OFFICE OF RESOURCE CONSERVATION

State of Illinois

Grant Proposal Final Report

PROJECT NUMBER: T-50

PROJECT TITLE: The Effects of Habitat Fragmentation on Sensitive Aquatic Species

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INTRODUCTION:

In the United States and throughout the world, contiguous habitats have undergone fragmentation into smaller, more isolated patches (Wilcove *et al.* 1986, Noss and Csuti 1997, Rosenblatt *et al.* 1999). Habitat fragmentation causes a reduction in total habitat area and redistributes the remaining area into patches (Wilcove *et al.* 1986), which may lead to a loss of habitat types and changes in both abiotic and biotic factors. Due to the modification of native landscape by human disturbance, less than 1% of the original landscape in Illinois remains (Page *et al.* 1997).

With habitat fragmentation the effective size of a population may be reduced and individuals may exhibit limited dispersal between patches (Wilcove *et al.* 1986). As an area becomes more fragmented, the effective population size, or the number of breeding individuals in a population, will be greatly reduced compared to the actual total census count (Gilpin and Soulé 1986, Lacy 1987). Breeding individuals are responsible for population expansion and the maintenance of genetic variability. If fewer individuals produce the next generation, this may lead to detrimental genetic effects, such as decreased genetic variability, inbreeding depression and a reduction of the ability to respond to environmental variability. Fragmentation can create a landscape structure that could result in limited dispersal rates of individuals among populations (Collingham and Huntley 2000). In fragmented habitats, dispersal is limited by an organism's ability to reach a patch of suitable habitat and as landscapes becomes more fragmented the dispersal rate of an organism decreases markedly (Wilcove *et al.* 1986, Lehtinen *et al.* 1999, Collingham and Huntley 2000), leading to an increase in genetic similarity within populations (F_{IS}) and a decrease in similarity among populations (F_{ST}).

Increasing physical isolation of populations heightens the concern about negative genetic consequences due to genetic drift and inbreeding. The longer isolation lasts, the greater the chance of inbreeding occurring within a population (decreases intrapopulation variability) and genetic drift taking place between populations (increases interpopulation variability). If high quality patches are extremely isolated from one another, dispersal between the populations may be so limited that loss of allelic diversity occurs.

There have been numerous studies that have investigated the effects of terrestrial habitat fragmentation on the survival and reproductive capabilities of organisms. Research has shown that, due to the increased isolation caused by habitat fragmentation, many terrestrial organisms such as plants, birds, and lizards, have decreased in their overall genetic variability. A reduction in genetic variation will likely reduce an organism's ability to adapt to environmental changes and/or respond to environmental stressors, therefore increasing the probability of population extinction.

Research on fragmentation of terrestrial ecosystems has been extensive but few studies have investigated fragmentation of lotic aquatic ecosystems. Aquatic habitat fragmentation is defined as a lack of connectivity between upstream and downstream populations along the longitudinal gradient and/or the lateral gradient. The longitudinal gradient is within stream disruption of flow brought about by dams and bridges. Fragmentation along the lateral gradient is any loss or modification of the riparian zone outside of the stream channel.

Within the last 100 years, Illinois stream habitats have become increasingly fragmented by dams and the loss of riparian zones, because of an increase in rates of channelization, drainage, groundwater exploitation, and most importantly, agriculture (Karr *et al.* 1985, Page *et al.* 1997, Pringle 1997, Jones *et al.* 1999). As in fragments of terrestrial systems, organisms subjected to aquatic fragmentation (i.e. >70% loss of riparian zone; Page *et al.* 1997) may form isolated populations, preventing migration and leading to a reduction in gene flow and/or a loss of genetic variation within populations (Tibbets and Dowling 1996, Page *et al.* 1997, Pringle 1997).

In general, the fragmentation of Illinois streams has led to the creation of small, discrete, isolated patches of stream habitat in a sea of low quality habitat. Thus small patches of high quality stream (stretches that meander, have rocky substrate, good tree cover, and good riparian zone) are separated from one another by large patches of low quality stream (channelized, silty substrate, poor tree cover, and little or no riparian zone). Fish populations isolated within high quality patches should exhibit small effective population sizes and little or no gene flow between populations resulting in a loss of genetic variability within the isolate due to the lack of gene flow and an increase in genetic variability between isolates due to genetic drift.

Darters are ideal model species for looking at the effects of aquatic fragmentation on dispersal rates and genetic variability. Darters are intolerant, bottom-dwelling habitat specialists that inhabit rocky or gravelly riffles with a swift current. Much of the darter's life is spent beneath or between rocks protected from the current. Reproduction occurs in the spring and early summer, and culminates with the attachment of eggs to the bottom substrate. Thus, darters require a fast flowing current and gravel bottom substrate to survive and reproduce, and may be unable to live or traverse bad patches of a stream (slow-moving or standing water).

Although aquatic systems in the Midwest have been shown to be fragmented by agricultural activity and urbanization (Page *et al.* 1997), it is unknown whether habitat specialists, such as darters, exhibit population isolation. Thus, the overall goal of this study is to determine if aquatic habitat fragmentation has had an isolating effect on darter populations. Specifically to estimate population size of isolated populations and determine dispersal rate of individuals between isolated high quality patches. “High Quality” sites consist of a meandering stream with rocky substrate, good tree cover (≥70%), a good riparian zone (containing relatively undisturbed soil and non-cultivated plants) and contain a series of riffles. Information from this study will be critical in designing proper management practices that will reestablish isolated habitats and native fish populations within a continuous and cohesive ecosystem that provides benefits to all members of the ecosystem, including humans.

MATERIALS AND METHODS:

Polecat Creek is located in Coles County, Illinois and is a 17.8-mile long, fourth-order stream that flows into the Embarras River located in east-central Illinois (Figure 1). This stream is ideal for a study of darter population isolation because it is highly fragmented and contains “high quality” sites that are separated from one another by long stretches of “low quality” areas. “High Quality” sites chosen along the length of Polecat Creek consisted of a meandering stream with rocky substrate, good tree cover (≥70%), a good riparian zone and contain a series of riffles. Each high quality site was spatially located with a GPS unit and integrated into a GIS coverage. Riffles were considered separate if there was a minimum distance upstream and downstream of 60 m to the next riffle. Because streams are dynamic systems we categorized each riffle into a 30 m distance class based upon its distance from the nearest upstream riffle. The initial survey resulted in 54 identified riffles of which, 31 riffles were considered temporally stable and “high quality” and were utilized for sampling (Table 1, Figure 2). Riffles were numbered starting at the furthest downstream site.

Initial sampling indicated two common darter species, the rainbow darter (*Etheostoma caeruleum*) and the greenside darter (*Etheostoma blenioides*). Sampling at each site was done blocking the creek with a seine from bank to bank just upstream and downstream from the riffle. Three people proceeded to kick the substrate as they moved from the downstream seine to the upstream seine. A total of five passes was performed at each sampling time to standardize effort. Sites were visited a total of 5 or 6 times and sampled whenever possible. This resulted in most sites being sampled a minimum of 3 times with only two sites sampled less than that (Table 2).

During each pass all members of the target species were collected and placed into holding containers and non-target species were released. Each individual darter was then marked with a site specific tag using a series of colored elastomers (Bonneau *et al.* 1995). After marking, each individual was placed in a holding container for 3 – 5 minutes to assure no ill effects from handling. A small piece of caudal fin was then collected and placed into a tube of 95% ethanol, which was then placed into a cooler with ice until it could be returned to the laboratory for storage in a dedicated refrigerator. Again each individual was placed into a holding container for 3 – 5 minutes and then released back into the stream. If a marked fish was collected its initial and current site of capture were recorded.

All data was transferred into Excel™(2007, 2008, 2011) for data storage as well as creation of tables and figures. All data analysis was performed in SAS© V. 9.1 and 9.2. All statistics are reported as calculated values and actual probabilities. If SAS© did not report the actual probability then it was calculated in Excel™ using the appropriate statistical distribution function. All models were fit as saturated models and then nonsignificant higher order effects were removed sequentially until a final model obtained. Capture and recapture data was too sparse to allow convergence of population models in program MARK (White 2007) and so simple minimum number alive estimates were utilized to provide an index of abundance. Turnover rate of each riffle (as defined by Rodríguez 2002) was calculated as the number of new individuals caught during capture times 2 through t divided by the total number of individuals caught during capture times 2 through t. Obviously recaptures have a probability of 0 during the first capture event and thus are not used for calculation.

RESULTS:

Captures and Abundances

A total of 2002 individuals were captured with rainbow darters being captured 3.53 times more frequently compared to greenside darters. Both species were captured at all sites except site 14 which only contained rainbow darters. This site was only sampled once and had a very low number of total captures (Table 3). Rainbow darters were more common at all sites except site 44 where greenside darters exhibited twice the total captures compared to rainbow darters (Table 3). Since the number of sampling bouts were the same within sites, abundances paralled the patterns for (but not necessarily the differences between) total captures for sites (Table 4) and distance classes (Table 5). The total captures differed significantly for the main effects of species (total captures for each species were different), distance class (total captures differed among distance classes) and year (total captures for each year were different) (Table 6). All two way interactions were also significant (Table 6). The difference in total captures between species varied among distance classes (Species x Distance Class) and between years (Species x Year) and the difference in captures between years varied among distance classes (Distance Class x Year). The three-way interaction was not significant. The pattern of captures among distance classes was similar for both species and within species between years (Figures 3 and 4). Within species, more rainbow darters were captured in 2009 (Figure 3) but more greenside darters were captured in 2008 (Figure 4). Mean abundances differed significantly between species but were not significantly different among distance classes or year (Figure 5, Table 7). Sites nested within distance class were significantly different. The two-way interactions of species and distance class and distance class and year were not significantly different but species and year showed a significant interaction paralleling capture analysis (Table 7).

Recaptures and Movements

A total 214 recaptures were recorded (greenside: 20, rainbow: 194). The overall recapture rate was 10.7% (greenside: 4.5%, rainbow: 12.4%). Of the recaptures 38 (greenside: 3, rainbow: 35) were recaptured in a site different from that of initial capture. This results in effective dispersal rates of 0.68% for greenside darters and 2.24% for rainbow darters. Greenside darters are slightly more philopatric compared to rainbow darters (greenside: 15% dispersers, rainbow: 22% dispersers). Recaptures were recorded at 28 sites for rainbow darters (Table 8) and 12 sites for greenside darters (Table 9). The total recaptures differed significantly for the main effects of species (total recaptures for each species were different), distance class (total recaptures differed among distance classes), movement (total recaptures differed for individuals that were recaptured at their initial capture site compared to those who dispersed) and year (total recaptures differed between years) (Table 10). The only two-way interaction that was significant was movement x year (the difference between the number of dispersers and non-dispersers differed between years) (Table 10). These results as well as the pattern of recaptures are illustrated in figure 6 for rainbow darters and figure 7 for greenside darters. Greenside darter movement was anisotropic as they only moved downstream (Table 9, Figures 8 and 9) while Rainbow darters moved both up and downstream (Table 8, Figures 8 and 9). Greenside darters tended to move greater distances (mean distance: Figure 8, mean number of riffles: Figure 9) compared to rainbow darters (distance in m: $t_{36} = 2.69$, $P = 0.005$, number of riffles: $t_{36} = 3.64$, $P = 0.0004$). Overall, rainbow darter movement was anisotropic based upon the number of movements (10 downstream, 25 upstream). However, movement distance was isotropic as the upstream and downstream movement distances were not significantly different for rainbow darters (distance in m: $t_{31} = 0.82$, $P = 0.42$, number of riffles: $t_{33} = 0.68$, $P = 0.50$). Population turnover rates were higher for Greenside darters ($m = 0.915$) compared to Rainbow darters ($m = 0.834$) and this difference is significant ($t_{23} = 2.88$, $P = 0.008$). The population turnover rate is also more variable for Greenside darters (Figure 10, $s^2 = 0.0139$) compared to Rainbow darters ($s^2 = 0.0074$) but this difference is not significant ($F_{23,29} = 1.876$, $P = 0.055$) although it is small enough to warrant interest.

Population Turnover

Turnover rate in these sites was high (Figure 10) with a mean turnover rate of 91.5% ± 4.99% for Greenside darters and 83.4% ± 3.22% for Rainbow darters. 12 sites showed 100% turnover for Greensides and only 2 sites showed 100% turnover for Rainbows. The turnover rate in Rainbow darters is significantly lower compared to Greenside darters ($t_{23} = 2.88$, $P = 0.0042$).

DISCUSSION:

Although both Greenside darters and Rainbow darters are considered common in East-Central Illinois and surrounding areas (Pflieger 1978, Smith 1979), in Polecat Creek Rainbow Darters were much more common and would be classified as the dominant darter species in terms of population parameters. Overall, Rainbow darters were 3.53 times more common than Greenside Darters. In the first year the ratio of Rainbow:Greenside was 2.13:1.00 but in the second year it had increased to 6.92:1.00. In addition there was one site where Greenside darters were never captured and six (6) sites where Greenside darters were only captured once. There was only a single site where Rainbow darters were captured only once. Greenside darters may also be on the decline in Polecat Creek as there were 313 captures in 2008 and only 129 captures in 2009. There were slightly more Rainbow darter captures in 2009 (892) compared to 2008 (668). However, sampling effort was greater in 2009 compared to 2008 so correcting for that both species were less common than expected, assuming we were in the linear part of the relationship between effort and number of captures. The number of captures of Greenside darters in 2009 was only 21% of that expected while for Rainbow darters it was 67% of that expected. This is only two years of data so we may be seeing normal annual fluctuations in population numbers. However, this is still of concern, especially for Greenside darters as population fluctuations of that magnitude means there is a large probability of population extinction in the short term (i.e. over periods of time less than 50 years) (Forney and Gilpin 1989, Boyce 1992).

It is clear from the statistical analyses that the two species of darters are not responding similarly, in terms of abundance and number of captures, to yearly variation, but only in terms of total captures to variation in distance class. Rainbow darters show less of an effect of yearly variation compared to Greensides but appear to show greater relative declines at higher distance classes (i.e. fragmentation effects). This could be a scale effect because Greenside darters are much less common and so the potential range of variation is smaller (this is likely based upon the reacapture data). Nevertheless, this does provide evidence that fragmentation effects are real and could potentially lead to population extinction, at least in localized populations.

Temporal and spatial variation are also not independent factors in determining population dynamics (Miller and Conner 2005). However, sampling designs for simultaneous testing are generally not feasible in terms of logistics and cost. In an unpublished study on mosquitofish, Novak *et al.* (unpub) determined that the overriding factor affecting local genetic and demographic variation was not spatial or temporal variation, but the interaction of the two. It is likely that this effect exists here and is common in most populations. This effect complicates both interpretation of results and makes the management of populations much more difficult since the main effects of space and time may not be interpretable in and of themselves.

Overall recapture rates (10.7% over years and species) were about as expected. Greenside darters appear more philopatric compared to rainbow darters and movement between populations is likely to be unintentional as all movements for Greensides was downstream. Rainbow darters tended to move upstream about 2.5x as often as they moved downstream although again, most recaptures were in the same population as initial capture although overall Rainbow darters exhibited more intersite movement, and smaller distances moved, compared to Greenside darters. Based upon population numbers and movement, either the habitats within Polecat Creek are preferred by Rainbow darters, the Rainbow darters are able to outcompete Greenside darters in these habitats, or the two species exhibit different fundamental population structures (Rainbow: metapopulation, Greenside: demic). Regardless, it appears that Greenside darters are a more marginal species in Polecat Creek, at least during the time period of this study.

The effects of fragmentation are much more easily observed in the recapture data for Rainbow darters. Most of the observed movements were between sites in the lower distance classes. Thus, at least for Rainbow darters, fragmentation would decrease the ability of individuals to move to different riffles. The ultimate effect would be to change the species from a metapopulation structure to an isolated deme model with attendant changes in population dynamics and genetic structure. Isolated demes are at greater extinction risk compared to groups within a metapopulation (Fagan 2002) due in large part to a decreased rate of dispersal and perhaps the attendant gene flow.

The darter populations in this creek are highly dynamic as exhibited by the capture and recapture data and accentuated by the turnover rate statistics. The root cause of this is likely the fact that lotic systems are fundamentally dynamic themselves and this variation drives the population dynamics of the attendant species. However, this variation makes populations of lotic species more susceptible to extinction (Hanski 1998) and thus it is more critical to have monitoring systems in place to determine if population number variation is becoming too extreme in such systems. Additional factors such as anthropogenic stressors such as contaminants, increased hydrological variation, reduction of habitat, increased fragmentation, etc. only lead to increased variation of the environment which exacerbates the problem.

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Table 1. Distance classes of sites initially surveyed. Sites used in the study are shaded in light gray. Distance class is the approximate upstream distance to the next riffle. Numbering started at the furthest downstream site.

Distance Class (m)	Site	Distance Class (m)	Site
90	1	90	28
120	2	90	29
120	3	90	30
90	4	60	31
120	5	90	32
150	6	120	33
90	7	90	34
90	8	120	35
60	9	90	36
60	10	90	37
90	11	90	38
90	12	120	39
150	13	90	40
150	14	120	41
120	15	60	42
240	16	120	43
120	17	180	44
120	18	120	45
180	19	120	46
120	20	90	47
90	21	60	48
90	22	60	49
60	23	120	50
120	24	150	51
120	25	60	52
120	26	60	53
60	27	90	54

Table 2. Number of sampling trips by site and distance class.

Distance Class (m)	Site	Number of Sampling Trips	Sampling Trips for Distance Class
60	9	5	35
	10	3	
	42	3	
	48	6	
	49	6	
	52	6	
	53	6	
90	7	5	41
	8	5	
	11	4	
	12	5	
	36	4	
	37	4	
	40	2	
	47	6	
	54	6	
120	15	5	44
	17	5	
	18	5	
	39	4	
	41	3	
	43	5	
	45	5	
	46	6	
	50	6	
150	13	5	11
	14	1	
	51	5	
180	19	5	11
	44	6	
240	16	5	5

Table 3. Total number of individuals captured for each species by site and distance class.

Distance Class (m)	Site	Greenside Total Captures		Rainbow Total Captures		Total Captures	
60	9	5	101	93	447	98	548
	10	6		22		28	
	42	10		27		37	
	48	14		79		93	
	49	23		104		127	
	52	20		45		65	
	53	23		77		100	
90	7	6	137	42	468	48	605
	8	1		59		60	
	11	10		40		50	
	12	18		40		58	
	36	11		35		46	
	37	3		27		30	
	40	8		11		19	
	47	63		123		186	
	54	17		91		108	
120	15	37	124	103	426	140	550
	17	5		25		30	
	18	4		38		42	
	39	5		51		56	
	41	5		26		31	
	43	5		46		51	
	45	18		34		52	
	46	36		57		93	
	50	9		46		55	
150	13	11	35	74	113	85	148
	14	0		6		6	
	51	24		33		57	
180	19	2	36	50	67	52	103
	44	34		17		51	
240	16	9	9	39	39	48	48
Total		442		1560		2002	

Table 4. Mean and standard deviation of abundance of each species per sampling time for each site.

Site	Greenside Abund.		Rainbow Abund.		Rainbow: Greenside
	Mean	Std. Dev.	Mean	Std. Dev.	
7	1.2	2.68	8.4	8.23	7.00
8	0.2	0.45	11.8	9.91	59.00
9	1.0	1.41	18.6	7.92	18.60
10	2.0	2.65	7.3	8.39	3.67
11	2.5	3.11	10.0	9.63	4.00
12	3.6	1.67	8.0	4.47	2.22
13	2.2	1.48	14.8	13.83	6.73
14	0.0		6.0		
15	7.4	6.58	20.6	24.95	2.78
16	1.8	2.49	7.8	3.56	4.33
17	1.0	2.24	5.0	2.12	5.00
18	0.8	1.10	7.6	6.91	9.50
19	0.4	0.89	10.0	12.08	25.00
36	2.8	2.06	8.8	4.35	3.18
37	0.8	1.50	6.8	1.71	9.00
39	1.3	1.50	12.8	2.06	10.20
40	4.0	5.66	5.5	26.50	1.38
41	1.7	1.15	8.7	7.37	5.20
42	3.3	2.31	9.0	7.00	2.70
43	1.0	1.73	9.2	6.14	9.20
44	5.7	7.39	2.8	2.14	0.50
45	3.6	6.43	6.8	5.54	1.89
46	6.0	10.84	9.5	6.41	1.58
47	10.5	16.07	20.5	15.16	1.95
48	2.3	3.83	13.2	6.34	5.64
49	3.8	3.06	17.3	3.27	4.52
50	1.5	1.05	7.7	4.03	5.11
51	4.8	4.21	6.6	3.91	1.38
52	3.3	3.72	7.5	6.38	2.25
53	3.8	8.42	12.8	2.86	3.35
54	2.8	3.66	15.2	6.01	5.35
All Sites	3.0	5.38	10.6	8.85	3.53
Mean	2.8	2.7	10.2	6.0	7.4
Std. Dev.	2.3	1.6	4.5	2.5	11.0
Max	10.5	16.1	20.6	26.5	59.0
Min	0.0	0.4	2.8	1.7	0.5

Table 5. Mean and standard deviation of abundance of each species per sampling time for each distance class.

Distance Class	Greenside Abundance		Rainbow Abundance	
	Mean	Std. Dev.	Mean	Std. Dev.
60	2.9	4.24	12.8	6.82
90	3.3	6.88	11.4	9.11
120	2.8	5.34	9.7	9.90
150	3.2	3.28	10.3	10.07
180	3.3	5.93	6.1	8.64
240	1.8	2.49	7.8	3.56

Table 6. Results of log-linear model analysis of captures.

Source	df	G	P
Species	**1**	**211.64**	**6.027×10^{-48}**
Distance Class	**5**	**496.61**	**4.305×10^{-105}**
Year	**1**	**7.97**	**0.0048**
Species x Distance Class	**5**	**22.96**	**0.0003**
Species x Year	**1**	**108.43**	**2.164×10^{-25}**
Distance Class x Year	**5**	**29.09**	**2.226×10^{-6}**
Species x Distance Class x Year	**5**	**5.01**	**0.4147**

Table 7. Results of Analysis of Variance of Abundances.

Source	df	F	P
Species	1	30.43	6.017×10^{-7}
Distance Class	5	1.11	0.3617
Year	1	0.41	0.5239
Site(Distance Class)	25	3.45	2.853×10^{-5}
Species x Distance Class	5	0.99	0.4332
Species x Year	1	9.04	0.0037
Distance Class x Year	5	0.74	0.5948

Table 8. Recapture Summary for rainbow darters. Numbers on the diagonal (shaded) indicate the number of recaptures in the same site as initial capture. Numbers above the diagonal indicate movement upstream and those below the diagonal indicate movement downstream.

Capture Site	Recapture Site																													
	7	8	9	10	11	12	13	14	15	16	17	18	19	36	37	39	40	41	42	43	44	45	46	47	48	49	50	52	53	54
7	11		1																											
8		7	2																											
9		1	12	2	1																									
10																														
11					4	1	1																							
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17											2																			
18												7																		
19													6																	
36														2																
37															4															
39																5		4		1										
40																1		1												
41																		2												
42																			2											
43																				4	2									
44																			1	2	2									
45																					1	4	1							
46																							6	1						
47																								12						
48																									5	1				
49																								1	1	8	2			
50																											3		1	
52																												7	1	
53																												1	9	1
54																												1		14

Table 9. Recapture Summary for greenside darters. Numbers on the diagonal (shaded) indicate the number of recaptures in the same site as initial capture. Numbers above the diagonal indicate movement upstream and those below the diagonal indicate movement downstream.

Capture Site	Recapture Site													
	9	11	12	13	15	36	44	47	49	50	51	52	53	54
9	1													
11		2												
12			1											
13				2										
15					2									
40						1								
44							2							
47								1						
49									1					
50								1						
51									1					
52												2		
53													2	
54														1

Table 10. Results of log-linear model analysis of recaptures.

Source	df	G	P
Movement	1	73.44	$1.037x10^{-17}$
Distance Class	4	53.62	$6.321x10^{-11}$
Species	1	93.60	$3.862x10^{-22}$
Year	1	71.88	$2.287x10^{-17}$
Movement x Distance Class	4	3.08	0.5445
Movement x Species	1	0.12	0.7290
Distance Class x Species	4	4.23	0.3758
Movement x Year	1	3.88	0.0489

Figure 1. Location of Polecat Creek, a fourth-order tributary of the Embarras River located in Coles County, Illinois

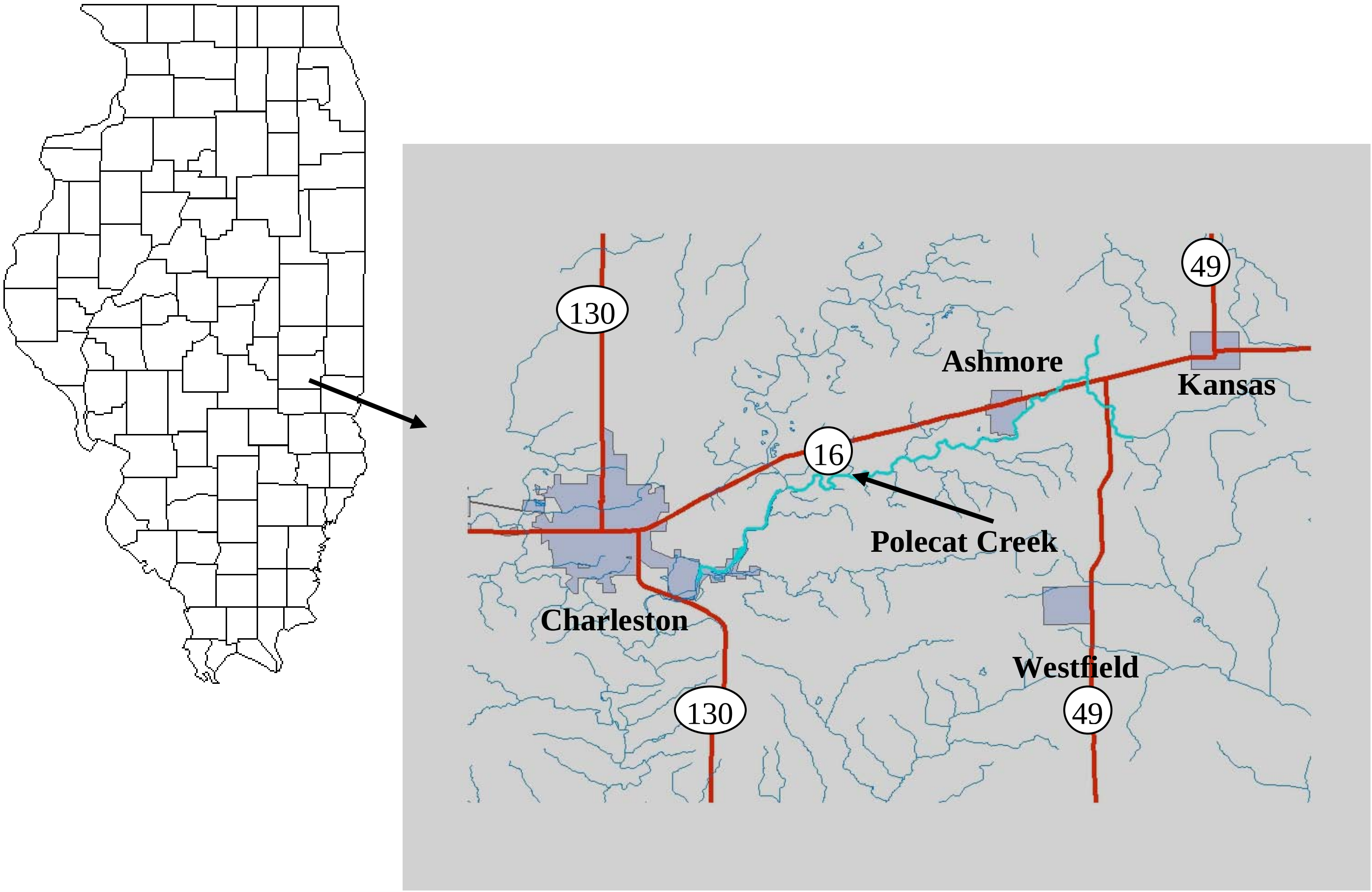

Figure 2. Location of sampling sites on Polecat Creek, Coles County, IL. Image saved as a image and thus the scale is only approximate.

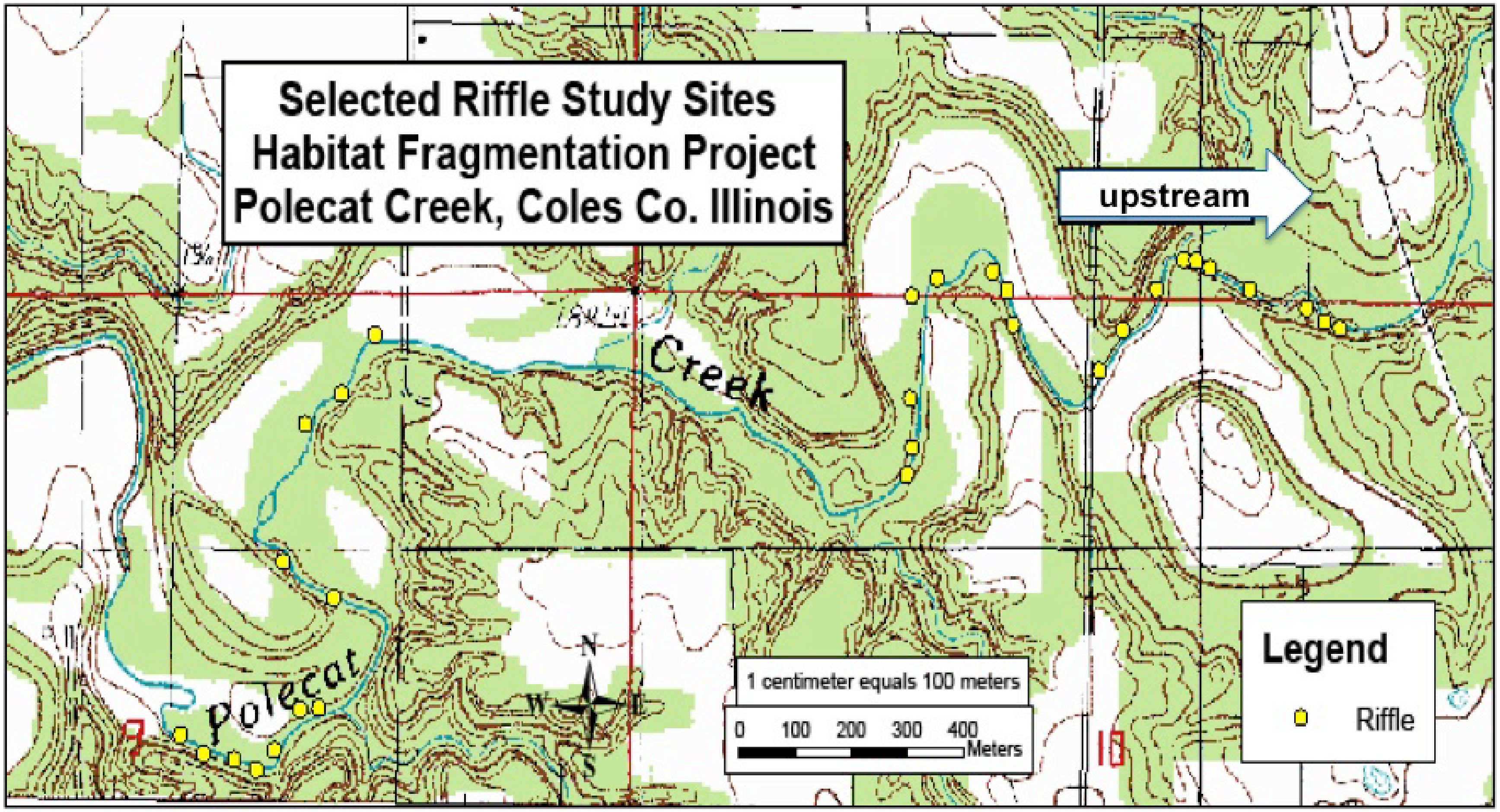

Figure 3. Number of rainbow darter captures by distance class for each year.

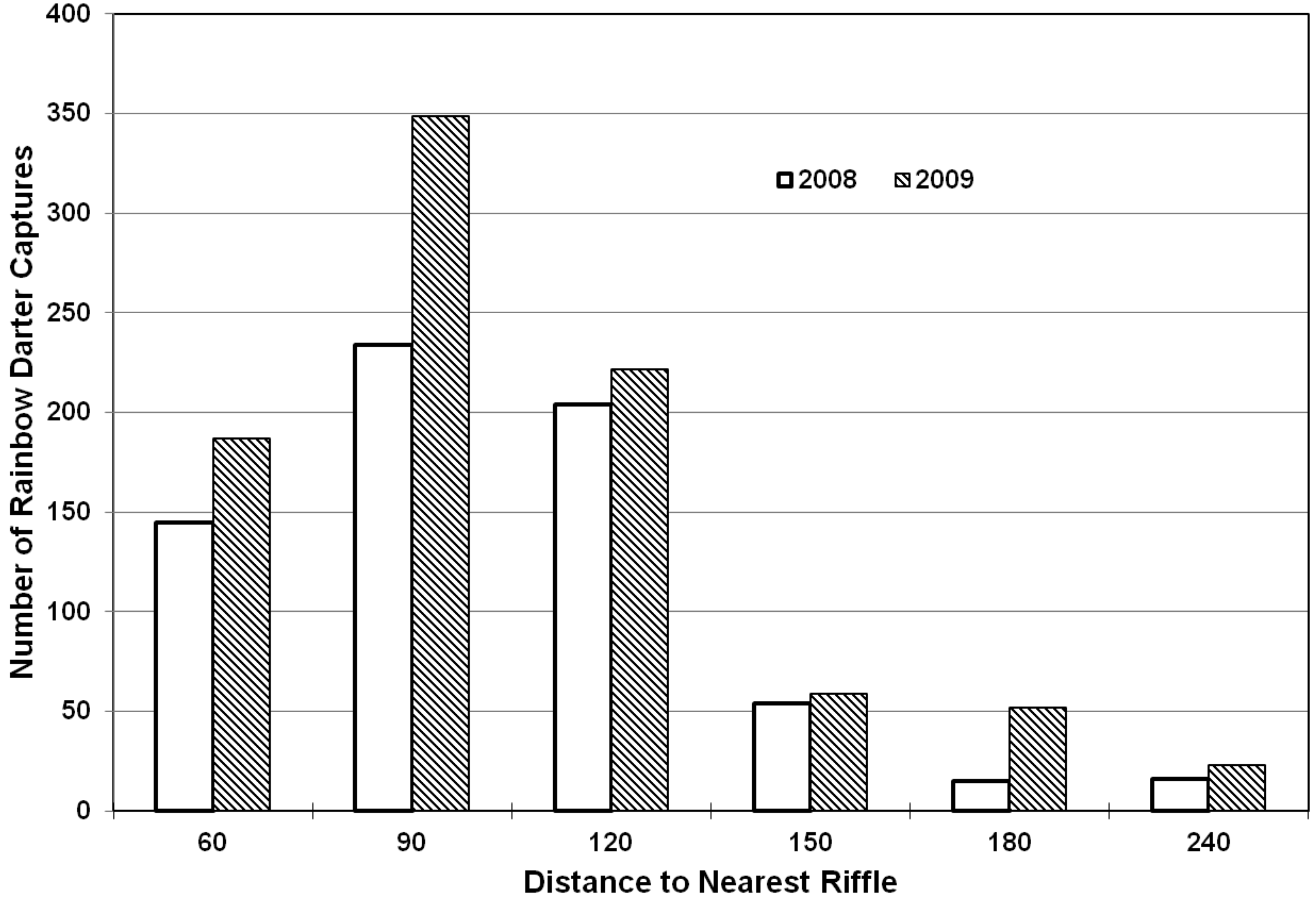

Figure 4. Number of greenside darter captures by distance class for each year.

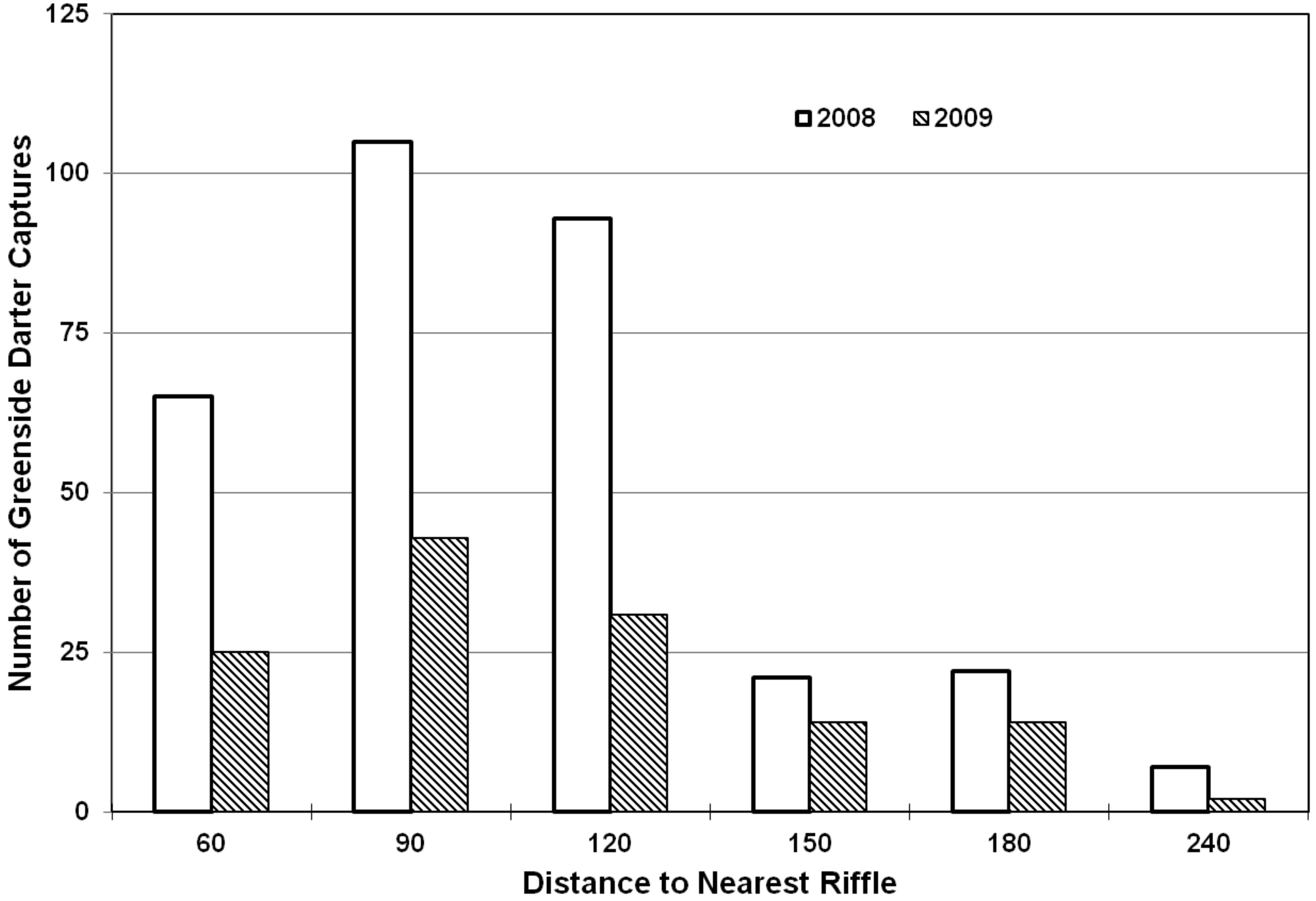

Figure 5. Means and 95% confidence intervals for abundance for each darter species by distance class.

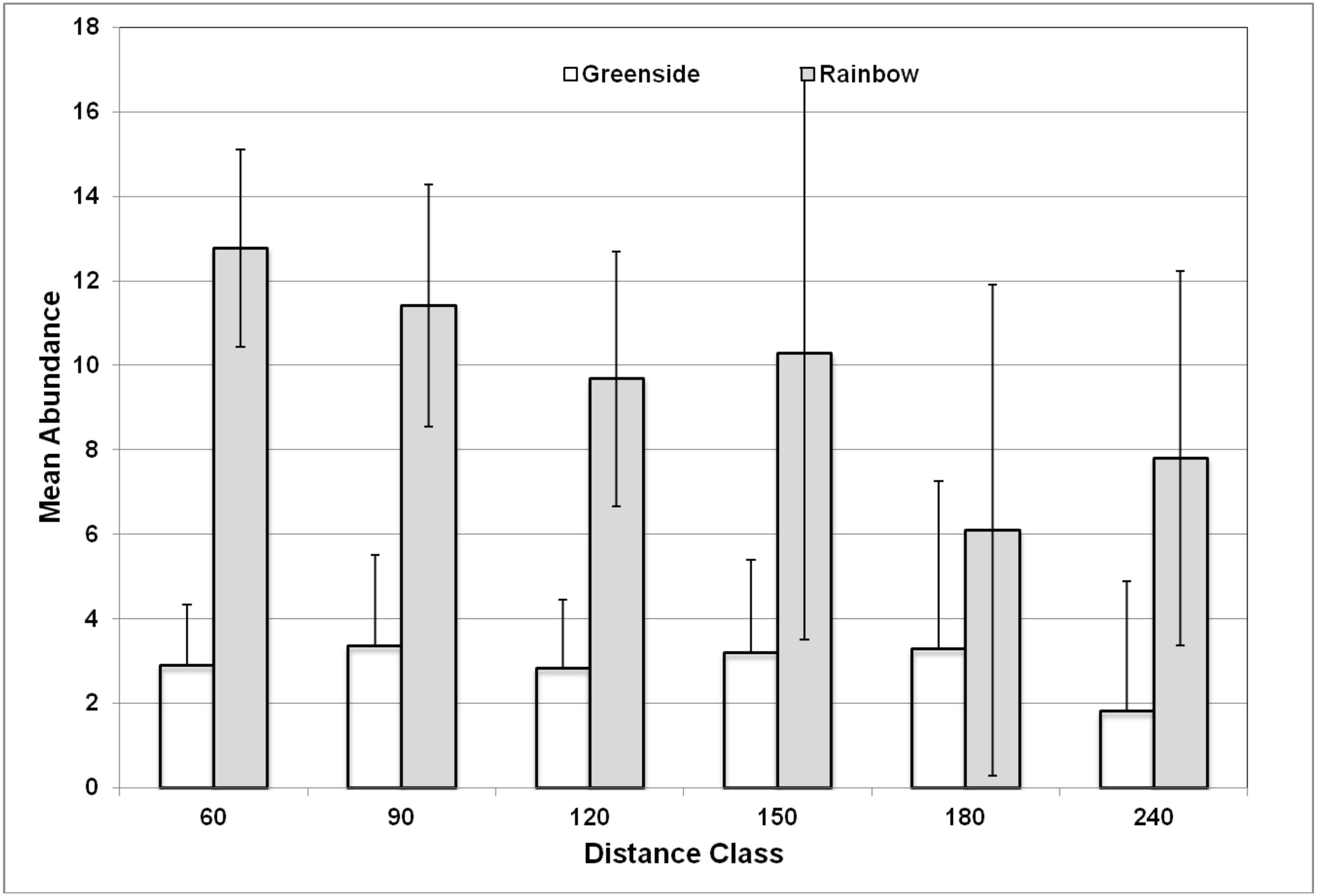

Figure 6. Number of rainbow darter recaptures, recaptured in the same or different riffle, by distance class for each year.

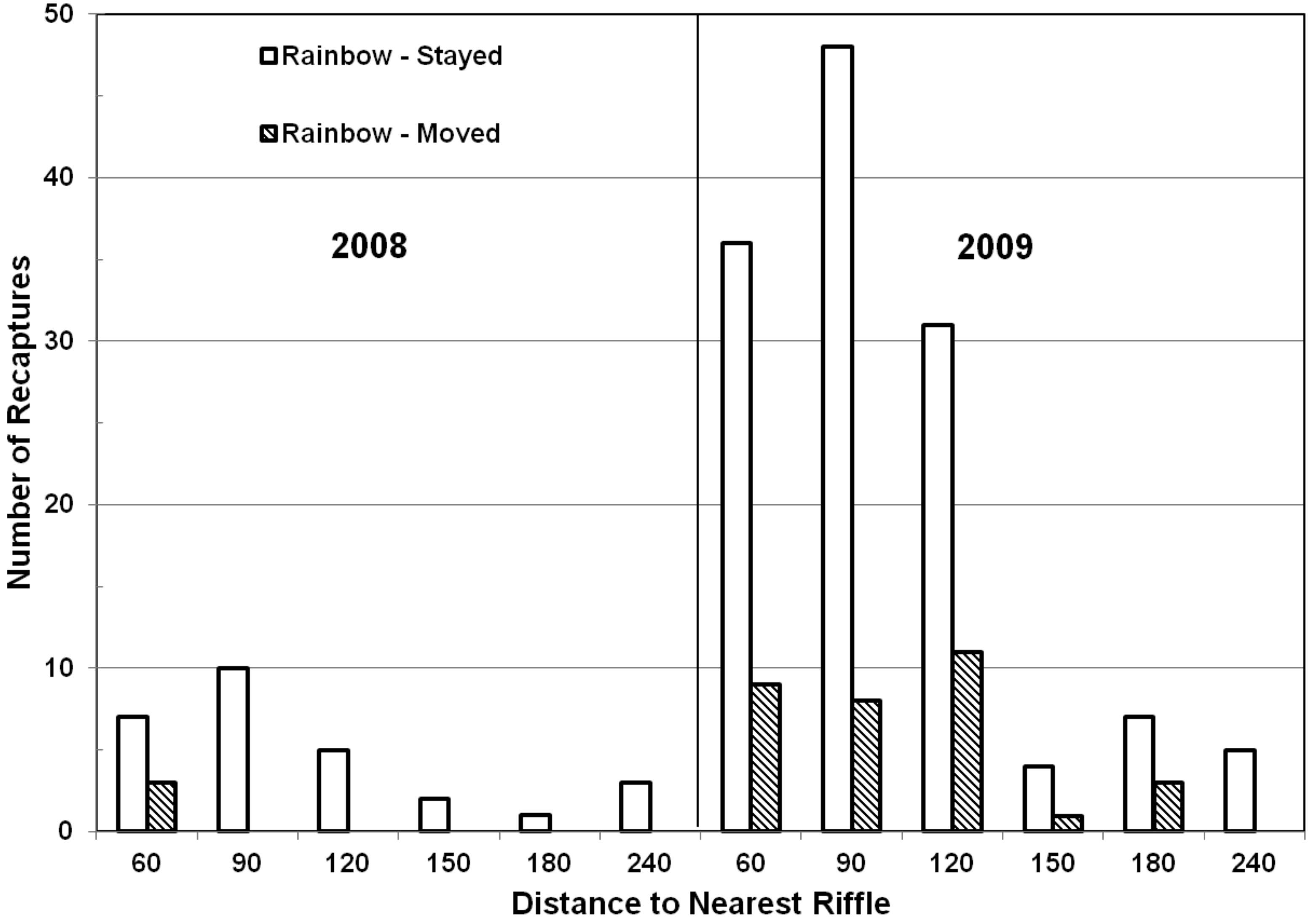

Figure 7. Number of greenside darter recaptures, recaptured in the same or different riffle, by distance class for each year.

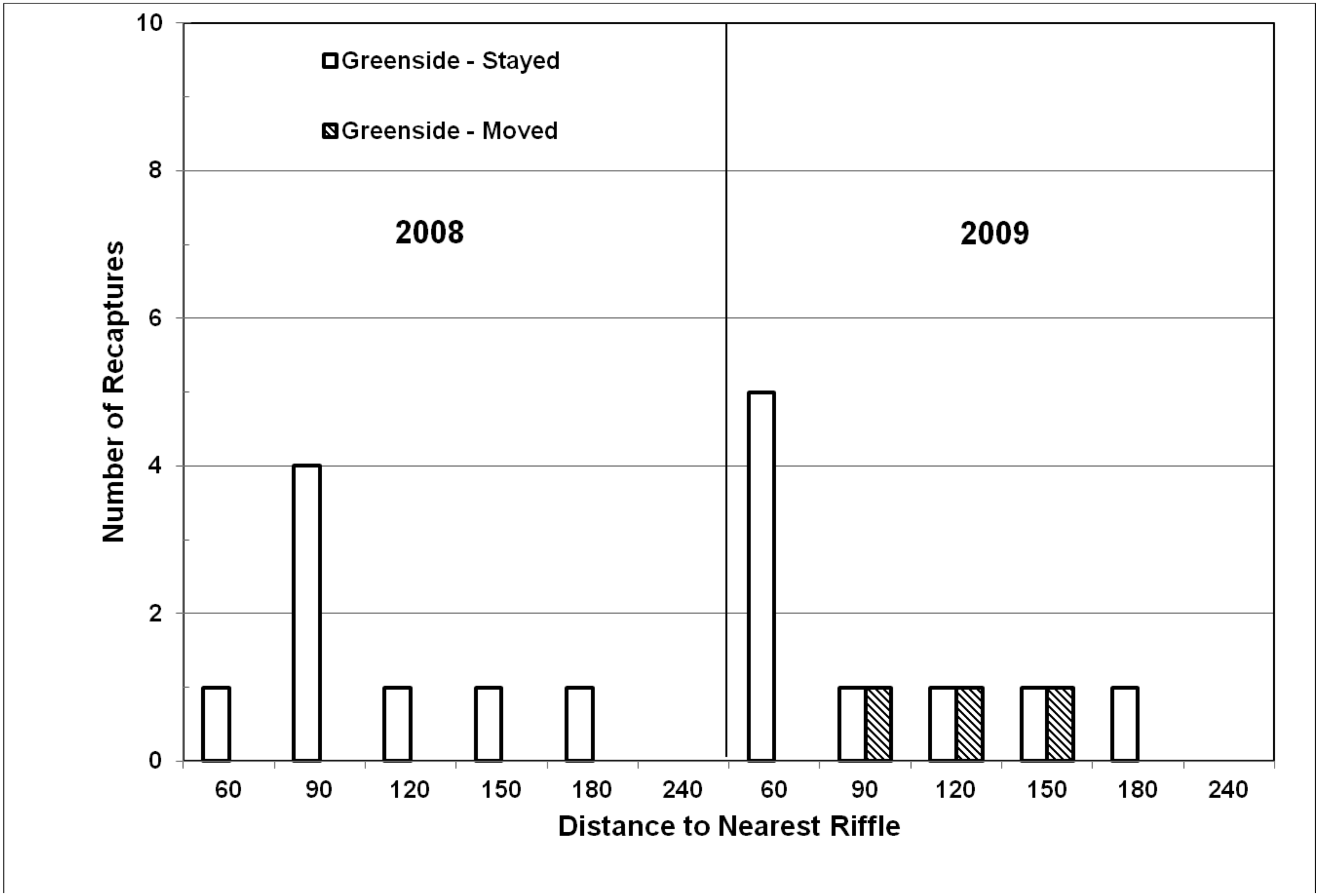

Figure 8. Mean and 95% confidence limit of distance moved by species and direction of movement.

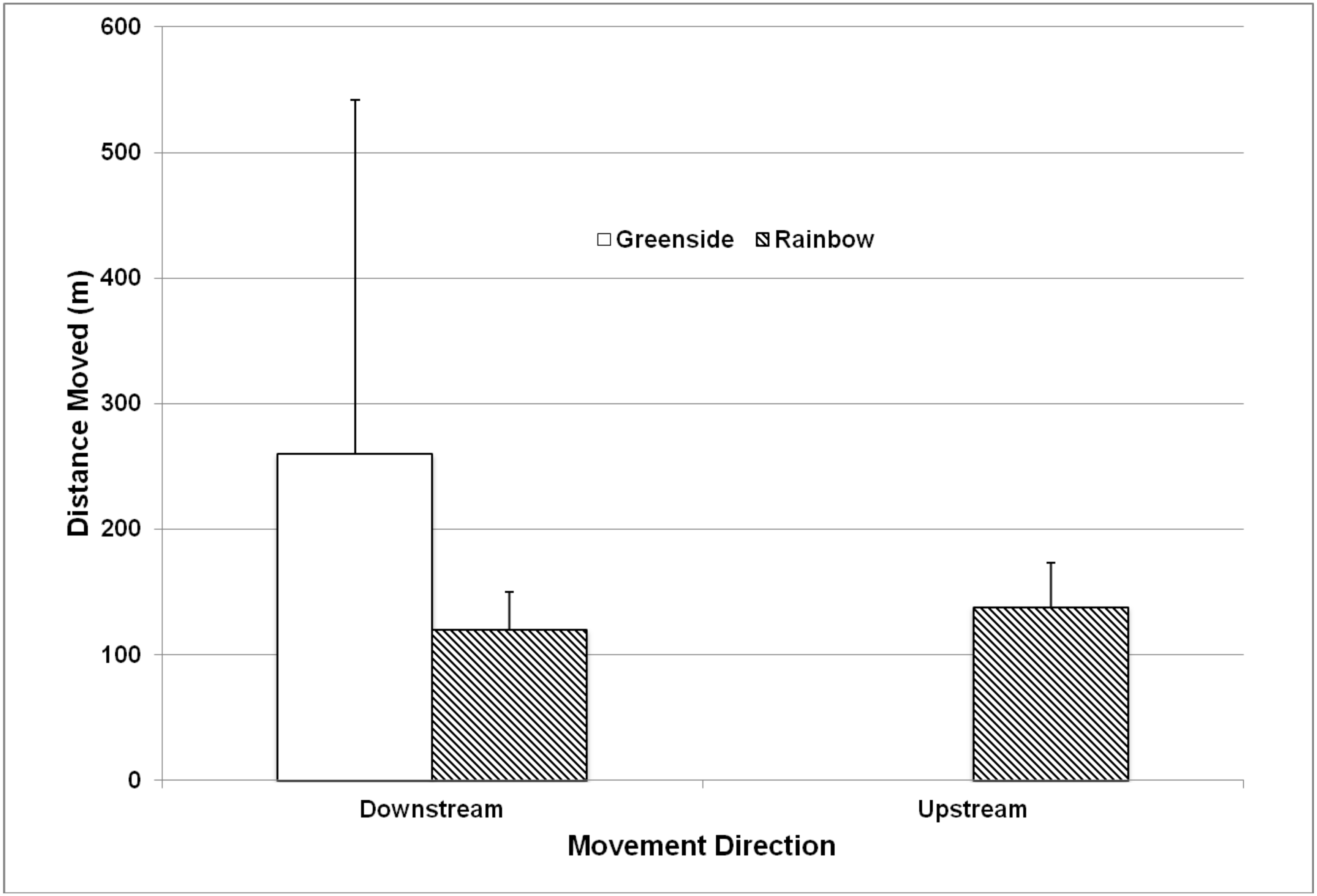

Figure 9. Mean and 95% confidence limit of number of riffles moved by species and direction of movement.

Figure 10. Population turnover rates for Greenside and Rainbow darters at each capture site.