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Effect of Season on Analysis of Growth in a Population of the Western Lesser Siren, *Siren intermedia nettingi*, in Northwestern Louisiana

Larry R. Raymond¹ and Laurence M. Hardy²

We analyzed growth in a population of *Siren intermedia nettingi*, Western Lesser Siren, from northwestern Louisiana using a mark–recapture technique employing PIT tags from January 1992 through March 1998. Traps were monitored for eight consecutive trap nights for all four seasons from 1992 to 1996, January and December winter trapping sessions in 1997, and late February through early March in 1998. A total of 1,004 siren captures included 575 original captures and 429 recaptures. A total of 223 sirens were recaptured at least once for a recapture rate of 38.7%. Thirty-five of the original sirens captured were recaptured in the same season and year and were not used in the analyses. Therefore, we had a usable recapture rate of 32.7%. Based on captures, bites by conspecifics, and presence of juveniles in the study pond, we concluded that sirens in this population were most active in autumn and winter and presumably had a winter breeding season. Males grew faster and reached larger sizes than females due to the large energy investment of females that produced ova and the importance of male agonistic behavior toward other male and female conspecifics. The greatest growth occurred in the spring, despite increased activity in autumn and winter. Sirens were least active in the summer. Growth was inversely proportional to size and smaller sirens grew at a faster rate than larger ones.

SIREN *intermedia nettingi*, the Western Lesser Siren, is an aquatic salamander belonging to the Sirenidae and is distributed statewide in freshwater to slightly brackish habitats in Louisiana (Dundee and Rossman, 1989; Boundy and Carr, 2017). Studies in other states analyzed growth in this species (Gehlbach and Kennedy, 1978; Frese et al., 2003; Hampton, 2009; Sawyer and Trauth, 2011) and some (Frese et al., 2003) were based on mark–recapture protocols of less than one year. Hampton (2009) and Sawyer and Trauth (2011) studied their populations for 28 months each. Other studies commented on growth and age at sexual maturity based on size classes (Davis and Knapp, 1953; Bennett and Taylor, 1968; Gehlbach and Kennedy, 1978; Trauth et al., 1990). Growth rates varied among populations and localities and there is still a paucity of data on many aspects of siren ecology (Frese et al., 2003; Sorenson, 2004; Graham et al., 2018).

We monitored growth of sirens over multiple years to determine when most growth occurred. We tested three hypotheses: 1) Males grow faster and larger than females. Several authors documented that males were larger than females (Smith, 1961; Martof, 1973; Sugg et al., 1988) and grew faster (Davis and Knapp, 1953; Gehlbach and Kennedy, 1978; Frese et al., 2003), although Hampton (2009) found no significant difference in growth between sexes. 2) Sirens grow more in the autumn and winter. Raymond (1991) documented that activity was greatest in the autumn and winter, suggesting that this was when sirens were most active. 3) Small sirens grow faster than larger ones. Davis and Knapp (1953), Gehlbach and Kennedy (1978), and Frese et al. (2003) suggested that smaller, presumably younger, sirens grew at a faster rate than larger ones. However, Sawyer and Trauth (2011) found no significant difference between the growth rates of small and large sirens.

MATERIALS AND METHODS

Study site and sampling design.—The study area encompassed a temporary pond in the southwestern corner of Walter B. Jacobs Memorial Nature Park in Caddo Parish, Louisiana (Hardy and Raymond, 1980; Raymond and Hardy, 1990). Sirens used in these analyses were captured in non-baited Gee’s minnow traps (6 mm mesh) during each season, beginning in January (1992) and ending in March (1998). Eight consecutive trap nights were conducted during each season in January (winter), April (spring), July (summer), and October (autumn) for the five years (1992–1996) used in many of the analyses. In 1993, the spring session began on March 30 and extended through April 7. After 1996, traps were monitored for eight consecutive nights in January and December of 1997, and 25 February through 5 March of 1998. Data from the captures in 1997 and 1998 were used in some of the analyses.

On 6 January 1992, we set a grid of numbered stakes in the pond. Thirty minnow traps were set at fixed positions in the pond at the numbered stakes during each trapping cycle. Most of the time in winter, and always in other seasons, the traps were placed in water shallow enough that trapped animals could gulp air (Brodman, 2008; Hampton, 2009). With few exceptions, the traps were checked daily during the trapping sessions. Captured sirens were anesthetized in a solution of Kodak’s Practical Quinaldine (5.3×10^{-5} mL/gallon) and then processed to determine sex, mass, SVL (measured from the tip of the snout to the posterior end of the cloaca), and total length. Measurements were taken to the nearest mm and mass was measured to the nearest 0.1 g. Sex was determined whether the siren was large enough to display external dimorphic characters (Martof, 1973; Gehlbach and Kennedy, 1978) or obvious female abdomen distension due to eggs during the breeding season (Frese et al., 2003). Sirens that died during the study were dissected to

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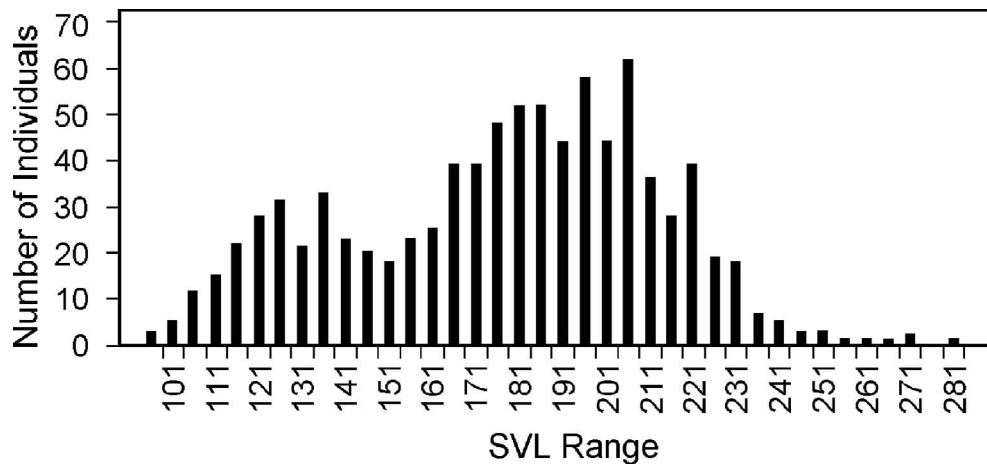


Fig. 1. First season capture SVL (mm) frequency ($n = 881$) for all individuals of *Siren intermedia* over the seven years of the study (1992–1998).

determine sex, preserved, and deposited in the collection of Louisiana State University in Shreveport (LSUS). In some cases, a siren too small to be sexed at the original capture was sexed at a later capture. The number of bite marks was counted on all individuals that displayed obvious bites. All sirens were marked with PIT tags injected into the abdominal cavity. Recaptures were confirmed with a Trovan LID500G Conventional RFID Reader. Captured animals were massed, measured, allowed to recover from anesthesia, and returned to the capture location with little disturbance. Six sirens captured on 13 October 1993 were kept in captivity while waiting for new PIT tags. They were tagged on 26 October 1993 and released the next day.

The LSUS Office of Sponsored Research and Technology Transfer approved this project which was conducted from 1 January 1992 to 31 March 1998.

Statistical analyses.—Biting was analyzed using the Kruskal Wallis Test in ProStat (version 3, Poly Software International, Pearl River, NY, USA) to determine whether there was a difference in the number of bites inflicted among the seasons. A non-parametric test was used due to the large differences observed in bites by season and the small number of individuals and bites per individual recorded during the summer. All other statistical analyses were performed using Vassarstats (Lowry, 2011), unless noted otherwise. The number of bites during the presumed winter reproductive season was compared between males and females using a t-test for independent samples. A basic correlation analysis was used to compare the number of bite marks with SVL.

The SVL data were used to determine size classes for known males and females separately using probability analyses as described by Harding (1949) and modified by Cassie (1954). The first capture of an individual for a given year was used for each of the years analyzed. These size classes were then compared to other studies that identified size classes.

Two-tailed t-tests were used to compare the means of mass, SVL, and total length between male and female captures for all years 1992–1998 combined. In all comparisons, the sample sizes were large enough that violation of the normality assumption should not have affected the tests of differences among group means (Snedecor and Cochran, 1989). We used the first capture measurement for each season if a siren was represented more than one time in the sample season of a year.

For each individual, daily growth in both mass and SVL was determined by subtracting the first measurements of mass and SVL for a season from the corresponding measurements in the first capture of the next season captured and dividing by the number of days between captures. Therefore, we compared growth in mass as g/day and SVL as mm/day among the groups tested. For some analyses, total growth in mm (SVL) based on the last capture of a recaptured individual (even if it was caught multiple times and displayed a higher SVL previously) was compared to the beginning SVL.

A one-way ANOVA was used to analyze growth in mass (g/day) and SVL (mm/day) in males and females separately and together by year and by season. If a statistically significant difference was noted ($P < 0.05$), a Tukey HSD test was used to determine which years and or seasons were statistically different. A correlation analysis was performed using the first capture of each year for all sirens to describe the relationship between SVL and mass. Growth in mass and SVL was regressed against beginning SVL to analyze influence of size on growth in males, females, and males and females combined. A three-way ANOVA was run in R (R Core Team, 2017) to compare growth in body mass and SVL separately for all years and seasons combined for both sexes.

Institutional abbreviations follow Sabaj (2020).

RESULTS

A total of 1,004 sirens were captured from January 1992 through March 1998; 575 were original captures and 429 were recaptures. The 429 recaptures included 118 duplicate season and year recaptures. A total of 223 sirens were recaptured at least once for a recapture rate of 38.7%. Thirty-five of the original sirens captured were recaptured in the same season and year and were not used in the analyses. Therefore, we had a recapture rate of 32.7% that was used in the growth analyses. We used only the first recapture of a siren for each season in all analyses. The SVL frequency of all first captures for an individual over the seven years of the study ranged from 91–278 mm (Fig. 1).

Based on number of captures per trap day during each season (0.29, autumn; 0.192, winter; 0.117, spring; 0.028, summer), sirens were most active in autumn, followed by winter, then spring, and displayed the least activity in summer (Raymond, 1991).

Table 1. Comparison of size of male and female *Siren intermedia* collected from 1992–1998. For each sex, the mean is followed by \pm confidence interval, sample size, and the range of variation expressed as minimum–maximum. The dataset used consisted of the first capture of each individually tagged siren during each year of the study.

	Male			Female			t	P
	$\bar{x} \pm \text{CI}$	n	Min–max	$\bar{x} \pm \text{CI}$	n	Min–max		
SVL	200.7 \pm 3.8	224	119–278	180.2 \pm 3.0	254	96–231	–8.12	<0.0001
Total length	309.5 \pm 6.2	225	179–429	273.6 \pm 4.7	254	144–364	–9.1	<0.0001
Mass	60.6 \pm 3.5	226	10–188.6	38.8 \pm 1.8	255	5.1–90.9	–11.08	<0.0001

The number of bite marks was recorded for all sirens captured. A Kruskal Wallis Test was used to compare the number of bite marks for each season (76, autumn; 1,010, winter; 313, spring; 6, summer) for males and females separately, and for males, females, and unknown sex sirens together. In all comparisons, there was a significant difference in the number of bite marks among seasons, and the number of bite marks in winter was greater than any of the other seasons. A total of 49 males captured in winter possessed 471 bite marks and 79 winter-captured females had 465 bites. A two-tailed t-test showed a significant difference in the total number of bites per individual between males and females ($t_{126} = 3.35$, $P = 0.001$). A basic correlation analysis of the number of bite marks per individual with SVL showed a significant positive correlation between the two ($r^2 = 0.1107$, $t_{230} = 5.35$, $P < 0.0001$).

Probability analyses produced seven size classes for both males and females, although the size ranges of classes differed between males and females. Individuals that could not be sexed accurately were not included in the size-class analyses. A total of 243 individuals for which the sex could not be reliably determined were classified as juveniles, and those individuals were not recaptured at a larger size to determine sex. The mean SVL of these individuals was 134.5 mm and the mean mass was 16 g; they were probably yearlings.

The first capture of an individual in each trapping session, 1992–1998, was used to compare sexual dimorphism in size between males and females. Males were larger than females in SVL, total length, and mass (Table 1).

We collected a series (LSUS 9237) of 13 juvenile sirens by dip netting on 13 May 2005. The mean SVL of these individuals was 21.4 mm ($n = 13$) and the mean total length was 29.1 mm ($n = 10$).

Males showed a significant difference (between years 1993 and 1994; $F_4 = 5.47$, $P = 0.0005$) in growth in mass over the five years (1992–1996) analyzed. Males also showed a significant difference among the four seasons ($F_3 = 4.25$, $P = 0.0071$, Table 2). Significant differences occurred between winter and summer ($P < 0.01$), spring and summer ($P < 0.01$), and summer and autumn ($P < 0.05$). Male growth in SVL was significantly different among years ($F_4 = 11.23$, $P < 0.0001$). Differences occurred between 1992 and 1995 ($P < 0.05$), 1993 and 1994 ($P < 0.01$), 1994 and 1995 ($P < 0.01$), and 1994 and 1996 ($P < 0.01$). Male growth in SVL was also significantly different among seasons ($F_3 = 4.58$, $P = 0.0047$, Table 2). Differences occurred between winter and summer ($P < 0.01$) and summer and autumn ($P < 0.01$).

Females showed a significant difference ($F_4 = 3.98$, $P = 0.0043$) in growth in mass over the five years analyzed. The difference occurred between 1994 and 1995 ($P < 0.05$). Female growth in mass by season also showed a significant

Table 2. MMpd = *Siren intermedia* growth in mass, calculated as increase in g per day, of males over the four seasons. Significant differences in growth occurred between winter and summer, spring and summer, and summer and autumn. $F_3 = 4.25$; $P = 0.0071$. MSpd = Growth in SVL, calculated as increase in mm per day, of males over the four seasons. Significant differences in growth occurred between winter and summer and summer and autumn. $F_3 = 4.58$; $P = 0.0047$. FMpd = Growth in mass, calculated as increase in grams per day, of females over the four seasons. Significant differences in growth occurred between winter and spring, winter and summer, winter and autumn, spring and summer, and summer and autumn. $F_3 = 20.98$; $P < 0.0001$. FSpd = Growth in SVL, calculated as increase in mm per day, of females over the four seasons. Significant differences in growth occurred between winter and spring, winter and summer, winter and autumn, spring and summer, and summer and autumn. $F_3 = 17.4$; $P < 0.0001$. MFMpd = Growth in mass, calculated as increase in g per day, of males and females combined over the four seasons. Significant differences in growth occurred between winter and spring, winter and summer, spring and summer, and summer and autumn. $F_3 = 17.51$; $P < 0.0001$. MFSpd = Growth in SVL, calculated as increase in mm per day, of males and females combined over the four seasons. Significant differences in growth occurred between winter and spring, winter and summer, spring and summer, and summer and autumn. $F_3 = 17.55$; $P < 0.0001$.

	Season	Winter	Spring	Summer	Autumn
MMpd	$\bar{x} \pm \text{SD}$	0.079 \pm 0.047	0.075 \pm 0.093	0.171 \pm 0.138	0.103 \pm 0.066
	n	26	18	10	56
MSpd	$\bar{x} \pm \text{SD}$	0.090 \pm 0.075	0.138 \pm 0.109	0.199 \pm 0.150	0.104 \pm 0.068
	n	26	18	10	56
FMpd	$\bar{x} \pm \text{SD}$	–0.007 \pm 0.051	0.037 \pm 0.054	0.104 \pm 0.050	0.052 \pm 0.040
	n	46	21	6	75
FSpd	$\bar{x} \pm \text{SD}$	0.019 \pm 0.058	0.078 \pm 0.077	0.161 \pm 0.088	0.078 \pm 0.046
	n	45	21	6	75
MFMpd	$\bar{x} \pm \text{SD}$	0.024 \pm 0.064	0.055 \pm 0.076	0.146 \pm 0.115	0.074 \pm 0.059
	n	72	39	16	131
MFSpd	$\bar{x} \pm \text{SD}$	0.045 \pm 0.073	0.105 \pm 0.097	0.185 \pm 0.128	0.089 \pm 0.057
	n	71	39	16	131

Table 3. Interaction of year, season, and sex on *Siren intermedia* growth in mass, calculated as an increase in g per day, for sirens captured 1992–1996. Significance codes: *** = 0.001; ** = 0.01; * = 0.05.

	Degrees of freedom	Sum of squares	Mean square	F value	P (>F)
Year	4	0.1947	0.04867	15.400	3.88e-11***
Sex	1	0.2220	0.22197	70.230	5.94e-15***
Season	3	0.1778	0.05925	18.747	7.02e-11***
Year:Sex	4	0.0086	0.00215	0.680	0.6062
Year:Season	10	0.0350	0.00350	1.108	0.3574
Sex:Season	3	0.0211	0.00704	2.227	0.0859
Year:Sex:Season	9	0.0354	0.00393	1.244	0.2695
Residuals	223	0.7048	0.00316		

difference ($F_3 = 20.98$, $P < 0.0001$, Table 2). Differences occurred between winter and spring ($P < 0.05$), winter and summer ($P < 0.01$), winter and autumn ($P < 0.01$), spring and summer ($P < 0.01$), and summer and autumn ($P < 0.01$). Female growth in SVL was significantly different among years ($F_4 = 3.75$, $P = 0.0062$). The difference occurred between 1994 and 1995 ($P < 0.01$). Female growth in SVL was also significantly different among seasons ($F_3 = 17.4$, $P < 0.0001$, Table 2). Differences occurred between winter and spring ($P < 0.05$), winter and summer ($P < 0.01$), winter and autumn ($P < 0.05$), spring and summer ($P < 0.01$), and summer and autumn ($P < 0.01$).

Combining growth in mass for males and females showed a significant difference among years ($F_4 = 10.22$, $P < 0.0001$). Differences occurred between 1993 and 1994 ($P < 0.01$), 1994 and 1995 ($P < 0.01$), and 1994 and 1996 ($P < 0.05$). Growth in mass for males and females combined by season was also significantly different ($F_3 = 17.51$, $P < 0.0001$, Table 2). Differences occurred between winter and summer ($P < 0.01$), winter and autumn ($P < 0.01$), spring and summer ($P < 0.01$), and summer and autumn ($P < 0.01$). Growth in SVL for both males and females combined was significantly different among years ($F_4 = 15.4$, $P < 0.0001$). Differences occurred between 1992 and 1995 ($P < 0.01$), 1993 and 1994 ($P < 0.01$), 1994 and 1995 ($P < 0.01$), and 1994 and 1996 ($P < 0.01$). Growth in SVL for both males and females combined differed among seasons ($F_3 = 17.55$, $P < 0.0001$, Table 2). Differences occurred between winter and spring (P

< 0.01), winter and summer ($P < 0.01$), spring and summer ($P < 0.01$), and summer and autumn ($P < 0.01$).

Males grew significantly more than females in both mass and SVL. Males grew 0.096 ± 0.016 ($\bar{x} \pm 95\%$ confidence interval [CI], range: -0.061 – 0.411 , $n = 111$) g per day compared to females' growth of 0.030 ± 0.001 (range: -0.275 – 0.147 , $n = 156$; $t_{187} = -6.84$, $P < 0.0001$) g per day. Males also grew significantly more than females in SVL. Males grew 0.112 ± 0.018 (range: -0.043 – 0.448 , $n = 108$) mm per day compared to females' growth of 0.061 ± 0.011 (range: -0.083 – 0.256 , $n = 155$; $t_{183} = -4.95$, $P < 0.0001$) mm per day. Both males and females showed a negative correlation between growth in mass (g/day) and SVL (mm/day) plotted against beginning SVL when analyzed separately and together.

Our data appeared to show that sirens grew the least in winter when they were most active. Therefore, we analyzed growth in SVL and mass for males and females that were captured in the winter of a year and recaptured in the following spring. Eleven males, excluding three juveniles (SVL < 180 mm, Martof, 1973), met this criterion and showed a mean growth in SVL of 0.036 mm per day and in mass of 0.079 g per day. Fourteen females also met this criterion and showed a mean SVL loss of -0.021 mm per day and a mean mass loss of -0.50 g per day. Compared to beginning SVL, growth in SVL showed a stronger relationship (males, $r^2 = 0.4141$, $t_{109} = -8.78$, $P < 0.0001$; females, $r^2 = 0.399$, $t_{154} = -10.11$, $P < 0.0001$; males and females, $r^2 = 0.3045$, $t_{265} = -10.77$, $P < 0.0001$) than growth in mass (males, $r^2 = 0.1224$, $t_{109} = -3.9$, $P = 0.0002$; females, $r^2 = 0.1573$, $t_{154} = -5.36$, $P < 0.0001$; males and females, $r^2 = 0.0796$, $t_{265} = -4.79$, $P < 0.0001$). An analysis of growth in total SVL compared to beginning SVL showed a strong correlation in both males and females (males, $r^2 = 0.6773$, $t_{72} = -12.29$, $P < 0.0001$; females, $r^2 = 0.6783$, $t_{79} = -12.91$, $P < 0.0001$).

An analysis of the correlation between SVL and mass for the first capture of each siren in each year showed a significant positive relationship ($r^2 = 0.875$, $t_{771} = 73.32$, $P < 0.0001$).

The effects of year, season, and sex on growth in mass and SVL were analyzed together in a three-way ANOVA to test for interactions among the three factors. Significant differences in growth in mass occurred among years, between the sexes, and among the seasons. No significant interactions occurred between year and sex, year and season, sex and season, or year, sex, and season (Table 3, Fig. 2). Similarly, growth in SVL showed significant differences in growth among years, between the sexes, and among seasons, but the only

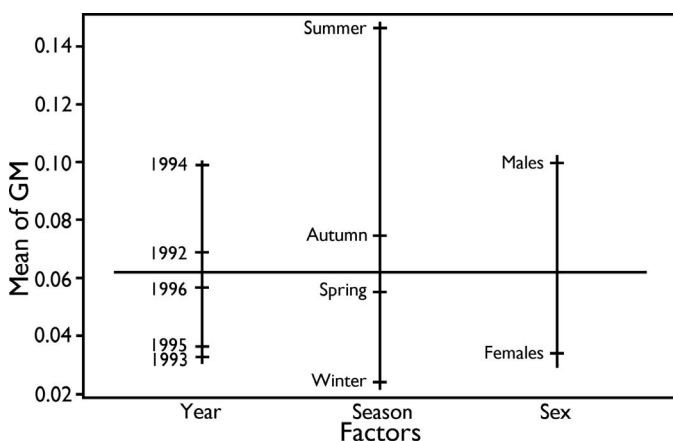
**Fig. 2.** Graph of interaction among years, seasons, and sex on growth in mass of *Siren intermedia* as calculated by increase in g per day. See Table 3 for statistics.

Table 4. Interaction of year, season, and sex on *Siren intermedia* growth in SVL, calculated as an increase in mm per day, for sirens captured 1992–1996. Significance codes: *** = 0.001; ** = 0.01; * = 0.05.

	Degrees of freedom	Sum of squares	Mean square	F value	P (>F)
Year	4	0.3361	0.08402	20.653	1.71e-14***
Sex	1	0.1090	0.10904	26.803	5.02e-07***
Season	3	0.1850	0.06167	15.159	5.18e-09***
Year:Sex	4	0.0381	0.00952	2.339	0.05615
Year:Season	10	0.0387	0.00387	0.952	0.48617
Sex:Season	3	0.0496	0.01654	4.066	0.00773**
Year:Sex:Season	9	0.0356	0.00395	0.971	0.46490
Residuals	223	0.9072	0.00407		

significant interaction occurred between sex and season (Table 4, Fig. 3).

DISCUSSION

Seasonal activity.—These results confirmed the earlier findings of Raymond (1991) that sirens were more active in autumn and winter based on captures. The increased activity during these seasons is presumably related to courtship and winter reproduction in this population. Reinhard et al. (2013) reported courtship and egg laying in winter under captive conditions for this species.

Another indicator of reproductive activity was the presence of bite marks on individual sirens. Godley (1983) reported bite marks on female *S. intermedia* in Florida and suggested that the bites were inflicted by courting adult males and that biting was a vigorous and important component of courtship. Raymond (1991) observed bite marks on both males and females in December, January, and March. Fauth and Resetarits (1999) analyzed biting in this species in natural populations and experimental enclosures. They concluded that biting was a male-biased agonistic behavior observed in male–female and male–male encounters. They further concluded that although bites were more prevalent in the breeding season, they also occurred in the nonbreeding season. Hampton (2009) showed that the number of captured individuals with bites was significantly correlated with the number of gravid females, implying a relationship

to reproductive behavior. He showed the greatest number of bite marks on males and females in winter and early spring. Reinhard et al. (2013) documented defense of nest sites through biting by males under captive conditions. They also documented males biting females on the flanks during courtship. Our study showed a significant positive correlation between the number of bite marks and SVL.

The smallest individual with bite marks recorded by Fauth and Resetarits (1999) was 128 mm SVL. The smallest individual with bite marks in our population was 116 mm SVL. We recorded one bite mark on sirens that measured 116, 122, 123, 125, 127, 130, 131, 134, and 141 mm SVL. A siren that measured 132 mm SVL had two bite marks and one that measured 146 mm had three bite marks. We concluded that the smaller, presumed sexually immature, individuals with bite marks were bitten by territorial males and not involved in courtship activities.

Most of the sirens with bite marks were captured in the winter season. Also, the number of bite marks was greater in the winter and greater in males than females. Although bite marks were observed in the other seasons, they were much reduced, especially in the summer. A careful examination of the recapture data on several individuals confirmed that most of the biting occurred in winter. For example, male #15B42F was captured on 13 January 1994 and had eight bite marks. This individual was captured two days later and possessed 14 bite marks. Male #4F0193 was captured on 11 January 1995 and had 20 bite marks. This individual was recaptured two days later and possessed 30 bite marks. Female #1C3A37 was captured on 13 January 1994 and had three bite marks. She was recaptured three days later and possessed ten bite marks.

It appeared that the bite marks inflicted in winter persisted into the spring. For example, male #15B9E9 was captured on 12 January 1995 and had 20 bite marks. This individual was captured again on 18 April 1995 and possessed 30 bite marks. Male #4D0176 was captured on 14 January 1996 and had ten bite marks. This individual was recaptured on 15 April 1996 and possessed ten bite marks, presumably the same ones inflicted in the winter season. Male #4D08BF was captured on 11 January 1995 and had 15 bite marks. This individual was recaptured on 20 April 1995 and possessed 17 bite marks. These observations confirmed previous studies that concluded that males engaged in biting other males to establish territories and bit females as a component of courtship, primarily during the winter season (Godley, 1983; Fauth and Resetarits, 1999; Reinhard et al., 2013).

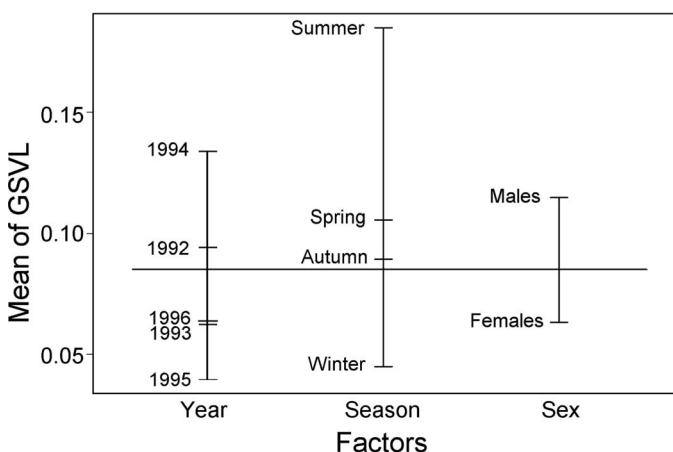


Fig. 3. Graph of interaction among years, seasons, and sex on growth in SVL of *Siren intermedia* as calculated by increase in mm per day. See Table 4 for statistics.

Size classes.—Male sirens were significantly larger than females in SVL, total length, and mass (Table 1). Males also grew significantly more in mass and SVL than females. Due to this size and growth difference between the sexes, we analyzed size classes separately for males and females.

Bennett and Taylor (1968) collected and preserved 25 sirens from a lake in Oklahoma. They identified four size classes based on SVL (70–120 mm, \bar{x} = 86 mm; 125–152 mm, \bar{x} = 137 mm; 183–204 mm, \bar{x} = 193 mm; and 239–286 mm, \bar{x} = 261 mm). Gehlbach and Kennedy (1978) also identified four size classes as determined by probability analysis based on weight (1–20 g, hatchlings; 20–50 g, yearlings; 50–70 g, 2- to 3-year-olds; and 70–160 g, > 3 years old). Brodman (2008) divided a northern population of *S. i. nettingi* into three size classes based on total length: juveniles (13–18 cm); intermediate-sized (19–22 cm, less than 6% of population), and adults (23–43 cm). Davis and Knapp (1953) and Trauth et al. (1990) indicated that female sirens reached sexual maturity and reproduced during their second year. All female sirens measuring 150 mm or less in SVL were sexually immature in the Oklahoma population (Davis and Knapp, 1953) and considered immature in an eastern Texas population (Hampton, 2009), where the smallest, visibly gravid, female measured 151 mm SVL. The smallest female siren that possessed yolked ovarian follicles was 165 mm in the Texas population studied by Gehlbach and Kennedy (1978).

The smallest gravid female we identified measured 149 mm in SVL, consistent with the size at sexual maturity reported in other populations. Males are considered sexually mature at SVL of 180 mm (Martof, 1973). Presumed yearlings in our population had a mean SVL of 134.5 mm and a mean weight of 16.0 g (n = 243). Our first two size classes probably represented older yearlings that were sexually immature with size class three representing sexually mature two-year-olds (Martof, 1973). Size class three males averaged 179.4 ± 3.8 mm SVL ($\bar{x} \pm SD$, range 173–185, n = 18) and females averaged 144.8 ± 3.5 mm (range 139–149, n = 8). Size class five represented the largest sample size for both sexes (males, 211.0 ± 7.2 mm, range 201–225, n = 91; females, 176.3 ± 5.4 mm, range 166–185, n = 92). The largest male size class was 266.2 ± 7.6 mm (range 256–278, n = 6) and the largest female size class was 219.5 ± 5.4 mm (range 211–231, n = 20).

Males grew faster and reached larger sizes than females, and their size classes would not be expected to be the same as females. Our seven size classes did not represent actual age classes, but probably represented differences in seasonal growth of sirens as shown in the results. For example, our siren female (#145EF1) was first captured on 8 April 1994 (127 mm SVL). This put her in our second female size class, but still too small to be sexually mature (< 2 years old). She was recaptured on 10 October 1995 (188 mm SVL), 550 days later, putting her into our female size class 6. She was subsequently recaptured on 21 October 1996 (196 mm SVL), 377 days later; 13 January 1997 (204 mm SVL), 84 days later; 3 December 1997 (217 mm SVL), 324 days later; and 5 March 1998 (214 mm SVL), 92 days later. Based on these captures, this female was at least five years old at her last capture. She showed growth of 0.111 mm/day, 0.021 mm/day, 0.095 mm/day, 0.04 mm/day, and –0.033 mm/day. The decrease in size from the December 1997 capture to the March 1998 capture may be related to the winter breeding season in this population. Although the decrease in SVL could be attributed to measurement error, it is plausible that the decrease was

due to the energetic stress involved in laying a large clutch of eggs (Bendik and Gluesenkamp, 2013).

Male siren (#DEDA0) was first captured on 16 July 1994 (143 mm SVL) putting him in size class one. He was recaptured on 11 October 1994 (155 mm SVL), 87 days later, placing him in size class two. Subsequent recaptures occurred on 13 October 1995 (188 mm SVL), 367 days later; 12 January 1996 (199 mm SVL), 91 days later; and 15 April 1996 (202 mm SVL), 94 days later. This male was at least three years old and showed growth of 0.138 mm/day, 0.09 mm/day, 0.121 mm/day, and 0.032 mm/day. Another male (#1C453F) was first captured on 11 October 1992 (186 mm SVL). This puts him in our size class four, and he was probably at least two years old. He was recaptured on 5 April 1993 (212 mm SVL, a growth of 0.148 mm/day), 7 October 1993 (242 mm SVL, a growth of 0.162 mm/day), and 9 October 1994 (270 mm SVL, a growth of 0.076 mm/day). This individual was at least four years old.

Growth.—Our study provided further support for other studies that documented that males are larger than females (our Table 1; Sugg et al., 1988) and that males grow faster than females (Davis and Knapp, 1953; Gehlbach and Kennedy, 1978; Frese et al., 2003). The largest male we processed (#215B7A) was trapped on 11 April 1992, and measured 278 mm SVL, 429 mm total length, and had a mass of 188.6 g. This individual was not recaptured. Our largest female (#159541) was trapped on 10 October 1995, and measured 231 mm SVL, 364 mm total length, and had a mass of 77.7 g. This female siren was not recaptured. A female with an even greater mass was trapped on 27 February 1998. She measured 225 mm SVL, 355 mm total length, and had a mass of 90.9 g, less than half the mass of our largest male.

Shine (1979) attributed larger size in amphibian males to the importance of male combat to reproductive success for some species. Since females were the same size or larger than males in most amphibian species, he determined that species with larger males were more likely to engage in physical combat. Reinhard et al. (2013) speculated that since males are involved in parental care, large size is an advantage in defense of territories and clutches against predators and might be advantageous in direct combat. This idea is supported by the population of sirens studied by Frese et al. (2003) and comments made by Godley (1983). As demonstrated by Fauth and Resetarits (1999), biting in sirens was an important component of male–male encounters. Our study confirmed the importance of male combat based on bite marks inflicted by conspecifics.

Hampton (2009) reported no significant difference in growth between males and females. He attributed the smaller body sizes and slower growth rates (0.022 mm/day in total length) of his study population to its relative isolation as an “island” population. This may have led to fewer available resources or reduced genetic variation. Our study pond was occasionally inundated by flood waters from a nearby creek and was occupied by a relatively diverse fish fauna in addition to amphibian and reptile populations (Snodgrass et al., 1999).

Male sirens showed a significant difference in growth in mass and SVL among years and seasons. Annual differences in growth may be related to weather and variation in average temperature and precipitation from year to year. Annual activity based on captures fluctuated seasonally over our

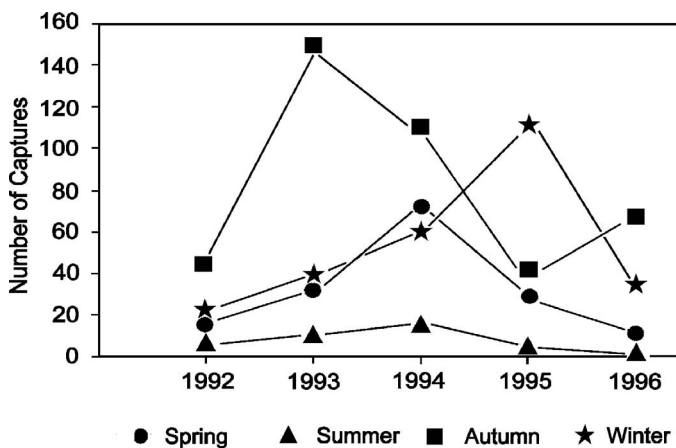


Fig. 4. Number of *Siren intermedia* captured per season and year over the five years of the study that sampled all four seasons.

study (Fig. 4). A comparison of captures per trap day, defined as one minnow trap set in the pond for a 24 h period, showed no obvious relationship to precipitation, mean temperature, minimum temperature, and mean minimum temperature. Other studies also found no significant correlation between captures and monthly average temperature or precipitation (Frese et al., 2003; Hampton, 2009). Gehlbach and Kennedy (1978) determined that the size of their catch was positively related to extremes of water temperature and was determined primarily by the variation in minimal temperature. They estimated that 71% of the variation in the size of the catch was determined by variation in thermal extremes. Hampton (2009) reported that the activity of his study population was significantly correlated with water temperature. Brodman (2008) suggested that siren populations fluctuated with the abundance of crayfishes and fishes.

The greatest growth that occurred in male sirens appeared to occur in spring, after breeding was completed. Measurements of growth in both mass and SVL were significantly higher by the summer, suggesting that foraging increased after breeding and before the decline in activity seen in the summer (Raymond, 1991). Males showed a small increase in growth in mass in winter and the smallest increase in growth in SVL in winter compared to other seasons. Although males were more active in the autumn and winter based on activity (Raymond, 1991), the greatest increase in growth occurred in the spring as documented by measurements made in the summer. This suggested that males spend more of their time occupied with establishing territories, courtship, and reproduction in the autumn and winter and do not spend as much time foraging until spring, after reproduction has occurred.

Female sirens also showed a significant difference in growth in both mass and SVL among years and seasons. Although differences among the years were minimal, the same trend of greater increases in growth in both mass and SVL recorded in the summer provided further evidence that most growth occurred in spring, after the breeding season for this population. The greater energy expenditure associated with production of ova (Duellman and Trueb, 1986) and loss of mass in females due to egg laying may also account for the smaller increase in size seen in females compared to males. Noble and Marshall (1932) reported two lots of siren eggs that contained 555 eggs and 260 eggs. They dissected a female in February 1931 that contained 299 eggs. Gehlbach

and Kennedy (1978) noted that three trapped female sirens laid 151, 190, and 226 eggs in field containers in late February and early March in Texas. Trauth et al. (1990) reported an average clutch size of 851.37 eggs (98–1506, $n = 8$) in sirens in Arkansas. Godley (1983) found two clutches of *S. intermedia* in Florida that contained 206 and 381 eggs. These clutch sizes represent a considerable mass lost by reproductive females.

Analysis of growth in female sirens on a seasonal basis showed a negative growth in mass in the winter and the smallest growth of the four seasons in SVL in winter (Table 2). Combining the data for males and females showed the same basic trends. Gravid females that oviposited their eggs would be expected to be smaller in mass, and possibly SVL (Bendik and Gluesenkamp, 2013), immediately following reproduction. An analysis of 14 recaptured female sirens that we captured in winter and spring of the same year demonstrated that females lost body size in both mass and SVL during the winter. We attributed this loss to the energy investment adult females required during egg laying.

The average growth in SVL for all sirens ($n = 307$) in our population was 0.086 mm/day. Males in our population grew 0.114 ± 0.017 mm/day ($\bar{x} \pm 95\%$ CI, $n = 111$). Females grew 0.030 ± 0.010 mm/day ($\bar{x} \pm 95\%$ CI, $n = 156$). Individuals that could not be sexed grew 0.108 ± 0.020 mm/day ($\bar{x} \pm 95\%$ CI, $n = 49$). This is within the range of variation reported by others (Hampton, 2009, 0.0005–0.113, $\bar{x} = 0.018$; Sawyer and Trauth, 2011, < 200 mm SVL = -1.00 – 1.40 , $\bar{x} = 0.055$, $n = 10$; > 200 mm SVL = -5.33 – 6.00 , $\bar{x} = 0.005$, $n = 6$), although our mean was larger. Frese et al. (2003) reported a mean growth in total length of 0.06 mm per day. Based on our analyses, males grew significantly more than females and combining growth of the sexes confounded this difference.

The average growth in mass for all sirens ($n = 307$) in our population was 0.072 g/day. Males in our population grew 0.096 ± 0.016 g/day ($\bar{x} \pm 95\%$ CI, $n = 111$). Females grew 0.061 ± 0.010 g/day ($\bar{x} \pm 95\%$ CI, $n = 156$). Individuals that could not be sexed grew 0.049 ± 0.016 g/day ($\bar{x} \pm 95\%$ CI, $n = 40$). As with SVL, males grew significantly more in mass than females and combining the sexes muddled the analysis of growth. Sawyer and Trauth (2011) reported a mean growth in mass of -0.203 g/day for *S. intermedia* < 200 mm SVL ($n = 10$) and 0.371 g/day for sirens > 200 mm SVL ($n = 6$). Although they reported no significant difference in growth between small and large sirens, they compared sirens < 200 mm to sirens > 200 mm. In our study, most of the growth of sirens occurred before they reached sexual maturity at an average of 150 mm for females and 180 mm for males (Martof, 1973). Neill (1949) collected 30 sirens on 18 May 1948 that had an average total length of 55 mm. He collected 46 individuals from the same pond on 18 July 1948, 61 days later, that had an average total length of 95 mm. This represented an average growth of 0.66 mm per day.

The smallest individuals we collected by dip netting had a mean SVL of 21.4 mm. Assuming an incubation period of 1.5–2.5 months (Petranka, 1998) and a hatching size of 11.5–11.6 mm in total length (Godley, 1983), these individuals probably came from eggs laid in February.

SVL was strongly correlated with mass in our study population. However, growth in both mass and SVL was weakly correlated to beginning SVL. The relationship was stronger for growth in SVL, providing more evidence that small, presumably younger, sirens grew faster than larger

sirens. However, this general trend of decreased growth as a siren increased in size was confused by seasonal differences in growth.

Juveniles collected in this population shortly after hatching showed a minimum increase of 113.8 mm in SVL (size class $1-\bar{x}$ SVL of juveniles) in males and 83 mm SVL in females as yearlings for this population. Dividing this increase in size by 365 days gave a conservative increase of 31% for males and 23% for females during their first year of growth.

We tested all the factors (sex, year, and season) influencing growth to determine whether any significant interactions contributed to our results. In terms of mass, all three factors showed significant differences in growth, but no combination of factors interacted in any significant way (Table 3, Fig. 2). When all three factors were tested for their influence on growth in SVL, besides each factor showing significant differences independently, the interaction of sex and season was significantly different (Table 4, Fig. 3). This finding supported the idea that ova are energetically more costly to produce than sperm (Duellman and Trueb, 1986) and that males grew larger because male rivalry takes the form of physical combat (Shine, 1979). As a result, females were smaller than males and grew at a slower rate.

Our study provided evidence for the effect of season on growth in sirens. More long-term studies of growth are needed to compare metapopulations throughout the species' range. Controlled studies focusing on the effect of other biotic and abiotic factors influencing growth and population trends in sirens are also needed to better understand the ecology of this species.

In conclusion, *S. intermedia* in northwestern Louisiana apparently bred in the winter and were most active in the autumn and winter. Biting occurred primarily in winter and was a component of male–male agonistic behavior and male–female courtship behavior. Male sirens grew faster and reached larger sizes than females. The larger size and increased growth in males were attributed to the greater energy investment of females in egg laying and the subsequent energy investment needed to recover lost body mass. The larger size in males was due to the importance of male combat as a component of reproductive activity in the species. Sirens showed the greatest increase in growth in spring, after establishing territories, courtship, and reproduction occurred. Although siren activity was greater in the autumn and winter, the energy investment required for courtship and breeding impacted increases in size. Increased foraging during the spring was expected if sirens were involved in preparation for courtship and actual courtship during the autumn and winter and did most of their foraging after the breeding season. Siren activity decreased dramatically in the summer due to high water temperatures and drying of water bodies (Hampton, 2009). Smaller sirens grew at a faster rate than larger sirens. In all cases, males, females, and males and females combined, a positive correlation between smaller size and greater growth in both SVL and mass occurred.

DATA ACCESSIBILITY

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