SPECIAL PUBLICATION SJ2012-SP1

SPAWNING HABITATS FOR AMERICAN SHAD AT THE ST. JOHNS RIVER, FLORIDA: POTENTIAL FOR USE IN ESTABLISHING MFLS

2718-08-11-F

Spawning Habitats for American Shad at the St. Johns River, Florida: Potential for Use in Establishing MFLs

Completion Report
November 2011

Andrew C. Dutterer
Dr. Micheal S. Allen
Dr. William E. Pine, III

Program for Fisheries and Aquatic Sciences
School of Forest and Resources and Conservation
The University of Florida

Submitted to the
Florida Fish and Wildlife Conservation Commission and
St. Johns River Water Management District

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Executive summary

The St. Johns River, Florida contains the southernmost population of anadromous American shad *Alosa sapidissma*. Given increasing demands for freshwater resources in Florida, variation in water levels within the St. Johns River could increase in the near future potentially altering access to spawning habitat for American shad. To help inform water and resource management decisions, a collaborative research effort between the St. Johns River Water Management District (SJRWMD), Florida Fish and Wildlife Conservation Commission (FWC), and University of Florida was initiated to expand on earlier research suggesting that spawning habitat use of migrating shad could be influenced by variation in water levels.

This report presents the conclusions of this collaboration. We assessed spawning habitat use of American shad over a three-year period using active and passive tracking of telemetered adult American shad. We then compared these movement patterns with habitat available in areas of high and low use to assess whether specific habitat characteristics (i.e., depth, substrate, flow) were selected. We assumed that during late winter and early spring American shad would migrate to areas in the St. Johns River favorable for staging prior to, or for spawning. We also assumed that areas of repeated occurrence for telemetered shad represented important habitat for spawning.

In Year 1 of this study, we determined that esophageal implants of acoustic telemetry tags in adult American shad combined with an array of fixed-position acoustic receivers would allow for continuous, large-scale, tracking of adult shad movement patterns in the St. Johns and Econlockhatchee rivers. These movement patterns were

used to draw inferences on the timing of seasonal spawning migration patterns and identified specific spatial areas that appeared to be used by adult American shad with high and low frequency. During Years 2 and 3, we expanded the spatial coverage of our fixed-position receiver array and added manual searches for telemetered fish in areas between the fixed-position monitoring stations using a directional hydrophone to increase spatial resolution of fish movements. In Year 3, we tested differences between used and available habitats for American shad to identify potential habitat selection patterns based on observed movement patterns during this study and previous observations of fish habitat use and movement by our agency partners. During our study, riverine flow conditions varied creating contrast in some aspects of in-river habitat conditions such as discharge with two years of relatively low-flow (2009 and 2011) and one high-flow year (2010) compared to historical water levels. We found that the river reach between Lake Monroe and Lake Jesup consistently received the highest use by telemetered American shad throughout the spawning period in all years, and many telemetered shad occupied this river reach nearly exclusively during assumed spawning activities. Secondary high use areas were also observed immediately upstream of Lake Harney, upstream of Puzzle Lake, and downstream of Lake Cone.

We observed differences in the upstream movement range of telemetered shad during low water years compared to the high water year. The upstream range for telemetered shad was lower (further downstream) during low water years compared to high water years. This suggests that low water levels may restrict, or discourage, upstream migration and may limit access to the most upstream spawning sites. When we compared habitat use patterns for American shad, we found some instances of telemetered shad selecting for deeper habitats that had higher flow velocities relative to available habitat conditions. This is consonant with previous American shad research and is likely explained by the species' requirement for turbulent or relatively high flows to transport and aerate slightly demersal eggs after spawning. Our findings were similar to previous research nearly 40 years prior in the St. Johns River as our high-use areas had previously been identified as important reaches for shad spawning. The patterns of habitat use we observed was also to similar to more recent findings from the FWC and SJRWMD. This suggests that spawning site selection has not changed in the St. Johns River from earlier research despite large changes in land use and human population density during this same time period within the river basin. Overall, our findings suggest that linkages between riverine flow conditions and adult American shad movement patterns likely do exist and under low-flow conditions upstream migration of adult American shad may be impaired. Whether this change in access to spawning habitat could lead to changes in adult American shad populations in the St. Johns River remains unknown. Future research could assess this question in a passive adaptive management framework by comparing adult shad spawning activities across a range of flow conditions with return rates of adult American shad from those same cohorts in future years.

Acknowledgements

This work would not be possible without extensive assistance from agency partners including FWC staff Reid Hyle, Jay Holder, Dick Krause, Jim Estes, Kevin Johnson, and Bob Eisenhauer. We thank Steve Miller for assistance with choosing receiver locations and provided habitat data collected by his group with the SJRWMD. Ken Snyder (SJRWMD) provided logistical support. Technical assistance at the University of Florida included Darren Pecora, Derrick Thrasher, Nick Cole, Zachary Martin and Zak Slagle. This work was supported by the Federal Sportfish Restoration Program.

Introduction

Water level and flow regime can strongly influence riverine fish communities by altering available habitat, water quality, food availability, spawning success, and predation risk (Cushman 1985; Freeman et al., 2001; Murchie et al., 2008). Across Florida, minimum flow and level regulations are being evaluated by natural resource management agencies to establish water levels that must be maintained to prevent ecological harm via anthropogenic alterations to water flows. Fish communities in Florida riverine ecosystems are unique in many aspects because of the strong linkages between marine and freshwater fish communities. Changes to ecosystem structure and function could occur due to alterations in riverine flow by altering essential habitats, trophic linkages, or changing predation risks potentially impacting fish communities within Florida waters. Because of these linkages between freshwater and coastal fish species, the diverse types of habitats found within these river systems, and the paucity of fish research that has been conducted in these systems, new technologies and sampling approaches are needed to rapidly assess fish communities and habitat quality so that ecological information can be incorporated into river flow and level regulation decisions.

American shad *Alosa sapidissma* are native to the east coast of North America ranging from the St. Lawrence River, Canada in the north to the St. Johns River, Florida in the south (Limburg et al. 2003). Within this latitudinal range, the species exhibits diverse life history characteristics, such as varying degrees of iteroparity (number of reproductive events within a lifetime) (Facey and Van Den Avyle 1986), age and size at maturity (La Pointe 1957), and increasing fecundity from north to south (Leggett and Carscadden 1978). Latitudinal variation in life history, historical importance as a fishery, and concerns over the status of this species have led to numerous reviews of the biology and ecology of this unique species (Facey and Van Den Avyle 1986; Stier and Crance 1985; MacKenzie et al. 1985; McBride 2000; Limburg et al. 2003).

In response to requests from the Atlantic States Marine Fisheries Commission, the Florida Fish and Wildlife Conservation Commission has been monitoring anadromous shad (*Alosa* spp.) populations from the St. Johns River, Florida. Present abundance of *Alosa* spp. in the St. Johns River and other rivers along the Atlantic seaboard is substantially lower now than in the mid-1900s due to a variety of factors including historical overfishing and habitat loss due to altered hydrology. Preserving anadromous shad stocks is an important goal for state and federal management agencies along the entire east US coast.

Historically, American shad supported important commercial and recreational fisheries in the St. Johns River. Although commercial fishing for shad in Florida was discontinued following the net limitation amendment in 1995 and recreational fishing is highly regulated, the American shad population in Florida has not rebounded to historic highs (McBride 2005). The status of American shad stocks across the Atlantic slope is of concern to resource managers with most management efforts focused on regulating fishing mortality and many research efforts focused on evaluating spawning and recruitment dynamics (Harris and Hightower 2010). A key management action designed to improve American shad abundance was the 2005 closure of a mixed-stock ocean intercept fishery along the US continental shelf. This fishery which captured a variety of *Alosa* spp. including American shad from a large number of natal east coast rivers. The expectation by managers is that the closure of this fishery will lead to reductions in total mortality, increasing the adult spawning stock size, and ultimately improving recruitment and population abundance.

Compared to the body of research on *Alosa* spp. in other Atlantic Coastal states, less research has been directed toward anadromous shads in Florida. However, details of American shad spawning migrations in the St. Johns River were documented by Walberg (1960), Nichols (1965 and 1966), and Williams and Bruger (1972). A central focus of those research projects was to document American shad spawning at the St. Johns River, which has generally been reported to span from Crows Bluff, west of DeLand, south to U.S. Hwy 192, near Melbourne. The range of spawning activities for American shad in the St. Johns River varies annually, and typically does not include the entire area of river described above, but across numerous studies over multiple decades the most consistent known areas of spawning activity, supported by larval and juvenile collections, exists between lakes Monroe and Poinsett. Williams and Bruger (1972) observed a large shift in the area of greatest American shad spawning activity between years of their study that was concurrent with changes in water levels. They suggested that anadromous shad spawning habitat in the St. Johns River was affected by river flows, and that primary spawning aggregations might shift spatial locations within the river from year to year as shad searched for areas of river with preferred high velocity regions.

Recent studies in Florida (McBride 2000; Harris and McBride 2004; McBride 2005; McBride and Holder 2008) including work by the FWC and the St. Johns River Water Management District indicate a renewed interests in Florida in the status and ecology of anadromous shad. These studies indicate that the current status of American shad is smaller than the historical biomass, but, that this stock is likely slowly rebuilding. Because of historical overfishing and a slow speed to recovery for American shad in Florida, McBride and Holder (2008) and Harris and McBride (2004) suggested that preservation of spawning habitats in the St. Johns River would be especially important for sustaining and rebuilding this southernmost American shad population. These earlier efforts combined with continuing research by SJRWMD and FWC personnel regarding habitat use and distribution of larval and juvenile American shad motivated this current collaborative work on adult spawning habitats.

Past research indicates that American shad are selective in spawning habitat use. Williams and Bruger (1972) reported that at the St. Johns River American shad spawning occurred in areas with current velocity of 1-1.5 ft $\cdot$ s^{-1} (0.3-0.46 m $\cdot$ s^{-1}). This range is similar to current velocity values reported for American shad spawning at other rivers within the southeastern U.S. (0.63 m · s^{-1}, Sparks and Hightower 1998; 0.4 m · s^{-1}, Beasley and Hightower 2000). Stier and Crance (1985) reported American shad spawning typically taking place in current velocities of 0.3-0.91 m · s^{-1}, over a variety of substrates, but generally sand and gravel, and within a wide range of depths (0.45-12.2 m). Sparks and Hightower (1998) and Beasley and Hightower (2000) reported American shad spawning over relatively shallow gravel, coble, and bedrock substrates in two North Carolina rivers. Williams and Bruger (1972) characterized high-use spawning areas in the St. Johns River as having relatively shallow depth and clean sand substrate. With the exception of Williams and Bruger (1972) much of what is presently known about American shad spawning habitat applies to river systems in the more northern range of the species where flow and substrate characteristics are inherently different than the low-gradient St. Johns River. Reducing this uncertainty in knowledge related to American shad spawning habitat requirements would help to inform water flow policies and improve fish management plans for American shad in the St. Johns River.

River flow conditions are known to affect habitat use, movement, growth, and survival of American shad at different life stages. In the St. Johns River, a recent review of the potential impacts of low-flows on American shad (Harris and McBride 2004) suggests that "upstream migration and spawning location of adult American shad and downstream migration of juveniles may be affected by flow rate in river systems…." These authors reviewed known spawning habitats and egg and larval requirements for American shad in the St. Johns and elsewhere and suggested that "maintaining appropriate flow rates during the period of the year (December to May) when eggs and larvae are developing in the St. Johns River may be very important to this population of American shad." Recommendations such as this one, and increasing demands for water resources in the St. Johns River basin, indicate a need for a better understanding of how river flow influences spawning habitat for American shad. Such information could provide quantitative assessment tools to diagnose the consequences of specific flow rates for these ecologically and economically important fishes. Thus, American shad and other *Alosa* spp. are likely good focal species for informing quantitative and science-based MFL regulations.

Objectives

The objectives of this study were to (1) evaluate the efficacy of tracking adult, spawning run American shad via esophageal implant acoustic telemetry tags within a passive receiver array during year-1, and (2) incorporate active tracking of spawning run adults to identify habitat characteristics of shad spawning locations during year-2 and year-3. This multi-year study provided the opportunity to monitor American shad spawning migrations under varying hydrologic conditions, giving insight into shad habitat use at different flow regimes during spawning.

Methods

American Shad Collection and Tagging

We began sampling for American shad between mid-December and early January, prior to the anticipated period of peak migration. During each year, we tagged fish over a protracted time period ("staggered-entry") such that we would tag representative fish from different entrant cohorts (entering the St. Johns River from the north moving south to spawn) of fish throughout the spawning migration. We collected adult American shad via boat electrofishing (Smith-Root, Inc. 9-kW generator powered pulsator) and selected individual fish >400-mm TL for tagging based on the length and weight values from McBride and Holder (2008) to ensure that the tag-weight: body-weight ratio was maintained at or below 2% (Winter 1996). In areas where catch of American shad was low or zero with electrofishing, we used a gill net (50 x 2 m, 100 and 150 mm stretched mesh), fished from substrate to 2 m above substrate, to verify that American shad were not present at depths below typical electrofishing efficacy. We did not tag American shad collected in gill nets. Gill nets were used as a second gear to provide inference about electrofishing efficacy (i.e., to verify that we were not missing an upstream migration of fish at deeper water depths).

We attempted to collect, tag, and release American shad downstream of spawning grounds, but much of the St. Johns River downstream of historic shad spawning areas is deep, lending to poor capture efficiency of shad with boat electrofishing gear. Thus, selecting effective tagging sites was an adaptive process and varied somewhat throughout our study. In 2009, most shad were collected, tagged, and released between rkm 279.5 to 280.5 (a small section of channels between Lake Monroe and S.R. 414). However, we observed restricted movement patterns from telemetered fish tagged in 2009 (i.e., telemetered shad did not migrate far beyond the primary tagging reach). Based on input from our agency partners, we interpreted this occurrence to suggest that during 2009 we may have tagged fish relatively close to their intended spawning area thus potentially fish did not migrate much further upstream (i.e., tagging shad on the spawning grounds rather than prior to reaching them). In an attempt to intercept American shad early in the migration (and further downstream) in 2010 and 2011, we directed initial American shad sampling efforts from rkm 136 (Palatka) to rkm 218 (Lake Dexter). However, while a relatively large amount of effort was expended (about 13 field days each year) in these downstream locations, our success rates were quite low (3 fish tagged in 2010, none in 2011). To increase catch-rates, we shifted collection efforts further upstream to areas where electrofishing was known to be more successful both from our 2009 efforts and earlier reports from McBride and others. During 2010 and 2011, the majority of our tagged fish were collected and tagged between rkm 266.6 and 267.4 (in the vicinity of I-4 and S. R. 17/92 bridges), and we did not tag any American shad further upstream than rkm 267.4. This general tagging location still represented a downstream shift relative to tagging that was done in 2009 where most tagged shad were collected and released approximately 12 km upstream between rkm 279.5 to 280.5.

American shad that met size requirements were implanted with acoustic transmitters using a non-surgical, esophageal implant method (Bowman 2001). To aid in insertion, tags were held within the end of a thin-walled acrylic tube (13.5-mm inside diameter; 15.8-mm outside diameter) and covered in water-soluble surgical lubricant. Tags were pushed completely past the esophagus into the stomach cavity and ejected from the insertion tube. Prior to release, we monitored tagged shad in a holding tank for approximately 30 s for any signs of tag regurgitation and to verify that the individual had recovered from the sedative effects of being subjected to electric shock (i.e., selfmaintained equilibrium and steady swimming speeds). All tags used were Vemco® V-13 ultra-sonic transmitter tags (13-mm diameter x 36-mm length, 10.6-g weight, 101-d projected tag life, 69.0-kHz frequency).

Fixed-Position Receiver Array

During all years of our study we relied heavily on passive tracking of telemetry tags via an array of fixed-position acoustic receivers (Figure 1). Our receivers consisted of Vemco® VR2 or VR2W omnidirectional hydrophones that provided continuous monitoring of water surrounding each receiver in a 200 – 300-m radius. Thus, we stationed acoustic receivers in areas of the river where the wetted channel was relatively narrow and less than the detection range of a receiver to obtain the greatest likelihood of detecting passing telemetered fish as they migrated upstream. Each receiver essentially served as a gate within the river that identified each telemetered fish as it passed, and recorded the date and time. Because locations of the autonomous receivers were known, movement patterns of all tagged American shad were reconstructed by merging files from each receiver in the array. The spatial span of our fixed-position array within the St. Johns River was designed cover reaches of the river previously identified to support American shad spawning. We also stationed at least 1-2 monitoring stations downstream of locations where shad were captured, tagged, and released so that we could easily identify any instances of a tagged shad abandoning its spawning migration and emigrating from the study area in a downstream direction. Consequently, our fixed-position receiver array was very similar during all years of the study; however, some minor characteristics did evolve from year to year. Figure 2 shows fixed-position receiver locations, scaled by rkm, for receivers used during each year of sampling.

In 2009, our fixed-position receiver array spanned from State Road (S. R.) 44 (rkm 237.0) to S. R. 528 (rkm 372.0; Figure 2). During this first year of sampling, we paired receivers so that there were two receivers at most monitoring stations to maximize the likelihood of detecting passing tags. Therefore, out of 19 total receivers, we created 11 monitoring stations (8 double receiver stations and 3 single receiver stations).

The transition from the 2009 American shad spawning season to 2010 spawning season marked the biggest changes in arrangement of receivers in the fixed-position receiver array between study years. Results from 2009 indicated that single receivers were just as effective at detecting passing tags as double receivers. Therefore in 2010, we used only one receiver at each monitoring station. This essentially freed eight receivers to be used in new locations and expanded the spatial extent of the array implemented in 2010 relative to the previous year (Figures 1 and 2). We expanded upstream monitoring by adding monitoring stations at S. R. 520 (rkm 372.0) and at Snowhill Road in the Econlockhatchee River (Econlockhatchee rkm 18.0). We also expanded the fixed-position receiver array downstream by adding monitoring stations at rkm 133.3, 150.4, and 201.6. Because American shad use of the river reach between Lake Monroe and Lake Jesup was high in 2009, we added one additional monitoring station to rkm 287.3 (just upstream of the Lake Jesup – St. Johns River confluence) to gain greater resolution in the receiver array into how that area was used by shad (Figures 1 and 2). In 2011, our fixed-position receiver array was similar to the one we used in 2010, but we removed the two monitoring stations located most-downstream. A total of 17 monitoring stations were used in the fixed-position receiver array in 2011 (Figure 2).

Each telemetry tag transmitted its identifying signal at a semi-random interval, ranging from 15 – 45 seconds, with a 30 second mean interval. This regularity in signal emission was important because it was sufficiently frequent such that migrating fish could not travel past a monitoring station without being detected and not so frequent that tag life did not last the entire spawning season. However, if tagged American shad regularly used areas of river that were within detection range of a fixed-position receiver, this receiver could, theoretically, detect a tag signal from an individual fish every 30 seconds for a period of minutes to weeks, resulting in thousands of tag detections. For our purposes, we were primarily interested in tag detections occurring on daily time steps to assess movement and migration patterns. Therefore, we collapsed our data logs from the fixed-position receiver array to construct daily records of individual fish being detected on a given receiver (a “fish-day”). With this format, a fish that briefly passed by a receiver had the same weight for comparison as a fish that stayed within detection range of a receiver an entire day. This did not preclude a fish being detected on multiple receivers on the same day.

Manual Tracking

During the 2010 and 2011 spawning seasons, we conducted manual telemetry of American shad as a complement to information gained in the fixed-position receiver array. Manual searches implemented a Vemco® VR-100 directional hydrophone deployed from a boat. During manual tracking, we generally oriented the boat in mid-channel, would submerse the hydrophone in the water, and search for tagged fish upstream, downstream, and then towards each shoreline for 30-60 seconds in each direction. Using the VR-100 directional hydrophone, our detection range for a tagged fish was usually 200-400 m; however, it was occasionally affected by conditions of high ambient noise, shallow depth, and braided channels. High velocities of water rushing past the directional hydrophone resulted in turbulence and “noise” obscuring tag detections; therefore, the directional hydrophone could not be effectively used from a moving boat. As a result, manual searches were conducted in a step-wise process, where the search boat was incrementally advanced along a river reach and tag searches were conducted when the boat was not under power. As manual searches were meant to provide a continuous “sweep” of river reaches, the spatial periodicity for each step-wise increment at which we listened for telemetered shad always reflected the expected tag detection range during working conditions (i.e., 200-400 m for optimal conditions). Thus, in areas where the detection distance was short (due to increased ambient noise, shallow depths, highly sinuous or braided channels, etc.), we decreased the linear distance increment between listening locations (i.e., searched more frequently within a given length of river channel).

When a tag was detected via manual tracking, we evaluated signal strength from multiple locations to triangulate the specific location of the telemetered American shad. Our margin of error for determining the position of telemetered shad via signal triangulation varied depending upon environmental conditions and tag strength. Under optimal conditions, we perceived that signal triangulation could be accurate to within 1-2 meters. Under adverse conditions, we perceived our triangulation accuracy to place us within tens-of-meters of a telemetered shad location. This was because tag signal strength was difficult to differentiate for triangulation at close range, when there was high ambient noise, or if a telemetered fish moved as a response to the presence of the tracking boat. Nonetheless, once the best position fix could be obtained, we recorded latitude and longitude with a GPS and measured habitat parameters (detailed below).

Habitat Assessment

At locations of manually telemetered American shad, we recorded depth, flow velocity, substrate type, and channel width. Because relocation accuracy varied and did not always allow us to confidently identify a single, precise spot in the river channel at which we could measure habitat parameters, we characterized the river channel at multiple points along a profile perpendicular to flow. These transect lines bisected the best position fix for each telemetered shad and ran from bank to bank. Along each transect line we measured depth (m) and flow velocity ($m \cdot s^{-1}$) at 10%, 50%, and 90% of channel wetted width and at the channel thalweg. When conditions allowed for precise triangulation, we also recorded habitat parameters at the location of the telemetered shad in addition to the four points along the channel transect.

We also recorded a categorical assessment of substrate type at each point along transects. We sampled substrate via a steel pipe dredge (4-in diameter, 16-in length, 10-lb weight) that was lowered to substrate and dragged for approximately 1-m at each habitat measurement location along transect lines. The dredge was retrieved, and we classified substrate based on particle size. The diversity of substrate particle size is low at the St. Johns River relative to rivers at higher latitudes. Most substrates were best described as sand, silt, or a mixes of the two substrates. Thus, we categorized substrate as: all sand (sand), sand particles dominant over silt (sand > silt), sand particles equal to silt (sand = silt), silt particles dominant over sand (silt > sand), or all silt (silt).

To determine if American shad selected for certain habitat conditions in the St. Johns River for spawning, we compared habitat parameters for areas where telemetered American shad occurred (i.e., recorded from transects where telemetered shad were located) to habitat parameters measured at randomized locations that represented available habitat. Our hypothesis was to determine whether habitat conditions at places where telemetered American shad were located (used) differed from random sites (available). We measured available habitat along transects using the same methods as for measuring habitat for manually telemetered shad. Prior to the onset of manual tracking for the 2011 spawning season, we created a bank of randomized locations for available habitat transects. Then for each day of manual telemetry searching, a subset of available habitat transect locations was randomly selected to be measured as they were encountered during the manual telemetry sweep of a river reach. Therefore, available habitat parameters were measured throughout the American shad spawning season and were reflective of any changes in water levels that occurred during the overall spawning window. We considered habitat selection to occur if there was differential use of habitat relative to overall or average conditions as measured by statistical comparison of habitat parameter measurements. We tested for differences in measured parameters from used and available habitats with two-sample t-tests ($\alpha = 0.05$).

Results

Water Levels During American Shad Spawning

Previous research of American shad spawning in the St. Johns River, Florida indicated that river discharge and water level likely influenced spawning fish distribution (William and Bruger 1972); therefore, knowledge of water levels during our research provides important context to the spatial distribution patterns of American shad that we observed. River discharge and water level varied somewhat among years of our study and resulted in one high water level spawning season (2010) and two low water level spawning seasons (2009 and 2011). The low water level spawning seasons had very similar patterns of river discharge and water level that were generally below median water levels for gauging station histories (Figure 3). The 2010 spawning season had higher flows where river discharge and water levels were generally higher than median water levels for gauging station histories. Figures 3-4 show river discharge and gauge height for three locations in the St. Johns and Econlockhatchee rivers (USGS gauge 02234500 on St. Johns River at U.S. Hwy 17/92, USGS gauge 02234000 on St. Johns River at S.R. 46, and USGS gauge 02233500 on Econlockhatchee River at Snowhill Rd.). We selected these three water level gauges because their locations were central to American shad activity in our study, and they best illustrated the water level conditions that may have influenced telemetered shad.

American Shad Collection and Tagging

During the 2009 spawning run, we tagged 15 American shad with ultra-sonic transmitters to address objective 1 (i.e., evaluating the efficacy of tracking shad in this system). Total length of American shad tagged in 2009 ranged from 400 to 483 mm (Figure 5). We did not record sex for telemetered shad during the first year. We staggered three tagging events over a period of approximately three weeks (26 January, 6 February, and 12 February 2009), and five tags were implanted on each occasion.

In 2010, we increased the number of tagged American shad to 59. Total length of shad tagged in 2010 ranged from 404 to 490 mm (Figure 5). Thirty tagged shad were female, and 29 were male. Because of a larger number of total tags used in 2010, we staggered tagging over a period of approximately five weeks (18 January – 22 February) with an even distribution of tags across tagging events within this timeframe.

American shad tagging in 2011 was very similar to tagging implemented in 2010. In 2011, we tagged 40 American shad, and again, staggered tagging over a five week period. We tagged shad on 12, 20, and 27 January and 2 and 10 February 2011. Total length of American shad tagged in 2011 ranged from 401 to 526 mm (Figure 5). Of the 40 tagged shad, 23 were female and 17 were male.

Fixed-Position Receiver Array

In 2009, we monitored 15 telemetered American shad. In aggregate, those tags were detected in the fixed-position receiver array over 29,000 times. Tag detections in 2009 accounted for 135 fish-days (i.e., unique combinations of tag, day, and receiver; Figure 6). We recorded tag detections at 8 of 11 monitoring stations (Figure 7), and the tag detections spanned from the most-downstream monitoring station at S.R. 44 (rkm 237) to S.R. 50 (rkm 350.5). We did not detect any telemetry tags at the two most-upstream monitoring stations near the Tosohatchee power line right-of-way (rkm 362.1) or S. R. 528 (rkm 372).

In 2010, we tracked 59 telemetered American shad, and in aggregate, those shad were detected in the fixed-position receiver array over 400,000 times. The total tag detections resulted in 1,020 fish-days. In 2010, some portion of telemetry tags were detected at every monitoring station ranging from Memorial Bridge in Palatka (rkm 133.3) to S.R. 520 (rkm 386.6), where five tags were detected at the most-upstream monitoring station (Figures 6 and 7).

In 2011, we monitored 40 telemetered shad, and in aggregate, those shad were detected in the fixed-position receiver array over 248,000 times. These detections represented 898 fish-day detections. We detected telemetered shad at 14 of 16 total monitoring stations, and those detections spanned from S. R. 40 bridge in Astor (rkm 209.4) to the Tosohatchee powerline right-of-way (rkm 362.1). We did not detect tagged shad at either of the two most-upstream monitoring stations located at S. R. 528 (rkm 272) and S. R. 520 (rkm 386.6; Figures 6 and 7).

Overall, shad movement patterns within the fixed-position receiver array were very similar from year to year over three spawning seasons of monitoring. In each year, highest shad activity occurred between lakes Monroe and Jesup, and detections of telemetered shad steadily declined with increased distance upstream from the Lake Monroe – Lake Jesup reach (Figures 6 and 7). Figure 8 shows detection histories for telemetered shad that were characteristic of this group, whose movement patterns focused on the Lake Monroe – Lake Jesup reach. Many of the telemetered shad whose activity was focused in the Lake Monroe – Lake Jesup reach never ascended beyond Lake Harney. During 2009 – 2011, 80%, 52%, and 53% of the viable telemetered shad during each year, respectively, did not ascend beyond Lake Harney as evident by their absence on the next upstream receiver located at C. S. Lee Park near S. R. 46 (rkm 316.4) or any other upstream receiver. However, the 80% value for 2009 may be biased high because fish in this year were tagged further upstream than in 2010 and 2011.

Detection histories from the fixed-position receiver array showed some portion of telemetered American shad entered the Econlockhatchee River during each year of our study (Figures 6 and 7). In 2009, we detected one telemetered shad (7% of all telemetered shad) in the Econlockhatchee River. In 2010, we detected eight shad (16% of all telemetered shad), and in 2011, we detected 7 shad (18% of all telemetered shad) there, which indicated somewhat consistent use of the Econlockhatchee River by American shad during spawning migrations. Of the telemetered American shad that entered the Econlockhatchee River, most stayed within the lower 18 rkm of river channel. However, during 2010 and 2011, the two years a monitoring station was in place at Econlockhatchee rkm 18, we detected two telemetered shad at this location during each year, indicating that these shad migrated at least as far as the lower 18 rkm of the Econlockhatchee River.

Although overall detection patterns among years shared several similar patterns, the number of telemetered shad that migrated to the upstream extents of the fixed-position receiver array varied somewhat among years (Figures 6 and 7). In 2009 and

2011, the lower streamflow years, telemetered shad were only detected as far upstream as S. R. 50 (rkm 350.5) or the Tosohatchee powerline right-of-way (rkm 362.1). During 2010, the high streamflow year, we detected 12 telemetered shad (24% of telemetered shad) at S. R. 50 (rkm 350.5) and five shad (10% of telemetered shad) that ascended within the river to the last upstream monitoring station at S. R. 520 (rkm 386.6). These results indicate that low water levels may limit the upstream movement of a portion adult American shad during their spawning migration. Thus, long spawning migrations upstream, such as shown in Figure 9, may be rare during years with low river flow conditions. Figure 9 shows detection histories for four telemetered shad that migrated to the most upstream area of our receiver array in 2010.

Previous American shad telemetry studies have reported “fall-back”, a delay or abandonment of typical upstream spawning migration post tagging, in American shad and other anadromous fishes (Olney et al. 2006). We observed some telemetered shad to exhibit fall-back behavior during all years of our study. The percent of telemetered shad that exhibited fall-back behavior was relatively similar across years and ranged from 6 to 10%. However, most of the telemetered shad that exhibited fall-back behavior did not completely abandon the spawning migration and eventually resumed upstream movement. Figure 10 shows example tag detection histories for four telemetered American shad in 2010 that displayed fall-back behavior, with three of the detection histories showing resumed upstream migration following the fall-back behavior.

Manual tracking

To obtain higher spatial resolution of American shad spawning migration movements and habitat use than could be inferred from fixed-position receiver array telemetry results alone, we conducted manual telemetry searches for American shad during the 2010 and 2011 spawning seasons. In 2010, manual searches were conducted during 35 cumulative days between 11 February and 6 May 2010. The spatial extents of 2010 manual tracking effort spanned from rkm 237 to 365 and rkm 372 to 420 (The short gap in coverage between rkm 365 and 372 was immediately downstream of S. R. 528). In the Econlockhatchee River, we conducted manual telemetry searches five times from the confluence of the Econlockhatchee River to its rkm 18 near Snowhill Road. In total, we conducted manual telemetry searches along approximately 690 cumulative km of river channel in the St. Johns and Econlockhatchee rivers.

In 2011, we conducted manual telemetry searches with the same methods and similar effort allocation as the 2010 sampling season. Our 2011 manual telemetry searches were conducted during 36 total days from 24 January to 18 May. Our manual tracking effort spanned from rkm 241 to 386, with all main channel sections between these two points having been searched at least once, and some river reaches were searched up to 10 times. Again in 2011, we searched the Econlockhatchee River from its confluence with the St. Johns River to Econlockhatchee rkm 18, near Snowhill Road, a total of five times. In total, we conducted manual telemetry searches along approximately 737 km of river channel in the St. Johns and Econlockhatchee rivers. Figure 11 shows manual telemetry effort expenditure per rkm for the St. Johns River in 2010 and 2011, where one unit of effort was equal to one passing “sweep” of the VR-100 directional hydrophone as described previously. The main difference between manual telemetry effort allocation in 2010 and 2011 was a result of low water levels in

2011 making access to upper river reaches difficult or impossible. As a result, our overall 2011 manual telemetry searching effort did not extend as far upstream in comparison to 2010. This created a slight shift in the overall effort allocation, from 2010 to 2011, toward the high use reaches for American shad between lakes Monroe and Jesup as seen in Figure 11.

Tag detection patterns via manual telemetry were similar in 2010 and 2011 and showed similar spatial distribution patterns for American shad as documented by the fixed-position receiver array during each year. In 2010, we detected 53 of 59 total telemetry tags via manual telemetry searches, and our total number of tag detections was 194 (Figure 12). Therefore, each tag was located via manual telemetry an average of 3.6 times in 2010. In 2011, we detected 34 of 40 total telemetry tags via manual telemetry searches, and our total number of tag detections was 141 (average of 4.1 times per tag, Figure 13). In both years, manual telemetry search results were consonant with results from the fixed-position receiver array, where the Lake Monroe – Lake Jesup reach was the highest use area during our study. In 2010, 113 manual telemetry tag detections (58%) occurred between lakes Monroe and Harney, and in 2011, we detected 101 (72%) tags via manual telemetry in the same reach. Manual telemetry tag detections from 2010 and 2011 between lakes Monroe and Harney also showed high use of this area, similar to the fixed position receivers (Figure 14). River reaches upstream of Lake Harney produced 50 (26%) and 36 (27%) tag detections by manual telemetry in 2010 and 2011, respectively. Figures 15 and 16 illustrate manual telemetry tag detection patterns at a smaller, reach-scale that focus on reaches from Lake Harney to Puzzle Lake and from Hatbill to S. R. 50 and show clusters of tag detections from 2010 and 2011. Included among manual telemetry tag detections that occurred above Lake Harney were shad that were manually telemetered in the Econlockhatchee River. During 2010, we had 10 manual telemetry detections in the Econlockhatchee River from four unique tagged shad, and in 2011, we had four manual telemetry detections that were attributed to two tagged shad. Figure 17 shows manual telemetry detections for American shad in the Econlockhatchee River from the 2010 and 2011spawning migrations.

The remainder of manual telemetry detections corresponded to tags relocated downstream of Lake Monroe. These included 30 locations (15%) in 2010 and 3 locations (2%) in 2011. The relatively large number of manual telemetry tag detections in Lake Monroe or downstream during 2010 was due to the group of “non-moving” tags (presumably mortalities or tag regurgitations) that existed near the tagging reach.

Because year-to-year manual telemetry effort differed somewhat and reach by reach effort differed markedly within each year, we standardized manual telemetry results as catch per unit effort (CPUE) to provide more accurate comparisons between years and between river reaches within each year (Figure 18). We calculated CPUE for each rkm that was searched at least once via manual telemetry methods, and CPUE was measured as the total number of telemetry tag detections divided by number of searching passes completed with manual telemetry gear. Telemetry CPUE could also be used to make general comparisons between this study and others that reported CPUE metrics related to American shad spawning in the St. Johns River.

The spatial distributions of telemetry CPUE were generally similar in 2010 and 2011 (Figure 18). In 2010, telemetry CPUE varied from 0 – 2.63 detections · $pass^{-1}$, and non-zero CPUE values occurred in 33.5% of surveyed rkms. In 2011, telemetry CPUE varied from 0 – 2.11 detections · pass^{-1} with 26.5% of surveyed rkm having CPUE values > zero. During both years, the highest telemetry CPUE for American shad occurred in the reach between lakes Monroe and Jesup (rkm 279 – 283). In 2010, we observed secondary peaks in telemetry CPUE at rkms 313, 326, and 357 (1 – 1.33 detections · pass^{-1}). In 2011, we observed secondary peaks in telemetry CPUE at rkms 326 and 341 (0.8 – 1.0 detections · pass^{-1}. Differences in telemetry CPUE between years primarily occurred in the most-upstream range of telemetered shad movements, with detections of telemetered shad extending much further upstream in 2010 (higher water conditions) relative to 2011 (lower water level conditions; Figure 18). Thus, the CPUE metric presented similar inference on habitat use to the overall detection data. Further, areas of highest CPUE based on telemetry also corresponded to highest electrofishing catches by FWC staff (R. Hyle, unpublished data).

In the Econlockhatchee River, CPUE of telemetered shad differed between years and was somewhat low relative to detection rates at reaches in the St. Johns River (Figure 19). In 2010, more American shad were detected via manual telemetry in the Econlockhatchee River and CPUE varied from 0 – 0.6 detections · pass^{-1}). Highest CPUE was observed at Econlockhatchee rkm 13, and 35% of rkm in the Econlockhatchee had CPUE greater than zero. In 2011, CPUE for telemetered shad in the Econlockhatchee varied from 0 – 0.4 detections · pass^{-1}, and the highest CPUE was observed at Econlockhatchee rkm 11. Approximately 17% of rkm in the Econlockhatchee had CPUE greater than zero.

Habitat Assessment

We compared measures of depth (m) and flow velocity ($m \cdot s^{-1}$) at channel thalwegs for used and available habitat transects to evaluate depth and flow selection patterns for American shad in the St. Johns River. Among the multiple points of habitat measurement along channel profile transect lines, we selected data collected at thalwegs for between-transect comparisons because these data represented profile maxima for depth and flow. Additionally, when we experienced greatest spatial precision for tag triangulation via manual telemetry, we found telemetered shad frequently occupied the channel thalweg. This suggested that habitat data collected at the thalweg in channel profile transects was likely a good proxy for shad position when we were unable to triangulate a precise position for a manually telemetered shad. We categorized used and available habitats by position in the river relative to large-scale patterns in channel morphology. Downstream of Lake Harney, discharge in the St. Johns is largely confined to one channel, and upstream of Lake Harney, discharge is often divided among multiple, smaller channels. Discharge in the lower Econlockhatchee River is largely confined to a single channel; however, its discharge is much less than the St. Johns River. Therefore, we made comparisons of used and available habitat for three spatial regions: downstream of Lake Harney, upstream of Lake Harney, and the Econlockhatchee River.

Overall, telemetered shad occurred in habitats with maximum flows that ranged from 0.01 to 0.31 $m \cdot s^{-1}$ and maximum depths that ranged from 0.5 to 7 m, and we identified instances of shad selecting for deeper depths and faster flows in reaches of the St. Johns River, but not in the Econlockhatchee River. Water depths for used versus available (random) habitats did not differ downstream of Lake Harney (used = 3.04 m; available = 3.34 m; $p = 0.251$; Figure 20). Depths for used habitats were significantly greater than available habitats in reaches upstream of Lake Harney (used = 1.84 m; available = 1.37 m; $p = 0.036$, Figure 20). Flow velocity was significantly greater for used habitats relative to available habitats for reaches downstream and upstream of Lake Harney in the St. Johns River (Figure 21, used downstream = 0.112 $m \cdot s^{-1}$; available downstream = 0.079 $m \cdot s^{-1}$; $p = 0.003$; used upstream = 0.133 $m \cdot s^{-1}$; available upstream = 0.090 $m \cdot s^{-1}$; $p = 0.023$). In the Econlockhatchee River, depths for used and available habitat did not differ (used = 2.23 m; available = 2.12 m; $p = 0.861$, Figure 22). In the Econlockhatchee River, flow velocity for used and available habitats did not significantly differ (Figure 22, used = 0.155 $m \cdot s^{-1}$; available = 0.136 $m \cdot s^{-1}$; $p = 0.632$). Therefore, when differences in used and available habitat were observed, we found that American shad selected for deeper sections of river with higher flow velocities.

Generally, telemetered American shad occurred at habitats with substrate categorization in similar proportion to the availability of those substrate categorizations (Figure 23). Thus, we did not observe evidence for selection of substrate type during our study. In the St. Johns (both upstream and downstream of Lake Harney) we observed all substrate categories (e.g. sand, sand > silt, sand = silt, silt > sand, and silt). The availability of these substrate categorizations varied somewhat, but the use of these habitats by American shad was similar to overall availability. In the Econlockhatchee River the availability of substrates was skewed towards sand substrates, and telemetered shad in the Econlockhatchee were always associated with sand substrates.

Discussion

We documented that adult American shad demonstrated spawning migration behaviors in the St. Johns River, Florida entering the river in late winter and early spring with the majority of fish migrating upstream to an area between lakes Monroe and Jesup where spawning likely took place. We did not document spawning first hand through egg collections, but behaviors observed by telemetered fish and habitats selected by these fish suggest that these locations were suitable spawning locations. Collections of juvenile American shad downstream of this area between lakes Monroe and Jesup by FWC personnel provide additional inference that this location was a spawning site.

Our observations of this area between these two lakes being a spawning site were consistent across contrasting riverine flow conditions of high and low water levels. However, we observed differences in upstream migration distances in the year with high flow relative to the two lower flow years, with telemetered shad making longer migrations under conditions of higher water levels. We observed that American shad selected areas of the St. Johns River that had higher flow velocities than average conditions. We also observed in upstream reaches, which are typically shallower than downstream reaches, that American shad selected for habitats that were deeper than average conditions. Thus, the velocity and stage of the St. Johns River likely influenced the habitats selected for spawning by adult American shad and modifications to discharge or stage may alter the availability of these habitat characteristics for American shad in the St. Johns River.

Locations of American shad during spawning were generally similar to conclusions from Williams and Bruger (1972), but there were some interesting differences. During all years of our study, highest occurrence of telemetered American shad was in the reach between lakes Monroe and Jesup (rkm 275 – 287). Above Lake Harney, we typically saw steep declines in the presence of telemetered American shad, but several secondary high-use areas were located among these reaches. In 1969 and 1970, Williams and Bruger (1972) generally observed highest measures of American shad spawning activity (eggs $\cdot$ hr^{-1}) well upstream of the Lake Monroe – Lake Jesup reach (Figure 24). However, in 1970, they reported relatively high catch rates at rkm 285.5, which is located within the Lake Monroe – Lake Jesup reach (Figure 24). Williams and Bruger (1972) went on to suggest that the relative importance of this reach for American shad spawning could be much greater than its absolute catch rates would imply. This reach is much wider than areas upstream producing higher catch rates, thus it may have supported a greater number of spawning shad. Nichols (1965 and 1966) also monitored American shad spawning on the St. Johns River by collecting eggs. In 1964, Nichols reported highest catch rates for shad eggs between S. R. 50 (rkm 350.5) and S. R. 520 (rkm 386.6), well upstream of our high-use area. In 1965, he reported highest American shad egg catch rates just upstream of Puzzle Lake (rkm ~330). Nichols (1965) also reported that second highest egg catches were observed at Marina Isle (rkm ~287), which lies near the upstream end of the Lake Monroe – Lake Jesup reach. This location was not a high use area at any time during our 2009-2011 study nor has it been observed to be a high use area by agency cooperators over the last 8 years (R. Hyle, FWC, personal communication). Also, in a study investigating larval densities for American shad at the St. Johns River, Boucher (2009) reported high catches of larval shad near S. R. 46 (rkm ~284 and ~290). He noted that this area contained one of only two large aggregations of shad larval identified in 2009. Although reaches of highest-use for spawning American shad have varied somewhat among years and studies, our results that showed the Lake Monroe – Lake Jesup reach as a high-use area do not drastically depart from previous research findings, as this reach has yielded high catch rates for eggs or larval shad in the past.

Overall, characteristics of the spatial patterns of our telemetered American shad related to habitat use and migration distance were relatively similar across the three years of our study; however, the upstream extent of telemetered shad varied and may have been influenced by water levels. During our high water year of 2010 we detected 10% (n=5) of the moving telemetered shad migrating to at least rkm 386.6 and we relocated three of these fish as far upstream as rkm 402.8. We did not detect any telemetered fish migrating this distance upstream during our low water years in 2009 (max upstream detection: rkm 350.5) or 2011 (max upstream detection: rkm 362.1). Our FWC agency partners have collected adult American shad during very low water in 2007 and 2009 via electrofishing airboat in these same areas with high catches in 2009 at rkm 356-358 but catches further upstream of this location were very low (R. Hyle, FWC, personal communication). Williams and Bruger (1972) collected American shad eggs as far upstream as just beyond Lake Poinsett in 1969 (rkm ~400) and to S. R. 192 (rkm 433) in 1970. Their low water year (1969) was actually intermediate to our low water and high water conditions, and water levels during 1969 were at or above median gauge heights for much of the shad spawning season (Figure 25). Therefore, their documentation of shad spawning activities beyond rkm 350 – 360 in 1969 does not necessarily contradict our suggestion that low water levels (such as those observed in 2009 and 2011) may restrict spawning migrations to the far upstream reaches of the St. Johns River.

We observed telemetered shad in velocities from 0.01 to 0.31 $m \cdot s^{-1}$ (average: 0.12 $m \cdot s^{-1}$), and this range of flows is lower than those reported in most other studies for American shad spawning habitat. In a review of characteristics for American shad spawning populations in the southern portion of their range, Facey and Van Den Avyle (1986) reported that most American shad spawn in flows between 0.305 and 0.914 $m \cdot s^{-1}$. In Virginia streams Massman (1952) reported that most American shad spawning took place between 0.61 and 0.88 $m \cdot s^{-1}$. For North Carolina rivers Hightower and Sparks (2003) reported mean current velocity of 0.63 $m \cdot s^{-1}$ for shad spawning grounds at the Roanoke River, and Bowman (2001) reported 0.20 – 0.60 $m \cdot s^{-1}$ as the range of flow conditions for American shad spawning at the Neuse River. Williams and Bruger (1972) reported that most of their American shad egg collections at the St. Johns River took place during flow conditions of 0.3 – 0.46 $m \cdot s^{-1}$. The velocity values reported by Williams and Bruger (1972) were greater than ours, but similar in that they were low compared to velocities reported from other river systems in the southern portion of American shad occurrence. Low velocities in the St. Johns River result from very little elevational drop from headwaters to river mouth. Outside of Florida, most other river systems that support American shad spawning flow through an area of relatively steep elevation and physiographic change, often referred to a “fall zone”, where river flows are generally increased and American shad spawning occurs. These conditions are not present at the St. Johns River, and this may help to explain why the range for American shad spawning there is large and dynamic from year to year.

When we compared flow measure at locations of telemetered shad to available habitat, we found that they selected for areas that had higher flow velocity than average conditions. The SJRWMD flow data support our observations of American shad selection for higher flows because areas of high shad use had higher than average velocities in 2009 and observational reports from agency cooperators confirm this for 2006 and 2007 as well (S. Miller SJRWMD, personal communication). Many studies have previously linked American shad spawning behaviors and habitat use with spatial distribution and variation in river velocities, suggesting that they select and need certain velocities (often the highest available flows) for spawning. Leggett (1976) suggested that American shad relied on steady, downstream flows as cues for finding spawning habitat. If downstream flows stopped or reversed (as influenced by tides), he observed American shad to stop upstream movement, or even reverse direction and move downstream. Following a large-scale re-distribution of flows at the Santee River, South Carolina in 1985, Cooke and Leech (2003) observed a re-distribution of American shad during spawning migration to follow where relatively high river flows occurred. In 2004, Harris and McBride conducted further analyses to data published in Williams and Bruger (1972) from the St. Johns River. They showed that catch rates of American shad eggs were significantly and positively correlated to river flow velocity at sampling stations. Using a similar methodology to ours, Bowman (2001) compared used to available habitat for spawning American shad at the Neuse River, North Carolina, and he found that American shad used areas of river channel that had significantly higher flow velocity than average conditions. Walberg and Nichols (1967) reported that shad select for higher flow for spawning to prevent their eggs from becoming trapped in silt and suffocating.

Substrate type may not be a good indicator of suitable spawning habitat for American shad at the St. Johns River. We observed low diversity of substrate in the river, and American shad were associated with substrate categories in the same proportions in which these categories occurred (i.e., no selection). Williams and Bruger (1972) reported that catch of American shad eggs in the St. Johns occurred over “clean sand” substrates, and this is somewhat inconsistent with our results as we did not observe selection of American shad for sand substrates. Williams and Bruger (1972) did not provide details for habitat categorization, and it is possible that differences in our methods or subjectivity in substrate categorizations were responsible the differences. Previous research at other river systems supporting American shad spawning indicated that shad spawn over relatively coarse substrates, such as gravel, cobble, and boulder substrates (Stier and Crance 1985; Bowman 2001; Hightower and Sparks 2003). These substrates are typical of “fall-line” river channel transitions, which do not occur in the St. Johns River.

We found that telemetered American shad selected for deeper habitats in the shallower reaches of the St. Johns River that are above Lake Harney. This result was similar to one observed by Bowman (2001) at the Neuse River, North Carolina. Some studies have suggested that American shad prefer to spawn over relatively shallow sandbars, sand flats, or rocky shoals (MacKenzie et al. 1985; Hightower and Sparks 2003). However, it has been commonly reported that American shad will spawn over a wide range of depths, sometimes up to 12.2 m (Massman 1952; Walburg 1960; Walburg and Nichols 1967; Stier and Crance 1985). These studies appear to indicate that American shad are habitat generalists in terms of depth and suggest that channel depth may not be nearly as influential as flow velocity on where American shad spawn. Our study seems to support that line of thought as we observed more widespread selection for flows than we observed selection for depths.

Comparisons drawn between our results and results from previous shad research could have been affected by differences in methodologies for tracking American shad spawning. We used acoustic telemetry tags to follow movements of adult American shad during annual spawning migrations. Our telemetry gear provided detailed movement histories of tagged shad and indicated areas where tagged shad occurred and areas where tagged shad did not occur. Our habitat measurements and patterns of spatial distribution for American shad in the St. Johns River were based only on occurrence of telemetered shad. We did not collected eggs as evidence of actual spawning. We assumed that the majority of our telemetered shad were not adversely affected by tag implants and that their movement patterns were representative of the aggregation of spawning shad during each year. We assumed that American shad would migrate to areas in the St. Johns River favorable for spawning, and we assumed that areas of repeated occurrence for telemetered shad represented important habitat for shad spawning. Much of the previous research to which we make comparisons was based on, or partially included, collection of recently spawned eggs (Walberg 1960;

Nichols 1965; Nichols 1966; Williams and Bruger 1972; Hightower and Sparks 2003). Because shad eggs are demersal, it has usually been assumed that shad eggs have been collected very near to spawning sites (Williams and Bruger 1972; Hightower and Sparks 2003). Previous research has indicated that most shad spawning occurs during nighttime hours (Facey and Van Den Avyle 1986; Bowman 2001). Our manual telemetry searches (on which used habitat measures relied) occurred during daylight hours, and it is possible that our telemetered shad could have made short movements from their telemetered locations during the day to locations where spawning occurred (possibly at night). Results from our fixed position receiver array provided constant monitoring at a large spatial scale and did not indicate any large shifts in telemetered shad at night relative to daytime positions. Therefore, if there were any shifts between telemetered shad locations and actual spawning locations, they would have been small.

Changes to long-term flow-regimes in the St. Johns River, especially reductions in long-term velocity, could negatively affect American shad spawning success. Under low-flow conditions we observed a reduction in the range of telemetered shad on their spawning grounds, suggesting that low water levels may limit access to the most-upstream reaches. We also observed that shad spawning in the St. Johns River selected for locations that had higher flow velocity than average conditions. As flow velocities in the St. Johns River are low relative to other rivers that support American shad spawning, it is very likely that shad select the highest flow velocities in the St. Johns River for their spawning. Large-scale and long-term reductions in discharge and water level could affect the success of shad spawning and the rebuilding of a reduced population by restricting access to spawning reaches or reducing the availability of habitat with sufficient flow velocities necessary for American shad spawning. Therefore, water use and regulation in the St. Johns River should take into consideration effects on American shad spawning habitat. Future research for American shad spawning in the St. Johns should investigate the population level impacts of flows on American shad spawning success by linking annual water level conditions experienced by eggs and juveniles with age specific abundance of adult cohorts when they return to the St. Johns River to spawn.

Conclusions and Future Recommendations

- Low discharge and water levels may restrict access to the uppermost reaches of the American shad spawning grounds at the St. Johns River, Florida, as the upstream range of telemetered shad was less during low flow conditions relative to high flow conditions. These observations were also supported by FWC electrofishing surveys. This suggests that long-term changes in discharge and stage may reduce available spawning habitat relative to historical areas.

- The river reach between Lake Monroe and Lake Jesup may support more spawning than previously documented, as a large proportion of telemetered shad activity was located in this reach during 2009 – 2011 spawning seasons.

- In the St. Johns River, habitats with higher than average flows and depths are likely important for American shad spawning, as telemetered shad selected areas with higher flow velocity in comparison to average habitat flow conditions. Similar observations have been found in previous years by SJRWMD personnel.

- Sections of relatively deep river channel are likely important for American shad spawning, possibly as refuge from aerial predators and staging areas in between spawning events, as telemetered shad selected areas with deeper depths in comparison to average habitat conditions.

- Decreased flow regimes in the St. Johns River could reduce the available spawning habitat for American shad and affect spawning success by reducing the number of areas having sufficient flow velocity for spawning or by restricting access to suitable areas via shallow water migration bottlenecks. Our results showed evidence for changes in spawning habitat use during low flow conditions, which could have implications for recruitment.

- While this and most previous efforts have focused on timing and location of spawning activities, future research efforts should consider assessing whether there is a relationship between spawning, recruits, and adult population size in subsequent years. Management goals for this species include recovery of the stock, and there is a need to know whether there is a relationship between spawning habitat area, juvenile production, and returns by adults in subsequent years. This would be a key research topic for assessing the recovery of this stock and in informing water policy concerns about impairment to the population due to changes in riverine flow conditions.

Significant Deviations:

None

Cost:

Associated SF425 will be sent under separate cover.

Figures

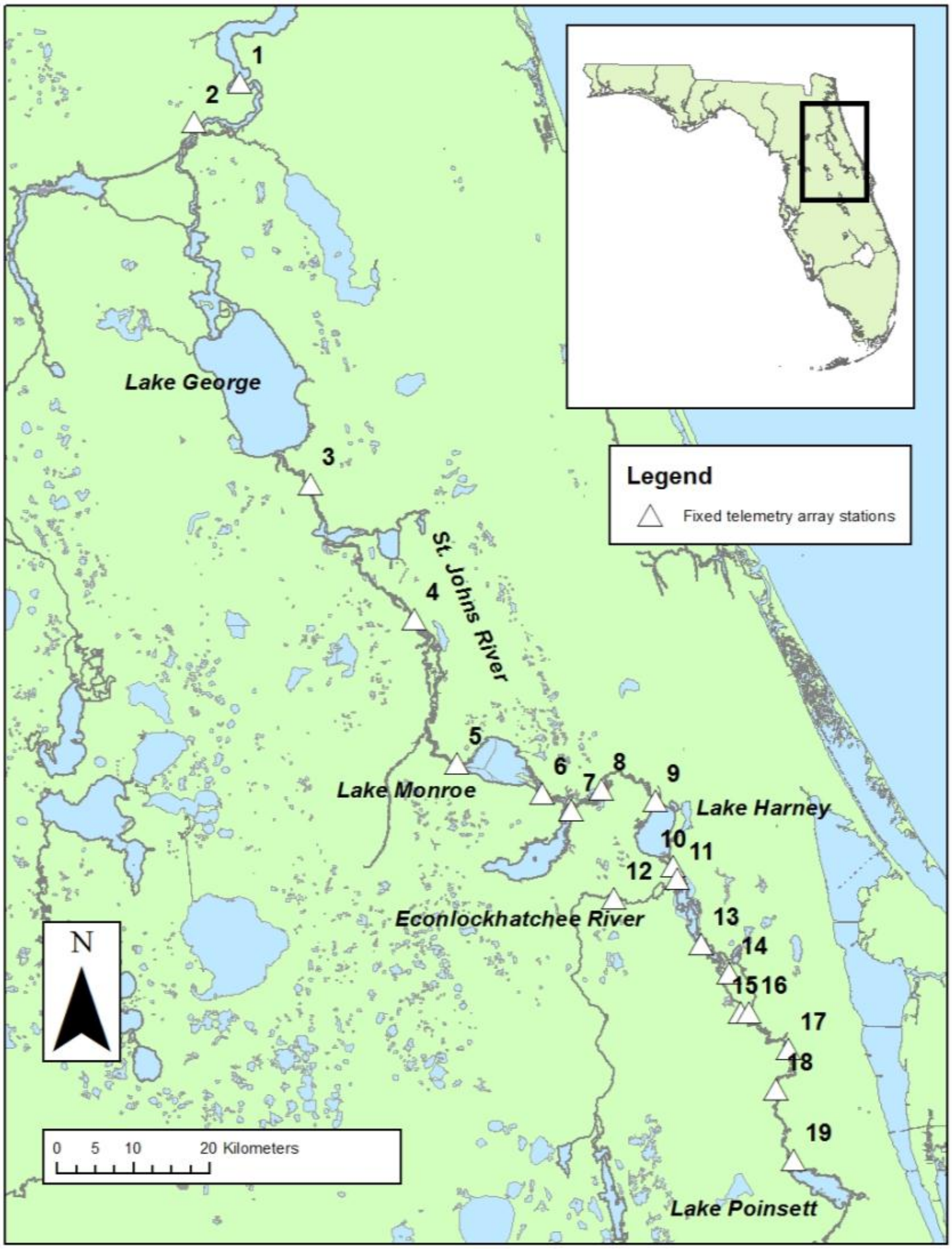

Figure 1. Map showing locations of fixed-position monitoring stations (numbered, white triangles) along the St. Johns River and Econlockhatchee River, Florida for monitoring adult American shad during the 2010 spawning migration. Total receiver array length was approximately 253 rkm. Slight modifications to this array design were implemented during each year of telemetry (see Figure 2 for further details). Note that the river flows from south to north.

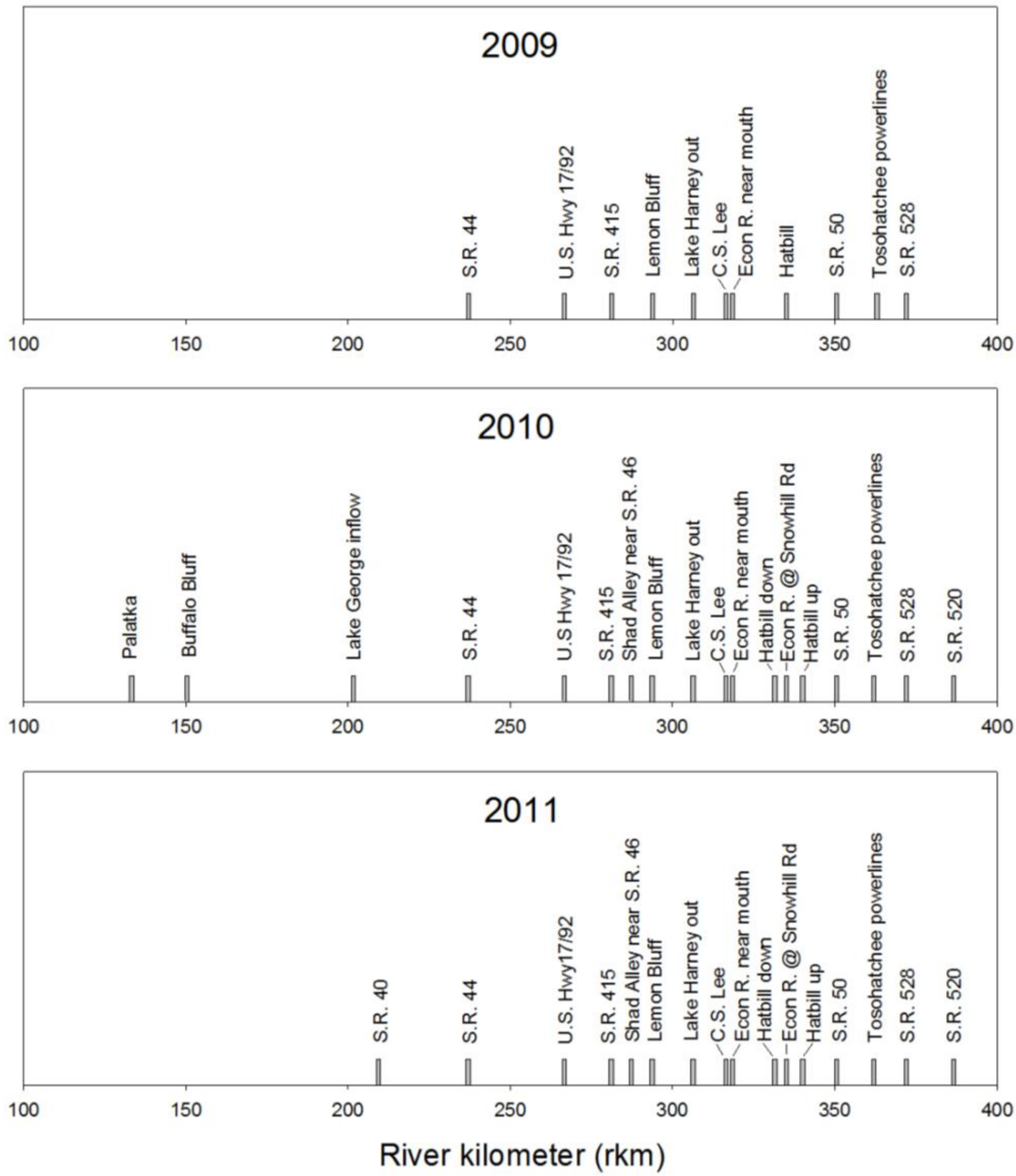

Figure 2. Locations of fixed-position acoustic receivers during three years of American shad telemetry. Receiver positions are scaled by river kilometer (rkm) along each horizontal axis. Total number and placement of receivers varied from year to year.

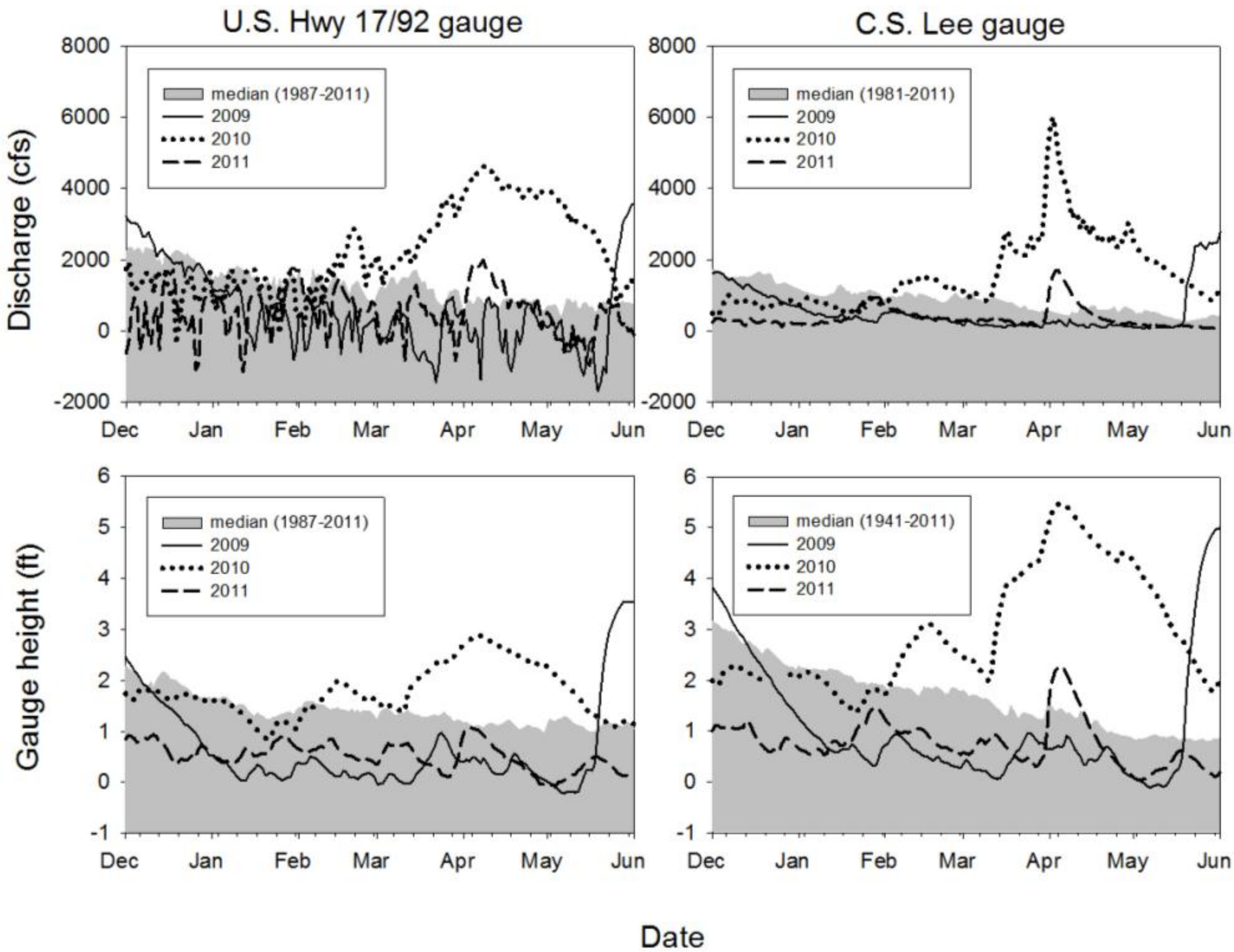

Figure 3. Discharge (cfs) and gauge height (ft) for two water gauging stations located near American shad spawning areas. Left panels display discharge and gauge height data from USGS gauge 02234500 at U.S. Hwy 17/92 (266.7 rkm). Right panels display discharge and gauge height data from USGS gauge 02234000 near C. S. Lee Park (rkm 316.6). Values for each sample year and the long term median values are shown.

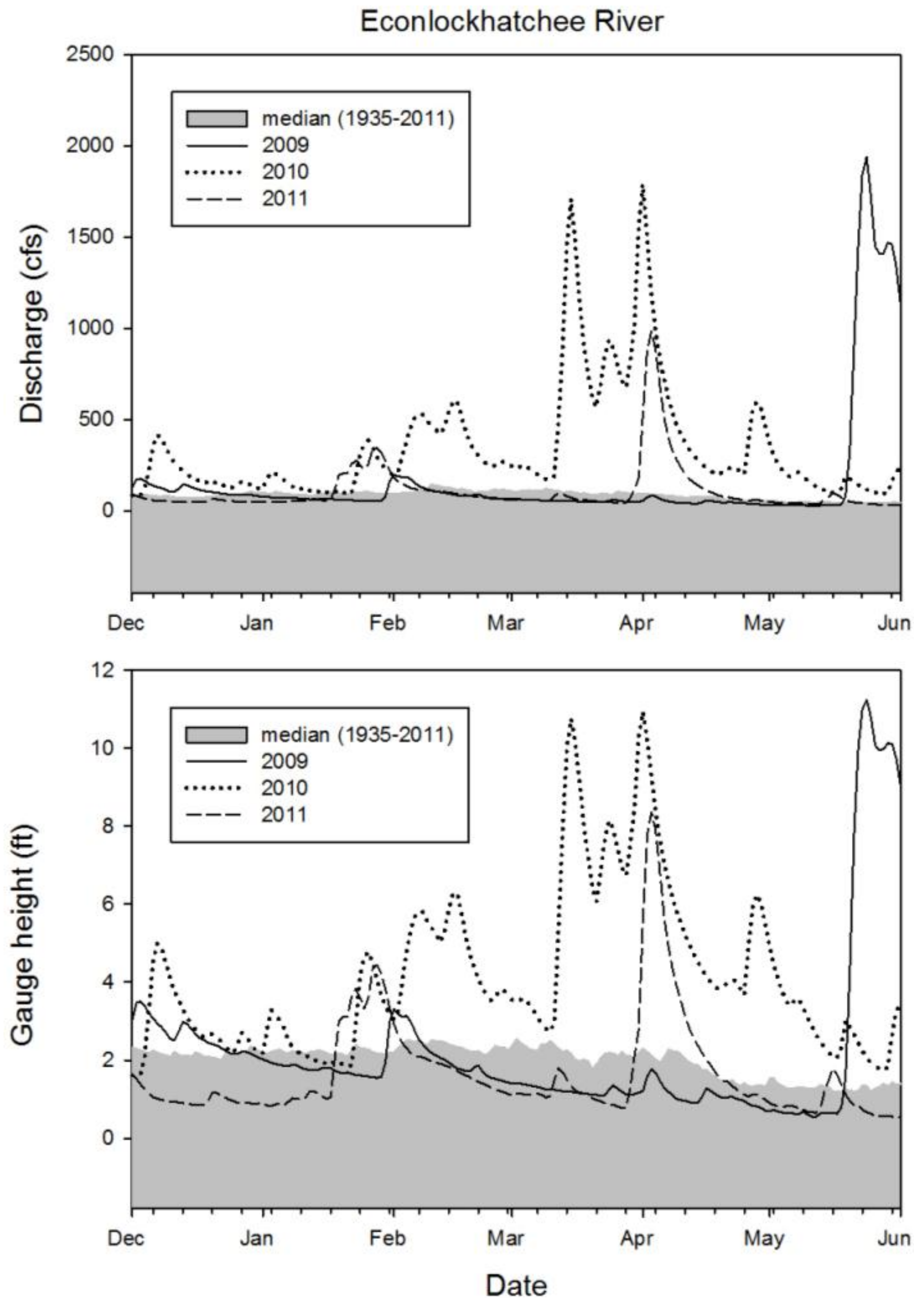

Figure 4. Discharge (cfs) and gauge height (ft) for the Econlockhatchee River during our study. Data were recorded at USGS gauging station 02233500 at Snowhill Road (Econlockhatchee rkm 18). Values for each sample year and the long term median values are shown.

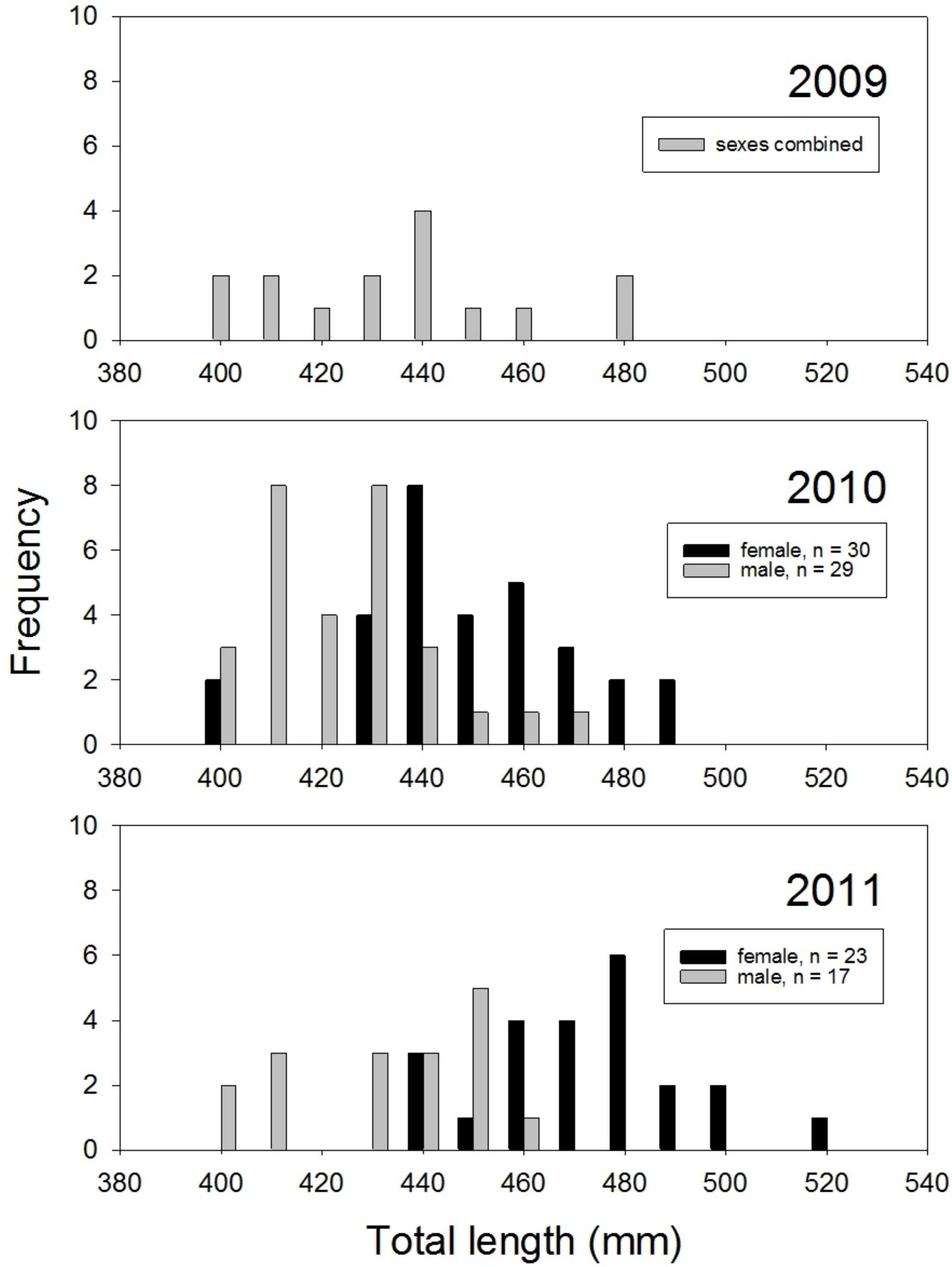

Figure 5. Length-frequency plots of American shad used for telemetry during three years of monitoring spawning migrations in the St. Johns River, Florida.

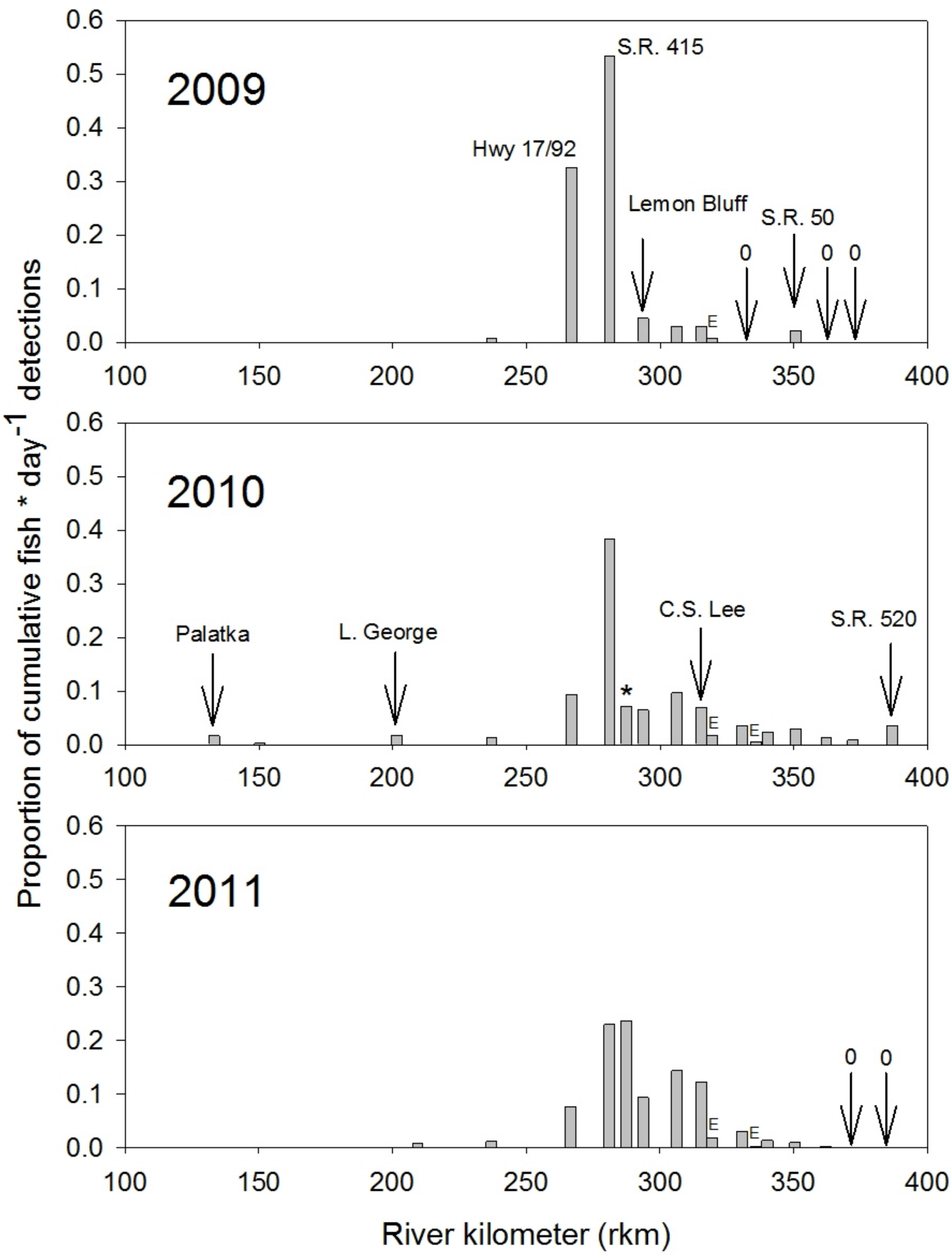

Figure 6. Plots of spatial distribution of tagged American shad based on tag detections within the fixed-position receiver array. Bars represent the proportion of total cumulative receiver fish*day^{-1}. One fish-day represents the detection of a tagged fish at a monitoring station during a 24-hour day (i.e., the unique combination of tag, receiver, and day). Arrows with a “0” above indicate a monitoring station that had no tag detections. An asterisk (*) indicates the receiver at rkm 287.3 that was deployed mid-way through our monitoring effort in 2010. Thus, totals from that location are not directly comparable to totals from other receivers during that year. An ‘E’ denotes receivers deployed in the Econlockhatchee River. Text labels are included for spatial reference.

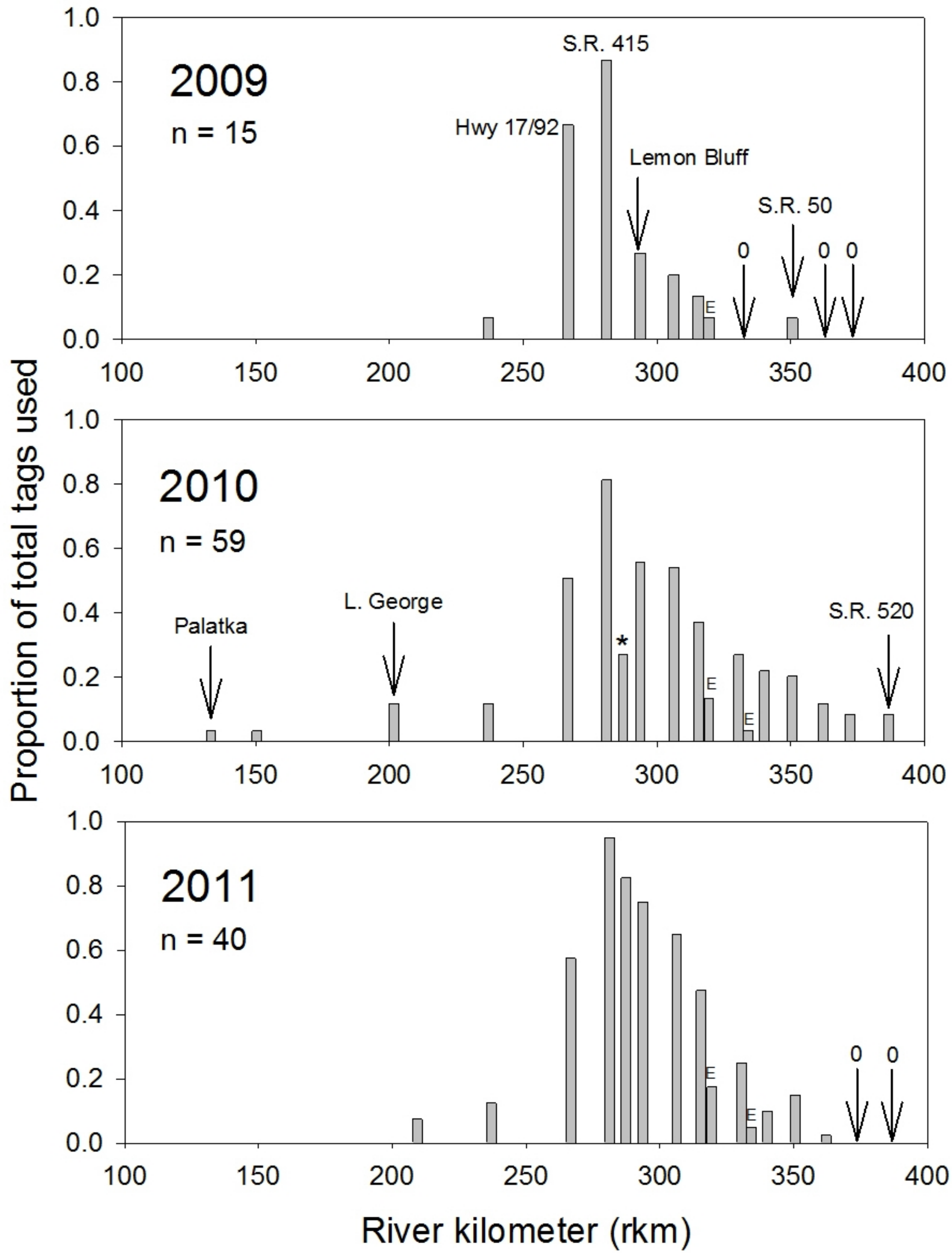

Figure 7. Plots of spatial distribution of tagged American shad based on tag detections within the fix-position receiver array. Bars represent the proportion of total tags used each year that were detected at each receiver. Arrows with a "0" above indicate a monitoring station that had no tag detections. An asterisk (*) indicates the receiver at rkm 287.3 that was deployed mid-way through our monitoring effort in 2010; therefore, totals from that location are not directly comparable to totals from other receivers during that year. An 'E' denotes receivers deployed in the Econlockhatchee River. Text labels are included for spatial reference.

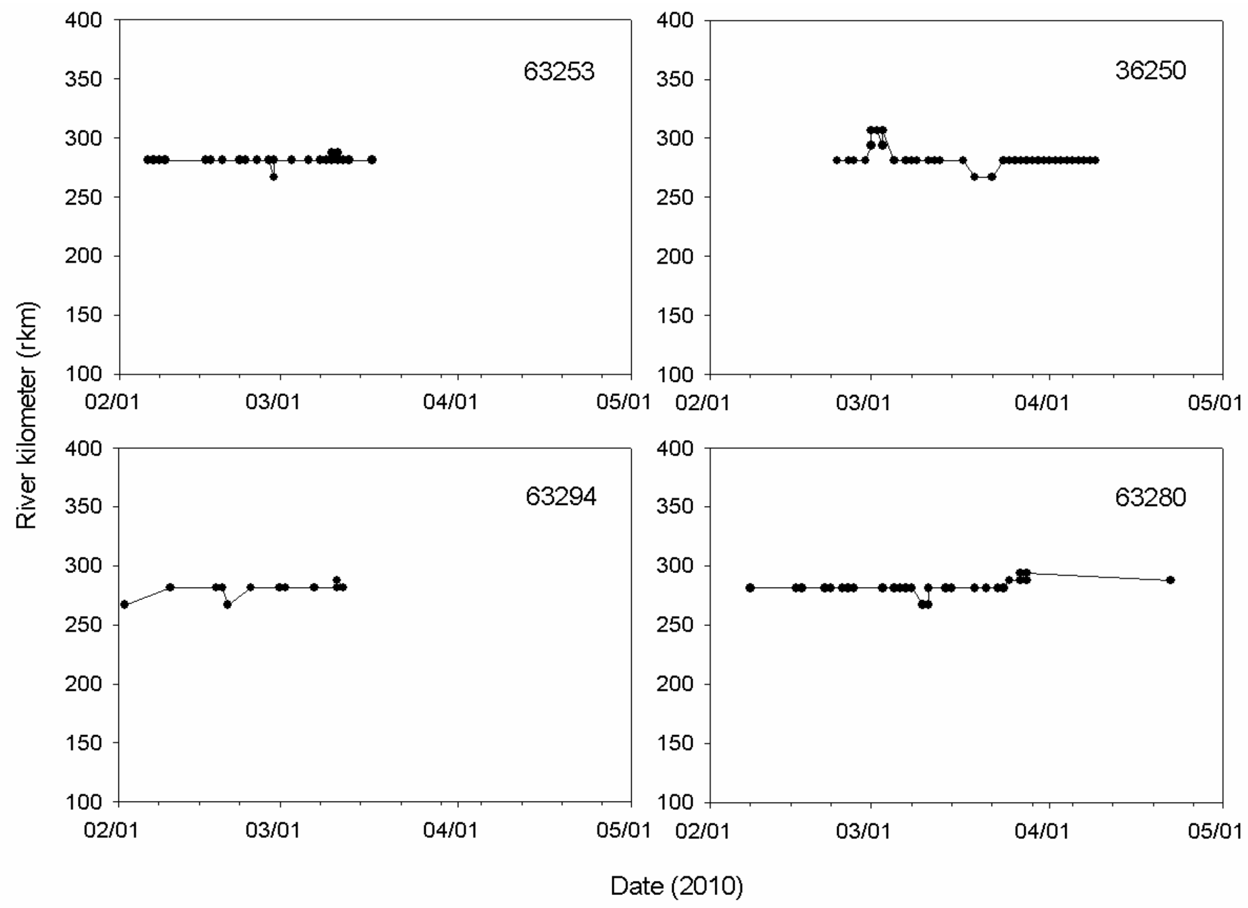

Figure 8. Examples of American shad tag detection histories that were typical of shad whose movement patterns focused on the Lake Monroe – Lake Jesup reach in 2010. River kilometers (rkm) are scaled along the y-axis, and date is scaled along the x-axis. Tag numbers are displayed in the upper right corner of each plot

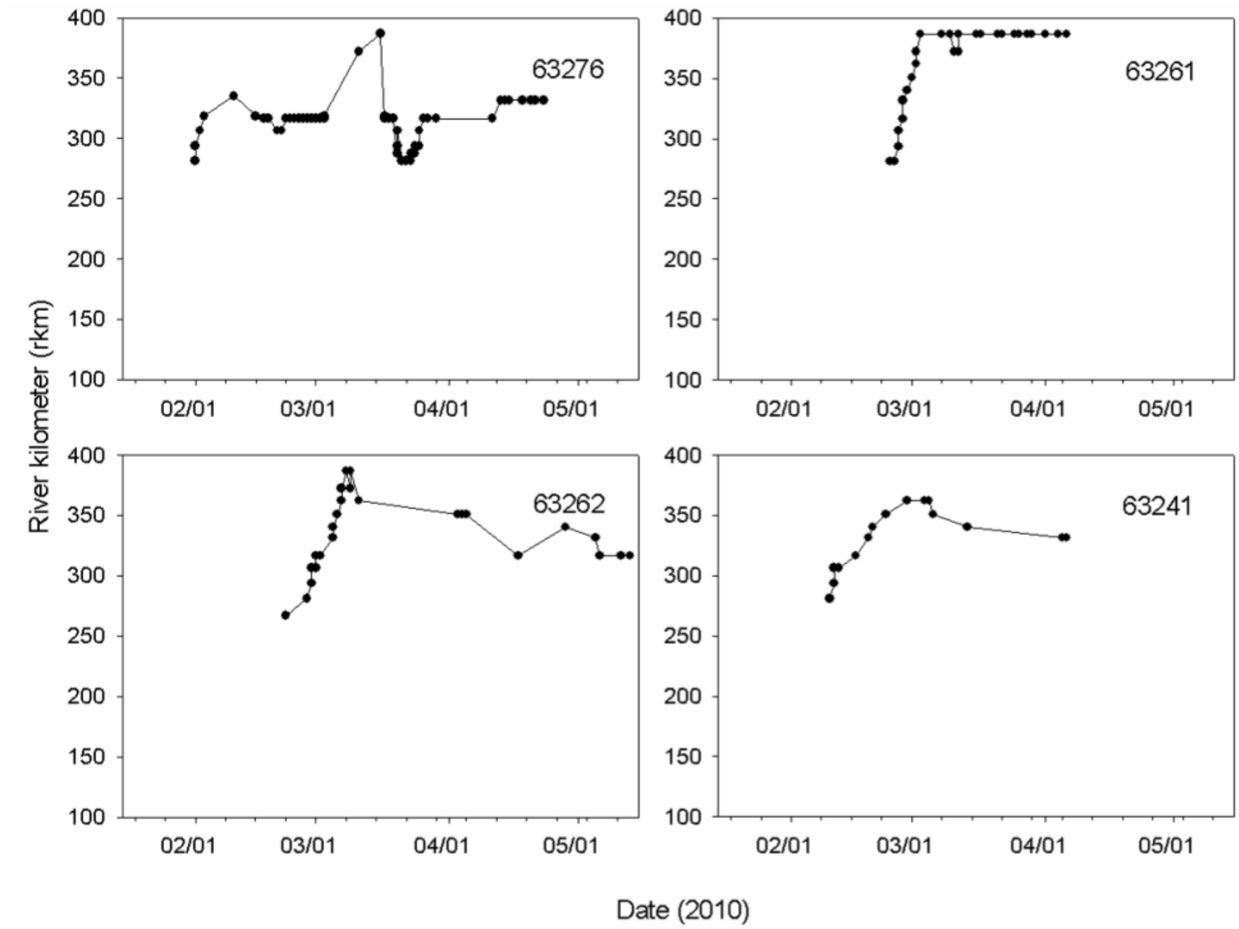

Figure 9. Examples of American shad tag detection histories that show spawning migrations that reached the upstream end of the fixed-position receiver array and the upper end of the historical spawning grounds in the St. Johns River in 2010. River kilometers (rkm) are scaled along the y-axis, and date is scaled along the x-axis. Tag numbers are displayed in the upper right corner of each plot.

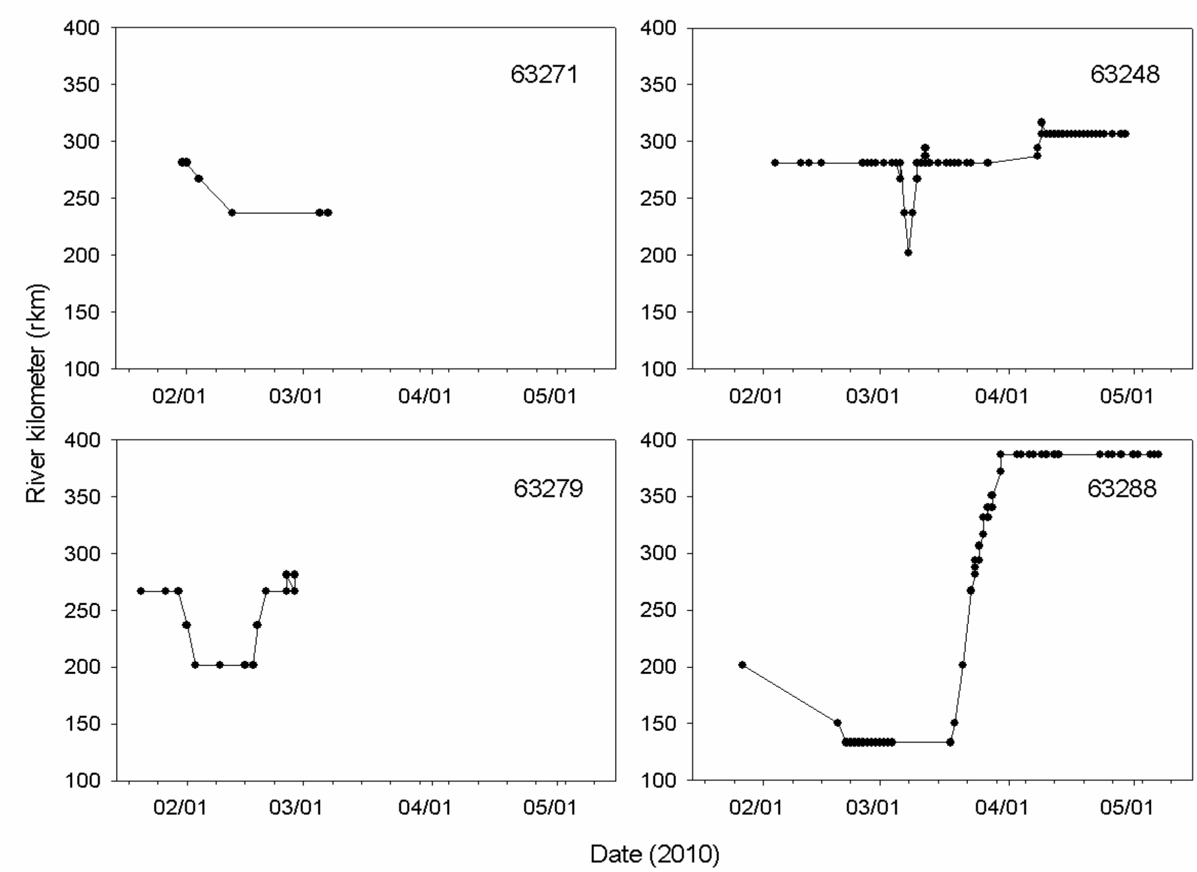

Figure 10. Example of American shad tag detection histories that show limited fall-back behavior post tagging in 2010. Most of the telemetered shad that showed fall-back behavior eventually returned to reaches that historically support American shad spawning. River kilometers (rkm) are scaled along the y-axis, and date is scaled along the x-axis. Tag numbers are displayed in the upper right corner of each plot.

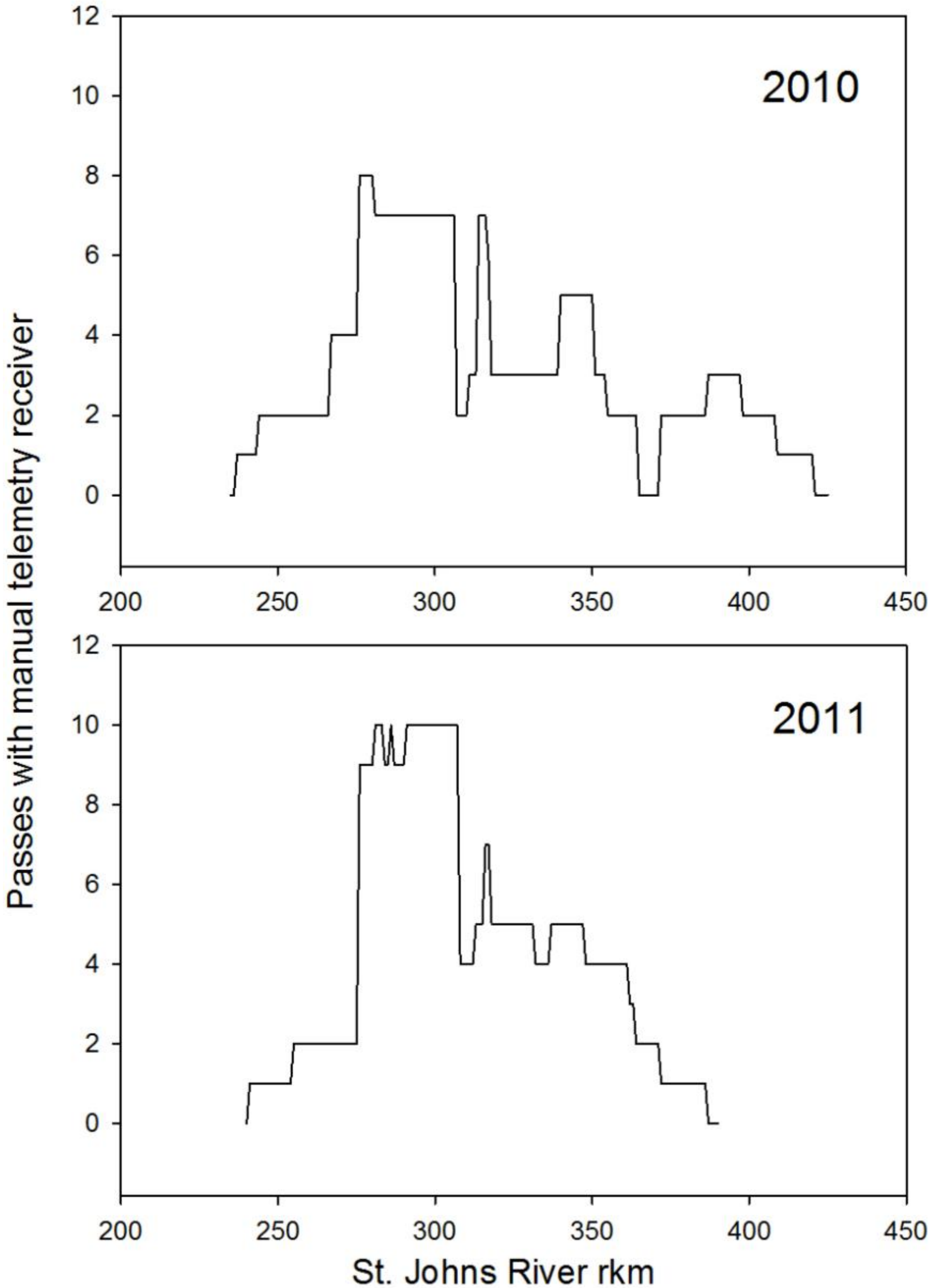

Figure 11. Number of passes for manual telemetry searches during the 2010 and 2011 American shad spawning seasons.

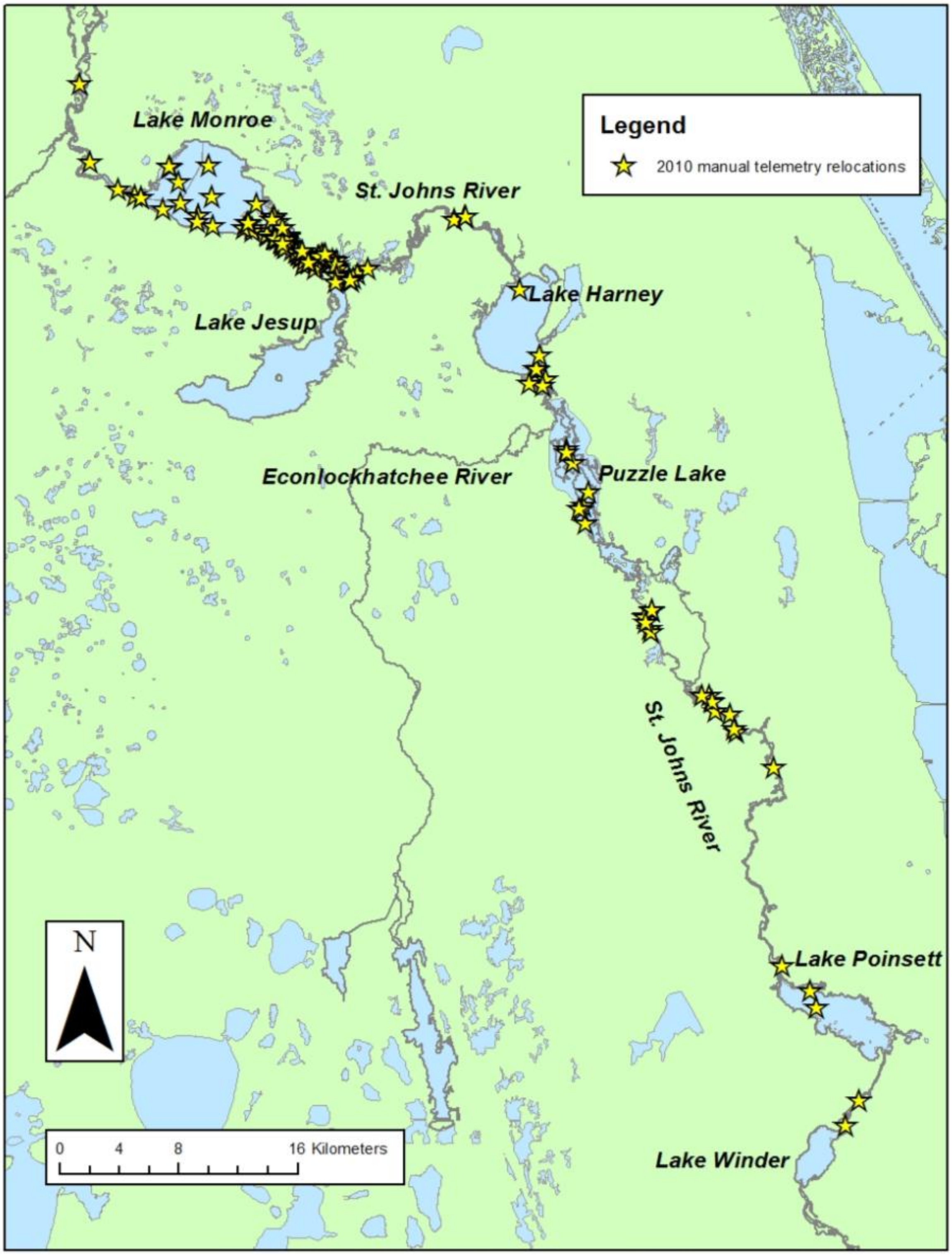

Figure 12. Map showing all manual telemetry tag detections (yellow stars) for American shad in the St. Johns River during the spawning migration in 2010.

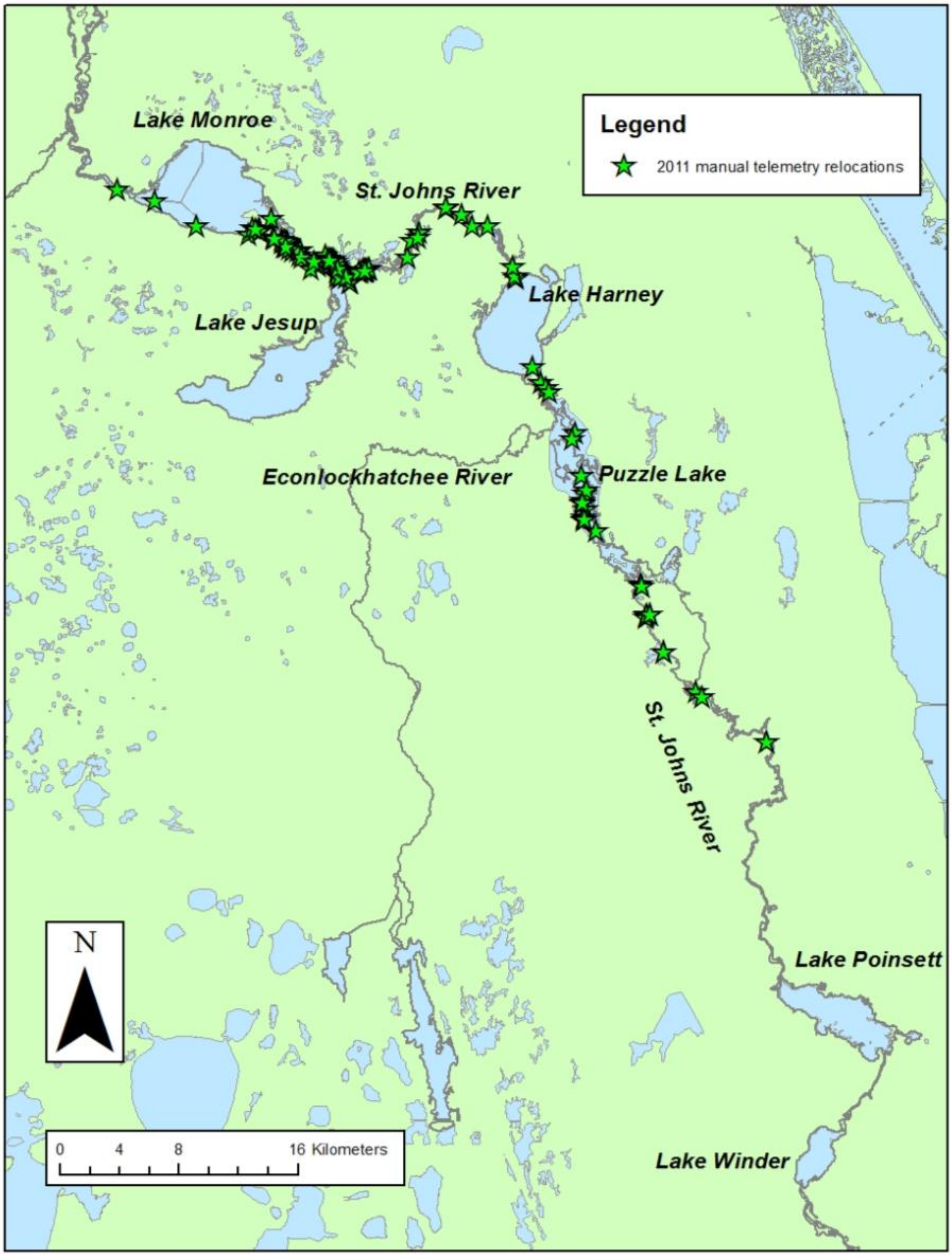

Figure 13. Map showing all manual telemetry tag detections (green stars) for American shad in the St. Johns River during the spawning migration in 2011.

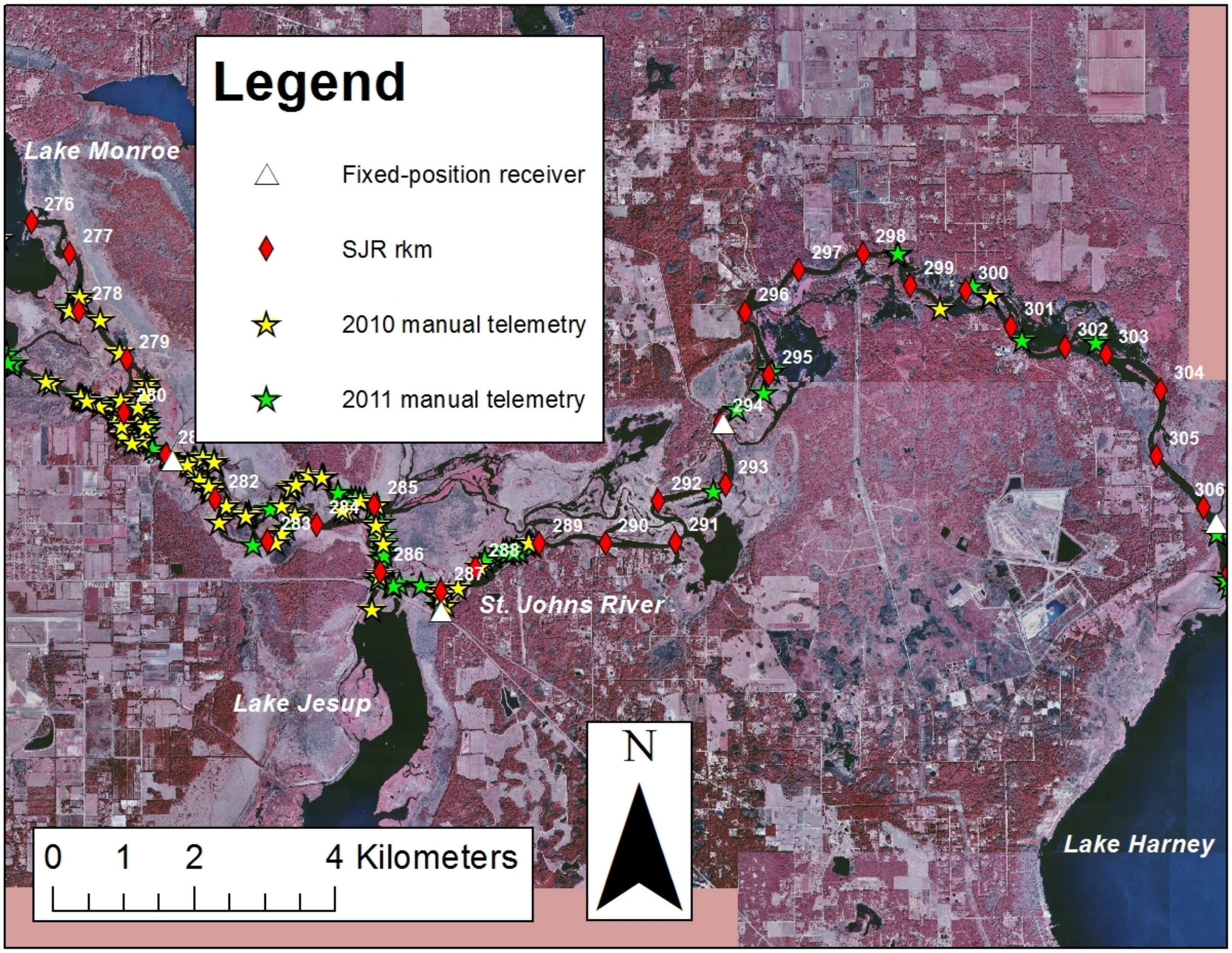

Figure 14. Map showing tagged American shad relocations by manual telemetry between Lake Monroe and Lake Harney. Results from 2010 (yellow stars) and 2011 (green stars) are shown together to for comparison of spatial similarity of tag relocation patterns.

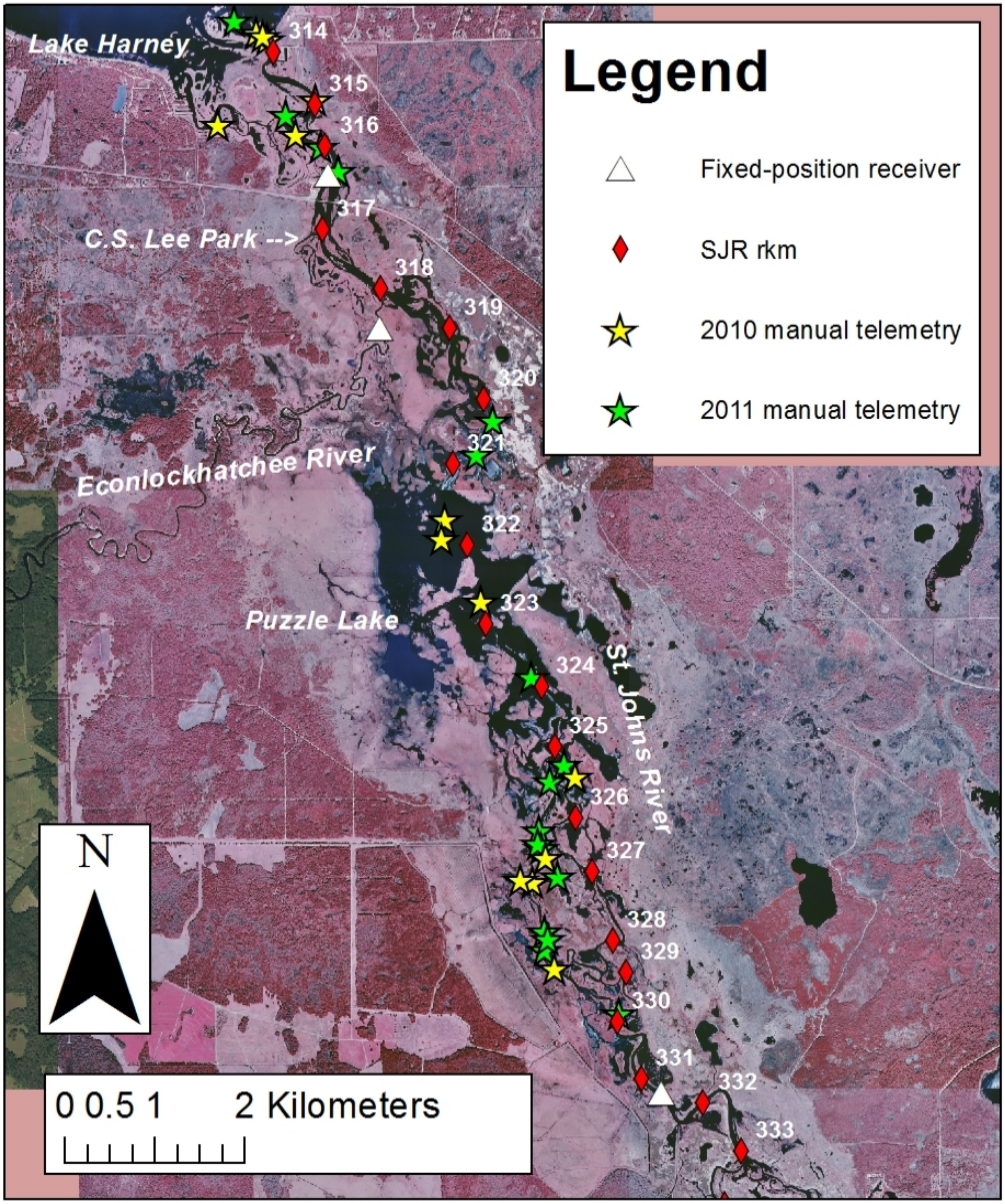

Figure 15. Map showing tagged American shad detections by manual telemetry near the confluence of the Econlockhatchee and St. Johns rivers. Results from 2010 (yellow stars) and 2011 (green stars) are shown together to for comparison of spatial similarity in tag relocation patterns.

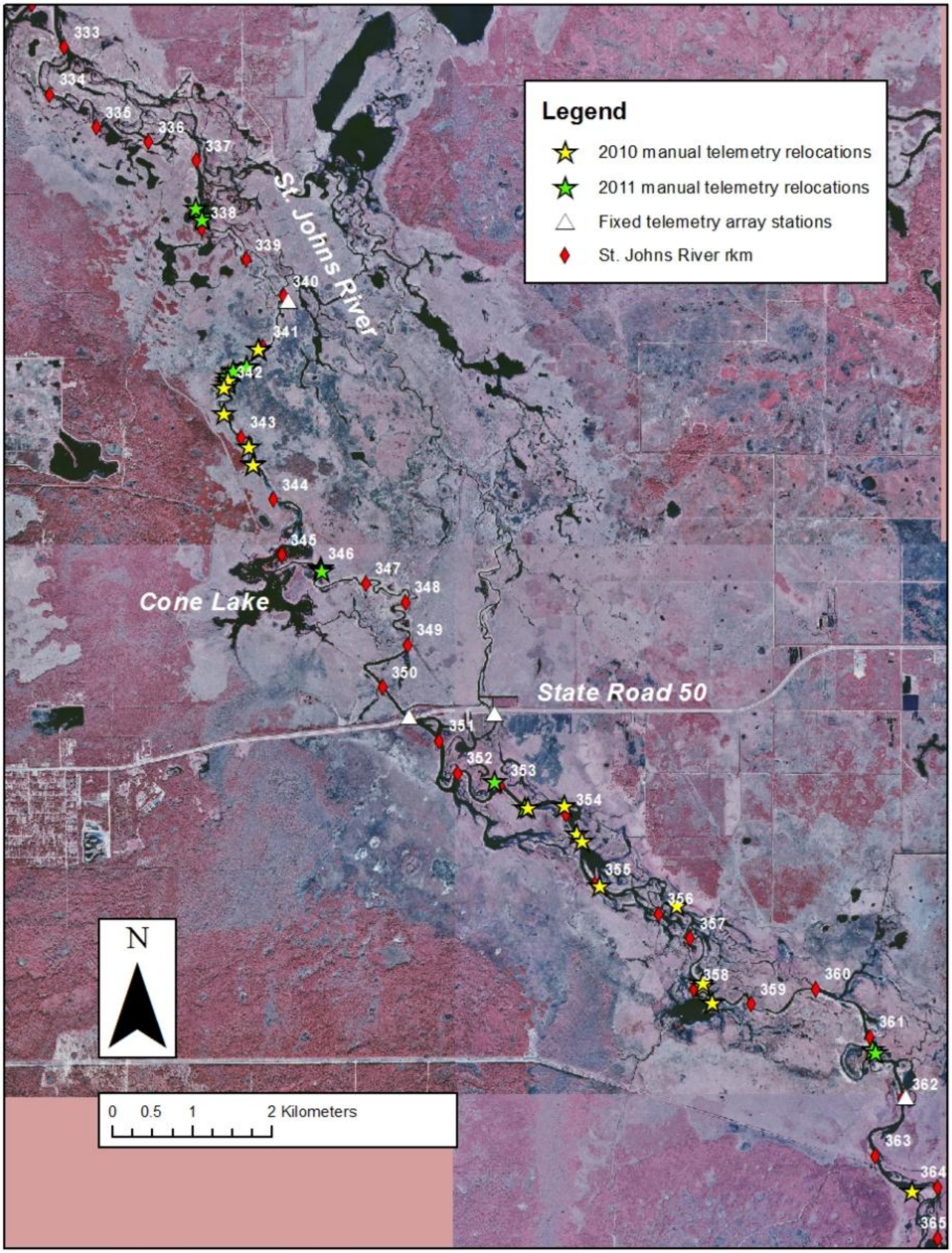

Figure 16. Map showing tagged American shad relocations by manual telemetry near the Cone Lake and state road 50. Results from 2010 (yellow stars) and 2011 (green stars) are shown together to for comparison of spatial similarity of tag relocation patterns.

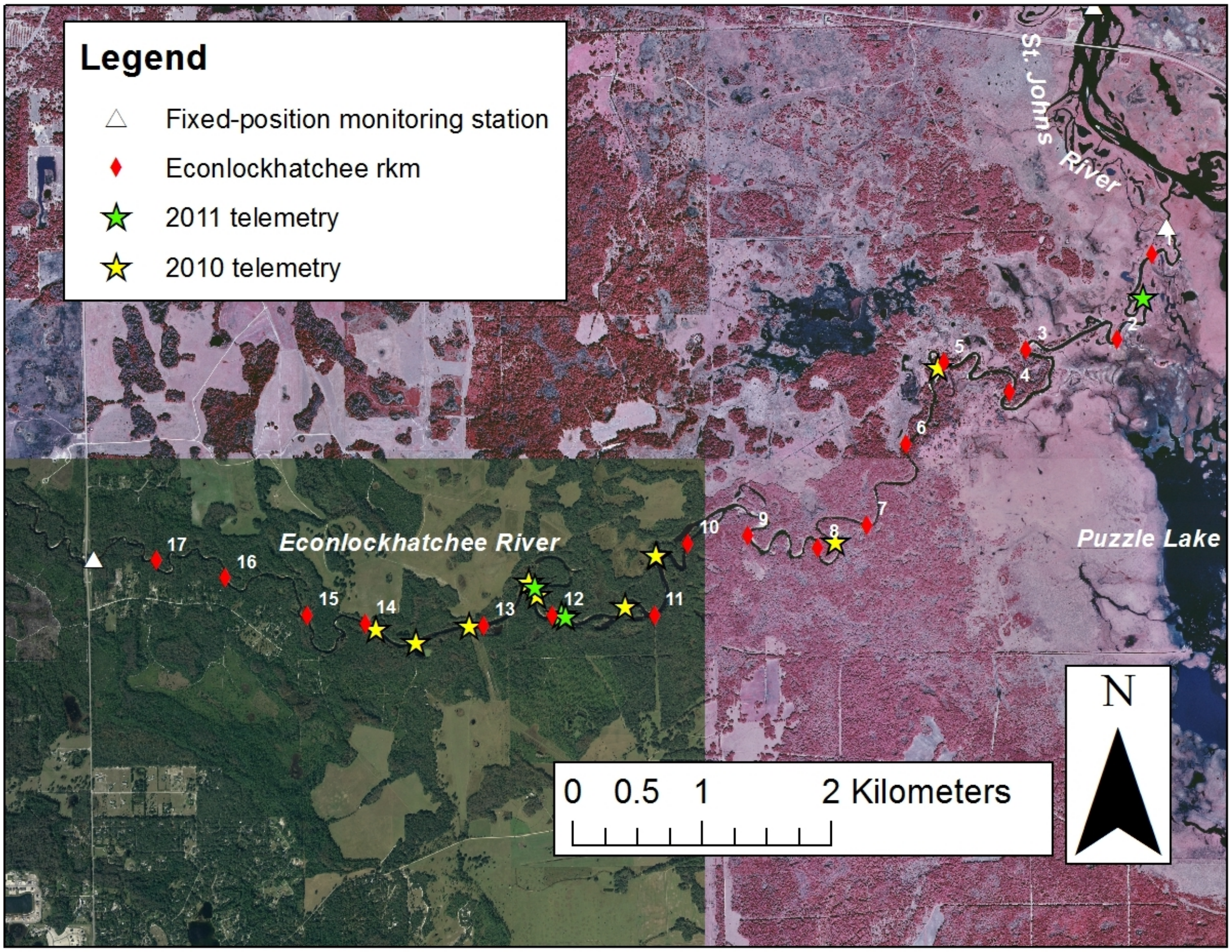

Figure 17. Map of the lower Econlockhatchee River with 2010 (yellow stars) and 2011 (green stars) manual telemetry tag relocations shown.

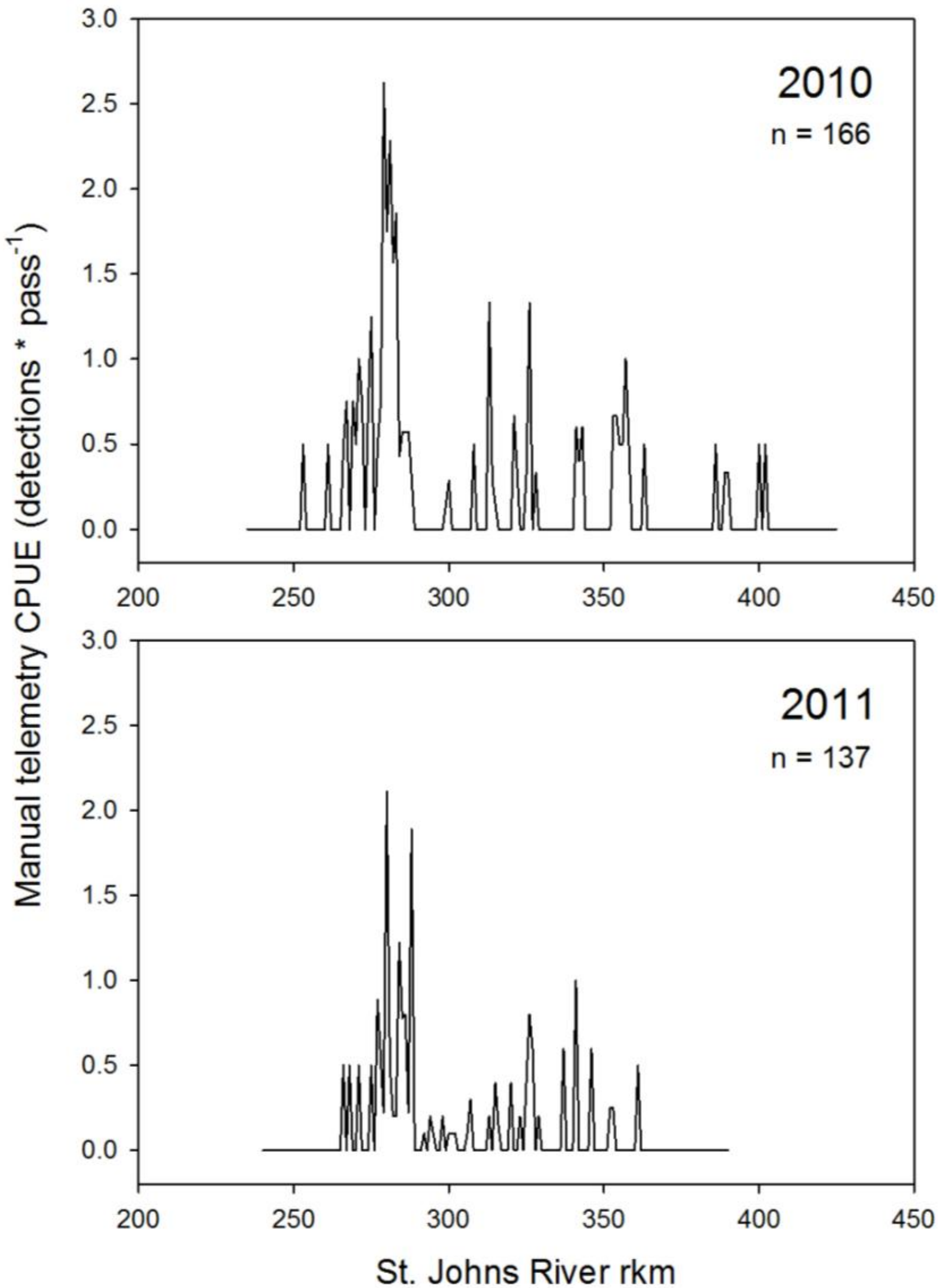

Figure 18. CPUE [catch per unit effort (tag detections · pass^{-1})] for 2010 and 2011 American shad manual telemetry searches in the St. Johns River. CPUE data were calculated for each river kilometer (rkm) of surveyed river channel. Sample sizes refer to the total number of tag detections contributing to each plot.

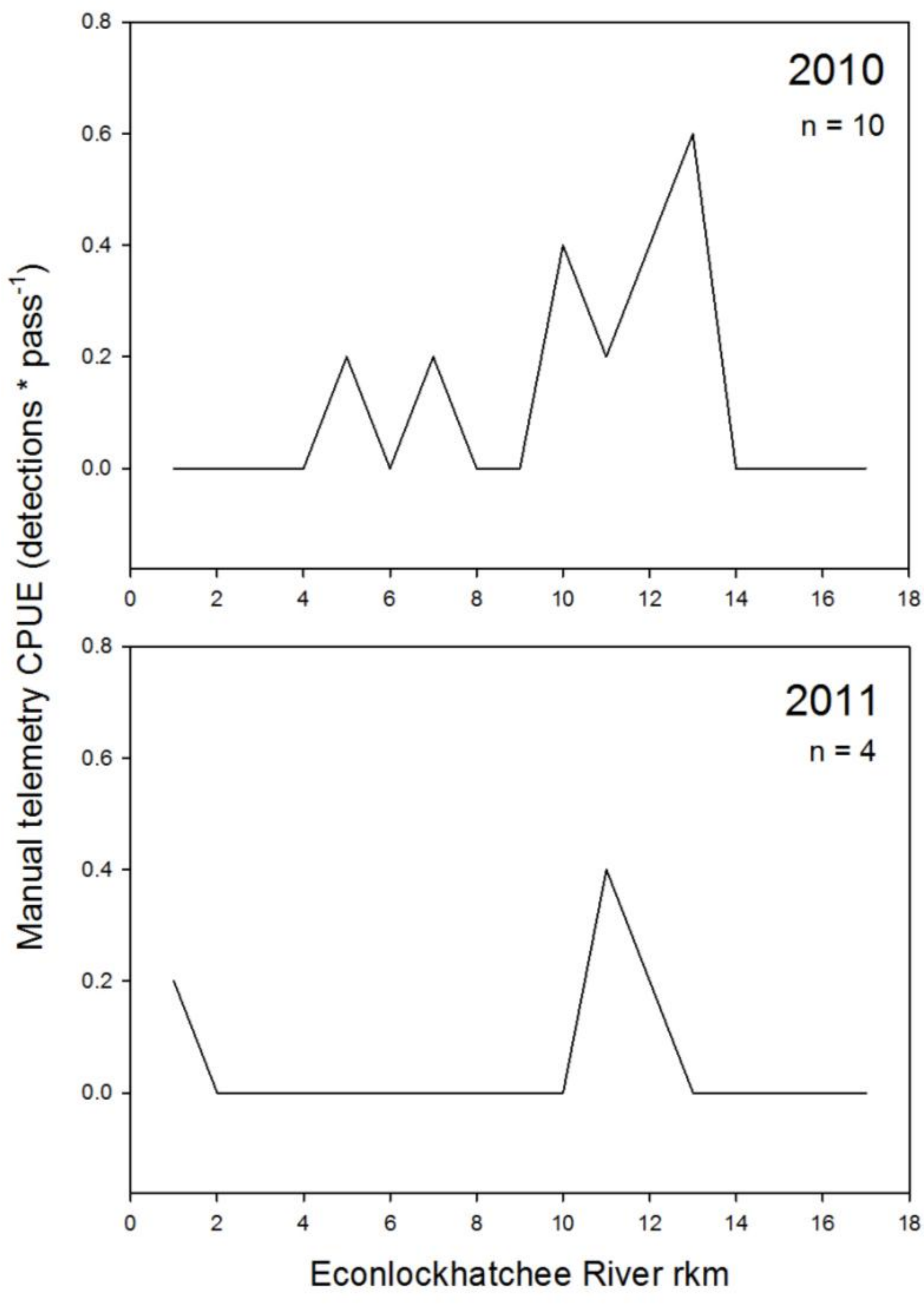

Figure 19. CPUE [catch per unit effort (tag detections · pass^{-1})] for 2010 and 2011 American shad manual telemetry searches in the Econlockhatchee River. CPUE data were calculated for each river kilometer (rkm) of surveyed river channel. Sample sizes refer to the total number of tag detections contributing to each plot.

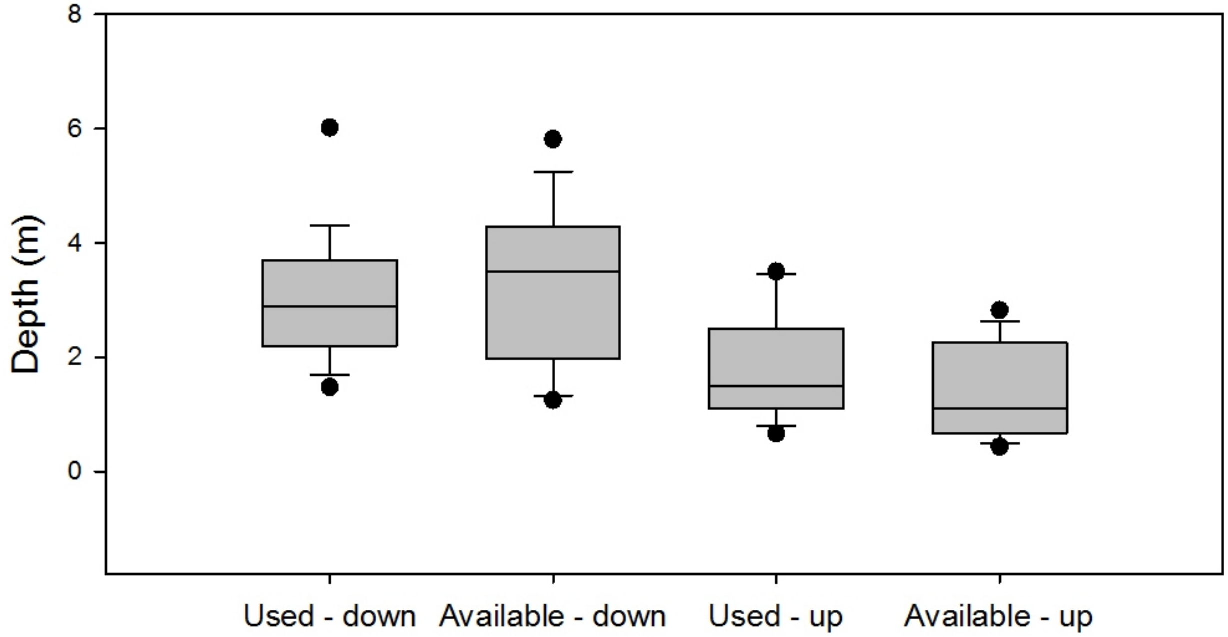

Figure 20. Box plots of used and available depth (m) for Amerian shad in the St. Johns River in 2011. Depths were measured at channel thalweg, and habitat types were categorized spatially as downstream (down) or upstream (up) of Lake Harney. Used and available depth measures did not differ downstream of Lake Harney; however, upstream of Lake Harney used depths were significantly greater than available depths in a two-sample t-test (p = 0.035).

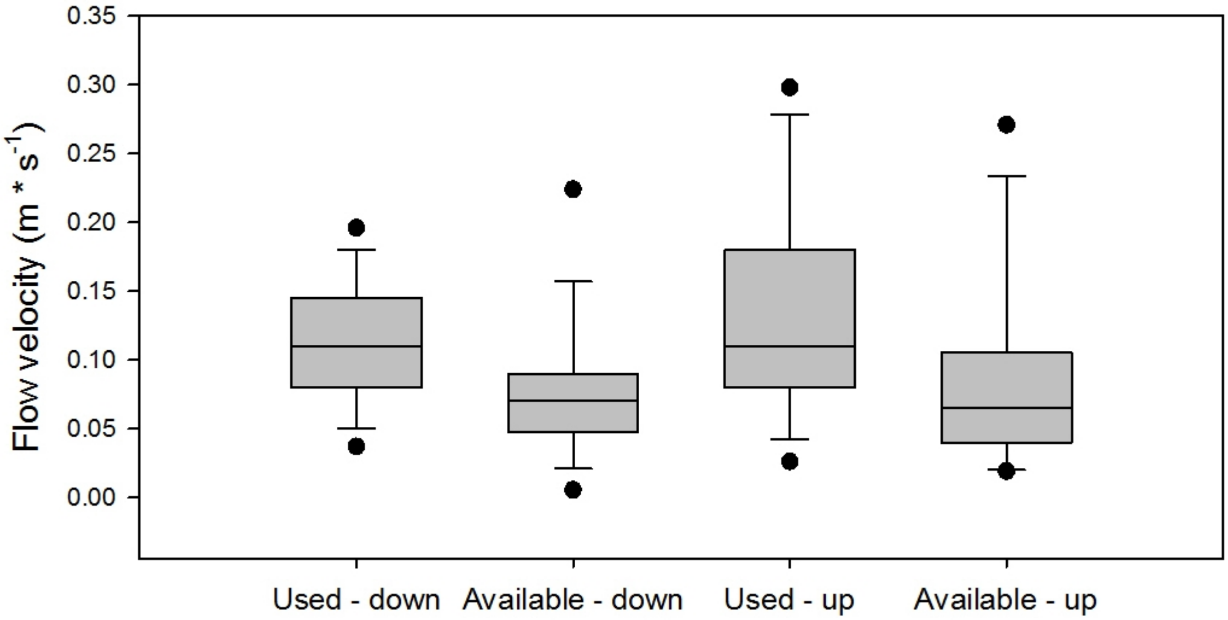

Figure 21. Box plots of used and available flow velocity (m · s^{-1}) for Amerian shad in the St. Johns River in 2011. Flow velocity measures were taken at 60% depth at channel thalweg, and habitat types were categorized spatially as downstream (down) or upstream (up) of Lake Harney. Flow velocity measures corresponding to used habitat were significantly greater than available habitat for reaches upstream and downstream of Lake Harney (both $p \leq 0.022$).

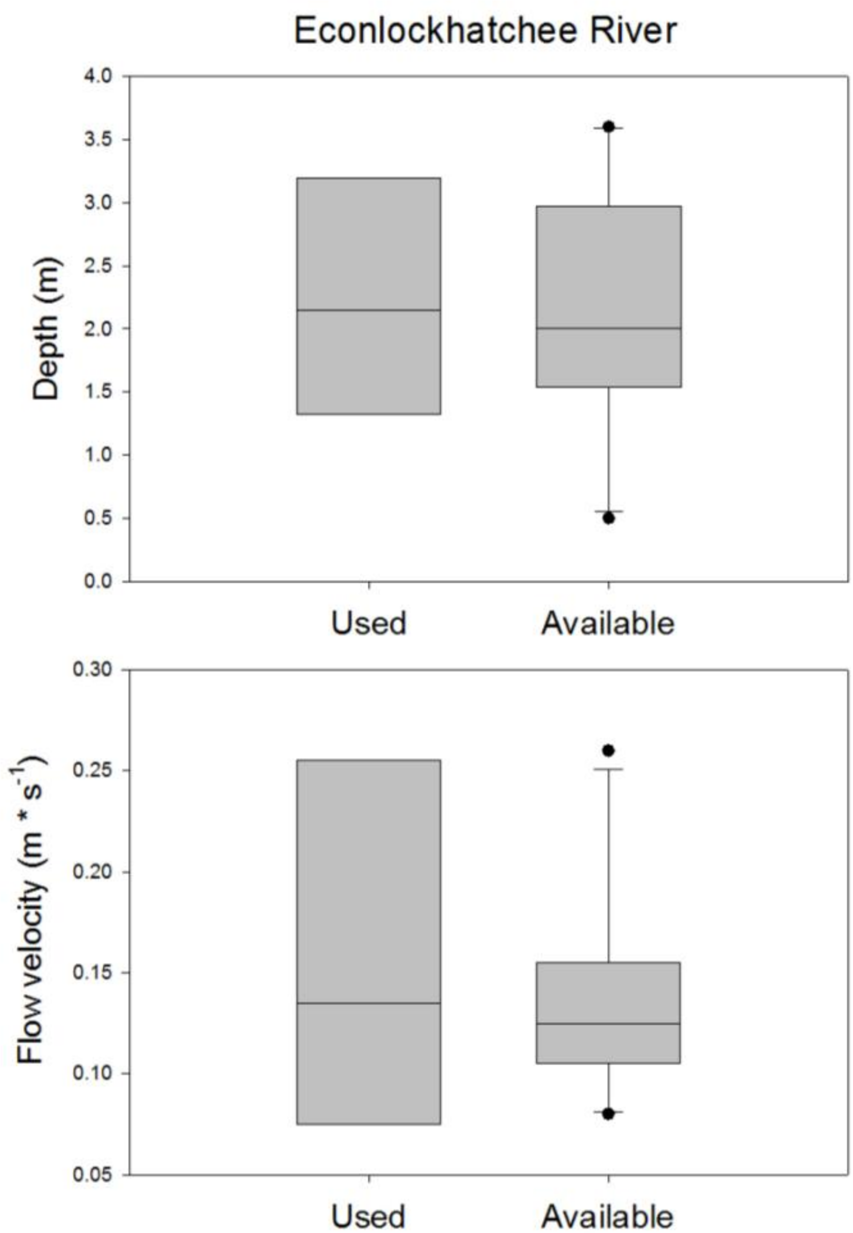

Figure 22. Box plots of depth (m) and flow velocity ($m \cdot s^{-1}$) measures from used and available habitat for American shad in the Econlockhatchee River in 2011. Two-sample t-tests indicated no difference in measure for either parameter between used and available habitats (both $p \geq 0.63$).

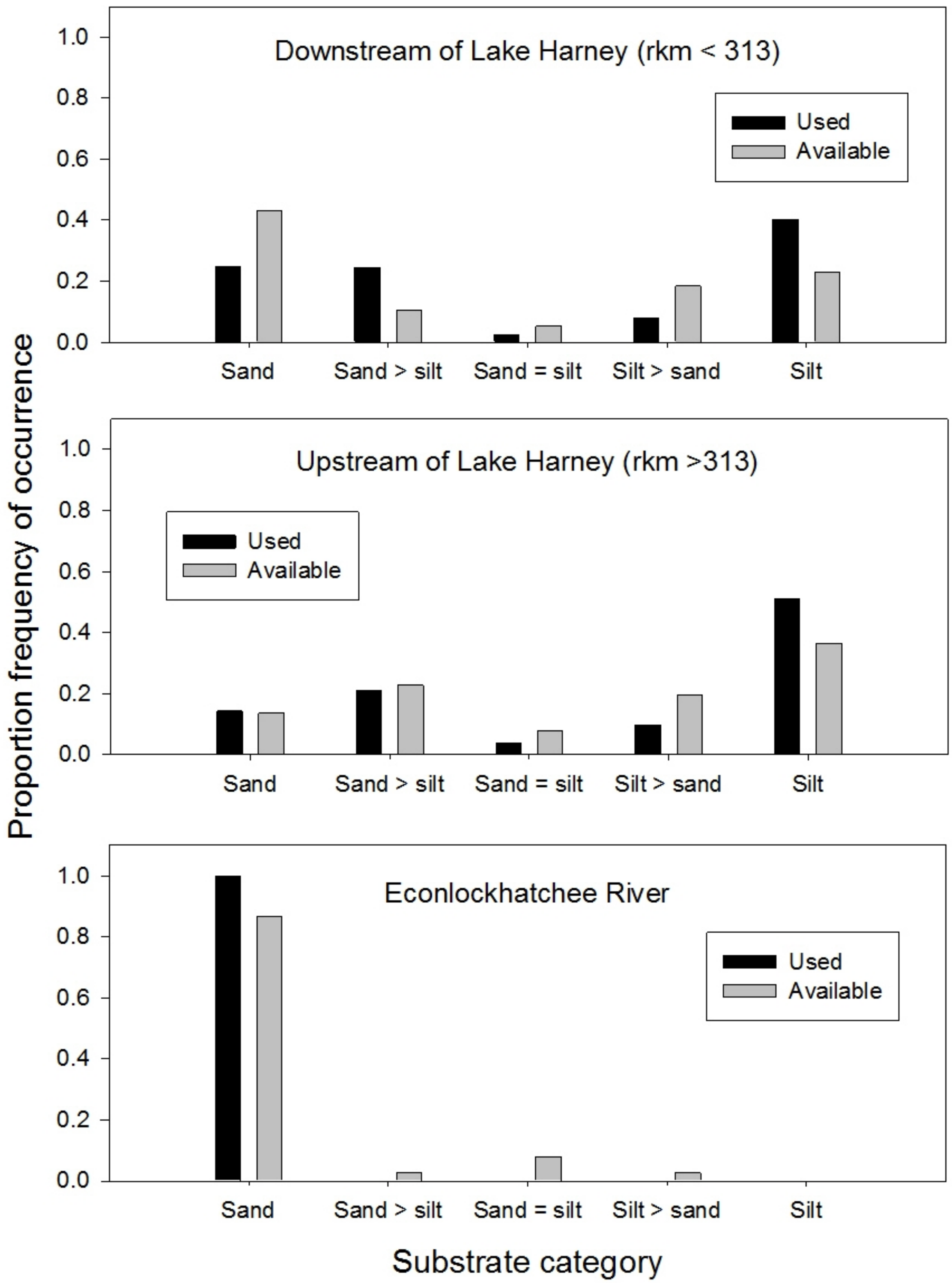

Figure 23, Plots of proportion of occurrence for substrate categorizations representing used and available habitats American shad in the St. Johns River downstream of Lake Harney, in the St. Johns River upstream of Lake Harney, and in the Econlockhatchee River.

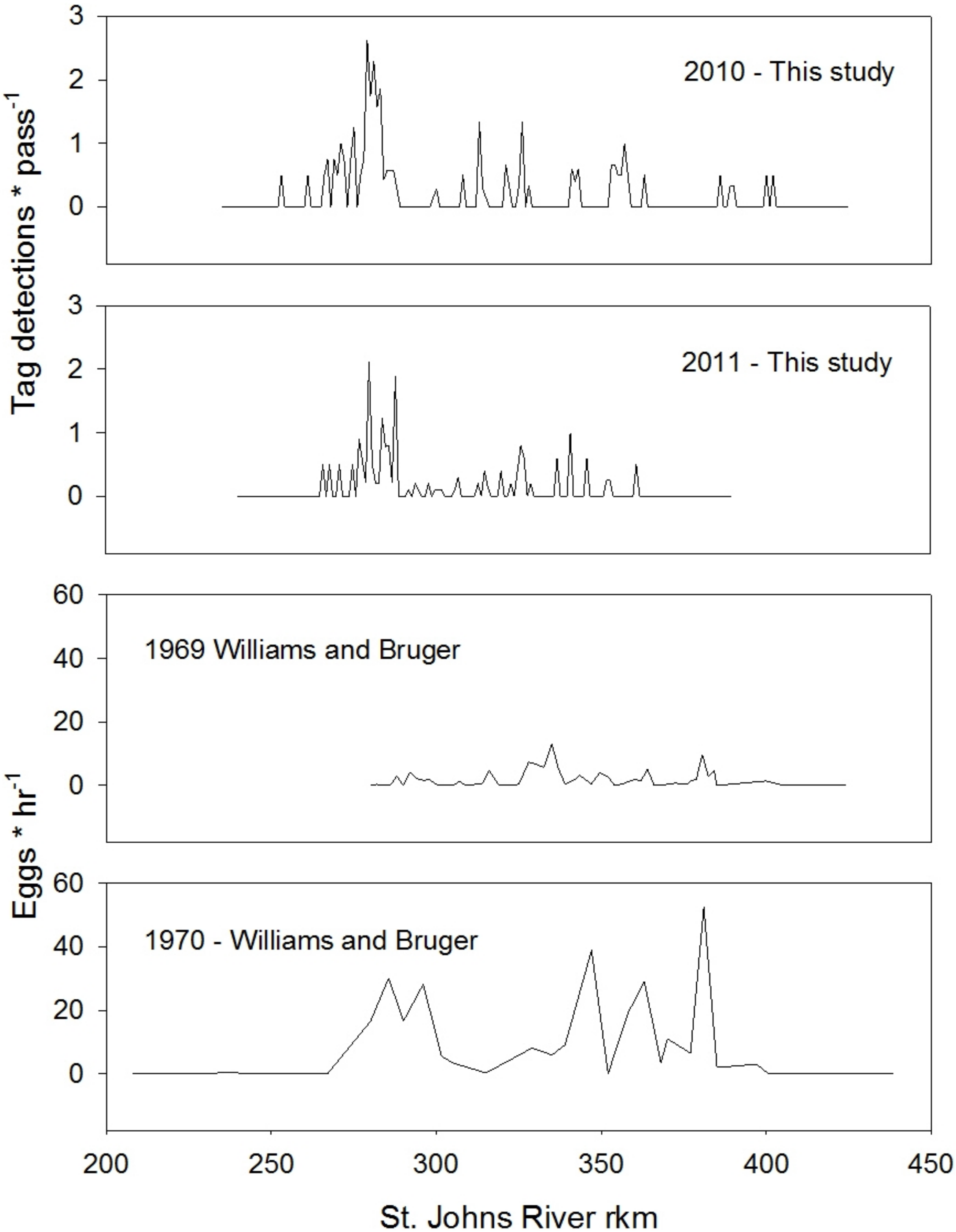

Figure 24. Plots of American shad egg CPUE (eggs * hr^{-1}) during 1969 and 1970 and telemetry CPUE (tag detections · $pass^{-1}$) in 2010 and 2011. Plots of shad egg CPUE were created from Tables 1 and 4 and Figure 3 in Williams and Bruger (1972).

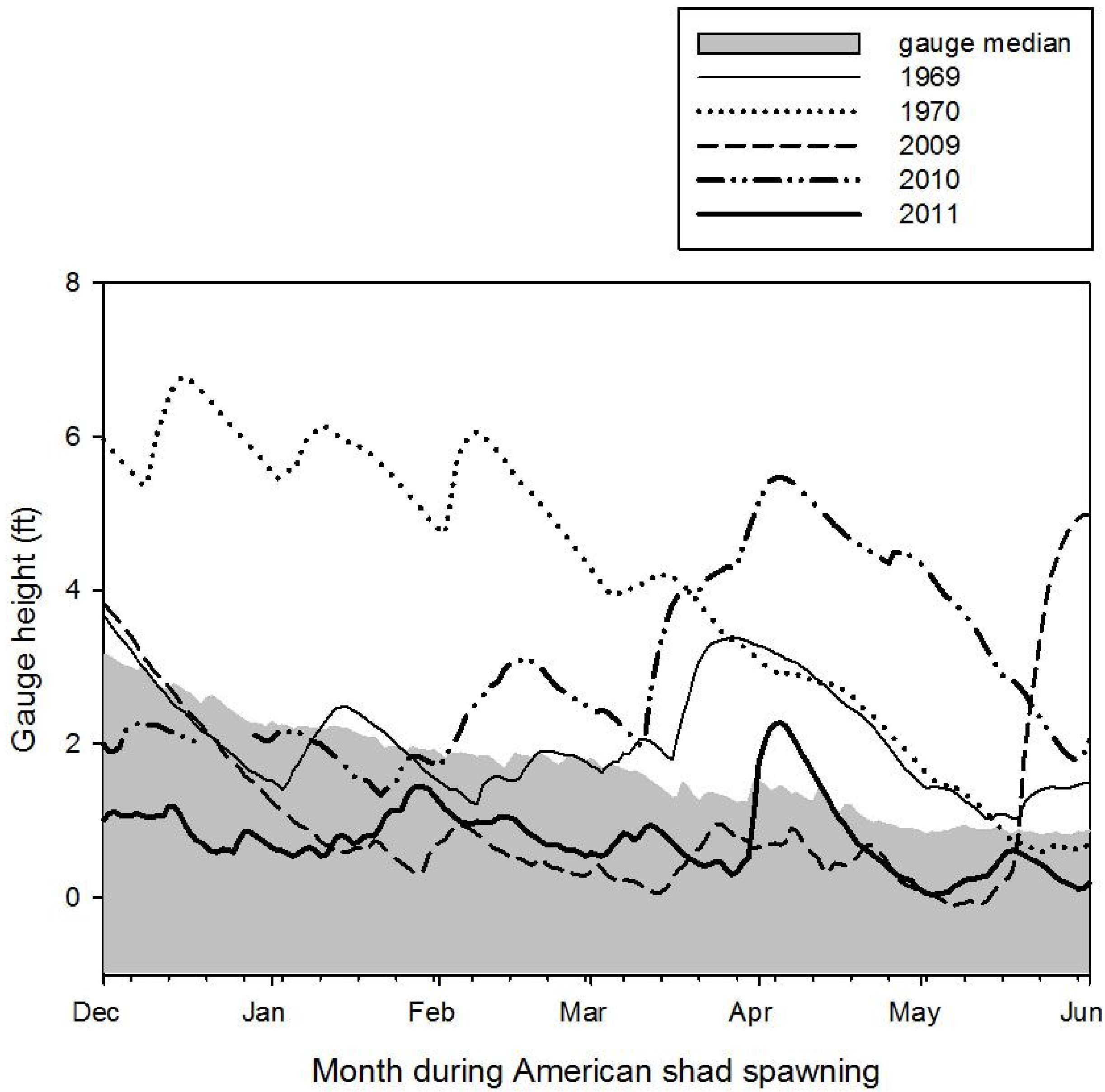

Figure 25. Plots of gauge height for St. Johns River during American shad spawning for 2009 – 2011 and 1969-1970. This plot provides comparisons of water levels encountered by Williams and Bruger (1972) and our study. Gauge height data were collected at USGS gauge 02234000 near C. S. Lee Park and S. R. 46. Median gauge height values were produced from data collected 1941 – present.

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