Spawning patterns and interspecific matings of sympatric white (*Catostomus commersoni*) and longnose (*C. catostomus*) suckers from the Gouin reservoir system, Quebec

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White (*Catostomus commersoni*) and longnose (*C. catostomus*) suckers from the Gouin reservoir, Quebec, and a small upstream lake (Lac des Cinq Miles) spawned in the same stream. White suckers numerically dominated the runs in all years; however, abundances of both species decreased eightfold during a year when the reservoir level was lowered for maintenance. Return rates of individuals of both species tagged during the spawning run were poor in the following year, and only a few fish (<0.6%) skipped a year to spawn 2 years later. Although some individuals of both species occurred at all monitored spawning areas, white suckers concentrated their spawning activity over sites with boulders, whereas longnose suckers were most abundant over gravel. Differences in the courtship behaviour of the two species initially discouraged interspecific matings. However, white sucker males ultimately participated in 32% of the female longnose sucker matings, though spawning of male longnose suckers with female white suckers was not observed. White suckers spawned in groups or in pairs, whereas in all instances longnose suckers spawned with two or more males.

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Les Meuniers rouges (*Catostomus catostomus*) et noirs (*Catostomus commersoni*) du réservoir Gouin (Québec) et du lac des Cinq Miles (un petit lac tributaire du réservoir) ont frayé dans le même cours d'eau. Durant toutes les années qu'a duré notre étude, les Meuniers noirs ont été plus nombreux durant la montaison, et, l'année où le niveau d'eau du réservoir a été abaissé pour des raisons d'entretien, les deux espèces ont été huit fois moins abondantes. Peu de poissons qui avaient été marqués durant la montaison sont revenus l'année suivante, et ce, pour les deux espèces; de même, un faible pourcentage d'individus, moins de 0,6%, ont sauté une année pour venir se reproduire deux ans plus tard. La fraye du Meunier rouge a eu lieu plus souvent sur un fond de gravier alors que le Meunier noir préférait un fond aux pierres plus grosses. Des poissons des deux espèces ont quand même été aperçu à toutes les frayères étudiées. Le comportement sexuel différait suffisamment chez les deux espèces pour empêcher tout accouplement interspécifique au début de la fraye. Mais, malgré tout, des Meuniers noirs mâles ont participé à 32% des fécondations d'oeufs déposés par des Meuniers rouges femelles. Les Meuniers rouges mâles, par contre, n'ont pas frayé avec les Meuniers noirs femelles. Les Meuniers noirs frayaient en groupes ou par paires, tandis que les Meuniers rouges ont toujours frayé avec au moins deux mâles.

Introduction

At many sites in North America, large numbers of white (*Catostomus commersoni*) and longnose (*C. catostomus*) suckers undergo concurrent spring spawning migrations (Olson and Scidmore 1963; Geen et al. 1966; Barton 1980; Dion and Whoriskey 1993). Crowding of these species into limited space could lead to hybridization (e.g., Nelson 1968, 1973; Dauble and Buschbom 1981). Sucker hybrids can be viable and fertile but apparently fail to reproduce (Nelson 1968, 1973). Interspecific matings are therefore costly and natural selection should favour reproductive isolation between the species (Ayala and Kiger 1984). Spatial, temporal, and behavioural isolating mechanisms that prevent interspecific fertilizations (premating barriers) would be the most energetically advantageous. As the species' mating times overlap (Dion and Whoriskey 1993), courtship incompatibilities (e.g., Dauble and Buschbom 1981; Nelson 1968) or use of different microhabitats for spawning could discourage interspecific pairings.

Anecdotal accounts (Nelson 1973; Scott and Crossman 1973) of similar courtship patterns of white and longnose suckers suggest the lack of a behavioural isolating mechanism. Males of both species arrive on the spawning grounds before the females, and hold station on loosely defined areas that are not aggressively defended. Receptive females join the males and courtship proceeds to fin erection. Body quivering precedes the release of eggs and sperm. However, hybridization is relatively rare and behaviour could exist that discourages inter-specific matings. The potential for spatial separation based on different spawning habitat preferences has not been examined.

This study investigated the courtship and spawning patterns of white and longnose suckers originating from two water bodies in northern Quebec, Lac des Cinq Miles (Five Mile Lake) and the Gouin reservoir, which are joined by a common stream. Our principal objectives were to (*i*) evaluate the numbers and sexes of fish using the spawning stream on a yearly basis and relate them to interspecific matings, (*ii*) determine if the two species occupied different spawning sites, (*iii*) describe courtship and spawning behaviour and determine if they differ between species, and (*iv*) calculate the frequency of interspecific matings. Our methodology involved counting and individually marking fish entering the stream from the lake and reservoir over a 3-year period. This permitted us to determine if the suckers from the two water bodies skipped years between successive spawnings, and if fish from the lake and the reservoir spawned together.

Study site

The Gouin reservoir (150 200 ha) is located about 350 km north of Montréal (Fig. 1) and was created by flooding in 1918. We worked

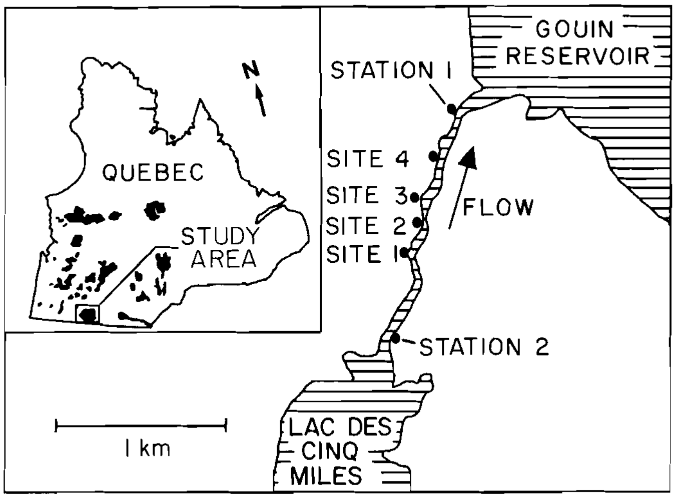

FIG. 1. The study area.

on the small clear unnamed outlet stream that connects Lac des Cinq Miles with the main reservoir (Fig. 1). This stream appears to be the only flowing-water habitat available for fish spawning in the southern portion of the reservoir. The stream is approximately 2 km long and its width varies from 10 to 15 m. There are two sections of rapids (water velocity 0.5–1.5 m/s), one at the junction with the reservoir and the second 0.6 km upstream from the reservoir. Average stream depth in spring was 1.5 m (range 0.2–2 m). Stream substrate was organic debris and sand in upstream areas and a mixture of sand, boulders, and fine gravel downstream of the first rapid.

Methods

Fyke nets facing both upstream and downstream were installed during the spawning seasons of 1986–1988 at the stream's junction with both the reservoir (station 1, see Fig. 1) and the lake (station 2, Fig. 1). These nets spanned the stream. We covered only the latter part of the run in 1986. Nets were tended daily. Captured fish were identified to species, measured (fork length, FL) for calculating growth rate, sexed on the basis of secondary sexual characteristics (presence or absence of breeding tubercles and nuptial coloration), and marked with an individually numbered Floy anchor tag (555 white suckers, 49 longnose suckers) or fin clip (5005 white suckers, 554 longnose suckers). Different-coloured tags or clips (combinations of pectoral and (or) pelvic clips) were used for fish from the lake and the reservoir, permitting us to identify fish origin and year of tagging either upon recapture or, in the case of the coloured tags, in situ. After tagging, fish were released to continue in the direction they had been moving. During peak migration periods we were unable to mark all the fish, and some were released after counting. Marked fish recaptured at the nets were identified as to origin and sex and remeasured before being released. Specific growth rates (SGRs) of Floy-tagged fish were calculated as (ln initial FL − ln final FL)/days at liberty.

Behavioural observations

Behavioural observations were made in the morning (07:00–11:00) and afternoon (17:00–20:00) at four spawning sites (Fig. 1) from 20 to 29 May 1988. These sites were chosen for their differing substratums: at site 1, average velocity was 0.45 m/s, average depth was 0.91 m, and the substratum consisted of large rocks; at site 2, average velocity was 0.62 m/s, average depth was 0.51 m, and the substratum consisted of large rocks; at site 3, average velocity was 0.43 m/s, average depth was 0.65 m, and the substratum was gravel; and at site 4, average velocity was 0.35 m/s, average depth was 0.60 m, and the substratum consisted of sand and gravel. Each site encompassed an area of 15 m^2 and was delineated by posts planted in the stream bottom.

We attempted to record the behaviour of at least four males and four females of each species at all sites during each morning and afternoon observation period. This was not always possible, owing to bad weather or the absence of a species from a site at a particular time. Observers positioned themselves either in the water or on the shore. If the fish were disturbed by our approach, we would wait for them to resume their normal activities before starting observations. The fish were not easily disturbed, and on occasion spawned on the observer's boots. Behaviour was recorded for 5 and 10 min for males and females, respectively. We noted the time spent in (1) holding station: the individual remained stationary within the stream and moved only to maintain its position against the current; (2) swimming: the fish actively moved about the stream; (3) feeding: the fish assumed a position at a 45° angle to the substratum and actively mouthed the bottom. Analysis of the stomach contents from a sample of fish obtained from the site by seining confirmed that the fish were feeding (Dion and Whoriskey 1992).

Spawning behaviour consisted of (1) aggression: a movement by an individual to hit or dislodge another from its position; (2) approach: a male or group of males moved close to a female; (3) chase: a male or a group of males left their position and followed a swimming female; (4) nuzzling: a male rubbed or brushed against the anal region of a female with its head; (5) rushes: observed only in matings involving longnose sucker females. The female and attendant males would circle around the spawning beds in alternate rushes up- and down-stream; (6) fin erection: exhibited by males in the latter stages of courtship, it consisted of a stiff erection of the dorsal, pelvic, and pectoral fins followed by body quivering; (7) spawning: release of gametes was observed. These behaviours were chosen following preliminary observations of spawning at the site in 1986.

Statistical analyses

Owing to small sample sizes, or violations of assumptions of normality and homogeneity of variance, appropriate nonparametric statistical methods were used (χ^2 test, Mann–Whitney U test, and Kruskal–Wallis ANOVA). Calculations were done with the STATGRAPHICS statistical package. Behavioural data from each species at our four sites did not differ significantly ($P_\alpha > 0.30$) and were therefore pooled.

Results

Fish abundance and return rates

White suckers were numerically dominant: we recorded 6974 and 1686 individuals entering the stream in 1987 and 1988, respectively, compared with 859 and 157 longnose suckers in the same years. Of the white suckers, 95 and 93% entered from the reservoir in 1987 and 1988, respectively. By contrast, 67 and 56% of the longnose suckers entered from the reservoir in 1987 and 1988, respectively. The drop in both species' abundances in 1987 coincided with a reservoir drawdown of 5 m, which increased the size and velocity of the rapids in the lower section of the stream.

Small percentages of the marked fish returned to spawn in the year following tagging (Table 1). A few fish of both species skipped a year and subsequently returned; however, only one fish (a male white sucker) returned to spawn in 3 consecutive years. Return rates of longnose and white sucker males significantly exceeded those of females in 1988 (χ^2, $P_\alpha < 0.05$), otherwise rates of return were similar between species and years (χ^2, $P_\alpha > 0.05$).

SGRs of Floy-tagged fish of both species returning to spawn again after 1 year were minimal and did not differ significantly between species or sexes (female white suckers, median SGR = 5.8×10^{-6}, $N = 19$; male white suckers, median SGR = 1.5×10^{-6}, $N = 14$; female longnose suckers,

TABLE 1. Return rates of marked fish

(A) Fish tagged in 1986

	No. marked	No. recaptured 1986	No. recaptured 1987
White sucker			
Males	1719	26 (1.5±0.6)	4 (0.2±0.2)
Females	1677	22 (1.3±0.5)	4 (0.2±0.2)
Total	3396	48 (1.4±0.1)	8 (0.2±0.01)
Longnose sucker			
Males	237	1 (0.4±0.8)	0 (0±0)
Females	167	4 (2.4±2.3)	1 (0.6±1.1)
Total	404	5 (1.2±0.6)	1 (0.3±1.0)

(B) Fish tagged in 1987

	No. marked	No. recaptured in 1988
White sucker		
Males	1261	91 (7.2±1.4)
Females	903	36 (4.0±1.3)
Total	2164	127 (5.9±1.0)
Longnose sucker		
Males	128	18 (14.1±6.1)
Females	71	2 (2.8±3.9)
Total	199	20 (10.1±4.2)

NOTE: Percentages given in parentheses are followed by binomial confidence limits. Only one fish, a white sucker male, returned in 3 consecutive years.

median SGR = -2.97×10^{-5}, $N = 2$; male longnose suckers, median SGR = -2.98×10^{-5}, $N = 2$).

The sex ratios of tagged fish of both species returning in 1987 did not differ significantly from those observed at the time of marking in 1986 (Table 2). By contrast, sex ratios of returned fish of both species in 1988 (the year of water level manipulation) were significantly biased in favour of males in comparison with the group initially marked.

Fish from the reservoir frequently mated with those from the lake. Thus, assortative mating of fish from the two sites was not occurring.

Spawning site use

Both species were found at all sites but species abundance differed among sites. White suckers predominated numerically at sites 1 and 2, whereas longnose suckers predominated at sites 3 and 4 (Fig. 2). Stream velocities and depths were relatively similar among sites. However, species distributions may be related to the substratum type. At sites 1 and 2 the bottom was covered with large rocks, whereas at sites 3 and 4 the substratum was gravel and sand.

TABLE 2. Ratios of male to female suckers at the time of marking, and of tagged fish returning 1 year later

	At tagging in 1986	Recapture in 1987	At tagging in 1987	Recapture in 1988
White suckers	1.02:1 (3396)	1.18:1 (48)	1.40:1 (2164)	2.53:1* (127)
Longnose suckers	1.42:1 (404)	0.25:1 (5)	1.80:1 (199)	9.0:1* (20)

NOTE: Numbers in parentheses are sample sizes.
*Sex ratio at recapture differs significantly (χ^2, $P\alpha < 0.05$) from that at marking.

Behaviour

Behaviour differed between species. Median percentages of time spent holding station were 82 and 71% for white sucker males ($N = 91$) and females ($N = 43$), respectively (Mann–Whitney U test, $P_\alpha > 0.05$), compared with 50% for both male ($N = 70$) and female ($N = 38$) longnose suckers (Mann–Whitney U test, $P_\alpha > 0.05$). Both white sucker males ($N = 91$) and females ($N = 43$) spent significantly more time holding station than their longnose counterparts ($N = 70$ males, $N = 43$ females; Mann–Whitney U test, $P_\alpha < 0.05$). White suckers rarely left their position during observations, and when they did they soon returned to the same spot. In contrast, longnose suckers showed no site attachment and moved throughout the spawning beds at each site. We observed no aggression within or between species.

Feeding was observed by only two (2.9%) of the male ($N = 70$) as opposed to five (13.2%, $N = 38$) of the female longnose suckers, and occupied 0 and 4% (median values) of male and female time budgets, respectively (male:female comparisons, Mann–Whitney U test, $P_\alpha < 0.05$). By contrast, 26.3% of male ($N = 91$) and 48.8% of female ($N = 43$) white suckers were seen feeding, for median values of 6.5 and 16% (Mann–Whitney U test, $P_\alpha < 0.05$) of male and female time budgets, respectively. Both male and female white suckers spent significantly more time (Mann–Whitney U test, $P_\alpha < 0.05$) feeding than their longnose sucker counterparts.

Courtship behaviour

Courtship and spawning behaviour did not occur frequently enough during our systematic observations to permit us to calculate their contributions to the species' time budgets. The following descriptions are based on additional observations targeted at courting groups. Courtship began with females leaving the shoreline and swimming into the main current, where the males were located.

Male white suckers would approach female white suckers, and if the female remained close would begin nuzzling. If she moved away from the spawning area to return to the bank, males did not pursue her. If she remained with the male, the male would show fin erection and vibration. This was followed by gamete release.

Male longnose suckers would also approach female longnose suckers and begin nuzzling. If the female was ready to spawn, she would initiate a chase, and the courting group would circle around the spawning area in a series of alternating rushes upstream followed by long runs downstream. The chase often attracted additional male longnose suckers, which joined in. Other individuals abandoned the group during the rush. If

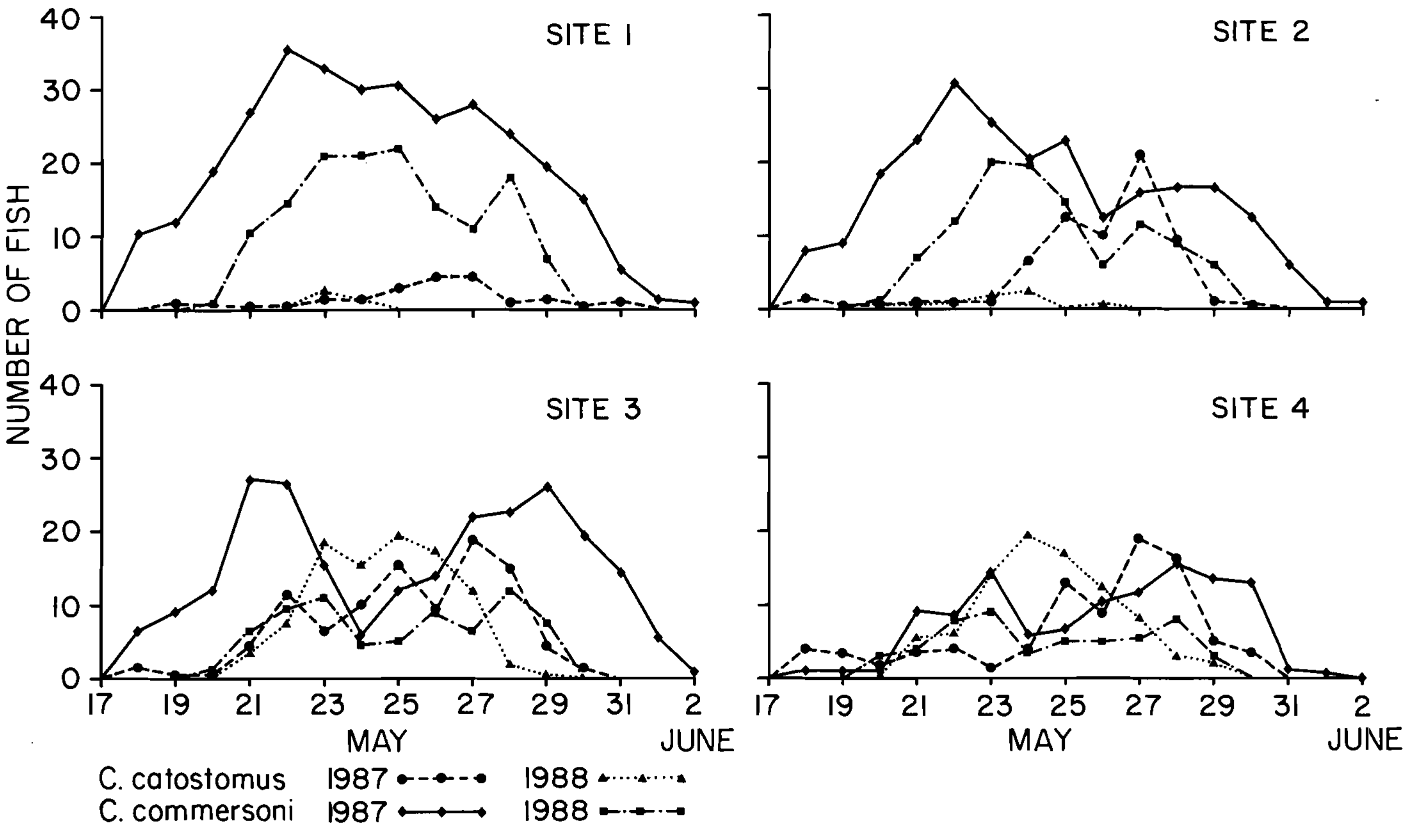

FIG. 2. Daily counts of fish occupying the 15-m^2 spawning sites.

TABLE 3. Mating events

	White suckers	Longnose suckers
No. of matings observed	6	19
No. of interspecific matings	0	6
% interspecific matings ±95% binomial confidence limits	0±0	32±22
Median no. of females per mating	1 (1–1)	1 (1–1)
Median no. of males per mating	2 (1–6)	3 (2–6)
No. of pair spawns observed	3	0

NOTE: Values in parentheses are ranges.

the female came to rest above the spawning bed, the males would erect their fins and begin vibrating and gametes would be released.

Interspecific courtship was also observed. Of the 88 recorded approaches towards female white suckers (involving 175 white sucker males and 15 longnose sucker males), 10 (11.4%) were by individual or groups of longnose suckers. Only once did a longnose sucker (a single male) approach a white sucker female together with male white suckers. All 10 of these interspecific interactions occurred at sites dominated by longnose suckers (sites 3 and 4). If the female remained close, male longnose suckers would begin nuzzling. However, when the female white sucker failed to initiate a chase, the longnose males would abandon the courtship and move off. By contrast, 32 (16.8%) of the 190 observed approaches by males towards longnose sucker females (a total of 567 longnose and 41 white sucker males participated) involved white sucker males. Of these 32 approaches, 23 occurred in multispecies groups composed of a median of 2 longnose sucker males (range 1–7) and 1 white sucker male (range 1–3), whereas 9 involved white sucker males only (median of 1, range 1–2). Thirty-one of 32 interspecific interactions were recorded at the sites dominated by longnose suckers. Male white suckers would nuzzle female longnose suckers, which would then start their chase. The 38 female longnose suckers observed were involved in 80 chases; white sucker males participated in only 6 (7.5%), and during some of these the white sucker males abandoned the females. However, groups courting longnose sucker females that came to rest for spawning were on occasion joined by white sucker males that had not participated in the chase. Courtship of both species would then proceed to male fin erection and vibration, followed by spawning.

Spawning groups and interspecific matings

In 32% of longnose sucker matings (19 matings were observed), white suckers participated (Table 3). All longnose sucker spawns involved a single female and varying numbers of conspecific and heterospecific males. A single interspecific mating involved white (2 individuals) and no longnose sucker males. In the six interspecific matings observed, a similar number (Mann–Whitney *U* test, $P_\alpha > 0.15$) of white (median 1, range 1–2) and longnose (median 1, range 0–4) sucker males participated. Overall, female longnose suckers spawned concurrently with a median of 3 males (range 2–6, including white suckers). All six white sucker matings observed involved a single female and conspecific males in varying numbers (median 2, range 1–6). Similar numbers of males spawned with white and longnose sucker females (Mann–Whitney U test, $P_\alpha > 0.25$). However, no female white sucker × male longnose sucker pairings were seen, and single white sucker males were able in some instances to pair spawn with a conspecific female. By contrast, all longnose sucker spawns were in groups.

Discussion

Abundances of spawning suckers of both species varied between years. A five- to eight-fold drop in numbers occurred in the year when reservoir levels were lowered for maintenance, creating rapids that may have blocked upstream movement of reservoir fish. Reservoir manipulations frequently disrupt the spawning of fishes (Olson et al. 1985; Hall and Avyle 1986; Deslandes et al. 1992). Curiously, the percentages of returning tagged males of both species actually increased significantly in the low compared with the high water year.

A biased sex ratio could be a factor promoting interspecific matings. Male-biased sex ratios of white suckers during spawning runs were observed by Quinn and Ross (1985). These authors attributed the bias to earlier maturation of males than of females, as well as the energetic demands on females of producing eggs, which could increase mortality rates or decrease spawning frequency (e.g., Potts and Wootton 1985). In our work, sex ratios did not differ from 1:1 males:females except for a preponderance of males in the low-water year. This suggests that female reproductive costs are not necessarily higher than those of males. Females of both species ate drifting sucker eggs during the spawning season (intra- and inter-specific egg predation; Dion and Whoriskey 1992). This energy-rich food source may have helped them recoup some of the energy drained by spawning.

Suckers are iteroparous and are often assumed to spawn yearly. Our fish apparently had a nonannual spawning pattern. Generally, less than 8% of the tagged fish of both species returned to the breeding grounds in consecutive years (Table 1). Quinn and Ross (1985) also found low rates of repeat spawning in consecutive years by white suckers (11 and 4% for males and females, respectively). Our data also show that very few fish (<1%) returned to spawn after skipping a year. However, the fish could have been spawning in the reservoir in the intervening period, although this seems unlikely, given reports of high annual mortality rates of suckers of spawning age (Verdon and Magnin 1977).

We found evidence for spatial separation of the two species into different spawning areas. White suckers outnumbered longnose suckers by up to 20:1 over spawning substratums composed of large rocks, whereas longnose suckers outnumbered white suckers by about 2:1 over gravel substratums. However, both species occurred at all sites, and this led to interspecific interactions. Males of both species would court conspecific and heterospecific females. However, a chase formed part of the courtship ritual of longnose suckers, but not of white suckers. This behaviour initially separated the species into same-species spawning groups (a premating barrier). However, the stream could contain 8000 or more suckers of the two species, depending on the year, with white suckers outnumbering longnose suckers by eight to one. Fish often joined spawning groups after courtship was finished and this led to interspecific matings. Virtually all of the interspecific courtship and spawning acts occurred at sites dominated by longnose suckers, probably because of displacement of the abundant white sucker males from preferred spawning habitats crowded with site-attached conspecific males. All the interspecific matings that we observed involved a longnose sucker female and various numbers of conspecific and heterospecific males. We do not know what percentage of the longnose sucker eggs were fertilized by white suckers. This probably depends on male proximity to the female when the group spawns (e.g., Hutchings and Myers 1988).

White suckers in three of the six matings we observed spawned in pairs, whereas all other spawns involved a single female and a group of males. By contrast, all longnose sucker spawns involved a single female and a group of males. Switches between pair and group spawning have been observed for other fishes (Warner and Hoffman 1980*a*, 1980*b*). In these systems, fish density determines the spawning mode, with pair spawning occurring at low density and group spawning (involving two or more of both males and females) at high density. Warner and Hoffman (1980*a*, 1980*b*) suggested that individual male reproductive success is much higher for males spawning in pairs than in groups, and males switch from pair to group mode only when competing males become so numerous that they can no longer be excluded. Given the high densities of white suckers, and their apparent displacement to longnose sucker sites, we were surprised that pair spawning occurred at all, and that we saw no male aggression. We were also surprised that pair spawns were not observed between longnose suckers despite their relatively low density.

Suckers can be important competitors of fishes more valued by humans (Magnan 1989; Lachance and Magnan 1990; Hayes et al. 1992) and their populations are assumed to be resilient (Bramblett and Fausch 1991). Their complicated spawning system and low rates of individual spawning may make them less resilient than they are assumed to be.

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Ayala, F.J., and Kiger, J.A., Jr. 1984. Modern genetics. Benjamin/Cummings Publishing Co., Reading, Mass.

Barton, B.A. 1980. Spawning migrations, age and growth, and summer feeding of white and longnose suckers in an irrigation reservoir. Can. Field-Nat. **94**: 300–304.

Bramblett, R.G., and Fausch, K.D. 1991. Variable fish communities and the index of biotic integrity in a Western Great Plains river. Trans. Am. Fish. Soc. **120**: 752–769.

Dauble, D., and Buschbom, R.L. 1981. Estimates of hybridization between two species of catostomids in the Columbia River. Copeia, 1981: 802–810.

Deslandes, J.-C., Fortin, R., Verdon, R., Roy, D., and Belzile, L. 1992. Évolution de la communauté de poissons du réservoir La Grande 2 à la suite de la mise en eau. *In* Les enseignements de la phase 1 du Complexe La Grande : actes du colloque. *Edited by* N. Chartrand and N. Thérien. Hydro-Québec, Montréal. pp. 106–120.

Dion, R., and Whoriskey, F.G. 1992. Lake whitefish *Coregonus clupeaformis*) predation on the eggs of longnose (*Catostomus catostomus*) and white (*C. commersoni*) suckers. Pol. Arch. Hydrobiol. **39**: 409–415.

Dion, R., and Whoriskey, F.G. 1993. Resource partitioning in a spring spawning freshwater fish assemblage dominated by catostomids (*Catostomus commersoni*, *C. catostomus*). Pol. Arch. Hydrobiol. **40**: 47–58.

Geen, G.H., Northcote, T.G., Hartman, G.F., and Lindsey, C.C. 1966. Life histories of two species of catostomid fishes in Sixteenmile Lake, British Columbia, with particular reference to inlet stream spawning. J. Fish. Res. Board Can. **23**: 1761–1788.

Hall, G.E., and Avyle, M.J. van den (*Editors*). 1986. Reservoir fisheries management: strategies for the 80's. Reservoir Committee, Southern Division, American Fisheries Society, Bethesda, Md.

Hayes, D.B., Taylor, W.W., and Schneider, J.C. 1992. Response of yellow perch and the benthic invertebrate community to a reduction in the abundance of white suckers. Trans. Am. Fish. Soc. **121**: 36–53.

Hutchings, J.A., and Myers, R.A. 1988. Mating success of alternate maturation phenotypes of male Atlantic salmon, *Salmo salar*. Oecologia, **75**: 169–174.

Lachance, S., and Magnan, P. 1990. Performance of domestic, hybrid and wild strains of brook trout, *Salvelinus fontinalis*, after stocking: the impact of intra- and interspecific competition. Can. J. Fish. Aquat. Sci. **47**: 2278–2284.

Magnan, P. 1989. The impact of cyprinid and catostomid introductions on brook charr. *Salvelinus fontinalis* populations: a review. Physiol. Ecol. Jpn. Spec. Vol. No. 1. pp. 337–356.

Nelson, J.S. 1968. Hybridization and isolating mechanism between *Catostomus commersoni* and *C. macrocheilus* (Pisces: Catostomidae). J. Fish. Res. Board Can. **25**: 101–150.

Nelson, J.S. 1973. Occurrence of hybrids between longnose sucker (*Catostomus catostomus*) and white sucker (*C. commersoni*) in Upper Kananaskis Reservoir, Alberta. J. Fish. Res. Board Can. **92**: 557–560.

Olson, D.E., and Scidmore, W.J. 1963. Homing tendency of spawning white suckers in Many Point Lake, Minnesota. Trans. Am. Fish. Soc. **92**: 13–16.

Olson, F.W., White, R.G., and Hamre, R.H. (*Editors*). 1985. *In* Proceedings of Symposium on Small Hydropower and Fisheries. May 1–3,1985, Aurora, Colo. American Fisheries Society, Western Division and Bio-engineering Section, Bethesda, Md.

Potts, G.W., and Wootton, R.J. (*Editors*). 1984. Fish reproduction: strategies and tactics. Academic Press, New York.

Quinn, S.P., and Ross, M.R. 1985. Non-annual spawning in the white sucker, *Catostomus commersoni*. Copeia, 1985: 613–618.

Scott, W.B., and Crossman, E.J. 1973. Freshwater fishes of Canada. Bull. Fish. Res. Board Can. No. 184.

Verdon, R., and Magnin, E. 1977. Dynamique de la population de meuniers noirs *Catostomus commersoni commersoni* (Lacépède) du lac Croche dans les Laurentides, Québec. Nat. Can. (Que.), **104**: 197–206.

Warner, R.R., and Hoffman, S.G. 1980*a*. Local population size as a determinant of mating system and sexual competition in two tropical marine fish (*Thalasomma* spp.). Evolution, **34**: 508–518.

Warner, R.R., and Hoffman, S.G. 1980*b*. Population density and the economics of territorial defense in a coral reef fish. Ecology, **61**: 772–780.