
THE FRESHWATER TURTLE COMMUNITY AT BLUE SPRING STATE PARK, VOLUSIA COUNTY, FLORIDA, USA

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Abstract.—Since 2007 the Turtle Survival Alliance - North American Freshwater Turtle Research Group (NAFTRG) has surveyed aquatic turtles in Volusia Blue Spring State Park, Orange City, Florida, USA. Here, we provide population parameters for the three most common freshwater turtle species, the Peninsula Cooter (*Pseudemys peninsularis*), Florida Red-bellied Cooter (*Pseudemys nelsoni*), and the Loggerhead Musk Turtle (*Sternotherus minor minor*), estimated from six years of mark and recapture data at Blue Spring State Park. The population estimates for the 1.9 ha study area were *P. nelsoni* 62 ± 2 , *P. peninsularis*, 240 ± 6 , and *S. m. minor*, 252 ± 7 . Although, the turtle population densities at Volusia Blue Spring appear robust for the habitat size, use of reverse-time capture-recapture models suggest that recruitment is minimal and recapture rates declined between sampling periods. Specific stressors that may be influencing population growth rates include bank erosion and lack, or loss, of nesting habitat, increasing winter use by West Indian Manatees (*Trichechus manatus*) and subsequent loss of aquatic vegetation, and additional competition with invasive fish and turtle species.

Key Words.—*Pseudemys nelsoni*; *Pseudemys peninsularis*; St. Johns River; *Sternotherus m. minor*; Volusia Blue Spring; West Indian Manatee

INTRODUCTION

Freshwater springs of Florida have been revered, worshipped, explored, and enjoyed by the peoples of Florida for over 2,000 y (Stamm 2008). Today, these springs appreciably contribute to the economy of Florida and provide recreational opportunities for millions of people every year (Stamm 2008). Likewise, the freshwater springs of Florida are vital to many freshwater organisms, including several rare, threatened, and endangered species (Hubbs 1995). These springs that are so integral to the economic, recreational, and environmental health of Florida are currently experiencing a variety of stressors. Over the past 30 y, the water table of Floridian springs has declined due to a reduction in recharge water (Shoemaker et al. 2004). This reduction is largely due to increased pavement and increased water consumption by residents (St. Johns River Water Management District 2006). Other anthropogenic influences include increased introduction of nitrites from farming and septic systems into many

springs (Toth and Fortich 2002; Wetland Solutions, Inc. 2007; Robert A. Mattson et al., unpubl. report). Most springs are also home to invasive flora and fauna, including the Red-eared Slider (*Trachemys scripta elegans*), Hydrilla (*Hydrilla verticillata*), Vermiculated Sailfin Catfish (*Pterygoplichthys disjunctivus*), and tilapia (*Oreochromis* spp.) that, in some cases, are displacing native species (Gibbs et al. 2008).

To combat the declining environmental quality of Volusia Blue Spring, the St. Johns River Water Management District (SJRWMD) adopted a strategic plan that includes a minimum flow regime (MFR; Wetland Solutions, Inc. 2007). According to the MFR, the minimum average long-term flow of Volusia Blue Spring will be increased 20% by 2016. Along with the set MFR, the SJRWMD plan includes monitoring indicators of the health and flow of the spring including water quality, aquifer levels, West Indian Manatee (*Trichechus manatus*) spring use, human use, and flora and fauna populations within the spring habitat (Wetland Solutions, Inc. 2007). Because Florida freshwater

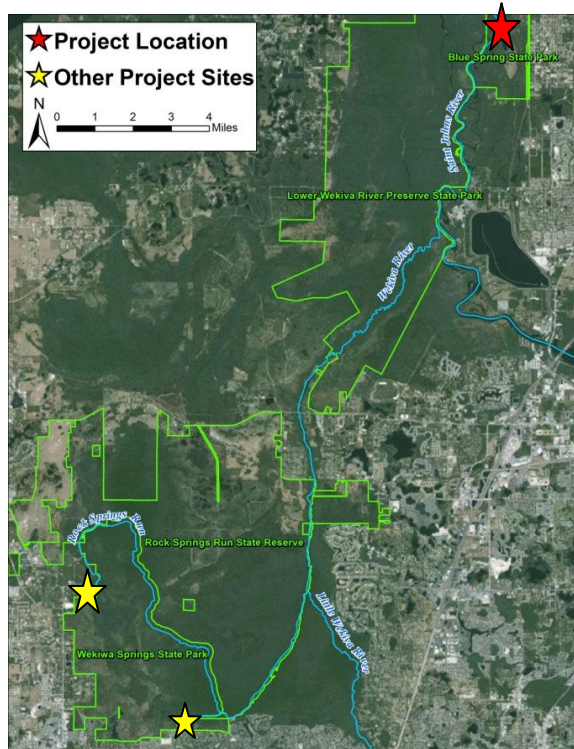


FIGURE 1. Map of St. Johns River watershed and associated study sites in Florida, USA.

springs are home to a myriad of organisms, monitoring the flora and fauna is a complex task.

Freshwater turtles are among the most conspicuous and ecologically important components of many freshwater spring ecosystems in Florida (Meylan 2006). Turtle populations in spring ecosystems have been studied throughout the state of Florida for over 70 y (Marchand 1942; Meylan et al. 1992; Jackson and Walker 1997; Chapin and Meylan 2011; Munscher et al. 2015a). Long-term mark and recapture studies (Meylan et al. 1992; Huestis and Meylan 2004; Chapin and Meylan 2011) have documented shifts in species composition, age structure, survivorship, and sex ratios in turtle assemblages in the Suwannee River drainage basin. However, knowledge of turtle species and population structure of turtles that inhabit other watersheds, including the St. Johns River watershed, are scarce or nonexistent. Only two studies have occurred here. At Rock Springs Run State Reserve (Fig. 1), Kramer (1995) studied the home range of Florida Red-bellied Cooters (*Pseudemys nelsoni*). He found that this species tends to reside in areas that offer ample food resources and basking sites. Hrycyshyn (2006) studied the turtle assemblage at Wekiwa Springs State Park (Fig. 1), approximately 9.3 km from Kramer's (1995) study site and preliminary findings suggest a very large, robust, turtle assemblage present at this site.

Both of the previously mentioned studies occurred at sites that are a part of the Wekiwa River drainage basin (Fig. 1), a small spring-fed river complex that feeds into the St. Johns River. Despite its proximity to Orlando, the area is highly regarded as high quality protected habitat (Wetland Solutions, Inc. 2007). The Wekiwa River is one of two designated wild and scenic rivers in Florida. Volusia Blue Spring is the largest spring in regards to water flow located within the St. Johns River Basin. However, the spring environment itself is relatively small and devoid of typical wetland / aquatic vegetation that are normally associated with freshwater spring habitats like Wekiwa Springs (Munscher et al. 2015 a, b).

We have been monitoring the freshwater turtle assemblage inhabiting Volusia Blue Spring since 2007. Our goal was to assess the turtle community and draw inferences on the quality and suitability of the spring habitat. Our objectives were to: (1) estimate the number of individuals in the populations for the three dominant species present in this spring: *P. peninsularis*, *P. nelsoni*, and *S. m. minor*; (2) quantify survivorship, biomass, recruitment, and sex ratios; and (3) identify key factors that may affect the turtle community and its use of the Volusia Blue Spring habitat to make management recommendations.

MATERIALS AND METHODS

Study site.—The study area encompasses the spring run of Volusia Blue Spring, located in Blue Spring State Park (BSSP), Orange City, Volusia County, Florida (28°56'N, 81°20'W; Fig. 2). The study area consists of a 0.72 km long spring run approximately 30 to 46 m wide encompassing 1.9 ha of protected aquatic habitat with depths up to 3 m. The very large boil at the head of the spring is over 24 m deep (Marella 2004). Volusia Blue Spring is a first magnitude spring that expels approximately 394 million L of water each day with an average temperature of 23.0° C (Saint Johns River Water Management. 2010. Water Supply, Blue Spring, Volusia County, Minimum Flow Regime, Available at <http://www.sjrwmd.com/technicalreports/spubs1.html> [Wetland Solutions, Inc: Accessed 8 August 2016]), and has the highest discharge of all of freshwater springs on the St. Johns River. The area that surrounds the spring boil has been modified over time with wooden retention walls to combat erosion. Steep forested banks 3–6 m high surround the spring boil except to the south, where the spring opens into the approximately 0.72 km long spring run. The confluence with the St. Johns River is the boundary between protected State Park habitat and the unprotected public waterway.

Methods.—We sampled the turtle assemblage of BSSP in March, August, and October 2007–2014;



FIGURE 2. Map of study area at Blue Spring State Park, Florida, USA.

however, due to flooding of the St. Johns River, we did not conduct October surveys in 2012 and 2014. For each sampling period, a variable number of people, typically between five and 10, snorkeled from about 0900 to 1600–1900, depending on time of year and weather conditions. We occasionally used double throated (1.9 m in diameter, 5.7 m long) hoop nets baited with fried chicken and melon rinds for trapping turtles. We placed all captured turtles in canoes and brought them to a central field location for data processing. We marked turtles using a variation of the shell notching technique described by Cagle (1939) and with passive intergraded transponder (PIT) tags.

Data collection.—We recorded straight-line measurements of maximum carapace length (CL), maximum plastron length (PL), carapace width (CW), and shell height (SH) to the nearest mm using large 40 cm size aluminum tree calipers (Haglof Inc., Madison, Mississippi, USA). We then determined the sex of turtles based on secondary sexual characteristics, such as tail and claw length (Ernst and Lovich 2009). We noted unique identifying features, damage, scars, or coloration for each turtle and aided in confirming identity. We determined the mass of all turtles using either Pesola spring scales (Pesola AG, Baar, Switzerland) or Ohaus

top loading scales (Ohaus Corp., Parsippany, New Jersey, USA) depending on the size and the species. We then released turtles back into the spring run at their approximate capture location.

Data analysis.—Due to the proximity to the St. Johns River, the largest river in Florida, and the relatively small size of Blue Spring, we treated it as an open system. We calculated population abundance for adults using POPAN parameterization of Jolly-Seber models (Jolly 1965; Seber 1965) in Program MARK (White and Burnham 1999). We calculated apparent annual survival (Φ) and recapture rates (p) using open population Cormack-Jolly-Seber models (CJS; Lebreton et al. 1992) in Program MARK (White and Burnham 1999). To test for differences in Φ and p between sexes, we generated CJS models to test whether Φ or p differed based on sex, time, or a sex-time interaction. We also generated Cormack-Jolly-Seber models to test whether Φ or p differed between species of *Pseudemys*, time, or a species-time interaction. We based model selection for all analyses on Akaike Information Criterion (AICc) values, with lower values denoting greater parsimony (Burnham and Anderson 2002).

To detect changes in population structures over time, we plotted recapture rates from fully time dependent models generated in Program Mark, calculated between early (March) and late (October) season sampling periods. We also used reverse-time, capture-recapture models to make inferences about local components of population growth (Pradel 1996; Nichols et al. 2000). We calculated seniority probability (γ) to better understand the proportional contribution of survival and recruitment to the population growth rate. Values of seniority approaching 1.0 suggest that there is little contribution to population growth rate by recruitment. Population growth rate (λ) can be estimated by rate of new individuals entering the population in relation to the survival rate. Recruitment (f) then is defined as the *per capita* addition of individuals to the local population. The parameters γ , λ , f were calculated using Pradel models in Program MARK.

We calculated biomass as the average mass of all initial captures in grams multiplied by the population size estimate for each species and by sex to account for sexual size dimorphism in some species. Total biomass was then the sum of the individual calculations for each sex. We excluded juvenile animals from calculations due to low capture-recapture rates. We estimated biomass per hectare by dividing the calculated total biomass for each species by 1.9 ha, the sampling area of the spring.

We calculated sex ratios based on total number of individual marked turtles, excluding juveniles. We used chi-square goodness of fit tests to determine if the observed proportion of male to female turtles was

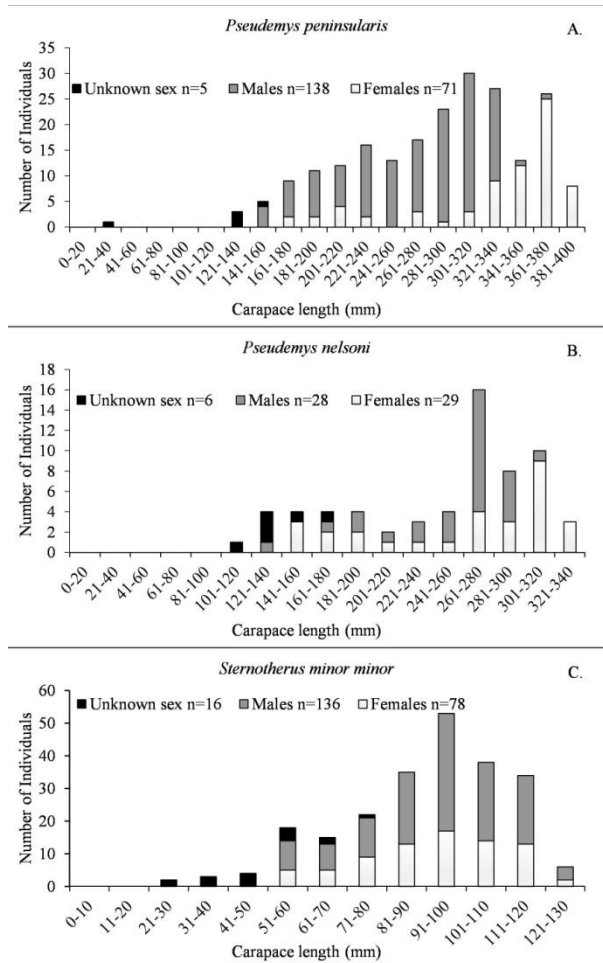


FIGURE 3. Size (carapace length) distributions of *Pseudemys peninsularis* (A), *P. nelsoni* (B), and *Sternotherus m. minor* (C) captured from 2007–2014 at Blue Spring State Park, Florida, USA.

significantly different from 1:1. We presented all data as mean \pm SE. We compared sexual size differences using ANOVA. For both tests, $\alpha = 0.05$.

RESULTS

We captured and marked 520 turtles of eight species (Table 1), and we calculated population parameters for the three most frequently captured species; *P. peninsularis*, *P. nelsoni*, and *S. minor* (Fig. 3). All other species had too few recaptures for statistical analysis. The population size estimate of adult turtles for the 1.9 ha study site for *P. nelsoni* was 62 ± 2 , for *P. peninsularis* was 240 ± 6 , and for *S. m. minor* 252 ± 7 .

We calculated the ratio of female to male individuals for all new captures for each species. *Pseudemys peninsularis* had a significantly skewed F:M ratio of 1:1.99 ($\chi^2 = 22.11$, $df = 1$, $P < 0.001$). Similarly, *S. m. minor* also had a significantly skewed F:M ratio of

TABLE 1. Chelonian species and the number of individuals (n) captured at Blue Springs State Park, Florida, USA, 2007–2014.

Species		n
Peninsula Cooter	<i>Pseudemys peninsularis</i>	214
Florida Redbellied Cooter	<i>Pseudemys nelsoni</i>	63
Loggerhead Musk Turtle	<i>Sternotherus minor minor</i>	230
Eastern Musk Turtle	<i>Sternotherus odoratus</i>	5
Eastern Snapping Turtle	<i>Chelydra serpentina</i>	6
Florida Softshell	<i>Apalone ferox</i>	3
Striped Mud Turtle	<i>Kinostemon baurii</i>	1
Yellow Bellied Slider	<i>Trachemys scripta scripta</i>	4
Red Eared Slider	<i>Trachemys scripta elegans</i>	14
False Map Turtle	<i>Graptemys pseudogeographica</i>	1
Eastern Painted Turtle	<i>Chrysemys picta</i>	1

1:2.13 ($\chi^2 = 21.36$, $df = 1$, $P < 0.001$). Only the sex ratio of *P. nelsoni*, with a F:M ratio of 1:1.23, was not significantly different from 1:1 ($\chi^2 = 0.532$, $df = 1$, $P > 0.05$).

Carapace length, shell height, plastron length, and mass measurements of female *P. peninsularis* were significantly larger than conspecific males ($F_{1,689} = 84.76$; $P < 0.001$; Table 2). While female *P. nelsoni* were also larger than their conspecific males ($F_{1,239} = 4.53$; $P = 0.001$), not all measurements were significantly larger (Table 2). Female *P. nelsoni* had significantly greater shell height and significantly greater mass than males. For any parameter measured, the sexes of *S. m. minor* were not significantly different ($F_{1,769} = 0.99$; $P = 0.08$; Table 2).

The biomass per species was 779 kg/ha for *P. peninsularis*, 173 kg/ha for *P. nelsoni*, and 16.4 kg/ha for *S. minor*. Biomass for the sexually dimorphic *Pseudemys* were calculated by summing the mean mass for males plus mean mass for females. The number of males and females were determined by population estimates and sex ratio.

Annual survival was similar between the sexes in *P. nelsoni* (Table 3). The model that best explained encounter rates for *P. nelsoni* was $\Phi(\text{constant}) p(\text{time})$, where survivorship was independent of group and time and recapture probability varied by time (Table 4). Survivorship was high for *P. peninsularis*, although recapture probability was much lower than for *P. nelsoni* (Table 3). The model that best explained encounter rates for *P. peninsularis* was $\Phi(\text{sex}) p(\text{time})$, where survivorship varied by sex and recapture probability varied across sampling intervals (Table 4). The best model to explain encounter histories between *P. peninsularis* and *P. nelsoni* was $\Phi(\text{constant}) p(\text{species} \times \text{time})$, where survivorship was independent of group and time but probability of recapture varied by

TABLE 2. Means comparisons between sexes of morphometric variables collected for three turtle species at Blue Spring State Park, Florida, USA. Shell measurements are in mm and mass in g (± 1 SE).

Variable	Male	Female	P
<i>Pseudemys peninsularis</i>			
n	135	69	
Carapace Length	267.9 \pm 4.5	331.6 \pm 7.3	<0.001
Carapace Width	183.0 \pm 2.5	226.5 \pm 4.4	<0.001
Plastron Length	234.8 \pm 3.8	297.6 \pm 6.6	<0.001
Shell Height	109.0 \pm 1.8	143.1 \pm 3.2	<0.001
Mass	2,387 \pm 100	4,989 \pm 241	<0.001
<i>Pseudemys nelsoni</i>			
n	24	24	
Carapace Length	257.9 \pm 6.7	272.4 \pm 11.4	0.27
Carapace Width	181.5 \pm 4.1	191.6 \pm 6.5	0.08
Plastron Length	236.7 \pm 10.4	251.3 \pm 6.2	0.23
Shell Height	110.1 \pm 2.9	122.8 \pm 5.3	0.04
Mass	2,417 \pm 171	3,169 \pm 302	0.03
<i>Sternotherus minor minor</i>			
n	135	77	
Carapace Length	93.5 \pm 1.4	93.15 \pm 1.9	0.86
Carapace Width	67.5 \pm 0.8	67.4 \pm 1.2	0.98
Plastron Length	66.6 \pm 1.1	68.6 \pm 1.5	0.27
Shell Height	36.2 \pm 0.4	37.5 \pm 0.7	0.13
Mass	126 \pm 5.0	128 \pm 7.3	0.83

species and sampling interval independently of each other (Table 5). Annual survival and capture rates were similar between the sexes of *S. m. minor* (Table 3). The best model to explain encounter histories for *S. m. minor* was Φ (constant) p (time) where survivorship was independent of group and time and recapture probability varied by time (Table 6).

In all models across all species, recapture probabilities varied by time. We plotted recapture probabilities between sampling periods from 2007–2012 and *P. nelsoni* showed considerable variation in recapture probability between early sampling sessions, with probabilities increasing slightly in later sessions (Fig. 4). Recapture probabilities decreased over time for *P. peninsularis* and *S. m. minor* (Fig. 4). Seniority values suggest that there is very little contribution to population growth rate from recruitment (Table 7). Recruitment values were very low for all species and population growth rates denoted a stable to declining population for *S. minor* and declining populations for both *Pseudemys* species (Table 7).

DISCUSSION

This study of the Volusia Blue Spring turtle community provides a clearer understanding of the use of springs in the river system at St. Johns by these species. Annual survival rates are high for all species, but there is evidence for slow population declines over time for some species. Other species may simply be

TABLE 3. Apparent annual survival (Φ) and recapture rates (p) of three turtle species at Blue Spring State Park, Florida, USA.

Species	Φ	p
<i>Pseudemys nelsoni</i>		
Male	0.97 \pm 0.01	0.37 \pm 0.04
Female	0.98 \pm 0.01	0.40 \pm 0.03
Pooled	0.98 \pm 0.01	0.39 \pm 0.02
<i>Pseudemys peninsularis</i>		
Male	0.97 \pm 0.01	0.07 \pm 0.01
Female	0.98 \pm 0.01	0.17 \pm 0.02
Pooled	0.97 \pm 0.01	0.09 \pm 0.01
<i>Sternotherus minor minor</i>		
Male	0.97 \pm 0.01	0.14 \pm 0.03
Female	0.96 \pm 0.02	0.08 \pm 0.03
Pooled	0.97 \pm 0.01	0.11 \pm 0.02

transients within the spring run. For *Pseudemys peninsularis*, the size classes of both males and females are skewed towards large individuals; however, the shape of the skew is more extreme among the females. In addition, the sex ratio is 1:2 in favor of males; whereas, most populations tend towards equal sex ratios (Ernst and Lovich 2009). Apparent survivorship and recapture probability differed by species (Φ) and by species and time (p). Additionally, juvenile turtles are underrepresented in our capture records. Although it is possible that this may be due to sampling bias, the presence of *P. nelsoni* juveniles suggests that our methods detect smaller *Pseudemys* when present. In addition, we also captured juvenile *Pseudemys* at other parks such as Wekiwa Springs, using the same sampling methods as in this study (Munscher et al. 2015b). Certain spring microhabitats that act as nurseries for juvenile *Pseudemys*, include floating and submerged vegetation, are exceedingly rare at Volusia Blue Spring. We believe that juvenile *P. peninsularis* may not be using the spring as their primary habitat as these shelter sites are absent. Additionally, we captured nearly four times more unique individuals of *P. peninsularis* than *P. nelsoni*, and *P. peninsularis* had much lower recapture rates. Taken together, these data suggest that *P. peninsularis* may be more transient in the spring system and may prefer using the St. Johns River habitat with visits to the spring.

Sternotherus m. minor size classes were approximately normally distributed for both males and females, but there was a male-biased sex ratio of 1:2. Other studies have reported 1:1 sex ratios for *S. m. minor* (Tinkle 1958; Meylan et al. 1992), while Sachsse (1977) reported female-biased sex ratios in laboratory hatchlings. Our most parsimonious model of

TABLE 4. Comparison of Cormack-Jolly-Seber models for apparent annual survival (Φ) and recapture rates (p) for *Pseudemys* sp. at Blue Spring State Park, Florida, USA. Models differ in whether Φ and p are assumed to be constant (.), fully time dependent (t), or differ between sexes (g), and whether there are interactions (*) among these factors.

Model	AICc	Delta AICc	AICc Weights	Number Parameters	Deviance
<i>Pseudemys nelsoni</i>					
$\Phi(.) p(t)$	610.806	0	0.674	19	451.049
$\Phi(g) p(t)$	612.263	1.457	0.326	20	450.036
$\Phi(.) p(.)$	632.777	21.971	0.000	2	511.182
$\Phi(t) p(t)$	633.788	22.983	0.000	35	430.888
$\Phi(g) p(.)$	633.792	22.986	0.000	3	510.135
$\Phi(.) p(g)$	634.412	23.606	0.000	3	510.755
$\Phi(g) p(g)$	635.647	24.841	0	4	509.908
$\Phi(.) p(g^*t)$	638.101	27.295	0	37	429.209
$\Phi(g) p(g^*t)$	640.896	30.090	0	38	428.952
$\Phi(t) p(.)$	645.470	34.664	0	19	485.714
$\Phi(t) p(g)$	647.742	36.936	0	20	485.515
$\Phi(t) p(g^*t)$	674.941	64.135	0	53	412.201
$\Phi(g^*t) p(t)$	677.066	66.260	0	53	414.326
$\Phi(g^*t) p(.)$	678.397	67.591	0	37	469.505
$\Phi(g^*t) p(g)$	681.409	70.604	0	38	469.465
$\Phi(g^*t) p(g^*t)$	728.360	117.555	0	69	398.519
<i>Pseudemys peninsularis</i>					
$\Phi(g) p(t)$	1110.668	0	0.605	20	505.267
$\Phi(.) p(t)$	1111.575	0.907	0.384	19	508.416
$\Phi(g) p(g^*t)$	1118.957	8.289	0.010	38	470.822
$\Phi(.) p(g^*t)$	1123.559	12.891	0.001	37	477.923
$\Phi(t) p(t)$	1125.556	14.888	0.000	35	484.872
$\Phi(t) p(g^*t)$	1138.420	27.752	0	53	450.844
$\Phi(g) p(g)$	1162.998	52.330	0	4	591.956
$\Phi(g^*t) p(g^*t)$	1164.013	53.345	0	67	435.983
$\Phi(g^*t) p(t)$	1164.172	53.504	0	53	476.597
$\Phi(g) p(.)$	1168.879	58.211	0	3	599.881
$\Phi(t) p(.)$	1169.773	59.105	0	19	566.615
$\Phi(.) p(.)$	1169.829	59.161	0	2	602.865
$\Phi(.) p(g)$	1170.348	59.680	0	3	601.351
$\Phi(t) p(g)$	1170.627	59.959	0	20	565.226
$\Phi(g^*t) p(g)$	1196.674	86.006	0	37	551.038
$\Phi(g^*t) p(.)$	1200.537	89.869	0	36	557.385

TABLE 5. Comparison of Cormack-Jolly-Seber models for apparent annual survival (Φ) and recapture rates (p) for *Pseudemys nelsoni* and *P. peninsularis* combined at Blue Spring State Park, Florida, USA. Models differ in whether Φ and p are assumed to differ between species (s) or over time (t), and whether there are interactions between these factors.

Model	AICc	Delta AICc	AICc Weights	Num. Par	Deviance
$\Phi(s) p(s^*t)$	1721.608	0	0.287	38	824.268
$\Phi(t) p(s^*t)$	1738.754	17.146	0	53	805.802
$\Phi(s^*t) p(s^*t)$	1756.510	34.902	0	70	780.562
$\Phi(s) p(s)$	1802.583	80.975	0	4	978.849
$\Phi(t) p(s)$	1807.797	86.189	0	20	950.580
$\Phi(s^*t) p(s)$	1814.470	92.862	0	38	917.130
$\Phi(s) p(t)$	1833.937	112.330	0	20	976.720
$\Phi(s^*t) p(t)$	1843.525	121.917	0	53	910.574
$\Phi(t) p(t)$	1847.366	125.758	0	35	956.905

survivorship and recapture probability reported that both parameters differed between sexes. Some of these differences may be best explained by ongoing changes to the spring itself, including lack of aquatic vegetation.

Our overall assessment is that the Volusia Blue Spring ecosystem is stressed from increased public use and bank erosion; as well as, limited submerged, emergent, and floating aquatic plants, and invasive species. These sources of degradation most likely contribute to the low

TABLE 6. Comparison of Cormack-Jolly-Seber models for apparent annual survival (Φ) and recapture rates (p) for *Sternotherus minor* at Blue Spring State Park, Florida, USA. Models differ in whether Φ and p are assumed to be constant (\cdot), fully time dependent (t), or differ between sexes (g), and whether there are interactions ($*$) among these factors.

Model	AICc	Delta AICc	AICc Weights	Num. Par	Deviance
$\Phi(\cdot) p(t)$	685.728	0	0.659	19	327.851
$\Phi(g) p(t)$	687.050	1.322	0.341	20	326.831
$\Phi(t) p(t)$	715.204	29.475	0	35	317.389
$\Phi(\cdot) p(g^*t)$	718.840	33.112	0	37	315.635
$\Phi(g) p(g^*t)$	721.464	35.736	0	38	315.528
$\Phi(\cdot) p(\cdot)$	725.805	40.077	0	2	404.997
$\Phi(\cdot) p(g)$	726.006	40.278	0	3	403.151
$\Phi(g) p(\cdot)$	726.903	41.174	0	3	404.048
$\Phi(g) p(g)$	728.049	42.321	0	4	403.132
$\Phi(t) p(\cdot)$	741.135	55.407	0	19	383.258
$\Phi(t) p(g)$	741.411	55.683	0	20	381.192
$\Phi(t) p(g^*t)$	754.850	69.121	0	53	304.830
$\Phi(g^*t) p(t)$	755.792	70.064	0	51	312.011
$\Phi(g^*t) p(\cdot)$	781.057	95.329	0	37	377.852
$\Phi(g^*t) p(g)$	783.406	97.678	0	38	377.471
$\Phi(g^*t) p(g^*t)$	798.431	112.703	0	67	301.179

recruitment rates observed in these populations. The strategic plan that includes a minimum flow regime (MFR) is a logical step towards increasing the water outflow and restoring spring habitat; however, this may not be enough to ensure the health of the spring ecosystem.

The manatee population at Volusia Blue Spring is exceeding the predicted growth rates, and the extra pressure from this population appears to be exhausting herbaceous food resources in the spring. The number of overwintering manatees at Volusia Blue Spring has grown from 11 individuals during the 1970–1971 season to 486 during the 2012–2013 season (Volusia Blue Spring State Park, unpubl. data). Both species of

Pseudemys studied here are primarily herbivorous (Ernst and Lovich 2009). Intense grazing of available vegetation by manatees in the spring may increase competition between the *Pseudemys* species for remaining resources. This may be one reason why recapture rates for *P. peninsularis* have declined over time. In contrast, *Sternotherus m. minor* are primarily molluscivorous as adults, preying predominantly on gastropods (Zappalorti and Iverson 2006). There is a strong negative relationship between algal biomass and gastropod biomass (Liebowitz et al. 2014). Severe reduction in vegetation would reduce habitat and food for gastropods, which in turn would have indirect effects on *S. m. minor* at Volusia Blue Spring, resulting in the decline in capture rates for this species.

This ecosystem would benefit substantially by increasing the abundance of native submerged aquatic plants, particularly because a large percentage of the turtle biomass is represented by herbivores. As of July 2013, the Parks Service began a reintroduction of eel grass (*Vallisneria* spp.) into the spring run. To protect these plants, metal cages were installed to prevent manatees from completely overgrazing this native aquatic plant, which provides important shelter for many species. The current use of caged eel grass is an excellent start for re-vegetating the spring run bottom. More abundant and varied aquatic vegetation would benefit the herbivorous turtles and improve the invertebrate abundance and diversity, which in turn would aid the carnivorous *Sternotherus* species.

The reduction of native aquatic vegetation may also be exacerbated by the presence of invasive fish. The Vermiculated Sailfin Armored Catfish (*Pterygoplichthys disjunctivus*), Blue Tilapia (*Oreochromis aureus*), Asian Grass Carp (*Ctenopharyngodon idella*), and Black Pacu (*Colossoma macropomum*) have been observed in the

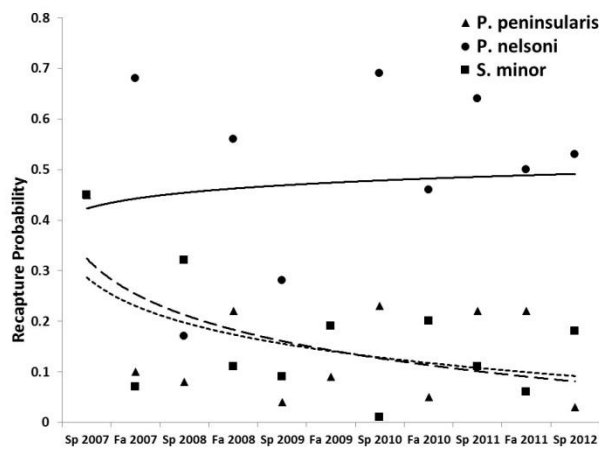


FIGURE 4. Trends in recapture rates between early (March) and late (October) season samples for turtles at Blue Spring State Park, Florida, USA. *Pseudemys nelsoni* is represented by the solid trend line, while *P. peninsularis* is represented by the small dashed trend line. *Sternotherus minor* is represented by the large dashed trend line.

TABLE 7. Seniority (γ), population growth rate (λ) and recruitment (f) for three species of turtles at Blue Spring State Park, Florida, USA.

	γ	λ	f
<i>Pseudemys peninsularis</i>	0.99 ± 0.001	0.97 ± 0.001	≤ 0.001
<i>Pseudemys nelsoni</i>	0.98 ± 0.001	0.98 ± 0.003	0.011 ± 0.003
<i>Sternotherus m. minor</i>	0.97 ± 0.013	1.00 ± 0.002	0.033 ± 0.005

spring run since 1999 (Gibbs et al. 2008; 2010; 2013). Over 5,800 Vermiculated Sailfin Armored Catfish have been removed over the past decade (Gibbs et al. 2008; 2013). Removal of these and other invasive fish will benefit populations of native competing fish and also limit further erosion of the spring banks that is caused by the Vermiculated Sailfin Catfish (Gibbs et al. 2013).

Additionally, several species of non-native turtles have been identified and removed. During previous monitoring sessions, 14 Red-eared Sliders, one False Map Turtle (*Graptemys pseudogeographica*), and one Eastern Painted Turtle (*Chrysemys picta picta*) have been removed, and four Yellow-bellied Sliders (*Trachemys scripta scripta*) have been marked since 2007 (Munscher et al. 2013a, b; 2014). We hypothesize that the three latter species pose little threat to the overall integrity of the Volusia Blue Spring turtle assemblage, although release from captivity could introduce diseases. The False Map Turtle and the Eastern Painted Turtle captures most likely represent individual releases of pet turtles, and the Yellow-bellied Slider is native to the state but is not native to the St. Johns river drainage (Krysko et al. 2011). Due to the consistent captures over the past six years, we suspect there may be a small breeding population of *T. s. elegans* residing in the Blue Spring / St. Johns River locality. Invasive *T. s. elegans* could directly compete with native *Pseudemys* species for scarce resources, as has been observed elsewhere when this invasive species competes with local species (Cadi and Joly 2004; Polo-Nuria et al. 2009). While this study provides important baseline data on turtle populations within Volusia Blue Spring, additional research in conjunction with continued monitoring will be needed to better manage this system. In particular, more research on the trophic ecology of Volusia Blue Spring must be undertaken to better understand the impacts of not only increasing populations of native imperiled species, but non-native species as well.

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Riedle et al.—Volusia Blue Spring turtle community.



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