THE SANTA FE RIVER IN NORTHERN FLORIDA: EFFECT OF HABITAT HETEROGENEITY ON TURTLE POPULATIONS

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ABSTRACT

The Santa Fe River (SFR) in northern Florida and its springs provide a unique ecosystem for a wealth of flora and fauna, and support a unique freshwater turtle assemblage. We conducted a 6-year mark-recapture study of ten turtle species to assess how habitat heterogeneity among sites affects riverine turtle populations. Because the SFR ecosystem has not been well described and the major emphasis of this paper is the effect of habitat variation on turtle populations, we provide thorough descriptions of the SFR basin and specific habitats in which we sampled turtles. The SFR originates as a tannin-stained blackwater river, but receives substantial input of clear, alkaline, thermally stable water from numerous artesian springs in its lower reaches. We used mark-recapture and demographic data to evaluate differences in turtle assemblages and population structure on a spatial scale. We compared turtle assemblages between a 5 km reach of blackwater river habitat and a 9 km reach of spring-influenced river habitat. We found the same ten species in both habitats. Hand capture while snorkeling suggested similar relative abundance of species in both river habitats, but baited hoop trap captures suggested that *Chelydra serpentina* (Snapping Turtle) and *Sternotherus minor* (Loggerhead Musk Turtle) are proportionately more abundant in the three spring-influenced habitats we sampled. The total density of all turtle species combined appears to be three to four times greater in the spring-influenced river reach than in the blackwater river reach. Examination of population structure of the three most abundant species (*Pseudemys suwanniensis* [Suwannee Cooter], *S. minor*, and *Trachemys scripta* [Yellow-bellied Slider]) in the river and adjacent spring habitats revealed that some springs feeding the SFR may function as nursery habitats. Results demonstrate the importance of habitat diversity (beta diversity) to the riverine turtle assemblage. If we had sampled turtles only in one section of the river or only in spring habitats in the lower SFR, our perceptions of assemblages and population structure would have been vastly different. The fate of the turtle populations in the SFR depends on the quantity and quality of water discharging from its springs. If the long-term trend of declining spring flows continues, we predict that SFR turtle populations will be detrimentally

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affected in multiple ways such as loss of nursery habitat and reduced recruitment. Less dilution of dark tannic water flowing down from the upper SFR may cause shifts in assemblage and population structure, as well as in population densities. Given the uncertain future of ecological conditions in the SFR, we advocate continued long-term monitoring of this unique turtle assemblage.

Key words: beta diversity, community ecology, freshwater springs, population structure, *Pseudemys suwanniensis*, river ecology, Santa Fe River, *Sternotherus minor*, *Trachemys scripta*, turtle.

INTRODUCTION

Rivers are structurally complex ecosystems that vary physically (e.g., width, depth, substrate type, flow velocity) and chemically (e.g., pH, dissolved oxygen, nitrate concentration) on a spatial scale influenced by local variation in elevation, geology, hydrology, and surrounding terrestrial environments as they flow from headwaters to mouth (Vannote et al., 1980; Minshall et al., 1985). The resulting mosaic of habitats with different abiotic and biotic parameters influences the distribution and abundance of many aquatic vertebrate species (Nickerson and Mays, 1973; Power, 1992; Robinson et al., 2002; Arrington et al., 2005; Sterrett et al., 2011; Pitt and Nickerson, 2014). In some species, habitat use also varies among demographic groups [life history stages], resulting in habitat-associated variation in size structure, age structure, and/or sex ratios (Hoxmeier and Devries, 1997; Nickerson et al., 2003; Martin and da Silva, 2004). Understanding variation in distribution, abundance, and population structure of species among habitats is essential to elucidating population dynamics, distributional relationships, and conservation status.

At least 150 turtle species occur in rivers throughout the world, and almost half of those species are listed as vulnerable, endangered, or critically endangered due to threats such as exploitation for food or medicinal use, anthropogenic alteration of habitat, and/or the pet trade (Moll and Moll, 2004; Turtle Taxonomy Working Group, 2014). However, little is known about distribution, abundance, and structure of most riverine turtle populations in the context of habitat heterogeneity. Available literature suggests most riverine species tend to use habitats non-randomly, with different species favoring different habitat types (Bury, 1979; Fuselier and Edds, 1994; Bodie and Semiltsch, 2000; Lescher et al., 2013; Lindeman, 2013; Paez et al., 2015). For example, Anderson et al. (2002) found distinctly different assemblages in open river, slough, and backwater habitats in the upper Mississippi River. In the middle Mississippi River, Smooth Softshell Turtles (*Apalone mutica*) were most abundant in open side channels and main channel borders where water was deeper and faster than in the tributaries and closed side channels in which Spiny Softshell Turtles (*A. spinifera*) were most abundant (Barko and Briggler, 2006). In the St. Croix River in Minnesota, Snapping Turtles (*Chelydra serpentina*), False Map Turtles (*Graptemys pseudogeographica*), and Painted Turtles (*Chrysemys picta*) were associated with muck substrate and snags, but no significant relationship was found between Northern Map Turtle (*G. geographica*) abundance and any measured habitat characteristic (DonnerWright et al., 1999).

Moll and Legler (1971) described habitat-associated variation in population structure for the Meso-American Slider (*Trachemys venusta*) population inhabiting the Rio Chagres in Panama. Ontogenetic stages in this population were segregated among habitats, with hatchlings and juveniles in backwaters and adults in fluvial parts of the river. Floodplain wetlands in other regions appeared to be nursery habitats for some populations of False Map Turtles (*G. pseudogeographica*), Red-eared Sliders (*T. scripta*), and Western Pond Turtles (*Actinemys marmorata*), with adults occurring in deeper water (Reese and Welsch, 1998; Bodie and Semiltsch, 2000; Bodie, 2001). Juvenile and subadult Central American River Turtles (*Dermatemys mawii*) occur in small tributaries of

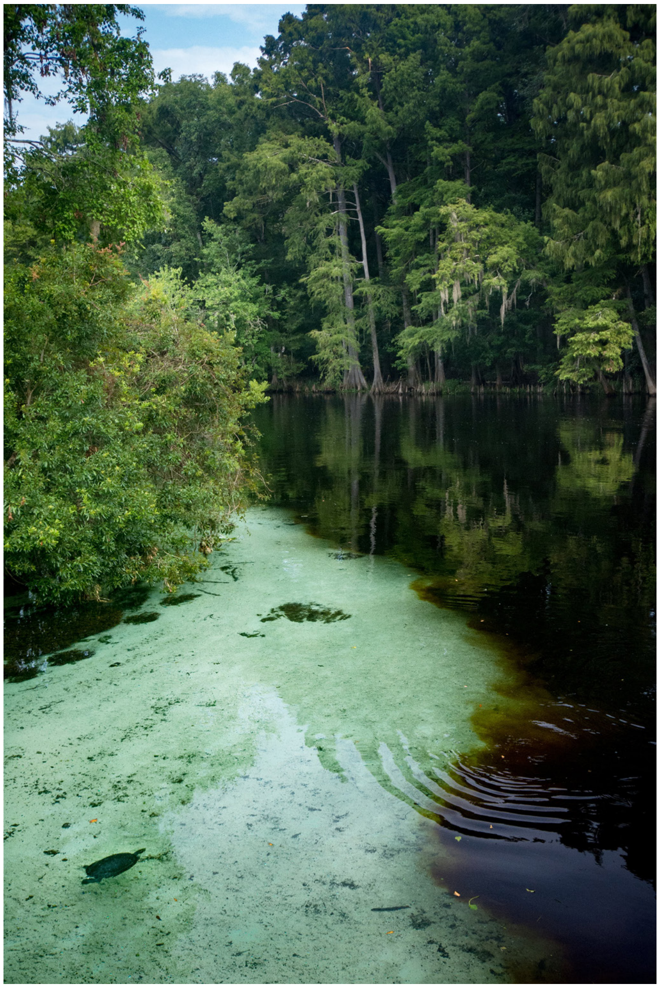

Figure 1. Clear spring water mixing with dark tannic water at the confluence of Gilchrist Blue Spring run and the Santa Fe River in northern Florida. The turtle is a *Pseudemys suwanniensis*. Photo by G. A. Shemitz.

large deep rivers inhabited by adults (Legler and Vogt, 2013). In the Amazon River basin, juvenile and subadult Giant South American River Turtles (*Podocnemis expansa*) and Yellow-spotted Amazon River Turtles (*P. unifilis*) occupy lakes, pools, and creeks during the dry season while adults remain in the river (Vogt, 2008). Differences in habitat use also occur between sexes in species such as Smooth Softshell Turtle (*A. mutica*), Cagle's Map Turtle (*G. caglei*), Yellow-blotched Map Turtle (*G. flavimaculata*), Northern Map Turtle (*G. geographica*), and Texas Map Turtle (*G. versa*) in the southeastern United States where females use deeper water farther from shore than the smaller males (Plummer, 1977; Pluto and Bellis, 1986; Jones, 1996; Lindeman, 2003). Thus, different demographic groups may be vulnerable to localized environmental impacts.

In this paper, we describe the Santa Fe River (SFR) ecosystem in northern Florida and examine how populations of ten native freshwater turtle species responded to habitat heterogeneity in this ecosystem during 2006–2012. The SFR originates as a blackwater river, but receives substantial input of clear water from artesian springs in its lower reaches (Fig. 1). Enhanced water clarity in the spring-influenced section of the river facilitates greater primary productivity than in the blackwater reach. To examine how turtles are affected by habitat variation, we describe the structure of the assemblage inhabiting a reach of spring-influenced river and make comparisons with an updated data set from the blackwater river habitat (Johnston et al., 2011). We also examine population structure of the three most abundant species (Suwannee Cooter [*Pseudemys suwanniensis*], Loggerhead Musk Turtle [*Sternotherus minor*], and Yellow-bellied Slider [*T. scripta*]) and compare samples from the two river habitats and three adjacent spring habitats that flow into the SFR. Because the SFR ecosystem has not been thoroughly described in published literature and the major emphasis of this paper is how turtle populations vary among habitats, we provide thorough descriptions of the SFR basin and specific habitats in which we sampled turtles.

MATERIAL AND METHODS

Study Area

The Santa Fe River (SFR) is a low gradient (0.36 m/km) river located in northern Florida that flows east to west for 113 km from its headwaters at Lake Santa Fe, Little Lake Santa Fe, and the Santa Fe Swamp to its confluence with the Suwannee River (Fig. 2; Nordlie 1990; Smock and Gilinsky, 1992). The river defines the borders of northern Alachua, southwestern Bradford, southern Union, southern Columbia, northern Gilchrist, and southeastern Suwannee Counties. The SFR basin occupies approximately 3,600 km^2 (Hunn and Slack, 1983; Florida Department of Environmental Protection, 2012). Land use is 47% upland (mostly managed) forest, 22% agriculture, 15% wetland, 11% urban, 3% rangeland, 1% water, 1% transportation, and 1% communication, utilities, and barren land (Florida Department of Environmental Protection, 2012).

In the eastern portion of the SFR basin, the Floridan Aquifer is confined by the Hawthorn Formation and overlain by a surficial sand aquifer. Surface streams and seepage from swamps in this area feed the SFR; its main tributaries are the New River and Olustee Creek (Fig. 2). The Floridan Aquifer in the western portion of the SFR basin is unconfined or semi-confined and receives direct recharge from local rainfall. The SFR flows through karst limestone terrain in the western basin and receives input from ≥ 45 artesian springs or spring groups. Historically, they include four first magnitude (> 2.8 m^3/sec [> 100 ft^3/sec]), 16 second magnitude (> 0.28–2.8 m^3/sec [> 10–100 ft^3/sec]), and 22 third magnitude (0.028–0.28 m^3/sec [1–10 ft^3/sec]) springs (Meinzer, 1927; Rosenau et al., 1977; Hornsby and Ceryak, 1998; Scott et al., 2004). Tributaries of the SFR in the western basin are Cow Creek, which provides surface drainage of swamps in the Waccasassa Flats, and the entirely spring-fed Ichetucknee River (Fig. 2). The Cody Escarpment, a relict Pleistocene shoreline running northwest to southeast, provides a rough demarcation between the Northern Highlands of the eastern SFR basin and the Gulf Coastal Lowlands of the western SFR basin (Fig. 2; Puri and Vernon, 1964; Upchurch, 2007).

Swallet and rise cave systems, which can take in significant portions of surface water flow, are numerous in the western portion of the SFR basin (Butt et al., 2007). The most prominent feature of the SFR is the 4.8 km-long natural land bridge located near the Cody Escarpment (Fig. 2). Here the SFR disappears underground into a large swallet in

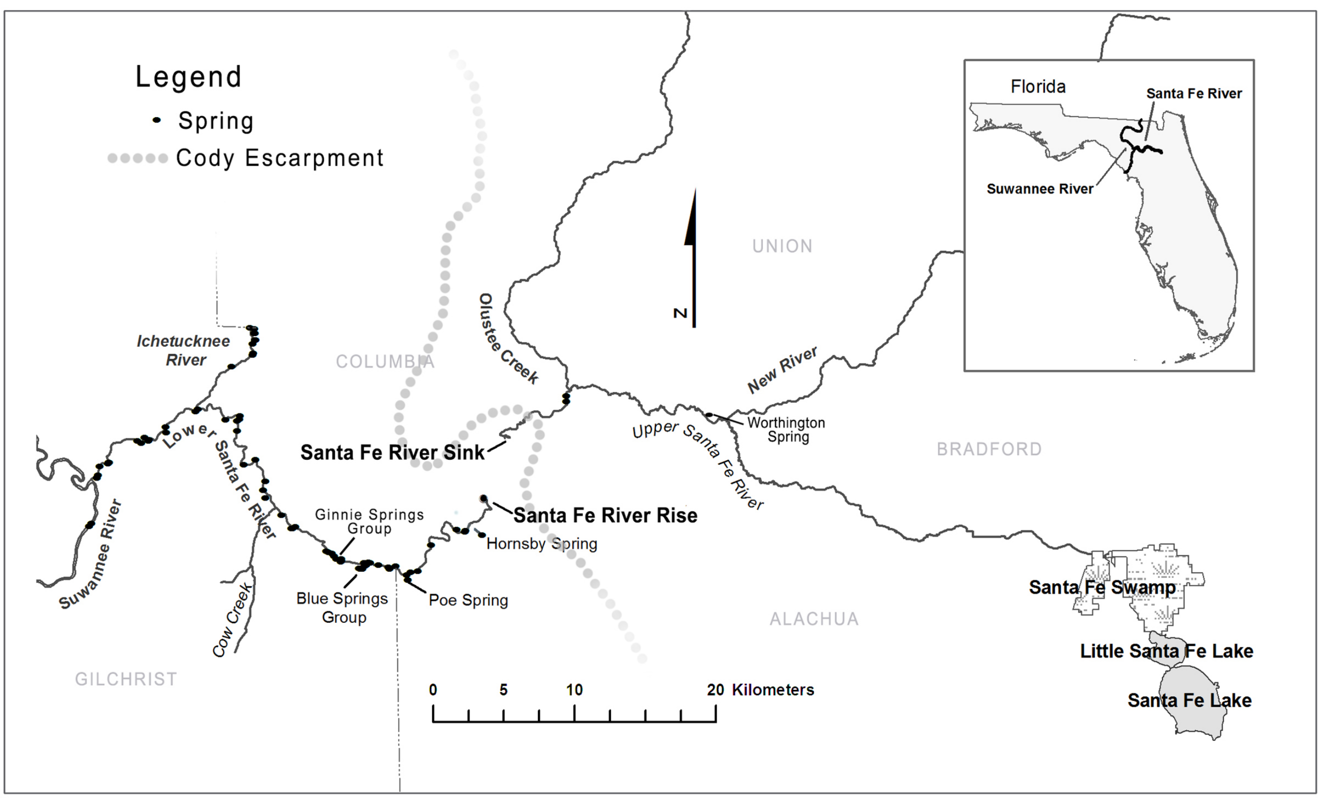

Figure 2. Santa Fe River basin in northern Florida illustrating pertinent geographic features and the two river reaches and three springs sampled in this study.

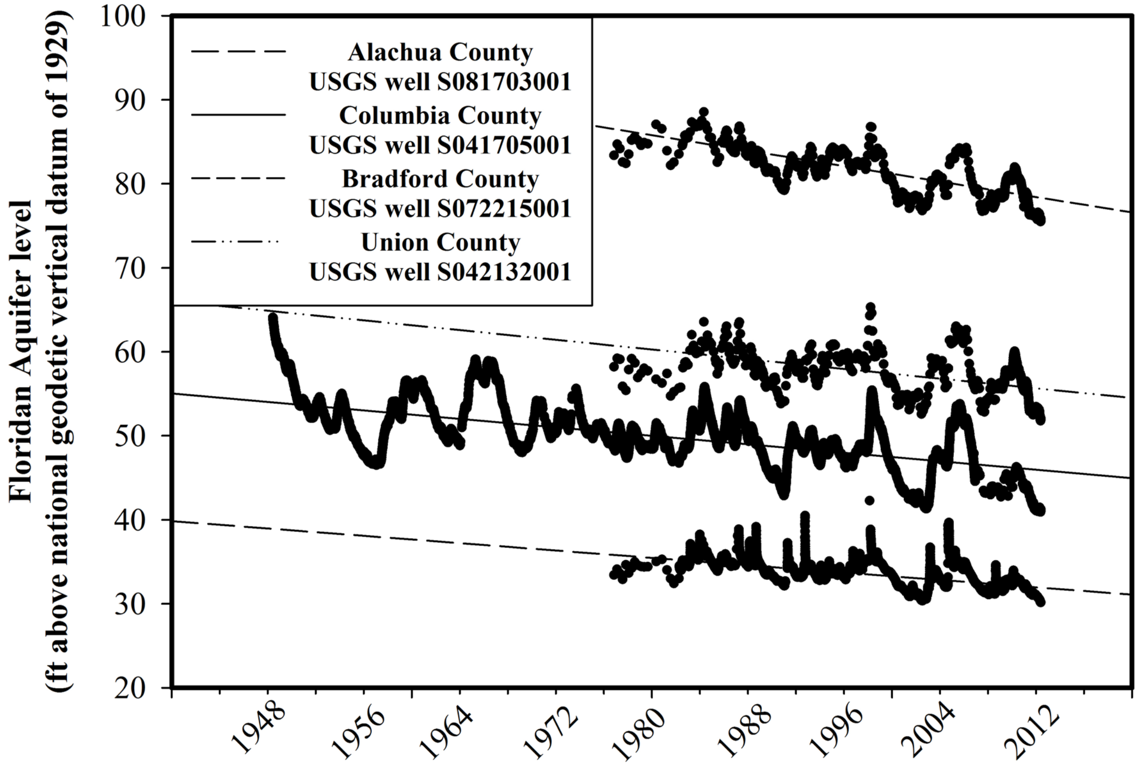

Figure 3. Groundwater levels in northern Florida, with linear regression trend lines. Data accessed from Suwannee River Water Management District Water Data Portal, Monitor Wells. Retrieved from http://www.mysuwanneeriver.org/portal/groundwater.htm on September 1, 2015.

Oleno State Park and then reappears downstream at SFR Rise in River Rise Preserve State Park. The land bridge is the geographical divide between the upper and lower SFR.

The SFR has two distinct hydrogeologic regimes. The upper SFR and upriver reaches of the lower SFR form a blackwater river, having dark, tannic, slightly acidic water with low nutrient levels under normal flow conditions. In the lower SFR, tannic flow receives initial significant augmentation of groundwater as it passes Poe Spring and a group of at least six smaller springs along an 1,100 m section of the river 13 km downriver from SFR Rise (Fig. 2). The Poe Springs area marks the transition from a dark, tannic water to a clearer, more thermally stable river with the addition of clear, mineral rich, alkaline, thermally stable spring water during non-flood conditions. During periods of high rainfall in the eastern SFR basin, large volumes of tannic water overwhelm clear water input from springs in the lower SFR causing the entire lower SFR to become tannic. During periods of low rainfall in the eastern SFR basin, the entire lower SFR may be clear because of groundwater input (Martin and Dean, 2001).

Water levels in the Floridan Aquifer have been declining in northern Florida over the past 70 years (Fig. 3; Knight, 2015). Declines are attributed to extraction of groundwater for human use and reduced groundwater recharge due to surface drainage alterations (Knight, 2015). When aquifer levels decline, the highest elevation springs are the first to lose their flow. The elevation of each spring along the SFR becomes progressively lower from upstream to downstream (e.g., Worthington Spring 16 m, Hornsby Spring 10 m, Poe Spring 8 m, Gilchrist Blue Springs 7.5 m; Fig. 2). Worthington Spring has not flowed for any significant period of time since the 1950s (Knight, 2015). Hornsby Spring was a first magnitude spring, but its flow has declined severely in recent years and even reversed direction during river flooding episodes (Fig. 4). Spring flows have also declined significantly in Poe Spring and Gilchrist Blue Springs (Fig. 4).

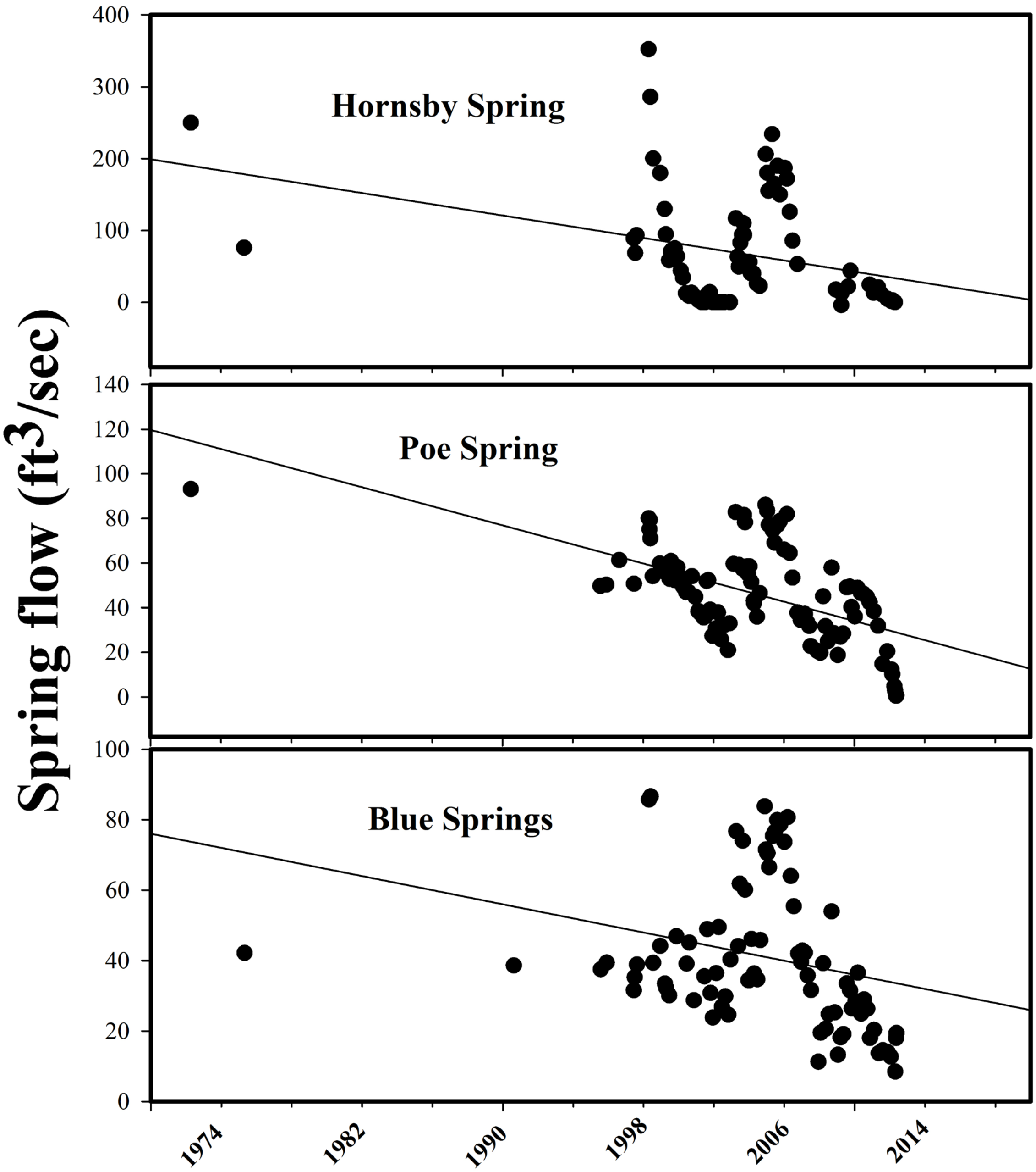

Figure 4. Spring flows in three springs along the lower Santa Fe River, with linear regression trend lines. Pearson Product Moment Correlation: Hornsby Spring ($r = -0.319$, $p = 0.005$), Poe Spring ($r = -0.561$, $p < 0.001$), Blue Springs ($r = -0.272$, $p = 0.011$). Data accessed from Suwannee River Water Management District Water Data Portal, Spring Stations. Retrieved from http://www.mysuwanneeriver.org/portal/springs.htm on September 1, 2015.

In addition to declines in water quantity discharging from many of the springs along the SFR, declines in water quality from springs have also been documented (Katz et al., 1999; Knight, 2015). Concentrations of nitrate, originating primarily from agricultural fertilizers and animal (cattle, poultry, swine) wastes, have been rising in Gilchrist Blue and Ginnie Springs during the past 20 years (Fig. 5; Katz et al., 1999; Knight, 2015). The average nitrate concentration at Gilchrist Blue Springs over this time was 1.76 mg/L, an estimated increase above natural background greater than

3,000% (Knight, 2015). Nitrate concentrations have been declining in springs upstream from Gilchrist Blue Springs (Fig. 5), perhaps due to an increased contribution of deeper, older aquifer water with lower nitrate concentrations (Katz, 2004). Demonstrated effects of elevated nitrate concentrations on aquatic animals include endocrine disruption in male Mosquitofish (*Gambusia holbrookii*, Edwards and Guillette, 2007), abnormal development in anurans (Xu and Oldham, 1997; Marco and Blaustein, 1999), and direct mortality of insects, larval fishes, and anurans (Kincheloe et al., 1979; Camargo and Ward, 1995; Hecnar, 1995). Elevated nitrate also contributes to enhanced growth of the invasive Hydrilla (*Hydrilla verticillata*, Kennedy et al., 2009).

Focal habitats

We sampled turtles in five focal habitats: two reaches of the lower SFR and three adjacent spring-fed habitats (Fig. 6). The upper river reach was the 5 km section of blackwater habitat immediately downriver from SFR Rise (blackwater river reach).. The lower river reach began 8 km farther downstream and consisted of 9 km of spring-influenced habitat between Poe Spring and Deer Spring (spring-influenced river reach). Spring habitats were Hornsby Spring (29.8503°N, -82.5933°W, WGS84), Poe Spring (29.8257°N, -82.6490°W, WGS84), and Gilchrist Blue Springs (29.8299°N, -82.6829°W, WGS84), along with their associated runs (Figs. 6, 7).

Blackwater river reach (BwR)—This section of the SFR flows through River Rise Preserve State Park and is surrounded by intact uplands consisting primarily of mesic flatwoods and upland pine forest (Florida Department of Environmental Protection, 2003). Bottomland forest is the most widespread floodplain habitat. The lowest elevations support a floodplain swamp forest dominated by Green Ash (*Fraxinus pennsylvanica*), Water Tupelo (*Nyssa aquatica*), and Bald Cypress (*Taxodium distichum*). The patchily distributed littoral vegetation occurs along ≤ 5% of the shoreline. Permanently inundated littoral areas support Creeping Burrhead (*Echinodorus cordifolius*) and Spatterdock (*Nuphar advena*). These emergent plants trap floating Water Hyacinth (*Eichhornia crassipes*; introduced), Duckweed (*Lemna* sp.), and Water Spangles (*Salvinia minima*) and anchor Alligator Weed (*Alternanthera philoxeroides*), Smooth Water-hyssops (*Bacopa monnieri*), Marsh Pennywort (*Hydrocotyle* sp.), Water Milfoil (*Myriophyllum* sp.), and Smartweed (*Polygonum densiflorum*) which extend out from the shoreline. Some of the species mentioned above entangle in the branches of fallen trees, sometimes forming large mats. Partially submerged fallen trees and large logs used by turtles for basking and refugia were abundant (typically 15–22 of these sites per km) during our study. Dark, tannic water generally inhibits growth of submersed aquatic macrophytes. However, population explosions of nuisance cyanobacteria (e.g., *Lyngbya wollei*) occur during periods of drought when current velocity slows and clear water conditions allow sunlight to reach all but the deepest parts of the river.

The BwR is usually 20–30 m wide. Water depths range from 0.1 m in the shallowest areas to 8.0 m in the deepest areas, with the majority of the site approximately 1.5–2.0 m deep. The substrate is primarily cobble in most areas, but solid limestone in deeper water. Water temperatures during our study varied seasonally between 12.6°C and 27.1°C (mean = 22.3°C) (Suwannee River Water Management District, 2015). Water chemistry and flow data are in Table 1.

Little is known about benthic macroinvertebrates in this section of the SFR. We observed Asian Clams (*Corbicula fluminea*; introduced), unionid mussels (*Elliptio*, *Villosa*), Apple Snails (*Pomacea paludosa*), and Banded Mystery Snails (*Viviparus georgianus*) during our study.

No published data describe the fish fauna in this section of the SFR, but Hellier (1967) found 43 species in the blackwater river habitat of the upper SFR. Mosquito Fish (*Gambusia holbrookii*), Brook Silverside (*Labidesthes sicculus*), Redbreast Sunfish (*Lepomis auritus*), Redear Sunfish (*L. microlophus*), Bluefin Killifish (*Lucania goodei*), Florida Largemouth Bass (*Micropterus salmoides*), and Golden Shiner (*Notemigonus crysoleucas*) were the most abundant species. We also frequently

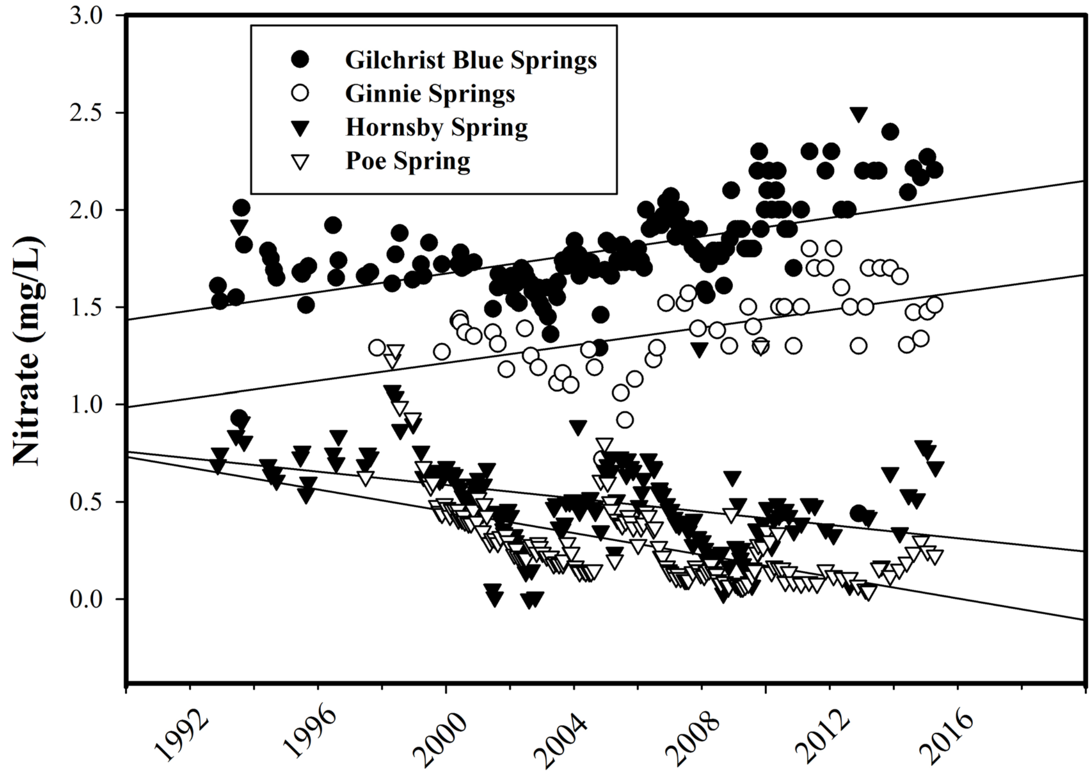

Figure 5. Nitrate levels in water discharging from four springs along the lower Santa Fe River, with linear regression trend lines. Pearson Product Moment Correlation: Blue Springs (r = 0.524, $p < 0.001$), Ginnie Springs (r = 0.527, $p < 0.001$), Hornsby Spring (r = -0.315, $p < 0.001$), Poe Spring (r = -0.554, $p < 0.001$). Data accessed from Suwannee River Water Management District Water Data Portal, Spring Stations. Retrieved from http://www.mysuwanneeriver.org/portal/springs.htm on September 1, 2015.

observed Florida Gar (*Lepisosteus platyrhincus*). We occasionally encountered American Alligators (*Alligator mississippiensis*), Plain-bellied Watersnakes (*Nerodia erythrogaster*), and Brown Watersnakes (*N. taxispilota*). We are unaware of any published studies of other vertebrates in this part of the river.

Recreational use of the upper section of the SFR is low; boating activity is generally limited to canoes and kayaks. Motorized boats are rare due to obstructions such as submerged logs and shallow riffle areas. We occasionally encountered recreational fishing activity.

Spring-influenced river (SiR)—This section of the SFR is bordered by the same floodplain habitats that occur in the previously described BwR habitat, but homes and parks (e.g., Poe Springs Park, Rum Island Park, Gilchrist Blue Springs Park, Ginnie Springs Outdoors) along the river create patches of open, non-forested habitat that are rare in the BwR habitat upriver. This section of the SFR receives input from at least 21 springs and generally exhibits more frequent and prolonged periods of clear water than the blackwater habitat. The SiR is also slightly wider, typically 35–50 m. During 2006–2012, the SFR in this section exhibited higher water visibility, dissolved oxygen, pH, calcium, nitrate, and faster current than the BwR (Table 1; Suwannee River Water Management District, 2015). Water temperatures were similar on average (22.1°C), but less variable (14.9–24.3°C) than in the BwR. Mid-channel water depth varied between 0.5 and 3.5 m. Although the mid-channel substrate is generally hard limestone, a soft sand/organic substrate (≤ 1 m deep) occurs along the edge of the river and in the spring runs feeding the river. Partially submerged fallen trees and large logs were abundant (14–24 per km) during this study.

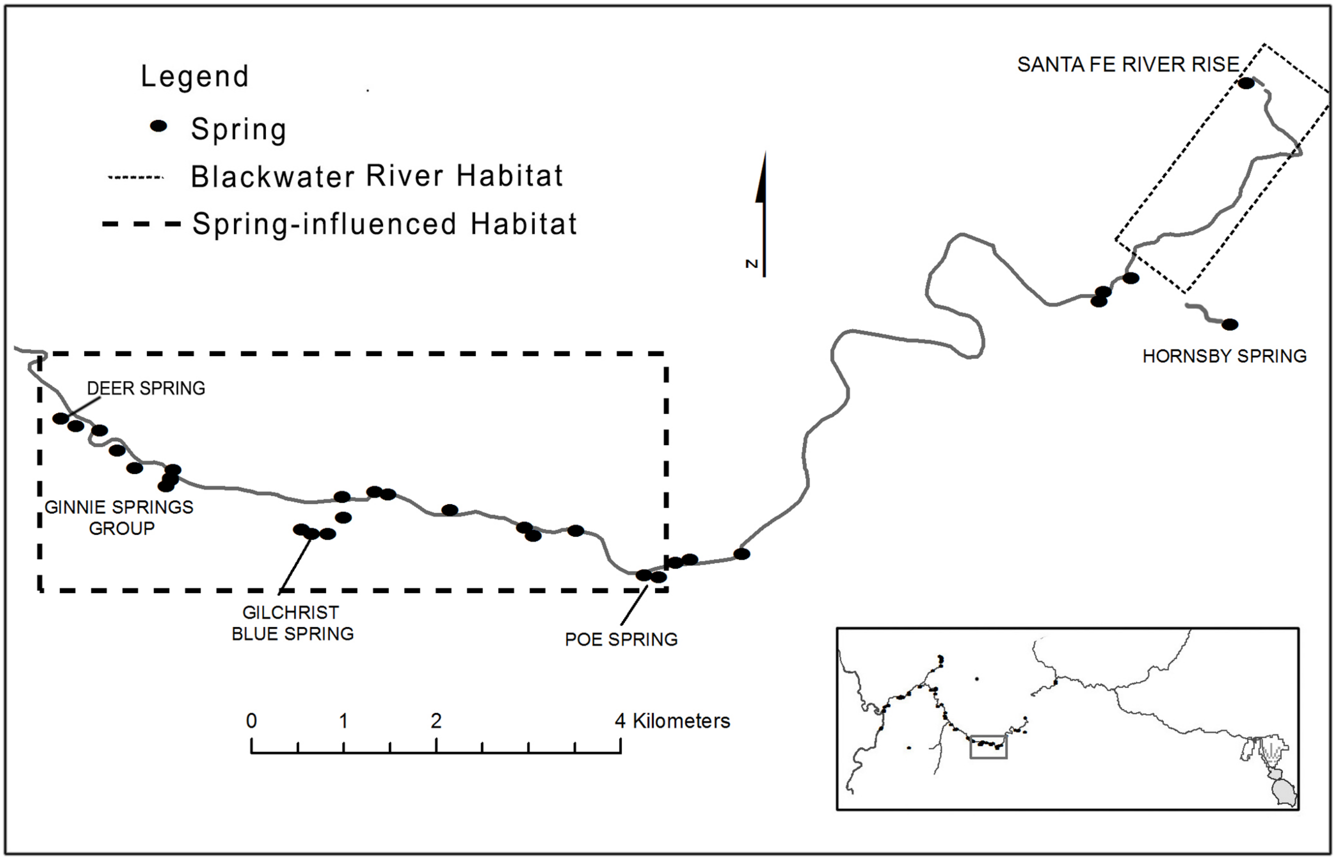

Figure 6. Geographic relationships of the two river reaches and three springs studied between May 2006 and May 2012 in the lower Santa Fe River in northern Florida.

Because of improved water clarity, this section of the SFR supports large patches of submerged aquatic macrophytes including Muskgrass (*Chara* sp.), Carpet Moss (*Fontinalis* sp.), invasive *H. verticillata*, invasive Indian Swampweed (*Hygrophila polysperma*), *Myriophyllum* sp., Springtape (*Sagittaria kurziana*), and Tapegrass (*Vallisneria americana*). During exceptionally prolonged periods of clear water, abundance of this vegetation in parts of the river channel may approach levels normally encountered in classic spring runs, but this abundance decreases with the return of dark water conditions. The invasive species (*Hygrophila polysperma* and *Hydrilla verticillata*) tolerate lower light levels than native species, which gives them an advantage over other species recovering from dark water periods (Bowes et al., 1977; Spencer and Bowes, 1985). Floating plants such as the introduced water hyacinth (*Eichhornia crassipes*), *Hydrocotyle* sp., *Lemna* sp., introduced Water Lettuce (*Pistia stratiotes*), and *S. minima* entangle in the branches of fallen trees and are unaffected by changes in water visibility.

Nuisance benthic and epiphytic algae (*Vaucheria* spp.) and *L. wollei* were first noticed in SFR in the 1990s (T. Morris, pers. obs.). They are most abundant during drought periods, when light penetration is highest and current velocity and dissolved oxygen are lowest. During these times, these algae and cyanobacteria can overgrow and shade out native aquatic macrophytes.

Mattson et al. (1995) described benthic algal and invertebrate communities in spring-fed north Florida streams, including this section of the SFR, and found that spring influence is a major factor affecting these communities. Periphyton production, dominated by diatoms, is highest where springs influence the clarity and chemistry

Table 1. Water parameters at five habitats along the lower Santa Fe River (May 2006–May 2012): blackwater river (BwR), spring-influenced river (SiR), Hornsby Spring (HS), Poe Spring (PS), and Blue Springs (BS). Numbers are mean and minimum-maximum. Data accessed from Suwannee River Water Management District Water Data Portal (http://www.mysuwanneeriver.org/portal.htm).

	BwR	SiR	HS	PS	BS
secchi (m)	0.72	1.88	7.1	2.3	3.7
	0.4–1.4	0.5–5.0	0.45–12.0	0.79–6.7	0.75–7.87
pH	7.42	7.52	7.32	7.36	7.45
	6.26–8.16	5.44–8.53	6.48–7.99	5.97–8.75	5.47–8.04
dissolved O_2 (mg/L)	4.9	5.5	1.0	1.0	5.4
	1.5–12.1	2.6–9.2	0.1–5.0	0.1–7.6	3.7–10.6
temperature (°C)	22.3	22.1	22.5	22.4	22.5
	12.6–27.1	14.9–24.3	21.1–25.8	22.0–25.2	21.8–23.4
nitrate (mg/L)	0.16	0.77	0.38	0.18	1.92
	0–0.68	0.22–1.2	0.01–1.29	0.06–1.3	1.56–2.3
calcium (mg/L)	57.9	63.0	75.5	71.4	65.7
	8.3–82.3	27.1–75.0	20.2–99.7	48.3–83.9	58.7–72.1
flow (ft^3/sec)	130.5	776.9	25.7	30.0	27.8
	24–1864	342 - 4470	-3.8 - 126	0.45–64.4	8.43–64.0

of the river. Benthic invertebrate species richness is also positively associated with spring input. Woody substrates support rich assemblages of invertebrates, dominated by aquatic insects such as Diptera (primarily chironomids), Ephemeroptera, and Trichoptera. Gastropod mollusks (primarily *Elimia floridensis*, Hydrobiidae, Ancylidae) and crustaceans (primarily the amphipod *Hyalella azteca*) are also characteristic of these substrates. Chironomids, oligochaetes, gastropods (*Campeloma*), and bivalves (*Corbicula*, *Elliptio*, *Musculium*, *Sphaerium*, *Villosa*) dominate sandy substrates. Submerged aquatic macrophytes are another major invertebrate habitat in this type of river, with *Sagittaria kurziana* supporting the highest densities, especially chironomids. Crayfish (*Procambarus* spp.) were the primary prey in diet studies of Suwannee Bass (*Micropterus notius*) and Largemouth Bass (*M. salmoides*) providing indirect evidence of their occurrence (Schramm and Maceina, 1986).

Hellier (1967) found 42 fish species in the upper SFR. The most abundant were *G. affinis* [*holbrooki*], *L. goodei*, Redeye Chub (*Hybopsis* [*Notropis*] *harperi*), Coastal Shiner (*Notropis petersi* [*petersoni*]), Tadpole Madtom (*Noturus gyrinus*), and Sailfin Molly (*Molliensa* [*Poecilia*] *latipinna*). Bluegill (*L. macrochirus*), *L. microlophus*, *M. notius*, and Blackbanded Darter (*Percina nigrofasciata*) were not common in the sample of captured fishes, but were reported to be abundant based on observations by Hellier (1967). During an electrofishing survey in this section of the SFR, Bonvechio et al. (2005) reported that capture rates of *M. notius* and *M. salmoides* were 22.6 and 19.8 fish/hr, respectively. During our study, we frequently observed Bowfin (*Amia calva*; Suarez et al., 2011), a species not reported by Hellier (1967) or Bonvechio et al. (2005). Nico et al. (2012) recently added South American Suckermouth Catfishes (*Pterygoplichthys* spp.) to the list of known species.

With the exception of our turtle studies, other vertebrates in this reach of the SFR have not been studied. We observed *A. mississippiensis*, *N. erythrogaster*, *N. taxispilota*, and Eastern

Figure 7. Illustrations of the three spring-fed habitats studied in the lower Santa Fe River in northern Florida. Upper left, Hornsby Spring, upper right, Poe Spring, lower left, Gilchrist Blue Spring, lower right, Gilchrist Blue Spring run. Photos by G. A. Shemitz, except lower right by J. C. Mitchell.

Diamondback Rattlesnakes (*Crotalus adamanteus*). We also frequently observed River Otters (*Lontra canadensis*; Mitchell and Johnston, 2012) and occasionally encountered Beavers (*Castor canadensis*), introduced Capybaras (*Hydrochoerus hydrochaeris*), and West Indian Manatees (*Trichechus manatus*).

Recreation in the lower reach of the SFR is high because the many parks located near springs provide easy access to the river. Poe Springs County Park, Rum Island County Park, Ginnie Springs Outdoors, and Blue Springs Park bring an average annual attendance of 246,530 visitor-days (Borisova et al. 2014). Picnicking and swimming are popular activities at Rum Island County Park that have an annual average of 9,800 visitor-days. At Ginnie Springs Outdoors, which has an average annual attendance of 205,000 visitor-days, activities such as picnicking, camping, swimming and scuba diving in springs, and tubing on the river are popular. Both parks also have boat ramps. Boating activity is higher in this section of the river than in the BwR. In addition to canoes and kayaks, motorized boats ranging from small jon boats with trolling motors to larger boats with 40 horsepower outboard motors are common. During a typical day of snorkeling, we encountered 2–5 motorized boats. We snorkeled only on weekdays when recreational activity of all types was lowest, so our estimate of boat activity is conservative. The parking lot at Rum Island Park has enough parking for six vehicles with boat trailers. During weekend days, these spots are usually full. Fewer boats typically enter the river at the Ginnie Springs boat ramp. Motorized boats also enter the SFR at the Poe Springs Park boat ramp, but those boats rarely exceed 10 horsepower (V. LeGree, pers. comm.).

Hornsby Spring (HS)—This is the largest spring in Alachua County (Scott et al., 2004). It was once considered a first magnitude spring, but it is now a second magnitude spring due to declining discharge (Fig. 3). Water temperatures during our study were 21.1–25.8°C (mean = 22.5°C) (Suwannee River Water Management District, 2015). Spring flow and water chemistry data are in Table 1. The spring basin is roughly 45 m in diameter. It averages 2 m deep and is approximately 10 m deep at the main vent. A smaller vent is approximately 5 m deep. The run flows west for 1.5 km to the SFR. The upper part of the run flows through floodplain swamp in a channel that varies in width (9–16 m) and depth (0.5–2.2 m). Some of the flow enters a swallet nearly 275 m downstream from the spring, and flows underground to the SFR. Downstream from this swallet, the run enters a broad swampy area and flows for 650 m to another swallet which directs more of the flow underground to the SFR. This was the historic end of the run until the 1930s, when a shallow (< 0.5 m), narrow (2–4 m) 625 m long canal was dredged to Darby Spring and the SFR.

Aquatic vegetation in the spring basin and run consists of patches of *E. cordifolius*, *E. crassipes*, *Hydrocotyle* spp., Red Ludwigia (*Ludwigia repens*), Naiad (*Najas guadalupensis*), Pickerel Weed (*Pontederia cordata*), *S. kurziana*, and *S. minima*. Benthic filamentous algae (*Vaucheria*) and cyanobacteria (*L. wollei*) occurred in scattered patches on the substrate. The majority of the aquatic vegetation occurs in and around the spring basin because the majority of the run is heavily shaded. Partially submerged fallen trees and large fully submerged logs are abundant along the run.

We observed nine native fish species, including Bowfin (*A. calva*), Lake Chubsucker (*Erimyzon sucetta*), *L. auritus*, *L. macrochirus*, *L. microlophus*, Spotted Sunfish (*Lepomis punctatus*), *M. notius*, *N. crysoleucas*, and Hogchoker (*Trinectes maculatus*). We captured and removed all non-native Sailfin Catfish (*Pterygoplichthys* spp.) we encountered (Nico et al. 2012). We also observed Spring Crayfish (*P. spiculifer*) and gastropods (*P. paludosa*, *V. georgianus*). We frequently encountered one or two small (< 2 m total length) American Alligators (*A. mississippiensis*).

A boardwalk partially surrounds the spring. Most of the uplands surrounding the spring are open, grassy low-rolling hills that rise 4–5 m above water level. The Church of the Seventh Day Adventists owns the entire property surrounding the spring and spring run and operates Camp Kulaqua, a retreat and conference center for schools, community programs, and various non-profit organizations. This is also a popular summer camp; hundreds of school children swim in the spring and canoe in the run each year. All animals are protected within the property.

Poe Spring (PS)—This is a second magnitude spring located within Poe Spring County Park. It is approximately 36 m in diameter; the vent is 5.7 m deep. Discharge flows swiftly through a short (23 m), shallow (< 1 m) run to the SFR. Water temperatures during our study were 22.0–25.2°C (mean = 22.4°C) (Suwannee River Water Management District, 2015). Spring flow and water chemistry data are in Table 1. The shallow parts of the basin and run have a sand or rock bottom kept free of benthic algae by swimmers. The deeper vent area is 90% covered in algae. The only aquatic vegetation we observed was along the basin's western margin that harbored small amounts of *B. monnieri, Chara* sp., *Hydrocotyle* sp., *Lemna* sp., *L. repens*, Browne's savory (*Micromeria brownie*), *Nitella* sp., and filamentous algae. We observed seven native fish species in the spring, including *A. calva*, *G. holbrooki*, *L. macrochirus*, *L. punctatus*, *L. goodei*, *N. harperi*, and *T. maculatus*. We also captured and removed non-native *Pterygoplichthys* spp. whenever encountered (Nico et al., 2012).

The north and west sides of the spring are surrounded by floodplain forest, but the east side of the spring is bordered by a 0.2 ha open, grassy picnic area and bordered by a retaining wall (built in 1991) which has vertical sides and steps for human access. Average annual attendance was 5,730 visitor-days (Borisova et al., 2014), but we observed substantially less activity during the majority of our study. We were the only people in the water during most of our sampling sessions at this location.

Gilchrist Blue Springs (BS)—This habitat is located within the privately owned Blue Springs Park in Gilchrist County. It is one of at least six locations in Florida called "Blue Spring." The most appropriate name of this location is Gilchrist Blue Springs, but for the purpose of this paper we refer to it as Blue Springs (BS). There are three springs in the park (Blue Spring, Naked Spring, Little Blue Spring) which flow into a main run that flows north through floodplain forest and feeds the SFR. Water in this habitat has substantially higher concentrations of dissolved oxygen and nitrate than in Hornsby and Poe Springs (Table 1). Water temperatures during our study were 21.8–23.4°C (mean = 22.5°C) (Suwannee River Water Management District, 2015).

Blue Spring is a second magnitude spring that is 40 m in diameter and has several vents 5.8 m deep, a wooden retaining wall on its south side, and a diving platform located on the west side. Naked Spring, located 140 m east of Blue Spring, is a third magnitude spring that is approximately 30 m in diameter and has two vents approximately 3–4 m deep. It has a short (100 m) run that flows west to join the main run. Naked Spring has a limestone substrate, but much of the run has a deep (up to 1 m) sand/organic substrate. Little Blue Spring, located 75 m west of Blue Spring, is a small (18 m diameter), heavily shaded fourth magnitude spring with a vent 3.1 m deep. A shallow (< 1 m) run flows 50 m to join the main run.

The total area of aquatic habitat created by the springs and their network of runs is 1.0 ha. The main run is 350 m long, 6–27 m wide and approximately 1 m deep. The majority of the main run has a hard limestone substrate, but several small patches of deep (up to 1 m) sand/organic substrate occur along the edges. Invasive *Hydrilla* is abundant and dominates all other aquatic vegetation in Blue Spring, Naked Spring, Naked Spring run, and the first 180 m of the main run. The downstream section of the main run is also heavily vegetated, but native species such as *L. repens*, *P. cordata*, *S. kurziana*, *V. americana*, and Atamasco Lily (*Zephyranthes atamasco*) are predominant.

Aquatic invertebrates and vertebrates are abundant. Liebowitz et al. (2014) reported high densities of gastropods (primarily *Elimia floridensis*) at this site. Spring Crayfish (*P. spiculifer*) were abundant. Fish species included *A. calva*, American Eel (*Anguilla rostrata*), Brown Darters (*Etheostoma edwini*), *G. holbrooki*, Least Killifish (*Heterandria formosa*), *L. platyrhincus*, *L. punctatus*, *L. macrochirus*, *L. goodei*, Spotted Suckers (*Minytrema melanops*), *M. notius*, *M. salmoides*, Mullet (*Mugil cephalus*), *N. gyrinus*, *N. harperi*, *P. nigrofasciata*, *P. latipinna*, Atlantic Needlefish (*Strongylura marina*), Gulf Pipefish (*Syngnathus scovelli*), and *T. maculatus*. We also observed *Castor canadensis*, *Lutra canadensis*, Lesser Siren (*Siren intermedia*), Greater Siren (*S. lacertina*), *N. erythrogaster*, and Banded Water Snakes (*N. fasciata*).

This park is a popular destination for aquatic activities such as swimming and jumping off the dive platform. Average annual attendance is 41,000 visitor-days (Borisova et al., 2014). A large area (> 2 ha) of the park just south of the springs is open sandy uplands used by park visitors for parking, picnicking, and camping.

Study Species and Methods

Eleven native freshwater turtle species occur in the SFR and its adjacent springs (Meylan, 2006; Johnston et al., 2011, 2012, 2015). This assemblage includes a unique combination of species whose geographic ranges overlap in the SFR basin to create a turtle diversity hotspot. Three species occur primarily in the Florida peninsula and are at the northern edges of their ranges (Florida Softshell [*A. ferox*], Florida Red-bellied Cooter [*P. nelsoni*], Peninsula Cooter [*P. peninsularis*]). Two species occur throughout most of eastern North America (Snapping Turtle [*C. serpentina*], Eastern Musk Turtle [*S. odoratus*]). Two occur primarily throughout the southeastern Coastal Plain, but rarely in rivers (Chicken Turtle [*Deirochelys reticularia*], Striped Mud Turtle [*Kinosternon baurii*]). One species occurs primarily in spring-fed habitats in the southeastern United States (*S. minor*), and one is at the southeastern edge of its range (*T. scripta*). The Suwannee Cooter (*P. suwanniensis*) is endemic to river drainages flowing into the northeastern Gulf of Mexico between the Ochlocknee River in the Florida panhandle and the Alafia River near Tampa. The Suwannee Alligator Snapping Turtle (*Macrochelys suwanniensis*) is endemic to the SFR and Suwannee River basins. We found two *D. reticularia* outside of our focal habitats and did not include this species in our analyses.

Sampling—We used two methods to capture turtles during our six-year study. We captured diurnal species by hand while snorkeling in each of the five habitats described above. During each snorkel session, a group of 4–8 experienced snorkelers attempted to capture all turtles observed during mid-morning to mid-afternoon (~0900–1500 h), placed them in canoes, and then returned to shore to measure and mark all individuals. We also used baited hoop traps to enhance capture of crepuscular and nocturnal species not easily observed during daytime snorkeling. We used single funnel nylon hoop traps baited with fresh cut fish. We used three different trap sizes (76 cm diameter, 2.5 cm mesh; 91 cm diameter, 6.4 cm mesh; 122 cm diameter, 6.4 cm mesh) to facilitate placement of traps in sites of varied water depths and to increase our capacity to detect a wide range of species and size classes. During each trap session, we set 8–20 traps (one 2.5 cm mesh trap for every three 6.4 cm mesh traps) with a minimum of 50 m between traps during late afternoon and checked them the following morning. Each trap set overnight constituted one trap-night (TN). Sampling occurred in all months as water visibility and human recreational activity permitted (May 2006–May 2012). Sampling sessions were not homogeneous among years, seasons, or sites due to irregular patterns of water clarity.

We measured each captured turtle for straight midline carapace length (CL) and straight midline plastron length (PL) to the nearest 1 mm using aluminum tree calipers (Haglöf®, Långsele, Sweden) or dial calipers (Scienceware, Wayne, NJ). We also measured the length of the longest foreclaw on the left forelimb on all *P. suwanniensis* and *T. scripta* using dial calipers. We marked small (< 120 mm PL) turtles individually by filing or cutting notches in the marginal scutes and peripheral bones using a standard numbering system (Cagle, 1939). We marked larger (> 120 mm PL) individuals with drill holes following the same system. *Apalone ferox* were marked by inserting passive integrated transponder (PIT) tags into the muscle and connective tissue between the plastron and pelvis lateral to the midline (Runyan and Meylan, 2005). Snapping Turtles (*C. serpentina* and *M. suwanniensis*) were also marked with PIT tags (in addition to carapace marking), but insertion was into the ventrolateral tail muscle (Johnston et al., 2012, 2015). We released all turtles at the capture site on the same day of capture.

We determined sex based on sexually dimorphic features reported by Jackson (2006), Thomas (2006), Zappalorti and Iverson (2006), and Ernst and Lovich (2009). We palpated female *P. suwanniensis* and *T. scripta* for eggs. Size at maturity for females was based on PL of the smallest gravid individual. Male *P. suwanniensis* and *T. scripta* were considered to have reached maturity when they attained the PL at which allometric elongation of the fore-claws occurs (Gibbons and Greene, 1990; Huestis and Meylan, 2004; Readel et al., 2008). Sizes at maturity of female and male *S. minor* were based on published data from the nearest studied populations (Iverson, 1978; Etchberger and Stovall, 1990; Cox et al., 1991). Because males mature at smaller sizes than females in *P. suwanniensis*, *S. minor*, and *T. scripta*, we considered immature females that were larger than the smallest mature male as subadult females. All individuals smaller than the smallest subadult female were considered juveniles.

Statistical Analysis—We categorized capture data by the five habitats we studied: (1) BwR, (2) SiR, (3) HS, (4) PS, and (5) BS (Fig. 5). To compare assemblage structure between the two river habitats, we calculated species richness, species diversity (Shannon H), and relative frequencies of species following Magurran (2004) for each snorkel session and then compared the values of each parameter between the two sites using a Mann-Whitney rank sum test (U). We followed the same protocol to compare the same assemblage parameters obtained from trap sessions. To compare capture per unit effort between river habitats, we used number of turtles captured per person-hour (T/PH) and per trap-night (T/TN) for each snorkel and trap session, respectively.

We evaluated differences in population structure of the three most abundant species (*P. suwanniensis, S. minor, and T. scripta*) in the five habitats. We first determined whether capture method affected our perception of population structure of each species (proportions of juveniles, subadult females, adult males and females) in each river habitat using the two sample z-test for comparisons of proportions of demographic groups. If capture method did not affect the proportion of any demographic group of a particular species in the river, we combined trap and snorkel capture data for that species for all subsequent comparisons among the five habitats. We based comparisons of results for snorkeling and trapping sessions only on the two river samples because we sampled the springs only by snorkeling. We tested the null hypothesis that population structure was not significantly different in all habitat pair combinations with a X^2 test of equality of demographic proportions in a 4 x 5 x 2 table. We then used the post hoc multiple comparisons Marascuilo procedure (https://www.statstodo.com/MultiProp_Pgm.php) to test whether proportions of the four demographic groups (population structure) were significantly different among the five habitat types. We used X^2 analysis to determine which demographic groups contributed to significant differences between habitat pairs; we used the Fisher Exact Probability Test when sample sizes were too small for the X^2 test. We used X^2 analysis to test whether the sex ratio of adults differed from 1:1 in each habitat. We accepted statistical significance at $\alpha \leq 0.05$. We performed analyses in SigmaPlot v12.3, except for the Marascuilo procedure calculated online. Turtle taxonomy and common names follow Crother (2012) and Thomas et al. (2014).

RESULTS

Assemblage structure

We captured 374 individual turtles of ten native species in the BwR and 1,798 individuals of ten native species in the SiR (Table 2). Nine individuals were captured in both river habitats (1 *C. serpentina*, 4 *P. peninsularis*, 4 *P. suwanniensis*). Species richness per snorkel session was similar in the BwR (mean = 4.7 ± 1.9, 3–9, 10 sessions) and SiR (mean = 5.2 ± 0.9, 4–7, 17 sessions; U = 56.00, $p = 0.14$). Using trapping data only, species richness per session was significantly higher in the SiR (mean = 4.1 ± 1.3, 2–7, 43 sessions) than in the BwR (mean = 1.5 ± 1.1, 0–4, 21 sessions; U = 55.50, $p < 0.001$). Species diversity (Shannon H) per snorkel session did not differ significantly between the BwR (mean = 1.0 ± 0.2, 0.675–1.538, 10 sessions) and SiR (mean = 0.92 ± 0.18, 0.678–1.392, 17 sessions; U = 65.00, $p = 0.327$). Trapping data indicated a significantly higher species diversity in the SiR (mean = 0.97 ± 0.24, 0.279–1.379, n = 43 sessions) than in the BwR (mean = 0.34 ± 0.40, 0–1.332, 21 sessions; U = 75.00, $p < 0.001$).

Relative abundances of all ten species were not significantly different between snorkeling sessions in the BwR and SiR (Fig. 8). Using trapping data only, relative abundance of seven species was similar in the two river habitats. Relative abundances of *C. serpentina* and *S. minor* were significantly higher during trapping sessions in the SiR than in the BwR. Relative abundance of *T. scripta* was significantly higher during trapping in the BwR than in the SiR.

We captured *S. minor* and *T. scripta* at significantly higher rates in the SiR than in the BwR using both sampling methods (Tables 3, 4). We also captured *C. serpentina* (trap sessions), *P. suwanniensis* (snorkel sessions), and *P. nelsoni* (trap sessions) at significantly higher rates in the SiR than in the BwR. Capture rates of *A. ferox*, *K. baurii*, *M. suwanniensis*, *P. peninsularis*, and *S. odoratus* did not differ between habitats using either method.

Population Structure

Pseudemys suwanniensis—Our total *P. suwanniensis* sample consisted of 418 (34.1%)

Table 2. Raw data for number of individuals of each turtle species captured in blackwater (BwR) and spring-influenced river (SiR) habitats in the lower Santa Fe River (May 2006–May 2012) using hand capture and trap capture methods. Percent of total sample in each habitat using each capture method is in parentheses. Sampling in BwR: 10 snorkel sessions, 142 person-hours; 21 trap sessions, 184 trap-nights. Sampling in SiR: 17 snorkel sessions, 250 person-hours; 43 trap sessions, 676 trap-nights.

	BwR		SiR	
	hand	trap	hand	trap
Apalone ferox	2 (0.6)	2 (2.9)	3 (0.3)	10 (1.1)
Chelydra serpentina	1 (0.3)	2 (2.9)	30 (2.7)	87 (9.9)
Kinosternon baurii	2 (0.6)	0 (0)	4 (0.4)	3 (0.3)
Macrochelys suwanniensis	9 (2.9)	4 (5.8)	9 (0.8)	18 (2.0)
Pseudemys nelsoni	11 (3.5)	0 (0)	17 (1.6)	9 (1.0)
Pseudemys peninsularis	9 (2.9)	0 (0)	18 (1.6)	2 (0.2)
Pseudemys suwanniensis	167 (53.2)	2 (2.9)	625 (57.0)	21 (2.4)
Sternotherus minor	84 (26.8)	5 (7.2)	228 (20.8)	233 (26.4)
Sternotherus odoratus	1 (0.3)	0 (0)	2 (0.2)	9 (1.0)
Trachemys scripta	28 (8.9)	54 (78.3)	160 (14.6)	491 (55.6)
All species	314	69	1096	883

juveniles (34–179 mm PL), 121 (9.9%) subadult females (182–295 mm PL), 287 (23.4%) adult females (296–381 mm PL), and 400 (32.6%) adult males (181–294 mm PL) (Fig. 9). The adult sex ratio (1.39M:1F) was significantly male biased ($X^2 = 18.587$, $p < 0.001$). We captured 167 individuals in the BwR, 625 in SiR, 227 in HS, 136 in PS, and 136 in BS (Fig. 10). We captured sixty-five individuals in more than one habitat. All 1,226 individuals were hand captured while snorkeling; 23 of those individuals also captured in traps. We therefore used only snorkel data for comparisons of population structure among habitats.

Population structure differed significantly among habitats (Table 5; Fig. 10). The overall X^2 indicated at least one significant difference in population structure among the ten combinations of habitat pairs (Table 5; $X^2 = 128.845$, df = 4, $p < 0.0001$). The Marascuilo procedure revealed there were six combinations of habitat pairs in which

Table 3. Capture rate (turtles/person-hr) per snorkel session of each species in two river reaches using the hand capture method: blackwater river (BwR), spring-influenced river (SiR). Data are presented as mean ± 1 SD, minimum-maximum. U = Mann-Whitney rank sum test for capture rates between habitats.

	BwR (10 sessions)	SiR (17 sessions)	U	*p*
Apalone ferox	0.011 ± 0.02 0–0.45	0.006 ± 0.02 0–0.05	75.0	0.512
Chelydra serpentina	0.006 ± 0.016 0–0.05	0.043 ± 0.054 0–0.167	55.5	0.093
Kinosternon baurii	0.007 ± 0.021 0–0.067	0.004 ± 0.017 0–0.071	78.0	0.598
Macrochelys suwanniensis	0.006 ± 0.016 0–0.05	0.008 ± 0.03 0–0.125	79.0	0.655
Pseudemys nelsoni	0.056 ± 0.064 0–0.20	0.053 ± 0.058 0–0.167	79.5	0.794
Pseudemys peninsularis	0.140 ± 0.086 0–0.30	0.147 ± 0.09 0–0.30	69.0	0.764
Pseudemys suwanniensis	1.344 ± 0.544 0.5–1.65	4.115 ± 1.279 1.1–6.3	8.0	<0.001
Sternotherus minor	0.317 ± 0.181 0–0.60	0.798 ± 0.548 0–2.38	29.0	0.005
Sternotherus odoratus	0.006 ± 0.016 0–0.05	0.005 ± 0.02 0–0.083	78.0	0.598
Trachemys scripta	0.185 ± 0.175 0–0.50	0.691 ± 0.187 0.45–1	3.0	<0.001
Total	2.08 ± 0.540 1.2–3.2	5.87 ± 1.451 2.6–9.25	1.0	<0.001

population structure differed significantly (Table 5). The high numbers of juveniles in HS and BS contributed to differences between HS-PS (X^2 = 44.94, $p < 0.001$), HS-BwR (X^2 = 72.89, $p < 0.001$), HS-SiR (X^2 = 98.34, p < 0.001), BS-BwR (X^2 = 43.5, p < 0.001), BS-SiR (X^2 = 37.25, $p < 0.001$), and BS-PS (X^2 = 23.43, $p < 0.001$). The low numbers of subadult females in HS and BS also contributed to differences between HS-PS (X^2 = 12.92, $p <$ 0.001), HS-BwR (X^2 = 13.43, $p < 0.001$), HS-SiR (X^2 = 13.29, $p < 0.001$), BS-BwR (X^2 = 13.52, $p <$ 0.001), BS-SiR (X^2 = 12.45, $p < 0.001$), and BS-PS (X^2 = 13.39, $p < 0.001$). The adult sex ratio was significantly male biased in the BwR (1.43:1; X^2 = 4.101, $p = 0.043$), SiR (1.32:1; X^2 = 8.01, $p = 0.005$) and PS (2.28:1; X^2 = 14.411, $p = 0.0001$), but did not differ significantly from 1:1 in HS (X^2 = 0.231, $p = 0.631$) and BS (X^2 = 0.018, $p = 0.8927$).

Sternotherus minor—Our total *S. minor* sample consisted of 96 (13.5%) juveniles (26–57 mm CL), 68 (9.6%) subadult females (58–79 mm CL), 193 (27.2%) adult females (80–128 mm CL), and 352 (49.6%) adult males (58–131 mm CL). The adult sex ratio (1.82:1) was significantly male biased (X^2 = 46.387, $p < 0.001$). We captured 89 individuals in the BwR, 453 in SiR, 65 in HS, 16 in

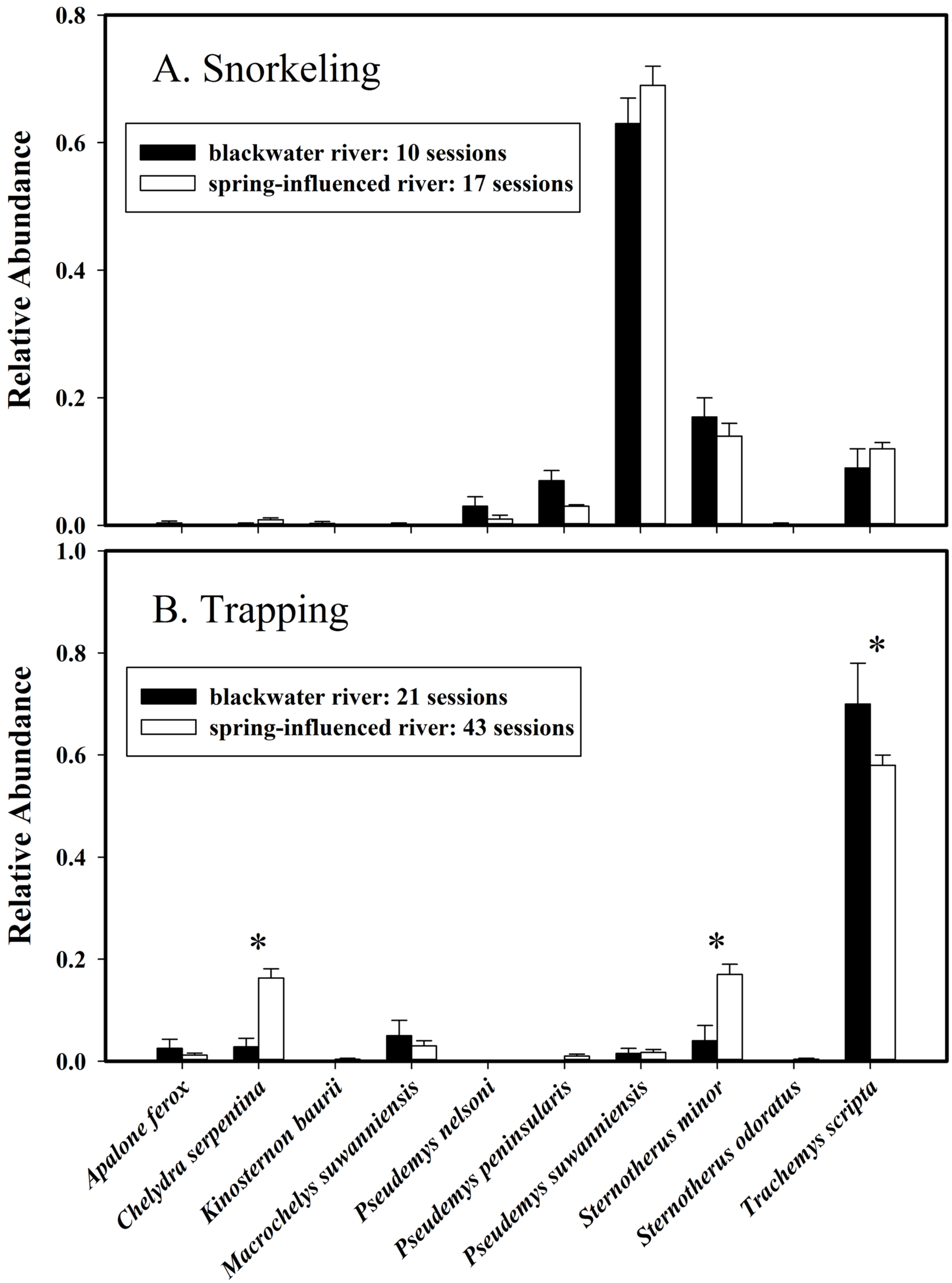

Figure 8. Relative abundance of all freshwater turtle species captured during snorkel (A) and trap (B) sessions in two different river habitats in the Santa Fe River in northern Florida. Results are means and standard errors of all sessions combined for each habitat sampled. Asterisk (*) indicates significant difference ($p < 0.05$) between habitats.

Table 4. Capture rate (turtles/trap-night) per trap session of each species in two river reaches using trap capture method; blackwater river (BwR), spring-influenced river (SiR). Data are presented as mean ± 1 SD, minimum-maximum. U = Mann-Whitney rank sum test for capture rates between habitats..

	BwR (21 sessions)	SiR (43 sessions)	U	*p*
Apalone ferox	0.017 ± 0.056 0–0.25	0.031 ± 0.106 0–0.10	411.0	0.416
Chelydra serpentina	0.011 ± 0.034 0–0.14	0.290 ± 0.201 0–0.58	34.5	<0.001
Kinosternon baurii	0 ± 0 0–0	0.011 ± 0.034 0–0.17	---	---
Macrochelys suwanniensis	0.037 ± 0.089 0–0.33	0.043 ± 0.065 0–0.30	374.0	0.199
Pseudemys nelsoni	0 ± 0 0–0	0.013 ± 0.03 0–0.10	---	---
Pseudemys peninsularis	0 ± 0 0–0	0.002 ± 0.011 0–0.05	---	---
Pseudemys suwanniensis	0.004 ± 0.015 0–0.07	0.049 ± 0.126 0–0.67	361.5	0.077
Sternotherus minor	0.021 ± 0.073 0–0.33	0.362 ± 0.454 0–1.85	112.0	<0.001
Sternotherus odoratus	0 ± 0 0–0	0.011 ± 0.03 0–0.15	---	---
Trachemys scripta	0.381 ± 0.477 0–2.17	1.070 ± 0.643 0.35–3.0	103.5	<0.001
Total	0.469 ± 0.539 0–2.5	1.957 ± 1.150 0.08–5.0	64.5	<0.001

PS, and 86 in BS (Fig. 11). Using data from SiR, we found no significant effect of sampling method on the proportion of juveniles (z = 0.0458, $p = 0.963$), subadult females (z = -0.166, $p = 0.868$), adult females (z = 1.221, $p = 0.222$), or adult males (z = 0.226, $p = 0.821$). The sample from the BwR was too small to permit similar statistical analysis. We therefore combined hand capture and trap capture data for comparisons of demographic structure among habitats.

Population structure differed significantly among habitats (Table 6; Fig. 11). Overall X^2 indicated at least one significant difference in population structure among the ten combinations of habitat pairs (Table 6; $X^2 = 16.522$, df = 4, $p = 0.0024$). The Marascuilo procedure revealed two combinations of habitat pairs in which population structure differed significantly (Table 6). The high number of juveniles in BS was the source of differences in BS-BwR ($X^2 = 6.1$, $p = 0.0135$) and BS-SiR ($X^2 = 10.17$, $p = 0.0014$). Adult sex ratio was significantly male biased in the BwR (2.33:1; $X^2 = 11.200$, p < 0.001), SiR (1.90:1; $X^2 = 34.984$, $p < 0.001$), and HS (1.93:1; $X^2 = 4.455$, $p = 0.035$), but did not differ significantly from 1:1 in BS ($X^2 = 0.148$, $p = 0.701$). The small sample of adults from

Table 5. Pairwise comparisons of *Pseudemys suwanniensis* population structure in samples from five habitats in the Santa Fe River using Marascuilo's post hoc multiple proportion procedure. Abbreviations are blackwater river (BwR), spring-influenced river (SiR), Hornsby Spring (HS), Poe Spring (PS), and Blue Springs (BS). Significant effects are in bold.

Habitat Pairs	Difference	X^2	*p*
HS-PS	0.4315	29.8800	**<0.0001**
HS-BS	-0.0196	1.2162	0.8754
HS-BwR	0.5733	50.9522	**<0.0001**
HS-SiR	0.3291	83.9665	**<0.0001**
PS-BS	-0.4511	32.7351	**<0.0001**
PS-BwR	0.1418	1.6289	0.8036
PS-SiR	-0.1024	1.4595	0.8338
BS-BwR	0.5929	54.6065	**<0.0001**
BS-SiR	0.3486	95.2706	**<0.0001**
BwR-SiR	-0.2443	8.0507	0.0897

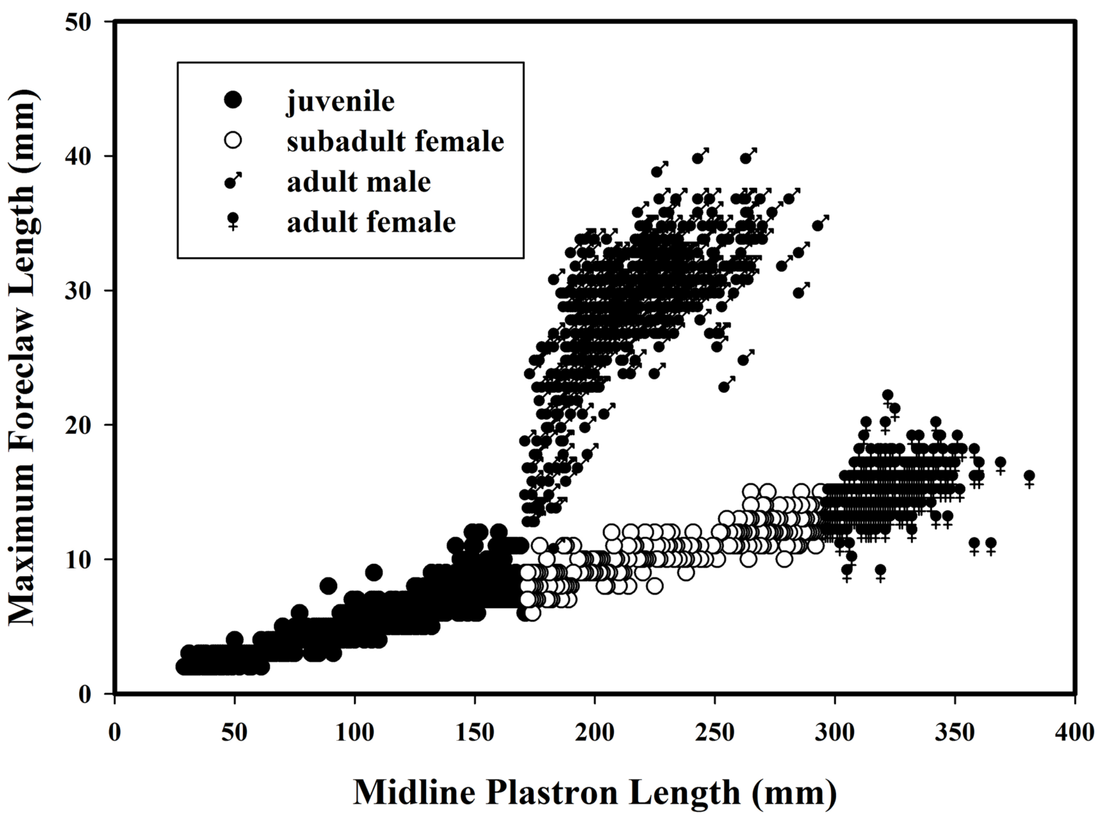

Figure 9. Relationship between straight-midline plastron length and maximum fore-claw length of male, female, and juvenile *Pseudemys suwanniensis* demographic groups in the lower Santa Fe River in northern Florida. Males matured at 181 mm PL (see text). The smallest gravid female was 296 mm PL.

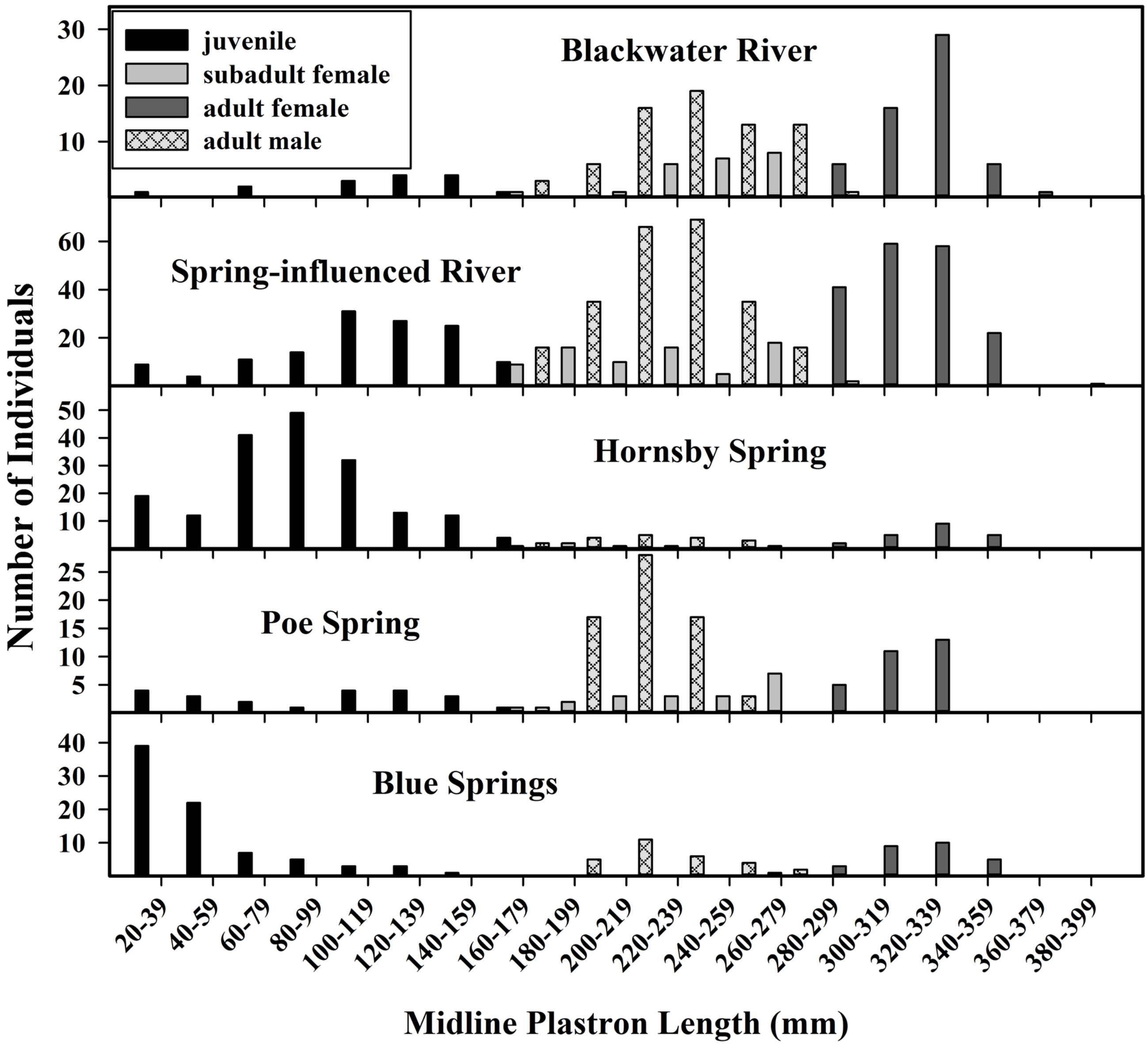

Figure 10. Size distributions of *Pseudemys suwanniensis* demographic groups hand-captured in the five study habitats in the lower Santa Fe River in northern Florida.

PS (n = 5) did not permit analysis.

Trachemys scripta—Our total *T. scripta* sample consisted of 64 (8.8%) juveniles (33–106 mm PL), 65 (9.0%) subadult females (107–187 mm PL), 264 (36.4%) adult females (188–255 mm PL), and 332 (45.8%) adult males (107–215 mm PL) (Fig. 12). Adult sex ratio (1.26:1) was significantly male biased (X^2 = 7.758, p = 0.005). We captured 75 individuals in the BwR, 544 in SiR, 29 in HS, 31 in PS, and 46 in BS (Fig. 13). We found no significant effect of sampling method on proportion of juveniles (BwR z = 0.137, p = 0.891; SiR z = 0.358, p = 0.720), subadult females (BwR z = 1.828, p = 0.068; SiR z = 1.848, p = 0.065), adult females (BwR z = 0.176, p = 0.860; SiR z = 0.353, p = 0.724), or adult males (BwR z = 1.439, p = 0.150; SiR z = 0.418, p = 0.676). We therefore combined hand capture and trap capture data for comparisons of demographic structure among habitats.

Population structure differed significantly among habitats (Table 7; Fig. 13). Overall X^2 indicated at least one significant difference in

Table 6. Pairwise comparisons of *Sternotherus minor* population structure in samples from five habitats in the Santa Fe River using Marascuilo's post hoc multiple proportion procedure. Abbreviations are blackwater river (BwR), spring-influenced river (SiR), Hornsby Spring (HS), Poe Spring (PS), and Blue Springs (BS). Significant effects are in bold.

Habitat Pairs	Difference	X^2	*p*
HS-PS	-0.2468	2.4176	0.6595
HS-BS	-0.3086	5.9938	0.1996
HS-BwR	0.203	1.7237	0.7864
HS-SiR	0.0487	0.1636	0.9968
PS-BS	-0.0618	0.2135	0.9946
PS-BwR	0.4498	7.8495	0.0972
PS-SiR	0.2955	5.3362	0.2545
BS-BwR	0.5116	15.8896	**0.0032**
BS-SiR	0.3573	18.0823	**0.0012**
BwR-SiR	-0.1543	1.5788	0.8126

population structure among the ten combinations of habitat pairs (Table 7; $X^2 = 35.580$, df = 4, $p < 0.0001$). The Marascuilo procedure revealed there were five combinations of habitat pairs in which population structure differed significantly (Table 7). Differences in the number of juveniles contributed to differences between HS-PS (Fisher Exact probability Test; Phi = -0.38, $p = 0.0016$), HS-SiR ($X^2 = 26.3$, $p < 0.001$), BS-PS (Fisher Exact Probability Test; Phi = -0.34, $p < 0.001$), and BS-SiR ($X^2 = 44.19$, $p < 0.001$). Adult sex ratio was significantly male biased in the BwR (2.58:1; $X^2 = 13.235$, $p = 0.003$) and HS (3.25:1; $X^2 = 4.765$, $p = 0.029$), but did not differ significantly from 1:1 in SiR ($X^2 = 1.061$, $p = 0.303$), PS ($X^2 = 0.310$, $p = 0.577$), and BS ($X^2 = 0.154$, $p = 0.695$).

DISCUSSION

The SFR and its springs provide a unique ecosystem that supports a wealth of flora and fauna, including a unique freshwater turtle assemblage. We have mostly observational information on plant, invertebrate, and vertebrate species that adds to the few in-depth scientific studies conducted in this riverine ecosystem. Documentation of the diversity of habitat characteristics offers the opportunity to understand variation in the biota at different spatial scales. On-going changes in the system due to declines in quantity and quality of water discharging from springs require an urgent and diverse response by scientists and local citizens to find ways to avert the possible collapse of elements of its biota (Knight, 2015).

We used six years of mark-recapture and demographic data on the freshwater turtles in the SFR ecosystem to evaluate differences in assemblage and population structure on a spatial scale. Results demonstrate the importance of habitat diversity among sites (beta diversity). Management of biotic communities in the SFR basin should focus on maintaining environmental heterogeneity and improving the health of the springs. Conservation of spatial heterogeneity will help preserve the natural beta diversity in the SFR.

The results of this study clearly demonstrate that turtle populations are not homogeneously distributed throughout the lower SFR ecosystem. Occurrence of springs appears to be a major factor affecting abundance and population structure.

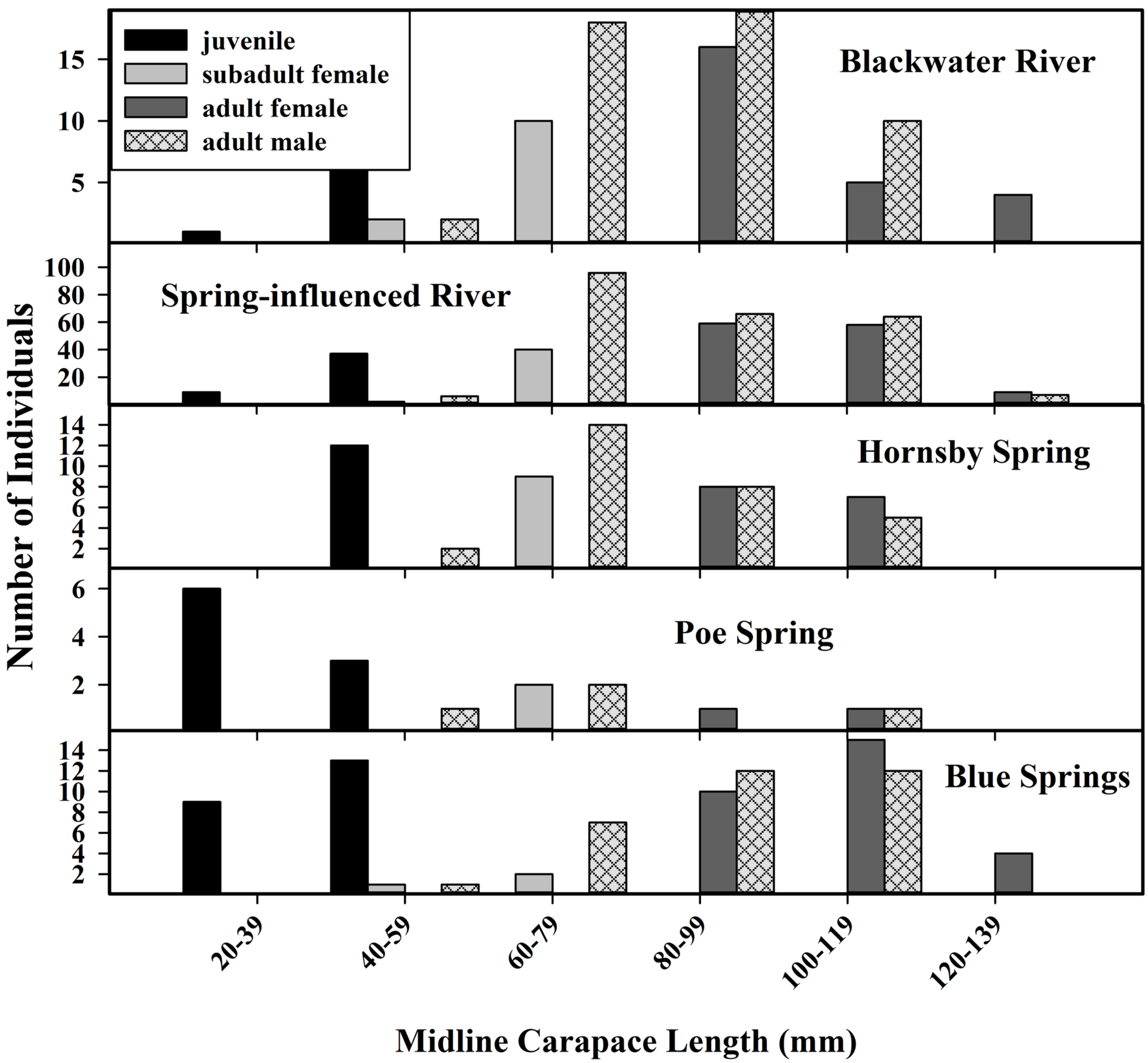

Figure 11. Size distributions of *Sternotherus minor* demographic groups captured in the five study habitats in the lower Santa Fe River in northern Florida.

However, a limitation of our study is the absence of quantitative statistical correlation analysis that identifies which habitat variables are responsible for the observed differences in turtle populations among the habitats in which we sampled. The small number of habitats and logistical constraints on our ability to gather appropriate biologically meaningful habitat data during each sampling session limited our ability to perform such analysis. Thus, this paper describes habitat-associated variation in turtle population attributes on a coarse spatial scale within a multiyear timeframe. Combination of turtle data from all sampling sessions in our 6-yr study also limits the meaningfulness of correlations with short term environmental measurements.

Turtle Assemblage structure

We found the same ten species in both river habitats, but perceptions of species diversity and relative abundance in each habitat depend, in part, on the sampling method used. Snorkel capture data suggest similar species diversity and relative

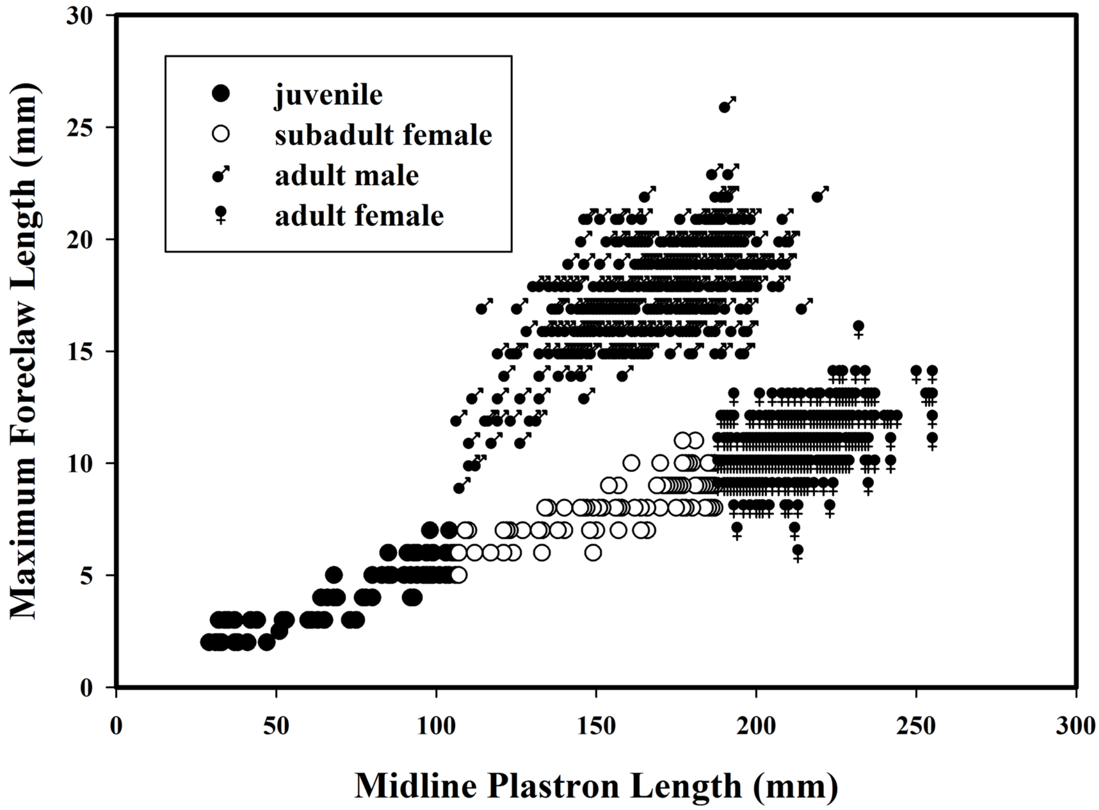

Figure 12. Relationship between straight-midline plastron length and maximum fore-claw length of male, female, and juvenile *Trachemys scripta* demographic groups in the lower Santa Fe River in northern Florida. Males matured at 107 mm PL (see text). The smallest gravid female was 188 mm PL.

Table 7. Pairwise comparisons of *Trachemys scripta* population structure in samples from five habitats in the Santa Fe River using Marascuilo's post hoc multiple proportion procedure. Abbreviations are blackwater river (BwR), spring-influenced river (SiR), Hornsby Spring (HS), Poe Spring (PS), and Blue Springs (BS). Significant effects are in bold.

Habitat Pairs	Difference	X^2	*p*
HS-PS	0.9167	132.0	**<0.0001**
HS-BS	-0.0333	0.127	0.9981
HS-BwR	0.3452	2.882	0.5777
HS-SiR	0.5758	37.167	**<0.0001**
PS-BS	-0.95	380.0	**<0.0001**
PS-BwR	-0.5714	9.333	0.0533
PS-SiR	-0.3409	45.517	**<0.0001**
BS-BwR	0.3786	3.836	0.4286
BS-SiR	0.6091	75.278	**<0.0001**
BwR-SiR	0.2305	1.416	0.8415

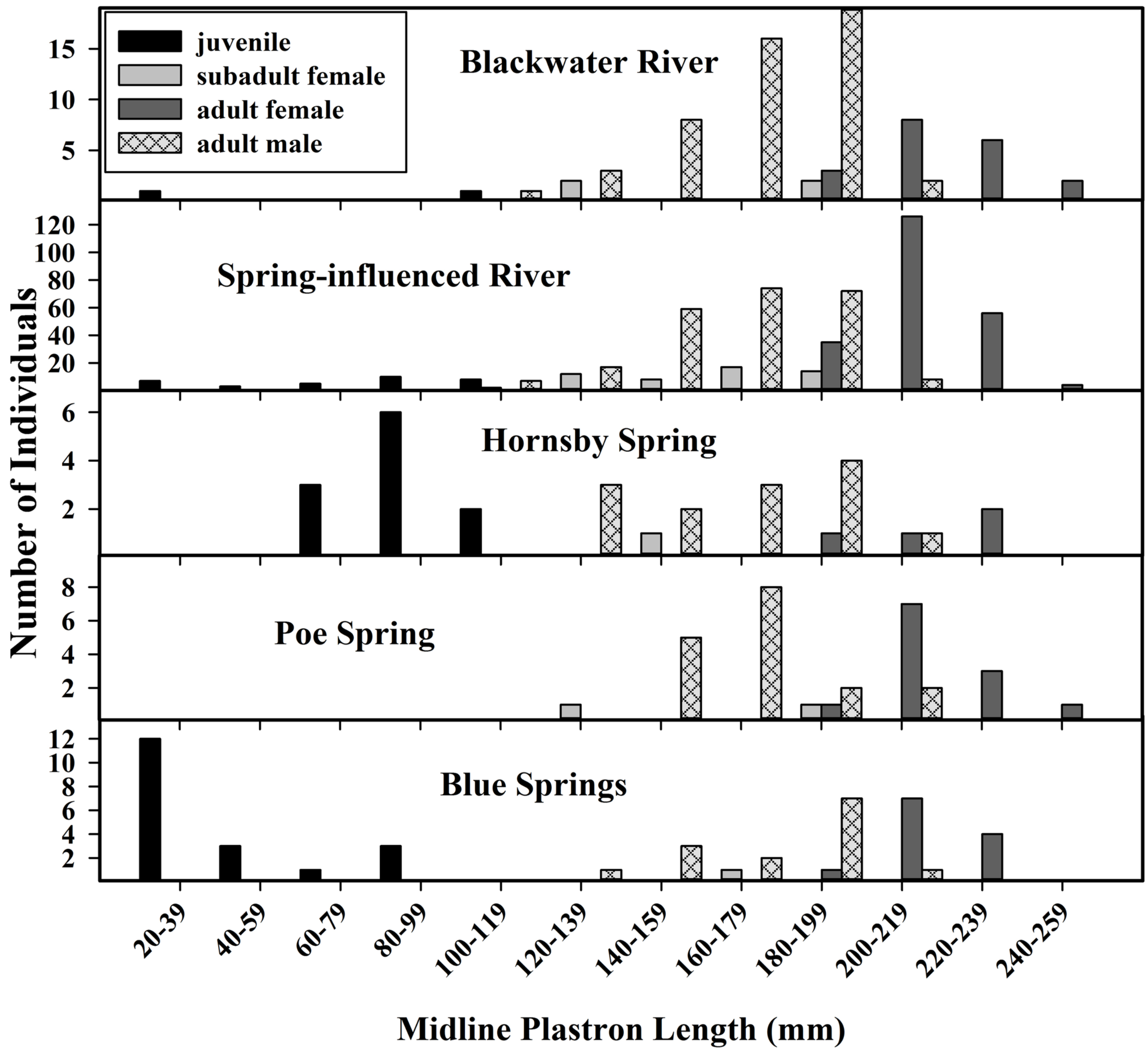

Figure 13. Size distributions of *Trachemys scripta* demographic groups captured in the five study habitats in the lower Santa Fe River in northern Florida.

abundance of species in both river habitats. Trapping data suggest species diversity was higher in SiR than in BwR. *Chelydra serpentina* and *S. minor* were proportionately more commonly trapped in the SiR, and *T. scripta* was proportionately more commonly trapped in the BwR. *Chelydra serpentina* is more abundant in habitats with soft substrate and abundant submerged aquatic vegetation (Aresco et al., 2006; Ernst and Lovich, 2009). They may be more sensitive than other species to the limited availability of these microhabitats in the BwR. *Sternotherus minor* has a restricted diet that shifts ontogenetically from primarily insects as juveniles to primarily mollusks as adults (Carr, 1952; Tinkle, 1958a). This species may be more sensitive than others to the availability of gastropods in the BwR. *Trachemys scripta* is a habitat generalist with an omnivorous diet (Gibbons, 1990a; Thomas, 2006; Ernst and Lovich, 2009), and may be less sensitive than *C. serpentina* and *S. minor* to habitat differences between the BwR and SiR.

Both capture methods indicate the primary difference between the two SFR assemblages was species abundance. The four dominant species (*C. serpentina*, *P. suwanniensis*, *S. minor*, *T. scripta*) in the river were captured at significantly higher rates in the SiR than in the BwR. Using capture rate as an index of abundance, turtles (all species combined) were 2.8 or 4.2 times more abundant in the SiR based on trapping and snorkeling data, respectively. Although we did not estimate density in this study, we can infer an approximate density based on the previously reported density of all turtles in the BwR (78.6 turtles/ha; Johnston et al., 2011). Our estimates are 220 turtles/ha from trapping and 330 turtles/ha from snorkeling in the SiR. This high density is likely a consequence of higher primary productivity in the SiR, as herbivores (*P. nelsoni*, *P. suwanniensis*), carnivores (*S. minor*), and omnivores (*C. serpentina*, *T. scripta*) were more abundant in this habitat. Density can be even higher in the Ichetucknee River, a large entirely spring-fed tributary of the lower SFR (Fig. 2). Chapin and Meylan (2011) estimated at least 487 turtles/ha in the 5.6 km (11 ha) section of river in Ichetucknee Springs State Park.

Our estimates of capture rates, and assumptions of abundance between the two river habitats, may be affected by differences in detectability of turtles when snorkeling in each habitat. We attempted to minimize the potential effect of this sampling bias by conducting all snorkel sessions when underwater visibility was similar. Appropriate clear water snorkeling conditions occurred less frequently in the BwR than in the SiR, thus allowing fewer snorkel sessions in the BwR.

Population structure

Pseudemys suwanniensis—Population structure was similar in both river habitats, but structures in HS and BS suggest these springs are important nursery habitats and likely sources of recruitment. At both sites, juveniles were abundant and subadult females were rare. We frequently captured gravid females in these springs during the nesting season. Nest construction was commonly observed in the uplands surrounding these springs (K. Davis, Owner of Blue Springs Park, pers. comm.; E. Esquivel, Manager of Camp Kulaqua, pers. comm.). Abundant aquatic vegetation at both of these sites provided the herbivorous juveniles with food, as well as shelter from swift current. The high human recreational activity at HS and BS may limit the frequency that predators such as American Alligators and River Otters use these sites.

Size structure data from BS and SiR suggest that juveniles may leave the nursery habitat and enter the SiR as they reach the 60–79 mm PL size class. These individuals may supplement juvenile cohorts that hatch from nests in open patches along the river shoreline and enter the river as hatchlings. Juveniles may leave HS as they reach the 100–119 mm PL class. Because HS is the nursery habitat closest to the BwR, juveniles from this site may be the primary source of new recruits in the BwR. This scenario is consistent with our observation that 80% of juveniles in the BwR sample were >100 mm PL .

Our observations at BS and HS parallel those made by Jackson (1970) at Fanning Spring (Levy Co.) along the Suwannee River, where juveniles comprised 48.1% of the population sample. However, we cannot generalize that all springs are nurseries for *P. suwanniensis*. Poe Spring, for example, does not appear to be a significant nursery habitat. We have observed nesting in the open sandy area on the east side of the spring, but the small amount of aquatic vegetation and woody debris in the spring and short run provides insufficient food and shelter for large numbers of hatchlings and juveniles.

Comparisons between SFR *P. suwanniensis* populations and other populations are limited by small numbers of published studies of this geographically restricted species (Meylan et al., 1992; Jackson and Walker, 1997; Huestis and Meylan, 2004; Jackson, 2006; Heinrich et al., 2010, 2012, 2015). In the Wakulla River, gravid females were 304–383 mm maximum PL (Jackson and Walker 1997). SFR adult females were 306–393 mm maximum PL (296–381 mm straight-midline PL), slightly larger than the Wakulla females. Because the Wakulla study focused on nesting ecology, similar data were not available for comparisons of adult male body sizes. Jackson (2006) stated that males may grow to at least 290 mm maximum PL, but three males from the SFR exceeded that size, the largest measuring 310 mm maximum PL (294 mm straight-midline PL). The size at which males attain maturity, based on allometric elongation of the fore-claws, was reported to be approximately 175 mm straight midline PL in the Rainbow Run (Marion Co.) population (Huestis and Meylan, 2004), slightly smaller than our 181 mm straight midline PL estimate for SFR males. The Rainbow Run population described by Huestis and Meylan (2004) had a lower percentage of adults (44%) and fewer large adults than the SFR population, but this population may be in the process of recovering from historical harvest (Meylan et al., 1992).

The *P. suwanniensis* population in the lower SFR basin appears to be healthy based on the large numbers of individuals in all size classes and large body sizes of both sexes. According to many long-term local residents, this population was apparently heavily harvested during the 1960s and 1970s (K. Davis, pers. comm.). Mark Wray (owner of Ginnie Springs Outdoors since 1971) observed that "turtles of all kinds were hunted by a group of local residents during the 1960s and 1970s to the point they were almost wiped out … all the turtles we see today, especially the big ones, weren't here 40 years ago." These anecdotal observations suggest our data describe a population that has recovered from harvest.

Sternotherus minor—Population structure was similar in both river habitats, but most of the variation occurred among springs. The population in BS exhibited the highest proportion of juveniles, suggesting that it is a nursery habitat for *S. minor*, as well as *P. suwanniensis*. Female *S. minor* lay their eggs at the base of trees or beside logs (Carr, 1952), microhabitats which are abundant in the uplands surrounding all of our study habitats. However, the aquatic habitat at BS has abundant woody debris that supports aquatic insect prey for juveniles, as well as high dissolved oxygen and associated high gastropod abundance that make this site ideal for *S. minor* in general. The PS population also had a high proportion of juveniles, but the sample size was very small. The small amount of woody debris (i.e., aquatic insect habitat) limits the value of this spring for juveniles. The low dissolved oxygen and associated low gastropod abundances in PS, as well as in HS, further reduce the value of these habitats for *S. minor*.

Adult sex ratios also varied among habitats in the lower SFR basin. Previous studies suggest that a 1:1 ratio is typical of *S. minor* populations, but the reported ratios have been from populations in entirely spring-fed habitats (Tinkle, 1958b; Cox et al., 1988; Meylan et al., 1992). In our study, the only habitat with a 1:1 adult sex ratio was BS, the habitat that most closely resembles those in which *S. minor* adult sex ratios were previously studied.

Our understanding of *S. minor* population structure was enhanced by increased sample sizes resulting from combined snorkel and trap captures. We were able to combine those data because we found no significant effect of sampling method on proportions of each demographic group captured. Sterrett et al. (2010) also found that snorkeling and baited traps in southwestern Georgia streams yielded similar distributions of sexes of *S. minor*, although snorkeling captured only juveniles. Our success capturing juveniles in traps may be due to the smaller mesh of our traps (2.5 cm) compared to the 3.8 cm mesh of those used by Sterrett et al. (2010).

The *S. minor* population in the lower SFR basin appears to be stable or growing given the abundance of individuals in all size classes and large adults of both sexes. Unfortunately, there are no historical baseline data for this population, and our limited number of recaptures prevents meaningful results from population models. In the late 1980s, hundreds of *S. minor* were collected for the pet trade from a portion of the SiR habitat in our study (Enge and Foster, 1986). The SFR population seems to have recovered, but we are unable to determine whether its structure is the same as the one before this massive collection occurred.

Trachemys scripta—Population structure of *T. scripta* differed among river and spring habitats. The primary difference between the two river habitats was adult sex ratio; male biased in the BwR, but 1:1 in the SiR. Captures of gravid female *T. scripta* and all nesting observations occurred downriver from the BwR, suggesting that turtles captured in the BwR originated downriver as hatchlings and later migrated upriver. The male biased sex ratio in the BwR may have resulted from males migrating upstream more frequently than females. Additional studies of *T. scripta* movements in the SFR will be required to test this hypothesis.

An alternative hypothesis is that differences in adult sex ratio between BwR and SiR are the result of differences in nesting habitat and the subsequent effect of different incubation temperatures on sex ratios of hatchlings entering each river habitat. *Trachemys scripta* exhibits temperature-dependent sex determination (Bull et al., 1982; Ewert et al., 1994). Incubation temperatures > 29.5°C produce females; those < 28°C produce males. The upland habitat along the BwR is more heavily shaded and nesting habitat may be cooler than in the uplands along the SiR. If nest temperatures < 28°C occur more frequently in BwR than in SiR, then male biased sex ratios would be more common in BwR hatchlings than SiR hatchlings. Future studies of *T. scripta* nesting ecology along the SFR could elucidate this hypothesis.

The high proportion of juveniles in BS and observations of nesting in the uplands surrounding these springs (L. Matthews, pers. comm.; W. Wollman, pers. comm.) suggest this location functions as a nursery for *T. scripta,* as well as for *P. suwanniensis* and *S. minor*. Population structure data from BS and the SiR suggest that juveniles leave BS as they reach 100 mm PL and enter the river to augment juvenile cohorts from nests laid in open patches along the river. Our observations are consistent with previous reports that riverine *Trachemys* use quiet backwater habitats as nurseries (Moll and Legler, 1971; Bodie and Semlitsch, 2000; Bodie, 2001). The spring and spring run habitat in BS is essentially a unique type of backwater.

We cannot generalize that all springs are important sites for juvenile recruitment in the SFR *T. scripta* population. Our HS sample had a high proportion of juveniles, although none was a hatchling. We also never captured a gravid female at this site. Open uplands surrounding the spring appear to provide appropriate nesting habitat, and the abundant aquatic vegetation and woody debris in the spring and spring run provided appropriate habitat for hatchlings and juveniles. The limited use of this site by nesting females may be a consequence of the rarity of gravid females in the nearby BwR. In PS, we captured no juveniles or gravid females, likely because it has insufficient food or shelter to function as juvenile habitat. We did not observe nesting or emergent hatchlings at PS. Low nest success may be another reason for the absence of juveniles in our PS sample. Our *T. scripta* sample included all captured individuals, regardless of capture method used, because data from snorkeling and baited traps provided similar perceptions of population structure. Sterrett et al. (2010) also reported no differences in distributions of sexes and size classes using snorkeling and baited traps to capture *T. scripta* in streams in southwestern Georgia.

In comparison with other *T. scripta* populations studied in Florida (Jackson, 1988; Aresco, 2004), females in the SFR reach larger body sizes (G. Johnston and J. Mitchell, unpublished). Prior to our study, the largest known female *T. scripta* in Florida was 230 mm maximum PL (Jackson, 1988). Twenty-six females from the SFR exceeded that size, the largest measuring 259 mm maximum PL (255 mm straight-midline PL). The largest male *T. scripta* in our study measured 220 mm maximum PL (215 mm straight-midline PL). No other published studies of Florida *T. scripta* populations have provided data on male body size (Thomas, 2006).

The *T. scripta* population in the SFR basin appears to be stable or growing due to the occurrence and abundance of all demographic groups. Occurrence of exceptionally large adults suggests food resources are not limiting. We are unable to compare our population structure data with those from other riverine *T. scripta* populations because most published studies of *T. scripta* populations occurred in lentic habitats (Gibbons, 1990a; Ernst and Lovich, 2009). Parameters of population structure such as proportions of demographic groups and adult body sizes vary substantially among populations in lentic habitats (Gibbons et al., 1979; Gibbons, 1990b; Gibbons and Greene, 1990; Mitchell and Pague, 1990; DeGregorio et al., 2012). We were unable to determine whether similar variation also occurs among populations in lotic habitats or whether our data are typical of a riverine population.

The future of turtles in the Santa Fe River

Although this study emphasizes spatial variation in freshwater turtle population characteristics, we must also consider the temporal component of variation in this ecosystem. Our study provides a brief snapshot of the turtle populations in the lower SFR basin over a 6-year period. The conditions we observed during our study were likely not the same as in years past. Previous conditions may have been more favorable for turtles. For example, spring flow was historically higher throughout the SFR basin, and lack of retaining walls or boardwalks around HS, PS, or BS did not affect movements of gravid females and hatchlings between springs and uplands. Other past conditions were certainly harmful for turtles (e.g., harvest for food and collection for the pet trade). Unfortunately, there are no historical baseline data that provide insight into how the SFR turtle populations may have changed over the past several decades. Thus, our data provide a baseline to which results of future studies of turtles in SFR can be compared.

The fate of turtle populations in the SFR is linked to the quantity and quality of water discharging from its springs. If the long-term trend of declining spring flows continues, turtle populations in the SFR will be detrimentally affected in multiple ways. For example, if HS and BS eventually stop flowing (as has already occurred at Worthington Spring), *P. suwanniensis*, *S. minor*, and *T. scripta* will likely lose nursery habitat. and population declines due to reduced recruitment may occur. Declining spring flows would also affect ecological conditions in the SFR downstream from PS. With reduced input of clear spring water, there will be less dilution of dark tannic water flowing down from the upper SFR. Thus, the BwR habitat will likely expand downstream into the present-day SiR. This expansion would include decreased abundance of submerged aquatic macrophytes during periods of normal rainfall and increased abundance of nuisance benthic algae and cyanobacteria during drought periods. We would then expect turtle assemblage and population structures, as well as population densities in the present-day SiR, to shift and resemble what we observed in the BwR.

Given the uncertain future ecological conditions in the SFR, we advocate continued long-term monitoring of this unique turtle assemblage. Monitoring of turtle populations in this ecosystem and riverine ecosystems in general should include as much habitat variety as possible. If we had sampled turtles in one or two habitats rather than five representative habitats in the lower SFR, our perceptions of assemblage and population structure would have been vastly different. Estimates of population parameters in studies of riverine turtles that focus only on one part of the river ecosystem, such as the mainstem or a single spring, may be inaccurate if they exclude other types of habitats used by freshwater turtles in that system.

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