POPULATION ECOLOGY OF GREATER SIREN, *SIREN LACERTINA*

by

THOMAS MARSHALL LUHRING

(Under the Direction of J. Whitfield Gibbons)

ABSTRACT

The greater siren, *Siren lacertina*, is the heaviest and third longest salamander in the western hemisphere, was described nearly two and a half centuries ago and is abundant in the core of its distribution range. However, there is relatively little information available regarding the natural history and population ecology of this presumed common large vertebrate. In addition to testing two temporary marking techniques, I used passive integrated transponder (PIT) tags to permanently mark individual greater siren in an isolated wetland. Thirteen months of trapping resulted in 470 *S. lacertina* captures. Of 271 marked animals, 83 (30.6%) were recaptured 174 times. Robust design top model estimates in program MARK estimated that 246.9 ± 29 (SE) *Siren lacertina* were in Dry Bay during the study period. Monthly survival rates were 0.88 ± 0.04 (SE) and 0.80 ± 0.03 (SE) for Robust design and Cormack-Jolly Seber top model estimates, respectively.

INDEX WORDS: Greater Siren, *Siren lacertina*, Mark-recapture, Population Ecology, Demography, Sirenidae

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DEDICATION

To my parents, James and Sue Luhring, who fostered my curiosity of the natural world at an early age, tolerated various aquaria, terraria, muddy shoes and the "occasional" muddy carpet. To Jimmy for often "graciously" taking the blame for said muddy carpet and for always being the older brother who "should have known better." Although there were several things in my childhood that I wanted and did not get (e.g., cookies before dinner, a corvette), I always had the things that I needed. I could not have asked for a better family or childhood and for that, I am eternally grateful.

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have been an indispensible part of my development to this point of my life. I could easily write tomes describing those who have touched my life in one way or another and the exclusion of your names here only reflects the brevity needed to have an acknowledgements section that is shorter than my actual thesis (which falls far short of the space needed to properly thank everyone to even a partial degree). Words fail to describe the thanks that I have for everyone that has lent me a hand in the field, given me words of encouragement, provided me with companionship and lifted my spirits during the tenuous periods of budget difficulties at the lab, guided my professional development, or for just being incredible friends, colleagues and mentors. It is hard to describe the welling up of deep sincere feelings that I have developed for many of those that have graced me with their presence during my graduate career as words are poor purveyors of such strong and intangible emotions. That I get choked up trying to find adequate words to properly acknowledge your contributions to my life, will hopefully be, in my own humble way, at least a suitable attempt at my most sincere thank you.

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CHAPTER 1

INTRODUCTION AND LITERATURE REVIEW

INTRODUCTION

Although the greater siren, *Siren lacertina*, was originally described nearly two and a half centuries ago (Linnaeus 1766), and has often been described as common or abundant throughout the core of its range during that time (Barton 1808; Jobson 1940; Petranka 1998), a paucity of information is available on its life history and population ecology. The following chapters investigate and assess population parameters and demographic characteristics for greater siren. Mark-recapture studies are one of the most effective ways of addressing demography questions. I used three concurrent marking techniques during a 13-month mark-recapture study to address many of the population ecology knowledge gaps of the greater siren.

To date, only one mark-recapture study has been published on *S. lacertina* (Sorensen 2004) and two on its close relative, the lesser siren, *Siren intermedia* (Gehlbach and Kennedy 1978; Frese et. al., 2003). A major challenge with population studies on either species is the difficulty in marking animals in a cost-efficient manner that fulfills the objectives of the study. Passive integrated transponder (PIT) tags are the best applicable permanent individual mark for greater siren (Sorensen 2003). I investigated the applicability of toe-clipping and tail-notching as cohort and non-specific marks, respectively. I tested these two techniques in the field to investigate mark persistence and readability on animals that had already been marked individually by means of a PIT tag.

These three marks were implemented during a mark-recapture study at Dry Bay, a 5-ha isolated herbaceous bay wetland in Aiken, South Carolina. The goals of this study were to: (1) test the applicability of three types of marking schemes on *S. lacertina* to provide options for future mark-recapture studies, (2) provide estimations for population size, size at first

reproduction, growth rates, movement within the wetland, and (3) record opportunistic natural history observations such as predators and prey of *S. lacertina*.

This thesis is written in manuscript style. Chapters 2 and 3 are formatted as journal articles that will be submitted to *Herpetologica* and *Herpetological Monographs*, respectively. Chapter 1 serves as an introduction to the thesis and provides a literature review of greater siren population ecology and natural history. Chapter 2 is a field test of two marking techniques for greater siren that uses passive integrated transponder (PIT) tags as a reference mark to track the individual performance of toe-clipping and tail-scooping. Chapter 3 provides estimates for population parameters from a 13-month mark-recapture effort at Dry Bay, an isolated 5-ha herbaceous bay wetland. Chapter 4 summarizes the conclusions of chapters 2 and 3 and provides suggestions for future studies to fill in current knowledge gaps.

LITERATURE REVIEW

Greater sirens are one of the largest salamanders in the western hemisphere, reaching nearly a meter in length (record of 97.8-cm; Conant and Collins 1998) and can weigh over a kilogram (personal observation). Only two-toed amphiumas, *Amphiuma means*, and three-toed amphiumas, *A. tridactylum*, grow longer (records of 116.2-cm and 106-cm, respectively; Conant and Collins 1998). Despite being common in the central areas of its range (Hendricks 2005) and occurring at high densities (1.3 siren per m^2; Sorensen 2004), surprisingly large gaps still exist in our understanding of even the most basic aspects of *S. lacertina* natural history.

Several factors contribute to the dearth of greater siren population ecology data. First, it is difficult to monitor permanently aquatic salamander populations (Hendricks 2005). The only mark-recapture study to date had low recapture rates (10 recaptures out of 66 marked greater siren) and low recapture probabilities (0.02-0.03) and, although it provided valuable data on

previously unknown population parameters, was limited in the conclusions that it could draw from mark-recapture estimates (Sorensen 2004).

A second difficultly with siren research is the inability to accurately and consistently distinguish between males and females. Hanlin and Mount (1978) determined that male head morphology was different from that of females, but Sorensen (2004) was unable to detect such a difference when taking the same morphometric measurements. The disparity in their findings is not surprising. First, Hanlin and Mount (1978) were taking measurements of preserved animals that were dissected to verify their sex. Sorensen (2004), took the same measurements, but did so on live animals that were not dissected to verify their sex. In addition to differences in site location, the sampling methodologies used by each group were themselves biased. Hanlin and Mount (1978) used baited hooks on fishing lines for sampling and caught larger and presumably sexually mature animals. Sorensen (2004) used passive-sampling minnow and crawfish traps and captured a variety of size-classes that presumably included both juveniles and sexually mature adults. If head shape morphology diverges after the onset of sexual maturity, then differences between the two studies would be expected. Male *Siren intermedia*, a close relative of *S. lacertina*, exhibit enlarged masseter muscles, like those observed by Hanlin and Mount (1978), as well as a suite of other morphological differences (Sugg et al., 1988) so it would not be surprising to find similar secondary sexual characteristics in *S. lacertina*.

The reproductive ecology of greater siren has many unresolved knowledge gaps. Minimum size and age at first reproduction are unknown. The mode of reproduction used to fertilize eggs is not known for certain. Ultsch (1973) posited that *S. lacertina* reproduced via external fertilization because females lack spermathecae, males lack cloacal glands, and females that laid eggs in the absence of males did not produce viable embryos. While these observations

suggest that fertilization is external, no conclusive evidence has been presented that fertilization is external or internal (e.g., chickens have internal fertilization, yet they lay infertile eggs in the absence of a rooster). In fact, greater siren lay their eggs singly, or in small clusters (Ultsch 1973), and external fertilization would presumably be an inefficient mode of reproduction for this strategy.

Seasonal activity has only been reported from the southerly portions of the distributional range of greater siren. Seasonal lows in activity occur in late fall and early winter in Alabama; activity (assumed to be feeding activity) peaks in June and July (Hanlin and Mount 1978). In northern Florida, capture rates were highest in January through March (Sorensen 2004), which coincides with reported breeding activity in Florida (Nobles and Richards 1932, Goin 1947, Ultsch 1973) and southern Alabama (Hanlin and Mount 1978). Eggs are deposited in February and March, and hatchlings emerge in late April and early May (Ultsch 1973). In Florida, one hatchling measured 13mm snout-vent length (SVL) and 16mm total length (Goin 1947) and young of the year may grow to 75mm SVL by mid-October (Ultsch 1973). No measurements are available for young of the year outside of Florida, and no estimates of size or age classes are available. Only scant information is available for growth rates of greater sirens in the wild (Sorensen 2004).

Because of the secretive life style of greater sirens and the difficulties associated with studying them, little is known regarding the most crucial life history, behavioral, and ecological traits of one of the largest amphibians in the western hemisphere. The scant information available for this enigmatic species is often based on one or a few animals in a limited number of locations in the southernmost portions of its range. Thus our current understanding of greater siren ecology and natural history is, at best, a piecemeal mosaic with many large gaps remaining

to be covered. The following chapters contribute to our knowledge base of several aspects of greater siren ecology.

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CHAPTER 2

USING PIT TAGS TO FIELD TEST TWO MARKING TECHNIQUES FOR GREATER SIREN (*SIREN LACERTINA*)[1]

[1]Luhring, T. M. To be submitted to Herpetologica.

ABSTRACT

Marking techniques for greater siren (*Siren lacertina*) are limited in applicability because of various morphological constraints and only one technique, passive integrated transponder (PIT) tags, has been tested in the field. I tested a cohort mark (toe clip) and a capture mark (tailfin scoop) for duration and readability in the field. All animals were given PIT tags, which permitted the tracking of individual healing rates for toe clips and tail scoops. Although most marks showed signs of regeneration after more than 30 days, most toe clips and tail scoops were discernable up to 180 days after the mark was administered. Although most tail scoops did not persist longer than 180 days, the majority of toe clips were discernable through the end of the study (i.e., up to 332 days).

INTRODUCTION

Mark-recapture models used in estimating population size require the capture, marking, and recapturing of marked animals (Donnelly and Guyer 1994). Although several methods are available for marking amphibians (see Ferner 1979), sirenids and greater siren (*Siren lacertina*), in particular, present several problems for marking schemes. Previous studies on lesser siren (*Siren intermedia*) used heat branding to create marks that lasted for up to 96 months (Gehlbach and Kennedy 1978, Raymond 1991, Freese 2000). The dark skin of greater siren prevents marks made by tattooing and injectable dyes from being easily read (Sorensen 2003). The only known test of marking techniques on *S. lacertina* was conducted on two captive animals (Sorensen 2003). The marking techniques used on the two captive animals included cyano-acrylic, tail-notching, heat-branding and Passive Integrated Transponders (PIT tags). Of these, only PIT tags were successful in creating a lasting mark and were later used in field studies.

The required level of identity (e.g., individual, cohort) and persistence (e.g., permanent, month, day) for a mark is dependent on the question being asked for a mark-recapture study. I

tested two types of non-individual-specific marks on greater sirens, *Siren lacertina*, in an isolated herbaceous bay wetland to determine their permanence and readability. Passive integrated transponder (PIT) tags are effective at providing a permanent individual mark in greater siren (Sorensen 2003). Their proven persistence as a mark for *S. lacertina* allowed me to use them as a redundant mark to ground truth other marking techniques used in this study. Additionally, PIT tags allowed me to record individual variation in the amount of time that the other two marks persist and to get the most accurate estimate of their applicability possible.

There are several individual marking schemes for toe clipping amphibians (see Donnelly et al., 1994). However the utility of toe-clipping for individually marking *Siren* is fairly limited as they only have eight total toes (most toe-clipping schemes are designed for amphibians with 18 total toes). For this reason, toe-clipping in this study was considered to be a cohort mark (i.e., different toe-clip combinations can be used in order to separate animals into smaller groups by a pre-defined criterion such as period of capture). Tail notching has been successfully used as a marking technique for larval anurans (Turner 1960). Sirens often have minor damage to their tailfins that can resemble a tail notch (personal observation). To avoid confusion with naturally occurring tailfin damage, I used an elongate arc or "tail scoop" (Figure 2.1) as a tailfin mark on each marked animal. Because there is not an effective way to vary the appearance of a tail scoop, this method was considered to be a non-specific capture mark (i.e., it only demonstrates that an animal has been previously captured and marked).

METHODS AND MATERIALS

All animals were captured from September 2006 to September 2007 as part of an on-going study on greater siren and two-toed amphiuma at Dry Bay, a 5-ha fishless Carolina bay located on the Department of Energy's Savannah River Site in Aiken County, South Carolina,

USA. A sampling period occurred each month for ten consecutive days (for a total of 130 trapping nights over 13 months). Upon return to the laboratory, animals were weighed to the nearest 0.1g on a Mettler PC 440 electronic scale (Mettler Instrument Corporation, Hightstown, NJ), measured on a meter stick for snout-vent length (SVL) and total length to the nearest 1.0mm, and were then marked. Animals were photographed with a Nikon D70 (model# 25218) or Nikon D200 (model# 25235) camera with a Nikon 18-70mm f/3.5-4.5G ED IF AF-S DX Nikkor Zoom Lens (model#2149) mounted on a Bogen TC-2 copy stand (Bogen Imaging Incorporated, Ramsey, NJ) to document mark regeneration and for later use in morphometric measurements. Animals were restrained for marking by placing them on a wet cloth. The cloth was folded over the animal's head and then the side of the cloth was folded over the animal. The animal and cloth were then rolled together to the opposite end of the cloth (Figure 2.2). This technique of restraining the siren permitted access to the area immediately posterior to the vent for injecting a PIT tag (AVID Marketing, Incorporated, Norco, CA) and administering a tail scoop while restraining the siren. Sirens did not need to be restrained for toe-clipping as they did not react to this type of mark. Larger sirens (>300mm SVL) also typically did not react to receiving a PIT tag, however, all animals were restrained in the cloth for PIT tagging and tail scooping.

All PIT tags were injected towards the distal end into the ventral side of the tail 1-3 cm posterior to the vent. This is the same area used by Sorensen (2003); however, I injected the PIT tag ventrally as the ventral aspect at this point was wider and doing so negated having to avoid the spinal column. Tissue from tail scoops was saved for genetic analysis and thus scissors were cleaned with a 10% bleach solution (to degrade any remnant DNA), run under tap water (to wash off any bleach), and then submerged in 70% isopropyl alcohol (to ensure sterilization) between

the marking of each animal. Syringe needles were stored in 70% isopropyl alcohol prior to being used on PIT tag applicators. All PIT tag applicators and needles were wiped with a paper towel (to remove tissue residue) and 70% isopropyl alcohol between animals to sterilize the equipment.

Markings on recaptured animals were given a four-stage rating based on a combination of photographic records and notes taken during laboratory measurements (Figures 2.3, 2.4). Toe clips and tail scoops were given a 1 if they were freshly clipped and did not show any evidence of regrowth (Figures 2.3a, 2.4a). They were given a 2 if there was only minor regrowth (Figures 2.3b, 2.4b). A toe clip was given a 3 if it was partially regrown (more than half the original size but less than ¾ the size of a full grown toe; Figure 2.3c). Tail scoops were given a 3 if the tissue had healed and the site of the mark was obviously discolored (Figure 2.4c). Toes and tails that were fully regenerated were given a rating of 4. If a mark was considered to be borderline between categories, it was given the higher numerical rating.

Toe clips were taken from the siren's second innermost toe (the longest toe) on the right foot by using a pair of sharp scissors to cut the toe at the base where it meets the hand. A few animals had deformities (not associated with toe-clipping) on their designated hand, in which case a toe was taken from the left hand and recorded. While toe-clipping was administered from the beginning of the experiment, tail-scooping was initiated in January of 2007 at which time all animals received a toe-clip, a tail scoop and a PIT tag. Animals recaptured within the same ten-day trapping period were recorded and released at the site of capture without taking additional measurements and were omitted from the analysis.

Mark ratings were tested for significant correlations to the age of the mark, and changes in SVL, total length, and mass since the original mark. Regressions were tested with an analysis of variance (ANOVA) with lack-of-fit and a comparison of alternative models (e.g., logarithmic-

x, s-curve model, squared-x) to determine which model best fit the data. Statistical analyses were run in Statgraphics (Centurion XV Version 15.2.06.).

RESULTS

A total of 102 recaptures of 72 toe-clipped animals and 94 recaptures of 58 tail-scooped animals were analyzed for mark durability and readability. These data were grouped into 30-day intervals to represent monthly sampling efforts (Tables 2.1, 2.2). Days between captures ranged from 20 to 332 days for toe clips (100.2 ±65.5 SD) and tail scoops (92.1 ±57.3 SD). Most toe clips showed signs of regeneration after more than 30 days (Figure 2.5) and the majority of tail scoops were partly regenerated 20-30 days after being administered (Figure 2.6). I grouped marks that were obvious (i.e., marks that were classified as a 1or 2) together to provide a conservative estimate of mark persistence (Figures 2.7, 2.8). Conservative estimates indicate that the majority of toe clips and tail scoops persisted 61-90 days and 20-30 days respectively (Figures 2.7, 2.8). The majority of toe clips and tail scoops were readable (i.e., classified as a 1, 2, or 3) for 180-332 days and 151-180 days, respectively (Figures 2.9, 2.10). The first toe clip that was fully regenerated occurred 127 days after being administered. The first tail scoop that was fully regenerated occurred 61 days after being administered. While the majority of toe clips were still readable within the 332 day maximum between captures (both recorded marks over 300 days were ranked as 3's) and one mark was a 1 at 216 days, most tail scoops were unreadable by 181 days (Figures 2.9, 2.10).

Toe clip and tail scoop mark readability were correlated to mark age, and growth rates (Figures 2.11, 2.12, 2.13, 2.14, 2.15, 2.16, 2.17, 2.18; Tables 2.3, 2.4, 2.5, 2.6, 2.7, 2.8, 2.9, 2.10). A Fisher's least significant difference (LSD) test was used to compare the mean mark age (days) to mark rating (1-4) within toe clips and tail scoops and between toe clips and tail scoops

(Table 2.11). There were three groupings of mark age and type (Figure 2.19). Two outliers were removed from the toe clip statistical analyses to create a better fit for the model without affecting significance. The outliers belonged to the same animal that did not regenerate any toe tissue after 194 and 216 days. One outlier was removed from the tail scoop analyses for similar reasons (no tail tissue regeneration in 63 days) and did not affect significance. All three outliers are included in non-statistical figures and tables (Figures 2.5, 2.6, 2.7, 2.8, 2.9, 2.10; Tables 2.1, 2.2).

DISCUSSION

Toe clips and tail scoops created distinguishable marks that were easily read within a finite period of time after being administered. Toe clips lasted longer than tail scoops and can also be used to create a finer level of distinction between groups of animals (cohorts). Most toe clips were still readable through the end of the study and one animal that was caught outside of the study period on 31 January 2008 had a readable toe clip that was 353 days old. Although there were five "lost marks" (a rating of 4) of toe clips, most of these were actually still distinguishable marks that surpassed the ¾ of original length threshold between a rating of 3 and 4. However, they were not easy to distinguish and may have only been distinguishable to someone familiar with what that specific toe should look like.

Toe clips would be best suited for mark-recapture studies lasting for a field season (January to September) and provide an opportunity for a cohort marking scheme. Toe-clipping may also be used in conjunction with studies on skeletochronology (Halliday and Verrell 1988; Bruce and Castanet 2006) or for any studies needing tissue samples. The number of toes on *S. lacertina* (8) limits toe-clipping schemes. Additionally, I caution against removing multiple toes on the same foot because *S. lacertina* use their feet as much, if not more than, their tail (personal

observation) to pull themselves through the water, vegetation, and organic debris, and the extent to which the loss of multiple toes would impact their survival is not known.

While one tail scoop was readable 332 days later, 11 out of the 12 tail scoop marks that were over 165 days old were completely regenerated and no longer visible. After 63 days, all tail scoops were healed and only discolored tissue (a rating of 3) in the area of the original mark distinguished these animals as having been given a tail scoop. Of all the techniques tested, tail scoops were likely the least invasive. The tissue in the mark area healed within 30 days for nearly all animals. Despite being structurally identical to the original tissue, the mark remained discernable for up to 180 days after implementation. Tail scoops would be ideal for marking efforts that last for a short period of time (<60 days) and do not require a specific mark. The tissue taken from tail scoops is sufficient for quality DNA extraction and the rapidity of tailfin regeneration suggests that there are not any likely long-term effects of tail scoops.

There are still several other types of marking techniques available for testing on sirens and other permanently aquatic salamanders. While PIT tags work well for permanent individual identification, they cannot be used in larva and small juveniles of *S. lacertina* because of the large gauge needle needed to insert the tag into the tail (Sorensen 2003, personal observation). The golden flecking on *S. lacertina* is highly variable in respect to the amount present, as well as the shapes and sizes of individual flecks. This variation is possibly unique and might be useable for individual identification with photo-identification programs (see Gamble et. al., 2008).

Until the validity of other such techniques are tested on *S. lacertina* in the field, I suggest using PIT tags for long-term studies or those requiring individual identification and either toe-clipping or tail scooping for short-term studies not requiring individual identification. The use of a PIT tag or other permanent individual mark is also useful for determining the applicability of

marking techniques in the field. Field testing marking techniques would presumably be the best indicator of how well those techniques would work in the field on the species or groups of species of interest.

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Figure 2.1. An example of a fresh tail scoop.

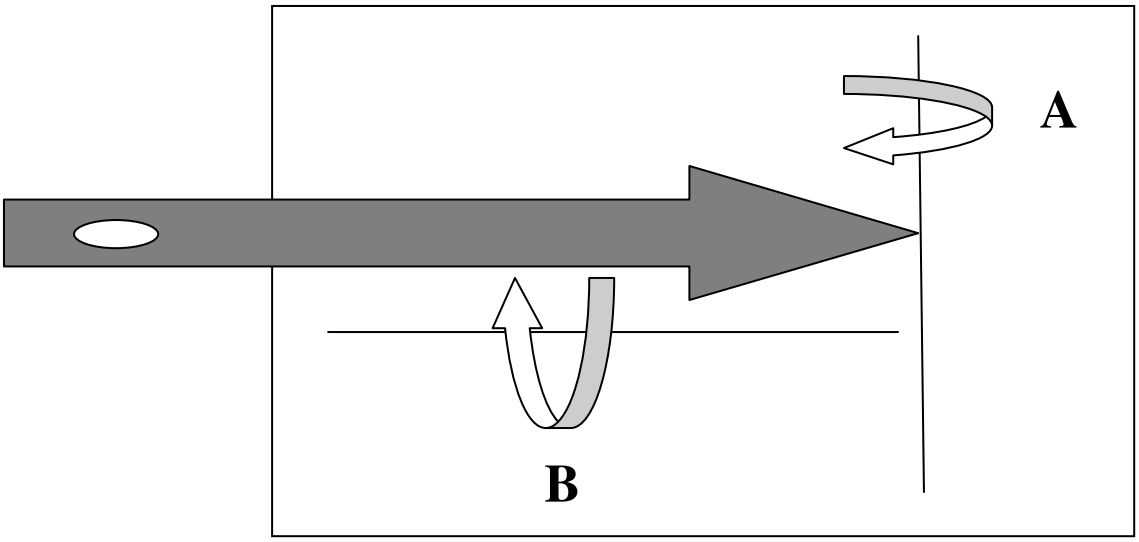

Figure 2.2. Diagram showing how a siren is restrained by rolling it in a damp cloth. The siren (large gray arrow) is placed partially on the cloth with its head (arrow head) on the cloth and its vent (open oval) and tail over the edge. The cloth is folded over the head of the siren at line A as indicated by the arrow. Then the cloth is folded over the siren at line B. At this point the siren and cloth are grabbed and rolled together towards the top of the cloth.

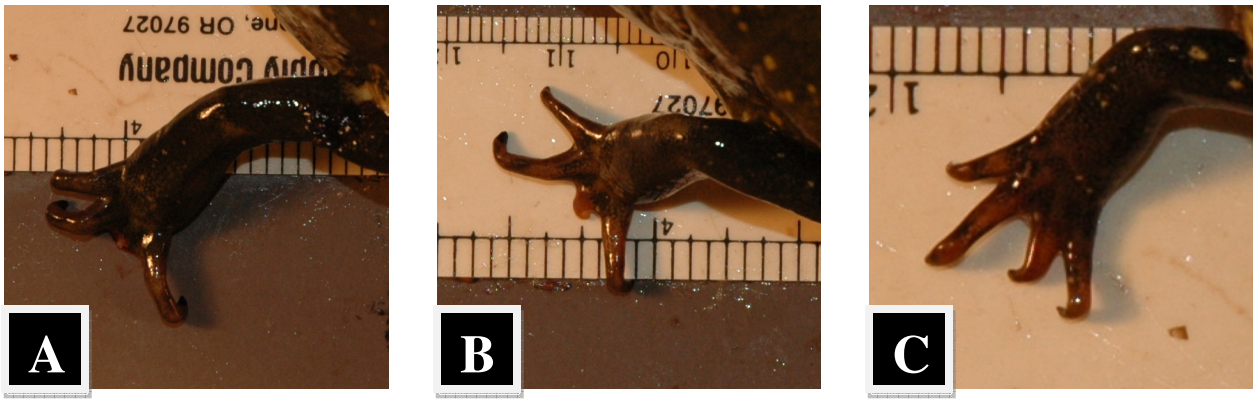

Figure 2.3. Siren toe clips in various stages of regeneration. A) Fresh mark. B) Minor regeneration. C) Partial Regeneration.

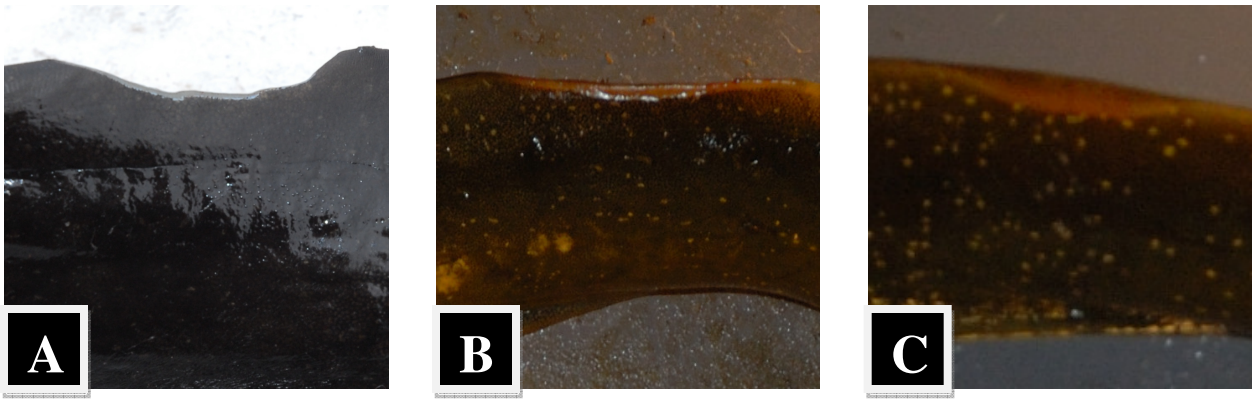

Figure 2.4. Tail scoops in various stages of regeneration. A) Fresh mark. B) Minor regeneration. C) Tissue regenerated but discolored.

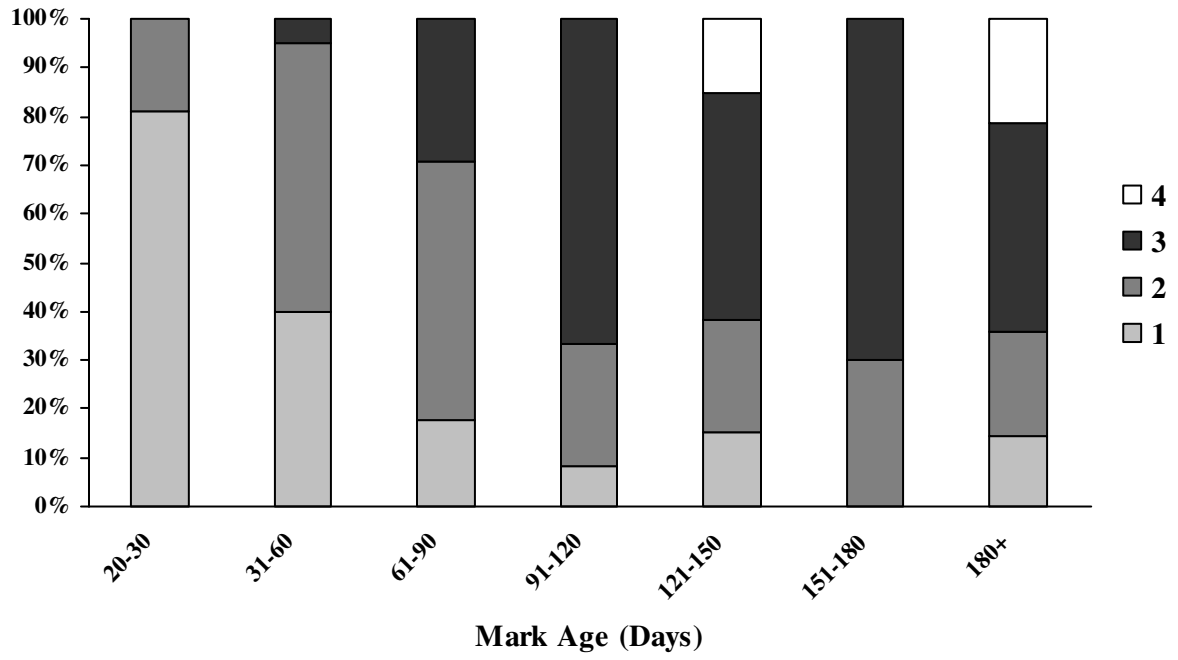

Figure 2.5. Proportion of toe clip ratings by mark age. 1=fresh, 2=minor regeneration, 3=partial regeneration, 4=loss of mark.

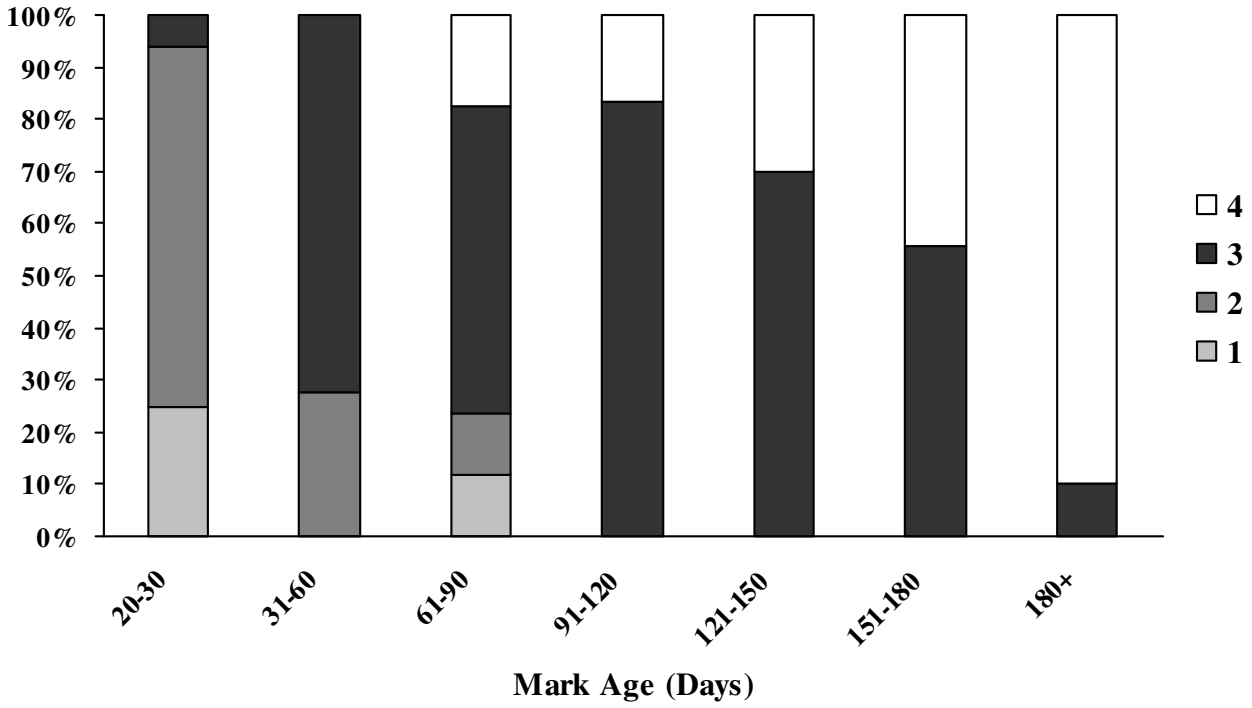

Figure 2.6. Proportion of tail scoop ratings by mark age. 1=fresh, 2=minor regeneration, 3=partial regeneration, 4=loss of mark.

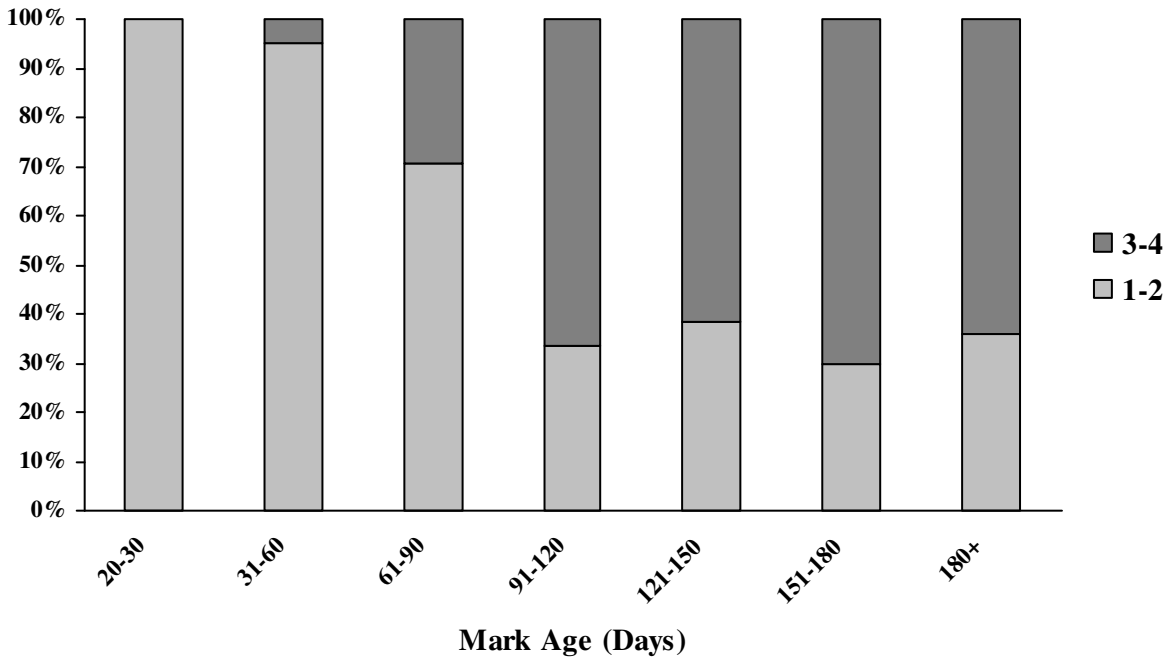

Figure 2.7. Proportion of obvious toe clips (ratings 1 and 2) compared to proportion of partially (3) or completely regenerated marks (4) by mark age.

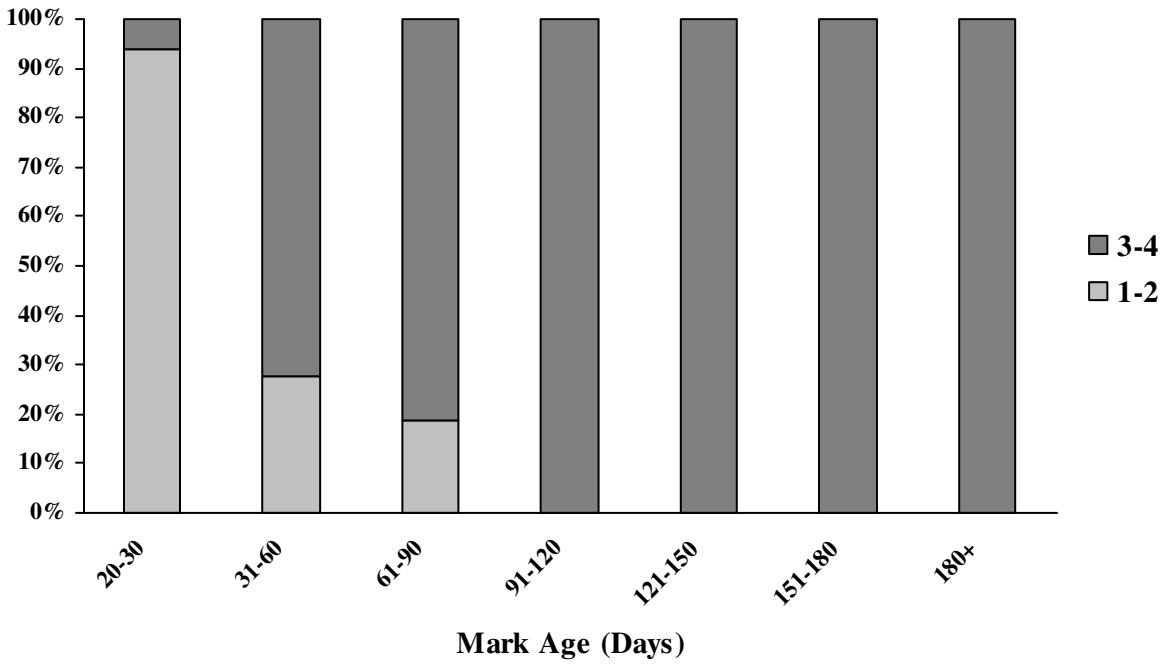

Figure 2.8. Proportion of obvious tail scoops (ratings 1 and 2) compared to proportion of partially (3) or completely regenerated marks (4) by mark age.

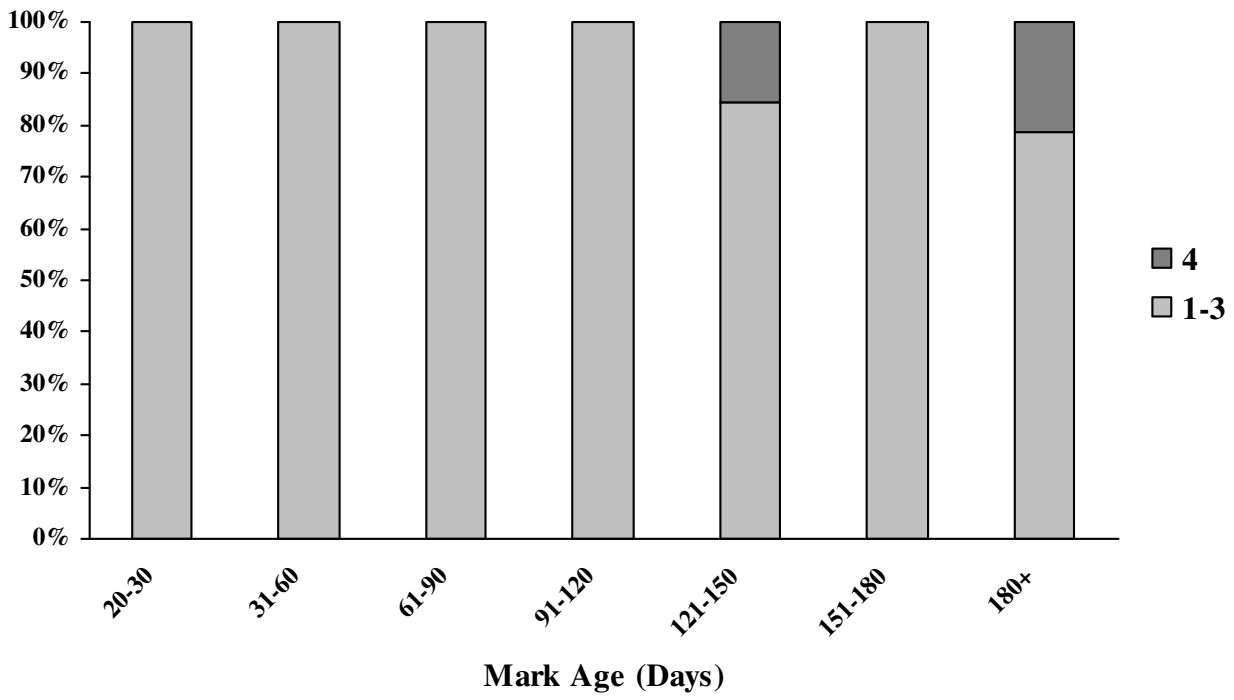

Figure 2.9. Proportion of readable toe clips (ratings 1, 2, and 3) to lost marks (4) by mark age.

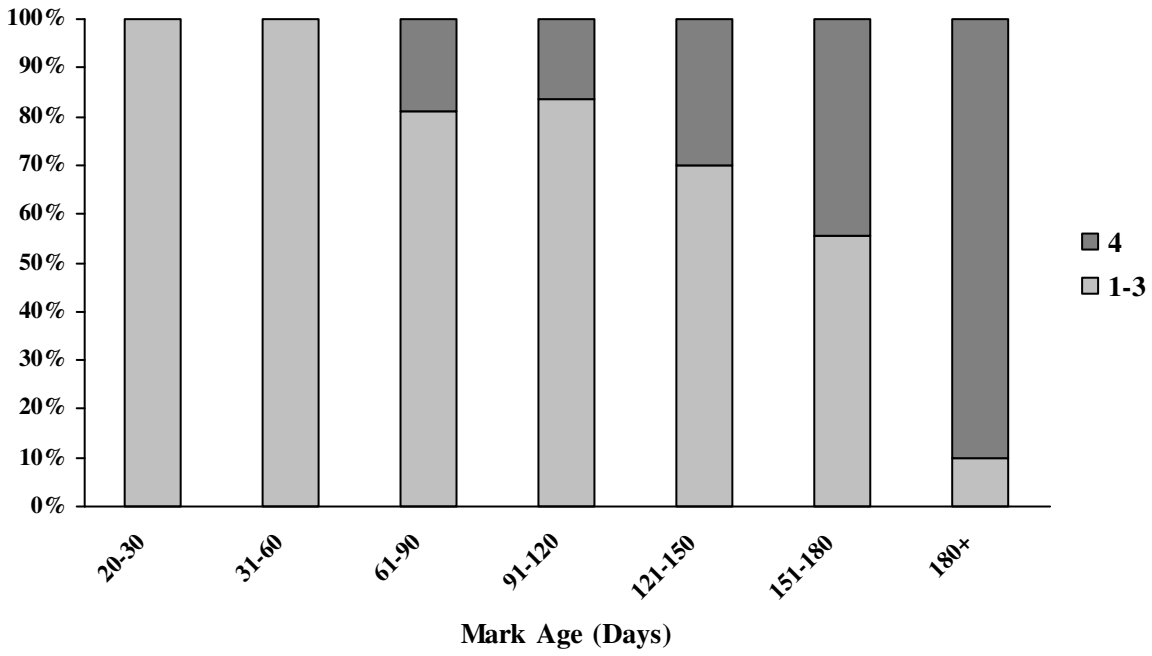

Figure 2.10. Proportion of readable tail scoops (ratings 1, 2, and 3) to lost marks (4) by mark age.

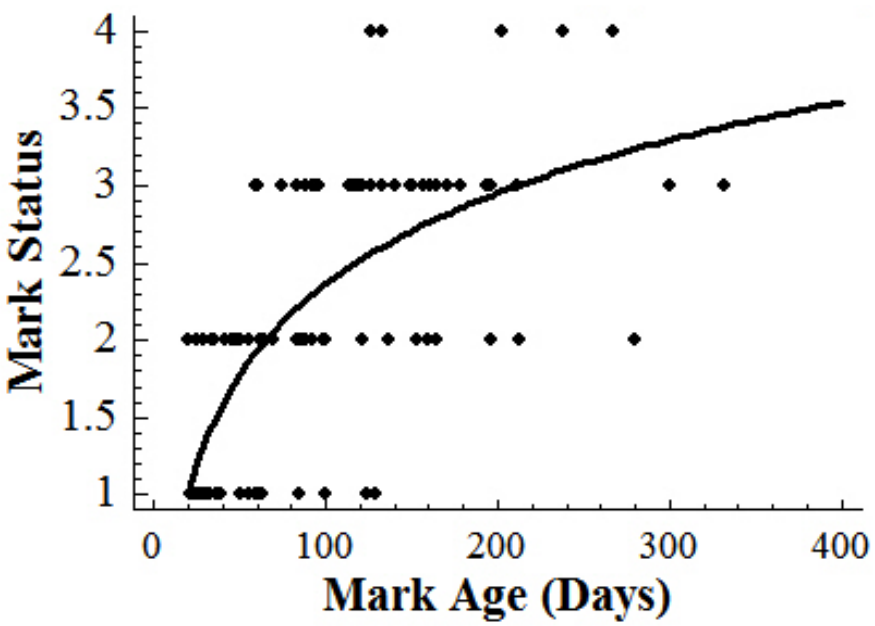

Figure 2.11. Relation of toe clip rating to mark age. Mark Status = -1.54 + 0.847*ln(Mark Age), $r^2 = 0.691$, $P < 0.0001$

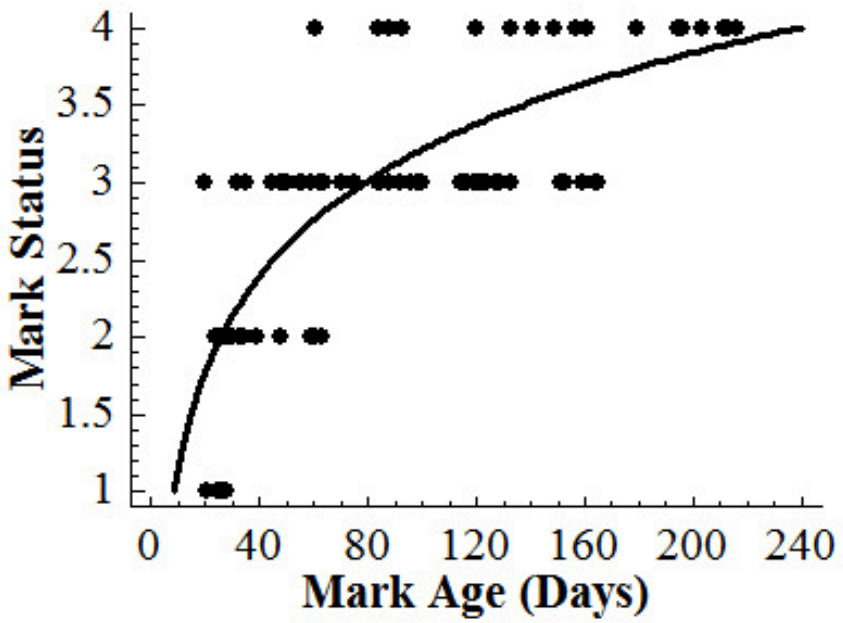

Figure 2.12. Relation of tail scoop rating to mark age. Mark Status = -0.929 + 0.899*ln(Days since first capture). $r^2 = 0.79$. $P < 0.0001$.

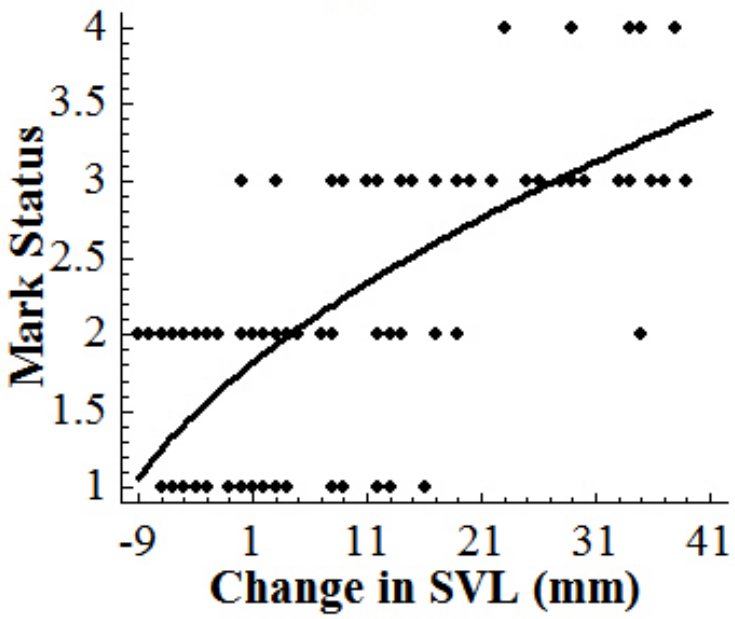

Figure 2.13. Relation of toe clip rating to change in snout-vent length (SVL). Mark Status = sqrt(3.08 + 0.215*Change in SVL). r^2 =0.70. P < 0.0001.

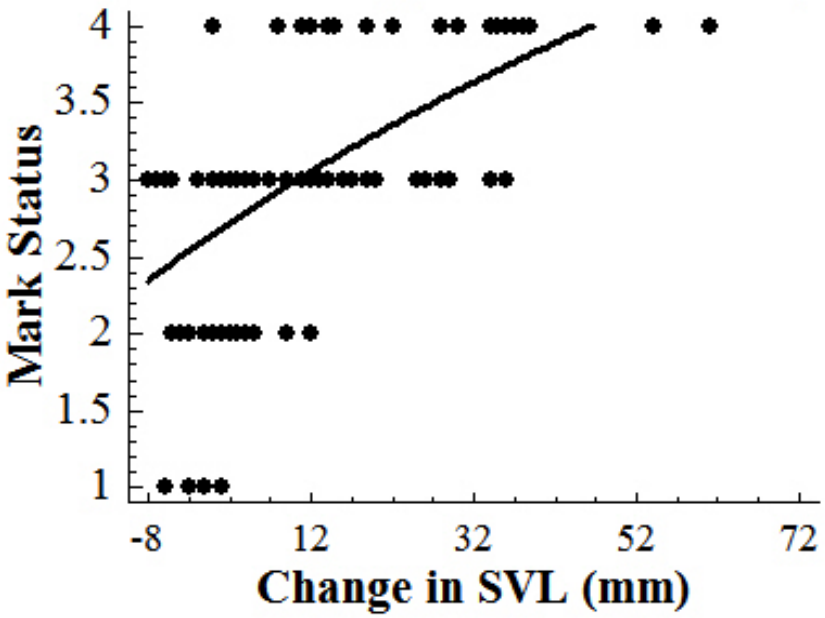

Figure 2.14. Relation of tail scoop rating to change in snout-vent length (SVL). Mark Status = sqrt(7.03 + 0.193*Change in SVL). $r^2 = 0.63$. $P < 0.0001$.

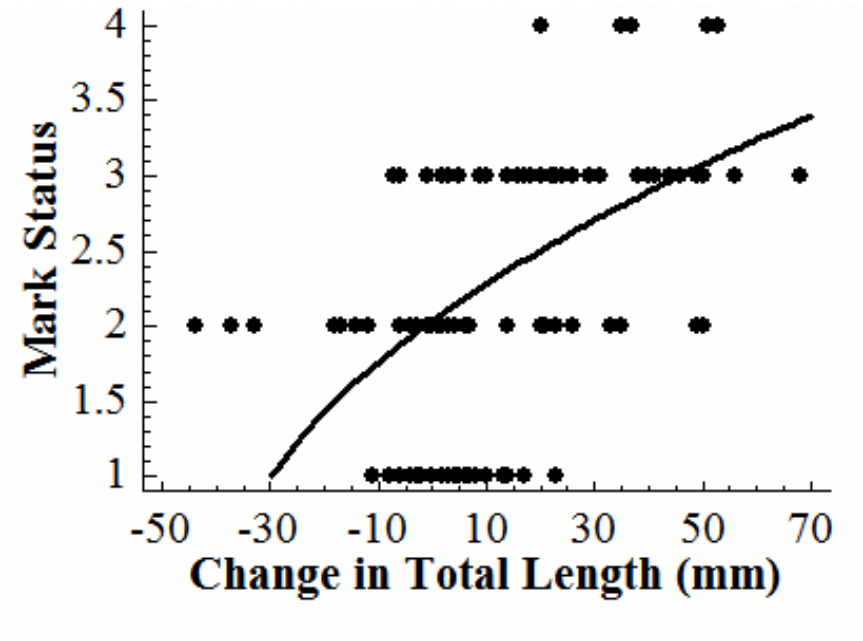

Figure 2.15. Relation of toe clip rating to change in total length. Mark Status = sqrt(4.15 + 0.106*Change in total length). $r^2 = 0.57$. $P < 0.0001$.

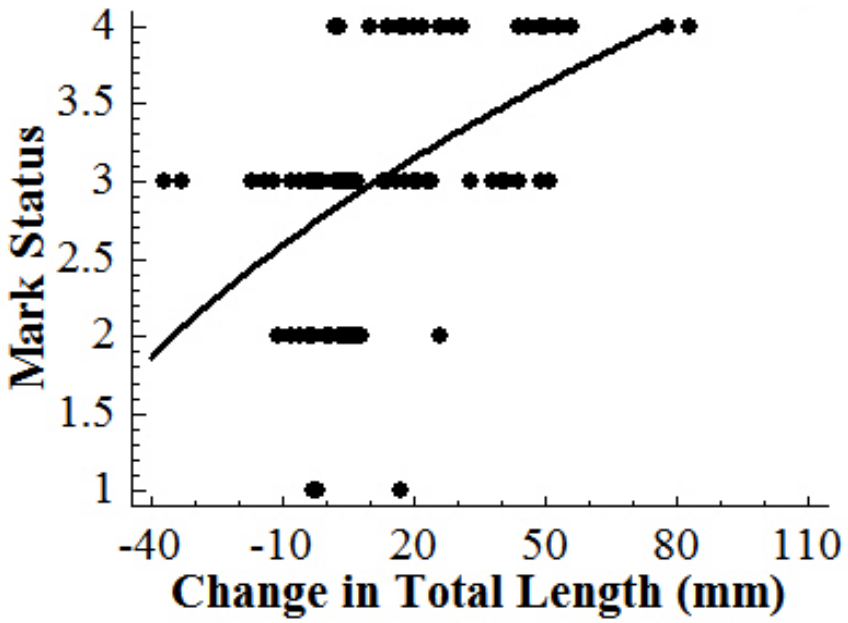

Figure 2.16. Relation of tail scoop rating to change in total length. Mark Status = sqrt(7.78 + 0.108*Change in Total Length). $r^2 = 0.55$. $P < 0.0001$.

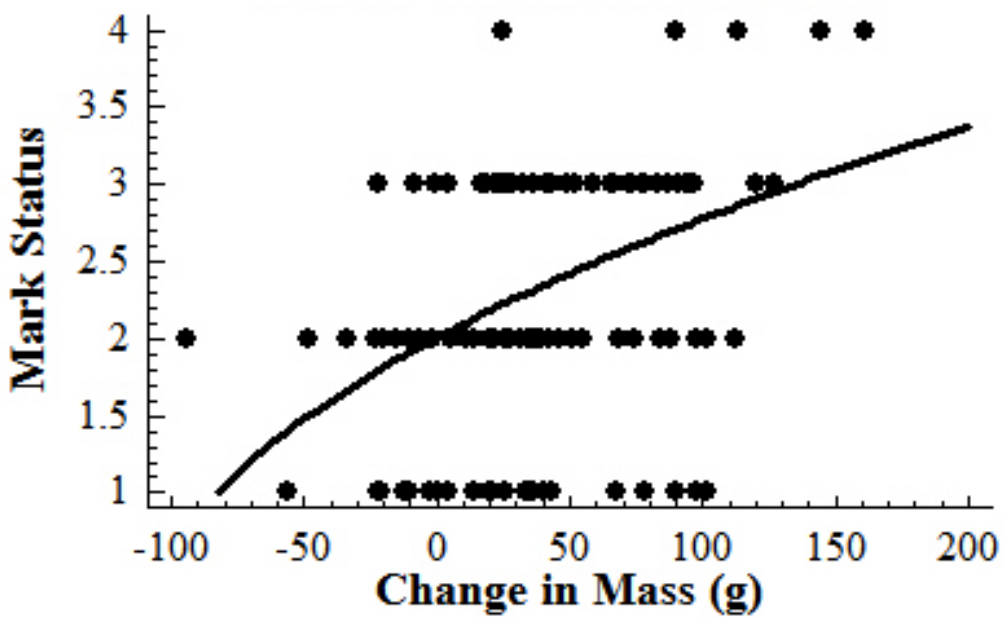

Figure 2.17. Relation of toe clip rating to change in mass (g). Mark Status = sqrt(4.03 + 0.0368*Change in Mass). $r^2 = 0.41$. $P < 0.0001$.

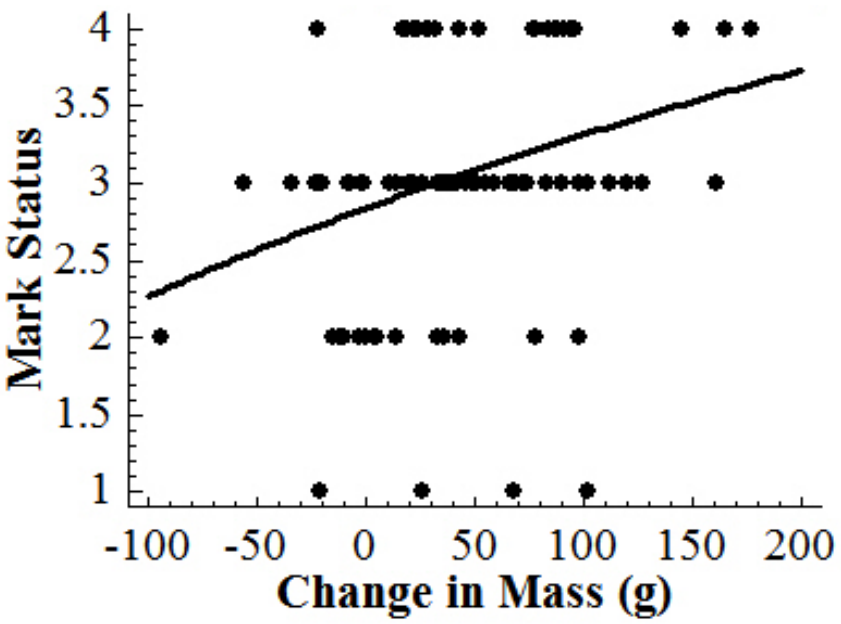

Figure 2.18. Relation of tail scoop rating to change in mass (g). Mark Status = sqrt(8.04 + 0.0292*Change in Mass). $r^2 = 0.32$. P = 0.0021.

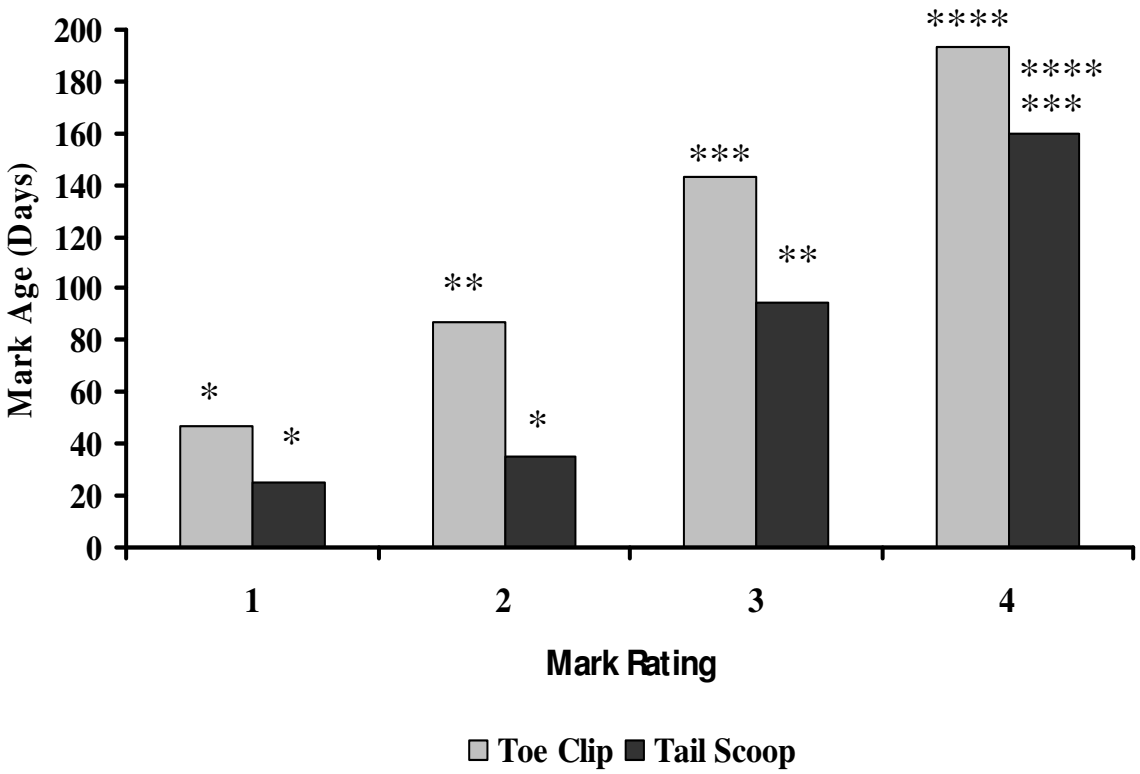

Figure 2.19. Comparison of mean mark age and rating between toe clips and tail scoops. Bars with different numbers of asterisks are significantly different from each other at the $p<0.05$ level.

Table 2.1. Breakdown of toe clip mark ratings (1-4) by mark age (days).

Rating	20-30	31-60	61-90	91-120	121-150	151-180	180+
1	13	8	3	1	2	0	2
2	3	11	9	3	3	3	3
3	0	1	5	8	6	7	6
4	0	0	0	0	2	0	3
Total	16	20	17	12	13	10	14

Table 2.2. Breakdown of tail scoop mark ratings (1-4) by mark age (days).

Rating	20-30	31-60	61-90	91-120	121-150	151-180	180+
1	4	0	1	0	0	0	0
2	11	5	2	0	0	0	0
3	1	13	10	10	7	5	1
4	0	0	3	2	3	4	9
Total	16	18	16	12	10	9	10

Table 2.3. Analysis of variance (ANOVA) with lack-of-fit test using toe clip mark rating as a response variable to mark age.

Source	*Sum of Squares*	*Df*	*Mean Square*	*F-Ratio*	*P-Value*
Model	37.00	1	37.00	89.65	<0.0001
Residual	40.44	98	0.41		
Lack-of-Fit	29.69	68	0.44	1.22	0.28
Pure Error	10.75	30	0.36		
Total (Corr.)	77.44	99			

Table 2.4. Analysis of variance (ANOVA) with lack-of-fit test using tail scoop mark rating as a response variable to mark age.

Source	*Sum of Squares*	*Df*	*Mean Square*	*F-Ratio*	*P-Value*
Model	34.16	1	34.16	144.59	<0.0001
Residual	20.56	87	0.24		
Lack-of-Fit	14.06	59	0.24	1.03	0.48
Pure Error	6.50	28	0.23		
Total (Corr.)	54.72	88			

Table 2.5. Analysis of variance (ANOVA) with lack-of-fit test using toe clip mark rating as a response variable to change in snout-vent length (SVL) from time of original mark.

Source	*Sum of Squares*	*Df*	*Mean Square*	*F-Ratio*	*P-Value*
Model	782.78	1	782.78	96.15	<0.0001
Residual	797.86	98	8.14		
Lack-of-Fit	342.76	39	8.79	1.14	0.32
Pure Error	455.10	59	7.71		
Total (Corr.)	1580.64	99			

Table 2.6. Analysis of variance (ANOVA) with lack-of-fit test using tail scoop mark rating as a response variable to change in snout-vent length (SVL) from time of original mark.

Source	*Sum of Squares*	*Df*	*Mean Square*	*F-Ratio*	*P-Value*
Model	693.53	1	693.53	58.33	<0.0001
Residual	1034.45	87	11.89		
Lack-of-Fit	508.05	38	13.37	1.24	0.23
Pure Error	526.40	49	10.74		
Total (Corr.)	1727.98	88			

Table 2.7. Analysis of variance (ANOVA) with lack-of-fit test using toe clip mark rating as a response variable to change in total length from time of original mark.

Source	*Sum of Squares*	*Df*	*Mean Square*	*F-Ratio*	*P-Value*
Model	505.95	1	505.95	46.14	<0.0001
Residual	1074.69	98	10.97		
Lack-of-Fit	541.71	51	10.62	0.94	0.59
Pure Error	532.97	47	11.34		
Total (Corr.)	1580.64	99			

Table 2.8. Analysis of variance (ANOVA) with lack-of-fit test using tail scoop mark rating as a response variable to change in total length from time of original mark.

Source	*Sum of Squares*	*Df*	*Mean Square*	*F-Ratio*	*P-Value*
Model	515.62	1	515.62	37.00	<0.0001
Residual	1212.36	87	13.94		
Lack-of-Fit	571.20	46	12.42	0.79	0.78
Pure Error	641.17	41	15.64		
Total (Corr.)	1727.98	88			

Table 2.9. Analysis of variance (ANOVA) with lack-of-fit test using toe clip mark rating as a response variable to change in mass from time of original mark.

Source	*Sum of Squares*	*Df*	*Mean Square*	*F-Ratio*	*P-Value*
Model	271.08	1	271.08	20.29	<0.0001
Residual	1309.56	98	13.36		
Lack-of-Fit	929.48	73	12.73	0.84	0.73
Pure Error	380.08	25	15.20		
Total (Corr.)	1580.64	99			

Table 2.10. Analysis of variance (ANOVA) with lack-of-fit test using tail scoop mark rating as a response variable to change in mass from time of original mark.

Source	*Sum of Squares*	*Df*	*Mean Square*	*F-Ratio*	*P-Value*
Model	179.14	1	179.15	10.06	0.0021
Residual	1548.83	87	17.80		
Lack-of-Fit	1231.41	69	17.85	1.01	0.52
Pure Error	317.42	18	17.63		
Total (Corr.)	1727.98	88			

Table 2.11. Results of a 95% Least Significant Difference (LSD) test on the mean ages of mark type ratings. Letters in homogenous groups column denote significantly different groups.

Mark Type-Rating	*Count*	*Mean*	*Homogeneous Groups*
Tail Scoop-1	4	25.0	A
Tail Scoop-2	18	35.5	A
Toe Clip-1	27	47.0741	A
Toe Clip-2	35	87.1429	B
Tail Scoop-3	47	94.2553	B
Toe Clip-3	33	143.242	C
Tail Scoop-4	21	160.095	CD
Toe Clip-4	5	193.6	D

CHAPTER 3

POPULATION ECOLOGY OF GREATER SIREN (*SIREN LACERTINA*)[1]

[1]Luhring, T. M., and B. D. Todd. To be submitted to Herpetological Monographs

ABSTRACT
Greater siren, *Siren lacertina*, population ecology is poorly known despite their relatively high abundance and large size. We used passive integrated transponder (PIT) tags to conduct a 13-month mark-recapture study at Dry Bay, a 5-ha herbaceous bay wetland in Aiken, South Carolina. Trapping at Dry Bay resulted in 470 *S. lacertina* captures. Of 271 marked animals, 83 (30.6%) were recaptured 174 times. Robust design top model estimates in program MARK estimated that 246.9 ± 29 (SE) *Siren lacertina* were in Dry Bay during the study period. Monthly survival rates were 0.88 ± 0.04 (SE) and 0.80 ± 0.03 (SE) for Robust design and Cormack-Jolly Seber top model estimates, respectively. Density was estimated to be 0.005 sirens/m^2 and biomass concentrations 1.5 g/m^2 (average mass of all animals equal to 297.8g). Greater sirens demonstrated a switching point when they reached approximately 400 mm snout-vent length (SVL), whereupon growth rate in mm/day (for SVL) decreased and the variability in mass gained or lost per day increased. Growth in mm/day was negatively correlated with SVL whereas growth in g/day was positively correlated with SVL. Seasonal peaks of activity were attributed to breeding activity in January and to foraging activity in May-June. Body condition varied by month with peaks in June and July.

INTRODUCTION

Although *S. lacertina* was originally described in 1766 (Linnaeus 1766), approaches a meter in length (Goin 1961; Conant and Collins 1998), is the heaviest salamander in North America (Martof 1973), and has often been described as common or abundant throughout the core of its range over the last two centuries (Barton 1808; Jobson 1940; Petranka 1998), a paucity of information is available on its life history and population ecology. This dearth of information on *S. lacertina* population ecology is due, in part, to their behavior and habitat preferences. Greater sirens are nocturnal (Hanlin and Mount 1978) and inhabit "muddy and

weed-choked" habitats (Martof 1973). Permanently aquatic salamanders, in general, are difficult to monitor (Hendricks 2005).

Dunn (1924), despite Linnaeus's original supposition that *Siren* ate serpents, and in light of more recent documentation that nothing but "mud" was found in the stomachs examined by Leconte (1824), suggested that *Siren* were herbivorous salamanders. In the 84 years since Dunn's suggestion, numerous studies established *S. lacertina* as a major invertivore that feeds heavily on mollusks such as snails (Burch and Wood 1955, Hanlin 1978, Moler 1994), as well as a variety of insects, pelecypods, annelids, and crayfish (see Carr 1940, Hamilton 1950, Duellman and Schwartz 1958, Hanlin 1978). Greater sirens also occasionally eat small fish (Duellman and Schwartz 1958, Hanlin 1978) and mole salamanders, *Ambystoma talpoideum* (Luhring 2007). However, vertebrates only rarely appear in diet records for *S. lacertina* and likely result from incidental opportunistic events.

Digestive tracts of greater sirens are often full of mud and filamentous algae (Leconte 1824, Burch and Wood 1955, Ultsch 1973, Hanlin 1978). The presence of this material in digestive tracts has been attributed to filter-feeding (Hanlin 1978) and would seem to be the unavoidable result of using negative pressure for capturing animals in the benthos. More recent analyses of gastrointestinal structure and microbial fermentation suggest that greater siren, although not as morphologically specialized as most herbivores, do have active microbial fermentation in the posterior intestine (Pryor et. al., 2006). However, the extent to which *S. lacertina* obtains nutrients from fermentation of plant material remains unknown.

Greater sirens likely feed opportunistically and are adapted to take advantage of available food resources. In addition to their varied omnivorous diet of living animal and plant matter, greater sirens scavenge opportunistically (TML personal observation). The ability to take

advantage of varied food sources, combined with fast growth rates (Tables 3.1, 3.2), high fecundity (1,400 enlarged, yolked, and pigmented ovarian follicles in one female; Hanlin and Mount 1978), high survivorship (0.88-1.00 monthly survival; Sorensen 2004), longevity (11-24.5 years in captivity; Flower 1925, Conant and Hudson 1949) and the high energy efficiencies of ectotherms in general (ectotherms have mass-specific energy requirements that are $1/7^{th}$ to $1/10^{th}$ that of endotherms of equal size; Pough et. al., 1998), may explain why sirens are able to reach high densities in a variety of locations (Tables 3.3, 3.4).

Lesser sirens, *S. intermedia*, a smaller and closely-related congener of *S. lacertina*, reduce the growth, survival and fecundity of eastern newts (*Notophthalmus viridescens*), a keystone species in some aquatic ecosystems (Fauth and Resetarits 1991). In addition to eating the larvae of newts, *S. intermedia* indiscriminately feed on several species of larval anurans (Fauth and Resetarits 1991). While greater sirens will eat adult salamanders (Luhring 2007), it is not known how they influence vital rates of conspecifics or affect amphibian community assemblages.

American alligators, *Alligator mississippiensis* (Delany and Abercrombie 1986), bald eagles, *Haliaeetus leucocephalus* (McEwan and Hirth 1980), bowfin, *Amia calva* (Jordan and Arrington 2001) and banded watersnakes, *Nerodia fasciata* (Gibbons and Dorcas 2004, Luhring, unpublished data) will prey on *S. lacertina*. However, greater sirens do not appear to be a major component of any of these species' diets. The mudsnake, *Farancia abacura*, is a specialist that eats mostly elongate permanently aquatic salamanders (*Amphiuma* spp. and *Siren* spp.; Mount 1975) and is known to eat greater sirens (Carr 1940). Other accounts of possible greater siren depredation events are limited in their specificity. Kilham (1984) witnessed American Crows, *Corvus brachyrhynchos*, robbing "large, eel-like salamanders" from Great Egrets, *Ardea alba*,

and White Ibis, *Eudocimus albus*, in south central Florida that were either two-toed amphiumas, *Amphiuma means*, or greater sirens. Wood Storks, *Mycteria americana* (Depkin et al., 1992), and several species of *Nerodia* (see Gibbons and Dorcas 2004) are known to eat *Siren*, but whether they consume *S. intermedia*, *S. lacertina*, or both is unspecified.

During periodic droughts, *Siren lacertina* aestivates in the bottom of dried wetlands (Carr 1940, Freeman 1958, Hanlin and Mount 1978). Cocoons made of dried squamous epithelial cells (Etheridge 1990a) and reduced resting metabolic rates of aestivating sirens (60-70% lower than active sirens; Etheridge 1990b) likely permit *S. lacertina* to survive periods of prolonged drought. Non-aestivating animals are capable of long-term (2.2-5.2 years) persistence without feeding and can survive losses of 45-86% percent of their body mass (Martof 1969). *Siren intermedia* is capable of aestivating for up to 35 weeks with larger animals losing mass at a slower rate than smaller animals (Gehlbach et. al., 1973). Greater sirens are larger than lesser sirens and have more mass per mm of body length (Figure 3.1), which would suggest that they are likely capable of persisting even longer periods of aestivation than previously recorded for *S. intermedia*. Etheridge (1990b) estimated that greater sirens with masses of 1, 500, and 1125g could potentially aestivate for 146, 386, and 842 days, respectively.

Although they can likely aestivate for over 2 years, *S. lacertina* are generally only found in wetlands that regularly hold water for at least six months (Snodgrass et. al., 1999). Sirens need reserves of body lipids to aestivate for long periods of time (Etheridge 1990b). Greater sirens have large fat reserves in their tails (Martof 1969) that are probably used for this reason. It is possible that sirens require several months to replenish these reserves to a sufficient level to aestivate successfully. Repeated bouts of aestivation without sufficient time to forage and

replenish fat reserves would be unsustainable and this likely precludes sirens from inhabiting wetlands with shorter hydroperiods.

While monitoring permanently aquatic salamanders is difficult (Hendricks 2005), crayfish traps (Johnson and Barichivich 2004) as well as steel and plastic minnow traps (Willson et. al., 2005) and hoop nets (Gibbons and Semlitsch 1991) reliably capture *S. lacertina*. Greater sirens can be permanently and individually marked with passive integrated transponder (PIT) tags (Sorensen 2003). Tail scoops and toe clips, while useful for tissue collection, are only effective marks for short-term marking purposes and last less than a year (Luhring unpublished data).

Our objectives in this study were to estimate relative population size and density of *S. lacertina* and to determine other population and ecological parameters including growth rates of individuals, seasonal activity periods, minimum size and age at first reproduction, and survivorship. Incidental natural history observations were also recorded in an effort to more fully understand the overall demography, behavior, and ecology of this enigmatic species.

METHODS AND MATERIALS

STUDY SITE

Dry Bay is a 5-ha, semi-permanent, herbaceous bay wetland that rarely dries completely (Davis and Janecek 1997). Although no fish are currently found in Dry Bay (Snodgrass et al. 1996, Luhring personal observation), fish were historically present prior to a drought in 1986 (Bennett and McFarlane 1983). The periphery of Dry Bay is mostly bottomland hardwoods (Davis and Janecek 1997) while the interior is dominated by maidencane, *Panicum hemitomon*, and floating macrophytes, *Nymphaea* spp. (Keough et. al., 1990). A historic ditch (Figure 3.2)

runs from the center of the bay through the northern end and to another depressional wetland to the north.

SAMPLING REGIME

Monthly trapping from September 2006 through September 2007 consisted of 10 consecutive nights of trapping. During 2006, all animals were measured and marked in the field prior to release. Starting in January 2007, all animals were returned to the lab in Rubbermaid® bins or large coolers for measurements prior to release. Animals captured in June through September of 2007 were released on the same day of capture. Each animal was released at the site of its capture.

We established four trapping arrays on 9 September 2006 using a total of 50 plastic minnow traps, 20 plastic-coated steel minnow traps, 24 trashcan traps (Luhring and Jennison in review), 4 hoop nets and a fyke net. The purpose of this initial trapping effort was to assess the effectiveness of the traps being used and to begin establishing a population of marked animals. Traps were redistributed among arrays starting October 2006 so that each array was composed of five trapping stations and three hoop nets. Trapping stations were distributed approximately 3-5m apart and were composed of a trashcan trap, a steel minnow trap and a plastic minnow trap placed within 1-2m of each other. Hoop nets were located within arrays between trapping stations. A fyke net was set in the ditch at the northern end of the first array (Figure 3.2) where the water was deep enough to permit its use.

The water level rose between December 2006 and January 2007 and the borders of the wetland expanded sufficiently to permit the addition of two more arrays for a total of six arrays. These six arrays were in place from January 2007 through August 2007. Water depth decreased

steadily during the summer. In September 2007 the water in the two additional arrays was not deep enough to sample and they were excluded from the trapping effort for that month.

All captures of vertebrates and invertebrates were recorded. All turtles, snakes, and alligators captured were returned to the laboratory to be measured and marked prior to being released. Invertebrates were recorded to the lowest possible taxonomic level (usually order) and counted. All traps except the fyke net were emptied of all contents prior to being reset. All vertebrates except for small tadpoles and mole salamanders were removed from the fyke net daily.

DATA COLLECTION

Sirens were measured in the field from September to December 2006. Wet body mass was measured with a 100g, 300g, 600g, or 1kg Pesola® scale while the animal was in a damp cotton mesh bag. The siren was then moved to another container and the mesh bag weighed to subtract from the total weight of the animal and bag. We initially used a squeezebox to measure sirens (Sorensen 2004) for the first day of captures in September 2006. However, we found it easier to measure all sirens by placing them directly on a meterstick; all subsequent measurements were taken in this fashion. Snout-vent length (SVL) and total length (TL) of each animal was determined to the nearest 1.0 mm. To approximate the relative physiological condition of captured animals, we used a body condition index (BCI), which was calculated as:

$$\text{Body Mass/Snout-Vent Length}^3 \times 10^6 \text{ (Romero and Wikelski 2001).}$$

Water depth was recorded daily from decimal-foot gages in the ditch (gage 31-2) and hole (gage 31-KM) arrays. The ditch array depth was the deepest point in the wetland (in the historic ditch), whereas the hole array depth was the deepest naturally-occurring point in the center of the wetland. Starting in January 2007, all captured animals were returned to the

laboratory for measurements, collection of tissue, and for marking. Sirens were weighed to the nearest 0.1g on a Mettler PC 440 electronic scale (Mettler Instrument Corporation, Hightstown, NJ), measured on a meterstick for SVL and TL to the nearest 1.0mm, and were then marked (Luhring unpublished data). Animals were then photographed dorsally with a Nikon D70 (model# 25218) or Nikon D200 (model# 25235) camera with a Nikon 18-70mm f/3.5-4.5G ED IF AF-S DX Nikkor Zoom Lens (model#2149) mounted on a Bogen TC-2 copy stand (Bogen Imaging Incorporated, Ramsey, NJ). Photographs were used to document mark regeneration and for later use in morphometric measurements. We recorded head-length (HL) and interocular (IO) distance (Hanlin and Mount 1978) with vernier calipers to the nearest 0.1 mm for later morphometric analyses.

Sirens were restrained for marking and tissue collection by placing them on a wet pillowcase, which was then folded over the animal's head. The side of the cloth was folded over the animal and then the animal and cloth were rolled together to the opposite end of the cloth (Figure 3.3). Restraining the siren permitted access to the area immediately posterior to the vent for injecting a PIT tag (AVID Marketing, Incorporated, Norco, CA) and collecting a tissue sample from the dorsal tail fin (each "tail scoop" doubled as a mark; Luhring unpublished data) without the use of anesthesia.

Syringe needles were stored in 70% isopropyl alcohol prior to being used on PIT tag applicators. All PIT tag applicators and needles were wiped with a paper towel (to remove tissue residue) and 70% isopropyl alcohol between animals to sterilize the equipment. Passive integrated transponder tags were injected ventrally 1-3 cm posterior to the vent towards the distal end of the animal. This is the same area used by Sorensen (2003); however, we injected the PIT tag ventrally as the ventral aspect at this point was wider and doing so negated having to avoid

the spinal column. Tissue from tail scoops was saved for genetics work, thus scissors were cleaned with a 10% bleach solution (to degrade any remnant DNA), run under tap water (to wash off any bleach), and then submerged in 70% isopropyl alcohol (to ensure sterilization) between the marking of each animal. Animals being returned to the lab often defecated prior to release, and we collected all opportunistic fecal samples from containers or directly from animals being weighed, measured and marked

POPULATION ANALYSES

We used Cormack-Jolly Seber (CJS) and Robust Design (RD) models to analyze mark-recapture data (Cormack 1964; Pollock 1982; Lebreton et al. 1992). The CJS model is an open population model used to calculate apparent survival rates and recapture probabilities across sampling intervals. For this model, we collapsed the consecutive daily sampling periods into single capture scores for each month. Specifically, we scored an animal with a '1' in its capture history for each month in which the animal was captured at least once during the 10-day capture period for that month. If the animal was not captured at least once during the sampling period each month it received a '0' for that period in its capture history. We used program MARK to construct four *a priori* CJS models with different permutations of time-varying or constant apparent survival and recapture probability (White and Burnham 1999). We provided resulting parameter estimates from the most parsimonious CJS model determined using an information theoretic approach (Akaike 1973; Burnham and Anderson 2002).

The Robust Design model combines open and closed population models to estimate temporary emigration, capture and recapture probabilities, survival, and population size (Pollock 1982; see also Bailey et al. 2004a). Data are structured so that primary periods are separated by monthly intervals, and each primary period consists of secondary samples conducted on 10

consecutive days (see Pollock 1982 for diagram). Only the months of September–December 2006 and June–September 2007 conformed to the statistical requirement of immediate release of animals on day of capture and therefore could be used in the RD models. We constructed simplified models with constant survival and constant population size and we constrained initial capture and recapture probabilities to be equal to each other and constant over daily secondary samples but time-varying among monthly primary periods. We tested for the presence of constant random, Markovian, or no temporary emigration (Bailey et al. 2004a) in models using an information theoretic approach to identify the most parsimonious model using program MARK. We provided model estimates of survival, temporary emigration, capture and recapture probabilities, and population size from the most parsimonious model.

STATISTICAL ANALYSES

All statistical analyses were run with Statgraphics (Centurion XV Version 15.2.06.). In addition to testing all regressions for significance with an analysis of variance (ANOVA), we ran a lack-of-fit test and a comparison of alternative models to determine the optimum equation for each model. For all statistical tests, significance was determined at the $\alpha = 0.05$ level. Analyses that included or were derived from body length (i.e., BCI) used SVL because total length (TL) was affected by the prevalence of tail damage in the population (personal observation).

RESULTS

Thirteen monthly trapping sessions were conducted from September 2006 through September 2007 for a total of 130 total nights of sampling and 12,650 trap-nights. The sampling effort resulted in 470 total captures of greater sirens. A total of 271 animals were marked and 83 (30.6%) were recaptured a total of 174 times. Of 25 unmarked captures, 13 sirens were too small to mark, 5 sirens escaped prior to receiving a mark, and a total of 7 animals were found dead (1

drowned in a plastic minnow trap, 1 unknown cause of death, 2 wading bird depredations, and 3 snake depredations). Almost half of all markable animals captured from May to September 2007 were recaptures (Figure 3.4).

Program MARK identified the CJS population model having constant survival and time-varying recapture probability as the most parsimonious model. The other three permutations of the CJS models all had ΔAIC values greater than 13. The most parsimonious model produced an estimate of 0.80 ± 0.03 (SE) for apparent survival across monthly intervals. Probability of recapture at least once during the multi-day sampling periods ranged from near zero in some months to a high of 0.30 ± 0.06 in June 2007 (Figure 3.5).

Using program MARK to analyze RD models, we found strong support for temporary emigration in the models. The model that excluded temporary emigration had a ΔAIC value of 17.5, whereas the two models incorporating some form of temporary emigration were separated by a ΔAIC value of 1. Although support for a single, most parsimonious model was equivocal, the model with constant random temporary emigration was ranked slightly higher and estimates of most parameters did not vary. The estimate of temporary random emigration was 0.67 ± 0.09 for each interval. Monthly survival was estimated to be 0.88 ± 0.04. Daily conditional capture and recapture probabilities ranged from a low of near zero to a high of 0.07 ± 0.01 (Figure 3.6). The population size for Dry Bay, conditional on having been available for capture, was estimated to be 81.5 ± 9.6 animals. After accounting for random temporary emigration (Bailey et al. 2004b), the total population was estimated to contain 246.9 ± 29 animals at each sampling period.

Activity varied monthly with spikes in array capture rates (excluding fyke net and intra-month captures) and total captures (excluding intra-month captures) occurring in January and

June (Figures 3.7, 3.8). Arrays differed in monthly capture rates, but we observed the same general trends of a decrease in late fall, a strong and well-defined peak in January followed by a depression of activity in February, and a later peak in late spring and early summer (Figure 3.7).

Siren lacertina in South Carolina had a growth curve that was intermediate between *S. lacertina* in North Florida (Sorensen 2004) and *S. intermedia* in East Texas (Gehlbach and Kennedy 1978; Figure 3.1). The rate at which *S. lacertina* increased in length (SVL) was negatively correlated ($r = -0.515$, $p = 0.0001$) with initial SVL (Figure 3.9, table 3.5). Growth rate (g/day) was positively correlated ($r = 0.482$, $p = 0.0003$) with initial SVL (Figure 3.10, Table 3.6). Body condition indices (BCI) varied monthly with a general increase from the beginning of the year until peaking in June and July and remaining relatively stable through August and September (Figure 3.11; Tables 3.7, 3.8).

Growth rates were estimated by subtracting the initial SVL or mass from the final SVL or mass and dividing the difference by the number of days between the first and last captures. We only included sirens with a minimum of 50 days between their first and last captures to minimize the influence of possible measuring error and temporal variation in growth. Of seven sirens with an SVL greater than 400mm and the requisite 50 days between captures, only one had positive growth in length. After limiting data to sirens with an SVL less than 400mm, we had a total of 45 *Siren lacertina* (ranging from 218 to 371mm SVL) to analyze for average growth rates. Growth rates for this size range conformed to a normal distribution (standard skewness = 0.425, standard kurtosis = -1.04) with an average growth rate (±SE) of 0.13 ± 0.013 mm SVL/day. Average yearly growth of sirens from 200-400 mm was then estimated by multiplying the average daily growth rate (0.13 mm/day) by 365 days for an estimate of 47.5 mm/year. Annual

growth for this size group was rounded to 50 mm/year for use in estimating size classes (Table 3.9).

Two females laid eggs in the lab prior to being returned to the field. The first female (298mm SVL, 446mm TL, 208.8g) deposited eggs on 14 February 2007 and the second female (273mm SVL, 418TL and 158.6g) deposited eggs on 12 March 2007. Both laid small clumps of eggs in groups of 2-5 that were distributed throughout the container. One dead female recovered from a submerged steel minnow trap on 15 April 2007 was returned to the lab, measured, frozen, and later dissected. This female (285mm SVL, 412mm TL, 224.9g) was gravid and had pronounced oviducts.

DISCUSSION

Greater sirens were active for 10 months out of the year starting in January and lasting through September with minor activity in October (Figure 3.8). There was a spike in activity in January 2007 followed by a sharp decrease in February 2007 and then a general increase of activity that peaked in June 2007. The spike in activity in January was likely associated with the initiation of breeding activity. This coincides with the breeding phenology of South Alabama females, which have greatly enlarged oviducts and eggs that are pigmented and yolked in January (Hanlin and Mount 1978). Based on known sizes of reproductive females at Dry Bay (273, 285 and 293 mm SVL), and estimated size class data (Table 3.9) we report that *S. lacertina* are reproductively mature by their 4th year with oviposition occurring from February through April. Reproduction may start as early as their 3rd year if the observed decrease in growth rate for that age group is the result of allocating energy to reproduction.

Siren intermedia mature in their second year (Davis and Knapp 1953, Trauth et al., 1990, Gibbons and Semlitsch 1991) after reaching 220-250mm TL (Davis and Knapp 1953). Bite

marks are frequently observed on adult *S. intermedia* during the breeding season and are attributed to breeding activity (Godley 1983, Petranka 1998). Bite marks were observed on nearly all of the reproductive adults in Dry Bay during the breeding season (especially during February) and were not evident during the rest of the year. *Siren lacertina* under 260mm SVL and 400mm TL did not have bite marks during the breeding season, nor did they lay eggs while at the laboratory. It is therefore likely that females in this population do not begin reproduction until their fourth year. The delayed maturity in *S. lacertina* (relative to *S. intermedia*) may result from a tradeoff for increased size and be an adaptation for increased survivorship through periods of drought (larger animals survive longer during periods of aestivation; Etheridge 1990b).

Large adults that were assumed to be males (animals at Dry Bay were not sacrificed to determine sex) had enlarged masseter muscles and broader tail fins than other large adults (Luhring unpublished data). This difference was seasonal, and size class specific, with secondary sexual characteristics appearing only in the larger males (>500mm TL) during the breeding season (January through April). The seasonality and restriction of secondary sexual characteristics to larger males may explain why these characters were not detected in the Florida population, if sexually dimorphic characteristics occur in Florida populations at all.

Activity levels did mirror water depth to some degree (Figure 3.8). Activity decreased from September 2006 to October 2006 as water level decreased (1.53 m to 1.40 m in the ditch). Although water depth increased in December 2006 to 1.47 m, the September 2006 depth was not surpassed until January 2007 (1.60 m), when reproductive activity spiked during this time. Although water depth continued to increase through February, a marked decrease in activity (a total of 31 individual sirens were captured in February as compared to 58 in January) was

apparent. Water depth continued to increase through March 2007 (reaching a peak average of 1.77 m) while activity slowly increased and reached a peak in June. After June, water level decreased every month until crossing below the September 2006 mark (1.53 m) by September 2007 (1.46 m). Few sirens (15) were caught in September 2007.

The peak of activity in June coincided with the highest average body conditioning in 2007 (Figure 3.11). Body conditioning did not increase significantly from January through April while reproduction was occurring (Figure 3.11, Table 3.8). Body condition dropped from September 2006 to October 2006 for similarly-sized animals, suggesting that conditions (possibly low water levels and reduced foraging opportunities) were not ideal for maintaining body mass. Average body condition for animals from January 2007 was also lower than those from September 2006, and individuals that were originally captured in September 2006, and subsequently recaptured in January and February 2007, generally lost mass between captures. Aestivating animals reduce their resting metabolic rate (Etheridge 1990b). Presumably, animals that went into a state of torpor during this time experienced a reduction in the rate of energy drawn from energy stores. Staying active during this time of reduced foraging opportunity would deplete active stores that could otherwise be allocated to drought survival or reproduction. Activity would be especially costly for larger animals with a higher basal metabolic requirement. The few sirens captured from October through December were generally smaller or had poorer body condition than those captured during the rest of the year. Of the 12 sirens captured in October 2006, only 5 had an SVL of 250 mm or longer, the highest BCI was 7.8 and only 3 animals had a BCI greater than 7.5 (the mean BCI for September 2006 was 8.3).The one capture in November 2006 was a young of year (110-120 mm SVL) and the only capture in December 2006 was an emaciated adult (364 mm SVL, 499 mm TL, 140 g) with a BCI of 2.9 (the lowest

BCI recorded for any live animal during this study). A similarly-sized siren (363 mm SVL) captured in September 2006 weighed 3.4 times as much (469 g) as the siren captured in December 2006.

Because our smallest captured siren was 80 mm SVL and only six total captures were less than 137 mm SVL, we used previously documented sizes to guide estimates of size classes from hatching to 200 mm SVL. *Siren lacertina* hatch at 13 mm SVL/16 mm TL (Goin 1947), reach 39 mm TL (this would probably be about a 30 mm SVL individual; TML personal observation) in mid-May (Neill 1949) and are 75 mm SVL by mid-October (Ultsch 1973). In 2006, the smallest *Siren lacertina* captured at Dry bay reached 113 to 127 mm SVL by mid-October. The smallest sirens captured in 2007 were 80 (August), 81 (July) and 88 mm SVL (August). We estimate that sirens in Dry bay reach 100 ±30 mm SVL during their first year and around 200 ±30 mm SVL their second year. Hatchling lesser sirens grow two to three times faster than older individuals (Gehlbach and Kennedy 1978). Juvenile *S. lacertina* also experienced periods of accelerated growth during their first two years with growth rates that were 2.6-3.6 times faster than sirens between 200-400 mm SVL (table 3.9).

Most growth rates for *S. lacertina* over 400 mm SVL were negative. One possible influence was the change in shape, size, and color of the cloaca and surrounding tissue throughout the year in these larger adults (TML personal observation). Larger adults likely grow so slowly that multiple years of recaptures would be needed to detect and provide an accurate estimate of their growth rate.

The shift from growing longer to growing in mass at 400mm SVL may be the result of several different selection pressures. Larger sirens lose less body mass when aestivating than do smaller sirens (Gehlbach et al., 1973). Selection for larger size in male sirens occurs in *S.*

intermedia with males growing faster during immaturity and growing larger than females (Davis and Knapp 1953, Gehlbach and Kennedy 1978). Fecundity is positively correlated to SVL in *S. intermedia* (Trauth et al., 1990) and increasing length would directly contribute to reproductive fitness. Sexual dimorphism with respect to absolute size does not appear to occur in greater sirens (Luhring, unpublished data), however, sex-specific growth rates are unavailable. The retardation of growth rate after 400mm SVL is possibly a physiological control to prevent larger sirens from becoming so large that their size becomes more of a liability than an advantage (e.g., impairment of mobility, energy that would otherwise go to reproduction has to be shunted to cell maintenance).

Siren lacertina at Dry Bay had an estimated density of 0.005 sirens/m^2 (246.9 sirens in 5-ha) and a biomass concentration of 1.5 g/ m^2 (average mass of all captures is 297.8 g). These estimates are much lower than others reported in the literature for *Siren*. For example, *S. lacertina* in North Florida are estimated to reach concentrations of 1.3 sirens/m^2 and 233 g/m^2 (Sorensen 2004). However, these estimates were accompanied by high variance (299-1377 estimated population) and are for a 50 m stretch of vegetation mat bordering a 34-ha pond (Sorensen 2003). The relatively high estimates for North Florida greater sirens are possibly the result of sirens spending a disproportionate amount of time in the vegetation mat foraging, seeking shelter from predators, residing, and depositing eggs. As a result, this favorable habitat of a thick vegetative matrix provided a higher concentration of resources (e.g., food, egg deposition sites, shelter) than the surrounding open water. The muddy layer beneath the vegetation mat on an otherwise sandy bottom (Sorensen 2003) is also likely the only suitable aestivation habitat. Receding water may have caused abnormally high concentrations of animals

to gather in this area. It is likely that thick vegetation mats provide the penultimate habitat in which *Siren lacertina* can reach extraordinary population densities.

For *S. intermedia*, which routinely reach high population densities (Table 3.2), females become reproductive in their second year (Davis and Knapp 1953). This is one to two years sooner than *S. lacertina* females. *Siren intermedia* are highly fecund salamanders that can produce over 1500 ova (Trauth et al., 1990); however, most records for females are much lower (299 ova, Noble and Marshall 1932; 130 and 269 ova, Collette and Gehlbach 1961; 151-226 ova, Gehlbach and Kennedy 1978). The only record of greater siren fecundity is a female from Alabama that had approximately 1400 enlarged ovarian eggs (Hanlin and Mount 1978). Age at first reproduction and fecundity greatly influence rate of population increase (Cole 1954, Lewontin 1965, Murphy 1968, Bell 1976). The earlier age of reproduction and smaller size of *S. intermedia,* when coupled with high fecundity, may allow them to naturally reach higher densities in a variety of habitats than their larger congener.

In regions where both *Siren* species are present, they are found in the same wetlands less often than would be expected if distribution was random, and *S. lacertina* is found more often in wetlands separated by an elevation gradient (Snodgrass et al., 1999). While this may suggest that greater sirens are better dispersers than the other two species, all three species need to be submerged to move any substantial distances and are therefore heavily dependent on the formation of temporary waterways that connect isolated wetlands during heavy rains and floods (Schalk and Luhring in review). Lesser siren (because of their smaller body size) require less water to remain submerged than their larger congeners and can also make substantial forays in temporary flooding events. If lesser sirens are the more vagile of the two species of *Siren*, then dispersal ability would not explain why greater sirens are found more often in more elevated

wetlands. These wetlands, by virtue of their higher elevation, are less often flooded or connected to other wetlands during flood events and immigration into these wetlands for permanently aquatic salamanders is infrequent at best. Even infrequent droughts (approximately every 10 years in the case of Dry Bay) occur with more frequency than do colonization opportunities. Greater sirens, being the more drought-adapted species, would likely out compete (if there is competition between the two species), or simply outlast its smaller congener through repeated episodes of drought without immigration from a source population.

Of the five predated animals found dead in Dry bay, two were killed by wading birds. Although wading birds are likely predators on *Siren lacertina* (Petranka 1998), to our knowledge no such events have been reported (but see Kilham 1984). On 21 April 2006, a green heron (*Butorides virescens*) was observed perched on top of a hoop net that was set in a small open area. The heron remained on top of the hoop net until approached and then flew off to a nearby tree. Presumably, the same heron had been observed on numerous occasions since the beginning of April 2007 at Dry Bay, but was never out in the open and never allowed TML to get as close to it as on this occasion. When the hoop net was lifted out of the water, a dead male *S. lacertina* was found inside with a puncture wound located 65 mm anterior to the vent. The puncture was located on the right aspect of the dorsum and directed through to the left side, although there was no apparent exit wound. The other presumed wading bird fatality was another large male siren with a similar puncture wound that was found floating in the same array (array 4) at 1640 hrs on 9 September 2007. The siren had only recently died (within an hour of discovery) and it is likely that the puncture wound was received during daylight hours by a diurnal wading bird. Great blue herons (*Ardea herodias*) are frequently seen at this fishless wetland and are also likely predators.

Three sirens were killed by snakes. One siren in a trashcan trap was killed by a *F. abacura* but not consumed on 11 June 2007. The other two deaths were associated with banded watersnakes. One live *S. lacertina* was regurgitated by a large *N. fasciata* captured in a steel minnow trap, the siren later died from injuries associated with digestion. The other greater siren killed by a large *N. fasciata* was also in a steel minnow trap. Juvenile *N. fasciata* in Dry Bay feed on mole salamander larvae (*Ambystoma talpoideum*) and small frogs and it appears that only large adults are successful predators of greater sirens.

Differences in selection pressures between populations create interpopulation divergence in life history parameters (Stearns 1976, 1977). The differences in growth curves and densities between the populations of greater sirens in South Carolina and Florida may be the result of different selection pressures from predators (the lack of fishes in Dry Bay may release siren there from otherwise intense selection pressure from gape-limited predators), wetland hydroperiod, or other constraints on life histories. Further studies into these processes would do much to explain differences in observed population characteristics. Currently, it is not known how prevalent these parameter differences are on the fine (inter-wetland) or coarse (inter-regional) scale, and whether enough divergence in some of these populations has led to enough genetic differentiation for them to be considered separate species. In the Florida panhandle alone, several populations of *Siren* sp. are likely new and undescribed species (P. E. Moler, personal communication in Sorensen 2003). *Pseudobranchus* in Florida were recently revealed to comprise two genetically distinct species (Moler and Kezer 1993) and further molecular analyses of sirenids throughout their distribution will probably reveal additional species.

The body of knowledge for greater siren biology is a chimera comprised mostly of studies and observations from Florida and South Alabama. Little to no information is currently

available for populations of greater sirens northward through Georgia, South Carolina, North Carolina, and Maryland. Future studies that investigate these populations would be of great value to a comprehensive understanding of *S. lacertina*. Movement patterns, fecundity, and reproductive mode have yet to be conclusively determined and these are crucial components for understanding the secretive lives of North America's largest salamander.

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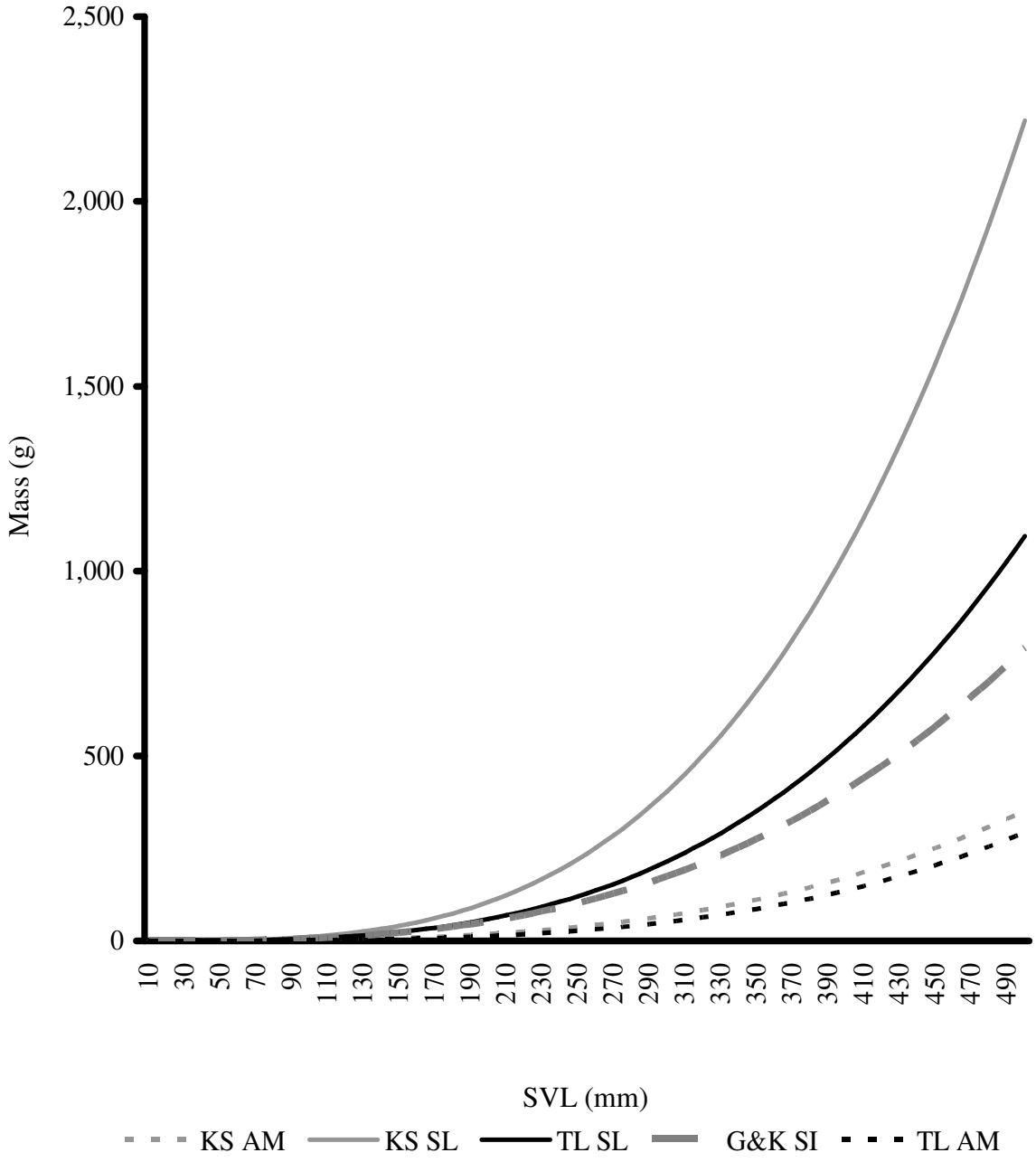

Figure 3.1. Growth rate curves for greater siren, *Siren lacertina* (SL), lesser siren, *Siren intermedia* (SI), and two-toed amphiuma, *Amphiuma means* (AM), from previous studies. KS = Sorensen 2004; TL = Luhring unpublished data; G&K = Gehlbach and Kennedy 1978.

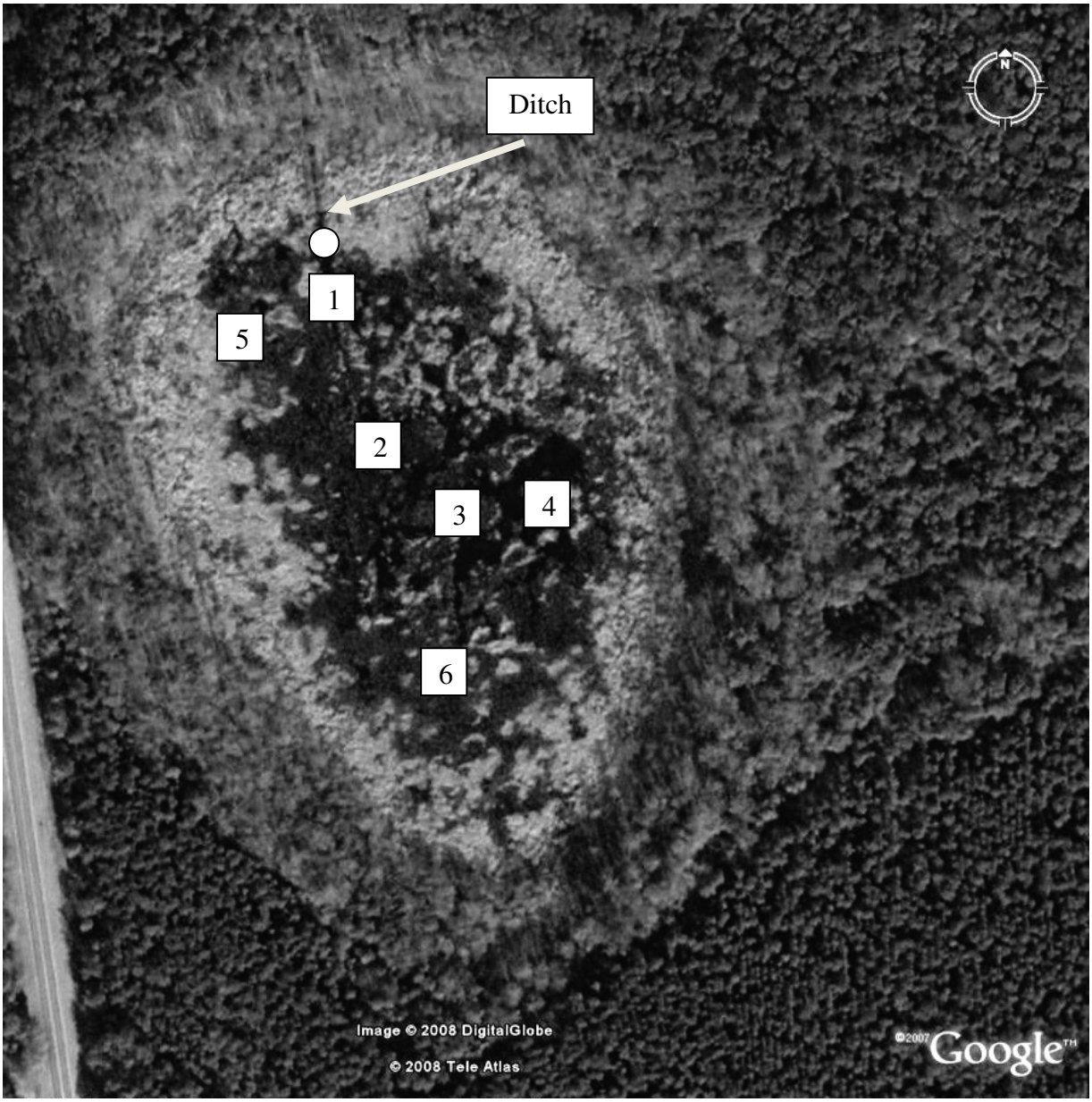

Figure 3.2. Illustration of Dry Bay showing locations of trapping arrays, fyke net, and ditch. Fyke net represented by circle. Approximate locations of trapping arrays are represented by numbered boxes. Arrays 5 and 6 were added in January 2007. Image courtesy of Google™ Earth.

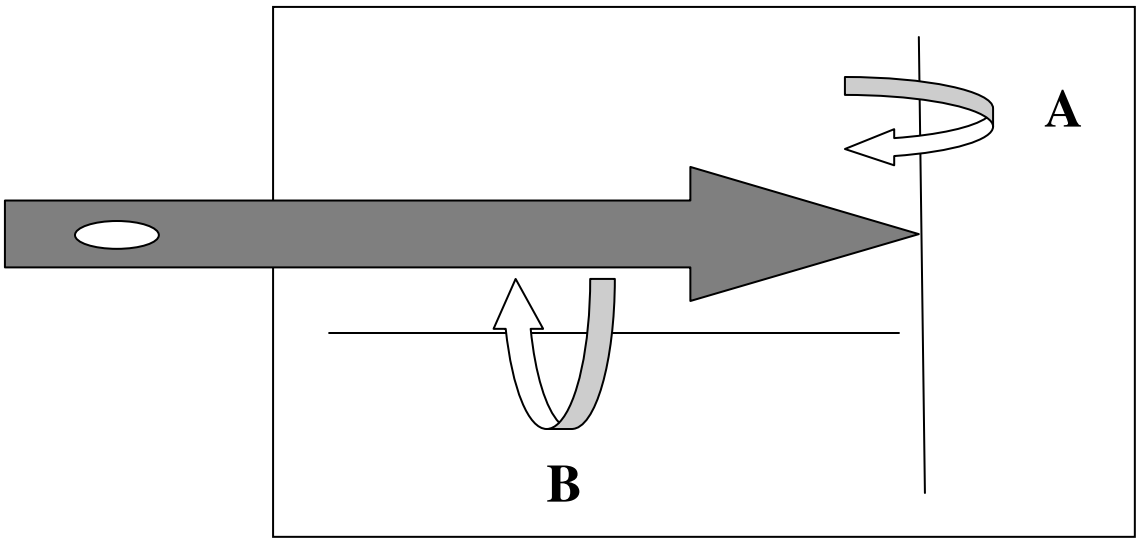

Figure 3.3. Diagram showing how a siren is restrained by rolling it in a damp cloth. The siren (large gray arrow) is placed partially on the cloth with its head (arrow head) on the cloth and its vent (open oval) and tail over the edge. The cloth is folded over the head of the siren at line A as indicated by the arrow. Then the cloth is folded over the siren at line B. At this point the siren and cloth are grabbed and rolled together towards the top of the cloth.

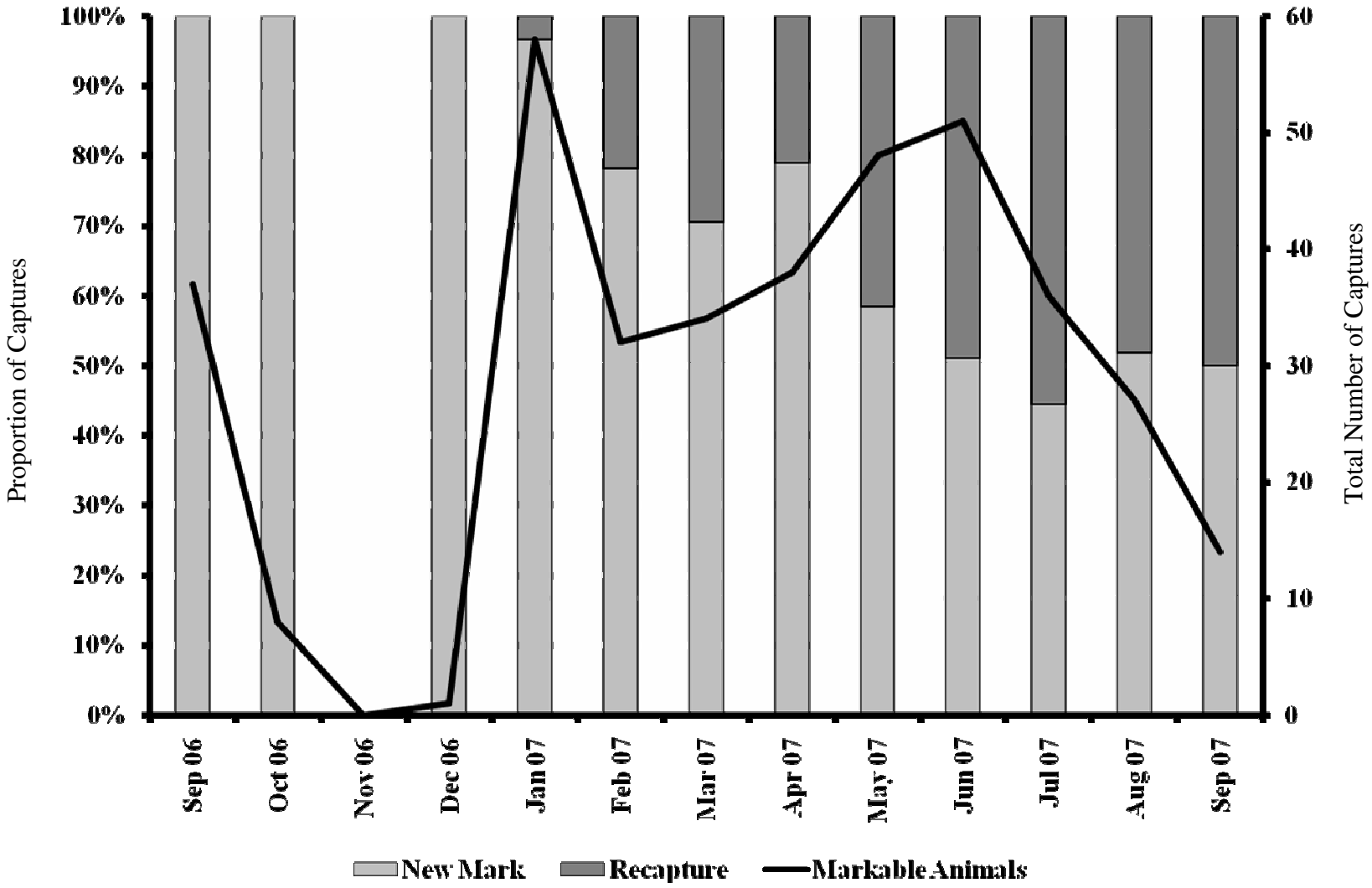

Figure 3.4. Monthly proportion of newly marked to recaptured sirens (bars on primary axis) with total number of markable animals captured (solid line on secondary axis).

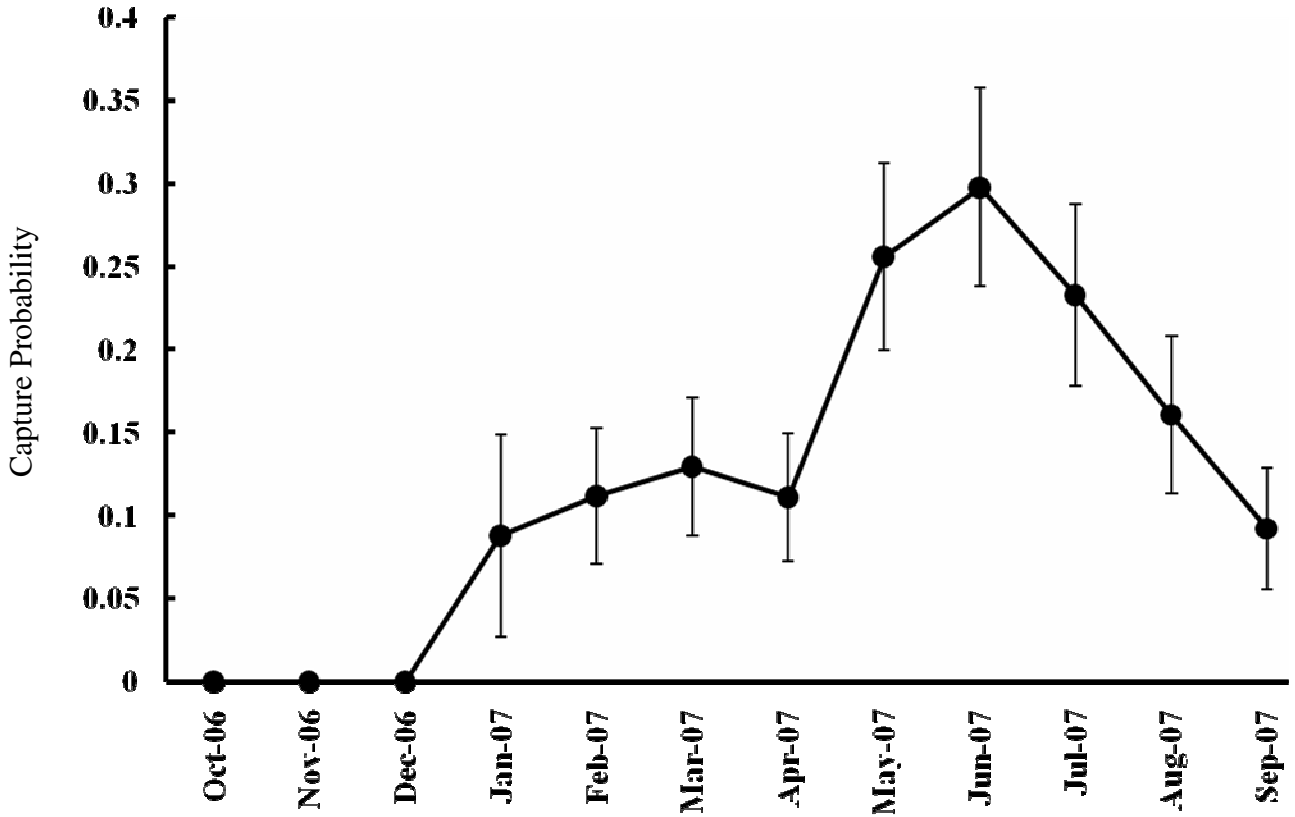

Figure 3.5. Cormack-Jolly Seber estimated monthly capture probabilities (±95% CI).

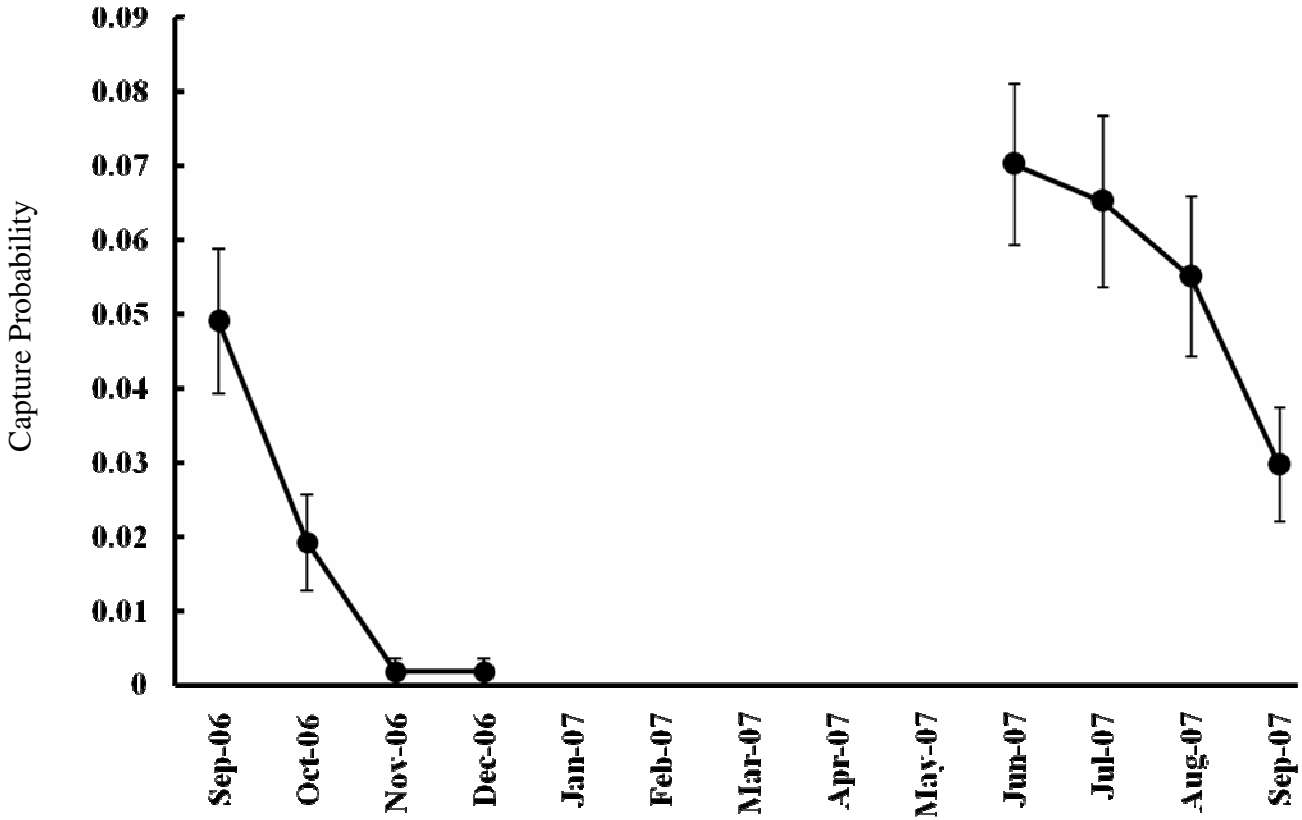

Figure 3.6. Robust design estimated daily conditional capture and recapture probabilities (±95% CI).

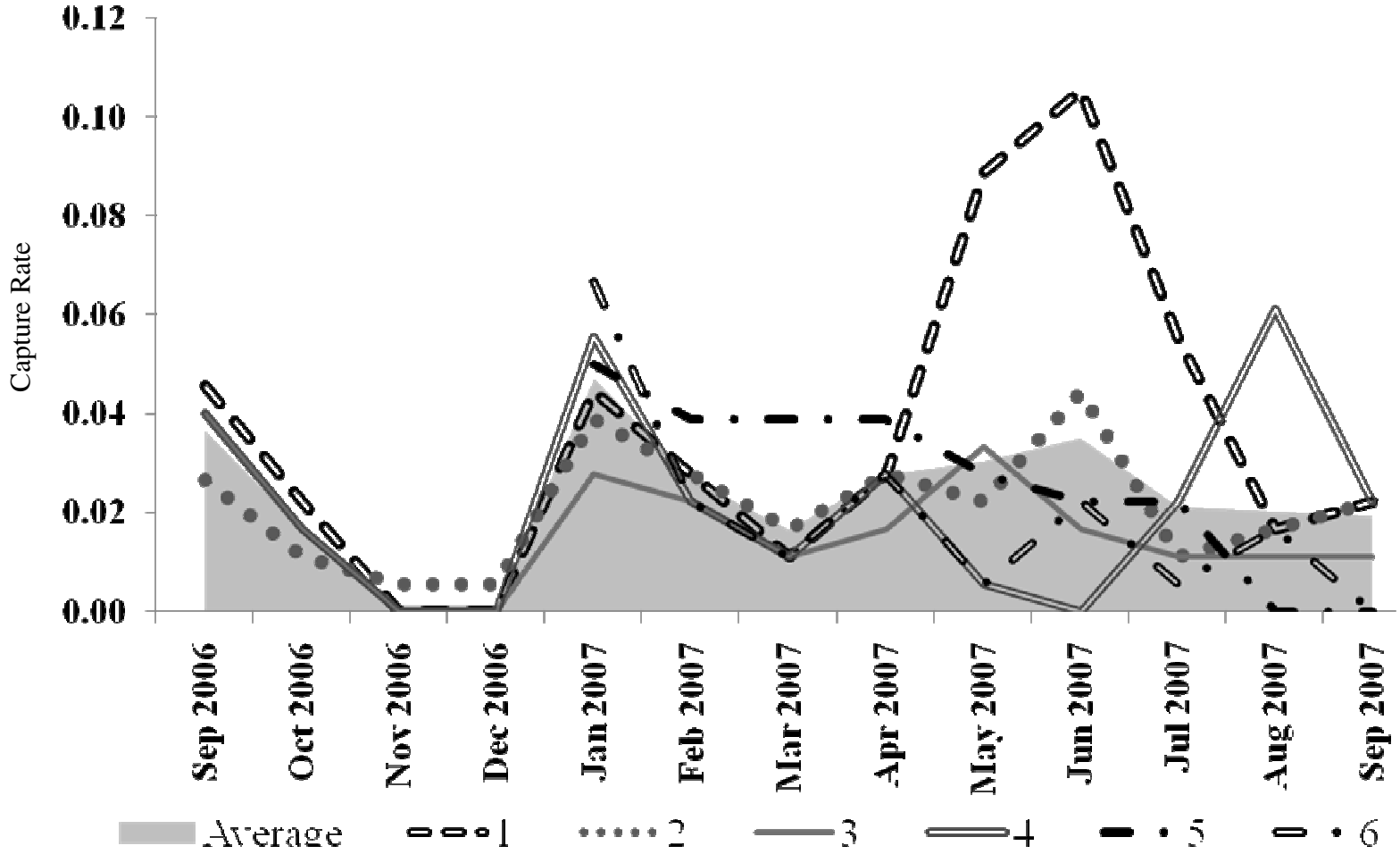

Figure 3.7. Monthly capture rates (total captures/total trap-nights) for each array. Fyke net and intra-month captures of individuals are not included.

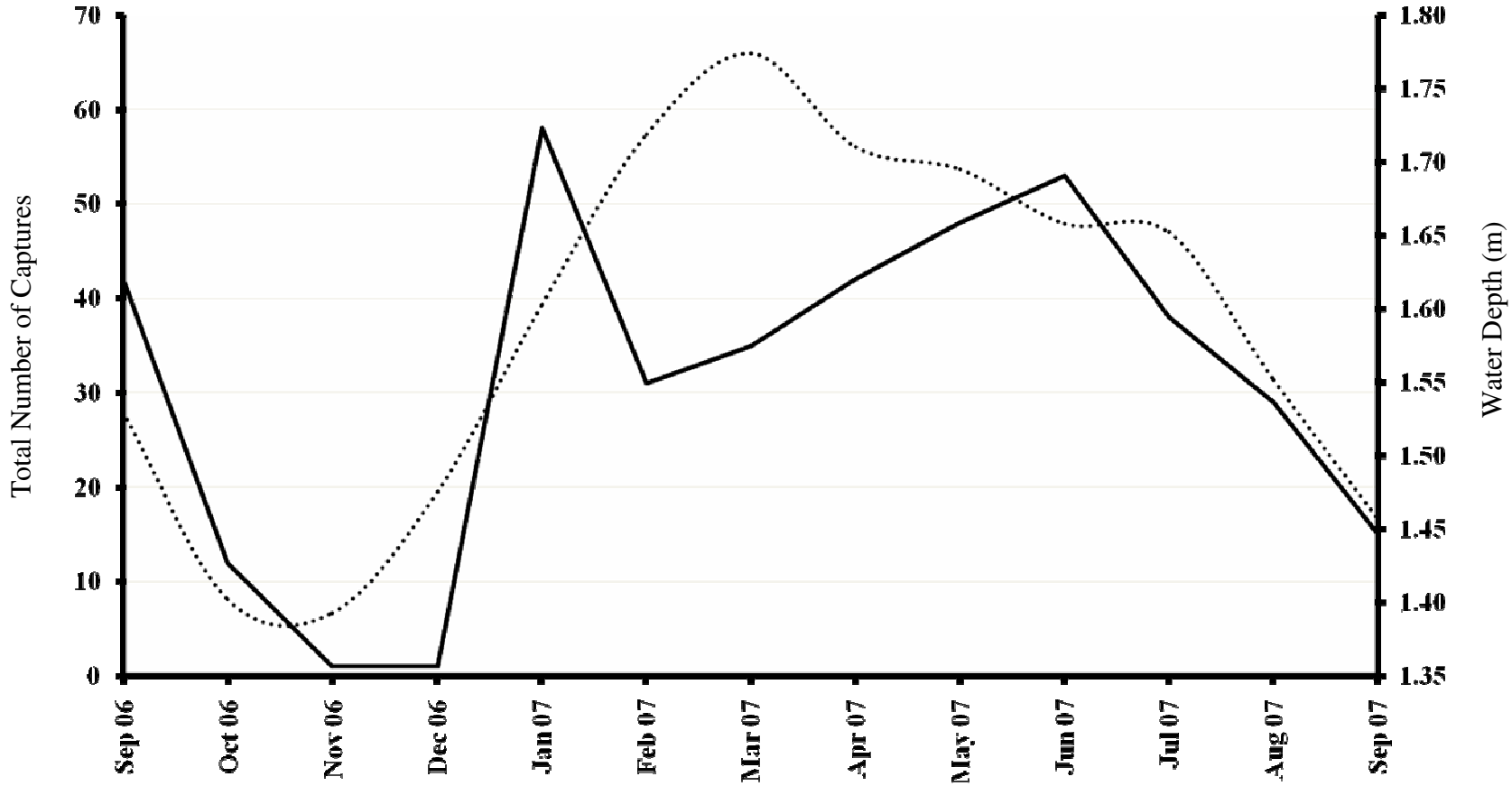

Figure 3.8. Monthly tally of all non-intramonth captures and average water depth (in meters) during sampling period (dotted line on secondary axis).

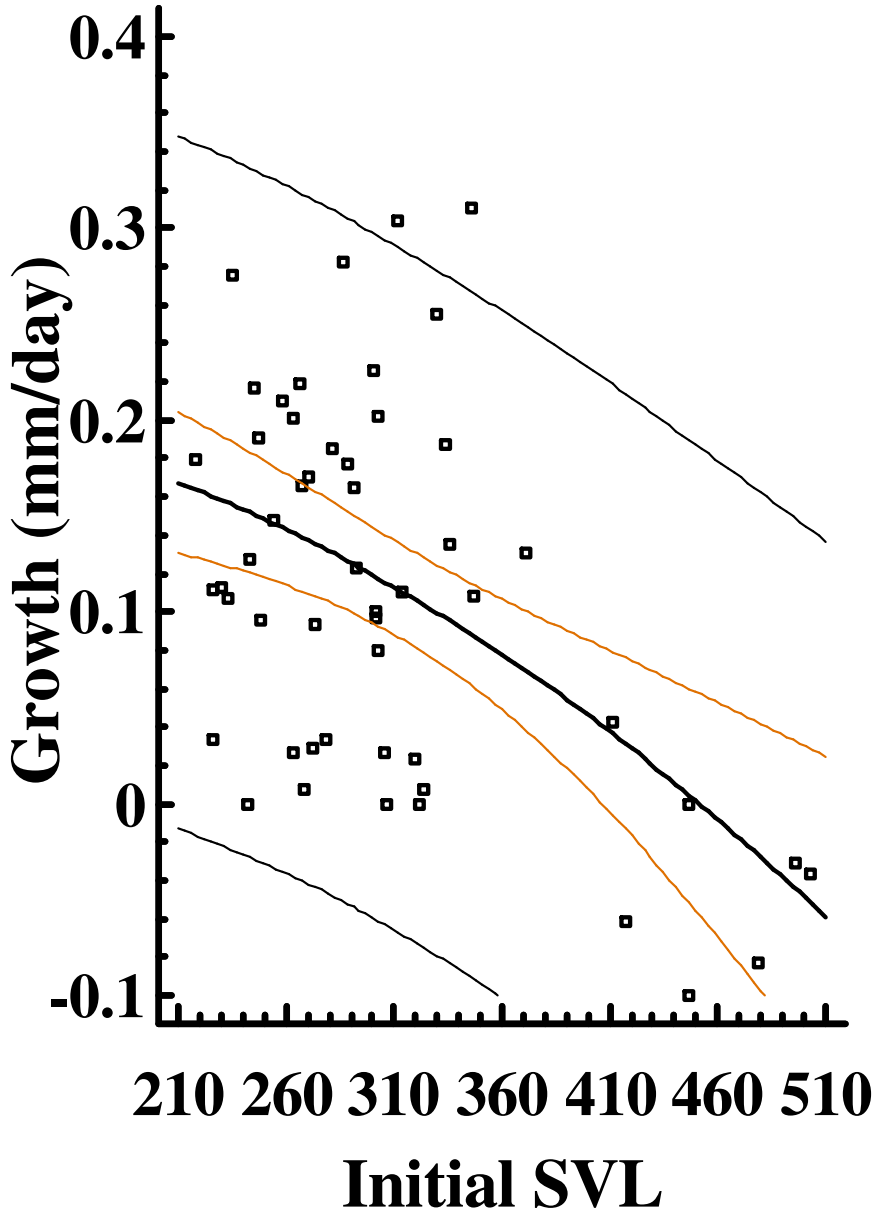

Figure 3.9. Growth rate (mm/day) between first and last captures (minimum of 50 days between captures) of 52 greater sirens as a function of size at initial capture. Middle line represents the line of best fit. The next innermost pair of lines define confidence limits. Outermost lines define prediction limits. Equation of line of best fit: Growth Rate (mm/day) = $0.214 - 1.047\ E^{-6} * \text{Initial SVL}^2$

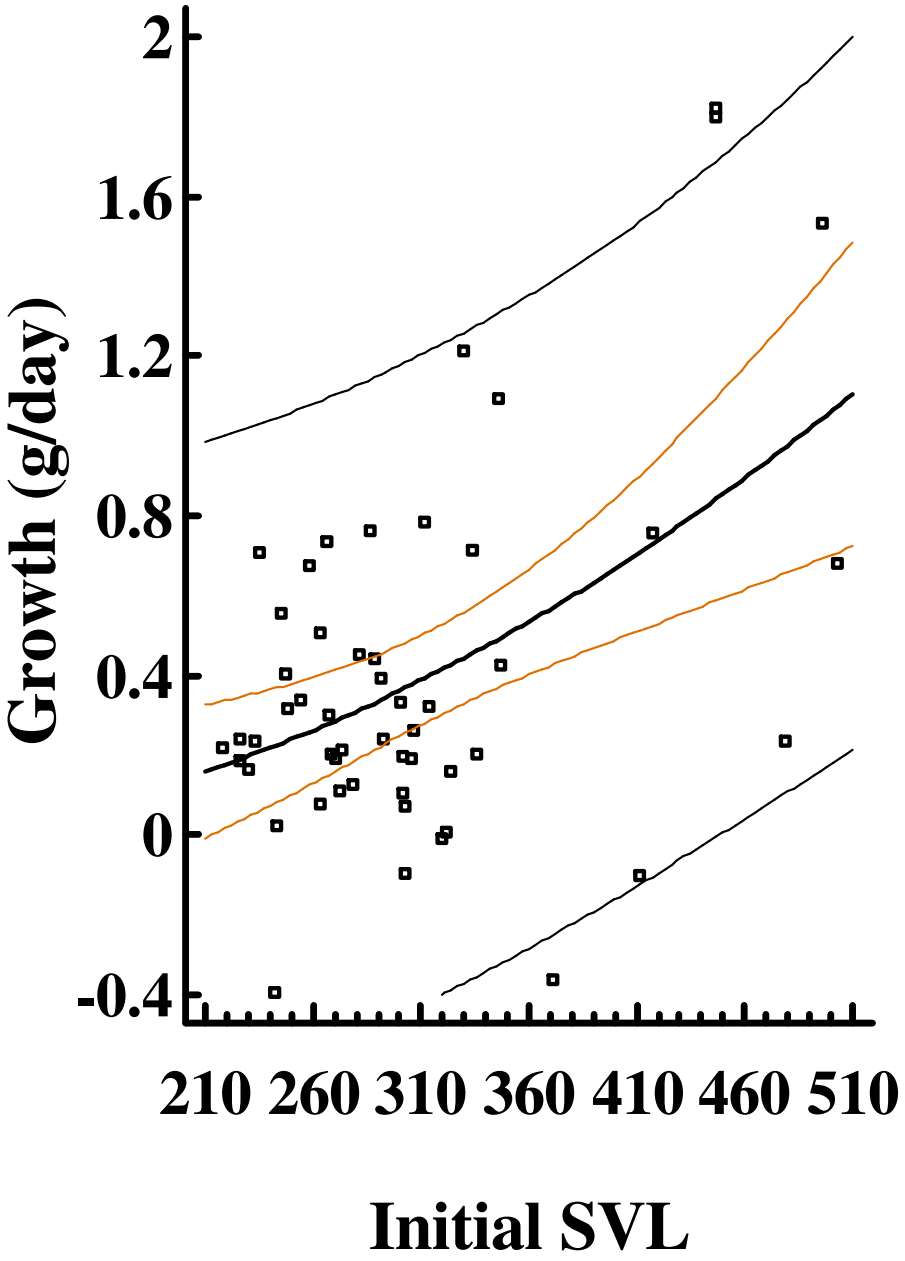

Figure 3.10. Growth rate (g/day) between first and last captures (minimum of 50 days between captures) of 52 greater sirens as a function of size at initial capture. Middle line represents the line of best fit. The next innermost pair of lines define confidence limits. Outermost lines define prediction limits. Equation of line of best fit: Growth Rate (g/day) = $-0.0329 + 4.375\ E^{-6} * \text{Initial SVL}^2$

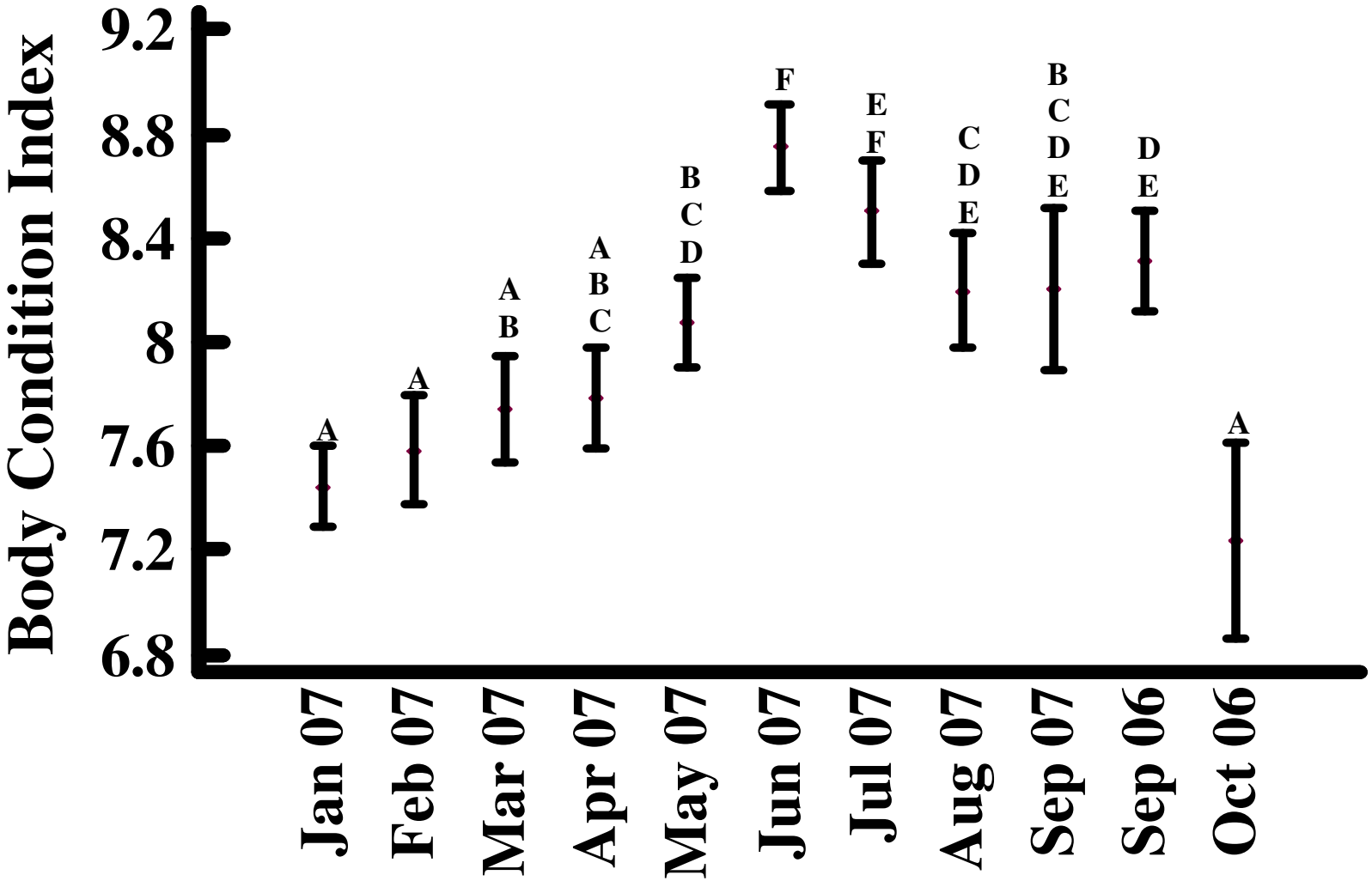

Figure 3.11. Means with 95.0% LSD intervals for monthly body condition index (BCI). Letters denote homogenous groups (i.e., months that do not share at least one letter are significantly different from each other).

Table 3.1. Estimated average growth rates of *Siren lacertina*. Asterisks denote estimates that were extrapolated from data provided from the author but not explicitly stated. SVL = Snout-Vent Length.

Sample (Method)	Location	Life Stage	Growth (Mass) g/day	Growth (Mass) g/year	Growth (SVL) mm/day	Growth (SVL) mm/year	Source
N=11 (Recaptures)	North FL	Adult	0.13 (0.0-0.66)	*47.5 (0.0-240.9)	0.91 (0.0-7.0)	*332.15 (0-2555)	Sorensen 2004
N=470 (Size Class)	West SC	Hatchling	n/a	n/a	0.48	87	This Study
		Year 2 Juvenile	n/a	n/a	0.35	100	
N=45 (Recaptures)		200-400mm SVL	n/a	n/a	0.133	48.5	
N=7 (Recaptures)		+400mm SVL	n/a	n/a	~0	~0	

Table 3.2. Estimated average growth rates of *Siren intermedia*. Asterisks denote estimates that were extrapolated from data provided from the author but not explicitly stated. TL=Total Length. SVL = Snout-Vent Length.

Sample (Method)	Location	Life Stage	Growth (Mass) g/day	Growth (Mass) g/year	Growth (TL) mm/day	Growth (TL) mm/year	Growth (SVL) mm/day	Growth (SVL) mm/year	Source
N=176 (Size Class)	East TX	Hatchlings	*0.24-0.36% of total	*25.4	n/a	n/a	n/a	n/a	Gehlbach and Kennedy 1978
		Year 2+	0.12% of total	*26.0-36.6	n/a	n/a	n/a	n/a	
N=116 (Size Class)	East TX	Hatchlings	n/a	n/a	n/a	n/a	*0.27 (female) *0.36 (male)	100 (female) 130 (male)	Davis and Knapp 1953
		2nd Year	n/a	n/a	n/a	n/a	*0.21 (female) *0.25 (male)	75 (female) 90 (male)	
N=50 (Recaptures)	Southwest MO	Juveniles and Adults	n/a	n/a	0.06	*21.9	n/a	n/a	Frese et al. 2003

Table 3.3. Estimated average population densities and biomass concentrations for *Siren lacertina*. Asterisks denote values that were extrapolated or estimated from data provided but not explicitly stated. SVL = Snout Vent Length.

Location	Model	Population Size (95% CI)	Wetland Size (Sample Area)	Animals/m^2 (95% CI)	Size Range (Mean Mass)	g/m^2 (95% CI)	Source
North FL	Jolly-Seber	639 (299-1377)	34ha (500 m^2)	1.3 (0.60-2.8)	>20g *(179.2g)	233 *(107.5-501.8)	Sorensen (2004)
West SC	Robust Design	248.4 (202.2-318.5)	50,000 m^2 (all)	0.005 (0.004-0.006)	>218mm SVL (297.8g)	1.5 (1.2-1.8)	This Study

Table 3.4. Estimated average population densities and biomass concentrations for *Siren intermedia*. Asterisks denote values that were extrapolated or estimated from data provided but not explicitly stated. For size range, total length or mass is given.

Location	Model	Population Size (95% CI)	Wetland Size (Sample Area)	Animals/m^2 (95% CI)	Size Range (Mean Mass)	g/m^2	Source
East TX	Total	209	9712 m^2	*0.02	129-465mm *(used 42g)	*0.84	Davis and Knapp 1953
East TX	Schnable	337 (273-401)	1082 m^2 (300 m^2)	1.1 (0.9-1.3)	> 2g (42g)	46.2	Gehlbach and Kennedy 1978
Southwest MO	Schnable	5,969 (3,880-8058)	11ha (2,750 m^2)	2.17 (1.14-2.93)	*100-460mm (33.26g)	72.2g/m^2	Frese et al., 2003
	Jolly-Seber	3,702 (1,202-8,606)		1.35 (-0.43-3.13)	*100-460mm (33.26g)	44.9g/m^2	
	Adjusted Peterson	3,793 (2,788-4798)		1.37 (1.01-1.74)	*100-460mm (33.26g)	45.6g/m^2	
Central AR	Total	~1200	Unknown (900 m^2)	1.3	Unknown	*43.2g/m^2	Sugg et al., 1988

Table 3.5. Analysis of variance (ANOVA) table for growth rate in mm/day versus initial snout-vent length (SVL).

Source	Sum of Squares	Df	Mean Square	F-Ratio	P-Value
Model	0.140	1	0.140	18.02	0.0001
Residual	0.387	50	0.00775		
Total (Corr.)	0.527	51			

Table 3.6. Analysis of variance (ANOVA) table for growth rate in g/day versus initial snout-vent length (SVL).

Source	Sum of Squares	Df	Mean Square	F-Ratio	P-Value
Model	2.438	1	2.438	15.11	0.0003
Residual	8.067	50	0.161		
Total (Corr.)	10.505	51			

Table 3.7. Analysis of Variance (ANOVA) table comparing monthly body condition index (BCI) values.

Source	*Sum of Squares*	*Df*	*Mean Square*	*F-Ratio*	*P-Value*
Between groups	77.147	10	7.715	10.39	< 0.0001
Within groups	285.002	384	0.742		
Total (Corr.)	362.149	394			

Table 3.8. Monthly mean body condition indices with homogenous groups.

	Count	Mean	Homogeneous Groups
January 2007	58	7.45	A
February 2007	32	7.58	A
March 2007	35	7.75	AB
April 2007	39	7.79	ABC
May 2007	48	8.08	BCD
June 2007	52	8.75	F
July 2007	37	8.50	EF
August 2007	29	8.20	CDE
September 2007	15	8.20	BCDE
September 2006	40	8.31	DE
October 2006	10	7.24	A

Table 3.9. Estimated size classes based on captures during 2006-2007, growth rates of recaptured animals and available literature. *Goin 1947.

Year	Initial Size (mm SVL)	Initial Month	Final Size (mm SVL)	Final Month	Approximate Growth Rate
1	13*	April	100	October	0.48mm/day
2	100	January	200	October	0.35mm/day
3	200	January	250	October	0.133mm/day
4	250	January	300	October	0.133mm/day
5	300	January	350	October	0.133mm/day
6	350	January	400	October	0.133mm/day
7+	400	January	400+		0.0mm/day

CHAPTER 4

CONCLUSIONS

In this study, I established population parameters for greater sirens, *Siren lacertina*, and quantified the utility of two new marking techniques. Prior to these investigations, population parameters based on mark-recapture studies for greater sirens outside of Florida did not exist. I found that population densities of *S. lacertina* in Dry Bay were much lower than previously reported for other locations and for closely related species, such as *S. intermedia*. Further investigations into population densities across wetland types and regions will provide more insight into the processes that determine population densities of permanently aquatic salamanders throughout their ranges.

Toe-clipping was an effective short-term mark that is generally readable for a field season. Tail-scooping, while not as long-lasting, was an effective short duration mark that healed quickly and had no discernable long-term effect. Tail-scooping would be an ideal mark for any short-duration study that needs to distinguish between new and recaptured animals. Both temporary marks complement studies that require tissue samples.

Population ecology of greater siren is relatively unknown. After thirteen months of sampling for 130 total nights of sampling and 12,650 trap-nights, we totaled 470 captures of *S. lacertina*. We marked 271 animals and recaptured 83 a total of 174 times. The resulting multiple recaptures of the same animals over several months enabled us to accurately describe several parameters that were previously unavailable or available only from rough estimates. The size classes presented in chapter 3 are the first for any species of *Siren* that are based on size classes and size-specific growth rates. The size at which *Siren* attenuate their growth in length had also not been available.

Presently, the sex-specific ecology and behavior of greater sirens are unknown. Future research aimed towards determining the sex of *S. lacertina* in the field or by any non-lethal

means would greatly enhance the expediency at which their natural history and population ecology can be revealed. The evaluation of an aging technique, such as skeletochronology, for sirens would be a boon to our understanding of their longevity in the wild.

Molecular investigations into phylogeography and phylogenetics would undoubtedly lead to fascinating discoveries about *Siren* evolution into different clades and their current distributions. Population genetics may also show how much gene flow occurs between *Siren* populations inhabiting isolated wetlands, as well as determine real versus perceived dispersal barriers. Many questions remain to be addressed in greater siren population ecology and most geographic regions are lacking much information about their location-specific natural history. Future investigations of populations in Maryland, North Carolina, South Carolina, and Georgia would aid in filling in what are currently large gaps in our understanding of greater siren biology.