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Spatial and temporal segregation of spawning habitat by catostomids in the Savannah River, Georgia and South Carolina, U.S.A.

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Spawning aggregations of five species of catostomids were observed on the two mid-channel gravel bars of the Savannah River, Georgia and South Carolina, in 2004 and 2005 to assess the degree of spatial and temporal overlap in the use of this habitat and determine the habitat preferences leading to segregation. Spawning catostomids showed a considerable amount of temporal overlap in their use of these mid-channel gravel bars. The observed temporal overlap was consistent between 2004 and 2005 and corresponded to temperatures at which species were present. The distribution of catostomids was not uniform at the upstream gravel bar. Carpsuckers *Carpiodes* sp., spotted sucker *Minytrema melanops* and robust redhorse *Moxostoma robustum* both demonstrated some spatial overlap with notchlip redhorse *Moxostoma collapsum*; however, their overall distributions were different from one another. Northern hogsucker *Hypentelium nigricans* was present across the gravel bars, apparently as an egg predator. Spawning catostomids segregated based on flow, depth, slope and substratum size. Whether due to limited habitat availability or changes in the timing of reproduction due to altered cues, temporal and spatial overlap occurs between spawning catostomids despite the apparent partitioning of available spawning habitat. It is unclear, however, if this overlap results in excessive mortality in the early life-history stages of these species. Results suggest spatial overlap among catostomid species was minimized due to species spawning in areas within a narrow range of conditions. Intraspecific interactions such as nest site superimposition or disturbance may be a concern.

Key words: Catostomidae; habitat segregation; nest site superimposition; regulated rivers; spawning aggregation.

INTRODUCTION

The deposition of eggs on or in gravel substratum during spawning is a reproductive strategy commonly employed by riverine fishes. The species employing this strategy share similar spawning habitat requirements that include clean

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gravel substratum of a particular size range and well-oxygenated, flowing water (Balon, 1975). Availability of suitable spawning habitat may be a limiting factor affecting both population and community structure of fishes utilizing this strategy (Benson, 1953; Ming & Noakes, 1984; Essington *et al.*, 2000). In salmonids, redd site superimposition has been identified as a significant source of mortality and reduced reproductive success (Fukushima *et al.*, 1998; Essington *et al.*, 2000). Redd site superimposition is commonly observed within a species due to the behavioural preferences of females to deposit eggs on existing nest sites even when suitable habitat is abundant (Essington *et al.*, 1998). Interference between sympatric salmonid species, however, is rarely observed unless they are closely related (Ming & Noakes, 1984; Essington *et al.*, 1998; Fukushima & Smoker, 1998). The underlying reasons for this have not been adequately investigated. It is likely in most systems, that enough suitable habitat is available to accommodate the number of spawning individuals of each species. It is also possible that sympatric species have microhabitat preferences different enough to segregate them spatially (Curry & Spacie, 1984; Kwak & Skelly, 1992; Essington *et al.*, 2000) or use the same habitats at intervals sufficient to allow for the completion of incubation and larval swim-up and thus reduce interference. Anthropogenic modifications to river systems, however, may alter the location and timing of spawning in riverine fishes (Paller & Saul, 1996; Pringle *et al.*, 2000; Cooke *et al.*, 2005) and in so doing increase the likelihood of nest site superimposition occurring.

The lower Savannah River represents a unique opportunity to assess the effects of dam construction and operation on the spawning habitat use of an assemblage of lithophilic spawners. As many as seven species of catostomids regularly inhabit main channel habitats within the Savannah River (Marcy *et al.*, 2005), including the imperilled robust redhorse *Moxostoma robustum* (Cope), notchlip redhorse *Moxostoma collapsum* (Cope), the currently undescribed brassy jumprock *Moxostoma* sp., quillback *Carpiodes cyprinus* (Lesueur), highfin carpsucker *Carpiodes velifer* (Rafinesque), spotted sucker *Minytrema melanops* (Rafinesque) and northern hogsucker *Hypentelium nigricans* (Lesueur). The members of this assemblage all have been reported to require clean gravel deposits in shallow flowing water for successful spawning (Balon, 1975; Page & Johnston, 1990; Marcy *et al.*, 2005). This habitat type is extremely rare in the main channel of the lower Savannah River, consisting of two mid-channel gravel bars, and dams impede access upstream where it is more abundant (Grabowski & Isely, 2006). The hypolimnetic discharge of these dams has altered the temperature and flow regimes of the lower Savannah River potentially altering important cues as to the timing of spawning (Paller & Saul, 1996; Cooke & Bunt, 1999). While some of the catostomid species present in the Savannah River are known to ascend tributaries during spawning migrations in other drainages (Curry & Spacie, 1984; Page & Johnston, 1990; Jenkins & Burkhead, 1993), available information regarding the life histories and preferences of these fishes suggests that many riverine populations complete this portion of their life cycle within the confines of the main channel (Jenkins & Burkhead, 1993; Marcy *et al.*, 2005; Grabowski & Isely, 2006). Catostomids that make spawning migrations into smaller tributaries have been observed to partition spawning habitat spatially and demonstrate distinct microhabitat preferences (Curry & Spacie, 1984; Kwak & Skelly, 1992; Dion & Whoriskey, 1993).

The lack of a sufficient quantity of suitable spawning habitat has been suggested as one of the factors contributing to the decline of robust redhorse and other catostomid populations (Cooke *et al.*, 2005). Potentially exacerbating this situation in many altered riverine systems is the presence of multiple species of catostomids sharing similar spawning habitat requirements leading to nest site superimposition. The objectives of this study were to document the specific spawning habitat requirements and determine the degree of spatial and temporal segregation of this habitat occurring among catostomid species in the lower Savannah River. The degree of intraspecific overlap in nest sites on each of the two gravel bars was also assessed. Catostomids in the main channel of the Savannah River were predicted to demonstrate a relatively high degree of interspecific superimposition because of the limited availability of spawning habitat and alterations in temperature.

MATERIALS AND METHODS

STUDY AREA

The Savannah River is one of the largest of the Atlantic Slope drainages and encompasses a watershed >25 000 km^2. This river forms the border between the states of Georgia and South Carolina in the south-eastern U.S. It is *c.* 500 km in length, but only the lower 300 km below the New Savannah Bluff Lock and Dam (NSBLD) at Augusta, Georgia, are free flowing. The Savannah River is a highly modified and regulated system with seven main stem dams, five of which have hydroelectric generation capabilities. The study area consisted of the two mid-channel gravel bars in the lower Savannah River. These structures are unique as they are the only two mid-channel gravel bars that have been found in the main channel of the lower Savannah River (Grabowski & Isely, 2006). The upper bar is located at rkm 299·4 just below the tailrace of NSBLD. It is *c.* 170 m long and 150 m wide, and is composed of a relatively thin layer of gravel over packed sand. This bar rises almost 3 m from the bottom on the Georgia side of the river channel at base flows and has a teardrop shape (Fig. 1). A smaller, secondary gravel bar is associated with the upper bar and is located immediately downstream. This secondary bar is located along the South Carolina bank and is separated from the upper bar by a narrow channel. Observations were made every other day at the upper bar during spring in both 2004 and 2005. The lower gravel bar is both smaller than the upper one, *c.* 60 m by 70 m, and lower relief, rising <2 m from the river bottom at base flows. Located at rkm 283·7, the lower bar is composed primarily of gravel over a layer of loosely packed sand and is shaped like the letter Y (Fig. 2). The lower bar was not part of the original study in 2004, but the chance observation of a large robust redhorse spawning aggregation there in May 2004 led to its inclusion in 2005. Observations were made every other day in spring 2005.

DATA COLLECTION

A combination of methods was used to assess how these habitats are partitioned and used by spawning catostomids. Visibility was such that fishes could be observed from the surface with the use of polarized sunglasses. The positions of fishes that were spawning, staging and holding position near the spawning grounds were recorded with a global positioning system (GPS) receiver while drifting over the deeper (>1·5 m) areas of the gravel bar in a boat. Boat observations were conducted over two 15 min periods

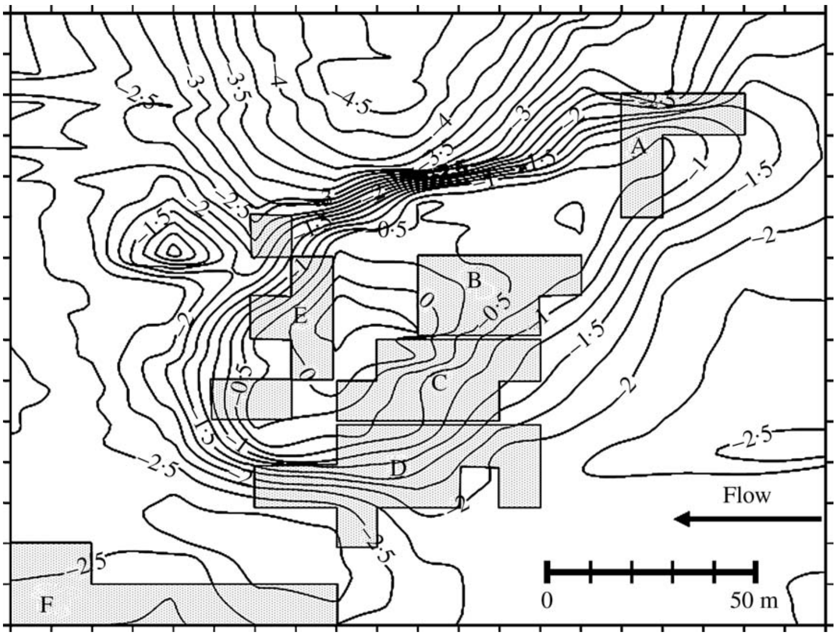

FIG. 1. Bathymetric map of the upper gravel bar at river kilometre 299·4 on the lower Savannah River. Contour lines represent a change in depth of 0·25 m. Depths indicate water depth under low flow conditions (*c.* 85 m^3 s^{-1}). The locations where catostomids were observed or captured (zones A–F) are delineated by shaded boxes.

everyday when conditions allowed. Fishes in shallower water were observed from a 3 m tall observation tower placed on the gravel bar. Tower observations typically lasted 60 min and were conducted two to three times each day when conditions allowed. The positions of fishes were marked with individually numbered weighted flags that were dropped upon the locations occupied by fishes. The fishes responded by moving a few metres away but generally returned within 2–3 min. Upon retrieval, the position of each flag was recorded using GPS and microhabitat variables were recorded. Depth was measured to the nearest 0·01 m using a metre stick. Current velocity was measured using a digital stream flowmeter. Riverbed slope (grade) parallel to the direction of flow was determined at each fish position using geographic imaging software and the bathymetric data were used to generate Figs 1 and 2. Substratum particle size distribution at each flag were determined in the field using a modified Wolman pebble count procedure (Wolman, 1954) on *c.* 50 pieces of substratum with a hand-held size analyser (gravelometer). This device consists of an aluminium plate with 14 square holes corresponding in size to common 0·5 ϕ unit classes and yields results effectively similar to sieving. Water temperature was measured everyday on site and recorded hourly approximately midway between the two gravel bars at rkm 289·7 by a Hobo Water Temperature Pro v.1 data logger. River discharge in cubic feet per second (cfs) was acquired from U.S. Geological Survey gauging station 02197000 (available online at http://waterdata.usgs.gov/ga/nwis/uv?2197000) and converted to m^3 s^{-1}.

Prepositioned grid electrofishers were deployed as described by Grabowski & Isely (2005) to capture spawning and staging fishes. A GPS waypoint, depth, current direction, current velocity and substratum particle size distribution was taken at each grid prior to retrieval. The primary purpose in capturing fishes was to confirm above-water species identifications and reproductive condition of individuals. The sex of all captured catostomids was determined based upon the expression of gametes and secondary sex

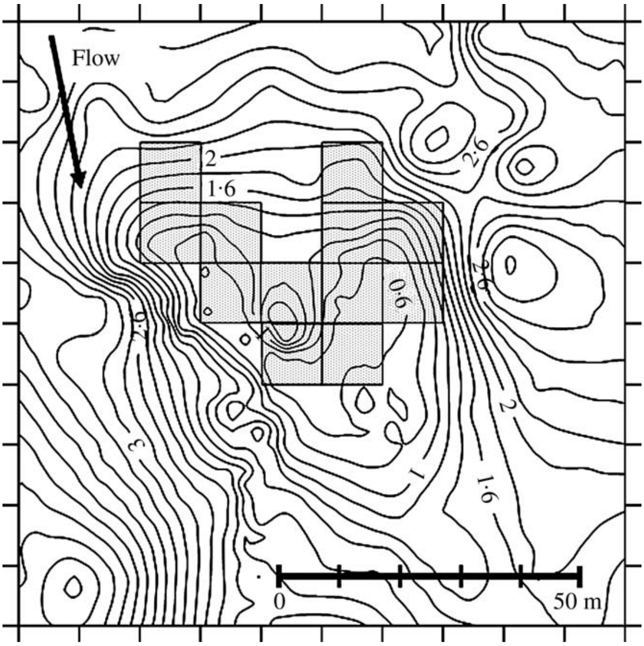

FIG. 2. Bathymetric map of the lower gravel bar at river kilometre 283·7 on the lower Savannah River. Contour lines represent a change in depth of 0·2 m. Depths indicate water depth under average flow conditions (*c.* 200 m^3 s^{-1}). The 10 m × 10 m areas in which catostomids were observed or captured are indicated by shaded boxes.

characteristics (presence of nuptial tubercles in males, loss of mucus in females) in reproductively active individuals and by the shape of the pelvic fins in individuals not reproductively active (W. C. Starnes, pers. comm.). At least one digital photograph was taken of each individual captured to serve as a voucher before releasing all fishes alive.

Emergent larvae were captured as they left the gravel bar using 1000 μm mesh, square frame plankton nets with a 0·125 m^2 opening. Five to six nets were deployed about each bar and allowed to fish for *c.* 1 h before retrieval. Depending upon conditions, this was repeated two to three times during each visit to the gravel bars. Ichthyoplankton samples were fixed in a 3·0% formalin solution, rinsed, and stored in 95% ethanol. Larval catostomids were identified to lowest taxa possible using Hogue & Buchanan (1977), Buynak & Mohr (1978, 1979), Fuiman (1979), Kay *et al.* (1994) and Bunt & Cooke (2004).

DATA ANALYSIS

Mixed model ANOVA with Dunnett's comparison tests was used to compare mean depths, current velocities, slopes and particle size among species (fixed effects) while controlling for year and location (random effects) (Zar, 1996). A paired *t*-test was used to test the hypothesis that species found on both gravel bars used areas with different depths, current velocities, slopes or particle sizes. Principle component analysis (PCA) was performed to visualize the relationships of these habitat variables among species and location. Spatial analysis of habitat partitioning on the upper bar was three-tiered. First, a 50 × 50 m grid was established and χ^2 analysis was performed to test for the uniform distribution of individuals over the upper bar. If fish distribution proved to be non-uniform on this coarse scale, then a 10 × 10 m grid was established. Only boxes with observations of fishes were considered for further analysis. χ^2 tests analysis was used to test for uniform fish distribution among the areas that were used. These 10 × 10 m boxes were then used to establish zones A–F (Fig. 1) on the basis of proximity, shared physical features and similar hydrologic conditions. Pair-wise χ^2 tests were employed to test the null hypotheses that distributions within the zones did not differ both among species and between 2004 and 2005 within species. ANOVA with Dunnett's comparison tests were used to confirm that each zone differed in at least one variable (depth, slope and mean particle size). Additionally, paired χ^2 tests were conducted to compare particle size distributions among zones. A similar analysis was completed for the lower bar with the exception of the coarse 50 × 50 m grid. This step was performed using a 20 × 20 m grid because of the smaller size of the lower bar. A finer scale 10 × 10 m grid was then established for areas occupied by fishes (Fig. 2) and was analysed as described for the upper bar. A significance level of $\alpha = 0{\cdot}05$ was used for all tests.

RESULTS

A total of 268 adult catostomids was captured consisting of 39 northern hogsuckers, 58 notchlip redhorse, 22 spotted suckers and 149 robust redhorse. The sex ratio for all species was heavily biased towards males (northern hogsucker: 2·3:1; notchlip redhorse: 7·3:1; robust redhorse: 4·5:1) except for spotted sucker (1:1). Each individual of all species except for northern hogsucker displayed signs of being reproductively active such as full tubercle development, loss of body slime, expression of gametes with the application of mild abdominal pressure, and wounds such as split fins and scale loss consistent with those found on spawning catostomids in other systems (R. E. Jenkins, pers. comm.). Northern hogsuckers in reproductive condition were only encountered in the first collections of 2004 and 2005. An additional 553 observations of adult catostomids were made during tower and boat observation periods in the course of this study. A total of 52 larval fishes were captured yielding an overall catch per unit effort of 0·14 larvae per net hour. The majority of larva ($n = 42$) consisted of catostomids represented by one unidentifiable individual, two *Carpiodes* sp., two northern hogsucker, two spotted sucker and 35 redhorses. Cyprinids (unidentified species; $n = 4$), clupeids (*Alosa* sp.; $n = 1$), percid darters ($n = 2$), and three unidentifiable larvae comprised the remainder of the ichthyoplankton samples. A large number ($n = 97$) of pre-hatching robust redhorse embryos at various stages of development were captured when ichthyoplankton nets were set behind actively spawning adults.

TEMPORAL DISTRIBUTION

Spawning catostomids showed a considerable amount of temporal overlap in their use of Savannah River main channel gravel bars in 2004 and 2005. This temporal overlap generally corresponded to the temperatures at which species were present (Fig. 3). Conditions on the Savannah River, however, varied considerably between 2004 and 2005. There were two major flood pulses in March 2005 caused by water releases from upstream reservoirs in an attempt to raise water levels in the river to allow fish passage at NSBLD. These were followed by a major natural flood pulse in April. Spring was relatively dry in 2004 with

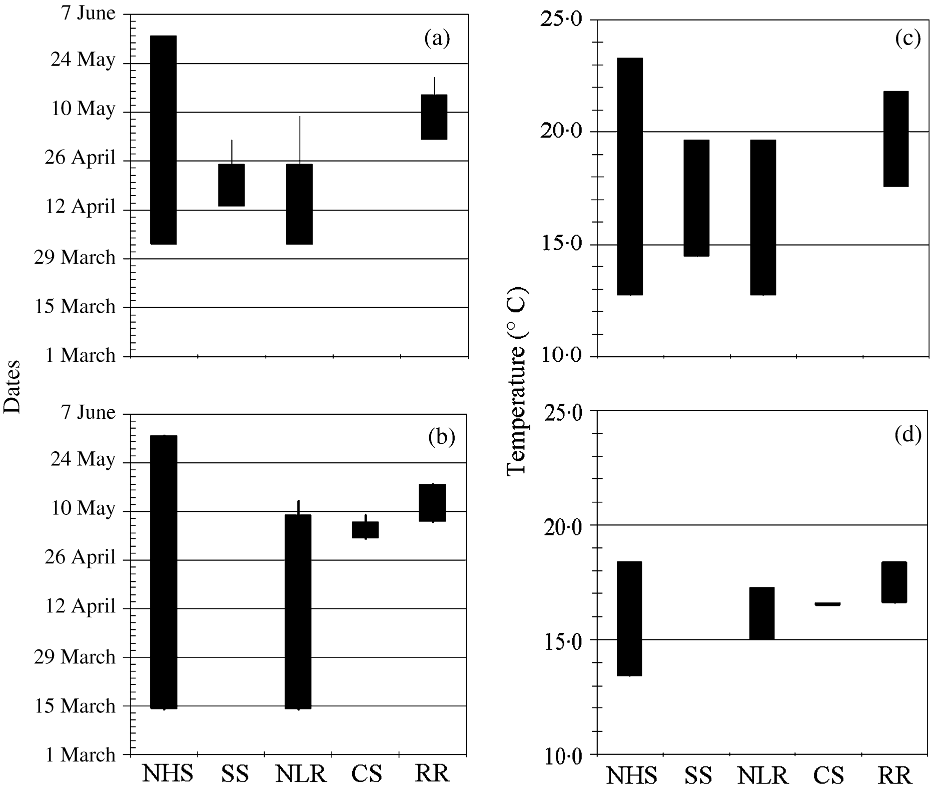

FIG. 3. (a), (b) Dates and (c), (d) temperatures when northern hogsucker (NHS), spotted sucker (SS), notchlip redhorse (NLR), carpsucker (CS) and robust redhorse (RR) were observed on the gravel bars in the lower Savannah River in (a), (c) 2004 and (b), (d) 2005. Vertical lines indicate the latest date larvae of that species were captured.

flows rarely exceeding the median daily streamflow except for a minor flood pulse in March 2004. Temperatures were depressed and exhibited less fluctuation in 2005 relative to those in 2004.

The spawning progression appears to be northern hogsucker, notchlip redhorse, spotted sucker, carpsucker and robust redhorse (Fig. 3). Northern hogsucker were present at each gravel bar throughout the duration of observations in both years. Individuals in spawning condition, however, were encountered only in early spring during both 2004 and 2005. Notchlip redhorse were present and observed spawning for a longer period of time than all other species except for northern hogsuckers. Two other species spawned on the upper bar during the period notchlip redhorse were present. While adult spotted suckers were observed or captured during 2004, no spawning was observed despite the capture of larvae. Carpsuckers were observed spawning and larvae were captured in 2005. Unfortunately, adult carpsuckers were not captured rendering it impossible to confirm which *Carpiodes* species was present. Robust redhorse arrived after the departure of adult notchlip redhorse. This species arrived earlier, was present in greater numbers, and stayed longer at the lower gravel bar.

SPATIAL DISTRIBUTION

Spawning catostomids were not distributed uniformly on the upper gravel bar based on a 50 × 50 m grid (χ^2, d.f. = 11, $P < 0{\cdot}001$) nor distributed uniformly among the 100 m^2 areas in which they did occur (χ^2, d.f. = 5, $P < 0{\cdot}001$). While species demonstrated some spatial overlap among the zones of the upper gravel bar (Table I), their distributions were different from one another (χ^2, d.f. = 5, $P < 0{\cdot}001$). There was no difference between 2004 and 2005 in the distributions of notchlip redhorse (χ^2, d.f. = 5, $P > 0{\cdot}05$) or robust redhorse (χ^2, d.f. = 5, $P > 0{\cdot}05$).

Robust redhorse and northern hogsucker were the only catostomid species observed on the lower gravel bar. More robust redhorse were observed or captured on the lower bar ($n = 226$) than the upper bar ($n = 29$). Their distribution on the lower bar was not uniform (χ^2, d.f. = 24, $P < 0{\cdot}001$) as they were found only along the upstream edge of the gravel bar. Their overall distribution along this edge also was not uniform (χ^2, d.f. = 11, $P < 0{\cdot}001$) with the largest concentration occurring along the Georgia edge of the bar. Northern hogsucker appeared to follow a similar distribution pattern. Their distribution over the entire gravel bar (χ^2, d.f. = 24, $P > 0{\cdot}05$) and among the 100 m^2 areas in which they were found (χ^2, d.f. = 5, $P > 0{\cdot}05$), however, was uniform. This is probably an artefact of the small number of individuals observed or captured ($n = 12$). Northern hogsuckers on the lower bar exhibited no signs of being reproductively active. Visual observations suggest that northern hogsuckers were present within active robust redhorse redds to feed on eggs and possibly benthic invertebrates dislodged from the substratum. Captured northern hogsuckers were frequently observed regurgitating intact eggs and a yolk-like material.

Depth and current velocity varied with stream discharge at NSBLD. Spawning catostomids on the upper bar were found consistently in the same areas regardless of spawning intensity or water level. These areas remained underwater and flow was maintained under all observed levels of stream discharge (85 to >850 $\mathrm{m}^3\ \mathrm{s}^{-1}$). On the lower gravel bar, robust redhorse initiated spawning on the Georgia side of the upstream edge and spilled over to the centre and South Carolina edge as spawning intensity increased. The Georgia edge, however,

TABLE I. Percentage of individuals of each catostomid species found in the zones of the upper gravel bar in the Savannah River (see Fig. 1) during spring 2004 and 2005

		Zone					
		A	B	C	D	E	F
Species	*n*	Percentage of individuals					
Carpiodes sp.	40	0·0	0·0	7·5	0·0	92·5	0·0
Hypentelium nigricans	108	0·0	13·9	33·3	8·3	5·6	38·9
Minytrema melanops	34	0·0	0·0	5·9	2·9	0·0	91·2
Moxostoma collapsum	610	2·6	27·9	39·0	20·8	0·7	9·0
Moxostoma robustum	29	0·0	6·9	3·4	75·9	3·5	10·3
Total	821	1·9	22·8	34·1	19·4	5·9	15·9

appeared to remain the area of greatest intensity. Redd sites along the Georgia edge were not exposed or degraded by fluctuating water levels as opposed to areas along the centre and South Carolina edge of the bar.

SPAWNING HABITAT SEGREGATION

Catostomids on the upper bar appeared to segregate based on microhabitat conditions of flow, depth, slope and substratum size (Table II). The PCA was able to account for 87·5% of the variability on two axes with eigenvalues $\geq 1{\cdot}2$. Current velocity, slope and mean particle size loaded onto PC-1 while depth was the only variable loaded onto PC-2 (Fig. 4). The zones of the upper bar where each species was predominantly found were basically defined by these conditions (Table III). Carpsuckers were excluded from further analysis because only one full set of habitat measurements was taken. Two of the three records of this species were made during boat observations over deep water. The mean depth of areas used for spawning differed among all other species ($F_{3,198}$, $P < 0{\cdot}001$) when controlling for year and location (upper *v.* lower gravel bar) despite the occupation of similar mean depths by robust redhorse and northern hogsucker (Table II). Spotted suckers were found in the deepest water, and robust redhorse and northern hogsuckers were typically observed in the shallowest. Similarly, the mean flow velocity of areas occupied by catostomids differed among all species ($F_{3,19,}$ $P < 0{\cdot}001$) when adjusted for year and location effects. Northern hogsuckers on average were found in the swiftest flowing water and spotted suckers were found in the slowest. The slopes of areas used by catostomids differed among species ($F_{4,230}$, $P < 0{\cdot}001$). Robust redhorse were captured in areas that were steeper than areas used by other species. Spotted sucker used areas of similar slope to those used by notchlip redhorse and northern hogsucker. Northern hogsucker, however, used areas with a greater slope than did notchlip redhorse. Both robust redhorse and northern hogsucker (*t*-test, d.f. = 81, $P < 0{\cdot}05$) used areas with a greater slope on the

TABLE II. Mean ± S.E. depth, velocity and slope, and mean ± S.E. and median substratum particle size of the Savannah River gravel bar locations from which catostomid species were captured or observed in spring 2004 and 2005

Species	*n*	Mean depth (m)	Mean velocity (m s^{-1})	Mean slope	Mean substratum diameter (mm)	Modal substratum diameter (mm)
Carpiodes sp.	2	1·25	0·63	0·04 ± 0·01	14·8 ± 1·2	5·7, 22·6
Hypentelium nigricans	30	0·74 ± 0·03	0·44 ± 0·03	0·05 ± 0·00	11·9 ± 0·5	11·3
Minytrema melanops	22	1·16 ± 0·03	0·17 ± 0·03	0·03 ± 0·01	9·4 ± 0·7	8·0
Moxostoma collapsum	56	0·98 ± 0·02	0·30 ± 0·03	0·04 ± 0·00	12·2 ± 1·1	16·0
Moxostoma robustum	96	0·74 ± 0·02	0·24 ± 0·01	0·07 ± 0·00	14·3 ± 0·3	32·0

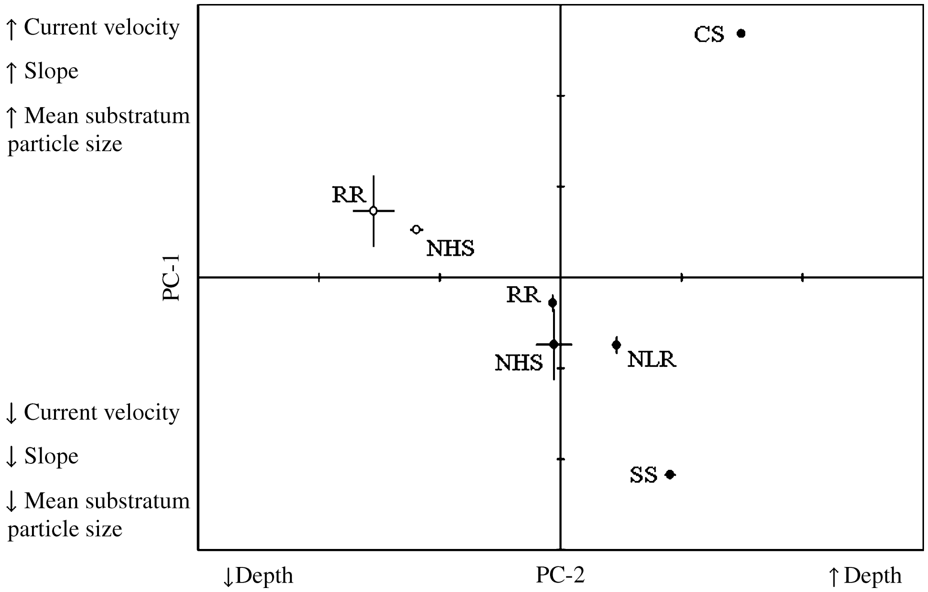

FIG. 4. Principle component analysis for habitat conditions in areas used by spawning notchlip redhorse (NLR), northern hogsucker (NHS), robust redhorse (RR), spotted sucker (SS), and carpsucker (CS) on the upper (●) and lower (○) gravel bars in the lower Savannah River in 2004 and 2005. Current velocity, slope and mean particle size loaded onto the first principle component while depth was the only variable loaded onto second component. Error bars are S.E.

lower gravel bar (robust redhorse: 0·08 ± 0·00; northern hogsucker: 0·09 ± 0·01) than on the upper bar (robust redhorse: 0·06 ± 0·01; northern hogsucker: 0·04 ± 0·01). In general, areas used by these species on the upper bar tended to be shallower with higher current velocities, steeper slopes and larger substratum (Fig. 4).

DISCUSSION

The two main channel gravel bars in the lower Savannah River represent an important, if not the sole, spawning habitat for catostomids in this system. The

TABLE III. Mean ± S.E. depth, depth range and slope, and mean ± S.E. and median substratum diameter of the zones of the upper gravel bar (see Fig. 1)

Zone	*n*	Mean depth (m)	Depth range (m)	Mean slope (per cent grade)	Mean substratum diameter (mm)	Median substratum diameter (mm)
A	21	1·66 ± 0·17	0·88–4·08	5·1 ± 1·0	10·5 ± 0·6	5·7, 11·3
B	39	0·23 ± 0·08	0·00–0·90	3·9 ± 0·3	9·1 ± 0·5	5·7
C	42	0·53 ± 0·07	0·00–1·10	3·9 ± 0·3	11·5 ± 0·7	5·7
D	25	1·00 ± 0·09	0·23–2·07	5·4 ± 0·8	12·5 ± 0·7	8·0, 16·0
E	44	0·16 ± 0·07	0·00–1·95	6·3 ± 1·2	9·7 ± 0·5	5·7, 8·0
F	15	0·62 ± 0·33	0·03–1·20	2·5 ± 0·2	10·5 ± 0·5	8·0

biased sex ratios of captured adult fishes and collection of emergent catostomid larva are consistent with the observation of catostomids using the upper and lower gravel bars for spawning and has been noted in other catostomid species (Peterson *et al.*, 2000; Vokoun *et al.*, 2003). These fishes are known to primarily spawn as 'trembling trios' or triads of a single female flanked by two males (Page & Johnson, 1990; Jenkins & Burkhead, 1993). Males hold position on the spawning ground and are approached by females arriving from nearby staging areas. Collections in active spawning areas would, therefore, result in the highly biased sex ratios observed in this study. It also suggests that spotted sucker were using the deeper, low current velocity area of zone F along the South Carolina bank as a staging area. The majority of individuals of this species (>90%) were captured here in equal proportions of males and females. Spotted suckers were probably spawning in zones C and D in high flow, shallow areas along the upstream edge of the gravel bar where only males were captured. The larvae of all species observed spawning or captured in spawning condition were captured during the course of this study. It is important to note that at present there is no reliable method of distinguishing between larval robust redhorse and notchlip redhorse aside from a mitochondrial DNA assay (Wirgin *et al.*, 2004). The results presented here are, therefore, conservative estimates of the temporal overlap between notchlip and robust redhorse as larval robust redhorse were not identified as such until 5 days after the adults were observed. This is well below the time reported by Weyers *et al.* (2003) of 5–10 days between hatching and emergence of larval robust redhorse under aquarium conditions.

The sequence of species arrival and the time spent spawning on gravel bars is probably heavily influenced by photoperiod, water temperature and flows. These factors have been identified as important cues for initiating spawning migrations (Quinn & Adams, 1996; McCormick *et al.*, 1998; Cooke & Bunt, 1999) and maturation of gonads (Huber & Bengtson, 1999). Catostomids in the lower Savannah River have to cope with a temperature and flow regime that is dramatically altered from its natural state as water temperatures tend to be consistently cooler than those prior to impoundment (Paller & Saul, 1996). Fishes may be spawning outside their preferred temperature range based on records for these species in other river systems in the south-eastern U.S. (D. J. Coughlan, pers. comm.). Alternatively, they may be delaying reproduction to later in the spring when temperatures are within this range which would probably have severe negative effects on young-of-the-year age class strength and survival due to failure in acquiring the energy reserves necessary to survive winter (Kipling & Frost, 1970; Buckley *et al.*, 1991). Species sequences and reproductive chronology can be highly variable among river systems (McHugh & Budy, 2004) necessitating comparative studies on larger geographic scales or site specific models. Complicating matters is interannual variability of environmental variables such as the difference in annual temperature regimes observed in 2004 and 2005. Fishes were present on the gravel bar at lower temperatures and narrower temperature ranges in 2005 than 2004. This may increase the likelihood of temporal overlap among species by decreasing the time between species or increasing the time early life-history stages are present on the gravel bar. Some species such as robust redhorse, however, arrived on the gravel bar at approximately the same time in 2004 and 2005 suggesting photoperiod may be just as important. Further investigation of the stability of the observed sequence of spawning fishes both in the Savannah River and throughout the south-eastern U.S. will be required to determine the relative role of photoperiod, temperature, flow or perhaps intrinsic factors not yet considered.

Whether due to limited habitat availability or changes in the timing of reproduction due to altered cues, temporal and spatial overlap occurs between spawning catostomids despite the apparent partitioning of available spawning habitat. This overlap can be broadly divided into two types: temporal overlap of spawning adults of different species, and temporal overlap of spawning adults with the early life-history stages of another species. The more common of these was the presence of spawning adults while early life-history stages of a previous species were still emerging from the gravel. This occurred in both years between spawning robust redhorse and larval notchlip redhorse. Other studies examining the spawning aggregations of catostomids have not incorporated ichthyoplankton sampling concurrent with sampling of spawning adults. This study confirms that larvae are present for a considerable period of time after spawning activity of other species has initiated. This is true in other fish groups such as salmonids. The long incubation periods and the relative ease of identifying redd sites of salmonids has lead to the recognition of redd site superimposition, both intra- and interspecific, as a serious concern (Sandercock, 1991; Essington *et al.*, 1998; Fukushima & Smoker, 1998; Fukushima *et al.*, 1998). For example, Fukushima *et al.* (1998) estimated redd site superimposition accounted for a loss of up to one-third of the daily reproductive output within an Alaskan pink salmon *Oncorhynchus gorbuscha* (Walbaum) population.

It is unclear how commonly temporal overlap occurs between spawning adults of two species. Notchlip redhorse overlapped with spotted sucker in 2004 and carpsucker in 2005. It is uncertain, however, how often and under what circumstances spotted sucker and carpsucker use the upper bar. These species occupied a limited area on the bar, were there for a short period of time, and were never observed at high densities. In other systems, spotted sucker have been reported to ascend tributaries to form large spawning aggregations (McSwain & Gennings, 1972; Mettee *et al.*, 1996) while carpsuckers have been reported to use a variety of different habitats in both the main river channel and in smaller tributaries (Harlan & Speaker, 1956; Scott & Crossman, 1973; Jenkins & Burkhead, 1993). Notchlip redhorse were present on the upper gravel bar in larger numbers, over a greater proportion of the available area, and for a longer period of time during both years. Temporal overlap in spawning between two or more species has been observed in other catostomid assemblages (Curry & Spacie, 1984; Kwak & Skelly, 1992; Dion & Whoriskey, 1993), salmonids (Fukushima & Smoker, 1998) and cyprinid nest associates of nest building cyprinids such as *Nocomis* spp. (Johnston, 1991). In these cases, authors generally reported a greater degree of spatial segregation than that observed at the gravel bars in the lower Savannah River in the case of catostomids and salmonids or non-invasive deposition of eggs as in the case of cyprinids. As previously mentioned, northern hogsucker did overlap with all other species but were probably present on the bars as either residents or egg predators and not for reproduction for the majority of that time.

Despite the considerable amount of both temporal and spatial overlap between notchlip redhorse and the other species, spatial segregation under observed conditions appears to be sufficient to prevent excessive mortality of early life-history stages due to interspecific nest site superimposition. For example, robust redhorse, considered the least abundant species in this assemblage, appears to experience lowest risk. This species not only spawns later in the spring than the other species, but also appears to be the only species to use the lower gravel bar for reproduction. Spotted sucker is one of the most common large fish species in the Savannah River (Marcy *et al.*, 2005). The relatively low number of individuals observed at the study sites, however, suggests the majority of individuals in the Savannah River population ascend tributaries to spawn as in other systems (McSwain & Gennings, 1972) or utilize as of yet unidentified habitat. Notchlip redhorse appear to be the predominant species spawning on the upper bar both in terms of number of individuals and time present on the bar. There is the potential for a relatively small proportion of their nests to be disturbed by spawning robust redhorse and spotted sucker. A much greater potential, however, exists for intraspecific nest site superimposition for fishes in the lower Savannah River dependent upon main channel gravel bars as their primary spawning habitat such as notchlip redhorse and robust redhorse.

Although the quantity of suitable habitat is limited, it appears that spatial overlap among catostomids was minimized due to species spawning in areas within a narrow range of conditions such as depth, slope, current velocity and substratum size distributions. This degree of spawning microhabitat specificity has been noted in other catostomids (Curry & Spacie, 1984; Kwak & Skelly, 1992). In fishes, this specificity probably has several functions ranging from acting as a reproductive isolating mechanism (Kwak & Skelly, 1992) to maximizing reproductive success (Hall, 1972; Itzkowitz, 1991; Maurakis & Green, 2001). Spawning habitat specificity may be a contributing factor to the spawning site fidelity observed in robust redhorse in the Savannah River (Grabowski & Isely, 2006). The microhabitat specificity demonstrated by spawning catostomids is probably the underlying reason for the observed differences in spatial distribution among species. For example, robust redhorse was the only species observed spawning on the lower gravel bar. This species used areas with the largest modal substratum particle size and slope relative to those used by the other catostomid species. The lower gravel bar would seem to be the logical choice for robust redhorse to meet these conditions. Spawning microhabitat specificity is also likely to partially explain why some species distributions varied between 2004 and 2005. Some of the microhabitat variables such as slope and substratum size remained relatively constant over the duration of this study. On the other hand, depth and current velocity changed by the hour in relation to water discharge upstream of the gravel bars. Hyporheic discharge, or upwelling water passing through the substratum, has been demonstrated to be a critical factor in spawning habitat selection in other species, such as brook charr *Salvelinus fontinalis* (Mitchill) (Benson, 1953; Bernier-Bourgault & Magnan, 2002; Blanchfield & Ridgway, 2005). Attempts to locate similar areas of hyporheic discharge at areas used by spawning catostomids using piezometers failed. Hyporheic flow is probably minimal if such areas are present on the gravel bars and probably not a major factor in habitat selection. Other factors which have probably contributed to the selection of spawning habitat include the presence of spawning conspecifics (Essington *et al.*, 1998; Danchin *et al.*, 2004) and competitive exclusion from preferred sites by larger conspecifics or other species (Ming & Noakes, 1984; Essington *et al.*, 2000).

Even though interspecific overlap is minimized, species dependent upon the two main channel gravel bars in the Savannah River are subject to intraspecific nest disturbance and site superimposition. This is illustrated by the developing embryos that were captured behind active nest sites on the lower bar in 2005. This number would have probably been higher, but there were also large numbers of cyprinids, such as bannerfin shiner *Cyprinella leedsi* (Fowler), whitefin shiner *Cyprinella nivea* (Cope) and spotfin shiner *Notropis hudsonius* (Clinton), blackbanded darters *Percina nigrofasciata* (Agassiz) and northern hogsuckers present on the lower bar (unpubl. data). These fishes were presumably feeding on dislodged embryos and eggs. Captured individuals had guts that were filled with eggs. This study did not have sufficient spatial resolution to assess the extent and impact of intraspecific nest site superimposition. Using the methods employed by this study, it was not possible to localize where the eggs had been deposited with the degree of accuracy necessary to reliably quantify intraspecific nest superimposition. The overlap in fish positions and the amount of disturbed gravel observed in this study, however, suggests that a high degree of superimposition occurs and warrants investigation into effects of intraspecific interactions on reproductive success. Species using these bars are probably vulnerable to the same stochastic events and anthropogenic influences that have been shown to effect spawning aggregations of fishes in other systems, such as pollution and siltation (Acornley & Sear, 1999; Spromberg & Birge, 2005), boat traffic and groundings (Boussard, 1981; Bettoli & Clark, 1992; Amoser *et al.*, 2004), fishing pressure (Scoppettone & Vinyard, 1991; Markle & Cooperman, 2002) and fluctuations in current velocities and water levels due to hydropower generation or water conservation at upstream reservoirs (Baxter, 1977; Bain *et al.*, 1988; Weyers *et al.*, 2003). Further, the small area readily available and used by Savannah River species may exacerbate these risks. The availability of suitable spawning habitat appears to have the potential to be a major limiting factor in the conservation and long-term viability of catostomid populations and the populations of other substratum spawning fishes in modified river systems.

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