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American Midland Naturalist, Vol. 144, No. 1. (Jul., 2000), pp. 187-201.

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Spawning Behaviors in the Bluehead Chub, *Nocomis leptocephalus*, River Chub, *N. micropogon* and Central Stoneroller, *Campostoma anomalum*

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ABSTRACT.—Spawning behaviors were filmed and observed in the nest-building minnows, the bluehead chub, *Nocomis leptocephalus*, and river chub, *N. micropogon*. Analysis of videotapes exposed previously unreported behaviors (*e.g.*, female retroflexure) and a precise sequence of male-female interactions that coordinated a successful spawn. Reproductive behaviors were classified into six sequential categories (interim, approach, alignment, run, clasp, dissociation) to facilitate interspecific comparisons. The most conspicuous differences between species involved the intensity of the female's retroflexure and the male's spawning clasp (strong in *N. leptocephalus* vs. weak in *N. micropogon*) and reproductive behaviors of subordinate males. In *N. leptocephalus*, subordinate males spawned concurrently and independently of the resident male over a communal nest, whereas in *N. micropogon* a subordinate acted like a satellite male and stole spawns from the nest-building male. In addition, heterogeneric spawning clasps involving a male and female *N. leptocephalus* and a male central stoneroller, *Campostoma anomalum*, are newly described.

INTRODUCTION

Nocomis Girard is a genus of nest-building chubs (Cyprinidae) widely distributed in the United States east of the Great Plains. Breeding males in all seven species of *Nocomis* use their jaws to transport pebbles (gravel) and build mound nests for spawning in slow to moderately flowing water (Reighard, 1943; Lachner, 1952; Jenkins and Burkhead, 1994). Internal mandibular surfaces of nest-building males in at least two species (*N. leptocephalus* and *N. micropogon*) are covered with a layer of keratin which may reduce abrasion during stone carrying (McGuire *et al.*, 1996; W. R. McGuire, pers. comm.).

Nest construction is a three-stage process (Reighard, 1943; Maurakis *et al.*, 1991; Jenkins and Burkhead, 1994). The male excavates a concavity which he fills with pebbles to form a platform and finally covers with pebbles collected from surrounding substrates to form a dome-shaped mound. During mound-building the male uses his jaws and snout to hollow out a pit (*e.g.*, *Nocomis biguttatus* and *N. leptocephalus*) or longer trough (*N. micropogon*) in which spawning takes place (Reighard, 1943; Pflieger, 1975; Vives, 1990; Johnston, 1991; Maurakis *et al.*, 1991; Wallin, 1992). Typically located on the mound's upstream slope, the

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spawning pit or trough creates a pocket of slack water and presumably enhances fertilization by allowing gametes to sink into the pebble interstices of the nest (Maurakis *et al.*, 1992). After a number of spawns a male *N. leptocephalus* covers the pit with pebbles and excavates another pit for spawning, whereas a male *N. micropogon* continually reshapes the original trough. Eggs become buried and are thought to receive a constant circulation of water (Vives, 1990) and remain well aerated in the clean interstices of the nest (Hubbs and Cooper, 1936; Raney, 1940a; Johnston, 1991; Jenkins and Burkhead, 1994). Burial of eggs also presumably reduces their risk of predation (Hubbs and Cooper, 1936; Raney, 1940a; Vives, 1990; Johnston, 1991; Jenkins and Burkhead, 1994). *Nocomis* also exhibits extreme sexual dimorphism during the breeding season (*see* figures in Jenkins and Burkhead, 1994). Nuptial males develop sharp cephalic tubercles and aggressively defend their spawning sites from conspecific intruders (Maurakis *et al.*, 1997) and potential egg predators such as suckers (Hankinson, 1932; Vives, 1990).

Other species of minnows, referred to as nest associates, often school and may spawn over active nests of *Nocomis* without contributing to the nest's construction. Twenty-seven minnow species are reported as nest associates of *Nocomis* (Johnston and Page, 1992; Maurakis and Woolcott, 1993; Johnston and Kleiner, 1994). Interaction of host and nest associate is thought to be mutualistic (Hubbs and Cooper, 1936; Wallin, 1992; Johnston, 1994). Eggs and larvae of associates benefit from the parental care of nesting chub, and offspring of both host and associate may benefit from a dilution effect whereby predation risk per egg is reduced in the nest (Wallin, 1992; Johnston, 1994).

Spawning behaviors have been reported in detail for redspot chub, *Nocomis asper*, in Missouri (Maurakis and Roston, 1998); hornyhead chub, *N. biguttatus*, in Missouri (Pflieger, 1975) and Wisconsin (Vives, 1990); river chub, *N. micropogon*, in Michigan (Reighard, 1943), New York (Miller, 1964) and Virginia (Sabaj, 1992; Jenkins and Burkhead, 1994); and bluehead chub, *N. leptocephalus*, in North Carolina (Johnston, 1991), South Carolina (Wallin 1989, 1992) and Virginia (Sabaj, 1992). Maurakis *et al.* (1991) hypothesized *N. biguttatus* and *N. leptocephalus* are more closely related relative to *N. micropogon* based on a cladistic analysis of reproductive behaviors in the three species using the central stone-roller, *Campostoma anomalum*, as an outgroup.

We filmed and observed spawning in *Nocomis leptocephalus* in Georgia, North Carolina and Virginia and *N. micropogon* in North Carolina and Virginia. Analysis of videotapes revealed previously unreported reproductive behaviors in *N. leptocephalus*, *N. micropogon* and the nest associate, *Campostoma anomalum*. Our objectives are to document these behaviors and to review, compare and discuss spawning in *Nocomis* based on our observations and those reported in the literature. In addition we comment on the potential adaptive significance and phylogenetic implications of these behaviors for *Nocomis* and other species of North American minnows, and note the use of behavioral categories (*i.e.*, Sabaj, 1992) to outline specific traits of minnow reproduction.

MATERIALS AND METHODS

Fishes were observed and videotaped from above the surface of the water using techniques discussed in Maurakis and Woolcott (1995). Behaviors on tape were reviewed at normal speed, in slow motion and frame by frame to record the movements and relative positions of fishes. Illustrations were drawn from a single frame of videotape viewed on a monitor. To facilitate direct comparisons between the two species of *Nocomis*, reproductive activities were resolved into six categories (Sabaj, 1992) that reflected the sequence of male-female interactions characteristic of a successful spawn. The categories are: interim (male behavior between spawns), approach (female behavior directed towards interim male),

alignment (behavior affecting precise orientation of spawning pair over substrate), run (initiated by female, synchronized movement of aligned pair over substrate), clasp (momentary flexure of male's body about an axis determined by female's position at the end of her run) and dissociation (pair separation immediately after the clasp). Qualitative treatment of behaviors in each category is followed by descriptions of events disruptive of the interim male or a successful spawning sequence.

Spawning was filmed and observed in *Nocomis leptocephalus* ($n = 19$ males; 34.2 h direct observations, 13.4 h videotape) in Georgia (Altamaha Drainage), North Carolina (Cape Fear, Roanoke, Savannah and Tennessee drainages) and Virginia (New-Kanawha and Roanoke drainages); and *N. micropogon* ($n = 5$ males, 13.3 h direct observations, 7.4 h videotape) in North Carolina (Tennessee Drainage) and Virginia (Potomac Drainage) from 1984 to 1993 (see Appendix for sites, times, temperatures and individuals studied). Behaviors described for *N. leptocephalus* in Sinking Creek and *N. micropogon* in Catocin Creek, Virginia, were corroborated by similar behaviors recorded at the additional study sites. Sinking Creek was a clear, small (about 7.5 m wide) and shallow (average depth about 0.5 m) upland stream with a substrate of loose gravel, cobble and small boulders. Catocin Creek was a clear, wide (about 30 m) and shallow (average depth about 1 m) piedmont stream with a similar substrate.

RESULTS

Spawning in Nocomis leptocephalus.—In Sinking Creek two males spawned over a single mound nest about 70 cm in diameter and 13 cm high at its center. Each male occupied a spawning pit approximately 4 cm wide, 6 cm long and 2.5 cm deep. The pits were within 10 cm of each other on the upstream slope, one slightly upstream of the other. The larger male (=resident) occupied the more upstream pit and had constructed the nest. Both males concurrently and independently spawned with females over their respective pits; however, the resident male participated in the majority of spawns. Numerous individuals of *Campostoma anomalum* (central stoneroller), *Luxilus cerasinus* (crescent shiner) and *Phoxinus oreas* (mountain redbelly dace) also schooled over the nest. We analyzed 58 successful and 5 unsuccessful spawns performed by the resident male and several female *Nocomis leptocephalus* and 10 spawns disrupted by a male *C. anomalum* over a 1 h period. Six categories of reproductive behaviors (Sabaj, 1992) were observed.

(1) Interim. The resident male engaged in mound-building, pit-digging, pit-posturing and anal-fin fanning between spawning sequences. During mound-building he used his jaws to collect pebbles from the surrounding substrate and deposit them on the nest. At various intervals he temporarily ceased mound-building to excavate a spawning pit. Pit-digging occurred as the male dipped his head and drove his snout into the pit floor while vigorously beating his tail. He either rooted with his snout or seized a pebble with his jaws, lifted his head and swam forward with tail quivering. As he deposited the pebble upstream he vibrated his extended anal fin in the pit for up to 2 s (anal-fin fanning, Fig. 1a). The male might fan the pit without prior digging; however, he first dipped his head into the pit before moving forward to coordinate placement of his anal fin.

Pit-posturing appeared to signal the male's readiness to begin a spawning sequence. Head facing upstream, the male hovered 2–4 cm above the pit floor. His dorsal and paired fins remained fully extended and his head was angled slightly downwards such that his body nearly paralleled the nest's upstream slope. Successful spawning sequences always began with the pit-postured male.

(2) Approach. About ten female *Nocomis leptocephalus* actively jockeyed for a position over the rear slope of the nest from which they might begin their approach. Although a

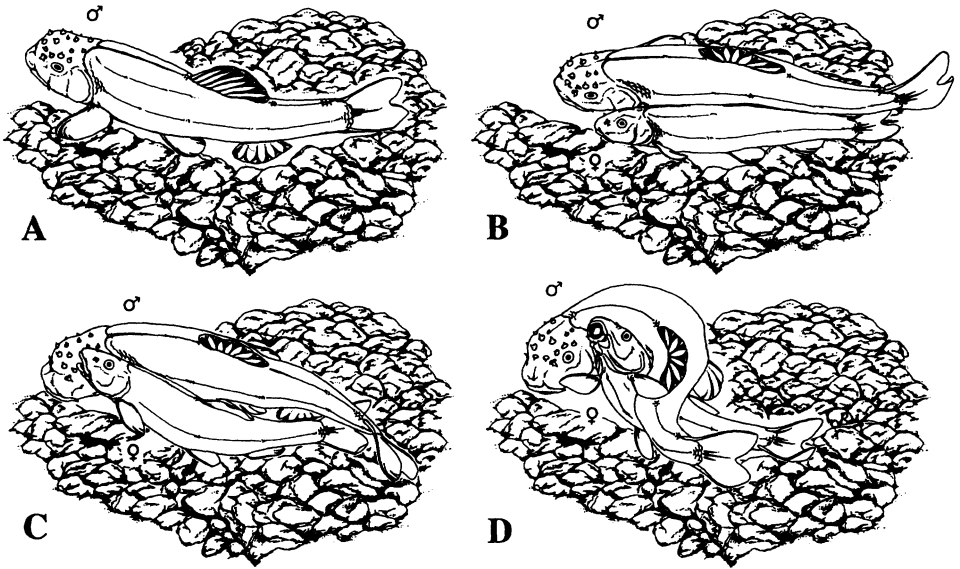


FIG. 1.—Spawning sequence in *Nocomis leptocephalus*. (A) Male anal-fin fanning (interim behavior). (B) Male tilts sideways after female enters pit (alignment). (C) Female swims forward along substrate, gapes and tosses head upwards over upstream rim of pit (run and retroflexure). Male turns head towards female and curves caudal peduncle over hers. (D) Male contracts body into semicircle and laterally compresses female as she twists anterior body away from male (clasp). Gametes presumably released at this moment

female might swim towards the nest from any direction, she always approached the postured male from downstream. She entered the pit either by darting directly beneath the male's tail or by swimming upstream to one side and sidling laterally into the pit.

(3) Alignment. The female, upon entering the pit, stationed herself beneath the male with her snout directly below or slightly ahead of his extended pectoral fins. Her body aligned parallel to the pit's long axis and remained pressed to its floor. She either remained posted beneath the male for a few seconds or immediately initiated the spawning run.

During alignment the male tilted the dorsal half of his body to one side as the female's snout moved beneath his pectoral region (Fig. 1b). The female's movement into the pit determined the direction of his sagittal tilt. If she sidled into the pit his dorsal surface tilted towards her entry; if she moved into the pit directly beneath his tail he might angle his body in either direction based on her final position.

(4) Run. A successful spawning run always was initiated by the female. With her body pressed to the substrate, she quickly swam about 3–5 cm upstream while quivering her tail and caudal peduncle. The male remained tilted as he promptly accompanied her short run with rapid tail beats. As the female moved forward over the upstream rim of the pit, she gaped and abruptly tossed her head vertically into the water column. She began her upward pitch with body upright and the ventral surface of her caudal peduncle still pressed to the substrate. Her snout traversed a 45° arc as the side of her head apposed either the male's operculum or his anterior flank just above the pectoral fin (Fig. 1c). As her snout approached vertical she rolled the anterior portion of her body away from the male placing her dorsum in contact with his anterior flank (Fig. 1d). This twisting motion continued

posteriorly along her body until the ventrolateral surface of her caudal peduncle became pressed to the substrate. At the height of her flexure, the anterior portion of the female (from snout to pelvic girdle) became nearly vertical and approximated a 45–90° angle with the substrate.

The female's motion at the end of her run (*i.e.*, frontal head pitch and sagittal twist) is termed "retroflexure" to distinguish it as a female-initiated behavior. Previous accounts described the female as having her head forced up and her body thrown into a vertical position by the male. Although the closely timed clasping maneuver of the male might exaggerate her vertical pitch and twist, the female initiated the retroflexed motion.

(5) Clasp. The male initiated his clasp as the female tossed her head vertically into the water column. He turned his head towards her and curved his posterior flank over her back (Fig. 1c). The male then drove his posterior flank into the female's side as she twisted sagittally. His anterior body (from snout to anal fin) contracted into a semicircle and resembled a horseshoe about the vertically arched female (Fig 1d). Facing away from the clasp, the female's abdominal region was compressed laterally as the male constricted his body. At the height of the clasp the male's vent pressed against the dorsolateral surface of the female's caudal peduncle and the female's vent remained over the upstream rim of the pit. Gametes presumably were shed at this moment. All male *Nocomis leptocephalus* ($n = 19$) observed in Georgia, North Carolina and Virginia performed spawning clasps.

(6) Dissociation. The spawning clasp was completed in about a second and the pair immediately separated. As the male's body relaxed parallel to the current, he drifted downstream to resume interim behavior (*e.g.*, pit-posturing). Once released, the female continued to rise vertically into the water column, then quickly rolled upright and either retreated downstream or drifted to a position behind the male from where she might initiate another spawning sequence.

Disruption of an interim male or spawning sequence resulted from aggressive interactions with conspecific males (*see* Maurakis *et al.*, 1997), nest associates and egg or fish predators. Disruption of a spawning sequence also resulted if a male or female responded inappropriately to their mate. For example, alignment failed if a female retreated or was displaced from the spawning pit prior to her run. Runs infrequently were disrupted when a female failed to retroflex and exited the pit over the upstream slope.

Three infrequent variations of the run and clasp were considered disruptive (*i.e.*, unsuccessful spawns). On two occasions the female vertically arched her head but failed to sagittally twist and appress her dorsum to the concave side of the constricted male. As a result of her partial retroflexure, the male's posterior flank impacted the female's dorsal surface during the clasp (Fig. 2a). On two occasions the female reversed her sagittal twist and appressed her breast and abdomen to the concave side of the male (Fig. 2b). The male did not appear to complete his clasp during these two reverse retroflexures. In the third variation, the lagging male failed to respond to a female's normal retroflexure and there was no spawning clasp (Fig. 2c).

The odd behavior of a small tuberculate male *Camptostoma anomalum* (stoneroller) in breeding color disrupted 10 spawning sequences between the resident male and several female *Nocomis leptocephalus* (chub). The stoneroller frequently held a position slightly upstream and next to the chub's spawning pit. On one occasion the stoneroller disrupted alignment. As the male chub tilted towards the female, the stoneroller darted towards her opposite side. The male chub promptly delivered a powerful downward head butt, expelling both fishes from the spawning pit. The stoneroller also accompanied nine separate spawning runs, disrupting six. As the female chub initiated her run with tail quivering, the stoneroller darted towards her and became appressed to her flank opposite the male chub.

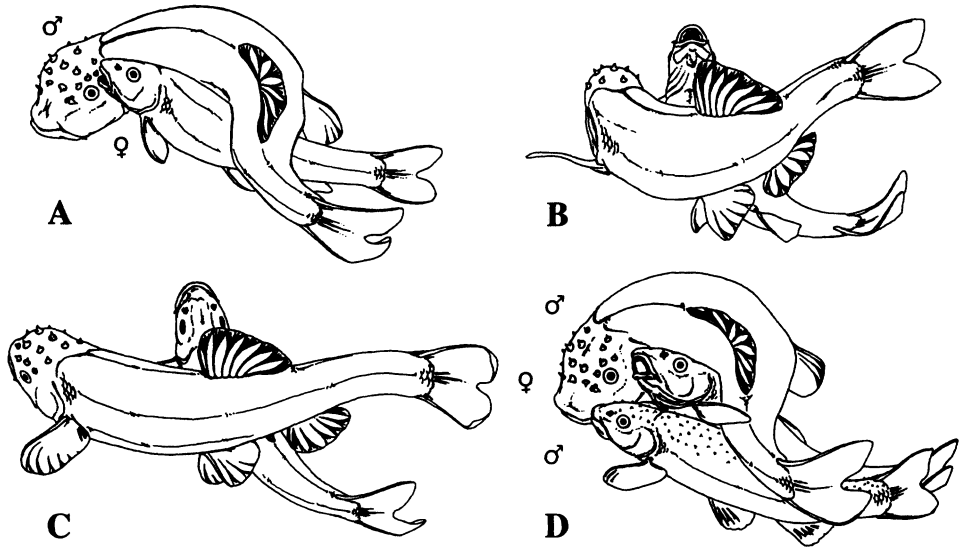


FIG. 2.—Disrupted spawns in *Nocomis leptocephalus*. (A) Female arches head upwards but fails to twist body away from male (incomplete retroflexure). Male's clasp does not laterally compress female. (B) Female twists body towards male (reverse retroflexure) and male fails to complete clasp. (C) Female performs retroflexure, but lagging male fails to apply clasp. (D) Male *Campostoma anomalum* accompanies spawning run and is clasped alongside female *Nocomis*

During six runs, the stoneroller physically obstructed both the female's retroflexure and the male chub's clasping motion. However, on three occasions, the male chub clasped simultaneously a retroflexed female chub and the stoneroller (Fig. 2d). The female did not appear compressed laterally during these clasps because the male chub's posterior flank impacted the stoneroller's dorsal surface. It is uncertain whether any of the fishes released gametes during these heterogeneric clasps.

Spawning in Nocomis micropogon.—In Catoctin Creek, the roughly circular mound nest of *Nocomis micropogon* was about 50 cm in diameter and 10 cm high at its center. A single spawning trough 20–25 cm long, about 4 cm deep and 10 cm wide extended the length of the mound's upstream slope parallel to the stream's current. The pebble nest was built, maintained and guarded by a single resident male. A smaller subordinate male often hovered over the rear slope and downstream of the nest, but did not contribute to its construction. We analyzed 23 successful spawns performed by the resident male and several females, and three spawns successfully stolen by the satellite male over a 2.6 h period. During this time, *Luxilus cornutus* (common shiner) and *Notropis rubellus* (rosyface minnow) schooled over the rear slope and immediately downstream of the nest.

(1) Interim. In *Nocomis micropogon*, interim behaviors (mound-building, trough-digging, -posturing, anal-fin fanning) of the resident male were similar to those described for *N. leptocephalus*, but slightly modified to accommodate the longer spawning trough. When anal-fin fanning, for example, the male dipped his caudal peduncle into the downstream end of the trough and swam forward with tail beating. Upon reaching the upstream end of the trough he paused and vibrated his extended anal fin at the base of the trough's upstream rim where spawning later occurred. Also like *N. leptocephalus*, a successful spawn-

ing sequence in *N. micropogon* began with the postured male. Facing upstream, the male hovered with dorsal and paired fins extended and his head positioned over the downstream end of the trough.

(2) Approach. As in *Nocomis leptocephalus*, a female *N. micropogon* began her approach from a position downstream of the postured male.

(3) Alignment. Similar to *Nocomis leptocephalus*, the male *N. micropogon* tilted sideways as a female aligned parallel in the downstream half of the trough.

(4) Run. As in *Nocomis leptocephalus*, a female *N. micropogon* initiated her spawning run as the male tilted. Following the contour of the substrate, she swam about 5–10 cm upstream with her dorsum appressed to the male's anterior flank and her side often crowded against a wall of the trough. The tilted male remained slightly ahead as he accompanied her run with 3–7 distinct tail beats. Once the female reached the upstream rim of the trough, she gaped, arched her head upwards and pressed her vent to the substrate in a manner similar to that of female *N. leptocephalus*.

Compared to *Nocomis leptocephalus*, the spawning run of *N. micropogon* appeared less vigorous as the pair swam forward with distinct tail beats (vs. tail quivering in *N. leptocephalus*). Also in *N. micropogon*, females' retroflexures were less acute and lacked the sagittal twist seen in female *N. leptocephalus*. A large female *N. micropogon* typically arched her anterior body about 30° from the substrate (Fig. 3a), whereas a small female arched 60–90°. In both species, the female's retroflexure was topographically fixed to the upstream rim of the pit or trough; however, spawning runs in *N. micropogon* were longer (ca. 5–10 cm) to accommodate its longer trough (20–25 cm).

(5) Clasp. As in *Nocomis leptocephalus*, the male *N. micropogon* initiated his clasp as the female arched vertically. The clasp began as he turned his head towards her and curved his posterior body over her back. His rear flank appeared to anchor the female posteriorly to the substrate as it slid over her tail and caudal peduncle (Fig. 3a). She pressed her vent to the upstream rim of the trough as the male's vent was positioned slightly to one side. Gametes presumably were extruded at this time.

In *Nocomis micropogon*, the curvature of the male's body at the height of the spawning clasp was less pronounced than in *N. leptocephalus*. Whereas in *N. leptocephalus* the male's anterior body (from snout to anal fin) contracted into a semicircle (strong clasp), in *N. micropogon* the male's body assumed a crescent shape (weak clasp).

(6) Dissociation. As in *Nocomis leptocephalus*, the pair immediately separated after the spawning clasp.

In *Nocomis micropogon*, the resident male was distracted by activities of conspecifics, nest associates and egg predators; however, subordinate males were more disruptive than in *N. leptocephalus*. A subordinate male stationed over the nest's rear slope usually did not provoke the resident male *N. micropogon*, but any movement of a subordinate towards the trough or onto the upstream slope elicited head butting and chasing.

Alignment was unsuccessful if a female withdrew or was displaced from the trough before initiating a run. Runs failed if a female overran the attending male. If the female's snout moved aside or ahead of the male's snout during their run, the male turned his head and displaced the female from the trough with a lateral head butt. Alternatively, the female might exit the trough upstream (with or without retroflexing) before the lagging male was able to clasp.

One tuberculate satellite male on four separate occasions accompanied the run of a spawning pair. The satellite male approached during alignment and tilted towards the female opposite the tilt of the resident male. With a male on either side, the female began her run towards the upstream rim of the trough. During three such runs, the satellite male

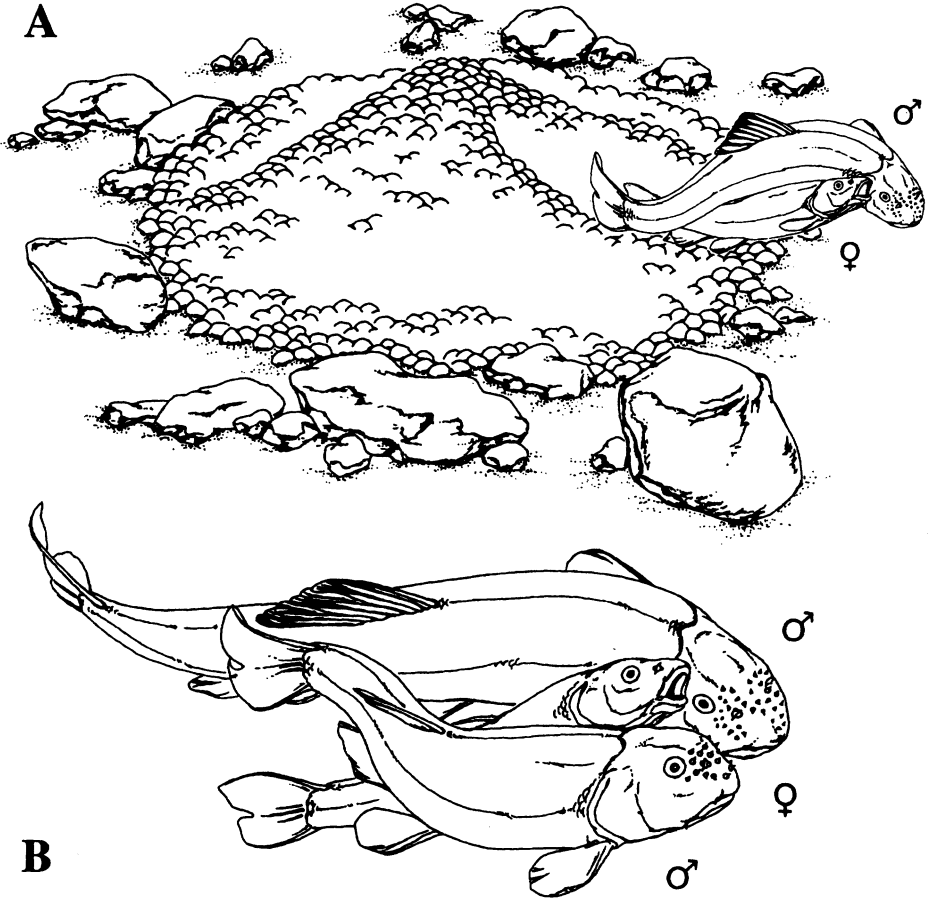


FIG. 3.—(A) Spawning clasp in *Nocomis micropogon* over upstream rim of spawning trough. (B) Satellite male (bottom) steals spawning clasp and presumably fertilization from larger resident male

was first to curve his posterior flank over the female's back as she arched her head upwards. He thereby displaced the resident male and effectively stole the clasp and presumably fertilization (Fig. 3b). During a fourth run, the female remained buried beneath the tilted males and was unable to vertically arch her head from the floor of the trough. Unable to clasp, the dominant male promptly dismissed the stalled female and satellite male with a single head butt.

Comparison of spawning in Nocomis spp.—The two species of *Nocomis* shared similar spawning behaviors (*e.g.*, interim, approach, alignment, dissociation) that were slightly modified to suit either a pit (*N. leptocephalus*) or longer trough (*N. micropogon*). Behaviors that consistently differed between species were the female's run and male's clasp. In *N. leptocephalus*, a female's run was abrupt (ca. 3–5 cm) and ended as she arched her head upwards and twisted sagittally (strong retroflexure). In *N. micropogon*, a female's run generally was longer (ca. 5–10 cm) and ended as she simply arched her head upwards (weak retroflex-

ure). Likewise, the spawning clasp of *N. leptocephalus* (semicircular) was more vigorous than that of *N. micropogon* (crescent shape).

Reproductive behaviors of subordinate males also differed between species. In *Nocomis leptocephalus*, 2–5 males spawned concurrently and independently of each other over a single nest in six of nine nests studied (average number of males per nest = 2.1; see Appendix). In contrast, the subordinate male observed in Catoctin Creek used the tactics of a satellite to effectively steal spawns from the resident nest builder on three occasions.

DISCUSSION

The reproductive behaviors described for *Nocomis leptocephalus* in Sinking Creek were largely similar to those observed for this species at separate sites in Georgia, North Carolina and Virginia. Likewise, behaviors of *N. micropogon* in Catoctin Creek were consistent with those observed at separate sites in Virginia and North Carolina. Various studies have described and commented on spawning behaviors in *Nocomis* and other species of nest-building and nest-associate minnows. Using the behavioral categories as a framework, we relate our observations to those of previous workers.

(1) Interim. Reighard (1943) suggested that anal-fin fanning in male *Nocomis micropogon* may clear debris from the recently excavated area or “may be an act of self-excitation preliminary to spawning.” Vives (1990) commented that in *N. biguttatus*, the male may add sperm to the spawning pit during similar behaviors. We propose that anal-fin fanning also may serve as a courtship display to attract females. In *N. leptocephalus*, the anterior anal-fin rays become bright white in breeding males compared to pale yellow or cream colored in nonbreeding males (Jenkins and Burkhead, 1994; pers. obs.). White anal-fin rays and anal-fin fanning may exaggerate the appearance of a male releasing milt and perhaps stimulate in females a sensory bias for such males. Anal-fin fanning also may facilitate the release of chemical cues (*e.g.*, milt, pheromones) into the spawning pit.

Male posturing behavior also occurs in *Campostoma anomalum*, another sexually dimorphic species in which the male excavates a pit for spawning (Burkhead, 1980; pers. obs.). Burkhead (1980) likewise hypothesized that the male’s pit posture might help signal a state of spawning readiness. *Campostoma* is considered to be closely related to *Nocomis* (Simons and Mayden, 1999), and male posturing over an excavation (*i.e.*, pit or trough) is presumably homologous in the two genera.

(2) Approach. Maurakis and Roston (1998) similarly noted that a female *Nocomis asper* approaches the postured male from downstream. In *N. leptocephalus* and *N. micropogon*, we did not observe females successfully approach a postured male from upstream, nor did we see the tail-first nest-entry behavior described for female creek chubs, *Semotilus atromaculatus* (Ross, 1976; Sabaj, 1992).

(3) Alignment. Male tilting behavior was first described for *Nocomis micropogon* (Reighard, 1943) and is newly described for *N. leptocephalus*. The tilting behavior is similar to that of males in the shiner genus *Luxilus* (Raney, 1940b; Miller, 1964; pers. obs.). However, *Nocomis* and *Luxilus* are not closely related (Coburn and Cavender, 1992) and this behavior is likely convergent. Both genera employ a spawning clasp and tilting behavior may afford the male the best position from which to apply his clasp. Miller (1964) also speculated that in *Luxilus*, the tilt display may serve as a species recognition cue for approaching females.

(4) Run. Female retroflexure also occurs in redspot chub, *Nocomis asper* (Maurakis and Roston, 1998) and was first discovered in two species of *Semotilus*, the creek chub, *S. atromaculatus* (Sabaj, 1992) and Dixie chub, *S. thoreauianus* (Maurakis *et al.*, 1993). *Semotilus* also exhibits male nest-building behavior and spawning clasps (Sabaj, 1992; Maurakis *et al.*,

1993). However, all of these behaviors are likely convergent because *Semotilus* and *Nocomis* are distantly related among North American minnows (Simons and Mayden, 1997, 1999).

In the *Nocomis* that we observed the spawning sequence was disrupted if an aligned female withdrew from the pit or trough without initiating a run. A female also might exit the pit or trough upstream (with or without retroflexing) before the lagging male was able to coordinate his clasp. Similar behaviors were reported for female *N. micropogon* (Reighard, 1943), *N. biguttatus* (Vives, 1990) and *N. asper* (Maurakis and Roston, 1998). Mock alignments and runs may serve as prespawning courtship behaviors and, as Vives (1990) noted, eventually stimulate the initiation of a successful spawning sequence.

(5) Clasp. We observed male *Nocomis leptocephalus* ($n = 19$) perform spawning clasps in Georgia, North Carolina and Virginia. However, based on her observations in South Carolina, Wallin (1989) described the spawning act: "The male chub would press laterally against the female for a brief moment of contact when eggs were released . . ." Thus, it is uncertain whether the clasp is characteristic of all populations.

Our observations of weak clasps by male *Nocomis micropogon* ($n = 5$) in North Carolina and Virginia are largely consistent with those reported by Reighard (1943) for males in Michigan. Reighard (1943) used the term "embrace" and similarly resolved the spawning act of *N. micropogon* into two separate behaviors interpreted accordingly: "She then rises from the bottom [retroflexure], and as she does so the male throws his body to one side and catches her between the body on one side and the upper surface of the spread tuberculate pectoral fin and lateral pearled surface of the head on the other side [weak clasp]." However, as in *N. leptocephalus*, the consistency of clasping behavior throughout the range of *N. micropogon* is uncertain. For example, Jenkins and Burkhead (1994) described the spawning act in *N. micropogon* as follows: "The male holds his body nearly straight and parallel to the female; he may hold the female with his posterior body over her, and with a tuberculate pectoral fin under her."

(6) Dissociation. As in *Nocomis leptocephalus* and *N. micropogon*, a spawning pair quickly separate after the clasp in *N. asper* (Maurakis and Roston, 1998) and *N. biguttatus* (Vives, 1990). This allows the male and female to promptly regain positions (*i.e.*, pit posture and downstream of male, respectively) from which they can repeat the spawning sequence in rapid succession. Vives (1990), for example, observed one pair of *N. biguttatus* perform 106 consecutive spawning sequences without interruption.

Communal nesting was previously reported for *Nocomis leptocephalus* in North Carolina (Johnston, 1991) and South Carolina (Wallin, 1989), and Johnston (1991) suggested that this behavior may be typical of the species. Based in part on the fish observed in this study, Maurakis *et al.* (1997) calculated that a male *N. leptocephalus* defended a relatively small territory around his spawning pit (*i.e.*, average area was 22% of total available substrate on upstream slope of nest). As a result, up to five subordinate males, termed "squatters," were able to establish territories over an occupied nest.

In *Nocomis micropogon*, subordinate males may occur over or near a nest; however, unlike *N. leptocephalus*, they contribute very little to the nest's construction and maintenance (Reighard, 1943; pers. obs.). Before our observations they were not known to spawn. R. E. Jenkins and E. A. Lachner (*in* Jenkins and Burkhead, 1994) speculated whether such males employ satellite or sneaker tactics as described for sunfishes (Gross 1982; 1984). In Catoclin Creek a subordinate male used the tactics of a satellite to effectively steal spawns from the resident nest-builder on three occasions. We did not observe the subordinate male align with and clasp a female independently of the resident male; although he occasionally postured over the trough for brief periods while the resident male temporarily left the nest to gather stones. Maurakis *et al.* (1997) calculated that in *N. micropogon* the resident male

defended a larger proportion of the upstream slope of the nest (74% compared to 22% in *N. leptocephalus*) and, as a result, subordinates were unable to establish their own spawning territories on the nest.

R. E. Jenkins (pers. obs. in Jenkins and Burkhead, 1994) and E. A. Lachner (pers. comm. in Jenkins and Burkhead, 1994) noted that subordinate males of *Nocomis micropogon* often resemble conspecific females in that they have a dark lateral stripe, lack nuptial color and either lack or have reduced tubercles. They questioned whether some of the unusual "female" behaviors (e.g., trough-digging) reported by Reighard (1943) were in fact subordinate males. Likewise, the subordinate male in this study resembled conspecific females. Female mimicry is thought to directly enhance the competitive ability of subordinate males by concealing their presence and potential threat to a resource-holding male (e.g., resident nest-builder) (Saetre and Slagsvold, 1996).

Heterogeneric spawning clasps.—Intergeneric breeding behaviors involving nest-building and nest-associate species have been reported for a few other minnows. Miller (1964) observed male *Luxilus cornutus* (nest associate) perform tilt displays toward female *Semotilus atromaculatus* (nest builder). Raney (1940b) observed several female *L. cornutus* approach and align beside a male *Exoglossum maxillingua* posturing over his nest. Raney (1940c) also reported twelve heterogeneric clasps between male hybrids, *L. cornutus* x *Notropis rubellus* (nest associate) and female *L. cornutus*, and one clasp between a male *L. cornutus* and a female hybrid.

Three heterogeneric clasps of a male and female *Nocomis leptocephalus* and a small male *Campostoma anomalum* offer some insight on the reproductive behaviors of *C. anomalum* and hybridization between the two species. *Campostoma anomalum* typically spawns over a pit excavated by the male in riffles where a number of males may guard and maintain spawning pits in close proximity (Miller, 1962, 1964; Burkhead, 1980; Jenkins and Burkhead, 1994). A female enters the pit and is immediately converged upon by the resident male and all nearby males (Miller, 1962; Burkhead, 1980). Males "twist and writhe" to get close to the female and presumably release their gametes (Miller, 1962). Spawning clasps between a male and female *C. anomalum* have not been reported.

In *Campostoma anomalum* the alignment of male and female in the spawning pit is evidently a powerful stimulus for nearby males to converge and participate in what Jenkins and Burkhead (1994) described as a "mating frenzy." Under some circumstances this stimulus may be sufficiently strong to override species recognition cues presumably serving as premating isolating mechanisms. The behavior of the small *C. anomalum* observed in this study was especially peculiar because the chub nest was occupied by an additional 10–12 larger male *C. anomalum* that wholly ignored the alignments of spawning *Nocomis leptocephalus*. *Campostoma anomalum* commonly schools over nests of *Nocomis*; however, it is often difficult to determine whether such congregations are composed of actively spawning males or post-nuptial males foraging for buried eggs (Miller, 1964; Jenkins and Burkhead, 1994). The school of large *C. anomalum* over the chub nest observed in this study did not appear to be spawning and were probably post-nuptial. Presumably, the small male *C. anomalum* reached reproductive condition late in the season and, in the absence of breeding conspecifics, responded to an interspecific, yet similar, cue afforded by the alignment of *Nocomis* in the spawning pit.

It is unconfirmed whether gametes were shed by the female chub and male stoneroller observed in this study. Hybrids of *Campostoma anomalum* and *Nocomis leptocephalus* are sometimes common in nature (e.g., Grady and Cashner, 1988). Hybridization between nest builder and nest associate is attributed to either chance cross-fertilization or mismating

(Raney, 1947; Jenkins and Burkhead, 1994). Our observations of heterogeneric clasps between *N. leptocephalus* and *C. anomalum* offer some evidence for the latter.

Behavioral categories.—In their classification of reproductive strategies in North American minnows, Johnston and Page (1992) highlighted the need for “detailed studies outlining specific traits of reproductive behavior.” Johnston and Page hypothesized the evolution of reproductive strategies by mapping them onto a phylogenetic tree based on morphology (Coburn and Cavender, 1992). They realized the potential usefulness of behavioral traits as character states in a phylogenetic analysis, but were unable to independently test the morphological phylogeny because of a lack of data for many species.

The categories (interim, approach, alignment, run, clasp, dissociation) proposed in Sabaj (1992) provided a useful framework for outlining and comparing spawning behaviors in *Nocomis* and were similarly applied to spawning in the minnows *Exoglossum laurae*, *Rhinichthys atratulus* and *Semotilus atromaculatus* (Sabaj, 1992), *Luxilus albeolus* and *L. cerasinus* (Maurakis and Woolcott, 1993), *Notropis alborus* (Newman and Maurakis, 1998) and *Nocomis asper* (Maurakis and Roston, 1998). The categories are particularly useful for lithophilous spawners (sensu Balon, 1975) and can help identify specific behavioral traits (e.g., female run with retroflexure) for phylogenetic analyses. However, we caution that similar behaviors may occur in phylogenetically unrelated minnows (e.g., female retroflexure and male nest building in *Nocomis* and *Semotilus*). Specific features of such behaviors (e.g., contortion of female’s body, nest construction and composition) can help evaluate homology and perhaps detect such convergences.

In both species of *Nocomis* the contour of the pebble nest was an important topographical cue for the sequence of male-female interactions. For example, interim males postured over a specific area of the nest. Likewise, a female’s run conformed precisely to the concave floor of the pit (*N. leptocephalus*) or trough (*N. micropogon*) and the location of her retroflexure was fixed to the upstream rim of the excavation. Therefore, both the architecture of the nest and sequence of male-female interactions coordinated the simultaneous release of eggs and milt over a discrete area specifically designed for gamete deposition and fertilization. Observations of nocturnal spawning in both species (Maurakis and Woolcott, 1996) further suggest that coordination of the spawning act is facilitated, at least in part, by tactile cues between the male, female and spawning substrate.

Acknowledgments.—We thank Lawrence M. Page, Brooks M. Burr, Jason H. Knouft and two anonymous reviewers for comments and suggestions on improving the manuscript. This study was conducted in partial fulfillment of requirements for a Master’s Degree and supported by the following grants and awards to MHS: Robert F. Smart Summer Research Award, John Neasmith Dickinson Memorial Research Award and a Graduate Research Program Grant from the University of Richmond. MHS and EGM dedicate this paper to Dr. William S. Woolcott (1922–1998), our great friend and mentor who was as fascinating as the chubs he studied.

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SUBMITTED 1 MARCH 1999

ACCEPTED 10 SEPTEMBER 1999

APPENDIX

List of chubs observed and videotaped (grouped by species, drainage, state). *Nocomis leptocephalus*.—**Altamaha Drainage**: Georgia: Hall Co., North Oconee River, 5.6 km WSW Lula at U.S. 23; E. G. Maurakis and J. J. Loos; EGM-GA-126; 1320–1700 h EDT, 25 May 1984; one male spawning over nest (20 C; direct observation); Stephens Co., North Fork Broad River, 2.7 km SW Toccoa at Pine View Rd.; E. G. Maurakis and J. Kahnke; EGM-GA-198; 1530–1830 h EDT, 13 April 1986; one male spawning over nest (18 C; 60 min recording time). **Cape Fear Drainage**: North Carolina: Chatham Co., Roberson Creek, Pittsboro at U.S. 15; E. G. Maurakis and G. P. Maurakis; EGM-NC-142; 1200–1300 h EDT, 26 May 1985; three males spawning over communal nest (21.1 C; direct observation). **New-Kanawha Drainage**: Virginia: Craig Co., Sinking Creek, 5 km SW Sinking Creek at SR 42; E. G. Maurakis, W. S. Woolcott and M. H. Sabaj; EGM-VA-225; 1330–1730 h EDT, 26 May 1989; two males spawning over communal nest (15.5 C, 64 min recording time). **Roanoke Drainage**: North Carolina: Rockingham Co., Cascade Creek, 4.2 km ENE Draper at SR 770, W. S. Woolcott and E. G. Maurakis; WSW-NC-378; 1530–1630 h EDT, 7 May 1988; two males spawning over communal nest (16 C; 60 min recording time). Virginia: City of Danville, Pumpkin Creek, SR 86; E. G. Maurakis and J. Kahnke; EGM-VA-203; 1115–1445 h EDT, 11 May 1986; five males spawning over communal nest (16 C; 140 min recording time); City of Danville, Pumpkin Creek, London Bridge Dr. 0.8 km E SR 86; E. G. Maurakis; EGM-VA-322; 2015 h EDT, 8 May to 0515 h EDT, 9 May 1993; one male spawning over nest (18.3 C; 60 min recording time). **Savannah Drainage**: North Carolina: Jackson Co., Horsepasture River, 3.4 km NE Cashiers at U.S. 64; E. G. Maurakis, W. S. Woolcott and J. T. Goodin; EGM-NC-210; 1230–1630 h EDT, 6 June 1988; two males spawning over communal nest (15 C; 180 min recording time). **Tennessee Drainage**: North Carolina: Macon Co., Satulah Branch, Highlands at SR 1603 bridge; E. G. Maurakis, W. S. Woolcott and J. T. Goodin; EGM-NC-211; 1100–1600 h EDT, 7 June 1988; two males spawning over communal nest (21 C; 240 min recording time).

Nocomis micropogon.—**Potomac Drainage**: Virginia: Loudon Co., Catoctin Creek, Taylorstown at SR 663; E. G. Maurakis; EGM-VA-254; 1300–1830 h EDT, 25 May 1990; one nest-building male and one subordinate male spawning over nest (15.0–17.0 C; 158 min recording time); EGM-VA-301; 2104–2337 h EDT, 22 May 1992; two nest-building males spawning over their individual nests (19.2 C, 80 min recording time); EGM-VA-302; 2100 h EDT, 23 May to 0050 h EDT, 24 May 1992; *ibid.* (18.9 C; 120

min recording time). **Tennessee Drainage:** North Carolina: Macon Co., Tennessee Creek, 1 km NE Otto; E. G. Maurakis, W. S. Woolcott and J. T. Goodin; EGM-NC-214; 1520–1645 h EDT, 8 June 1988; one male spawning over nest (17 C; 85 min recording time).

SUBMITTED 1 MARCH 1999

ACCEPTED 10 SEPTEMBER 1999