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RENÉ D I O N, F R E D W H O R I S K E Y

RESOURCE PARTITIONING IN A SPRING SPAWNING FRESHWATER  
FISH ASSEMBLAGE DOMINATED BY CATOSTOMIDS  
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ABSTRACT

Fishes may partition spawning habitat either spatially or temporally to reduce the negative effects of competition, which include interference, egg/larvae destruction and hybridization. For three consecutive years, we monitored the spring stream residency and spawning of five fishes using a tributary stream of the Gouin Reservoir (North Central Québec). Timing of spawning of the distantly related species was different whereas the spawning activity of the closely related suckers overlapped in time and space. Intra- and inter-specific egg predation by the two sucker species was observed as well as predation by lake whitefish (*Coregonus clupeaformis*) on sucker eggs. Synchronisation of the spawning of the suckers may allow them to "swamp" egg predators with drifting eggs. Abundance of spawning fish was affected by water management practices in the reservoir. When water levels were low, fewer fish of all species had access to the stream possibly because of the development of rapids.

Key words: suckers, spawning, habitat partitioning

1. INTRODUCTION

Multispecies fish spawning assemblages can show spatial and temporal separation of spawning activity, possibly to avoid the negative effects of adult spawning competition for spawning sites (C u r r y, S p a c i e 1984) or to permit larvae to hatch at different times, decreasing the possibility of competition for food (C o r b e t, P o w l e s 1986). Temporally or spatially different spawning activity can also act as an isolating mechanism to prevent the mixing of different stocks adapted to local conditions, thereby minimizing the risk of breakdown of coadapted gene complexes (L e i d e r e t a l. 1985; S a i t o h 1990). It can also prevent hybridization of closely related species (B a r t n i k 1970). However, the synchronization of spawning periods of many species may decrease predation on eggs or larvae through a "predator swamping" effect (M c K a y e 1977).

Human activities often alter flow patterns of streams. These changes can have important effects on fishes (I n s k i p 1986; N e l s o n 1968). Most temperate freshwater fish prefer flowing water for reproduction (M a n s f i e l d 1984). Decreased flows caused by damming of streams to create reservoir-

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irs, or by drought, can limit available flowing water habitats causing spawning fishes to congregate together and concentrate their spawning activity. Competitive interactions may then negatively affect some species (Inskip 1986; Nelson 1965, 1973).

For three consecutive years (1986, 1987, 1988), spawning activity of fishes was monitored in a 2 km long stream that forms the outlet of Lac des Cinq Milles (100 ha surface area) and drains into the Gouin Reservoir (150,200 ha surface area). This reservoir was flooded in 1918, transforming a large portion of the St-Maurice River into lacustrine habitat. The assemblage of species found in these bodies of water is typical of northern boreal lakes.

Each spring, northern pike (*Esax lucius*), (*Stizostedion vitreum*), white and longnose suckers (*Catostomus commersoni*, *C. catostomus*), and fallfish (*Semotilus corporalis*) from both the lake and the reservoir spawn in this stream. Lake whitefish (*Coregonus clupeaformis*) are also present as egg predators (Dion, Whoriskey 1992). Although some form of resource partitioning in time or space might be expected to lower interspecific competitive interactions at spawning sites, it is not clear that the limited space available to this fish assemblage permits partitioning of resources during reproduction. Geen et al. (1966) suggested that in temporary streams, early spawning might have selective advantages. However, Hayes (1987) reported that for benthic spawners which lay eggs in nests, late spawning might be advantageous to avoid nest (egg) destruction by fish which subsequently spawn in the same place and turn up the gravel substrate. Temporal overlap in spawning might be selected for by a high predation rate on eggs and young (predator swamping effect, McKaye 1977).

We studied the stream residency and spawning of the fishes of the Lac des Cinq Milles outlet stream. Our objectives were to: (1) quantify the spatial and temporal partitioning of this habitat among the fishes, (2) verify if fish populations from the reservoir and from the lake segregate on spawning grounds, and (3) document egg predation by fishes in the stream, and its potential influence on spawning success.

## 2. MATERIALS AND METHODS

The study was conducted in the clear water stream that joins Lac des Cinq Milles with the Gouin Reservoir (48°15' N, 74°30' W). The reservoir is located in North Central Quebec. The stream is approximately 2 km long, and its width varies from 10 to 15 m. Two sections of rapids where water velocity varies from 0.5 to 1.5 m s<sup>-1</sup> are present, one at the junction with the reservoir and the second located approximately 0.6 km upstream from the reservoir. Average depth is 1.5 m but varies between 0.5 to 2 m during spring. The substrate is composed of organic debris and sand in the upstream section, and a mixture of sand, boulders and fine gravel downstream from the first rapid.

To monitor stream entry of fishes, two way traps were operated at two points along the stream: 1) near the junction of the stream with the reservoir, just above the first section of rapids (station 1), and at the inlet from the Lac des Cinq Milles (station 2) (Fig. 1).

The traps were installed after ice breakup, and were fished from 20 May to 15 July 1986, 1 May to 30 June 1987 and from 10 May to 10 June 1988. In 1986, the traps were installed after suckers had started spawning. Groups of suckers entering from the reservoir and the lake were tagged with different colored (blue and yellow respectively) floy tags, permitting us to determine if fish of these different origins associated together on the spawning sites. In 1987 and 1988 the traps were installed the day following ice break-up. The number of fish captured leaving the river was low which probably indicates the poor efficiency of the traps for departing fish. This is probably an effect of fluctuating water levels and the debris that accumulated in the wings of the net.

Daily maximum/minimum water temperatures were recorded. All fish captured were counted, and sexed where possible from secondary sexual characteristics. Large fish were given a distinctive fin clip identifying origin, and were tagged in 1987 for visual observations with Floy spaghetti tags (blue for fish entering from the reservoir and yellow for those entering from the lake). Small fish were only given a fin clip. After tagging, all fish were returned to the stream in the direction they were moving.



to 4 June 1987, and from 20 May to 31 May 1988 to enumerate the species present and to determine their sex and origin (reservoir versus Lac des Cinq Milles). This period corresponded with the peak of sucker spawning activity.

Fallfish nesting activity was also monitored in 1987 and 1988. Their gravel nest mounds were easily located. Visual observations were taken twice a day to determine a time budget of dominant males (observations of 15 minutes) and to count the total number of fish of all species present around the nests.

The intensity of sucker spawning was determined by measuring the volume of eggs captured in drift nets (750  $\mu\text{m}$  mesh) installed downstream from the four observation sites. Drift nets were emptied at 12-h intervals and eggs were preserved in 4% formalin, for later volumetric quantification in the laboratory. In 1987, three series of 48-h sets of the drift nets starting on May 21, May 26 and May 30. In 1988, egg drift was monitored daily throughout the spawning season (May 20 to May 31). Eggs of the two species of suckers could not be differentiated.

Non-parametric methods (Kendall's tau) were used to determine correlations between the abundance of each species present and the volume of eggs on the four sites.

### 3. RESULTS

#### STREAM ENTRY

Complete data on stream entries are available only for 1987 and 1988. In 1987 and 1988 fishes started entering the stream in early May, within a week after ice break-up, and 50% of the total number for all species had entered the stream by the end of May. The number of each species counted at station 1 was lower in 1988 than 1987, probably because of low water levels maintained to permit repairs on the reservoir dam. The low levels created rapids which might have prevented upstream migration of some fishes from the reservoir (walleye and lake whitefish). The lake and the reservoir were free of ice on 3 May 1987 and on 10 May 1988. Warming of the stream was interrupted by a cold period in 1987, which prolonged the spawning season by approximately five days as compared to 1988.

#### NORTHERN PIKE (*ESOX LUCIUS*)

Sixteen pike were caught in 1987 and 8 in 1988, virtually all from station 1. The absence of northern pike in the catches at station 2 would suggest that pike from the lake do not spawn in the stream. Northern pike from the reservoir have to ascend rapids where water velocity reaches 1.0 to 1.5  $\text{m s}^{-1}$  to reach spawning sites. In both years pike and walleye were the first entrants (10 May in 1987 and 12 May in 1988), when the daily average water temperature was 7°C (1987), or 5°C (1988; Tables II and III).

#### WALLEYE (*STIZOSTEDION VITREUM*)

A total of 115 entered the stream in 1987, 109 from the reservoir and 6 from the lake. In 1988, only 1 was caught moving from the reservoir, and none from the lake. This was probably because the low water levels in 1988 prevented upstream migration. These data suggest that lake residents are rarely using the stream for spawning. In 1987, walleye preceded suckers into the stream for spawning (50%

passed by May 9). Daily water temperature averaged 8°C during their upstream movement (Tables II and III).

Table II. Station 1 catch data on fishes entering the stream from the reservoir in 1987 and 1988

Species	Total number	Date first capture	Date 50% passed	Date peak migration	Avg. temp. at peak (°C)
Northern pike					
1987	16	3 May	10 May	10 May	7
1988	8	11 May	12 May	12 May	5
Walleye					
1987	109	1 May	9 May	6 May	8
1988	1				
Longnose sucker					
1987	575	6 May	15 May	14 May	8
1988	71	21 May	24 May	29 May	14
White sucker					
1987	6630	5 May	21 May	21 May	10
1988	1564	18 May	29 May	31 May	15
Lake whitefish					
1987	65	5 May	29 May	30 May	14
1988	2				
Fallfish					
1987	89	5 May	4 June	6 June	16
1988	18	18 May	29 May	31 May	15

WHITE AND LONGNOSE SUCKERS (*CATOSTOMUS COMMERSONI* AND *C. CATOSTOMUS*)

The timing of stream entry was similar (Tables II and III). Entry occurred when average temperature was over 10°C. Catch numbers were lower in 1988 than in 1987 at both stations. In both years, white sucker numerically dominated the catches at station 1 (ratio of 11.5:1 and 22:1, for 1987 and 1988, respectively) but similar numbers of both species moved in from the lake (1.2:1 and 1.4:1 for 1987 and 1988,  $X^2 p > 0.05$  for both years). White suckers entered the stream before longnose suckers in both years at both stations. However, the date by which 50% of the spawning fish of both species had entered the stream differed between stations in 1987 whereas it was similar in 1988 (Tables II and III).

FALLFISH (*SEMOTILUS CORPORALIS*)

Fallfish was the last species to enter the stream. Individuals from both the lake and the reservoir used the stream for spawning. The migration peak occurred earlier

Table III. Station 2 catch data on fishes entering the stream from Lac des Cinq Milles in 1987 and 1988. Low capture rates of northern pike, walleye and lake whitefish precluded calculation of some statistics

Species	Total number	Date first capture	Date 50% passed	Date peak migration	Avg. temp. at peak (°C)
Northern pike					
1987	1				
1988	0				
Walleye					
1987	6				
1988	0				
Longnose sucker					
1987	284	15 May	25 May	25 May	10.5
1988	85	18 May	21 May	21 May	16
White sucker					
1987	344	12 May	16 May	15 May	8.5
1988	122	18 May	21 May	21 May	16
Lake whitefish					
1987	0				
1988	0				
Fallfish					
1987	31	15 May	16 June	16 June	6
1988	27	18 May	25 May	25 May	14

for the fish coming from the lake than for those coming from the reservoir. Average daily temperature at peak migration times was 15°C except at station 2 in 1987 when it occurred when daily temperature averaged 9°C. Fewer fallfish were captured at station 1 (reservoir) in 1988 than in 1987 whereas similar numbers were captured in both years at station 2 (lake) (Tables II and III).

#### LAKE WHITEFISH (*COREGONUS CLUPEIFORMIS*)

Lake whitefish, a fall spawning species (Scott, Crossman 1973) were observed on spawning sites preying upon eggs of suckers and possibly walleyes (Dion, Whoriskey 1992). They were only captured moving to the stream from the reservoir. Most lake whitefish entered the stream after 50% of the suckers had completed their upstream migration. In 1987, 65 individuals were captured whereas only 2 were captured in 1988 (Tables II and III).

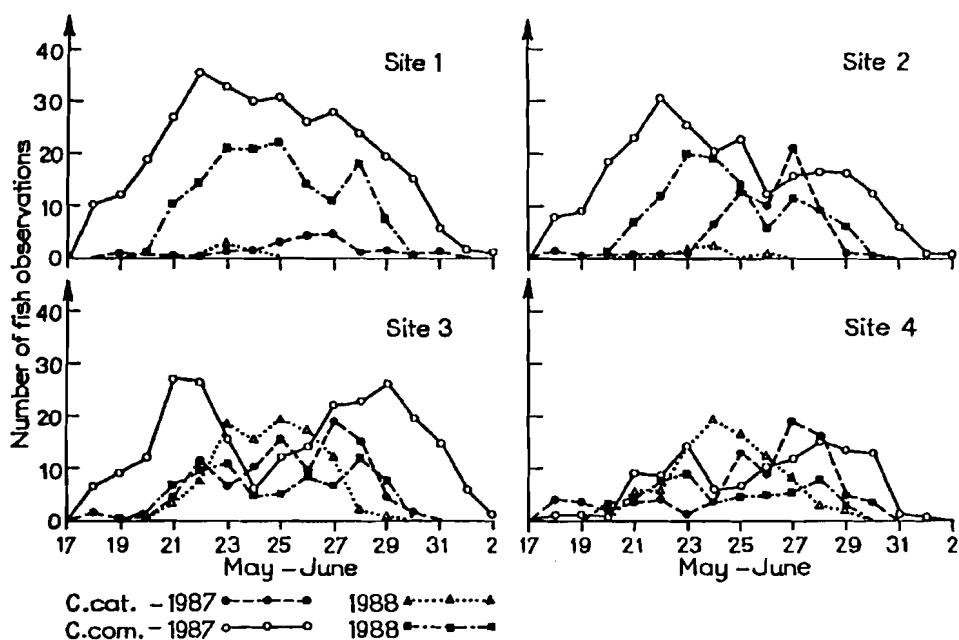


Fig. 2. Number of suckers observed on monitored sites in 1987 and 1988, in relation to date

#### FISH SPAWNING OBSERVATIONS AND EGG DRIFT

Spawning of pike and walleye was not observed during the three seasons but walleye eggs were found in drift nets and young pike were captured in fry traps later in the season (Dion, unpubl.). The white and longnose suckers were frequently observed spawning in 1987 and 1988. During 1987 and 1988 (Fig. 2) the two species were only partially spatially segregated on the spawning sites. Some individuals of both species occurred at all sites monitored. The abundance of white suckers decreased in a downstream direction in both years. Longnose suckers were equally abundant at sites 2, 3 and 4 in 1987 but numbers increased in a downstream direction in 1988. Overall, sites 1 and 2 were used most intensively by the white sucker whereas sites 3 and 4 were preferred by the longnose suckers.

Temporal separation of the spawning activity of the two suckers was not observed. Both species appeared over spawning substrate (sites 1 to 4) on 17 May in 1987 and on 19 May in 1988 and had left the sites by 1 June in 1987 and 30 May in 1988. Egg drift patterns overlapped at the four sites in 1987, and were similar at all sites in 1988 (Fig. 3), suggesting a concurrence of the spawning periods.

In 1988, the volume of drifting eggs at site 1 and 2 correlated positively and significantly with white sucker counts (site 1:  $T = 0.65$ ,  $p < 0.0006$  and on site 2:  $T = 0.60$ ,  $p < 0.0029$ ). Significant correlations were also obtained between egg drift volume and longnose sucker abundance at site 3 ( $T = 0.74$ ,  $p < 0.0003$ ) and site 4 ( $T = 0.67$ ,  $p < 0.0009$ ).

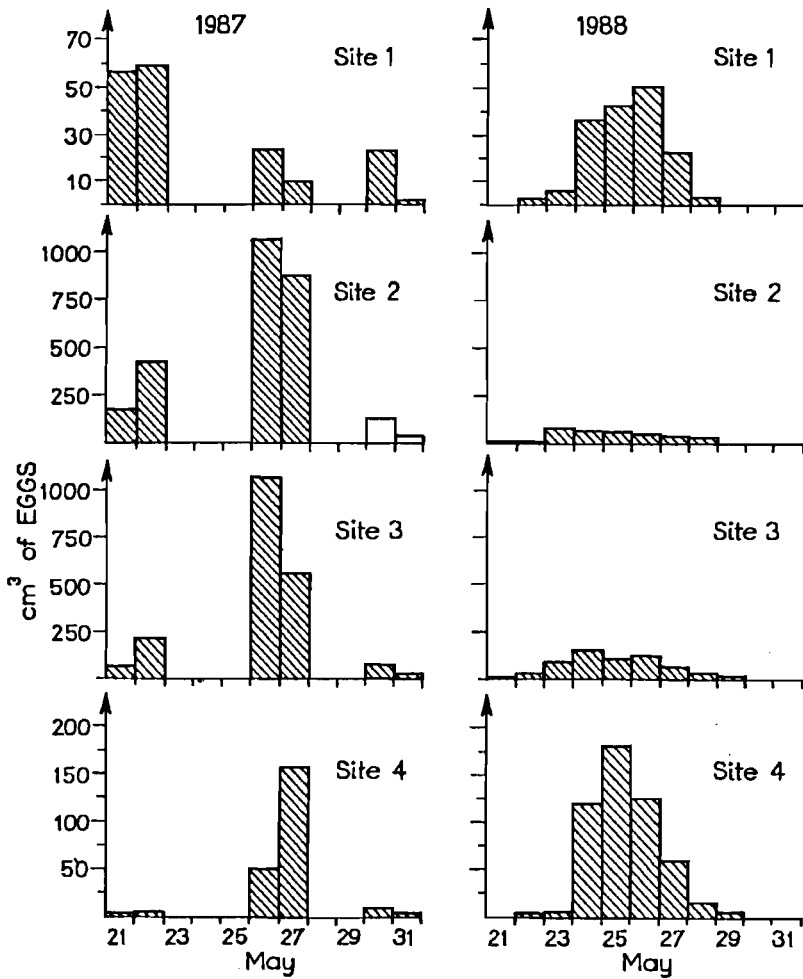


Fig. 3. Volume of eggs in the drift on monitored sites in relation to date for May 1987 and 1988. No sampling was conducted on 23–25 May and 28–29 May in 1987. Note that scales on the y axes vary among sites

Fallfish spawning activity was observed in 1987 and 1988. In 1987, nest building began on 22 May, when the water temperature first reached 12°C. Ten nests were built, eight of them above site 1. At this time, many suckers were present around fallfish nests and fallfish males directed 80% of their aggression against suckers attempting to spawn over their nest. When sucker spawning ceased, most aggression (90%) of dominant fallfish males was directed towards other intruding fallfish males. Throughout these observations, pike were observed in the vicinity of the nests, presumably attempting to prey on small fallfish. Large dominant males chased pike away from their nests. In 1988, fallfish nest building began on 21 May when the temperature again first reached 12°C. Eight nests were built that year, and spawning took place without any suckers present around the nests.

## EGG PREDATION

During the three years of the study, whitefish from the reservoir followed suckers into the stream and preyed on sucker eggs (Dion, Whoriskey 1992). The number of whitefish on spawning sites correlated positively and significantly with sucker abundance (Kendall's tau 0.40,  $p < 0.001$ ), and the stomach contents of the whitefish sampled were dominated by sucker eggs. Whitefish were not observed preying on eggs deposited in the substrate following spawning but rather they concentrated on the abundant drifting eggs. The lack of correlation between the number of whitefish occupying sites and the quantity of eggs in the drift may indicate that they were "swamped" by the large number of available eggs (Dion, Whoriskey 1992).

Throughout the spawning period, after spawning by a group of suckers had occurred, others of both species would move towards the site where spawning took place, and would root in the bottom apparently preying on the eggs. All the white suckers seined on the 26 May 1988 had eaten eggs as had seven out of 11 longnose suckers (64%). All fishes with eggs in their stomachs had fed exclusively on eggs.

No segregation of lake and reservoir suckers was observed during spawning. During visual observations of sucker spawning on the four sites in 1987, tagged white suckers and longnose suckers from the 2 water bodies were observed together on all sites at least once. At sites 1 and 2, white suckers from the two water bodies were observed together during 6 days whereas longnose suckers were seen together on one day at site 1 and on two days at site 2. On site 3, lake and reservoir white and longnose suckers were seen together for 9 and 3 days respectively. Finally, at site 4, white suckers from the two water bodies were observed together once and longnose suckers were observed together on two days.

Fallfish were generally too small to be tagged (except dominant males) so that segregation of the two stocks could not be determined. However, three observations of a tagged female from the reservoir spawning above observation site 1 on a nest guarded by a dominant male from the lake were recorded.

## RIVER EXIT

The number of fish captured leaving the stream was low compared to the number which entered. We cannot attribute this to post-spawning mortality or predation, indicating that many fish avoided capture by the traps as they left.

The data from 1987 and 1988 on origin versus return of pike (no recaptures) and walleye (3 recaptures from reservoir, returning to reservoir) were poor. Tag returns from sport fishermen in 1987 indicated that walleye and pike captured and tagged when moving from the reservoir into the stream in 1987 were mostly recaptured in the Lac des Cinq Mille. Out of the 109 walleyes tagged at station 1 in 1987, 8 were captured by sport fishermen on the lake (3 from the reservoir) whereas 5 pike out of the 16 tagged at station 1 were recaptured from the lake (none from the reservoir).

Longnose and white suckers left the river at the same time. The date when 50% of the suckers had left the stream coincided with the date when 50% had moved in, suggesting that during peak spawning activity, fish stayed on the spawning ground for only a short period.

Eighty five percent of the recaptured white suckers tagged entering from the reservoir returned to the reservoir compared to 30% for longnose suckers (Table IV). All recaptured longnose suckers tagged entering at station 2 from the lake returned to the lake, whereas only 26% of the white suckers moving from the lake returned to the lake. Overall, the majority of white suckers moved back to the reservoir whereas a majority of the longnose suckers moved towards the lake after spawning.

Table IV. Longnose and white suckers recaptures in 1987

Origin:	Reservoir	Reservoir	Lake	Lake
Recaptured moving to:	Reservoir	Lake	Reservoir	Lake
White sucker	414 (85%)	70 (15%)	37 (74%)	13 (26%)
Longnose sucker	11 (30%)	26 (70%)	0	17 (100%)

Lake whitefish tagged at station 1 were only recaptured moving back to the reservoir. Fallfish were generally the last ones to leave the stream and only four individuals were recaptured. All were dominant males (size 35 cm) and were recaptured moving back to the lentic system from which they originated.

#### 4. DISCUSSION

Walleye and pike were the first to enter the stream but the spawning activity was not observed. They were absent from the sucker's spawning sites during visual observations of the sucker spawning activity, which suggest that they spawned at a different time or on different sites. Temporal and spatial partitioning of spawning habitat was absent in the closely related sucker species. Timing of fallfish spawning activity overlapped with the suckers but spawning sites were aggressively defended by fallfish males.

Egg predation by both species of suckers was observed. It is likely that both intra- and interspecific predation was occurring because of the overlap in spawning times and habitat use, and because the eggs were similar in appearance (at least to a human observer). It is not known what percent of the eggs spawned by suckers was preyed upon by suckers. Lake whitefish preyed on sucker eggs, but the low abundance of whitefish and the fact that they preyed on eggs drifting out of favorable incubation sites suggests that this probably had a marginal effect on recruitment patterns.

Suckers from the reservoir and the lake did not segregate on spawning sites and the timing of stream entrance and spawning activity of the two populations was not different. This suggests that spawning activity of the two sucker species was triggered by the same cue, which is likely to be temperature (Tremblay 1962). The observation that many fish entering the stream from one site left the stream heading to the other suggests these are not distinct "stocks" but rather fish move freely between the two systems. Post-hatch larvae are transported downstream, but

movement upstream to Lac des Cinq Milles by small juveniles occurs later in the season (Dion unpubl.).

Competitive interactions between suckers and other species were rarely observed. However, we do not know if suckers prey on the eggs of the walleye and pike. Spawning of the suckers appears to be separated from spawning of other species utilizing the stream for reproduction. Fallfish and suckers competed for access to spawning at fallfish nests in one year, and male fallfish aggressively chased away the suckers. This was the only example of interspecific aggression observed. In both years the spawning activity of the fallfish continued after the suckers had left their spawning sites.

Temporal partitioning of spawning sites may be detrimental to early spawning benthic species which suffer egg uprooting by the subsequent reproduction of other species. Moreover, high egg predation rates might select for synchrony in the spawning activity of species in order to "swamp" predators (McKaye 1977). Both of these selective pressures may act on the suckers although it is worth noting that the suckers have to "swamp" other egg predators as well as congeners.

The system studied is under the influence of water level control structures. However, the spawning fish assemblage found in this stream is widespread across Eastern Canada and it is probable that synchrony in spawning activity of the two suckers is common (Walton 1979, Barton 1980). Since hybridization is possible (Nelson 1973, Hubbs 1955) in the absence of temporal and spatial separation, but occurs rarely, some other isolating mechanism such as behavioral differences in courtship or species recognition may be acting to prevent high hybridization rates.

## 5. SUMMARY

The species except for the suckers had temporally or spatially different spawning periods. Pike and walleye were the first entrants followed closely by the suckers. Fallfish were last to complete their stream entry. Most lake whitefish entered the stream after the suckers had started to spawn, allowing whitefish to prey upon sucker eggs. Egg predation by the two species of suckers was also observed. Segregation of stocks from the lake and the reservoir was not observed and the two sucker species were observed together on spawning sites. We believe that high egg predation rates or egg destruction by superimposed spawning might select for synchrony in the spawning activity of the suckers. The low water level of 1988 compared to 1987 probably prevented upstream migration of some fishes, especially walleye and whitefish.

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