GREAT LAKES FISHERY COMMISSION

Project Completion Report[1]

The interaction among male, female and sterile male sea lampreys during spawning in the Carp River, Lake Superior

by:

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Introduction

Petromyzon marinus usually migrate into Great Lakes tributaries to spawn in early spring (April) but some adult lampreys can be found in streams in summer and as late as September (Skidmore 1959; McLain et al. 1965; Manion and Hanson 1980; Noltie and Robilliard 1987). Hanson and Manion (1980) suggested that introducing sterile male sea lampreys into these spawning populations would be an effective adjunct to an integrated program for lamprey management; they demonstrated that the reduction in reproductive success was related to the ratio of sterile to male sea lampreys in a population in the Big Garlic River, Michigan.

Although interspecific breeding has not been documented, all species of lampreys require suitable stream bottom substrate, water velocities and water temperatures for successful spawning (Manion and Hanson 1980). Lampreys may spawn communally (Huggins and Thompson 1969), may be monogamous (Applegate 1950; Hanson and Manion 1980) or may exhibit little fidelity to a mate (Case 1970; Noltie and Robilliard 1987). Some form of nest construction by mature, usually male, lampreys is common (Brigham 1973; Case 1970; Coventry 1922; Huggins and Thompson 1970; Hussakof 1912; Manion and Hanson 1980; Young and Cole 1900) and some species may be cryptic spawners (Cochran and Gripentrog 1992; Kelso and Glova 1993). Regardless of the behaviour of *P. marinus* during spawning, the net effect of introducing non-indigenous sterilized male lampreys into a spawning population on the production of larvae within a stream should be a reduction of the number of viable offspring (Hanson and Manion 1980). However, if little fidelity exists among mating pairs of sea lampreys or if females mate and deposit eggs in more than one nest, assessment of the effect of introducing sterilized male sea lampreys should, of necessity, be directed at assessing larval abundance at the stream level as opposed to determining the abundance of viable eggs in nests. Therefore, to determine a) the interaction of non-indigenous sterilized male sea lampreys with other spawning lampreys and b) the fidelity among animals engaged in reproduction, we continuously followed sea lampreys fitted with radio transmitters and observed the interactions of lampreys at a subset of nests during spawning in the Carp River, a tributary to Lake Superior.

Methods

The Carp River (46° 57'N, 84° 35'W) is some 70 km north of Sault Ste. Marie, Ontario, on the eastern shore of Lake Superior (Nolte and Robillard 1987; Kelso and Noltie 1990). A low-head barrier designed to stop upstream progress of sea lampreys is located 1.2 km from the river mouth (Fig. 1) and was constructed in the winter of 1983/84. One hundred and thirty non-indigenous male, 130 non-indigenous female and 390 non-indigenous sterile male sea lampreys were released above the low-head barrier in each spring of 1996 and 1997. These sea lamprey were introduced above the low-head barrier (Sterile male assessment program, GLFC) to determine the number of progeny produced by this mix of fertile and infertile sea lampreys. Each animal was marked by a distinctive tag and fin mutilation (1996) or fin mutilation (1997) such that sex was readily distinguishable by visual examination.

We externally attached radio transmitters to 21 male, 10 female and 21 sterile male sea lampreys from the population delivered to the site from the United States Fish and Wildlife Service sea lamprey sterilization facility at Hammond Bay, Michigan (Table

1). Lampreys provided by the Hammond Bay facility were captured in Lake Huron or in the St. Mary's River. Transmitters were externally attached anterior to the anterior dorsal fin with two stainless steel surgical wires. Animals were observed for 10-30 minutes following transmitter attachment and only apparently healthy fish were allowed to swim from the 60L holding container.

Sea lampreys fitted with radio transmitters were located using a hand-held receiver equipped with a directional antenna as we walked the bank or waded the stream. We walked and waded the stream 3-4 times per week on an irregular schedule prior to spawning to locate and account for animals with radio transmitters. We adjusted receiver gain, the orientation of the directional antenna and our location in the stream to locate sea lampreys with attached transmitters. At night, we confirmed locations and pairings periodically by activating battery powered headlamps. To detect the emigration of animals with transmitters, we installed a continuously recording receiver at the low-head barrier (Fig. 1). The continuously recording receiver focused on a 150m section of the stream and completed a scanning cycle in 63 (1996) or 93 (1997) seconds. We did not attempt to locate sea lampreys that passed downstream over the barrier. The portion of the stream above the barrier was walked and the location of each nest (a cleaned or disturbed area (with or without sea lamprey present), usually depressed, often with a downstream or upstream crest of rocks removed from the depression (see Manion and Hanson 1980)) was marked with a coloured, numbered marker. The stream was walked on a daily basis once the first nest was observed. Nest assessment was conducted by trained observers, Department of Fisheries and Oceans, Sea Lamprey Control Centre.

Once nests were identified in the river system, we observed the nightime movement and pairings of sea lampreys with radio transmitters. Prior to following individual sea lampreys, all the animals with radio transmitters that remained in the stream were located. Those sea lamprey that were near areas with nests were continuously observed from just before dusk until just before dawn. When a sea lamprey left a refugia, their location within ±1.5m as they travelled was determined and their encounters with other lamprey were recorded. The battery powered lights that were periodically activated to observe lamprey and confirm location did not appear to disturb lampreys (see also Manion and Hanson 1980). When a sea lamprey left its refugia, attention was focused upon that individual and others were ignored until that active sea lamprey returned to a refugia and became quiescent again. We were able to continuously monitor the movement and pairing of 2-6 animals with radio transmitters each night depending upon their activity, proximity to one another and the sequence of the activity by individual sea lampreys in the group that was near the area with nests.

To determine the number and sex of sea lampreys using a nest, we found, marked and observed 7 nests in 1996 and 4 nests in 1997 that were within 30 m of the refugia used by sea lampreys with radio transmitters. On occasion during each night, a low voltage incandescent light or a battery powered headlamp was focused on the nest and individuals were identified by the distinguishing mark provided to each non-indigenous male, sterile male and female lampreys introduced into the stream.

Results

In all, we placed radio transmitters on 8% of those sea lampreys introduced above the barrier in the Carp River (Table 1). In 1996, two sea lampreys with transmitters died late in the study and two were missing from the watershed but were not detected by the continuously operating receiver (Fig. 1) as they passed downstream. In 1997, three sea lampreys with transmitters emigrated and were detected by the continuously operating receiver, 5 died over the 26 days of observation and 10 were missing from the watershed but were not detected by the continuously operating receiver. Those lampreys that were not found in the watershed i.e. that were "missing" and not detected by the continuously operating receiver at the barrier, either passed the receiver operating at the barrier too quickly to be detected, were removed from the river by predators, or the transmitter failed. We suspect that the sea lampreys with transmitters that were missing from the watershed passed the receiver too quickly to be detected in the scanning cycle.

Sea lampreys remaining in the Carp River commonly were secreted beneath undercut banks and in log and woody debris piles (Fig. 2). Animals were found less frequently (<10% of observations) under boulders and in deep pools. There was no significant difference (analysis of variance, $P_{.05}$) between the habitat selected during the day and night and there was no significant difference in the habitat used between years. We did not test for differences in the habitat type selected by the non-indigenous male, female and sterile male sea lampreys (Fig. 1); however, there was no evidence to suspect any difference among the sexes. The amount of available habitat, habitat type and location of the habitats used as refugia varied with discharge between and within years. We suggest that discharge and its influence on the availability of habitat types will have a greater effect on the type of habitat in which sea lampreys are found than any preference affected by sex.

More nests (~4X), constructed earlier, were found in the early summer of 1996 than in 1997 (Fig. 3). Rainfall, stream discharge and water temperature were also very different between years (Figs. 3 and 4). Our measurement of discharge in the Carp River was infrequent; however, rainfall (Turkey Lakes Watershed, Environment Canada) and discharge continuously measured in a nearby river (Batchawana River, Environment Canada) and our few measurements of discharge in the Carp River indicate that flow was much greater in 1997 (Fig. 4). The three animals that emigrated from the Carp River in 1997 passed the continuously recording receiver during peak, June 23-26, 1997, flows and 10 other sea lampreys with transmitters were missing from the watershed on the day following this freshet. In addition to the strong freshet, water temperature was greater in 1997, the year in which fewer nests were found. From these data and data from the Wolf, Pancake and Bad rivers, we infer that freshets probably increase emigration in spawning sea lamprey populations.

Sea lampreys with radio transmitters that remained in the Carp River, near areas where nests were found, were more active in 1996 than 1997 and none of the animals with transmitters was seen actively spawning in 1997 (Fig. 5, Table 2). In both years, the sea lampreys we continuously observed at night spent most (between 75 and 100% of observations) of their time in refugia and some (4 of 12 animals continuously observed in 1996; 5 of 6 animals in 1997) did not leave their refugia during the study period. Travel upstream or downstream for distances >100m was also rare once nest construction began. The time spent constructing nests and in spawning was, logically, brief (an association with a nest lasted 30 sec.- 120 min.). In 1996, 3 of 21 sea lamprey with radio transmitters spawned and each visited more than one nest (Fig. 6). We followed and observed a non-indigenous sterile male and two non-indigenous male sea lampreys with radio transmitters in the act of successful mating with a female. Each male visited several nests (Fig. 6), and was observed with other non-indigenous males, sterile males and females although only one mating event that resulted in eggs being deposited in the nest was observed for each male. Nests were either in gravels of riffles or in gravel substrates sequestered beneath root masses and under large woody debris. In 1997, only one of 31 sea lamprey with radio transmitters was found on a nest, that animal remained alone and was not observed spawning during the period of observation. During both years, male sea lampreys with radio transmitters were observed constructing nests, altering nests and were in nests without a female(s). Between 2 and 4 male and sterile male sea lampreys were observed on a nest at the same time.

At night, we repeatedly checked 7 nests in 1996 and 4 nests in 1997 for the presence of sea lampreys. On 57 occasions (47% of the times that we inspected the nests) in 1996, we observed non-indigenous male or sterile male sea lampreys on the nests without a female and we also saw 14 mating pairs on the 7 nests. In 1997, we observed 10 male or sterile male on 4 nests at various times and observed 10 mating pairs of non-indigenous sterile male and female lampreys on the same 4 nests. Non-indigenous female lampreys were infrequently unattended in either year on these nests. The same individual may have made repeated visits to this subsample of nests but distinguishing features of individuals – scars, colour, fin damage - and the activity of sea lampreys with transmitters around some of these and other nests suggest that we probably observed a number of different individuals. In 1996 almost equal numbers of non-indigenous male (6) and sterile male (8) lampreys were mating with females but in 1997 we saw only non-indigenous sterile male lampreys mate.

Year	Number of nests	Total number of observations	Number of nights	Empty	Males only	Sterile males only	Males with female	Sterile males with a female	Female only
1996	7	120	6	46	15	42	6	8	3
1997	4	71	6	50	4	6	0	10	1

Consequently, from these data we infer that infidelity to a nest is normal and that the frequency of nest construction and the number of sea lampreys in the population that mate varied between years.

Discussion

Sea lampreys with radio transmitters spent most of their time in refugia prior to spawning and we saw nest building and spawning only during 12 days in late June and early July, 1996, and 9 days in late June and early July, 1997, in the Carp River. The timing of nest construction was similar between 1996 and 1997 but the number of nests found in the stream varied by about a factor of 4 between years. In 1996, 20% (4 of 20) of sea lampreys released with radio transmitters spawned while in 1997 0% (0 of 31) of sea lampreys were observed spawning. The inference from these data is that, perhaps apart from the timing of spawning, emigration from the spawning population and reproduction in the population will vary annually depending, we think, upon discharge.

Manion and Hanson (1980) in their summary of the spawning behaviour of lampreys and Applegate (1950) in his study of sea lamprey spawning in the Ocqueoc River suggested that polyandry was rare and monogamy was common. Polyandrous spawning i.e. one female spawning with several males (definition from Applegate 1950) and polygamy (one male spawning with >1 female) was not observed for sea lampreys with transmitters or those visiting 11 nests in the Carp River. Sea lampreys spawning in the Carp River spawned in pairs, changed mates and used more than one nest. Consequently, from the movement of non-indigenous male, sterile male and female sea lampreys among nests and the changes in mates, the ova deposited in a nest will not likely be the result of spawning by a single pair of lampreys. Although we monitored nest construction and relocated sea lampreys with radio transmitters 2 weeks before and after the short (9-12 day) spawning period in late June and early July, we saw no new nests and no further pairings other than during this brief period.

We summarized information about lamprey spawning (Table 3) available in the literature. All lampreys appear to spawn in the coarse substrates that commonly occur in riffles and in waters of higher velocity. Generally, nest construction occurs by male(s) or female(s) lampreys prior to and during spawning, nests may overlap, nests may become superimposed and nests may be used and altered by animals spawning later. Non-indigenous sea lampreys spawning in the Carp River, 1996 and 1997, followed these norms. Some lamprey spawning may be cryptic (Table 3) and we saw sea lampreys spawn under cover in sequestered nests in the Carp River. From Hussakoff (1912), Coventry (1922), Applegate (1950), Hanson and Manion (1980), Noltie and Robilliard (1987) and this study, we also suggest that spawning by sea lampreys, as with other lampreys, is likely to be monogamous i.e. one male and one female, but that pairing will not likely be sustained until all the eggs of that female are deposited. From earlier studies, we expect that polygamy and polyandry may also occur in sea lamprey spawning populations. Consequently, spawning habitat used and spawning behaviour by lampreys may be facultative and will be variable among streams and years.

We concur with Hanson and Manion's (1980) conclusion from their field study that sterilization of male sea lampreys with bisazir had no detectable effect on their nest building and spawning behaviour and did not alter their mating competitiveness with indigenous male sea lampreys. Consequently, the introduction of sterile male sea lampreys into spawning populations continues to have potential for management of lamprey abundance. The short duration of spawning in the Carp River, the possible influence of freshets upon spawning success (Noltie and Robilliard 1987) and the possibility that sea lampreys may spawn in the autumn indicates that recruitment may be quite variable annually. If the contribution of sterile male lampreys to reducing the abundance of viable offspring remains proportional to their abundance in the spawning population, reproductive success of a sea lamprey population may vary annually but the contribution of sterile males should still remain proportionate to their abundance in the population. The observed behaviour of spawning by sea lampreys indicates that an assessment of the effects of introducing sterile males upon recruits should be conducted at the stream level because nests a) may contain progeny from more than one pair and b) nests may be destroyed and altered by other lampreys.

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Figure Legends

Fig. 1 Spawning areas for sea lampreys and the location of the continuously operating data logger (radio receiver), Carp River.

Fig. 2 Habitat selected (refugia) by non-indigenous sea lampreys with radio transmitters released in the Carp River, 1996 and 1997. Day and night observations were combined.

Fig. 3 Cumulative number of nests constructed by sea lampreys in the Carp River, period of continuous observation and water temperature, 1996 and 1997.

Fig. 4 Discharge in the Batchawana River (Environment Canada) and Carp River and rainfall at the Turkey Lakes Calibrated Watershed (Environment Canada), 1996 and 1997.

Fig. 5 Nocturnal movement, including spawning, of sea lampreys with radio transmitters in the Carp River 1996 and 1997.

Fig. 6 Nocturnal travel of 2 male sea lampreys (frequency 150.041 and 150.170 MHz, see also Table 1) during spawning in the Carp River, 1996.

Table 1: The number of non-indigenous sea lampreys with radio transmitters, number emigrating, and movement in the Carp River, 1996 and 1997.

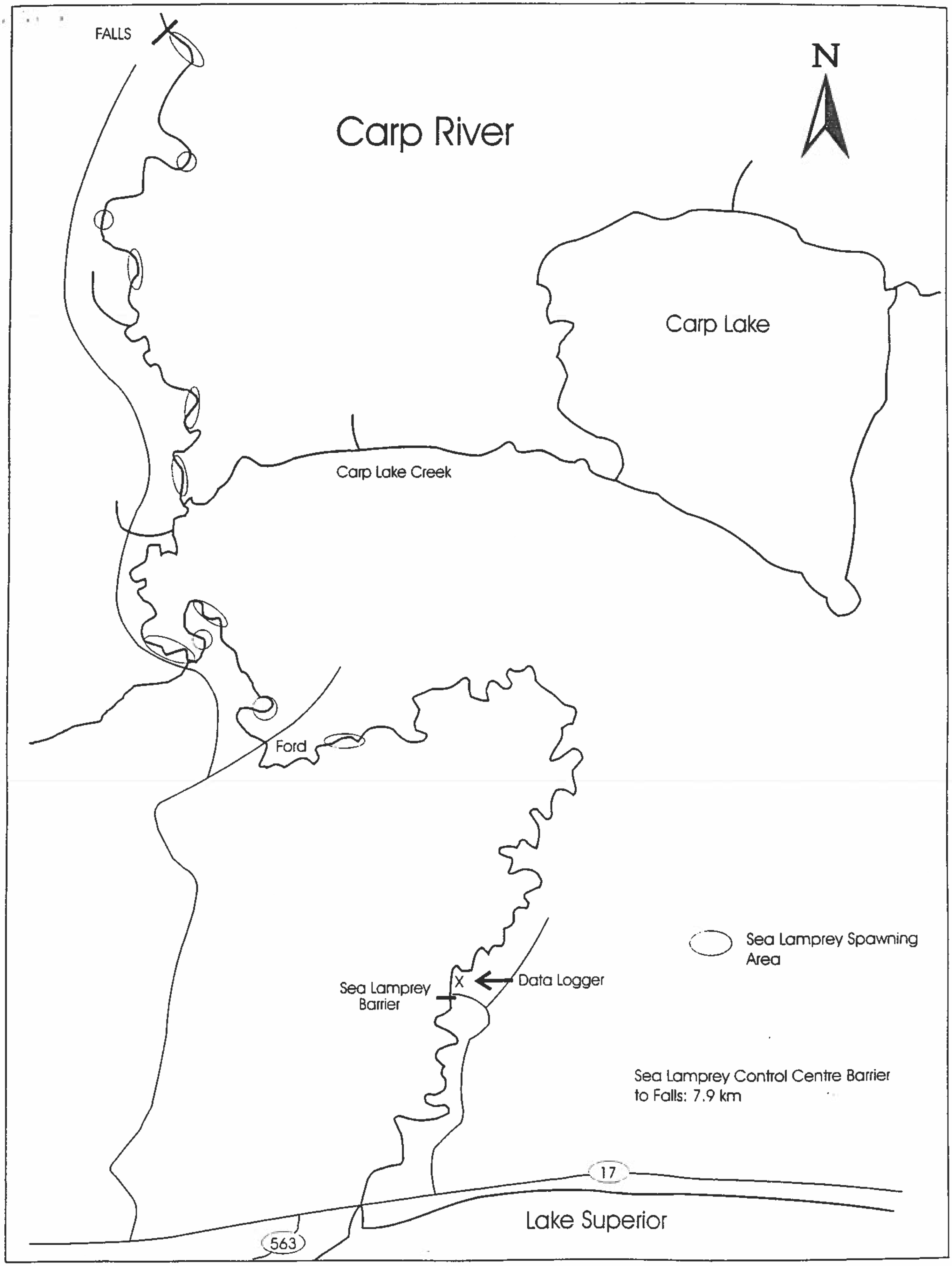
	1996	1997
Carp River		
Duration of study (d)	31	26
Number of lamprey with Radio transmitters	21	31
Male	10	11
Female	0	10
Sterile male	11	10
Number emmigrating, M	0	2
Number emmigrating, F	-	0
Number emmigrating, S	0	1
Number Dead	2	5
Number missing	2	10
Mean maximum distance travelled (km)		
Males	0.33	-0.86
Females	-	0.97
Sterile males	-0.21	-0.95
Average daily movement (km)		
Males	0.05	-0.59
Females	-	0.14
Sterile males	-0.14	-0.42

Table 2: Nests visited with and without female sea lampreys in the Carp river, 1996 and 1997.

	Animal #	Sexual Condition	#of nights observed	#of nights on "spawning areas"	#of nests visited	#of nests with females	Net Result
1996	170.010	S	6	0	0	0	did not appear to spawn.
	170.021	S	7	0	0	0	did not appear to spawn.
	170.041	S	6	2	4	1	spawned multi-nest visits seen with female
	170.100	S	1	0	0	0	did not appear to spawn.
	170.120	M	1	1	0	0	unknown
	170.130	M	1	1	0	0	did not appear to spawn.
	170.150	M	7	0	0	0	did not appear to spawn.
	170.159	M	4	0	0	0	did not appear to spawn.
	170.170	M	6	5	3	1	spawned multi-nest visits seen with female
	170.191	M	6	6	2	1	spawned multi-nest visits
	170.201	M	4	0	0	0	did not appear to spawn.
	170.211	M	2	0	0	0	did not appear to spawn.
1997	171.148	M	5	5	1	0	did not appear to spawn.
	171.190	M	5	5	0	0	unknown
	171.366	F	3	3	0	0	unknown
	171.389	F	1	1	0	0	unknown
	171.447	S	5	5	0	0	unknown
	171.510	S	3	3	0	0	unknown

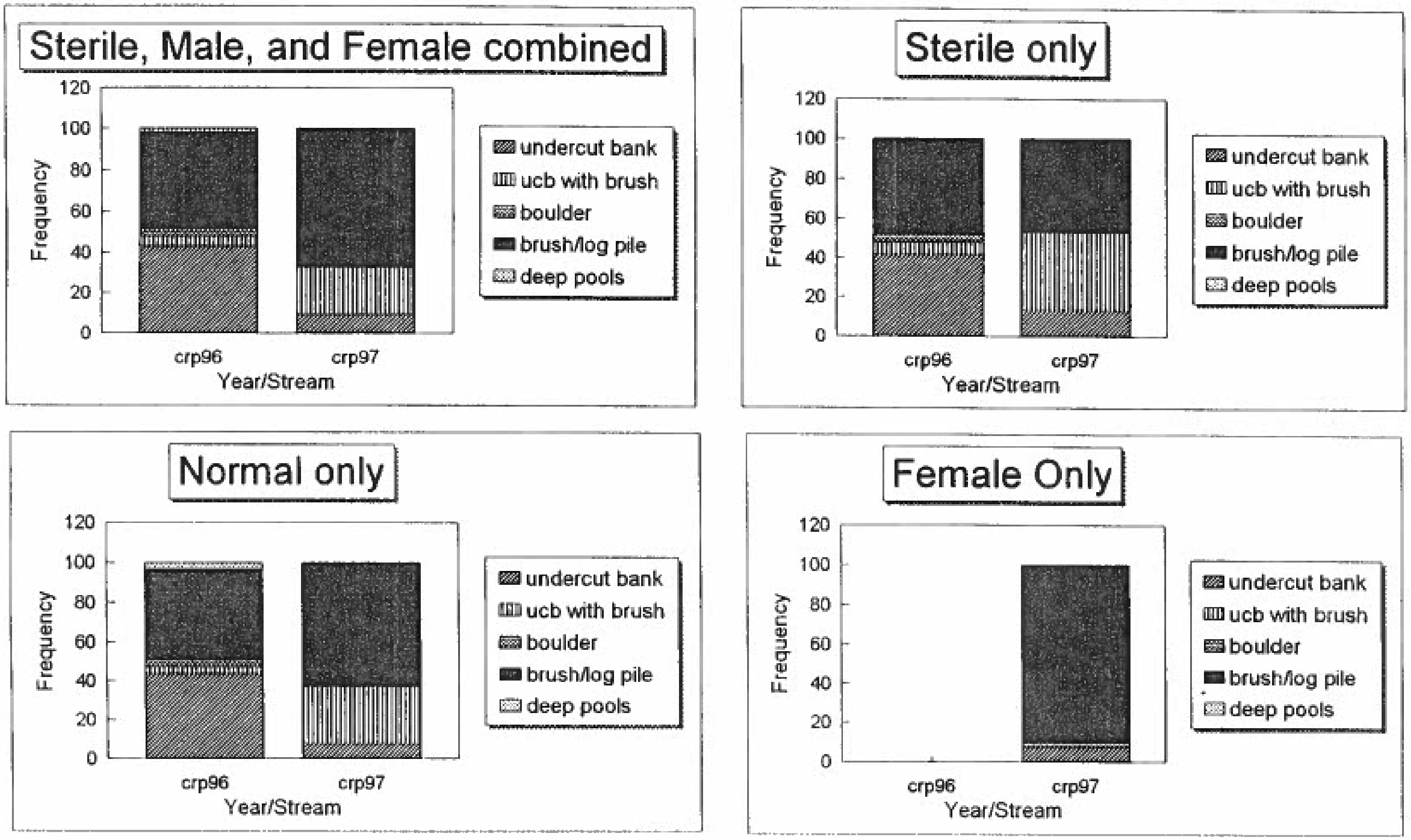
Species	Substrate	Preparatory Activity	Spawning Notes	Post-spawning Activities
Ichthyomyzon castaneus (Case 1970) Entosphenus lamottei (Gage 1928) Lampetra richardsoni (McIntyre 1969 and Case 1970) Ichthyomyzon gagei (Dandy and Scott 1953) Lampetra fluviatilis (Hagelin 1959; Huggins and Thompson 1970) Entosphenus tridentaties (from Case 1970) Lampetra aepyptera (Bingham 1973)	Small rocks, pebbles, gravel, course sand, often or usually in riffles	- create depressions and nests, reorganize substrate – nests/depressions may be made by an individual (L.aepyptera) or large group (I.castaneus)	- mating ranges from one female with several to many males to communal spawning – may be cryptic (Cochran and Gripentrog 1992) i.e. under cover	- substrate usually rearranged after spawning occurs
Petromyzon marinus	Cleaned gravel, shingle, small and large boulders, coarse pebbles, in riffles and rapids	- create shallow depressions or defined nests, nests may overlap – nest construction usually by males (Manion and Hanson 1980) but may be by females (Applegate 1950)	- generally monogamous (Manion and Hanson 1980; Applegate 1950) – male may mate with successive females (Coventry 1922; Hussakoff 1912) – degree of monogomy can vary (Hanson and Manion 1980) but is high >50%, conversely, polyandry low, <5% (Applegate 1950; Manion and McLain 1971)	?
Petromyzon marinus (this study)	In riffles, mixed gravel, pebbles and small boulders	- created shallow depressions and defined nests, nests may overlap and were constructed over existing nests, a nest/depression can be result of activity by several males and females	- no evidence of sustained pairing, males most often visited several nests, no nest fidelity observed – all animals in a population may not spawn	?

Table 3. Summary of substrate used, preparatory in-stream activity and spawning behavior of lampreys



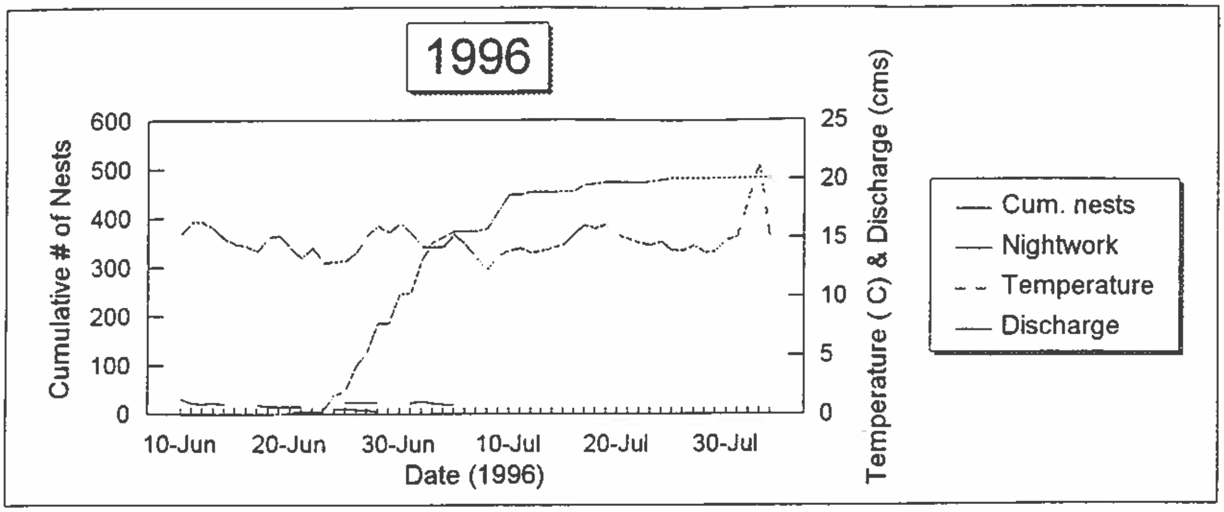
Carp River
N
FALLS
Carp Lake
Carp Lake Creek
Ford
Sea Lamprey Spawning Area
Sea Lamprey Barrier
X
Data Logger
Sea Lamprey Control Centre Barrier to Falls: 7.9 km
17
563
Lake Superior

Figure 1:



Sterile, Male, and Female combined
Sterile only
Normal only
Female Only
Frequency
120
100
80
60
40
20
0
crp96
crp97
Year/Stream
undercut bank
ucb with brush
boulder
brush/log pile
deep pools

Figure 2:


1996
Cumulative # of Nests
600
500
400
300
200
100
0
10-Jun
20-Jun
30-Jun
10-Jul
20-Jul
30-Jul
Date (1996)
Temperature (C) & Discharge (cms)
25
20
15
10
5
0
Cum. nests
Nightwork
Temperature
Discharge

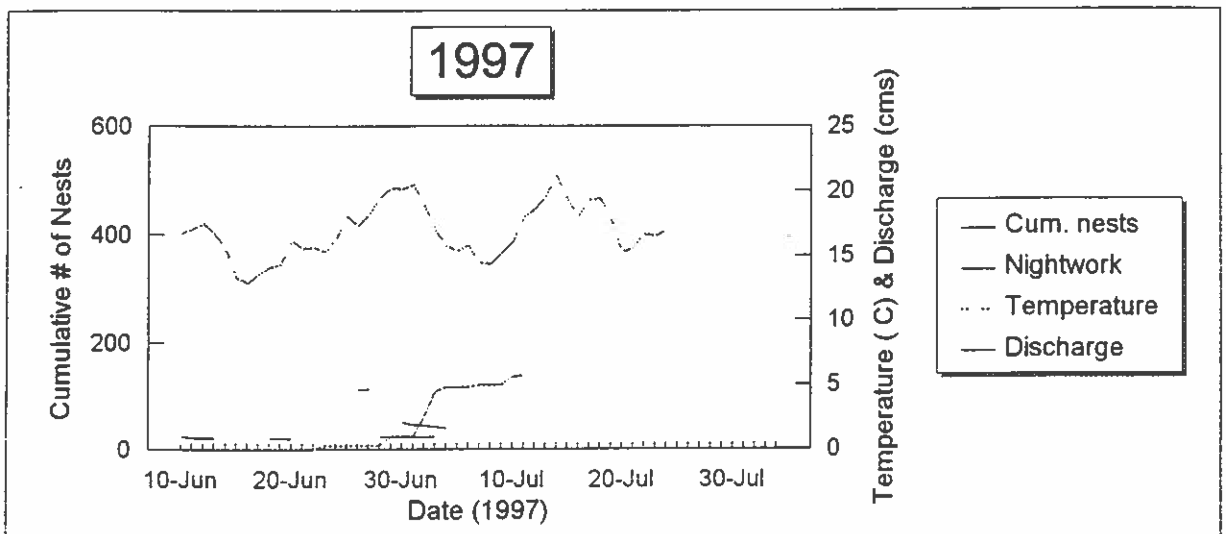

1997
Cumulative # of Nests
600
400
200
0
10-Jun
20-Jun
30-Jun
10-Jul
20-Jul
30-Jul
Date (1997)
Temperature (C) & Discharge (cms)
25
20
15
10
5
0
Cum. nests
Nightwork
Temperature
Discharge

Figure 3:

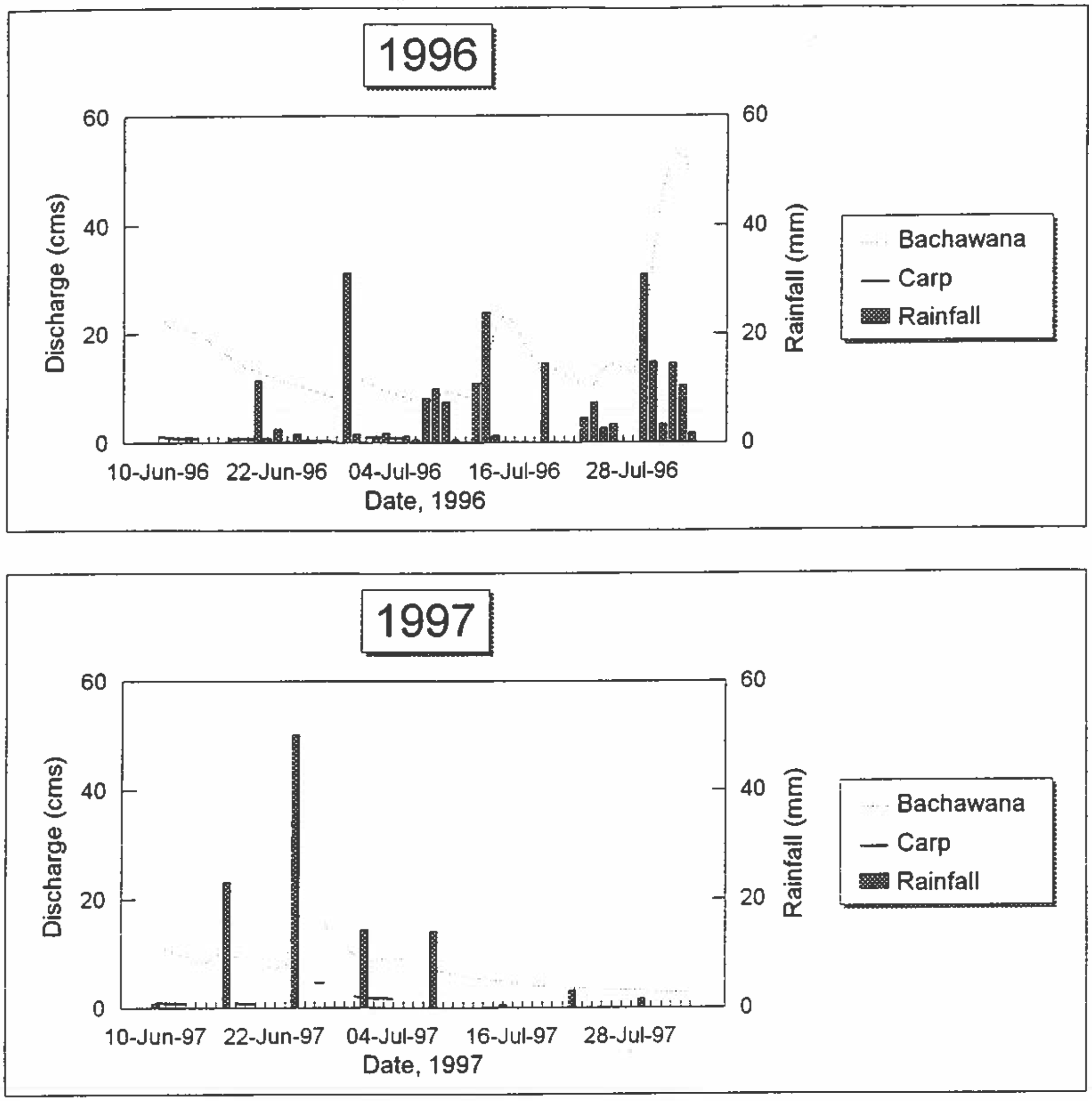

1996
Discharge (cms)
Rainfall (mm)
60
40
20
0
10-Jun-96
22-Jun-96
04-Jul-96
16-Jul-96
28-Jul-96
Date, 1996
Bachawana
Carp
Rainfall
1997
Discharge (cms)
Rainfall (mm)
10-Jun-97
22-Jun-97
04-Jul-97
16-Jul-97
28-Jul-97
Date, 1997
Bachawana
Carp
Rainfall

Figure 4:

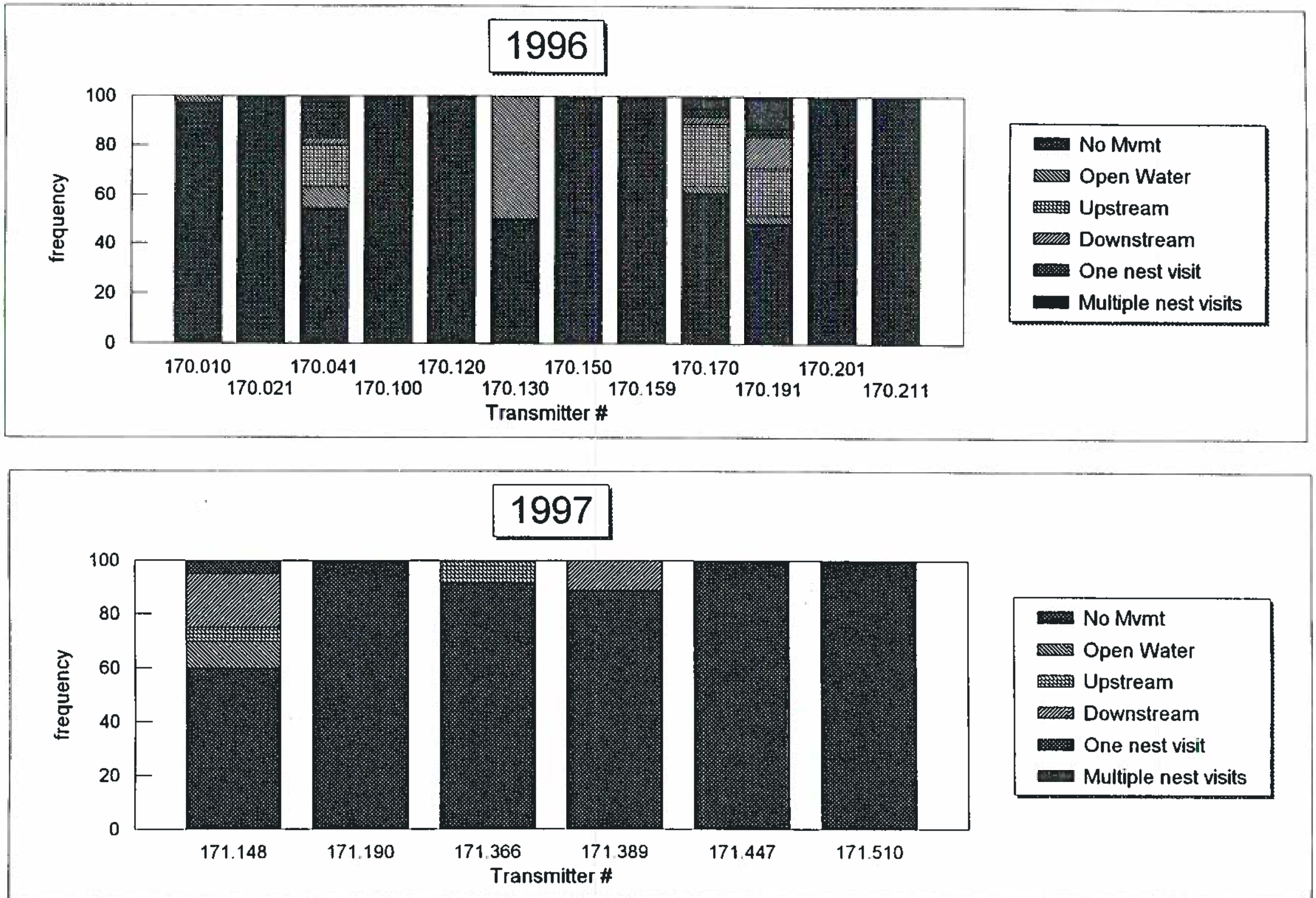
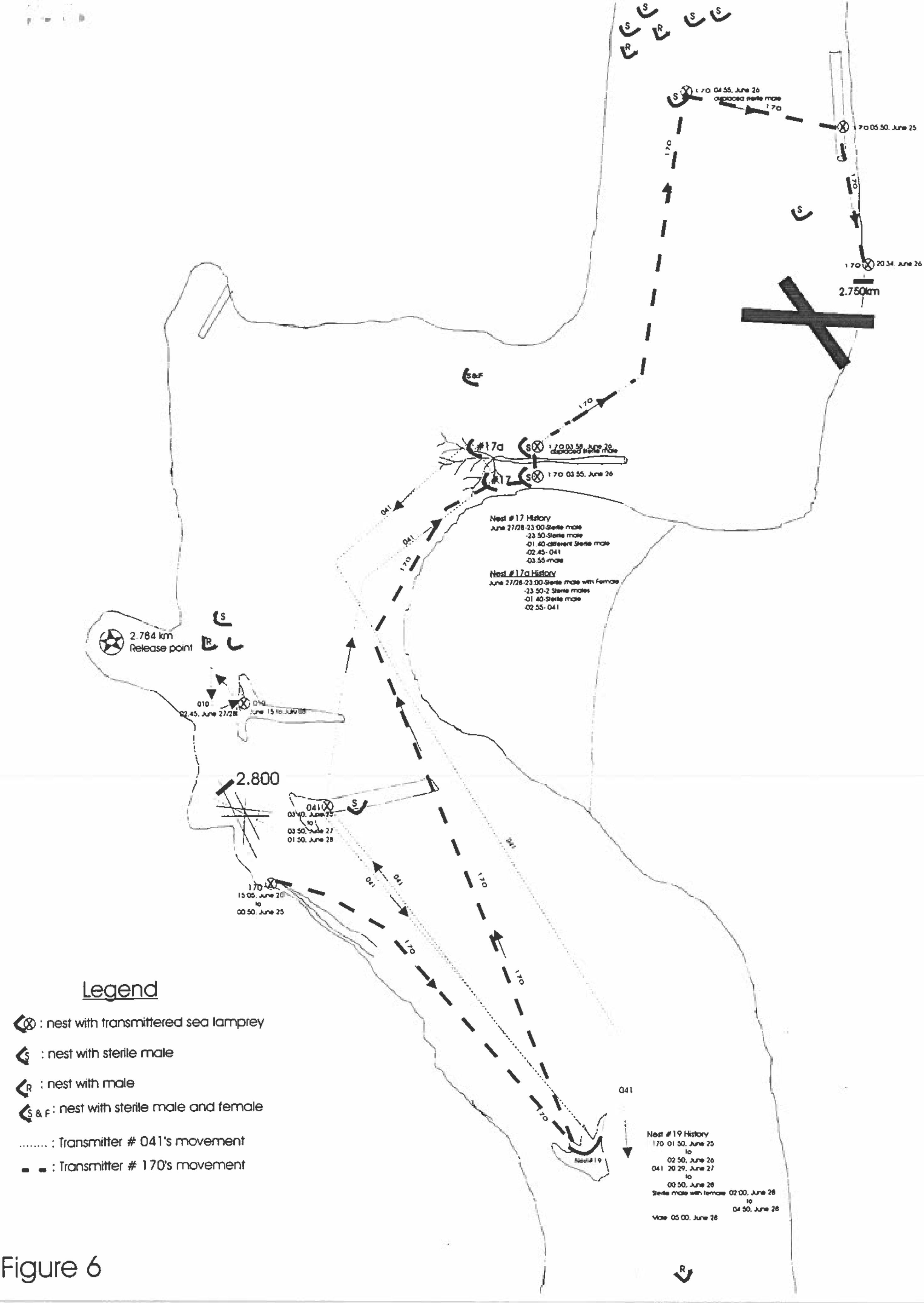

1996
100
80
60
40
20
0
frequency
170.010
170.021
170.041
170.100
170.120
170.130
170.150
170.159
170.170
170.191
170.201
170.211
Transmitter #
No Mvmt
Open Water
Upstream
Downstream
One nest visit
Multiple nest visits
1997
171.148
171.190
171.366
171.389
171.447
171.510

Figure 5:



170 04 55, June 26
displaced sterile male
170 05 50, June 25
170 20 34, June 26
2.750km
#17a
170 03 58, June 26
displaced sterile male
#17
170 03 55, June 26
Nest #17 History
June 27/28-23:00-Sterile male
-23 50-Sterile male
-01 40-different Sterile male
-02 45- 041
-03 55-male
Nest #17a History
June 27/28-23:00-Sterile male with Female
-23 50-2 Sterile males
-01 40-Sterile male
-02 55- 041
2.784 km
Release point
010
02.45, June 27/28
010
June 15 to June 28
2.800
041
03 40, June 25
to
03 50, June 27
01 50, June 28
170
15 05, June 20
to
00 50, June 25
Nest#19
Nest #19 History
170 01 50, June 25
to
02 50, June 26
041 20 29, June 27
to
00 50, June 28
Sterile male with female 02 00, June 28
to
04 50, June 28
Male 05 00, June 28
Legend
: nest with transmittered sea lamprey
: nest with sterile male
: nest with male
: nest with sterile male and female
: Transmitter # 041's movement
: Transmitter # 170's movement

Figure 6