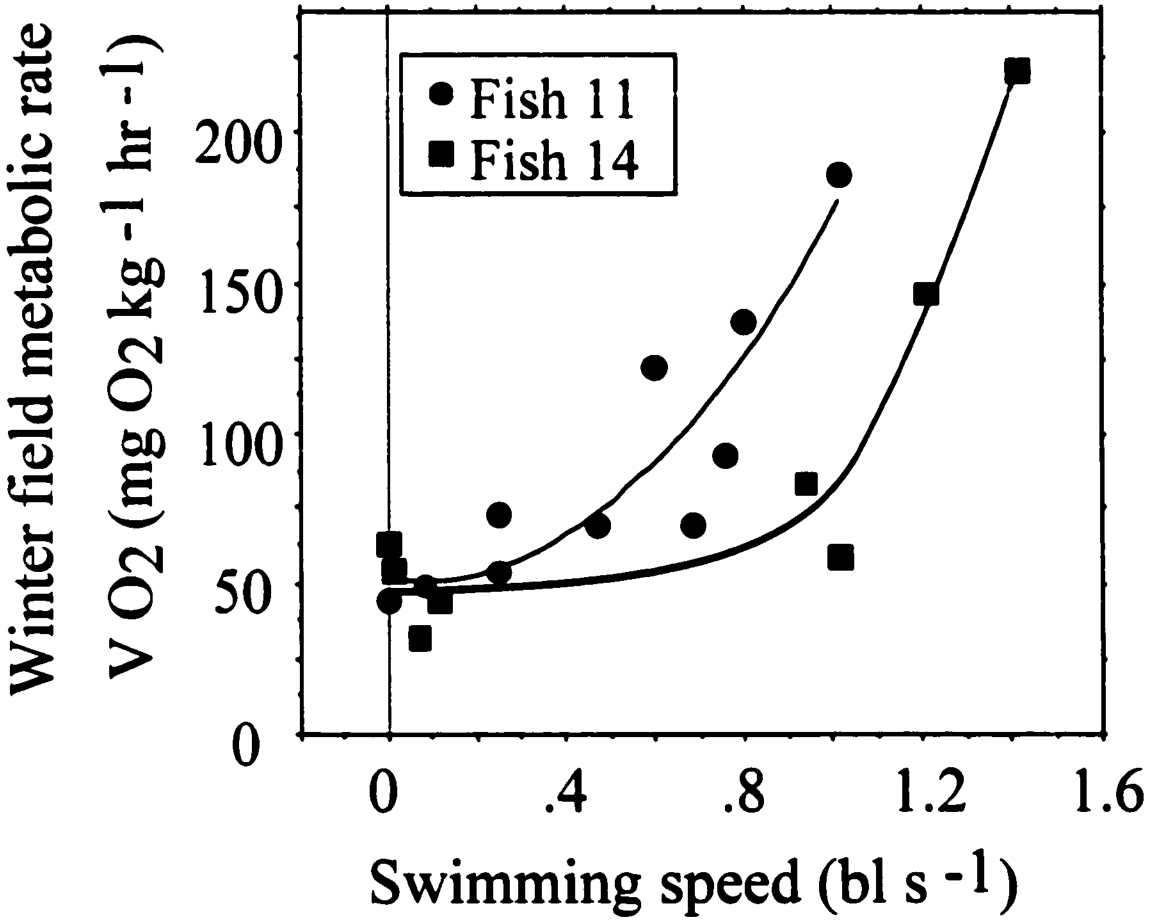

Figure 3-12. The relationship between VO_2 and swimming speed (body lengths s^{-1}) for two brown trout radiotagged with EMG radiotransmitters.

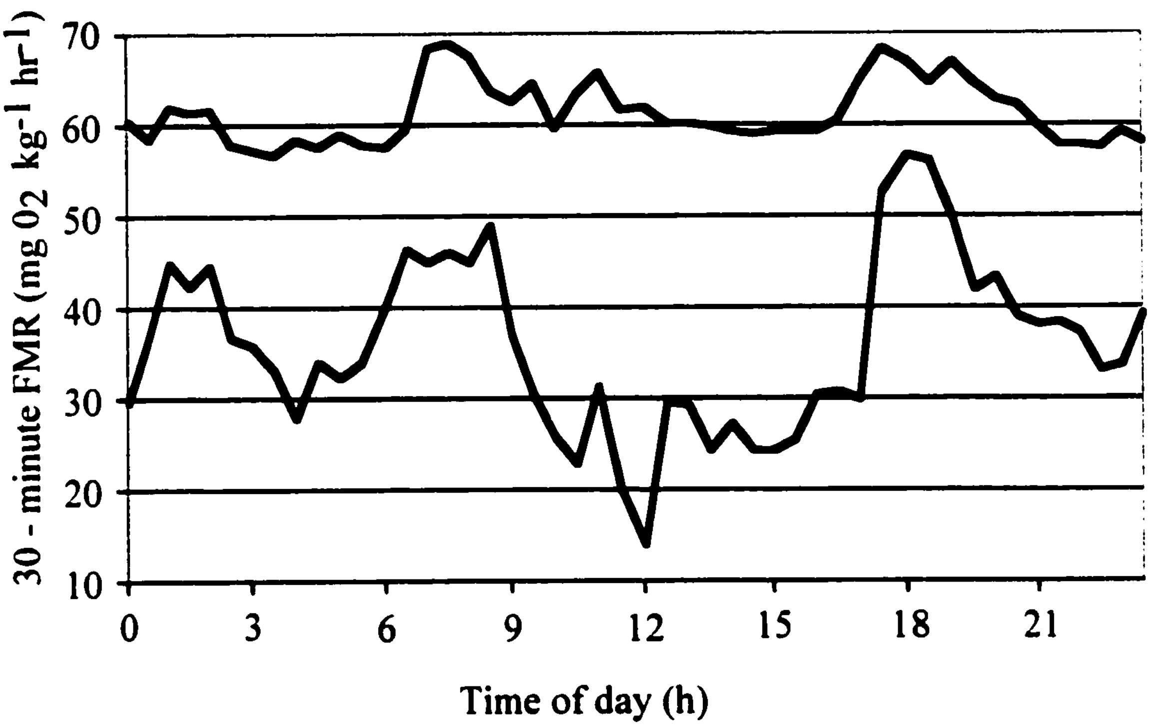

Figure 3-13. Winter field metabolic rates (at 1.7 - 2.7°C) of two brown trout in the Grand River, Ontario. The top line represents fish 11 and the bottom line fish 14.

Discussion

Diel Patterns

During winter, our results suggest there was no clear consistent pattern in diel patterns of swimming activity among riverine brown trout, white sucker or common carp. This inconsistency in diel activity patterns of fish is not uncommon and it may be more prevalent in winter due to the consistently low temperatures and light levels under ice. Richardson and McCleave (1974) found variations in diel patterns among juvenile Atlantic salmon (*Salmo salar*) studied during the same ten day experimental periods. Alanara and Brannas (1997) had similar findings for juvenile Arctic char (*Salvelinus alpinus*) and rainbow trout.

While many white sucker were generally arrhythmic, several were less active at night than the rest of the day. In contrast, by visual observation, Emery (1973) found that white sucker in Ontario lakes fed during dusk and at night but during the day swam in schools and did not feed. He did not, however, state how much activity changed over the diel period. Also, contrary to the results of this study, Reynolds and Casterlin (1978) in a laboratory study found that eighty-nine percent of activity in white sucker occurred during darkness at water temperatures from 22°C to 27°C.

It is not surprising that many of the white sucker were arrhythmic since they are not visual feeders. Feeding may be done effectively any time of the day, and it may be timed to avoid competing with other species with specific feeding patterns. For example, feeding less at night may be a mechanism to avoid competition with common carp, which are generally more active during twilight or night than during the day. Observations from underwater videotape indicate that when common carp moved into a part of a pool where white sucker were feeding, the white sucker moved to other parts of a pool (Brown, unpublished data) However, since some white sucker resided in run habitats where common carp were seldom observed, these fish may be more active during the night than white sucker which reside in the pools with common carp.

Most of the common carp were less active during the day than either twilight or night, while the rest of the fish were arrhythmic. These results are similar to Spencers (1929) who found common carp more active at night than day. In laboratory studies, Martin et al. (1998) reported that 10 cm common carp selected the lowest light levels available along a range from 100 to 2000 lux during all seasons (water temperatures ranging from 10.6 to 26.7 °C). Almost half of the common carp in this study had peaks in activity which occurred at the overlap of night and twilight in both the morning and evening. This activity is similar to crepuscularity but with a slight shift to the darker portions of the night.

Although there was no consistency in the time of day when fish were most active, the length of the winter night meant that most swimming activity was performed, and thus energy was expended, during the 13-14.5 h night. For all species studied, this was followed by the 5.5-8 h day and the brief 4 h twilight period. Young (1999) likewise found that during summer, stream dwelling brown trout were most active and moved more during night and twilight than during the day. Young et al. (1997) indicated that from May to February, stream dwelling brown trout were most active at night, followed by twilight and day, respectively. Bunnel et al. (1998), however, found that during winter, stream dwelling brown trout moved more just after sunrise than during the rest of the day. Young (1999) estimated that fish were active for only 11 h of the day during summer. Our data suggests, however, that river dwelling fish have no specific time period when they are consistently quiescent during winter.

Diel rhythms in some brown trout varied with surface ice cover. After a solid surface ice cover formed, swimming activity generally decreased at night relative to day and twilight. After ice cover melted or broke up, activity became more randomly distributed among day, night, and twilight with no clear trend present. These changes may be due to the decrease in light intensity in the river when surface ice cover (and sometimes snow cover) is present. Young (1999) found that steam dwelling brown trout activity was negatively correlated to light intensity during the summer. In winter, fish may be more active during periods of higher light intensity since the probability of predation by mammalian and avian predators is decreased by the presence of a surface ice cover and visual foraging is enhanced.

Swimming Activity

All of the fish species studied were active in the winter. White sucker and brown trout had similar swimming activity levels, swimming a mean of 14.8 – 18 km a day through the water respectively. Common carp had a much higher activity rate than either brown trout or white sucker. The two calibrated common carp swam a mean of 25 and 40.1 km per day. There was a large amount of variance among distances swum per day by fish which may be an indication of how environmental factors influence fish.

For example, swimming activity varied with the type of river ice present. The most notable change in activity was in brown trout 10, which was exposed to an approximately two week period of anchor ice formation. This fish displayed a large increase in activity during this period. However, since this was only one fish, and there was a great deal of variability in the activity of fish throughout the river, the influence of anchor ice on fish activity should be verified with further research. Anchor ice probably has broad impact on fish activity, as was seen in this one fish, because it is known to exclude large amounts of riverine habitat and is associated with fish movements (Brown and Mackay 1995a; Jakober et al. 1998; Brown 1999).

Another environmental factor which influenced swimming activity was surface ice. The activities of most brown trout changed when a solid surface ice cover formed, however, the direction of change was not consistent, half of the fish became more active, and the rest became less active. Activity levels may vary with different river environments or with the body reserves of the fish. Fish may become more active since the threat of predation from birds and mammals is eased with the formation of a solid surface ice enabling them to forage more freely with less risk. Some fish may have moved more than others due to lower body reserves and an increased need to forage. Juvenile Atlantic salmon have been found to have different behavioural patterns depending on their physiological condition. Metcalfe et al. (1998) found that fish in poorer condition were more diurnal than fish in better condition. They suggested that fish in poorer condition must forage more during the day (a more optimal time for feeding) even though there is more of a risk of predation during this time.

Conversely, if fish don't have a large physiological need to feed, a decrease in predator attacks, as a result of a solid surface ice cover, may lead them to decrease swimming activity. Underwater video cameras have recorded brown trout in the Grand River being attacked on several occasions by both mink (*Mustela vison*) and common mergansers (*Mergus merganser*) (Brown unpublished data) under both ice free periods and when there was border ice present. This predation was not observed when there was a solid surface ice cover.

Another environmental factor which may influence swimming activity is riverine habitat. The type of riverine habitat may be a deciding factor in how swimming activity changes with ice cover. Both of the brown trout which became less active under a surface ice cover were in more restricted areas of the river, while the two brown trout which became more active resided in large, long pools. These unrestricted habitats may allow fish to move about more easily.

Water discharge also had an influence on riverine fish, but some species responded more than others. The swimming activity of white sucker and common carp was much more influenced by water discharge than that of brown trout. Although there was a significant negative relationship between water discharge and swimming activity for brown trout when data for all fish were grouped, it is likely not biologically significant since there was no similar trend among all individuals. However, for both white sucker and common carp, there was a significant negative relationship between swimming activity and water discharge when data were grouped, and this trend was also obvious among individuals. Activity may decrease during high water discharge periods since the habitats suitable for the fish are drastically reduced. During periods of high water discharge white sucker and common carp moved from main channel habitats into backwater habitats (as shown in chapter two). This movement may be to avoid the high water velocities in the main channel which likely are very energetically expensive, and are also associated with large displacements of fish. Brown trout, however, were less likely to move to backwater habitats, instead they remained more often on the edge of the main channel. Swimming activity therefore stays at a higher level than if the fish take refuge in small backwater habitats. These differences in response to water discharge are likely due to the relative differences in body shape and swimming ability among the species. White sucker and common carp are unlikely to be able to perform at the same level as salmonids which are more adapted to life in swift water.

The positive correlation between fish swimming activity and water discharge was weakly reflected in their response to increasing water temperature. Brown trout did not have a consistent relationship between swimming activity and water temperature, while both common carp and white sucker had a negative relationship between the two variables. However, since the swimming performance of fish should increase with increasing temperatures (Videler 1993), this relationship is likely driven by the positive relationship between water temperature and water discharge. This seems most likely, since the range in water temperature was small, and since flooding events coincide with periods of warmer water.

Some of the differences in activity levels between species may be due to their physiological differences. The higher rate of swimming activity in common carp may be due to the ability of their muscles to acclimate to cold water. Unlike brown trout and white sucker, the swimming activity of some cyprinids, such as common carp, goldfish (*Carassius auratus*), and roach (*Rutilus rutilus*), is improved at low temperatures following a period of acclimation (Videler 1993). They exhibit changes in the contractile properties of the muscles by inducing changes in the molecular structure of myosin in the thick filaments (Johnston et al. 1990; Videler 1993).

Metabolic Rate

Field metabolic rates of the two brown trout from which EMG signals were calibrated to swimming speed and oxygen consumption were 36.0 and 61.4 O_2 kg^{-1} hr^{-1} at temperatures which were usually between 0°C and 1°C. These rates are similar to the FMR rates of approximately 55 and 80 mg O_2 kg^{-1} hr^{-1} reported by Briggs and Post (1997a) for two rainbow trout held in a 400 m^2 experimental pond at 4°C. The slight differences might be species specific or related to the conditions of measurement. The slightly lower rates I estimated were for brown trout in a river environment. Fish may be more adapted to such an environment since they are able to select their microhabitat. On the other hand the river might be expected to be more energetically demanding because of the current and because predators occasionally caused the fish to escape. The low rates are perhaps a measure of how able the fish are to minimize their energy cost in their natural environment.

Since both brown trout were active, usually swimming over 10 km a day, they are presumed to have been actively foraging as they lost little body mass. At low water temperatures the digestive rates are decreased along with consumption rates, and it is likely the fish could feed at or near their maximum rates. This lack of weight loss corresponds to findings by Cunjak (1988) who found that adult brown trout had a rapid depletion of lipids during early winter but levels remained stable or increased during the remainder of the winter.

Conclusions

This research shows that river dwelling brown trout, white sucker and common carp are active during the winter, sometimes very active. Activity varies diurnally, with changing ice conditions, as well as fluctuations in water discharge and temperature. The influence of these environmental variables differ among species, with common carp and white sucker being more influenced by high water discharges than brown trout. Field metabolic rates of brown trout were similar but slightly lower than rainbow trout which were studied at 4°C. These results indicate that winter is a time when fish have varying energetic demands and that environmental factors influence these demands just as they do during other seasons. Further work needs to be done to determine how swimming activity is influenced by some of the large fluctuations in water discharge seen during mid-winter freshets and spring floods. Although my data on the topic are preliminary, they suggest that frazil and anchor ice events may be very energetically demanding periods for fish, likely because habitats are rapidly changing and constantly in flux.

One recurring topic throughout this work is that fish are active during the winter, more active than previously believed. The commonly held belief that fish are inactive during the winter prevails because water temperatures are low and fish can digest little food, thus, feeding rates of fish are greatly reduced during winter. Also, swimming ability is reduced at lower temperatures (Rimmer et al. 1985; Videler 1993). During winter, juvenile salmonids do exhibit a strategy of reducing activity in an attempt to reduce energy consumption, and are inactive at least part of the day (Heggenes et al. 1993; Fraser et al. 1993; Whalen and Parrish 1999). However, my research shows that adult fish are active during winter, likely more active than necessary for simply limited feeding and digestion. Despite being active, my data, where available, shows fish lost little if any weight over the winter. This active strategy may be at least partially to avoid predators, or to stay aware of the constantly changing environment around them, and the availability of refuges. Obviously, further research is needed to more fully understand the energetics and behaviour of fish during winter.

Chapter 4

Effects of hanging ice dams on winter movements and swimming activity of fish

Introduction

River ice can have many negative effects on fish (Brown et al. 1994). Laboratory studies have shown that supercooled temperatures and subsurface ice can stress fish and reduce their swimming activity and escape response (Brown et al. 1999). Subsurface ice can also have negative impacts on fish habitat. When frazil ice adheres to stream substrate and other submerged objects it forms anchor ice (Tsang 1982). Anchor ice has filled large portions of streams and small rivers and excluded fish from riverine habitats causing them to move (Brown and Mackay 1995a; Jakober 1998; Brown 1999). Frazil ice can also have negative impacts on fish habitat by forming hanging dams. Hanging dams are created by thick sub-surface accumulations of frazil ice (Michel 1975). They form in low velocity reaches of rivers below surface ice, typically located downstream of more turbulent faster water sections that retard ice cover formation. Here, in freezing weather, conditions are ideal for generation of frazil ice since in open water there is continuous heat loss to the atmosphere and maintenance of a slight amount of supercooling of the river water (Tsang 1982). There is usually sufficient turbulence to entrain frazil particles, from the surface where they first form, into the main flow. When these are carried into the section downstream, buoyancy causes the frazil particles to deposit underneath the existing ice cover. As the deposit thickens, a hanging dam is formed, blocking the river flow, which produces an increase in the local flow velocity (Cunjak and Caissie 1994; Komadina-Douthwright et al. 1997). The deposition continues until either the upstream supply of frazil ceases, or until the local velocity increases to the point that it is sufficient to suppress the effects of buoyancy and carry the frazil past the hanging dam (Beltaos and Dean 1981). Hanging dams can be quite large, (at least 90 m deep and 1200 m long (Gold and Williams 1963)) and persistent features (they can last several months (Komadina-Douthwright et al. 1997)) during winter, yet little is known about their influence on fish.

While several authors have surveyed hanging dams, their formation has not been correlated with fish movements, changes in fish habitat use, or other behavioural responses of fish. This is somewhat surprising given that hanging dams have been found to influence large pools which were suspected to be good overwintering areas for Atlantic salmon (Cunjak and Caissie 1994; Caissie et al. 1997; Komadina-Douthwright et al. 1997).

To determine how hanging dams influence fish, common carp and brown trout were implanted with radiotransmitters in the Grand River, Ontario during the winters of 1996-97 and 1997-98 and their movements, habitat use, and swimming activity were monitored through these changing conditions. We hypothesized that fish would move out of overwintering pools if hanging dams formed in them, and that fish would be forced to be more active while outside of the overwintering pools.

Methods

This project is part of a wide-ranging radiotelemetry study, covering a larger portion of the Grand River. In this chapter I focus on the radiotagged fish which were known to be influenced by hanging dams. This research was carried out along a 4 km reach of the Grand River, Ontario (43°38'-43°41'N, 80°26'-80°29'W). The study area runs through Elora Gorge, which is a high gradient (mean 5.3 m/km) channel cut through a limestone gorge with abundant bedrock substrate.

Preliminary work was done in the winter of 1996-7 and more intense work was done in the winter of 1997-8. One adult brown trout (351 mm fork length (L_F), 480 g) and one adult common carp (568 mm L_F, 3269 g) were implanted with radio transmitters on Dec. 12, 1996 and Jan. 2, 1997 respectively. Five adult common carp (mean L_F = 594 mm, SD = 25; range = 560 - 620; mean weight 4122 g; SD = 794; range = 3060 - 4785) were implanted with radiotransmitters October 21-22, 1997. All but three common carp were surgically implanted with locational radiotransmitters using methods similar to Brown and Mackay (1995b). Locational radiotransmitters weighed 8.1 g in air and had a predicted lifetime of 425 days. Three of the common carp were implanted with electromyogram (EMG) radiotransmitters. Fish were collected by electrofishing and surgery was performed on the river bank near the site of capture. After implantation, fish were released at their capture point. All radiotransmitters were less than 2% of the weight of implanted fish in air. Fish were tracked at least every fifth day from Jan. 1 to Apr. 2, 1997, or from Dec. 6, 1997 to Mar. 8, 1998. Tracking was done on the ground and fish locations were fixed with a three element YAGI antenna and recorded on aerial photographs (scale 1:20000). Signals were received using a SRX_400 receiver (Lotek Engineering Inc.). The accuracy of the locating method was estimated to be within ±5 m. Integrated EMG signals were collected from the three common carp from Dec. 6, 1997 to Mar. 8, 1998.

The EMG transmitters were surgically implanted into the intraperitoneal cavity of three common carp. These transmitters (Lotek Engineering Inc.) weighed 18 g in air, 8 g in water, and were 5 cm long by 1.6 cm in diameter. They have two Teflon coated electrode wires which were anchored in the red muscle band and held in place by small (1 mm diameter, 5 mm long) 9 K gold rods, through which the end of the electrode is threaded. These electrodes feed electrical impulses into the transmitter which are emitted when the fish perform non-burst swimming. Since the electrodes are not placed in the white muscle, burst swimming was not quantified. The radiotransmitter stores the electrical impulses in a capacitor and when this is full, the transmitter emits a signal. Thus, when fish swim faster, signals are emitted more frequently by the transmitter (see Beddow and McKinley (1999) for further details). A datalogging radio receiver (Lotek Model SRX-400 with W20 firmware, Lotek Engineering Inc.) was used to receive and store radio signals. The receiver software records the amount of time between subsequent signals.

Although signals emitted from EMG radiotransmitters are correlated with swimming activity (Briggs and Post 1997a, 1997b; Beddow and McKinley 1999), EMG signals alone can only provide a relative index of swimming activity. Since each EMG radiotransmitter has different specifications (different pulse rates at resting and at a given swimming speed) and the same radiotransmitter will even have different pulse characteristics in different fish (R. Brown and T. Beddow unpublished data), EMG data cannot accurately be grouped among fish unless the pulse rates of the transmitters are known at resting and at several swimming speeds.

Although water discharge did fluctuate more during the study period (Figure 4-1), EMG data were only logged on days when water discharge was a mean of 8.1 m^3s^{-1} (range 4.9 - 14.1) and water temperatures were at or below 2.0° C. Since, only a limited amount of radio receivers were available for this study, and fish were widespread throughout the study area, signals from all implanted fish could not be logged at the same time. The proportion of the time that EMG data were logged thus depended on how widespread fish were and the number of radio receivers available at any time. EMG signals were recorded for a mean of 202 h for each fish. EMG signals were recorded for a mean of 112 h (range 76 - 135) while fish were in an overwintering pool and a mean of 91 h (range 65 - 104) while they were out of an overwintering pool. Activity was averaged over 0.5 h increments similar to Briggs and Post (1997a). Since fish may have daily activity patterns, data were averaged for each half hour of the day for the entire period in or out of an overwintering pool for each fish. To determine if swimming activity differed when fish were in or out of an overwintering pool, data for each individual were compared using a paired *t*-test.

Water depths, velocities and ice thicknesses were measured along three transects in a pool at the lower end of Elora Gorge. This pool was surveyed since preliminary work showed that a hanging dam had formed in this pool the year before. Surveys were done once on three transects when they were ice free (Dec. 14 1997, or Feb. 4, 1998) and once when a hanging dam was present (January 19-20, 1998). Since surveys of hanging dams are slow and difficult, time only permitted three transects to be surveyed. Bottom velocities (10 cm above the substrate) were measured and "mean" water velocities were

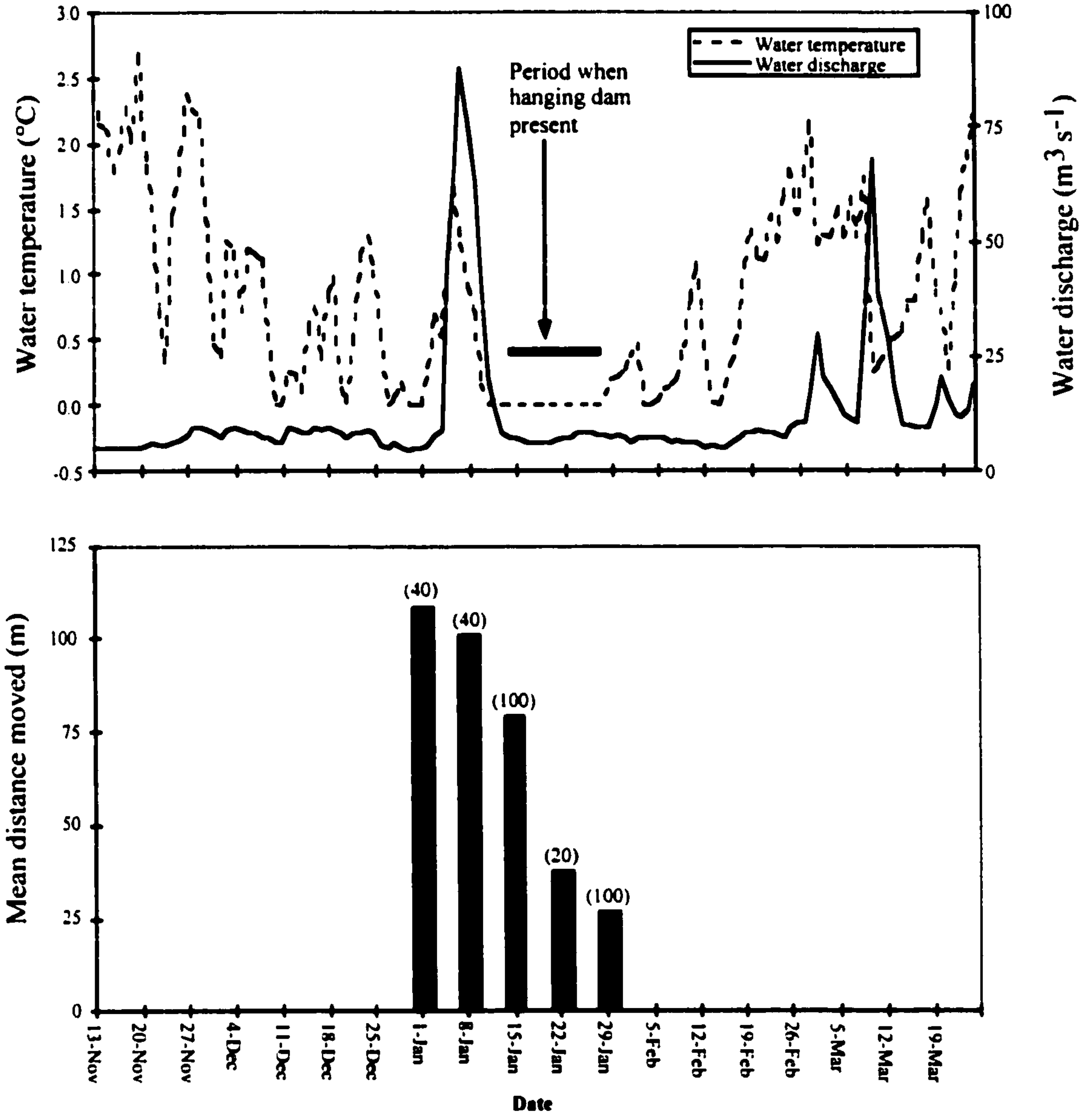

Figure 4-1. Top panel; winter water temperatures, water discharge, and presence of a hanging dam in the Grand River, Ontario. Bottom panel; mean weekly distance moved by radiotagged common common carp. The number in brackets above each bar represents the percentage of fish that moved during that week.

estimated every 4 m along each transect. "Mean" water velocity was estimated by averaging point measurements taken at 20 and 80% of the water column when ice cover was not present and at 20, 50, and 80% when ice cover was present. Water velocity was measured using a Sigma Doppler flow meter. Frazil slush was measured using a video camera submerged in the slush, or by pushing a rod with a flat plate on the end into the ice and noting the resistance to the ice (similar to Komadina-Douthwright et al. 1997). This method may slightly overestimate the thickness of frazil deposits by pushing the frazil down further into the pool. Transects were marked so that measurements could be taken at the same spots on subsequent occasions. Environment Canada provided water discharge data from the gauging station at the town of West Montrose (15 km downstream of the hanging dam site). Air and water temperatures (°C) were obtained using thermisters within the study area (Hobo Temp, Onset Computer Corp.).

Results

Preliminary investigations of the relationship between hanging dam formation and fish displacement during the winter of 1996-97 suggested that fish moved away from the vicinity of hanging dams. One radiotagged common carp occupied a pool at the lower end of Elora Gorge from Jan. 10 to Feb. 19, except for a short period (Jan. 29 – Feb. 3). During the fish's absence, several holes were drilled in the ice cover of the pool revealing 2-3 meters of frazil slush. Movements of a brown trout in the middle of the gorge also appeared to be influenced by a hanging dam. On 16 March, a brown trout moved into a part of a pool out of the main flow where a small spring entered. There was no frazil slush under the ice near this spring. Farther downstream in the pool, where the fish had previously been located since Feb. 3, frazil slush filled the entire water column forming a hanging dam. Previously, on Jan. 29, the same fish had made a similar movement. Although the pool was not surveyed for hanging dam formation at this time, the date of movement coincides with the suspected formation of a hanging dam in the downstream pool.

In 1998, a hanging dam formed in the same pool between Jan. 14 and Jan. 16 and lasted about two weeks (Figure 4-1). The hanging dam was surveyed Jan. 19-20 and was gone by Jan. 29 when a period of warm weather occurred and water temperatures increased to a mean daily temperature of 2°C. This warmer water quickly melted away the hanging dam. An estimated mean of 80.1% (range 78.1% – 83.7% at three transects) of the pool was filled with frazil ice (Figure 4-2). Mean and bottom water velocities in the pool changed (Figure 4-3) from a mean of 6 to 27 cm s^{-1} and 4 to 21 cm s^{-1} respectively when the hanging dam was present, and water depth decreased from a mean of 2.25 to 0.45 m. When these changes in habitat occurred, fish moved out of the pool (Figure 4-4).

Five common carp were in the pool on most occasions when the hanging dam was not present. Three of the common carp were in the pool during the entire study period except when the hanging dam was present (Figure 4-1). Two of the common carp were in the pool the entire study period except during the presence of the hanging dam and for a short move upstream to another pool during a period of high water discharge (Figure 4-1). All fish were in the pool on Jan.13 , but had moved out by Jan. 19 when the hanging dam

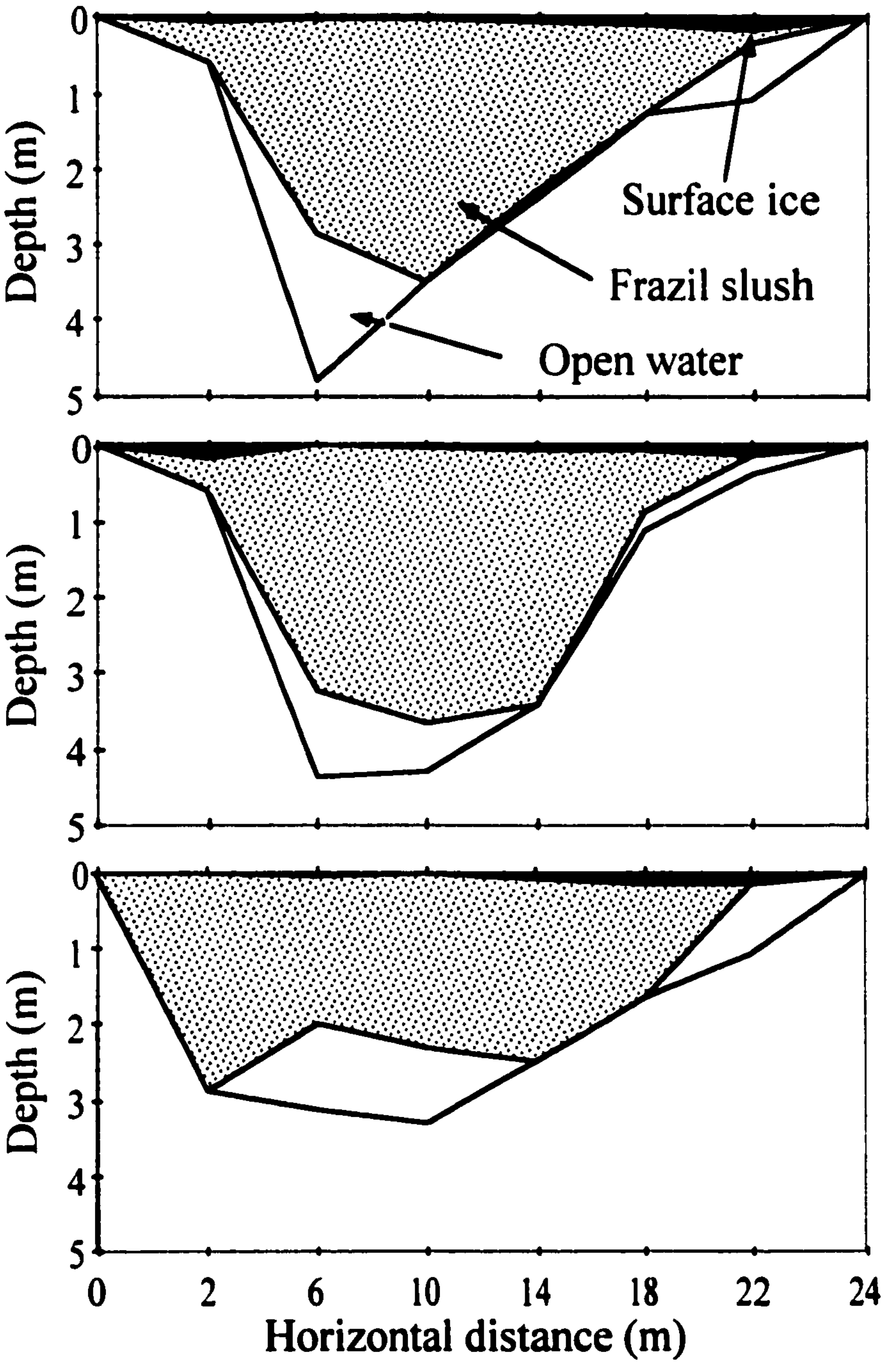

Figure 4-2. River cross sections at hanging dam site in the Grand River, Ontario, January 1998. The top panel shows the farthest upstream transect, the bottom panel shows the farthest downstream. Surface ice is shown in black while frazil ice deposits are shaded.

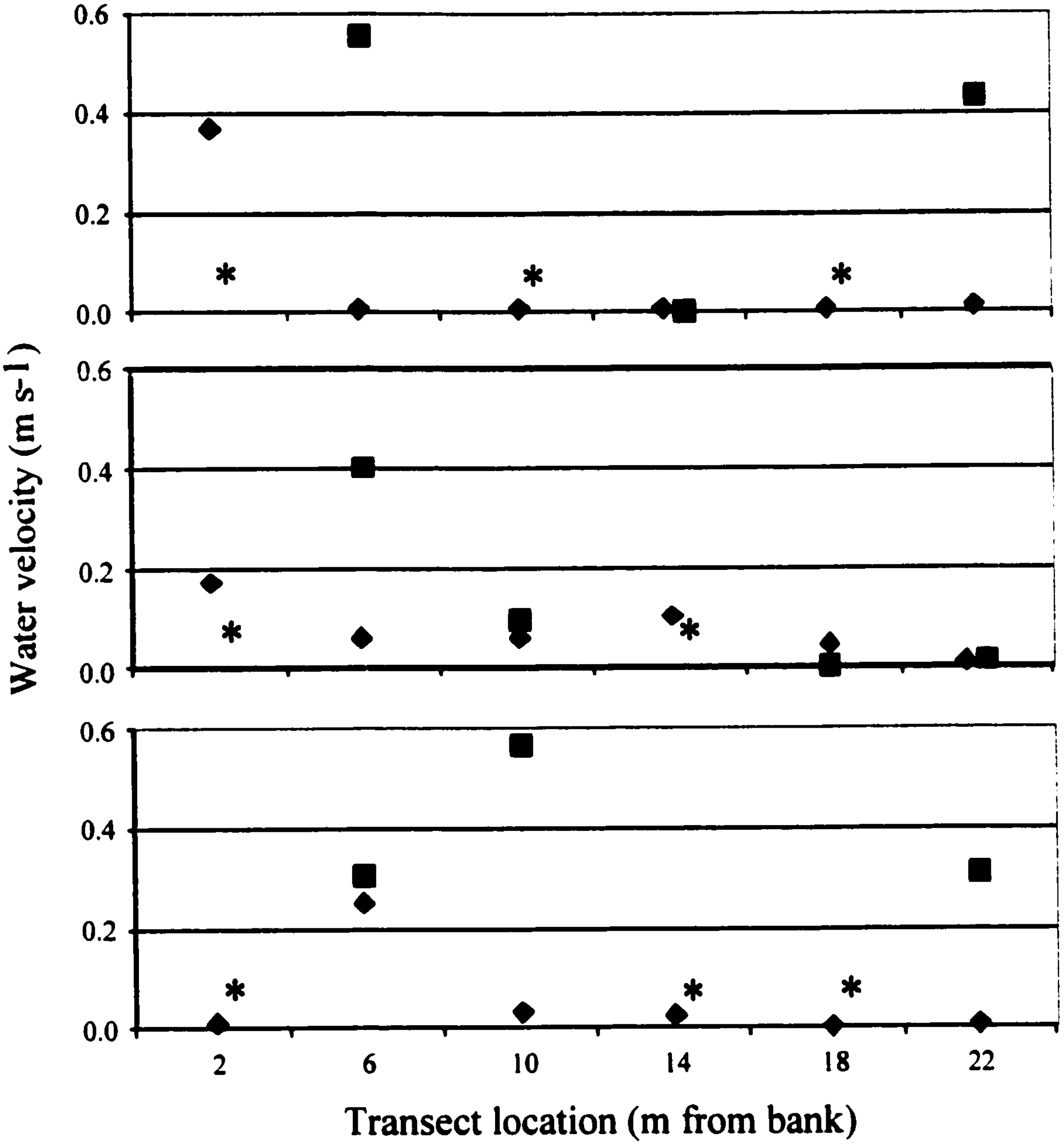

Figure 4-3. Mean water column velocity at survey points along three transects across an overwintering pool. Measurements when the pool was ice free are represented by diamond, while squares represent measurements when a hanging dam was present. Transect points where the entire water column was filled with frazil ice are shown by asterisks.

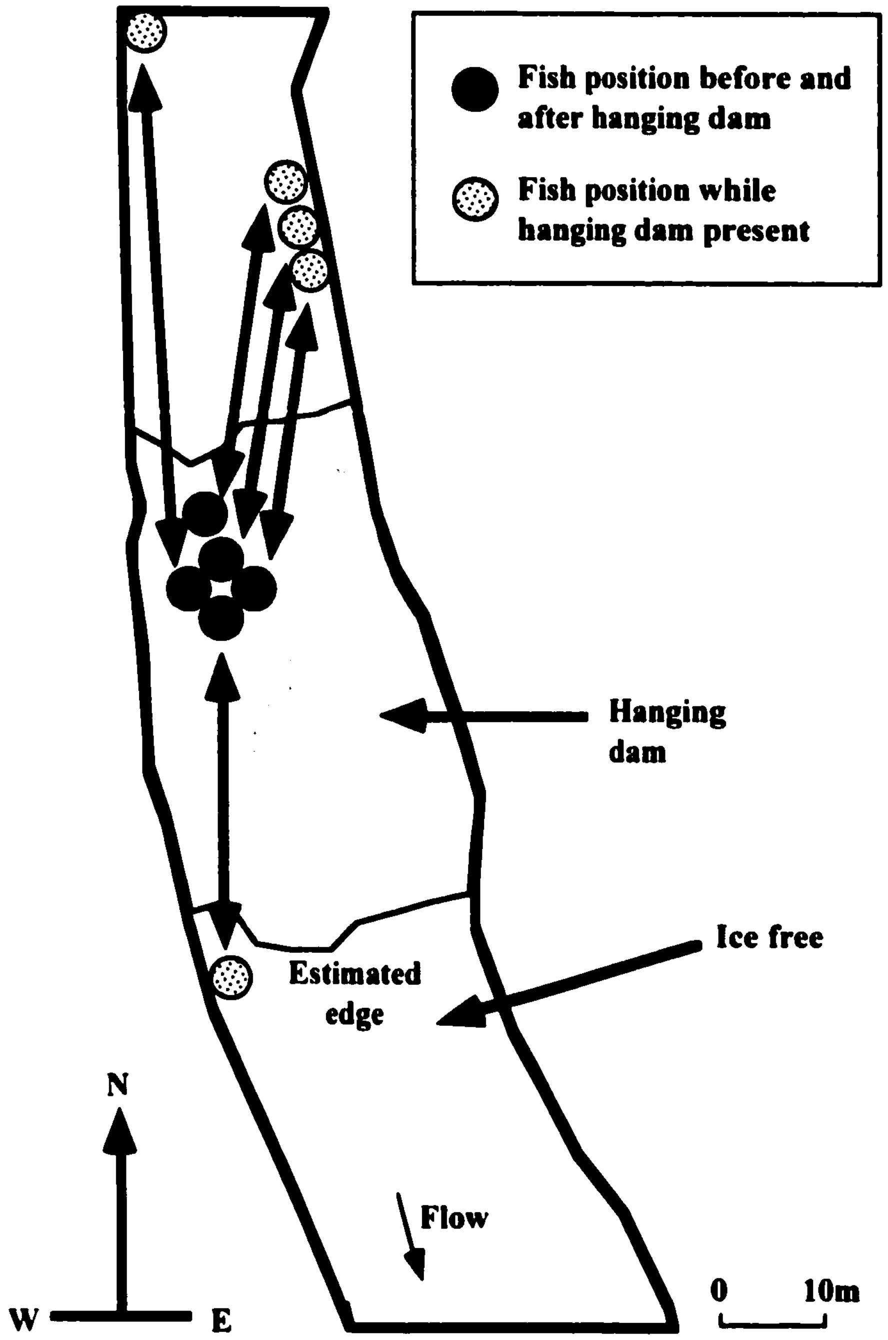

Figure 4-4. Movements of radiotagged common carp associated with the formation of a hanging dam in the Grand River, Ontario, January and February 1998. Arrows trace movements of fish out of the pool when the hanging dam forms, and back into the pool after the hanging dam is gone.

was surveyed. Four of the fish moved upstream and one moved downstream. The fish returned to the area where the hanging dam formed when it disappeared (Jan. 30). When the hanging dam formed, one fish moved 35-45 m downstream and remained in the lower end of the pool at the ice edge. The lower end of the pool and the river below the pool were not ice covered. One fish moved about 200 m upstream to another smaller, shallower pool and the other three fish moved 30-50 m upstream to the run above the pool and stayed along the edge of a border ice strip where water velocities were low. These three fish were observed in an aggregation with several other common carp. No depth or velocity data are available for locations fish used while they were out of the overwintering pool.

Being out of their overwintering pool did not have a consistent influence on swimming activity. Two of the common carp had significantly ($P<0.05$) higher swimming activity when in the overwintering pool, than the period when they were out of it (Figure 4-5). The swimming activity of a third common carp was significantly ($P<0.05$) higher during the period it was out of the pool. The two common carp which were less active while outside the overwintering area resided in the tail end of the pool or in the run above the pool while the hanging dam was present. The third fish, was upstream in another pool.

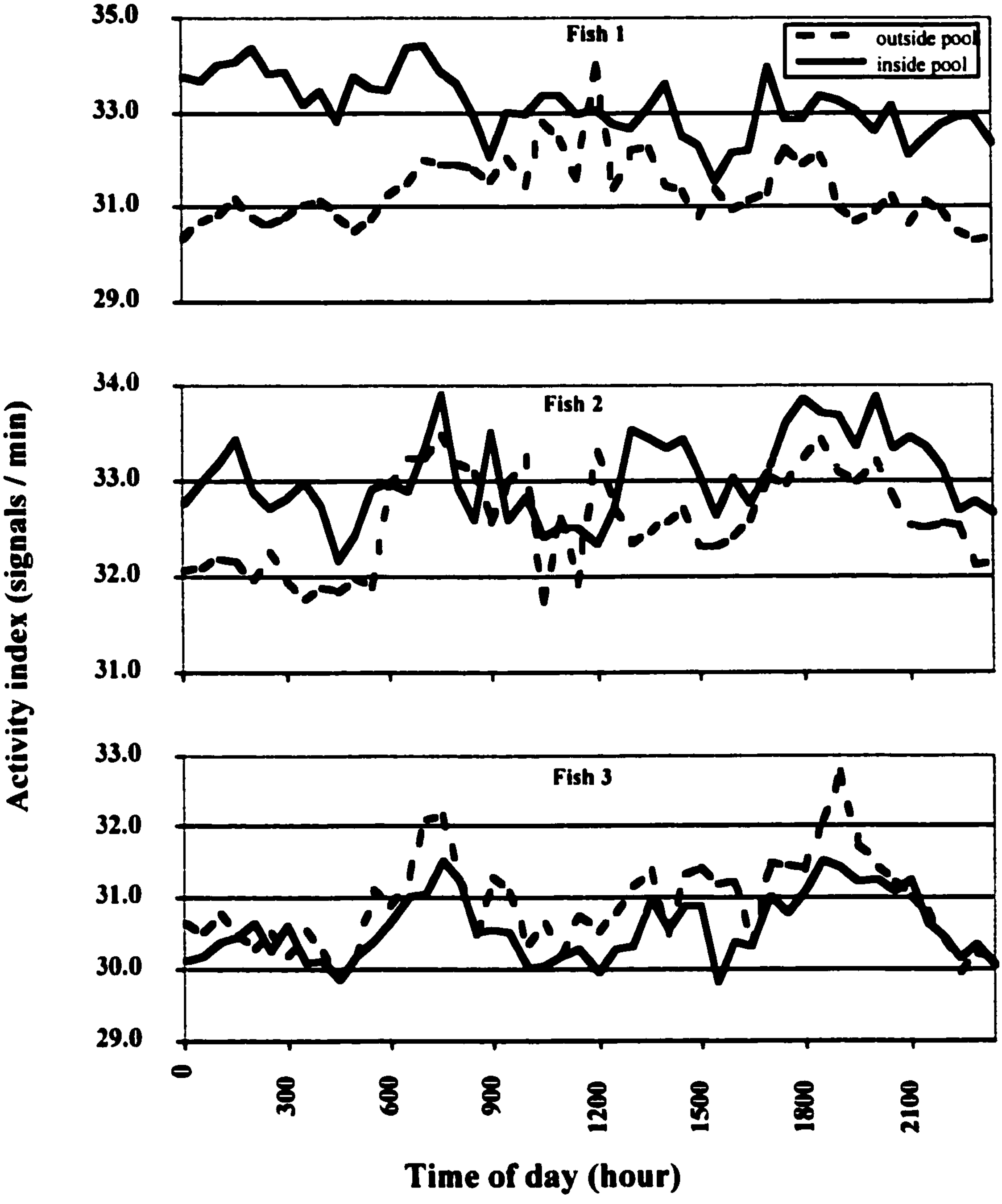

Figure 4-5. Mean daily swimming activity patterns of three common carp implanted with electromyogram radiotransmitters while they were in an overwintering pool and during a period they were outside the pool and the pool was filled by a hanging dam. The fish are swimming less as the activity index decreases; the lower end of the scale does not refer to a swimming speed of zero.

Discussion

In cool temperate and colder climates, hanging dams frequently form in some rivers during winter (Komadina-Douthwright et al. 1997) and fish have to cope with the resultant changes in their habitat. In this study, 80% of the overwintering pool was filled by the hanging dam and this caused a dramatic change in physical environmental conditions. Both bottom and mean water velocities were much higher when the hanging dam was present. This increase in water velocity coupled with a reduction in free water volume likely changed this pool from being a preferred overwintering site to unsuitable habitat virtually overnight. This is probable since as water temperatures decrease in the fall, fish such as riverine salmonids often make less use of shallower areas with higher water velocities and instead use deeper, slower habitats (Hartman 1965; Cunjak and Power 1986; Chisholm et al. 1987; Heggenes et al. 1993; Baltz et al. 1991; Brown and Mackay 1995a; Jakober et al. 1998). So when the hanging dam formed, the fish responded by moving out of the pool and seeking refuge elsewhere. Surveys of hanging dams by others (Cunjak and Caissie 1994; Caissie et al. 1997; Komadina-Douthwright et al. 1997) showed over 80% of the pool volumes were frazil ice.

While the hanging dam in the Grand River lasted for only about two weeks, in colder seasons or climates, hanging dams remain in place for long periods of time. Some remain in place for months (Komadina-Douthwright et al. 1997) or even from fall freeze up to spring break up (Beltaos and Dean 1981). This could influence large sections of rivers making them unusable during winter even though surface observations during summer suggest they are good overwintering areas.

Hanging dams may cause major difficulties for fish during winter, however, they have gone largely unnoted since they form under ice and are difficult to observe. Many of the other ways that river ice can influence fish and their habitats are much more visible. Frazil ice adhering to the substrate forms anchor ice (Tsang 1982) which can fill large portions of streams and small rivers excluding habitat and forcing fish to move (Brown and Mackay 1995a; Scruton et al. 1997; Jakober 1998; Brown 1999; Whalen et al. 1999). Thick anchor ice deposits forming in riffles create what is called an ice dam (Gerard 1989). Ice dams can block a large amount, or even temporarily can block all of the water discharge in a stream. Trout have been found lying on the substrate in dewatered pools below ice dams (Maciolek and Needham 1952). Thus, while fish habitats in shallower, faster areas of streams may be influenced by anchor ice and ice dams, habitats in the deeper, slower areas are susceptible to hanging dams. This makes most riverine fish habitat susceptible to ice exclusion at some time during the winter. Even surface ice can increase in thickness over the winter until it excludes large portions of overwintering habitats in streams and small rivers (Chisholm et al. 1987; Berg 1994; Scruton et al. 1997).

The formation of hanging dams would also force fish to move to new habitats during dangerous times, such as heavy frazil production, which may increase the chance of mortality. During frazil and anchor ice events, Brown et al. (1999) found that rainbow trout had a reduced escape response. If brown trout and common carp have a similar reduced escape response, they are more likely to be preyed upon by avian and mammalian predators while moving out of excluded habitats during frazil events. Similarly, fish may also be more likely to be stranded upstream of breaking ice dams.

Since ice dams impede river flow (Gerard 1989) and impound water, fish may move to the sides of newly immersed floodplain, and be stranded when the ice dam breaks and the floodplain is quickly dewatered.

Being forced out of an overwintering pool by a hanging dam did not appear to have consistent effects on the swimming activity of common carp. Two of the common carp were significantly more active when in the overwintering pool, than during the period when they were forced out of it. The fish may have changed their activity patterns to deal with unfamiliar or different types of habitat. Fish may be less active in a more constricted and unfamiliar area or they may be more active exhibiting exploratory behaviour. The pool that the fish used for overwintering was almost 5 m deep and very long, providing a large, low velocity area to move around in. When the pool was filled with the hanging dam, and the fish moved out, they occupied much more restricted habitats; the tail end of the pool they normally occupied or the margin of a run. These habitats did not provide the large areas of low velocity pool habitat the fish seemed to prefer. The fish likely couldn't make as wide a range of movements and still avoid areas with high water velocities. One of the fish, however, had higher swimming activity rates when it was forced out of its overwintering pool. This may be because it moved from its normal overwintering pool to another pool.

Conclusions

Hanging dams do influence fish, however, the extent of their effect is difficult to determine, especially since it is often difficult to determine where and when these formations occur without extensive, difficult surveys. Fish move out of pools where hanging dams form, and hanging dams can make pools unsuitable for fish for a short period, or for the entire winter. For fisheries managers to properly manage fish and fish habitats during winter, our knowledge of hanging dams must be expanded. Managers cannot simply consider excavating a deep pool a valid option for creating overwintering habitat. The negative effects of hanging dams on overwintering habitats emphasize the importance of areas with warm groundwater upwelling as overwintering habitat (Power et al. 1999). In these areas, hanging dams will not occur and winter habitats will be more stable. However, at the lower end of warm groundwater fed stream sections, frazil ice may form during colder weather, producing frazil which may contribute to hanging dams farther downstream.

Future work should be done to see how swimming activity is changed when fish are forced out of overwintering areas for longer periods of time and forced into less suitable habitats. It is recommended that more inter-disciplinary work such as this be done, bringing together biologists and river ice scientists.

Chapter 5

Swimming activity of rainbow trout exposed to supercooling and frazil ice

Introduction

Several authors have shown that frazil and anchor ice can have effects on fish habitats in rivers and streams. Fish move out of pools in rivers when frazil ice fills much of them creating hanging dams (Brown et al. 1998). Anchor ice can also fill large parts of rivers excluding fish habitat and forcing fish to move to new habitats (Brown and Mackay 1995a; Jakober et al. 1998; Brown 1999). Other effects of anchor ice formations on fish are also reviewed by Brown et al. (1994). However, while it is known that frazil and anchor ice can influence fish habitat, the physiological effects of supercooling, and frazil ice on fish are unknown.

Although little evidence exists that frazil ice directly kills fish (other than Tack 1938), mortalities of several juvenile trout have been noted after cold spells and frazil and anchor ice events (Brown et al. 1994). Brown et al. (1994) also speculated that frazil ice can plug the mouths and gills of fish, or abrade the gills. It has also been suggested that conditions during frazil ice events may be unsuitable for night active juvenile salmonids (Whalen et al. 1999). However, no strong direct links between frazil ice and physical damage have been found. However, if fish are forced to increase activity to avoid frazil ice, or due to anchor ice exclusion of habitats, an increased weight loss may occur making survival over the winter less likely. Since supercooling and frazil and anchor ice are common throughout winter below hydroelectric facilities, this topic is of particular interest.

To determine if fish activity is influenced by supercooling or frazil and anchor ice, the activity levels of adult rainbow trout were examined when exposed to these conditions in a large refrigerated flume. It was hypothesized that swimming activity levels would increase when fish were exposed to supercooled water and frazil and anchor ice.

Methods

The experiments were done in a refrigerated flume at the Ice Engineering Division of the U.S. Army Cold Regions Research and Engineering Laboratory. The set up of the flume and the conditions during the experiments are described in detail by White et al. (1999) and Kerr et al. (1997). Briefly, the flume is situated in a room where the temperature can be regulated between +18 and –29 °C. The flume is 0.61 by 1.22 m in cross section and 36.6 m long. It can tilt from +2 to –1° slope, has a flow capacity of nearly 0.4 m^3 per second and has a refrigerated bottom. For these experiments, the bed of the flume was insulated and covered with two layers of clean, uniform, well-rounded cobbles having a median diameter of 4 cm. Boulders with a nominal diameter of 19 cm were placed in the flume at irregular intervals to provide areas of lower velocity during the activity tests.

Rainbow trout were obtained from High on a Hill Hatchery (Plainfield, NH) and held at 0-1 °C in flow-through tanks for 1 week before the beginning of the experiments. Fish were not fed during the week preceding the experiments.

Adult rainbow trout were implanted with electromyogram (EMG) radiotransmitters which allow swimming activity to be quantified. Implanted fish were exposed to supercooled temperatures, frazil ice, and anchor ice. Two replicates of fish were implanted with EMG radiotransmitters using methods similar to McKinley and Power (1992) The first group (N=7, weight 1154 ±95 g; fork length 446 ±16 mm; mean

± SE) was implanted on November 19, 1998. The second group (N=5, weight 1026 ±46 g; fork length 425 ±3 mm; mean ± SE) was implanted on November 21, 1998. After fish had recovered from anesthesia, they were put back in a holding tank and allowed to recover for three days before signals were recorded.

The fish that were implanted with EMG transmitters on November 19 were placed in the flume in the afternoon of Nov. 22. EMG signals were recorded from the evening of Nov. 22 through the afternoon of Nov. 24. The temperature in the cold room was decreased in the early morning of Nov. 23 and the fish were exposed to two periods of supercooling, one 3.3 hours long and one 4.9 hours long, with a minimum water temperature of -0.011 °C. The second replicate of fish (implanted on Nov. 21) were placed in the flume in the afternoon of Nov. 24. EMG signals were recorded from the evening of Nov. 24 through the afternoon of Nov. 26. The temperature in the cold room was decreased in the early morning of Nov. 25 and the fish were exposed to two periods of supercooling, one 3.7 hours long and one 3.2 hours long, with a minimum water temperature of -0.018 °C. During both replicates, fish were allowed to acclimate to the flume for four hours before EMG signals were used. Fish were monitored in a 10 m long section of the flume which included a boulder randomly placed in each 1 m^2.

Fish were held in different sections of the flume by plastic screen dividers, which gradually accumulated anchor ice which impeded water flow. To prevent this, the anchor ice was scraped off the dividers when necessary. This was done carefully so that fish were disturbed as little as possible. However, since disturbing fish at some times was inevitable, the data for a period of five minutes (starting at the beginning of divider clearing) was removed from the fish swimming activity data used to calculate differences between the test and control period. To determine if the amount fish were disturbed (as indicated by swimming activity) was related to the amount of time in supercooled water (since the amount of frazil and anchor ice increases the longer the supercooling period), the swimming activity data for each five minute clearing period was averaged across all fish and regression analysis was performed on these data at different amounts of time since supercooling had commenced. There were two separate supercooling events on both test days, since water temperatures rose above freezing when the refrigeration units had to be defrosted.

Differences in swimming activity between the control period and the test period were determined for each fish. These differences were compared with a *t*-test or with a Mann-Whitney *U*-test when data were not normally distributed.

Results

Fish swimming activity was changed by the presence of supercooled water, frazil and anchor ice. Out of the 12 fish exposed to test conditions, 6 (50%) were significantly ($P<0.05$) less active during the test period than the control period (Fig. 5-1). None of the fish were significantly ($P<0.05$) more active during the test period.

The escape response of rainbow trout decreased as the length of time they were exposed to supercooled water and frazil and anchor ice increased (Fig. 5-2). As the supercooling events progressed, visual observations showed that frazil and anchor ice became increasingly more abundant. However, since the density of frazil ice could not be quantified, fish activity was compared to the amount of time water was supercooled. The fish gradually became less disturbed when they were approached while anchor ice

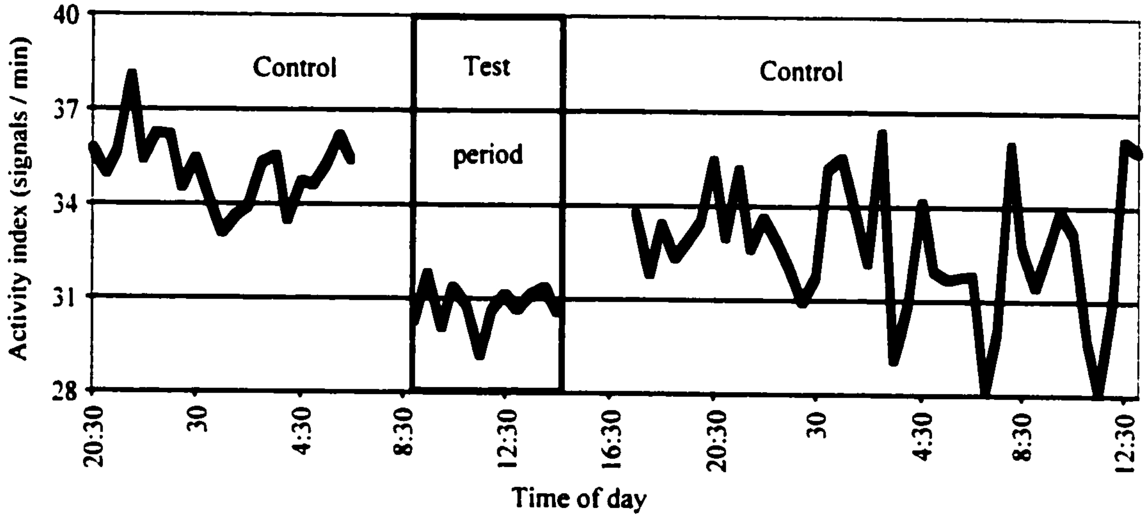

Figure 5-1. An example of the swimming activity of one EMG transmitter implanted rainbow trout during a test period of supercooling and frazil and anchor ice formation and during a control period. Lower levels on the activity index indicate lower swimming activity.

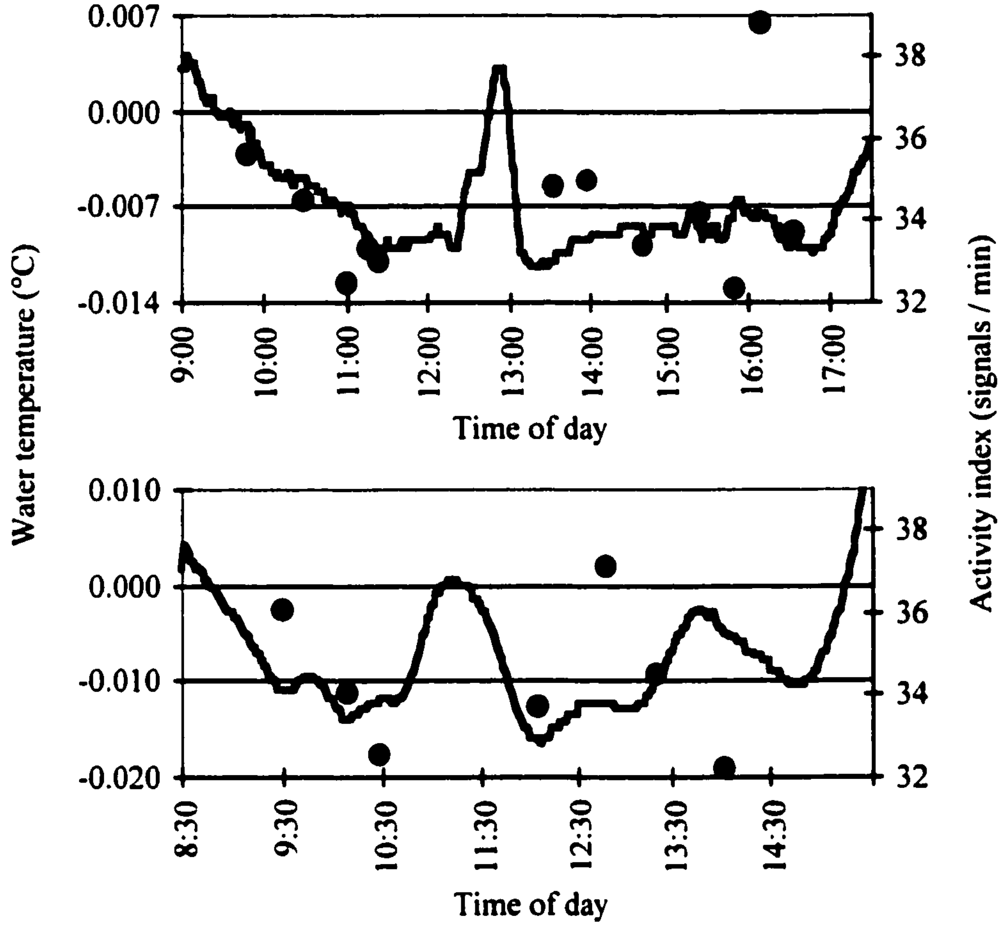

Figure 5-2. Water temperatures and swimming activity of EMG transmitter implanted rainbow trout during two test periods of supercooling and frazil and anchor ice formation. Lower levels on the activity index indicate lower swimming activity. The black circles indicate the mean swimming activity of implanted fish during five minute periods when ice was cleared from flume dividers. Frazil and anchor ice generally became more abundant as the amount of time the water was supercooled increased.

was scraped off the dividers that enclosed the fish in different sections of the flume. During supercooling, there was a significant (*P*<0.05) decrease in swimming activity as the amount of time fish were exposed to supercooling increased (Fig. 5-3). As Figure 5-3 shows, this analysis was performed after one outlying point was removed. During the test period, visual observations also showed that fish moved less as the duration of supercooling increased. At first, fish would swim away as they were approached to clear the dividers but as the duration of supercooling lengthened the fish did not appear disturbed even when approached to within 1 m.

Discussion

Through changes in the rate of swimming activity and escape response, an effect was seen from the exposure to supercooling and frazil and anchor ice. Half of the fish studied were less active during periods of supercooling and subsurface ice formation compared to control periods, none were more active. This decrease in activity may have broad implications for many areas of river management. This is especially true since, due to exclusions of habitat, fish are often forced to move during periods of subsurface ice formation to find more suitable habitats (Brown and Mackay 1995a; Jakober et al. 1998; Brown 1999).

Fish also moved less when approached as the amount of time they were exposed to supercooling and subsurface ice increased. Since supercooling and frazil ice events make fish less responsive to the approach of possible predators, predation is likely to increase substantially during this period. The combination of a repressed escape response and reduced activity at a time when habitats are changing dramatically, leaves fish

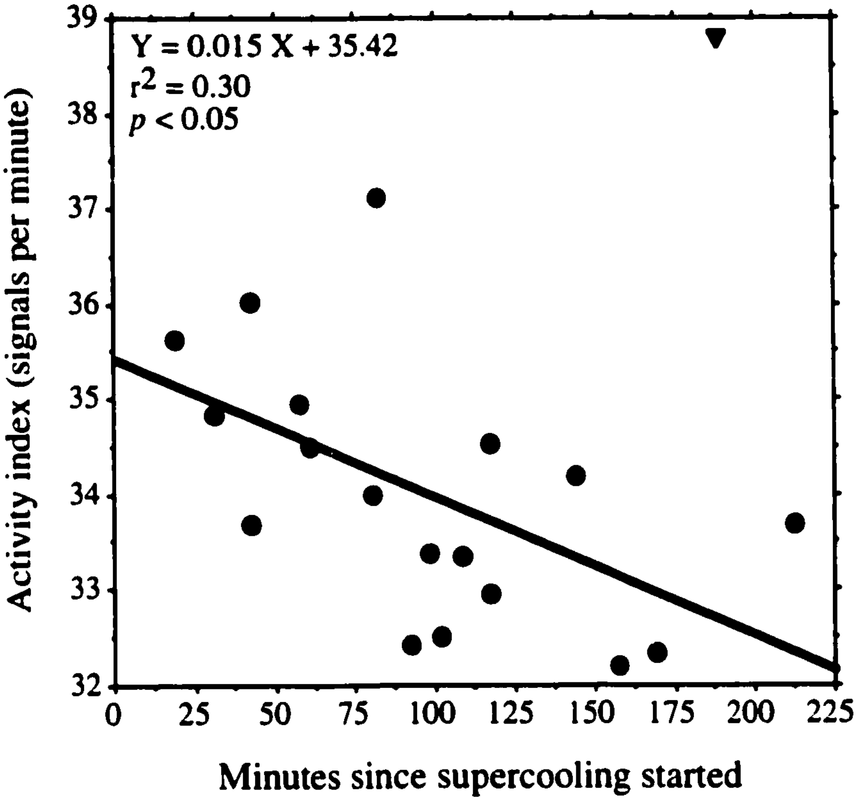

Figure 5-3. A regression plot of the activity index of EMG transmitter implanted rainbow trout at different periods of time after supercooling started. Mean swimming activity was calculated for all implanted fish during five minute periods when anchor ice was cleared off dividers which enclosed fish in a refrigerated flume. Lower levels on the activity index indicate lower swimming activity. Frazil and anchor ice generally became more abundant as the amount of time the water was supercooled increased. The activity of fish during one clearing interval was not included in this analysis (but it is graphed as a triangle) since it was an outlier.

particularly vulnerable to avian and mammalian predators which are not restrained by low temperatures.

Since trout are less active and appear to repress their escape response when exposed to supercooling and subsurface ice, moving into aggregations may partially offset the increased danger of predation. Many species of salmonids move into aggregations during winter. Brown (1999), reported that the percentage of radiotagged cutthroat trout in aggregations was negatively correlated with mean weekly water temperatures in the fall and early winter. Many other authors have also noted trout in large aggregations during winter (Hartman 1965; Cunjak and Power 1986; Brown and Mackay 1995a; Jakober et al. 1998). Brown (1999) suggested that this increasingly gregarious behaviour as temperatures decrease may reduce the chances of predation during cold winter temperatures when swimming ability is decreased (Videler 1993). Aggregation in deeper pools correlates well with a reduction in activity and repression of the escape response as well as providing some protection against frazil and anchor ice. Shoaling behaviour (such as aggregation) provides many advantages in predator avoidance (Pitcher 1986), and may partially offset the increased danger of predation fish experience during frazil ice events.

Many salmonids make behavioural changes in the fall and early winter which allow them to avoid or at least decrease their exposure to frazil and anchor ice. Many species of trout move out of shallow, faster habitats and into deeper, lower velocity habitats in the fall or early winter (Chisholm et al. 1987; Baltz et al. 1991; Heggenes et al. 1993; Brown and Mackay 1995a; Jakober et al. 1998). Shallow, turbulent mountain streams are often fully mixed throughout the water column with the result that suspended frazil is encountered at all depths. In deeper, slower water, the frazil tends to accumulate into buoyant flocs that rise to the surface. Because full mixing is less likely in deeper, slower water, anchor ice is also less likely to occur in deeper areas than in shallower habitats. Thus, movement towards deeper habitats should decrease the amount of frazil ice that fish are exposed to in the water column.

As temperatures decrease in the fall and early winter many salmonids move into areas kept warm by groundwater influx (Cunjak and Power 1986; Brown and Mackay 1995a; Brown 1999). These groundwater inflows often provide refuges from exposure to frazil and anchor ice (Power et al. 1999). However, as Brown (1999) warns, these groundwater sources must have sufficient influx of warm water during winter, or during very cold periods they may become filled with anchor ice and be much less suitable for fish.

Further work should be carried out to determine the response of fish to supercooling and frazil ice events. Activity of trout in tailraces of dams should be examined to determine if adult fish move out of these areas when multiple frazil events occur, as should the behaviour and success of juvenile fish in these areas. The behaviour of avian and mammalian predators should also be examined to see if they are more numerous or more successful in tailraces than in other areas. Studies are needed on the influence of supercooling and subsurface ice on other species of fish, especially fish that are not hatchery reared. Wild fish may respond quite differently than hatchery fish. In our work, the hatchery fish were exposed to supercooling and frazil ice for the first time so they may have acted differently than wild fish. However, the fish we tested should represent the large number of fish which are stocked into rivers and streams each year.

Tests should also be done to determine if fish become less influenced after multiple exposures to supercooling and frazil ice. The fish may become accustomed to the conditions and act more normally.

In conclusion, effects of supercooling and frazil and anchor ice were found. Adult fish were less active and had a reduced escape response. Supercooling and subsurface ice conditions may greatly increase the likelihood of predation to fish. These effects may also make areas where supercooling and subsurface ice occur of lower suitability than other areas. This important, and chronically overlooked area of fisheries management merits much more attention and future research.

Chapter 6

General Discussion

General Discussion

It can be seen from the previous chapters that many of ideas people have about overwintering fish are false. Fish are surprisingly active. But then again, the winter environment of rivers in temperate climes is likely much more dynamic than generally realized, and fish are forced to respond appropriately if they are to survive.

Many scientists suggest that fish exhibit energy efficient strategies (Smith and Li 1983; Bachman 1984; Fausch 1984; Cunjak and Power 1996). Such strategies would include conservation of energy by minimizing metabolic costs, such as swimming activity, during the winter. This concept may apply with young of the year or juvenile fish, or even adults of other species, but does not seem to fit for adult riverine brown trout, white sucker or common carp. Cunjak and Power (1987) noted that many fish had winter metabolic deficiencies which may make reducing activity attractive. However, even though it may result in a loss of weight, remaining active may be advantageous in avoiding the many dangers present in riverine environments during winter, thus increasing survival.

As can be seen throughout this thesis, and the work of others, temperate riverine environments can be highly variable during winter (Cunjak et al. 1998). Few if any habitats are stable, and fish have to cope with this constantly changing environment. Hanging dams fill otherwise suitable looking overwintering pools, and anchor ice can fill shallower habitats. The break-up of river ice and flooding can change habitats throughout the river both quickly and dramatically. Fish appear to be very adaptable, however, changing behaviours, staying active, and making movements to place themselves in suitable habitats throughout all of these changes. Fish moved when hanging dams formed and during winter flooding and ice break-up. Had they been in a state of near hibernation, they may have been surrounded by frazil ice and frozen when hanging dams formed. If fish did not remain sufficiently active, they would have an increased chance of being washed downstream during floods and possibly being physically damaged or stranded. As described in chapter 2, under certain circumstances, many fish can be stranded on the floodplain following the break-up of river ice and mid-winter flooding which emphasizes the problems they must cope with. Remaining active and maintaining searching behaviour may provide an advantage for fish returning to the main channel of rivers as flood waters subside and the main channel once again becomes suitable.

The effects of flooding on fish differed among species and was reflected in both changes in movement, habitat use, and swimming activity. Increases in water discharge had much less of an influence on brown trout than on white sucker and common carp. For brown trout there was no consistent change in swimming activity with increasing water discharge, and no consistent increases in movement either. With both white sucker and common carp however, swimming was curtailed during periods of high water discharge, as many fish moved out of their regular habitats into backwaters. At the same time, many white sucker and common carp made downstream movements, possibly being caught in the current while trying to retain their original positions. These differences in response to water discharge are likely due to the relative differences in body shape and swimming ability among the species. White sucker and common carp are unlikely to perform at the same level as salmonids which are more adapted to life in swift water. Thus a lack of refuge habitats, such as backwaters, will make some river sections less suitable for certain fish species. This could be why large adult white sucker are seldom captured in Elora Gorge (Brown, unpublished data), while they are common below the gorge. Habitat diversity is necessary to maintain species diversity.

The presence fo numerous ice break-ups and floods may make riverine habitats more demanding in milder climates than the colder areas of North America where only one spring break-up is observed. One of the primary dangers posed by these additional break-ups is that fish may be stranded on the shores of rivers. This appeared to be one of the few times that mortalities of many fish was easily observed. Multiple floods may also increase the energetic demands of fish since increasing movements were observed. However, this may be offset by decreased activity of fish which was observed in some common carp and white sucker while they were taking shelter in backwaters during floods. Predation may also be very different depending on the duration of ice cover. The shorter period of ice cover seen in milder portions of Canada may drastically increase the amount of predation or predatory attacks, making these climates even more harsh and energetically demanding for riverine fish.

The dynamic environment of rivers in winter may be one reason fish did not have any consistent diel patterns. Fish were often shifting habitats and moving as water discharge changed, as ice excluded habitats, and as frequent loads of frazil ice passed through the water column, making a consistent diel pattern difficult. This dynamic environment would also explain why there was a large amount of variance among distances swum per day by fish. Laboratory results confirmed that swimming activity of many fish was changed by the presence of frazil ice. However, even under stable surface ice cover diel patterns varied among individuals, possibly stemming from the different energy stores/reserves of fish or different habitat types.

Some of the variability in diel patterns of fish may have been due to the presence of other species. Common carp are very large and often were in aggregations during winter. They appeared to be forcing white sucker out of habitats in videotaped observations (Brown, unpublished data). This may be why those white sucker which were not arrhythmic had opposite diel patterns to many common carp. As common carp become acclimated to the cold, their swimming ability improves (Videler 1993). They are about twice as active as white sucker and brown trout, which may be forced to increase activity to avoid them, or change their activity patterns to be active when common carp are not. Clearly there are many variables that can influence fish during winter.

A contradiction seems to exist between trout activity during periods of frazil and anchor ice production in the field and in laboratory conditions. One brown trout had a large increase in activity during an approximately two week period of anchor ice formation. This pattern is expected since several other researchers have found fish moving more during periods of anchor ice formation (Brown and Mackay 1995a; Jakober et al. 1998; Brown 1999). However, half of the rainbow trout studied in the laboratory, as described in chapter 5, were less active during periods of supercooling and subsurface ice formation. While fish may be less active during the actual supercooling period, during the day when frazil is unlikely to be forming, the fish are likely forced to be more active, searching for new habitats not filled with anchor ice. Clearly this is both an area of concern and an area in need of further research.

This research points out that fish do require special habitats during winter. Groundwater inflows often provide refuges from exposure to frazil and anchor ice (Power et al. 1999). In this study, some brown trout took refuge from hanging dams by moving into a small groundwater area. Backwaters are also valuable habitats and should be protected as areas of refuge.

The results of this thesis, while answering many questions, have posed a series of new questions which identify areas for future research. Are the changes in activity and movement totally due to the variable nature of the riverine environment? Is there similar variability among individuals in regard to activity and movement in lakes as in rivers? Are fish which tend to aggregate more during winter less mobile and active? How do fish respond to an increased level of environmental fluctuation such as that caused by hydropeaking operations below dams? How is activity influenced by the higher incidence of frazil ice events which are expected below dams? Do fish become more active and have larger energetic deficits in more dynamic temperate rivers than in more stable Arctic rivers? Is mortality and predation higher in dynamic rivers? Small rivers and streams in colder climates usually have a short freeze-up period followed by a fairly stable period of surface ice cover (Prowse 1995). Fish in these habitats may have lower energetic demands and different diel patterns than in a river in southern Ontario where air temperatures often fluctuate around the freezing point all winter, and mid-winter floods are common. Global warming may have large implications in this area. A rise in air temperatures would reduce the amount of time surface ice is present on many of Canada's rivers (Beltaos 1997). This decrease in the duration of surface ice cover may make habitats more variable and have negative influences on fish.

Much more research needs to be done to determine the effects of river ice on fish and their habitats. With more cooperative work between fisheries scientists and river ice scientists, as was seen in this thesis, in a short period of time, major advances could be made in understanding how river ice influences fish and fish habitat. As can be seen, there are many areas where further research is needed, but the difficulties in completing winter field work do not outweigh the benefits of the results.

References

Alanara, A., and E. Brannas, 1997. Diurnal and nocturnal feeding activity in Arctic char (*Salvelinus alpinus*) and rainbow trout (*Oncorhynchus mykiss*). Canadian Journal of Fisheries and Aquatic Sciences 54: 2894-2900.

Allen, W. T. R. 1977. Freeze-up, break-up and ice thickness in Canada. Report No. CLI-1-77, Atmospheric Environment, Fisheries and Environment Canada, Downsview, Ontario, 185 pp.

Bachman, R. A. 1984. Foraging behaviour of free-ranging wild and hatchery brown trout in a stream. Transactions of the American Fisheries Society 113: 1-32.

Baltz, D. M., B. Vondracek, L. R. Brown, and P. B. Moyle. 1991. Seasonal changes in microhabitat selection by rainbow trout in a small stream. Transactions of the American Fisheries Society 120: 166-176.

Beddow, T. A., and R. S. McKinley. 1999. Importance of electrode positioning in biotelemetry studies estimating muscle activity in fish. Journal of Fish Biology 54: 819-831.

Beltaos, S. (Ed.) 1995. *River Ice Jams.* Water Resources Publications, Highlands Ranch, Colorado.

Beltaos, S. 1997. Effects of climate on river ice jams. *Proc. 9th Workshop on River Ice*, Fredericton, N. B., 24-Sept. 1997:225-240.

Beltaos, S., and A. M. Dean. 1981. Field investigations of a hanging ice dam. In IAHR International Ice Symposium pp. 475-485. Quebec, Canada.

Berg, N. H. 1994. Ice in stream pools in California's central Sierra Nevada: spatial and temporal variability and reduction in trout habitat availability. North American Journal of Fisheries Management 14: 372-384.

Bisson, P. A., J. L. Nielsen, R. A. Palmason, and L. E. Grove. 1982. A system of naming aquatic habitat types in small stream, with examples of habitat utilization by salmonids during low streamflow. Pages 62-72 *in* N. B. Armantrout, editor. Symposium on Acquisition and Utilization of Aquatic Habitat Inventory Information. Western Division, American Fisheries Society, Portland, Oregon, USA.

Bowerman, B. L., and R. T. O'Connell. 1990. *Linear Statistical Models: An Applied Approach*. PWS-Kent Publishing Company, Boston.

Briggs, C. T., and J. R. Post. 1997a. Field metabolic rates of rainbow trout estimated using electromyogram telemetry. Journal of Fish Biology 51: 807-823.

Briggs, C. T., and J. R. Post. 1997b. In situ activity metabolism of rainbow trout (*Oncorhynchus mykiss*): estimates obtained from telemetry of axial muscle electromyograms. Canadian Journal of Fisheries and Aquatic Sciences 54: 859-866.

Brown, R. S. 1999. Fall and early winter movements of cutthroat trout, *Oncorhynchus clarki*, in relation to water temperature and ice conditions in Dutch Creek, Alberta. Environmental Biology of Fishes 55: 359-368.

Brown, R. S., J. C. Brodeur, G. Power, S. F. Daly, K. D. White, and R. S. McKinley. 1999. Blood chemistry and swimming activity of rainbow trout exposed to supercooling and frazil ice. *Proc. 10th Workshop on River Ice*, Winnipeg, Manitoba.

Brown, R. S., and W. C. Mackay. 1995a. Fall and winter movements of and habitat use by cutthroat trout in the Ram River, Alberta. Transactions of the American Fisheries Society 124: 873-885.

Brown, R. S., and W. C. Mackay. 1995b. Spawning ecology of cutthroat trout (*Oncorhynchus clarki*) in the Ram River, Alberta. Canadian Journal of Fisheries and Aquatic Sciences 52: 983-992.

Brown, R. S., G. Power, R. S. McKinley, and S. Beltaos. 1998. Effects of hanging dams, surface ice break-up, and flooding on fish. Proc. of the 14th International Symposium on ice. Potsdam, NY, Volume 1, p. 175-181.

Brown, R. S., S. S. Stanislawski, and W. C. Mackay. 1994. Effects of frazil ice on fish. In Proceedings of the Workshop on Environmental Aspects of River Ice (T. D. Prowse, T. D. ed.) pp. 261-278. Saskatoon, Sask: NHRI Symposium No. 12., National Hydrology Research Institute, Environment Canada.

Brown, T. G., and G. F. Hartman. 1988. Contributions of seasonally flooded lands and minor tributaries to the production of coho salmon in Carnation Creek, British Columbia. Transactions of the American Fisheries Society 117: 546-551.

Bunnel, D. B. Jr., J. J. Isely, K. H. Burrell, and D. H. Van Lear. 1998. Diel movement of brown trout in a southern Appalachian river. Transactions of the American Fisheries Society 127: 630-636.

Caissie, D., S. M. Komadina-Douthwright, R. A. Cunjak, and B. Burrell. 1997. Ice conditions in the Southwest Miramichi River and its possible influence on winter movement of post-spawned Atlantic salmon. *Proc. 9th Workshop on River Ice*, Fredericton, N. B., 24-Sept. 1997:371-390.

Carlander, K. D., and R. E. Cleary. 1949. The daily activity patterns of some freshwater fish. The American Midland Naturalist 41(2): 447-452.

Chisholm, I. M., W. A. Hubert, and T. A. Wesche. 1987. Winter stream conditions and use of habitat by brook trout in high-elevation Wyoming streams. Transactions of the American Fisheries Society 116: 176-184.

Clapp, D. F., R. D. Clark Jr., and J. S. Diana. 1990. Range, activity, and habitat of large, free-ranging brown trout in a Michigan stream. Transactions of the American Fisheries Society 119: 1022-1034.

Cunjak, R. A. 1988. Physiological consequences of overwintering in streams: the cost of acclimitization. Canadian Journal of Fisheries and Aquatic Sciences 45: 433-452.

Cunjak, R. A., and D. Caissie. 1994. Frazil ice accumulation in a large salmon pool in the Miramichi River, New Brunswick: ecological implications for overwintering fishes. In Proceedings of the Workshop on Environmental Aspects of River Ice (T. D. Prowse, T. D. ed.) pp. 279-295. Saskatoon, Sask: NHRI Symposium No. 12., National Hydrology Research Institute, Environment Canada.

Cunjak, R. A., and G. Power. 1986. Winter habitat utilization by stream resident brook trout *Salvelinus fontinalis* and brown trout *Salmo trutta*. Canadian Journal of Fisheries and Aquatic Sciences 43: 1970-1981.

Cunjak, R. A., and G. Power. 1987. The feeding and energetics of stream-resident trout in winter. Journal of Fish Biology 31: 493-511.

Cunjak, R. A., T. D. Prowse, and D. L. Parrish. 1998. Atlantic salmon (*salmo salar*) in winter: "the season of parr discontent"? Canadian Journal of Fisheries and Aquatic Sciences 55(Suppl. 1): 161-180.

Demers, E., McKinley, R. S., Weatherley, A. H. and D. J. McQueen. 1996. Activity patterns of largemouth and smallmouth bass determined with electromyogram biotelemetry. Transactions of the American Fisheries Society 125: 434-439.

Emery, A. R. 1973. Preliminary comparisons of day and night habits of freshwater fish in Ontario lakes. Journal of the Fisheries Research Board of Canada 30: 761-774.

Eriksson, L-O. 1978. Nocturnalism versus diurnalism – dualism within fish individuals. In *Rhythmic activity of fishes* (Thorpe, J. E., ed.), pp. 69-89 New York, Academic.

Ettema, R., J. F. Kennedy, and F. Karim. 1982. Influence of turbulence and temperature of frazil ice formation. Pages 176-195 *in* D. D. Andres and R. Gerard, editors. Proceedings of the workshop on hydraulics of ice covered rivers. National Research Council of Canada, Subcommittee on Hydraulics of Ice Covered Rivers, Ottawa.

Fausch, K. D. 1984. Profitable stream positions for salmonids: relating specific growth rates to net energy gain. Canadian Journal of Zoology 62: 441-451.

Fraser, N. H. C., N. B. Metcalfe, and J. E. Thorpe. 1993. Temperature-dependent switch between diurnal and nocturnal foraging in salmon. Proceedings of the Royal Society of London B, Biological Science 252: 135-139.

Gerard, R. 1989. Hydroelectric power development and the ice regime of inland waters: a northern community perspective. National Hydrology Research Institute Contract Report No. 89001. Saskatoon, Saskatchewan.

Giannico, G. R., and M. C. Healey. 1998. Effects of flow and food on winter movements of juvenile coho salmon. Transactions of the American Fisheries Society 127: 645-651.

Gold, L. W., and G. P. Williams. 1963. An unusual ice formation on the Ottawa River. Journal of Glaciology 4(31): 569-573.

Hartman, G. F. 1965. Role of behavior in the ecology and interaction of underyearling coho salmon (*Oncorhynchus kisutch*) and steelhead trout (*Salmo gairdneri*). Journal of the Fisheries Research Board of Canada 22: 1035-1081.

Heggenes, J., T. G. Northcote, and A. Peter. 1991. Spatial stability of cutthroat trout (*Oncorhynchus clarki*) in a small, coastal stream. Canadian Journal of Fisheries and Aquatic Sciences 48: 757-762.

Heggenes, J., O. M. Krogg, O. R. Lindas, J. G. Dokk, and T. Bremnes. 1993. Homeostatic behavioral responses in a changing environment: brown trout (Salmo trutta) become nocturnal during winter. Journal of Animal Ecology 62: 295-308.

Helfman, G. S. 1986. Fish behaviour by day, night, and twilight. In, Tony J. Pitcher editor, *The Behaviour of Teleost Fishes*. The Johns Hopkins University Press, Baltimore, Maryland.

Hinch, S. G., R. E. Diewert, T. J. Lissimore, A. M. J. Prince, M. C. Healey, and M. A. Henderson. 1996. Use of electromyogram telemetry to assess difficult passage areas for river-migrating adult sockeye salmon. Transactions of the American Fisheries Society 125: 253-260.

Jakober, M. J., T. E. McMahon, R. E. Thurow, and C. G Clancy. 1998. Role of stream ice on fall and winter movements and habitat use by bull trout and cutthroat trout in Montana headwater streams. Transactions of the American Fisheries Society 127: 223-235.

Johnston, I. A., J. D. Fleming, and T. Crockford. 1990. Thermal acclimation and muscle contraction properties in cyprinid fish. American Journal of Physiology 259: R231-236.

Kerr, D. J., H. T. Shen, and S. F. Daly. 1997. Anchor ice formation and growth on gravel channel bed. *Proc. 9th Workshop on River Ice*, Fredericton, N. B., 24-Sept. 1997:153-171.

Komadina-Douthwright, S. M., D. Caissie, and R. A. Cunjak. 1997. Winter movement of radio-tagged Atlantic salmon (*Salmo salar*) kelts in relation to frazil ice in pools of the Miramichi River. Canadian Technical Report of Fisheries and Aquatic Sciences 2161: 66p.

Maciolek, J. A., and P. R. Neeham. 1952. Ecological effects of winter conditions on trout and trout foods in Convict Creek, California, 1951. Transactions of the American Fisheries Society 81: 202-217.

Martin, J., E. Garcia-Ceballos, J. C. Escudero, and J. J. Perez-Regardera. 1998. Interspecific relationships between tench, *Tinca tinca* (L.) and carp, *Cyprinus carpio* L., relative to preferred light intensity. Polski Archiwum Hydrobiologii 43:393-398.

Matheney, M. P., and C. F. Rabeni 1995. Patterns of movement and habitat use by northern hog suckers in an Ozark Stream. Transactions of the American Fisheries Society 124: 886-897.

McKinley, R. S. and G. Power. 1992. Measurement of activity and oxygen consumption for adult lake sturgeon (*Acipernser fulvescens*) in the wild using radiotransmitter EMG signals. Pages 307-318 *in* I. G. Priede and S. M. Swift, editors. *Wildlife telemetry: remote monitoring and tracking of animals*. Ellis Horwood, New York.

McMahon, T. E., and G. F. Hartman. 1989. Influence of cover complexity and current velocity on winter habitat use by juvenile coho salmon (*Oncorhynchus kisutch*). Canadian Journal of Fisheries and Aquatic Sciences 46:1551-1557.

Metcalfe, N. B., N. H. C. Fraser, and M. D. Burns. 1998. State-dependent shifts between nocturnal and diurnal activity in salmon. Proceedings of the Royal Society of London B 265: 1503-1507.

Meyers, L. S., T. F. Thuemler, and G. W. Kornely. 1992. Seasonal movements of brown trout in northeast Wisconsin. North American Journal of Fisheries Management 12: 433-441.

Michel, B. 1975. The formation of ice covers. Universite Laval Report GCS-75-09-05.

Pearsons, T. N., and H. W. Li. 1992. Influence of habitat complexity on resistance to flooding and resilience of stream fish assemblages. Transactions of the American Fisheries Society 121: 427-436.

Pitcher, T. J. 1986. Function of shoaling behaviour in teleosts. In, Tony J. Pitcher editor, *The Behaviour of Teleost Fishes*. The Johns Hopkins University Press, Baltimore, Maryland

Power, G., R. S. Brown, and J. G. Imhof. 1999. Groundwater and fish – insights from northern North America. Hydrological Processes 13: 401-422.

Prowse, T. D. 1995. River ice processes. In, S. Beltaos editor, *River Ice Jams*. Water Resources Publications, Highlands Ranch, Colorado.

Reynolds, W. W., and M. E. Casterlin. 1978. Behavioural thermoregulation and diel activity in white sucker (*Catostomus commersoni*). Comparative Biochemistry and Physiology 59A: 261-262.

Richardson, N. E., and J. D. McCleave. 1974. Locomotor activity rhythms of juvenile Atlantic salmon (*Salmo salar*) in various light conditions. Biological Bulletin 147: 422-432.

Rimmer, D. M., R. L. Saunders, and U. Paim. 1985. Effects of temperature and season on the position holding performance of juvenile Atlantic salmon (*Salmo salar*). Canadian Journal of Zoology 63: 92-96.

Rosgen, D. 1996. *Applied River Morphology*. Printed Media Companies, Minneapolis, MN.

Saunders, R. L. 1963. Respiration of the Atlantic cod. Journal of the Fisheries Research Board of Canada 20: 373-385.

Scott, W. B., and E. J. Crossman. 1998. *Freshwater fishes of Canada*. Galt House, Oakville, Ontario, Canada.

Scruton, D. A., K. D. Clarke, F. A. Bowdring, and C. J. Pennell. 1997. Winter habitat availability for salmonids in Newfoundland streams: a comparison between stream order and habitat type. *Proc. 9th Workshop on River Ice*, Fredericton, N. B., 24-Sept. 1997:425-439.

Smith, J. J., and H. W. Li. 1983. Energetic factors influencing foraging tactics of juvenile steelhead trout, *Salmo gairdneri*. p. 173-180. *In* D. L. G. Noakes et al.

(ed.) *Predators and prey in fishes*. Dr. W. Junk Publishers, The Hague, The Netherlands.

Smith, L. S., and T. W. Newcomb. 1970. A modified version of the Blazka respirometer and exercise chamber for large fish. Journal of the Fisheries Research Board of Canada 27: 1321-1324.

Spencers. W. F. 1929. Day and night periodicity in the activity of four species of freshwater fishes. Anatomical Record 44: 197.

Spoor, W. A., and C. L Schloemer. 1938. Diurnal activity of the common sucker, *Catostomus commersonnii* (Lacepede), and the rock bass *Ambloplites rupestris* (Rafinesque), in Muskellunge Lake. Transactions of the American Fisheries Society 68: 211-220.

Tack, E. 1938. Trout mortality from the formation of suspended ice crystals. Progressive fish Culturalist 37:26.

Tsang, G. 1982. Frazil and anchor ice, a monograph. NRC Subcommittee on Hydraulics of Ice-Covered Rivers, Ottawa.

Tschaplinski, P. J., and G. F. Hartman. 1983. Winter distribution of juvenile coho salmon (*Oncorhyncus kisutch*) before and after logging in Carnation Creek, British Columbia, and some implications for overwintering survival. Canadian Journal of Fisheries and Aquatic Sciences 40: 452-461.

Videler, J. J. 1993. *Fish swimming*. Chapman and Hall, London. 260 pp.

Weatherley, A. H., P. A. Kaseloo, M. D. Gare, J. M. Gunn., and B. Lipicnik. 1996. Field activity of lake trout during the reproductive period monitored by electromyogram radiotelemetry. Journal of Fish Biology 48: 675-685.

Whalen, K. G. and D. L. Parrish. 1999. Nocturnal habitat use of Atlantic salmon parr in winter. Canadian Journal of Fisheries and Aquatic Sciences 56: 1543-1550.

Whalen, K. G., D. L. Parrish, and M. E. Mather. 1999. Effect of ice formation on selection of habitats and winter distribution of post-young-of-the-year Atlantic salmon parr. Canadian Journal of Fisheries and Aquatic Sciences 56: 87-96.

White, K. D., S. F. Daly, and J. J. Gagnon. 1999. Simulating Winter Environments for Aquatic Life in the CRREL Refrigerated Flume. *Proc. 10th Workshop on River Ice*, Winnipeg, Manitoba.

Young, M. K. 1999. Summer diel activity and movement of adult brown trout in high-elevation streams in Wyoming, U.S.A. Journal of Fish Biology 54: 181-189.

Young, M. K., R. A. Wilkison., J. M. Phelps III, and J. S. Griffith. 1997. Contrasting movement and activity of large brown trout and rainbow trout in Silver Creek, Idaho. Great Basin Naturalist 57: 238-244.