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Size of Spawning Population, Residence Time, and Territory Shifts of Individuals in the Spawning Aggregation of a Riverine Catostomid

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Abstract - Little is known about the behavior of individual fish in a spawning aggregation, specifically how long an individual remains in an aggregation. We monitored *Moxostoma robustum* (Cope) (Robust Redhorse) in a Savannah River spawning aggregation during spring 2004 and 2005 to provide an estimate of the total number of adults and the number of males comprising the aggregation and to determine male residence time and movements within a spawning aggregation. Robust Redhorse were captured using prepostioned grid electrofishers, identified to sex, weighed, measured, and implanted with a passive integrated transponder. Spawning aggregation size was estimated using a multiple census mark-and-recapture procedure. The spawning aggregation seemed to consist of approximately the same number of individuals (82–85) and males (50–56) during both years of this study. Individual males were present for a mean of 3.6 ± 0.24 days (± SE) during the 12-day spawning period. The mean distance between successive recaptures of individual males was 15.9 ± 1.29 m (± SE). We conclude that males establish spawning territories on a daily basis and are present within the spawning aggregation for at least 3–4 days. The relatively short duration of the aggregation may be the result of an extremely small population of adults. However, the behavior of individuals has the potential to influence population estimates made while fish are aggregated for spawning.

Introduction

Fishes have been hypothesized to form spawning aggregations for a number of reasons including spawning habitat limitations, fertilization enhancement, and swamping potential egg predators (Claydon 2005, Domeier and Colin 1997). Although this behavior is exhibited over a wide range of taxa, little is known about the length of time individuals remain a part of a spawning aggregation or how the positions or territories of individuals change over that period of time. The majority of work on spawning aggregations has focused on coral reef and estuarine fishes. Serranids, such as *Epinephelus guttatus* (Linnaeus) (Red Hind; Colin et al. 1987, Whiteman et al. 2005) and *E. striatus* (Bloch) (Nassau Grouper; Smith 1972); lutjanids such as *Lutjanus cyanopterus* (Cuvier) (Cubera

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Snapper; Heyman et al. 2005); and *Centropomus undecimalis* (Bloch) (Common Snook; Lowerre-Barbieri et al. 2003) are known to form aggregations that last weeks. It has been noted that individuals of these fishes likely enter and leave aggregations (Lowerre-Barbieri et al. 2003, Whiteman et al. 2005), but it is generally not known how long an individual remains in an aggregation. It is unknown if riverine species in spawning aggregation behave in a similar manner.

Moxostoma robustum (Cope) (Robust Redhorse) is an imperiled, large, riverine catostomid found in three Atlantic slope drainages in North Carolina, South Carolina, and Georgia (Bryant et al. 1996, Cooke et al. 2005). This species has been reported to form spawning aggregations in shallow, flowing water over a clean gravel substrate (Bryant et al. 1996, Grabowski and Isely 2007a) similar to other members of its genus (Jenkins and Burkhead 1994, Page and Johnston 1990). Males establish territories that are vigorously defended from rivals. However, these fish generally spawn as a "tremoring trio" consisting of a female flanked by two males (Jenkins and Burkhead 1994, Page and Johnston 1990). The formation of at least two Robust Redhorse spawning aggregations during late spring has been documented in the lower Savannah River in South Carolina and Georgia (Grabowski and Isely 2006, 2007a). Both aggregations are associated with relatively small, mid-channel gravel bars. Individuals make upstream migrations potentially in excess of 100 km to reach these habitats and seem to have a high degree of fidelity to one of the gravel bars (Grabowski and Isely 2006). It is not known how long the same individuals remain in an aggregation or if they maintain the same position throughout their residence in the aggregation. These are important considerations for monitoring programs for this species, since sampling programs are frequently focused on spawning aggregations (Robust Redhorse Conservation Committee 2002), which could contribute bias in population estimates.

As part of a larger study examining spawning habitat partitioning among catostomids in the Savannah River, we marked and recaptured a significant number of Robust Redhorse (Grabowski and Isely 2005, 2007a). Our objectives were to provide an estimate of the size of the spawning population of Robust Redhorse and to document the residence time and movements of individuals within these spawning aggregations. We further attempted to correlate residence time to size and interpreted differences in residence time between sexes.

Methods

We captured Robust Redhorse from the lower Savannah River below New Savannah Bluff Lock and Dam (NSBLD) in Augusta, GA, between river kilometers (rkm) 300 and 280. Our efforts were restricted to the two mid-channel gravel bars that occur within this reach. These structures are unique in the lower Savannah River and have been identified as important spawning habitat for catostomids (Grabowski and Isely 2006, 2007a). The upstream gravel bar (hereafter referred to as the upper gravel bar) is located at rkm 299.4, immediately downstream of the tailrace of NSBLD. This structure encompasses an area of approximately 25,500 m^2 and consists of a thin layer of gravel mixed with sand. The upper gravel bar attracts spawning aggregations of *Carpiodes* spp. (carpsuckers), *Minytrema melanops* (Rafinesque) (Spotted Sucker), *Moxostoma collapsum* (Cope) (Notchlip Redhorse), and a relatively small number of Robust Redhorse (Grabowski and Isely 2007a). The other gravel bar (hereafter referred to as the lower gravel bar) is approximately 16 rkm downstream of NSBLD and is only about 4200 m^2 in area. The lower gravel bar is composed of a relatively thick layer of coarse gravel over sand and appears to be used as spawning substrate only by Robust Redhorse (Grabowski and Isely 2007a).

We captured Robust Redhorse primarily from the lower gravel bar using an array of six prepostioned grid electrofishers (PGEs) as described in Grabowski and Isely (2005). Sampling was conducted every other day from 02–14 May 2004 and daily from 07–18 May 2005. We measured, weighed, and checked each captured fish for tags. We determined the sex of each individual based upon development of secondary sexual characteristics (such as nuptial tubercle development) and expression of gametes in reproductively active individuals. We retained at least one digital photograph of each individual to serve as a voucher. A passive integrated transponder (PIT) tag (Biomark, Inc., Boise, ID) was implanted into the dorsal musculature immediately posterior to the dorsal fin of untagged individuals prior to release. Various state and federal agencies and researchers have tagged Robust Redhorse on the lower Savannah River since 1998, so fish possessing existing PIT tags were not re-marked, but were included in the study. All fish were allowed to recover (approximately 20 minutes) prior to release. Each PGE was operated a maximum of two times a day for a total of 20–30 seconds. The position of the center point of each PGE was recorded with a WAAS-enabled handheld GPS unit (Garmin International, Olathe, KS) prior to sampling, and this position served as the location of all Robust Redhorse captured within each PGE.

Estimates of the total number and number of males in the spawning aggregation were made for each year using a multiple census mark-recapture model (Darroch 1958, Seber 1986). GPS waypoints were used to determine distance between capture and recapture locations. Pearson's correlation was used to evaluate the relationship between residence time and total length of individuals. A significance level of $\alpha = 0.05$ was used for all tests. Means are reported ± standard error.

Results

A total of 169 Robust Redhorse have been captured and tagged (48 prior to this study, 121 during it) in the lower Savannah River consisting of 109 males (mean = 590.7 ± 3.18 mm TL; range = 450–692 mm TL), 42 females (mean = 636.2 ± 7.80 mm TL; range = 368–710 mm TL), and 18 individuals of unknown sex (mean = 583.4 ± 11.98 mm TL; range = 420–621 mm TL). We recaptured a total of 53 fish in 2004 and 2005. Three of these individuals were tagged and recaptured on the upper gravel bar, while the remainder was tagged and recaptured from the lower gravel bar. All fish were recaptured from the gravel bar where they were originally tagged; we did not encounter any movement between spawning aggregations. The majority of recaptured individuals were male (n = 51). We estimated that the spawning aggregation on the lower bar in 2004 consisted of about 83 individuals (95% C.I. = 66–100) of which 51 (95% C.I. = 40–62) are male. For 2005, we estimated that the spawning aggregation on the lower bar consisted of approximately 85 individuals total (95% C.I. = 74–95) of which about 56 (95% C.I. = 51–62) were male.

During 2005, we captured 14 individuals multiple times. These individuals ranged in size from 530 to 634 mm TL (mean = 593.5 ± 8.47 mm TL; range = 530–634), and all were male. One individual was recaptured twice, while the remaining fish were only recaptured once each. The recaptured males averaged a minimum residence time in the spawning aggregation of 3.6 ± 0.24 days (range = 3–5 days) while the aggregation was present on the lower gravel bar for 12 days in 2005. There was no significant relationship between male size and residence time ($r = 0.32$; $P = 0.25$). No individuals were recaptured in the same PGE, but three pairs of individuals were recaptured together. The estimated mean distance between capture locations was approximately 15.9 ± 1.29 m (range = 6.7–24.0 m).

Discussion

Robust Redhorse in the lower Savannah River form large spawning aggregations relative to the size of the available spawning habitat, leaving the aggregation vulnerable to decreased reproductive success due to nest-site superimposition (Grabowski and Isely 2007a) and the dewatering of nest sites due to fluctuations in river flow (Grabowski and Isely 2007b). Despite the appearance of localized, high-density aggregations of Robust Redhorse, it seems that the overall spawning population in the lower Savannah River is small. It is also possible that the assumptions of no mortality or recruitment inherent in the multiple census model (Darroch 1958, Seber 1986) were violated. While it is unlikely that there was an appreciable amount of mortality and recruitment occurring during the spawning season, the movement of individuals into and out of the spawning aggregation may have an effect similar to that of recruitment and mortality on the population estimate

(Kendall 1999, Williams et al. 2001) at the small temporal and spatial scales at which the model was employed. Our estimates may actually be a better reflection of the number of individuals present on the gravel bar at any given time and probably underestimate the number of individuals that comprise the aggregation over the entire spawning period. Further studies on the behavior of Robust Redhorse in spawning aggregations are necessary to be able to select a model to adequately address this turnover and more accurately estimate population size.

The sensitivity of multiple census models to the turnover of individuals in the spawning aggregation is potentially illustrated in our mark-recapture data and the disparity between the estimates of the number of males and the total number of individuals. Males seem to comprise more than two-thirds of the actively spawning adults in the spawning aggregation of a catostomid species at any given time. This finding is most likely an artifact of sampling due to the mating system of redhorses where a single female spawns as part of a triad with two males (Jenkins and Burkhead 1994, Page and Johnston 1990) and not an actual deviation from a 1:1 sex ratio in the population. Low catch rates of female catostomids in spawning aggregations have been noted previously (Grabowski and Isely 2005, Vokoun et al. 2003). Females are likely present in the vicinity of the aggregation in deep-water holding areas, but spend much less time within the spawning aggregations since they do not establish or maintain territories. The lack of female Robust Redhorse recaptures suggests they are present in the spawning aggregation for much shorter periods of time and thus are less susceptible to capture. Females of other species such as *Morone saxatilis* (Walbaum) (Striped Bass; Carmichael et al. 1998) and *Plectropomus leopardus* (Lacepède) (Coral Trout; Zeller 1998) have been observed to spend less time within spawning aggregations than male conspecifics. While it is true that fewer females were captured and tagged, the number recaptured was still disproportionately small. It is also possible that differential stress of capture and handling would cause female Robust Redhorse to cease spawning as has been noted in other species (Pankhurst and Van Der Kraak 1997, Zeller 1998). This possibility should be investigated further even though no such effects have been noted previously with radio-tagged Robust Redhorse (T.B. Grabowski, unpubl. data; D. Coughlan, Duke Energy, Huntersville, NC, pers. comm.) when handled in reproductive condition.

In contrast, male Robust Redhorse appear to remain within a spawning aggregation for a considerable portion of the spawning period. We did not find any evidence of a correlation between male length and residence time. This finding may be an artifact of a small sample lacking representatives from the smallest and largest size classes; however, our results are consistent with other studies examining Coral Trout (Zeller 1998) and *Gadus morhua* Linnaeus (Atlantic Cod; Robichaud and Rose 2003). Males seem to establish multiple territories during their time within the spawning aggregation. While it seems likely that the disturbance caused by our sampling induced captured males to establish new territories, there are two lines of evidence to suggest that males normally shift the locations of their territories during their time in a spawning aggregation. First, the spawning aggregations appeared to disband during the night and reform each day. Individuals were not observed holding positions on the lower gravel bar until several hours after sunrise (Grabowski and Isely 2005, 2007a). Additionally, flow fluctuations in the Savannah River would have forced males to change position with changing water levels (Grabowski and Isely 2007b). There is some evidence to suggest individual males may recognize other males and form partnerships to establish and co-defend territories; however, our study lacked sufficient spatial resolution to definitively say these males were immediately adjacent to one another and co-defending a territory.

Based on our observations, we conclude that male Robust Redhorse establish daily spawning territories based on prevailing conditions at the spawning site and possibly their relative, time-specific, dominance hierarchy. Females select their mates and likely expel their entire spawn over a relatively short period (1–2 days). Although both sexes may spawn with multiple partners, males expend their sperm supply over a longer period of several days. The relatively short duration of the aggregation may be the result of an extremely low abundance of adults.

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