

GREAT LAKES FISHERY COMMISSION

Project Completion Report¹

Upstream migration of sea lampreys with radio transmitters in three tributaries to Lake Superior

by:

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February 1998

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Introduction

Two present alternatives to the use of lampricides to manage sea lamprey populations (*Petromyzon marinus*) in the Great Lakes include the release of sterile males (Hanson and Manion 1980) and the installation of barriers to the upstream migration of adult sea lampreys (GLFC 1992). The success of these alternative control measures will be affected by migratory tendencies and the behaviour of adult sea lampreys in streams. Upstream migration precedes spawning by all species of lampreys (Malmqvist 1986). However, the distance, destination and rate of upstream travel varies by species and their life style. Barriers, especially those with traps, should be more effective if sea lampreys move aggressively upstream and remain committed to the stream. Release of non-indigenous sterile male sea lampreys into indigenous stream populations will be more effective at reducing recruitment if the sterile males are at least as aggressive in reaching spawning areas and in mating as indigenous male sea lampreys. Beamish (1979) determined that the energetic cost of locomotion during upstream migration was considerably less than that of activities associated with spawning. Although energy costs of migration may be low, the rate of upstream progress, the habitat selected during travel and for rest and the fidelity of sea lampreys to the stream they have entered will affect the success and distribution of the population in general and the choice of and benefit from management actions applied to reduce abundance of adult sea lampreys in the Great Lakes in particular.

Adult sea lampreys moved upstream in the Connecticut River at a mean daily rate of 1.01 km h^{-1} (Stier and Kynard 1986) and early arrivals may move upstream at a slower (Stier and Kynard 1986) or faster rate (Wigley 1959) than later arrivals. Emigration, too, from the population in a spawning stream may be high (Applegate and Smith 1951), moderate (Wigley 1959; Skidmore 1959) or emigration rates may vary over the duration of the spawning period (Moore and Schleen 1980). Malmqvist (1986) suggested that lampreys migrating long distances to spawn must possess a good means of orientation but noted that, when captured and re-released, neither *Petromyzon marinus* nor *Lampetra fluviatilis* showed a strong tendency to return to the stream first selected. From these diverse results, sea lampreys in the Great Lakes may fall somewhere in the continuum from facultative wanderers to those that are strictly diadromous. This apparent plasticity in stream selection, stream fidelity and variability in upstream migration patterns could favour population success of sea lampreys within the Great Lakes.

During the upstream migration and prior to spawning, lampreys are not usually observed during daylight hours (Manion and McLain 1971; Manion and Hanson 1980; Malmqvist 1986; Kelso and Glova 1993 and others). Malmqvist (1986) indicated that, shortly before spawning, lampreys increase their daytime activity. The cryptic behaviour during day or night prior to spawning of adult sea lampreys should favour survival during upstream migration as well as satisfy their intolerance of light; however, these daytime refugia apparently have been described only for *Geotria australis* (Kelso and Glova 1993). Understanding upstream migration as well as the habitat selected between travel periods may offer opportunities for developing or modifying management strategies that are alternatives to the use of lampricides.

To investigate the upstream migration of adult sea lampreys, we attached radio transmitters to sea lampreys and relocated them in three tributaries to Lake Superior. Because male sea lampreys are captured in Lake Huron, sterilized and then introduced into a target stream, we attached radio transmitters to these non-indigenous sterile males and released them into the same three tributaries to determine if this history affected upstream migration. To determine if sterilized indigenous male sea lampreys migrated upstream in the same manner as the non-indigenous sterile males, we captured males in the Bad River, sterilized them and released them, after attaching radio transmitters, in the Bad River. Each time we located a sea lamprey fitted with a radio transmitter, we described the habitat in which it was found. We therefore estimated emigration and the upstream rate of travel, determined the final destination in the stream and described the daytime refugia selected during upstream migration of sea lampreys in three tributaries to Lake Superior prior to spawning.

Methods

We released sea lampreys fitted with radio transmitters in the Wolf, Pancake and Bad rivers, all of which are tributaries to Lake Superior (Fig. 1). The Wolf River is a brown water river with a low-head barrier 5.9 km upstream from the estuary that blocks upstream passage of migrating sea lampreys (Fig. 2b). Spawning still occurs below the barrier (Department of Fisheries & Oceans, personal communication and personal observation). The Pancake River has a falls that acts as a natural barrier to upstream passage of sea lampreys some 7.4 km upstream from the estuary and a low head barrier is

in Gimlet Creek 0.2 km upstream from its confluence with the main stem (Fig. 2a). The Bad River is a dendritic system and access for fishes is limited only by natural conditions with the exception of the Meringo and Brunswailer rivers where man-made dams, constructed for flow regulation, restrict upstream passage (Fig. 2c). Mean annual flows are 6.88 (1971-1992), 2.83 (1993-1994) and 13.03 cms^{-1} (for the years 1993-1995) for the Wolf, Pancake and Bad rivers, respectively.

Adult sea lampreys indigenous to the stream were captured in permanent traps that are part of the low head barriers to upstream passage in the Wolf River and Gimlet Creek, in fyke nets installed 100-200m upstream from the mouth of the Pancake River and in portable traps installed at a natural falls some 16 km upstream from the estuary of the Bad River (Fig. 2c). Non-indigenous sterile male sea lampreys were haphazardly selected from the population of sterile males delivered from the sterilization facility at Hammond Bay, Michigan. Male sea lampreys destined for sterilization at Hammond Bay were from tributaries in Lake Huron or the St. Marys River. The origin of these sterile male sea lampreys not indigenous to Lake Superior essentially was unknown. Male sea lampreys also were captured in the portable trap installed at the falls in the Bad River, transported to the sterilization facility at Hammond Bay and sterilized (referred to as indigenous sterile males). Between 1993 and 1996, 149 radio transmitters (Lotek or Advanced Telemetry Systems) were attached externally (97%) or surgically implanted (3%) in sea lampreys in the three rivers (Table 1). Each sea lamprey was measured, the colour and external features subjectively described and a radio transmitter was attached prior to release. Transmitters were attached anterior to the anterior dorsal fin with two stainless steel surgical wires. Surgical wires were sutured through proximal and distal

neoprene pads and the dorsal musculature. Wires were tightened to secure the transmitter firmly to the sea lamprey and then both wires were crimped in a small metal tube. Neoprene pads cushioned the transmitter lateral to the mid-dorsal line of the sea lamprey and created tension on the surgical wires to reduce movement of the transmitter on the body surface and the wires in the musculature. For internal implantation of radio transmitters, sea lampreys were anesthetized with MS-222 (tricaine methanesulfonate) and transmitters were inserted through an incision lateral to the mid-ventral line using a technique similar to Ross and Kleiner (1982). Surgeries lasted 3-5 minutes. Animals were held in river water until equilibrium was recovered, observed for 5-30 minutes following transmitter attachment and only apparently healthy fish were allowed to swim from the 60L holding container. Because space in the sea lamprey coelom was limited even for our small transmitters (9-10.5mm diameter by 20-28mm in length) and because external attachment of transmitters was quick and seemed to have little effect on lamprey vigour, we attached all transmitters externally after 1993. Transmitters were active for more than 60 days, weighed 3.3 (Lotek) and 2.0 g (Advanced Telemetry Systems) in air and, in water, did not exceed 2% of the live body weight as suggested by Winter (1996). On occasion (6% of releases) transmitters were found detached from the lamprey. In these situations, we attached the transmitter externally to another indigenous male or non-indigenous sterile male sea lamprey and released it. Each transmitter, and subsequently each sea lamprey, was recognizable by its unique frequency.

Sea lampreys carrying transmitters were located using a hand-held receiver equipped with a directional antenna by canoeing the navigable portion of the river system (all rivers), by walking the stream in 1-3 km sections beginning at road access points (all

rivers) and by aircraft (Bad River). Animals were located 2-6 times per week on an irregular schedule. We did not locate sea lampreys with radio transmitters on days when rainfall was heavy or lightening occurred and we located sea lampreys less frequently when movement was minimal between successive days. Lampreys with transmitters were located 1-3 times each day that the Wolf River was canoed and once each day that the Pancake River was canoed. When a transmitter was detected by the receiver, we used signal strength and the antenna's direction to locate the sea lamprey. By changing position of the receiver operator in the stream, by adjusting receiver gain, by rotating the antenna, and by observing signal strength readings we were able to locate transmitters within ± 1.5 m as determined on 15 occasions in blind trials. In blind trials, transmitters were sequestered in a stream and the receiver operator determined the location of these transmitters whose location was unknown. The course of the Bad River, including its tributaries, was flown twice each day that an aircraft was used to locate animals with transmitters. In 1995, we combined walking and canoeing navigable portions of the Bad River with overflights by helicopter to determine locations of sea lamprey in the Bad River. Blind trials indicated that our determination of sea lamprey location by aircraft was approximate to within 100 m. We used only aircraft in the Bad River in 1996 to determine the location of sea lampreys with radio transmitters. We were able to cover by canoe, foot or aircraft the portion of the three watersheds that were accessible to sea lampreys.

We also installed continuously recording data loggers (receivers) at two locations in the Pancake River (Fig. 2a) and at three locations in the Bad River (Fig.2c) to record

upstream and downstream passage of sea lampreys with radio transmitters at those locations. The continuously recording data loggers were installed in stream sections such that at least 100 m of stream was in the receiver range. The receiver was programmed to scan each frequency for 3 sec.; therefore, the receiver completed its scan for transmitters in 60-90 sec depending upon the number of transmitters at large in the watershed.

For each sea lamprey fitted with a radio transmitter, we determined the daily movement, averaged the daily movement from the time of introduction to the time the animal reached its final location in the stream, measured the maximum distance traveled upstream and determined the net displacement (total of upstream and downstream movement) within the stream. We used analysis of variance to test for significant differences among tributaries and among indigenous male, indigenous sterile male, non-indigenous sterile male and indigenous female sea lampreys for each of these measures.

Sea lampreys with transmitters were recorded by the data logger as they passed downstream and emigrated from the tributary. If a sea lamprey was located further downstream on successive days, was not detected by the data logger and was not found in the watershed on successive days, we assumed that the animal had emigrated. If a sea lamprey died (we saw evidence that mink, otter and raptors captured sea lampreys) and the transmitter was removed from the watershed, our estimate of emigration rates would be inflated. We used χ^2 to test for significant differences in emigration for the different sexes with radio transmitters released in each stream.

In 1994, in the first 2 km of the Pancake River below the natural falls, changes in transmitter signal strength and direction were used to direct divers to the location of the

lamprey. Visual observation was used to describe attributes of the habitat in which sea lampreys were found and water depth was measured. In 1995, we used divers to characterize sea lamprey refugia in the Wolf and Pancake rivers, measured water depth, measured light levels using a Licor light sensor, and took a water sample for turbidity measurement using a Hach turbidity meter. We also measured water depth, light and turbidity at a mid-stream location adjacent to the location of the sea lamprey. At all other times, once a lamprey fitted with a transmitter was located, the habitat was described using features i.e. among boulders, under large woody debris, under an overhanging bank, etc. observable from the stream surface. The same observers were used in the same streams each year and, although habitat assessment was subjective, it was at least consistent. We used the split-plot design analysis of variance (Snedecor and Cochran 1967) to test for significant differences in habitat selected by indigenous male, and non-indigenous sterile male sea lampreys in the three tributaries.

Results

We followed 75 non-indigenous sterilized male, 52 indigenous male, 17 indigenous sterile male and 5 indigenous female sea lampreys equipped with radio transmitters between 25 and 66 days in three tributaries to Lake Superior (Table 1). Few indigenous male sea lampreys were captured in the Pancake River in 1993 and 1995 and in the Wolf River in 1995; therefore, we placed more transmitters on non-indigenous sterile males and attached five transmitters to indigenous female sea lampreys.

For all years and all tributaries, 25% of sea lampreys released with radio transmitters emigrated from the stream in which they were released (Table 1, Fig. 3). Overall, 31% (23 of 75) of the non-indigenous sterile male, 23% (12 of 52) of the indigenous male, 6% (1 of 17) of the indigenous sterile male and 60% (3 of 5) of the indigenous female sea lampreys emigrated. Emigration of sea lampreys from the tributary in which they were released was variable among years (Fig. 3) and was highest in 1995 in both the Wolf and Pancake rivers. Emigration was variable among rivers and was highest in the Wolf River (51% of total sea lampreys that emigrated, 49% of those released in that stream), intermediate in the Pancake River (38%, 26%) and lowest in the Bad River (10%, 8%). We grouped years and found that there was no significant difference (χ^2 , $P_{.05}$) in the emigration of indigenous male and non-indigenous sterile male sea lampreys from the three tributaries. Although emigration of female sea lampreys with radio transmitters was high in the Pancake River, the sample size was small, was not included in the statistical analysis, and the result must be considered inconclusive.

Emigration from the tributary in which sea lampreys were released occurred in May, June and July (Fig. 3). Although measurements of discharge, or staff gauge height readings that could serve as a surrogate for discharge, were not continuously available, emigration seemed to occur in the Pancake and Bad rivers during the several days during and immediately following a freshet (Fig. 4). However, in the Wolf River, emigration occurred throughout June in 1994 and 1995 even though discharge was variable and freshets occurred, particularly in 1995. We suspect, therefore, that

emigration is intrinsically variable among streams and may be exacerbated by increased discharge.

Some sea lampreys (8 of 149) with radio transmitters remained in the tributary (Table 2) but made no progress upstream and some sea lampreys (5 of 149) went downstream from the release point (Table 2) but did not exit the tributary. However, most (64% of the total released with radio transmitters) of the sea lampreys went upstream by making unidirectional progress (40%) or by migrating upstream, retreating, and then moving upstream again (24%). Consequently, animals with radio transmitters were distributed throughout accessible portions of each tributary (Fig. 2, parts a, b and c) late in the study when spawning occurred.

Sea lampreys with radio transmitters went upstream faster in the Bad River, 0.68 km day⁻¹, all animals that went upstream, than in the Pancake (0.25 km day⁻¹) and Wolf (0.25 km day⁻¹) rivers. Because the upstream rate of travel was so different among streams (Table 3), we compared travel rates only within streams. Non-indigenous sterile male sea lampreys with radio transmitters, on average, moved upstream at a greater daily rate in the Bad River in both years, in the Pancake River in 1993 and 1995 and in the Wolf River in 1995 than did indigenous male sea lampreys (Table 3). Indigenous male sea lampreys moved upstream at a slightly greater rate than non-indigenous sterile males in the Wolf and Pancake rivers in 1994. However, the difference in daily upstream movement was significantly different only between indigenous male (mean=0.50 km day⁻¹) and non-indigenous sterile male (mean=1.02 km day⁻¹) sea lampreys in 1995 in the Bad River (analysis of variance, $F=5.38$, sig. $P_{.05}$). Consequently, we assume that, overall, there was no difference in daily upstream travel rates of indigenous male, indigenous

sterile male and non-indigenous sterile male sea lampreys within the three tributaries to Lake Superior.

Non-indigenous sterile male sea lampreys with radio transmitters travelled farther upstream than indigenous males in the Bad River in both years and in the Pancake and Wolf rivers in 1995 (Table 3). Conversely, indigenous male sea lampreys travelled upstream farther than non-indigenous sterile males in the Wolf River in 1994 and in the Pancake River in 1993 and 1994. The maximum upstream displacement of non-indigenous sterile male sea lampreys was significantly different from that of indigenous male and indigenous sterile male sea lampreys in the Bad River only in 1996 (analysis of variance, $F=5.29$, $P_{.05}$). There was a significant difference between the maximum distance travelled upstream between years ($F = 6.69$, $P_{.05}$) in the Wolf River but not in the Pancake River. The distances travelled upstream i.e. the final upstream location relative to downstream release, may be significantly different among years and between sexes but we suspect that, overall, the differences will remain inconsistent and are not likely to be biologically significant.

To determine if progress upstream was sustained over the period of tracking, we plotted the distance and direction travelled between sitings for all sea lampreys with radio transmitters (Fig. 5). In the Wolf River, most movement upstream occurred prior to mid-June in the tracking period. In the Pancake and Bad rivers, some animals moved actively upstream until mid-July. Downstream movement of sea lampreys rarely occurred in any tributary after late June. However, some animals, after entry into any one of the three tributaries, remained stationary throughout each year's study. We are unable to account

for this disparate behaviour of sea lampreys on release into the tributaries in part because the range in size and external appearance, as it might reflect maturity, was not large.

We used χ^2 contingency tables to test whether there was any significant difference in the overall incidence (Table 2) of emigration, no movement, upstream progress only, upstream or downstream progress by indigenous male and non-indigenous sterile male sea lampreys within a tributary. In all cases, there was no significant difference attributable to sex. Therefore, we conclude that origin, sex or the sterilization process does not affect the migration behaviour patterns in sea lampreys.

Although continuously recording data loggers were installed downstream of release locations to detect emigration of sea lampreys with radio transmitters from the Pancake and Bad rivers, we also installed recording data loggers upstream (Fig. 2) of release locations to determine when animals travelled upstream. Few sea lampreys moved upstream in the early morning, 0500 to 0800, or in mid-afternoon, 1300 to 1600 h (Fig. 6). The period of greatest upstream movement was between 2200 and 0300 h over the duration of tracking. Although sea lampreys with radio transmitters moved upstream (Fig. 6) throughout the day, animals were clearly most active at night.

Sea lampreys were located in a variety of habitats but almost always under cover or in refugia (Fig. 7). Sea lampreys were found, to differing degrees, in each classification of habitat type in all study streams. Sea lampreys were commonly found (Fig. 8) in brush piles, under overhanging banks, under boulders and, in general, in locations where light and, perhaps, water velocity were reduced, but the exact location of an animal was difficult to determine without diving or excavating. During the day,

animals were seen travelling in shallow open waters as they actively moved upstream; however, sighting in open water was infrequent (<5% of observations). There was no significant difference (split-plot design, analysis of variance) in the habitat in which indigenous male and non-indigenous sterile male sea lampreys were found ($F=0.373$; not significant $P_{.05}$) and there was no significant difference in the habitat in which lampreys were found in the three tributaries ($F=0.006$, not significant $P_{.05}$). Sea lampreys were most commonly found (Fig. 8) within the tangled brush and log piles that accumulate in the bends of these northern streams. Sea lampreys were also commonly found in spaces under boulders and out of sight beneath undercut banks. We could not determine where animals were in the pools that could not be waded but we assume that sea lampreys were probably under boulders or among woody debris. Light levels at the lamprey location were significantly different from the mid-stream reference (one way analysis of variance $F=3952$, significant $P_{.05}$) but turbidity and water velocity were similar between the sea lamprey location and the mid-stream reference.

In the Wolf River, 2 of 21 (10%) and 4 of 20 (20%) sea lampreys with radio transmitters were captured in the trap at the low-head lamprey barrier in 1994 and 1995, respectively. No lampreys with transmitters were captured in the trap at the barrier in Gimlet Creek, Pancake River. Of the animals released in the Wolf River carrying transmitters, only 13 and 9 sea lampreys progressed far enough upstream such that they may have encountered the barrier (Table 2, Fig. 2); therefore, capture rates for those lampreys with the potential for encountering the barrier would be between 15 and 45% for the two years of study in the Wolf River.

Sea lampreys released into spawning migrations in the three tributaries may emigrate (25% of the total sea lampreys released with radio transmitters) or may not move upstream (17%) but the majority proceeded upstream to areas where spawning is likely to occur. We plotted the stream sections where nests were found in the Wolf and Pancake rivers (Fig. 2 a, b, c) and interpolated that at least 35% of our released animals were within 10m of a region in the stream on 2 or more occasions where nests were located. In the Bad River (Fig. 2c) extensive coarse substrate existed; however, we had no assessment of whether nests were made in these substrates and were unable to locate lampreys with radio transmitters as precisely as in the Wolf and Pancake rivers. Annual variability in final resting locations of sea lampreys entering streams prior to spawning is particularly evident in the Wolf River where the number of animals near spawning habitat differed by an order of magnitude between years (Tables 2 and 3 and Fig. 2). Determining the number of lampreys with the potential for spawning will be complicated by the temporal variability in discharge, affecting not only the area of watered gravels, but also emigration rates.

Discussion

Homing behaviour of *Petromyzon marinus* may not be strongly expressed in the Great Lakes (Skidmore 1959; Applegate and Smith 1951; Moore and Schleen 1980; Wigley 1959; Smith and Elliott 1953). Further, diadromous species vary in their instinctive drives to move upstream and their ability to migrate past hindrances to migration (McDowall 1993). Sterilization of male sea lampreys including the transfer of

these animals from watershed to watershed, if it causes even a minor reduction to inherently weak homing and migration tendencies, will result in a less than expected reduction in reproductive success in the target population. If sea lampreys exhibit weak homing behaviour and a low drive to move upstream, traps will produce low capture rates relative to the in-stream population.

Our studies indicate that, once committed to a tributary in which they might spawn in the Great Lakes, 26% of animals with transmitters emigrated from the stream in which they were placed. Emigration varied among years and streams and the difference among tributaries was large, from 5 to 60% in our 3 study streams. Applegate and Smith (1951) found that a dam in the Cheboygan River resulted in sea lampreys contributing to spawning migrations in other tributaries in inverse proportion to the distance from the blockaded stream. Smith and Elliott (1953) suggested that adult sea lampreys were dispersed in Lake Huron with no distinct pattern of migration. Taken together these studies would indicate that homing and fidelity to a spawning stream are not strong traits of maturing sea lampreys. Those animals that left our study streams usually progressed upstream only a few km beyond the release point and sea lampreys left the stream at any time from a few days to 7 weeks after release (Fig. 4). Although the stress of transmitter attachment may have heightened the tendency of sea lampreys to emigrate, we suggest that this influence was minor because emigration rates varied among streams and years and occurred continuously during the migration period but the application of radio transmitters and handling of animals was consistent among streams and years. Emigration was greatest in the Wolf River where the distance to a barrier was least and lowest in the Bad River where the distance to impediments to upstream passage was the

greatest (Table 4). It is more likely that the location of impediments, natural or man-made, to upstream movement by sea lampreys affects the level of commitment to a spawning stream. Increased ease of access to upstream reaches and greater distances from estuary to an impediment to upstream migration likely promote greater fidelity to a stream.

Although some sea lampreys emigrated (26%) after entering a potential spawning stream and some (8%) may not progress upstream beyond the lower reaches, most, $\approx 65\%$, of sea lampreys released with radio transmitters made net upstream progress. Once in a potential spawning stream, sea lampreys commonly retreat then travel upstream over the duration of the spawning migration. However, most (33%) animals moved aggressively upstream, more so soon after entry into a tributary. There was no difference in tendencies to emigrate, maintain location or the process of achieving upstream progress among indigenous male, non-indigenous sterile male, indigenous sterile male and, probably, indigenous female sea lampreys within the three study streams. Upstream rate of progress of lampreys in rivers has been reported to vary between 0.6 and 3.2 km day⁻¹ in Cayuga Inlet (Wigley 1959), to differ by sex (6.5 km day⁻¹ for male and 6.2 km day⁻¹ for female sea lampreys) in the St. John River (Beamish 1979), range up to 1.0 km h⁻¹ in the Connecticut River (Stier and Kynard 1986) and decline from 88 m day⁻¹ to 0 for *Geotria australis* over several months (Kelso and Glova 1993). The different methods used by the different studies precludes comparing rates of travel but we confirm that the upstream rate of progress will likely decline over the duration of upstream migration and will vary among watersheds (Table 4). Because we followed few females, we can only argue that

upstream travel rates do not differ between indigenous male, indigenous sterile male and non-indigenous sea lampreys within a stream.

Sea lampreys are rarely seen before spawning even during intense searches made in daylight (Manion and McLain 1971) but they appear to become tolerant to light once nesting and spawning begins (see Manion and Hanson 1980). Selection of refugia during upstream migration may serve several functions. First, the locations selected for resting during upstream migration are clearly in areas of reduced light and travel by sea lampreys is predominantly at night; therefore using these habitats during daylight reduces exposure to higher light levels. Second, these habitats may be reduced in water velocity and do provide a variety of surfaces for attachment. As a result of “resting” in refugia, the energy expenditure required to reach spawning areas may be reduced and predation risk, also, may be lowered. Although the benefits of selecting these refugia may be uncertain, cryptic behaviour by lampreys appears to be common during migration and, often, during spawning (this study, Cochrane and Gripentrog 1992; Kelso and Glova 1993). Cryptic behaviour may be common to lampreys, but, by its very nature, is difficult to determine and assess as a survival strategy. Native New Zealanders commonly capture lampreys (*Geotria australis*) from their refugia, resting places and attachment surfaces (McDowall 1990; Kelso unpublished report submitted to the Great Lakes Fishery Commission); however, to our knowledge, this type of “fishery” does not occur elsewhere. Habitat used as refugia by sea lampreys during upstream migration in our study streams was common and, as is evident from their distribution, sea lampreys are unlikely to be concentrated in number (and vulnerable to removal), when the supply of refugia is abundant.

It is difficult to determine the proportion of the population in a stream that either spawns or is vulnerable to capture in traps placed in streams. Emigration and non-random distribution within the watershed will complicate any estimation of abundance using mark-recapture methods. If our interpolation of the likelihood of spawning, based on proximity to areas where spawning redds are located is reasonable, then approximately 44 and 28% of sea lampreys with transmitters in the Wolf and Pancake rivers, respectively, could have spawned (Table 5). Emigration and the failure to progress upstream reduced the proportion of animals in proximity to known spawning areas. Our estimate of the number of animals, primarily males, that may spawn would be biased by our ability to recognize spawning areas and any effect of transmitter attachment on sea lamprey behaviour. In the Wolf River, only 10 and 20% of sea lampreys released with transmitters were captured in the trap at the low head barrier in 1994 and 1995. Although this proportion seems low, not all animals progressed upstream to the point where they would encounter the barrier and be vulnerable to capture. If these observations are reasonable for migrating adult sea lampreys in Great Lakes tributaries, lamprey behaviour during migration is such that the capture efficiency of traps and the proportion of animals likely to spawn will be stream dependent but will be low and is not likely to exceed half the population entering a stream.

In summary, we found that capture, sterilization and transport to a different stream does not affect migration tendencies of adult male sea lampreys. However, the instinctive drive of sea lampreys to move upstream and their fidelity to a potential spawning stream is, in our view, generally modest. Fidelity to a stream and the aggressiveness of upstream migration also varies, particularly, with stream characteristics e.g. fidelity and rate of

upstream movement was greatest in the Bad River, a large and complicated drainage system with low slope and with only minor natural impediments to progress in its lower reaches. Among stream differences in watershed size, in the distance between the estuary and an impediment to passage, and in freshet occurrence were the likely causes of the differences in emigration rates and travel rates reported in the literature.

Acknowledgements

Many helped by providing data (Andy Edwards, R. MacDonald) or sea lampreys (K. Mullett, M. Toohey, R. MacDonald) and locating sea lampreys with transmitters (T. Stemmler, J. Syme, D. Kelso and L. O'Connor). The enthusiastic and committed help that we received is appreciated. D. Ghan provided helpful advice to revise the manuscript. This study was funded by the Great Lakes Fishery Commission and the Department of Fisheries and Oceans.

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Figure Legends

Fig. 1 The location of the 3 study streams (Wolf, Pancake and Bad rivers) in Lake Superior.

2. Maximum upstream displacement of sea lampreys in the Pancake (2a), Wolf (2b) and Bad rivers (2c). The release locations (R), data logger locations (D), areas in which sea lamprey nests were found (shaded) and barriers and natural falls are included as appropriate. The shaded area shown for the Bad River (2c) only indicates areas where gravel and rubble occur; nest assessment was not conducted.

3. The timing of emigration of sea lampreys with transmitters from the Wolf, Pancake and Bad rivers. The number of sea lampreys released with radio transmitters and the number emigrating is provided in each panel.

4. The timing of emigration in relation to water temperature and discharge or water depth taken from an *in situ* staff gauge, 1993-1996.

5. The distance between successive locations showing progress upstream (+) or downstream (-), all sea lampreys released with radio transmitters.

6. The number of animals passing the upstream data logger (see Fig. 2) in the Pancake and Bad rivers, all years combined.

7. Frequency of refugia (ucb = undercut bank) selected by all lampreys for each stream, all years.

8. Classes of habitat used by sea lampreys migrating upstream in three tributaries to Lake Superior.

Table 1: Duration of tracking, number of transmitters attached, number emigrating, and the maximum distance travelled upstream by sea lampreys.

	1996	1995	1994	1993
Bad River				
Duration of study (days)	45	33	-	-
Number of transmitters	30	20	-	-
Indigenous male (IM)	10	6	-	-
Non-indigenous sterile male (NISM)	10	7	-	-
Indigenous sterile male (ISM)	10	7	-	-
Number emmigrating, IM	1	0	-	-
Number emmigrating, NISM	1	1	-	-
Number emmigrating, ISM	1	0	-	-
Number not-moving	0	0	-	-
Mean maximum distance (km)				
IM	20.34	18.49	-	-
NISM	35.81	28.64	-	-
ISM	20.48	24.49	-	-
=====				
Wolf River				
Duration of study (d)	-	27	29	-
Number of tagged lampreys	-	20	21	-
Indigenous male (IM)	-	6	10	-
Non-indigenous sterile male (NISM)	-	14	11	-
Number emmigrating, IM	-	3	4	-
Number emmigrating, NISM	-	9	4	-
Number dead	-	0	1	-
Number not-moving	-	0	0	-
Mean maximum distance (km)				
IM	-	0.730	2.09	-
NISM	-	1.060	2.07	-
=====				
Pancake River				
Duration of study (d)	-	25	32	66
Number of lamprey tagged	-	23	20	15
Indigenous male (IM)	-	8	10	3
Indigenous female (IF)	-	5	0	0
Non-indigenous sterile male (NISM)	-	10	10	12
Number emmigrating, IM	-	1	3	0
Number emmigrating, NISM	-	4	0	4
Number emmigrating, IF	-	3	0	0
Number not-moving	-	0	2	3
Mean maximum distance (km)				
IM	-	2.360	3.57	4.36
IF	-	1.690	-	-
NISM	-	2.750	3.49	2.3
=====				

Table 2: The type of movement for each group of sea lampreys for each stream for each year.

	No Movement			Upstream Progress only			Downstream Progress only			Upstream then Downstream			emigrated		
	NISM	IM	Other*	NISM	IM	Other*	NISM	IM	Other*	NISM	IM	Other*	NISM	IM	Other*
Pan93	2	1	-	3	2	-	1	0	-	2	0	-	4	0	-
Pan94	4	1	-	3	6	-	0	0	-	3	0	-	0	3	-
Pan95	0	0	0	4	6	2	2	1	0	0	0	0	4	1	3
Wf94	0	0	-	1	2	-	0	0	-	6	4	-	4	4	-
Wf95	0	0	-	1	3	-	0	0	-	4	0	-	9	3	-
Bad95	0	0	0	4	4	5	0	0	0	2	2	2	1	0	0
Bad96	0	0	0	4	6	2	0	0	0	5	3	7	1	1	1

* denotes ISM in Bad River, 1995 and 1996, and IF in Pancake River, 1995

Table 3a: The mean daily movement (km/day) for sea lampreys released with radio transmitters for each stream for each year.

	NISM	ISM	IM	IF	Significant F P(.05)
Pan93	0.27	-	0.24	-	NS
Pan94	0.14	-	0.25	-	NS
Pan95	0.27	-	0.21	0.38	NS
Wlf94	0.12	-	0.67	-	NS
Wlf95	0.10	-	0.09	-	NS
Bad95	1.02	0.64	0.53	-	S
Bad96	0.70	0.70	0.50	-	NS

NS=non-significant difference (A=.05), S=significant difference (A=.05)

Table 3b: The mean maximum (km travelled upstream) movement for sea lampreys released with radio transmitters for each stream for each year.

	NISM	ISM	IM	IF	Significant F P(.05)
Pan93	2.30	-	4.36	-	NS
Pan94	3.49	-	3.57	-	NS
Pan95	2.75	-	2.36	1.69	NS
Wlf94	2.07	-	2.09	-	NS
Wlf95	1.06	-	0.73	-	NS
Bad95	28.64	24.49	18.49	-	NS
Bad96	35.81	20.48	20.34	-	S

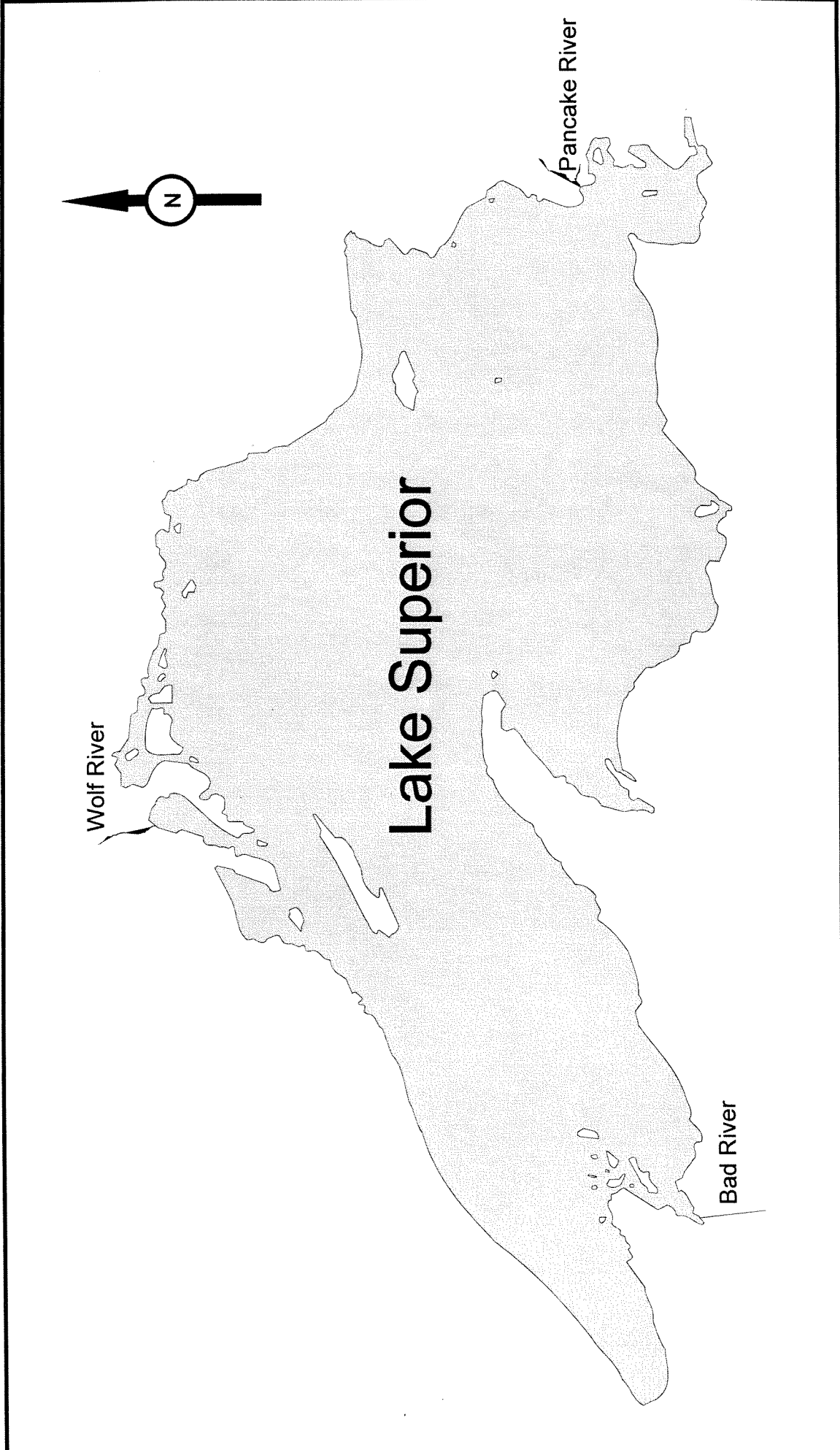
NS=non-significant difference (A=.05), S=significant difference (A=.05)

Table 4: Average daily movement and emigration rates, sexes combined, of sea lampreys for the three study streams.

River	Distance to Barrier (km)	Mean Annual Flow (cms)	Slope (m/km of river)	Average daily movement rate (km/day)	Emigration % all years
Wolf	5.9	6.8	2.58	0.25	49
Pancake	7.4	2.8	2.06	0.25	22
Bad	>50	5.803	1.01	0.68	8

Table 5: Interpolation, by in stream location, of the number of sea lampreys with radio transmitters near spawning areas (potential spawners) and near a sea lamprey trap (vulnerable to capture) in the pancake and Wolf rivers.

River	Year	#released	#captured in trap	# near spawning habitat
Pancake	1993	15	0	4
	1994	20	0	6
	1995	23	0	6
Wolf	1994	21	4	12
	1995	20	3	6



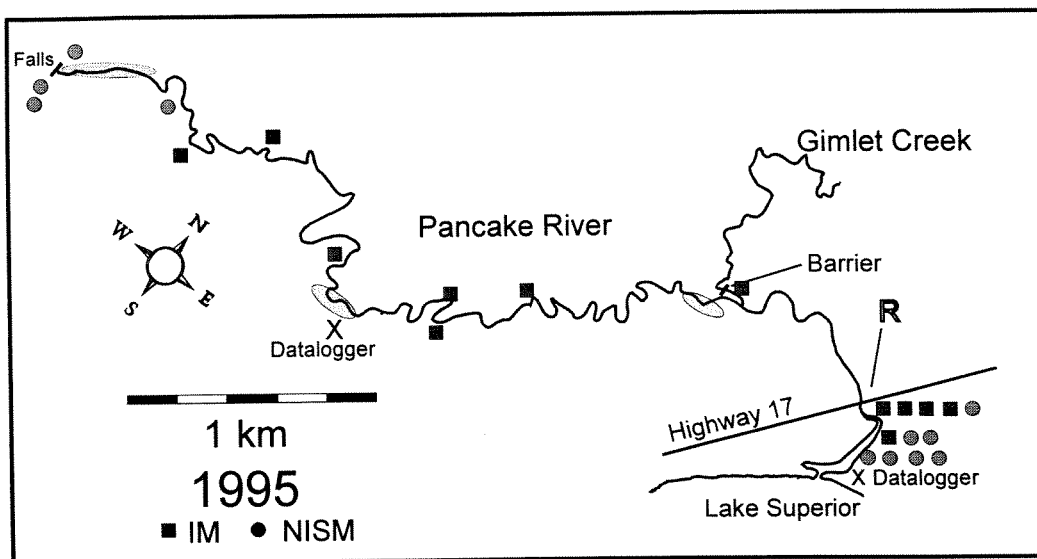
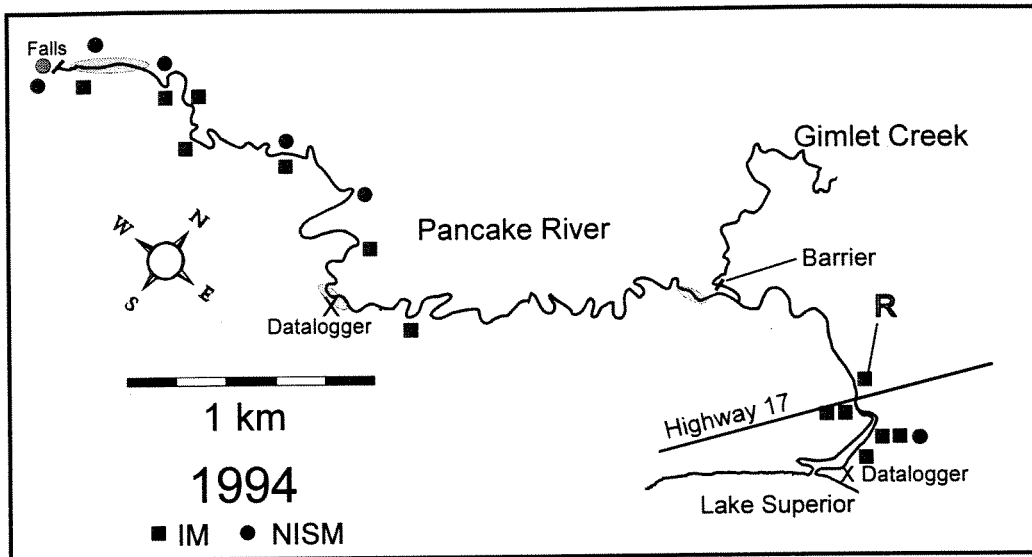
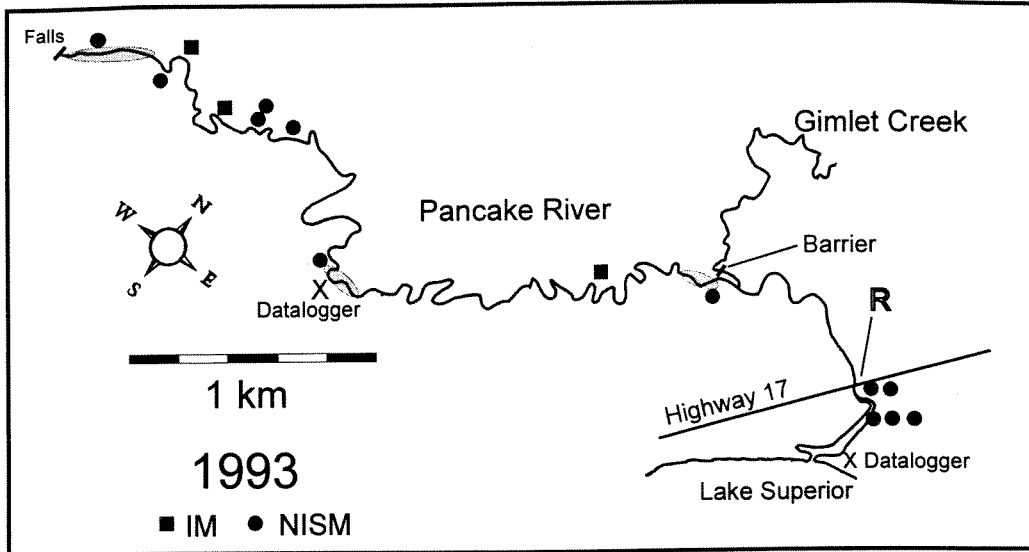


Figure 2a:

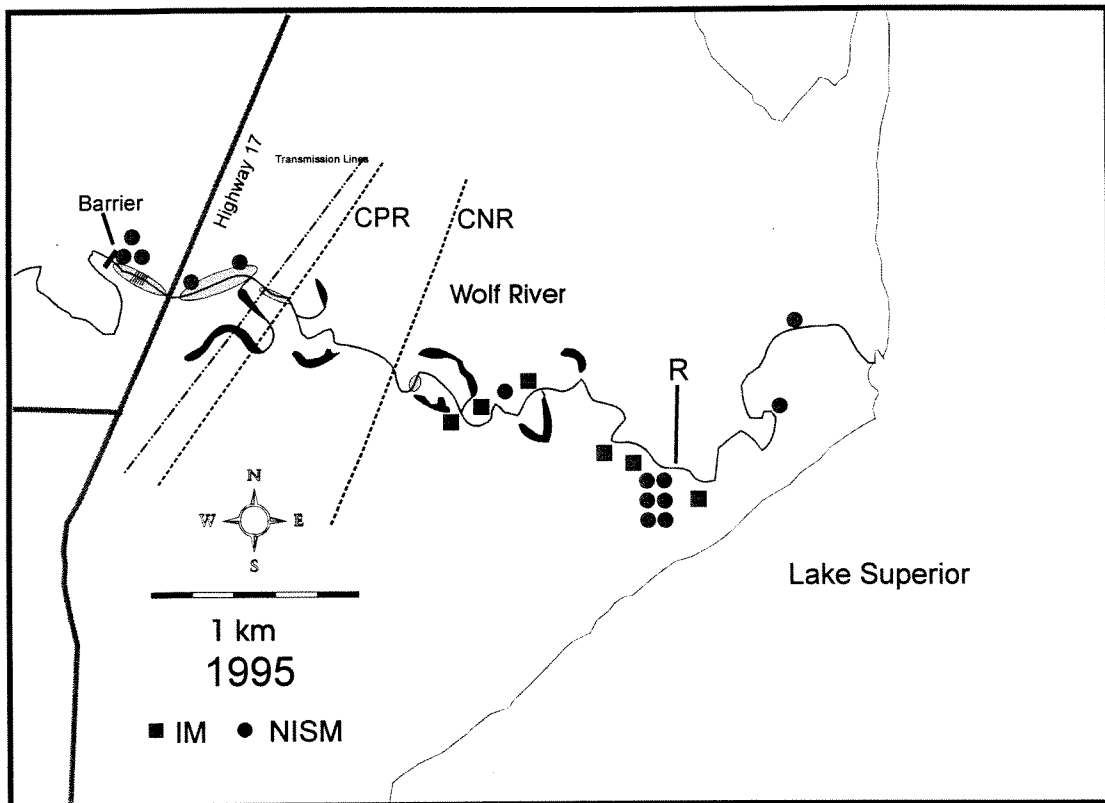
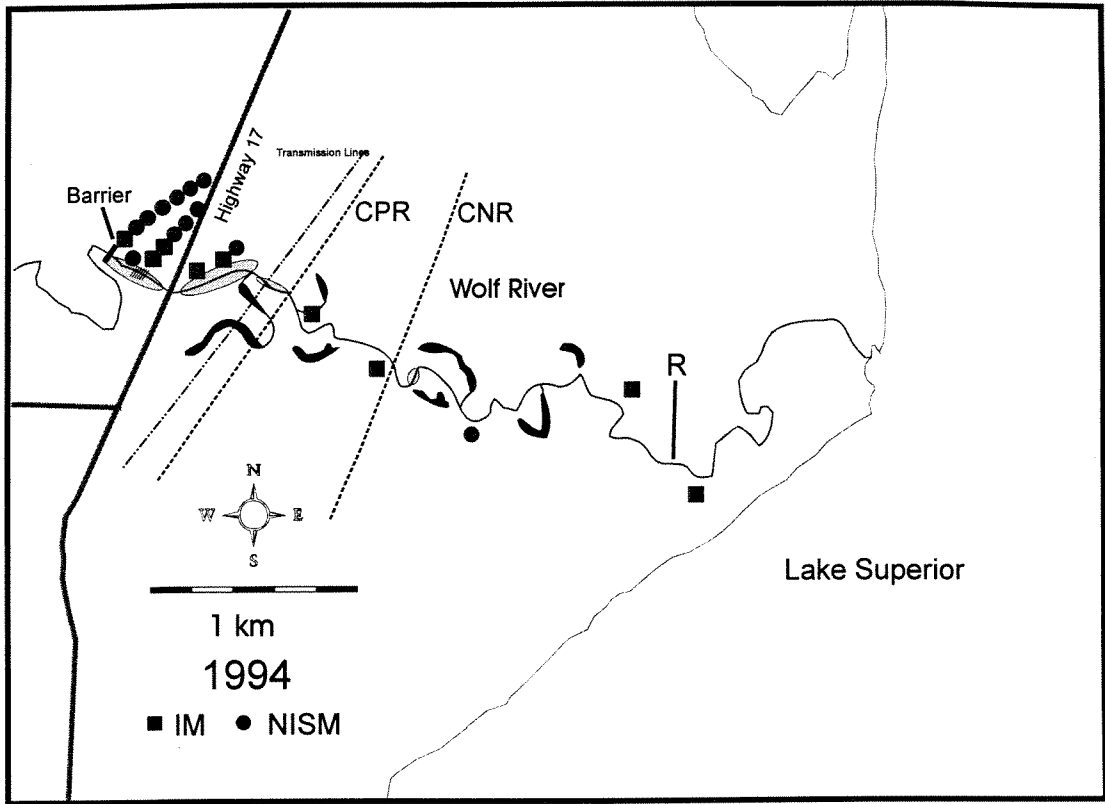


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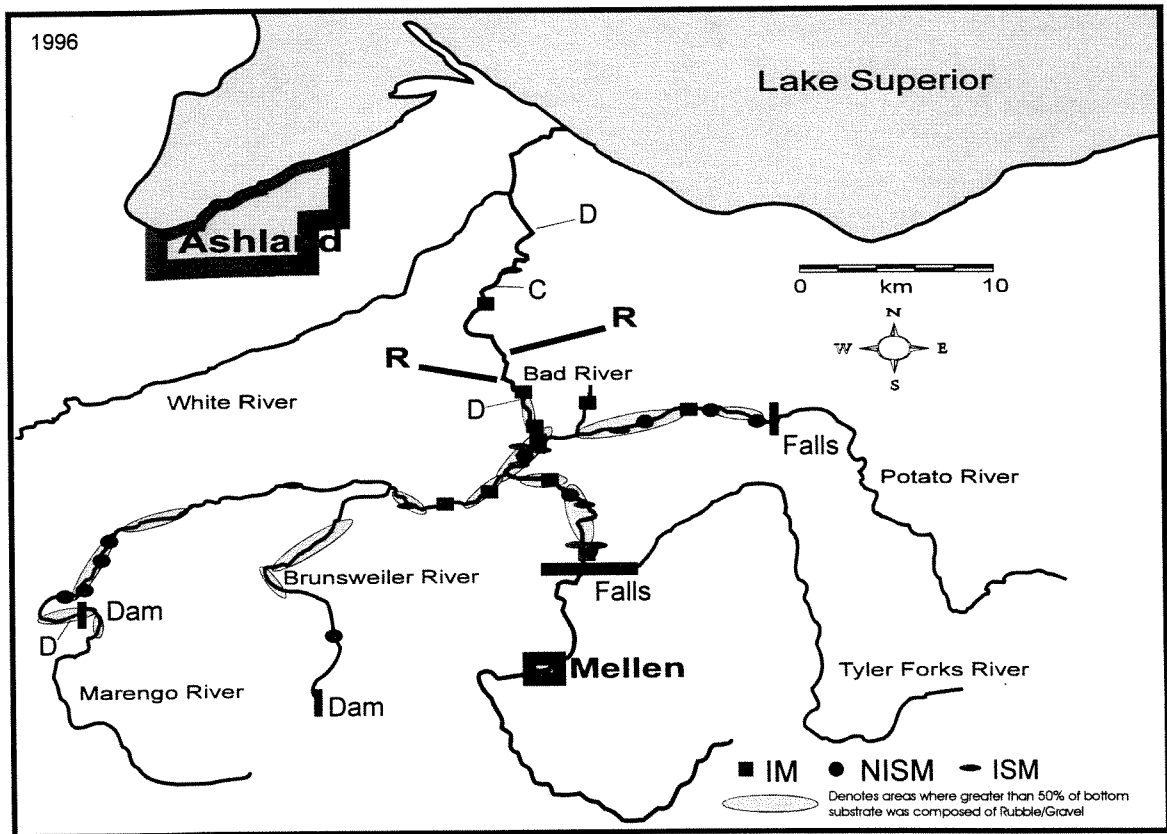
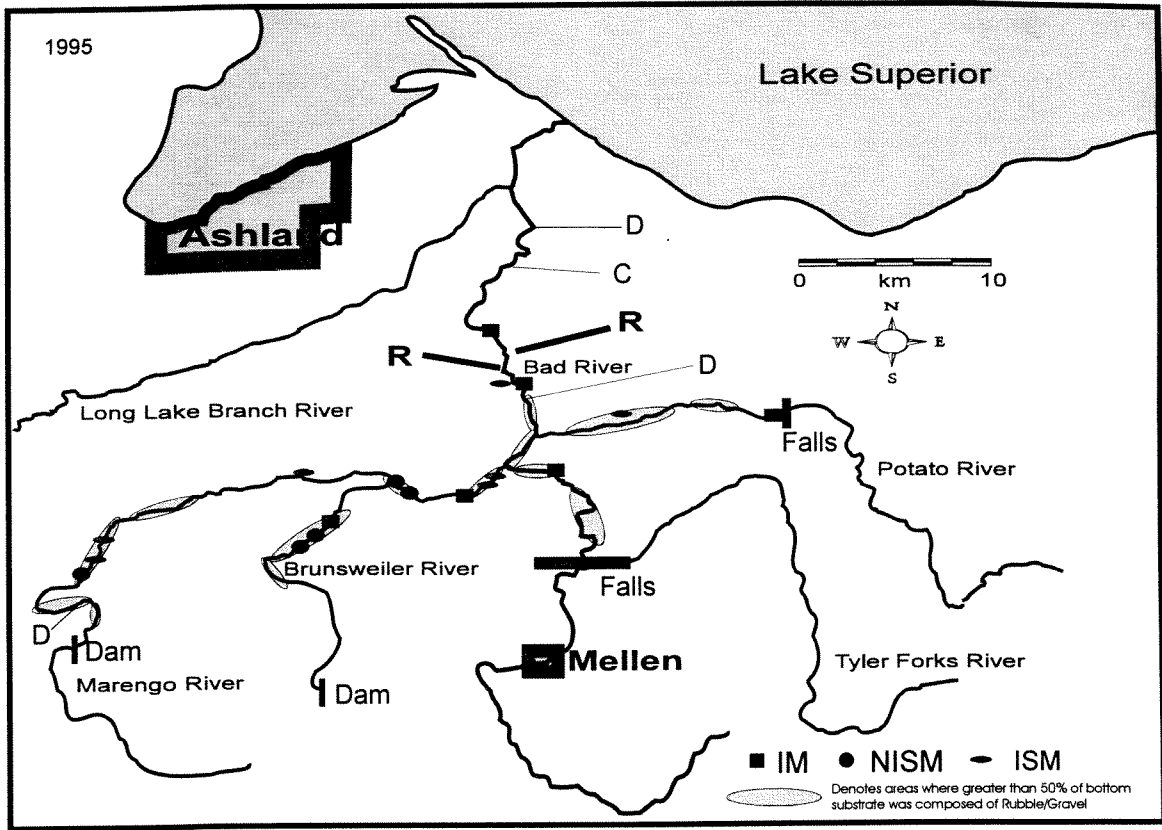


Figure 2c:

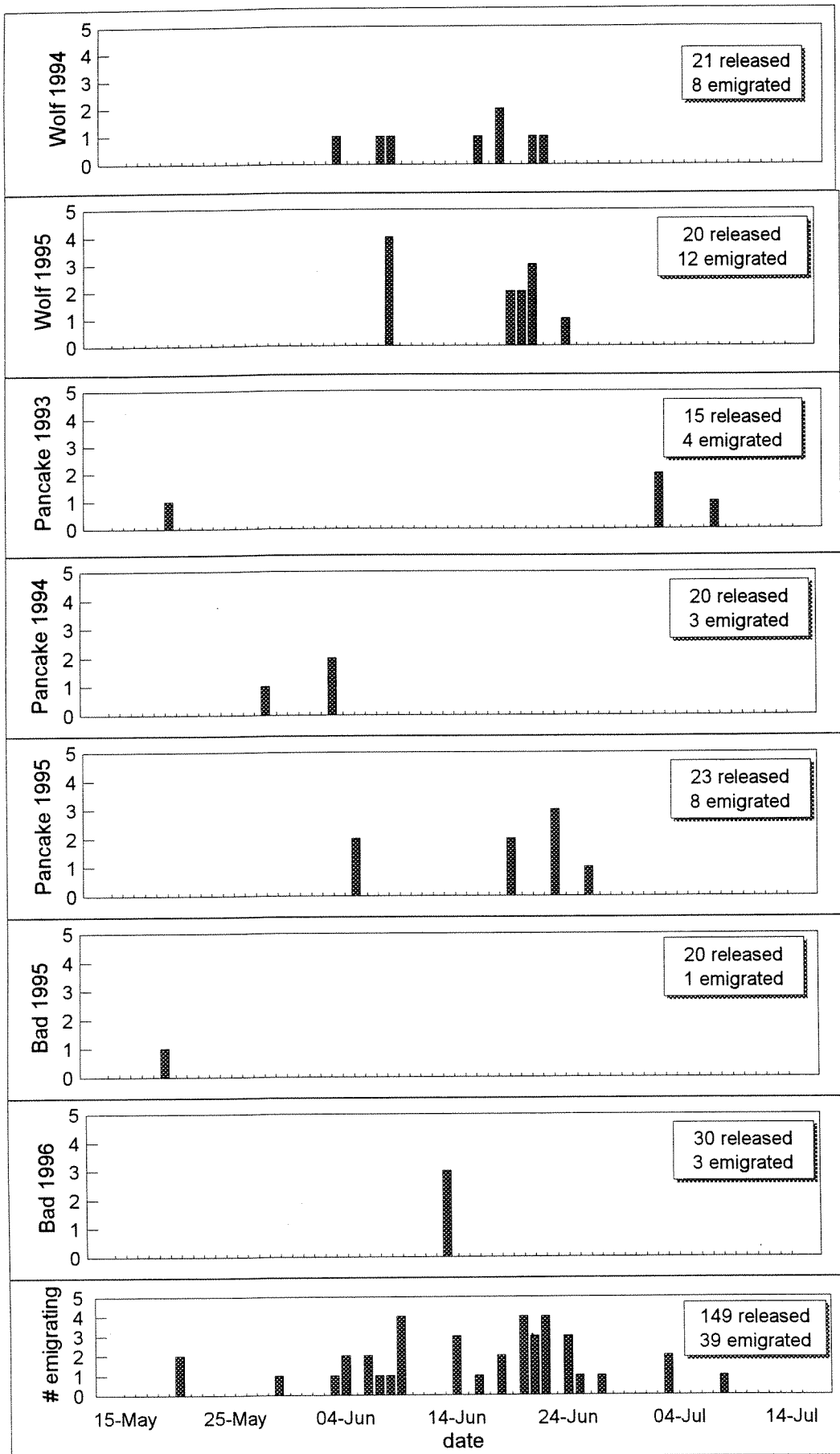


Figure 3

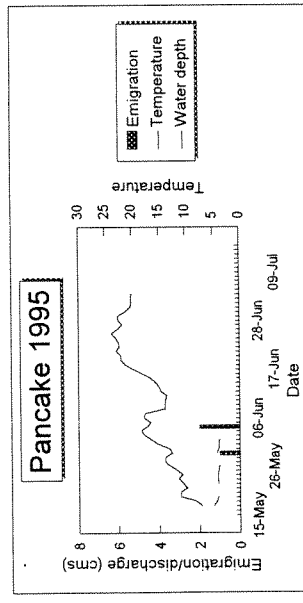
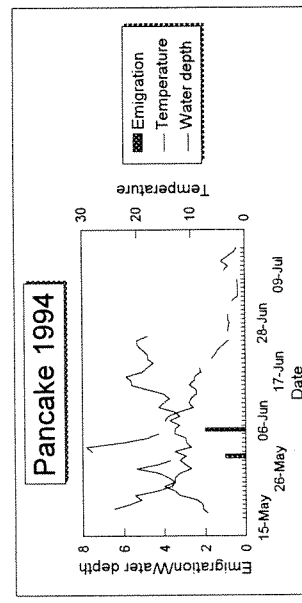
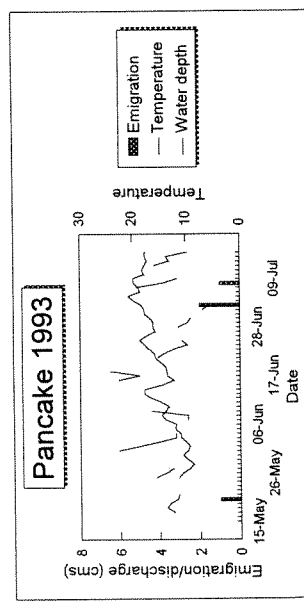
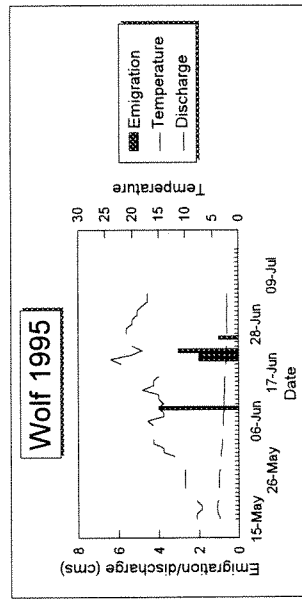
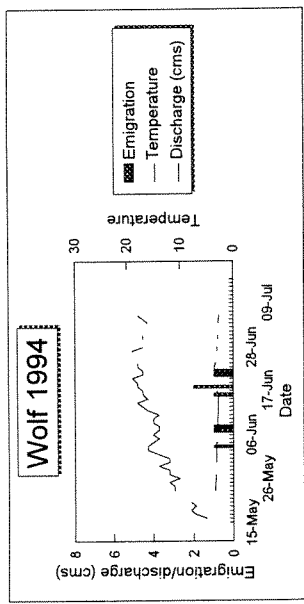
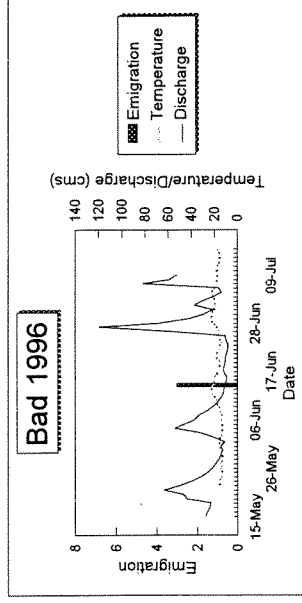
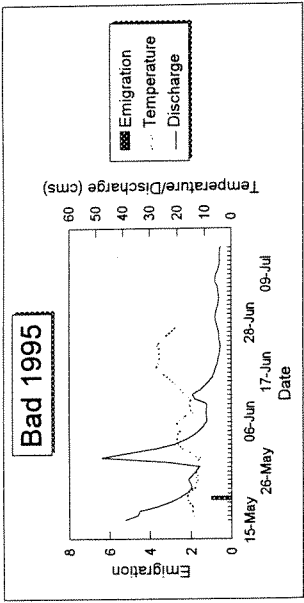


Figure 4

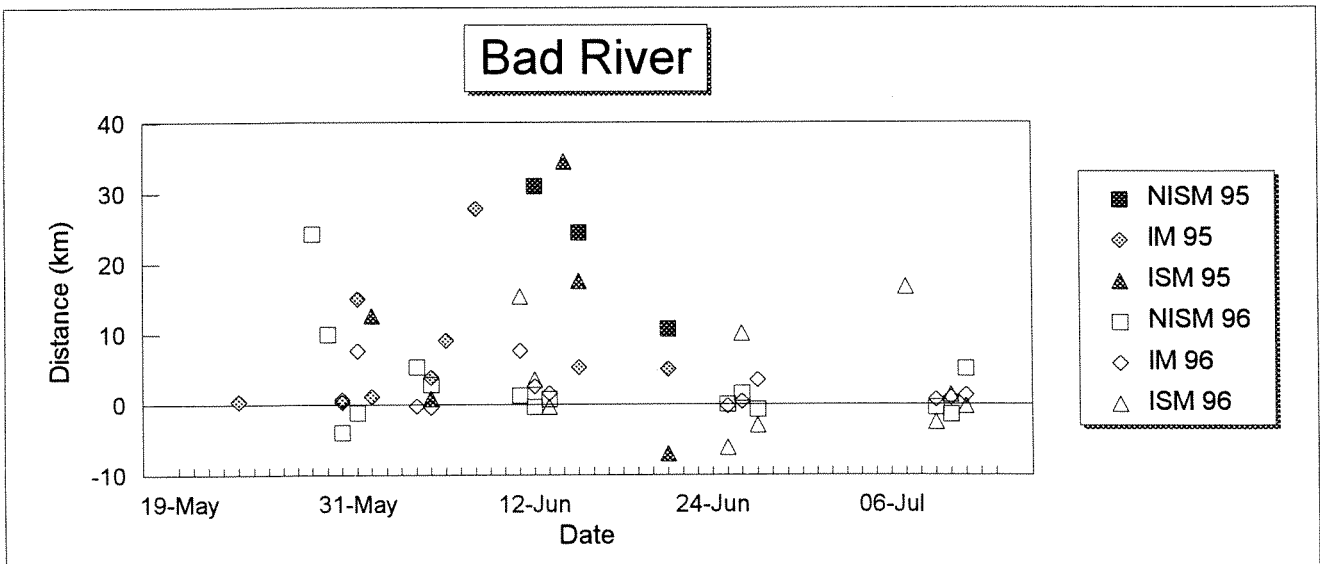
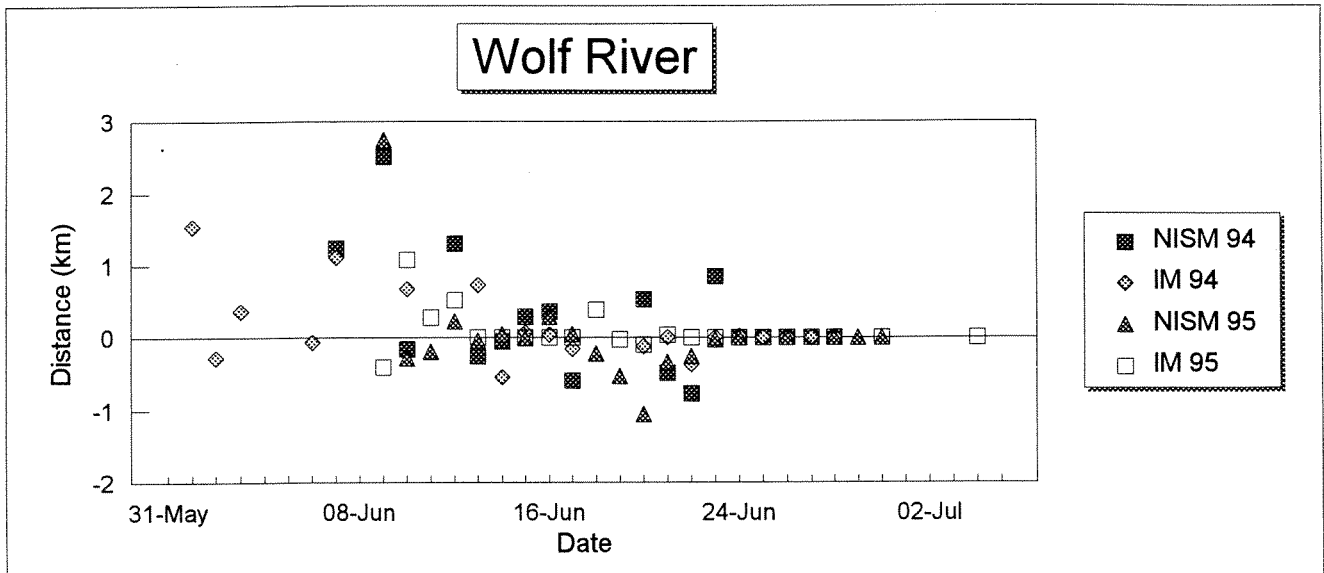
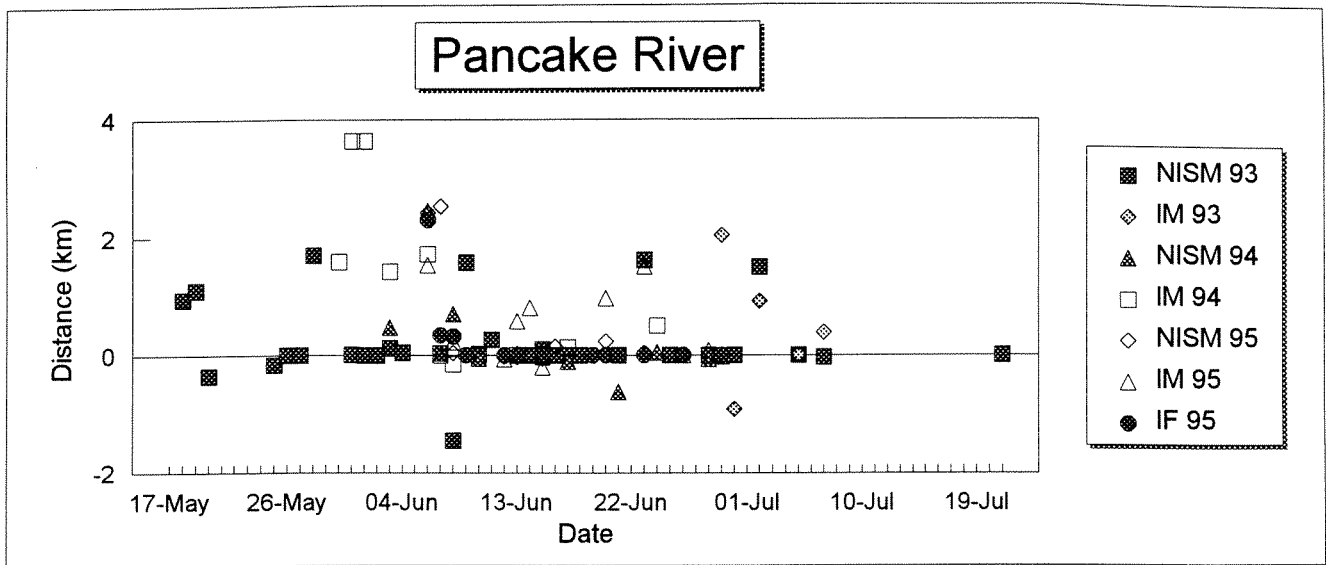


Figure 5

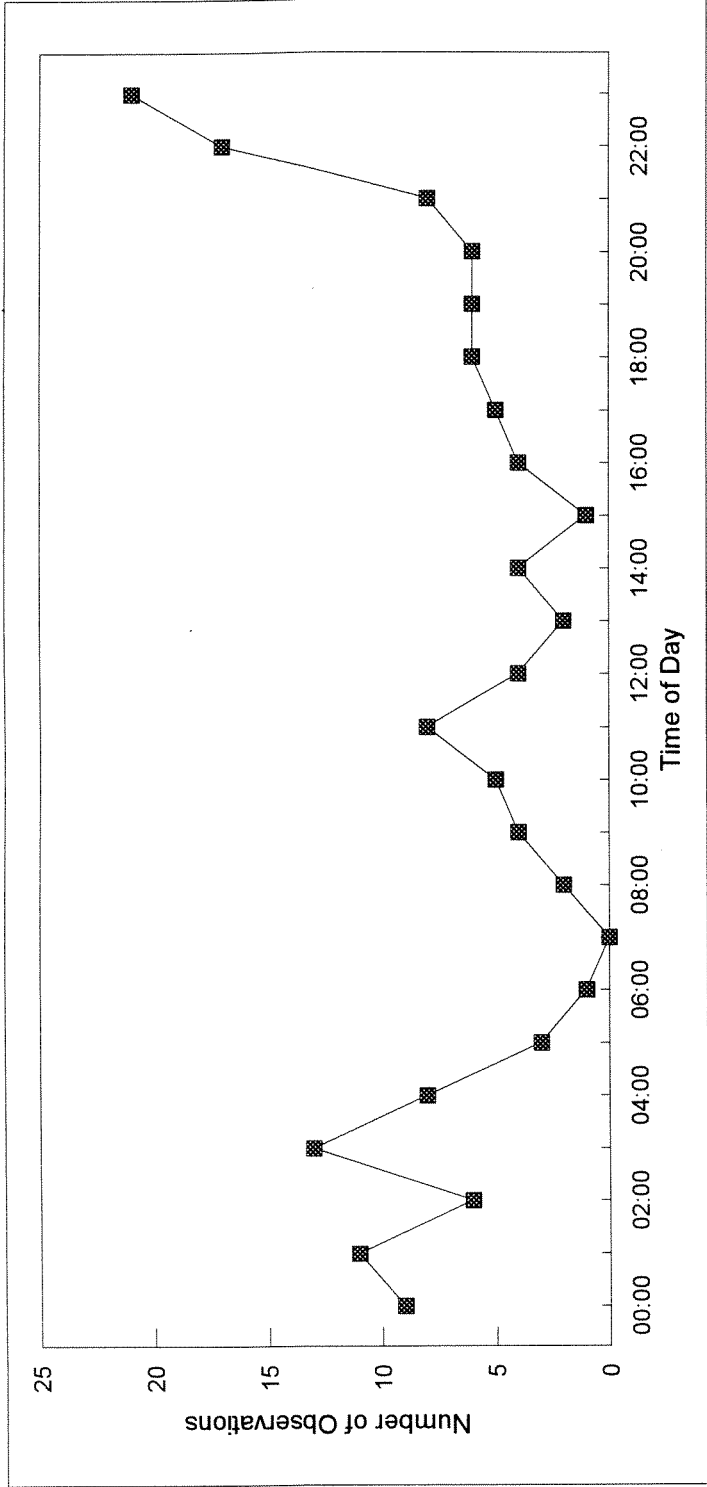


Figure 6

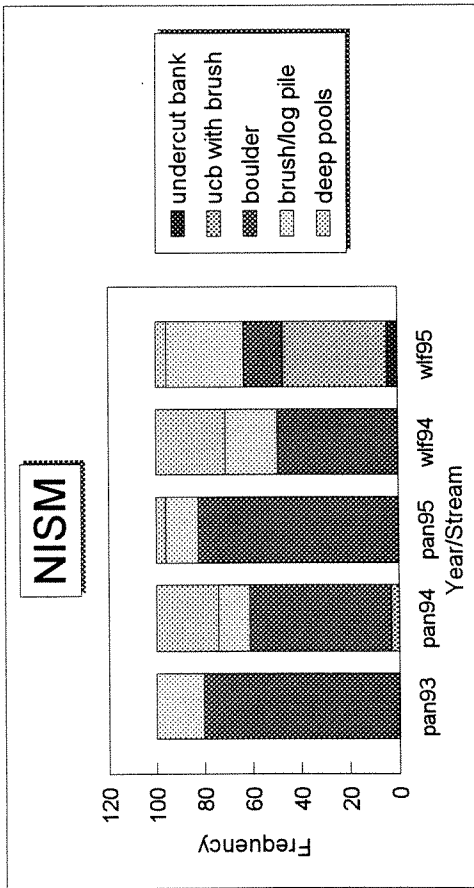
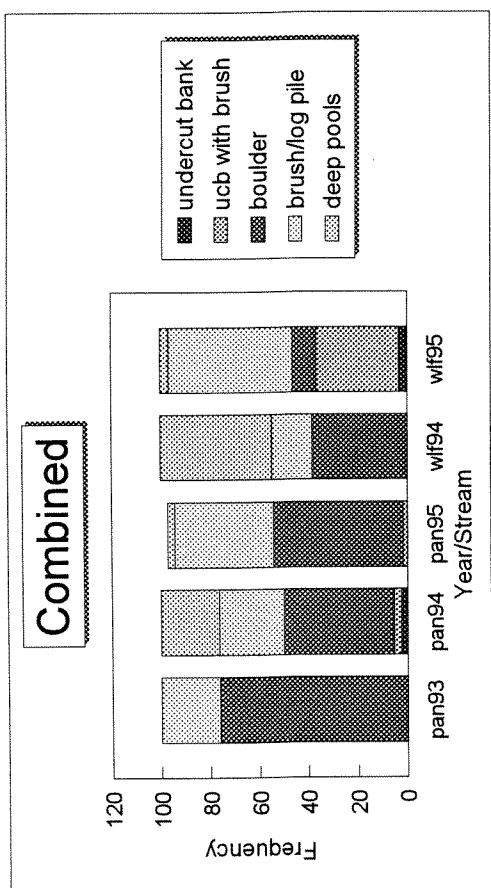
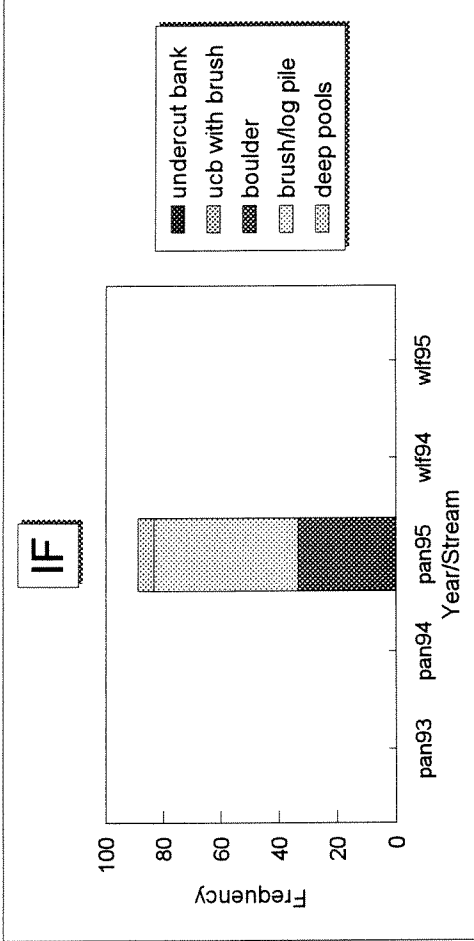
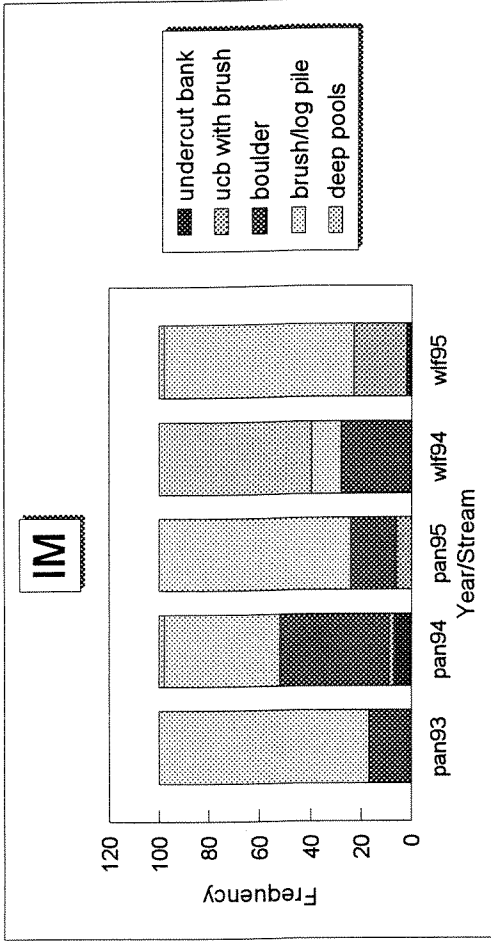


Figure 7

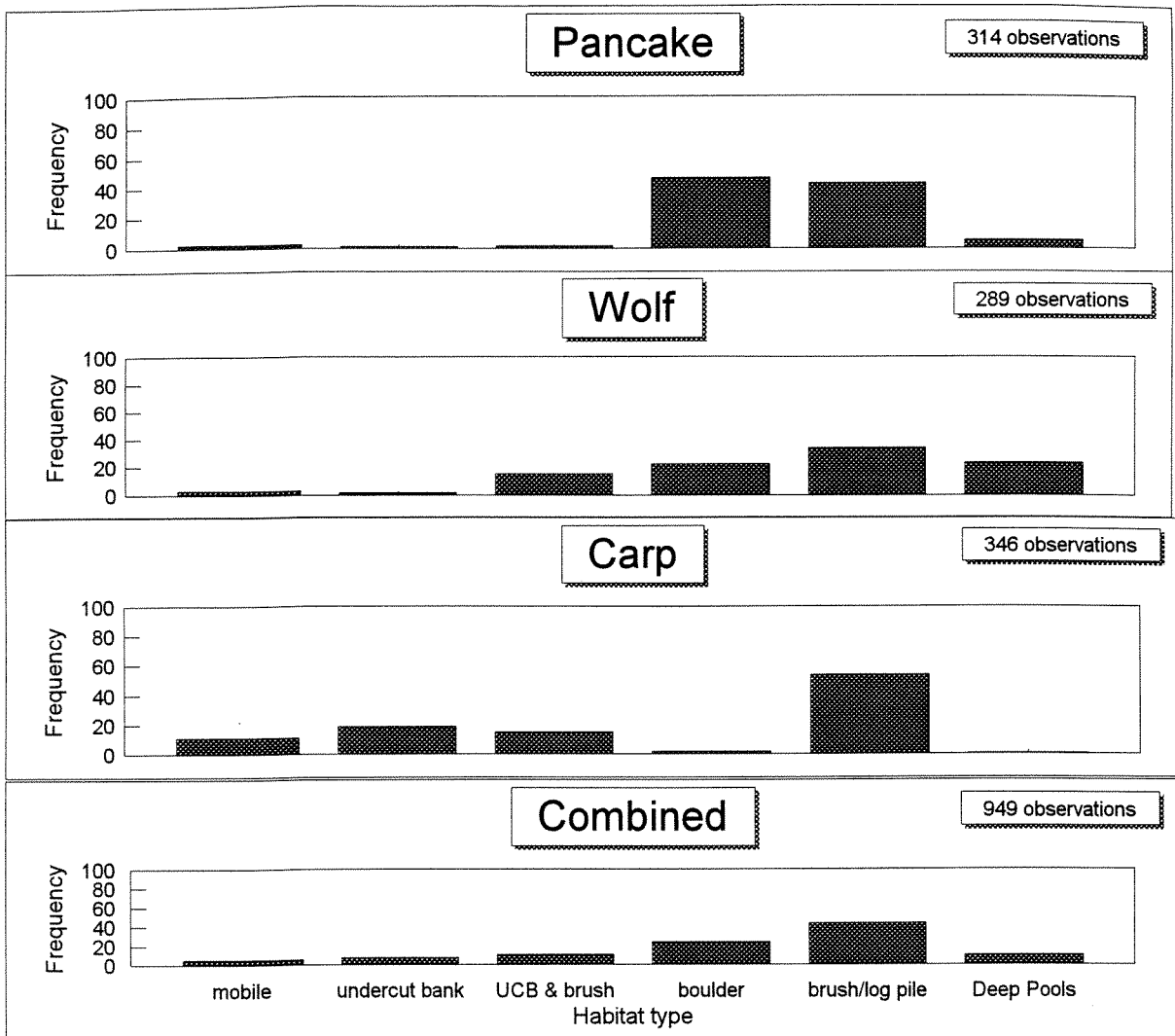


Figure 8