

Breeding Behaviors in *Nocomis platyrhynchus* and *Nocomis raneyi* (Actinopterygii: Cyprinidae)

Eugene G. Maurakis, Science Museum of Virginia, 2500 West
Broad Street, Richmond, VA 23220 and Biology Department,
University of Richmond, Richmond, VA 23173

ABSTRACT

Breeding behaviors in *Nocomis platyrhynchus* and *Nocomis raneyi*, described from direct observations and review of videotapes made in Little River (New River drainage) in Virginia, and Johns Creek and Maury River (James River drainage) in Virginia in 1998, respectively, are compared to those in *Nocomis micropogon*. The three-stage sequential process of nest construction [i.e., excavating a concavity with a central channel parallel to water current; constructing a platform (with central upstream channel) in the concavity with stones from the lateral margins of the concavity; and building a mound (with a spawning trough on the upstream slope of the nest) over the platform with pebbles from the streambed] in the two species is like that reported in *Nocomis micropogon*. Spawning behaviors in the two species are comparable to those in *N. micropogon* where a single male of each species spawns with individual females in the trough on the upstream slope of his nest where water currents are reduced. Nest associate species (those that congregate and may spawn over a nest but do not contribute to its construction) of *N. platyrhynchus* were *Campostoma anomalum*, *Luxilus chrysocephalus*, *Lythrurus ardens*, *Notropis rubellus*, and *Phoxinus oreas*; those of *N. raneyi* were *C. anomalum*, *Luxilus cornutus*, *L. ardens*, *N. rubellus*, and *P. oreas*.

INTRODUCTION

Nocomis platyrhynchus (New River drainage) and *Nocomis raneyi* (James, Roanoke-Chowan, Neuse and Tar River drainages), members of the *Nocomis micropogon* species-group, are two of seven species of *Nocomis* in which males of the species use their jaws to construct gravel nests for spawning in spring (Lachner and Jenkins, 1971). Spawning behavior has been described for populations of a close relative, *Nocomis micropogon* (Reighard, 1943; Maurakis et al., 1991; Sabaj, 1992) but not for *N. platyrhynchus* and *N. raneyi*. This paper describes nest building and spawning behaviors in *N. platyrhynchus* and *N. raneyi* and compares them with those in *N. micropogon*.

MATERIALS AND METHODS

Observations and videorecordings of fishes and collection of nest characteristics and materials (number of nests in parentheses) of *N. platyrhynchus* were made in Little River (New River drainage), Montgomery-Floyd Co. line at St. Rt. 8 bridge, 16 May 1998, 1050-1220 EDT, water temperature=19 C (EGM-VA-416)(3); Little River (New River drainage), Montgomery Co. at Co. Rt. 693 and 613 junction, about 8 km W of Riner, 16 May 1998, 1245-1545 EDT, water temperature=20 C (EGM-VA-417)(2); and Little River (New River drainage), Montgomery Co. at Co. Rt. 613, about 1 km E of Snowville, 1610-1845 EDT, water temperature=19 C, 16 May 1998 (EGM-VA-

418)(5). Nests of *N. raneyi* were studied in Johns Creek (James River drainage), Craig Co. at Co. Rt. 632 below dam at stone house about 1.6 km N of Maggie, 17 May 1998, 0800-1115 EDT, water temperature=16 C (EGM-VA-419)(1); John's Creek (James River drainage), Craig Co. at Co. Rt. 632 at Maggie, 17 May 1998, 1240-1400 EDT and 1655-1800 EDT, water temperatures=19 and 19.5 C (EGM-VA-420 and EGM-VA-422)(2 and 1), respectively; Johns Creek (James River drainage), Craig Co. at Co. Rt. 632 bridge about 5.6 km N of Maggie, 17 May 1998, 1440-1645 EDT, water temperature=19.5 C (EGM-VA-421)(1); John's Creek (James River drainage), Craig Co. at Co. Rt. 632 at Maggie, 23 May 1998, 0725-0840 EDT, water temperature=17.5 C (EGM-VA-423)(2); and Maury River (James River drainage), Rockbridge Co. at US Rt. 60, 23 May 1998, 1100-1240 EDT and 1250-1355 EDT, water temperatures=18 and 19 C (EGM-VA-424 and EGM-VA-425)(7 and 2), respectively. Nest of *N. micropogon* were studied in Catoctin Creek (Potomac River drainage), Loudon Co. at Co. Rt. 663, 0.1 km from jct. with Co. Rt. 665 at Taylorsville, 25 May 1990 and 27 May 1998, 1300-1830 EDT and 1025-1430 EDT, water temperature=19 C and 18.5 C (EGM-VA-254 and EGM-VA-426) (2 and 2), respectively); Thumb Run (Rappahannock River drainage), Fauquier Co. at Co. Rt. 688 bridge, 1630-1800 EDT, water temperature=17.5 C (EGM-VA-427)(5).

Videorecordings were made with a Sony CCD videocamera according to methods in Maurakis and Woolcott (1995). Activities recorded on film for each species were reviewed at normal speed, in slow motion, and frame by frame to identify specific behaviors of female and male *N. platyrhynchus* and *N. raneyi* following methods in Maurakis and Woolcott (1995). Six chronological categories that reflected the sequence of male-female interactions characteristic of a successful spawn, following those in Sabaj (1992) and Maurakis and Woolcott (1993), were used to resolve reproductive activities of male and female *N. platyrhynchus* and *N. raneyi*: *interim* (behavior of male between spawns), *approach* (behavior of female directed towards interim male), *alignment* (behavior affecting orientation of a spawning pair over substrate), *run* (initiated by a female, synchronized movement of aligned pair over substrate), *clasp* (spawning act, i.e., momentary flexure of male's body about that of female at end of her *run*), and *dissociation* (behaviors of male and female affecting their separation immediately following the clasp). Behaviors other than those associated with the spawning sequence were considered disruptive of a successful spawn.

A satellite male is one that deceptively mimics females and pairs simultaneously with true females and parental males (Gross, 1984). Nest associates are species that congregate and may spawn over a nest but do not contribute its construction.

Velocity of water currents (taken 1 cm over nests and substrates), measured with a Marsh-McBirney current meter, was recorded 0.5 m upstream of nests, 0.5 m downstream of nests, and over crests of nests; and in the spawning trough on the upstream slope of nests of each species. Nest length, height, and width, and spawning trough length, width, and depth were measured at nests of each species.

Pebble samples were collected from upstream, middle, and downstream parts of nests of each species with a 1 liter plastic beaker. Substrate samples, collected with the same device, were taken at random as far as 10 m from nests. Nest and substrate samples, stored in tagged plastic bags, were returned to the laboratory. Each sample was air-dried and sifted through five custom-built wire sieves. Mesh sizes, restricted to commercially available prefabricated screen sizes, were 23.0 mm, 11.3 mm, 6.0 mm,

2.5 mm, and 0.8 mm. Material that sifted through the smallest size mesh was collected in a pan. Weight of material in each sieve or pan was used to calculate percentage of material per mesh size. Hereafter, all references to percentage of mesh size classes are based on weights.

An electivity index (Ivlev, 1961) was calculated for each pebble size class per nest of each species. The equation $E = \frac{(n - p)}{(n + p)}$ (where E = pebble size selection, n = percentage of a particular pebble size in the nest, and p = the percentage of a particular pebble size in the substrate of the stream) was used to determine if selection of pebble size from the substrate was random. Percentages and electivity values were transformed to arcsin equivalents.

ANOVA and Duncan's Multiple range test (SAS, 1985) were used to compare average values of stream depth, substrate composition, nest composition, current velocity, and electivity of pebble sizes in each species.

RESULTS

Nest building and spawning behaviors were observed at water temperatures ranging from 19-19.5 C in *N. platyrhynchus*, and from 18-19.5 C in *N. raneyi* in May. Average water depth (50.6-51.7 cm) at nests of *N. platyrhynchus* and *N. raneyi* were significantly greater than that (21.2 cm) at nests of *N. micropogon* (Table 1).

Nest Construction: As nest construction was similar between the two species, that in *N. platyrhynchus* is presented with annotations of variations observed in *N. raneyi*. A nest was constructed and guarded by a single male. Nest construction began when a male used his jaws to excavate a concavity. Excavated stones were placed on the lateral margins of the concavity parallel to the water current. A nest-building male frequently aligned himself (head upstream) in the concavity. Then the male collected stones from the lateral margins of the concavity and covered the concavity. This resulted in a relatively flat horse-shoe shaped platform of stones with a central flow-through trough. Upstream margin of the platform had fewer pebbles than posterior and lateral margins. A male periodically fanned his trough with his anal fin. At the end of platform formation, the male collected pebbles as far as 10 meters from the nest and placed them on the platform to form a conical mound nest with a well-defined trough on its upstream slope. Male *N. raneyi* gathered stones as far as 20 m from their nests. One *N. raneyi* nest at end of platform stage was constructed simultaneously in the downstream end of the pit of a pit/mound nest being built by a male *Semotilus corporalis*. The male *S. corporalis* (~85 % total length of the nest-building male *N. raneyi*) excavated stones from his pit and deposited them on his mound where it interfaced the upstream portion of the pit. After 15 minutes, the male *N. raneyi* ended platform construction. He then began mound building by collecting and transporting stones from a nearby (2 m) inactive nest of *S. corporalis*, and from the streambed as far as about 5 m from the nest. During this time, the male *S. corporalis* continued nest-building and periodically engaged in chases and parallel swims with satellite conspecific males. Neither the nest-building male *N. raneyi* nor *S. corporalis*, however, was aggressive towards the other. Even when side by side with bodies nearly touching, the male *N. raneyi* and *S. corporalis* continued their nest-building activities as if the other was not present.

TABLE 1. Comparison of average stream depth, (cm), and nest characteristics (cm) of nests of *Nocomis micropogon*, *Nocomis platyrhynchus* and *Nocomis raneyi*. Underscored means do not differ significantly; df=12).

Parameter	Species		
Stream Depth (cm)	<i>N. micropogon</i>	<i>N. raneyi</i>	<i>N. platyrhynchus</i>
\bar{x}	21.2	<u>50.6</u>	<u>51.7</u>
F=5.31; p=0.01			
Nest Width	<i>N. platyrhynchus</i>	<i>N. micropogon</i>	<i>N. raneyi</i>
\bar{x}	<u>53.0</u>	66.0	<u>70.5</u>
F=1.22; p=0.31			
Nest Length	<i>N. platyrhynchus</i>	<i>N. raneyi</i>	<i>N. micropogon</i>
\bar{x}	<u>67.2</u>	70.6	<u>75.0</u>
F=0.37; p=0.69			
Nest Height	<i>N. platyrhynchus</i>	<i>N. micropogon</i>	<i>N. raneyi</i>
\bar{x}	<u>17.1</u>	20.4	<u>25.7</u>
F=2.5; p=0.10			
Trough Length	<i>N. micropogon</i>	<i>N. platyrhynchus</i>	<i>N. raneyi</i>
\bar{x}	<u>27.0</u>	<u>27.8</u>	<u>29.9</u>
F=0.28; p=0.76			
Trough Width	<i>N. platyrhynchus</i>	<i>N. micropogon</i>	<i>N. raneyi</i>
\bar{x}	<u>12.5</u>	12.8	<u>13.8</u>
F=0.22; p=0.81			
Trough depth	<i>N. platyrhynchus</i>	<i>N. micropogon</i>	<i>N. raneyi</i>
\bar{x}	<u>5.5</u>	5.8	<u>6.1</u>
F=0.12; p=0.88			

There were no significant differences in average values of nest width (\bar{x} range=53-70.5 cm), length (\bar{x} range=67.2-75 cm), and height (\bar{x} range=17.1-25.7 cm); and spawning trough length (\bar{x} range=27-29.9 cm), width (\bar{x} range=12.5-13.8 cm) and depth (\bar{x} range=5.5-6.1 cm) among the three species (Table 1). Stream substrates where nests were constructed by each species were dominated by the 23 mm stone size class (Table 2).

In nests, percentages (\bar{x} range=64.5-68.8 %) of the 11.3 mm size class pebbles were significantly higher those for other size classes in nests of all species (Table 3). In *N. micropogon* and *N. platyrhynchus*, average electivity values (\bar{x} range=0.57-0.60) for the 11.3 mm size class of stones were significantly greater than those (\bar{x} range=-0.99-0.19) for other size classes (Table 4). In *N. raneyi*, electivity values for the 11.3 (0.68) and 6.0 stone size classes (0.42) were significantly greater than those (\bar{x} range=-0.94 - -0.63) for other size classes (Table 4). Average water currents (\bar{x} range=0.01-0.06 cm/sec) in spawning troughs on the upstream slope of nests of all three species were significantly lower than those 0.5 m upstream of the nest (\bar{x} range=0.27-0.32 cm/sec),

TABLE 2. Average percentage of substrate material by size class in streams of *Nocomis micropogon*, *Nocomis platyrhynchus*, and *Nocomis raneyi*. Underscored means do not differ significantly.

Species	% substrate size class (mm)					
<i>N. micropogon</i>	0.8	2.5	6.0	<0.8	11.3	23.0
\bar{x}	1.06	2.30	4.42	7.40	17.06	67.76
F=14.82 ; p=0.0001; df=5						
<i>N. platyrhynchus</i>	0.8	<0.8	2.5	6.0	11.3	23.0
\bar{x}	0.17	0.90	1.33	3.46	15.63	76.27
F=16.41; p=0.0001; df=3						
<i>N. raneyi</i>	0.8		2.5	6.0	11.3	23.0
\bar{x}	1.77	4.90	6.30	13.97	18.37	54.67
F=4.6; p=0.0141; df=3						

TABLE 3. Average percentage of material by size class in nests of *Nocomis micropogon*, *Nocomis platyrhynchus*, and *Nocomis raneyi*. Underscored means do not differ significantly.

Species	% nest pebble size class (mm)					
<i>N. micropogon</i>	0.8	<0.8	2.5	6.0	23.0	11.3
\bar{x}	0.03	0.05	0.27	7.8	23.0	68.8
F=92.8; p=0.0001; df=5						
<i>N. platyrhynchus</i>	<0.8	0.8	2.5	6.0	23.0	11.3
\bar{x}	0.12	0.2	0.9	11.5	22.8	64.5
F=44.28; p=0.0001; df=3						
<i>N. raneyi</i>	<0.8	0.8	2.5	6.0	23.0	11.3
\bar{x}	0.07	0.1	0.78	15.78	18.75	64.6
F=28.8; p=0.0001; df=3						

0.5 m downstream of the nest (\bar{x} range=0.26-0.30 cm/sec), and at the crest of the nest (\bar{x} range=0.28-0.33 cm/sec)(Table 5).

Nest associate species of *N. platyrhynchus* were *Campostoma anomalum*, *Luxilus chrysocephalus*, *Notropis rubellus*, and *Phoxinus oreas*; those of *N. raneyi* were *Campostoma anomalum*, *Luxilus cornutus*, *Lythrurus ardens*, *Notropis rubellus*, and *Phoxinus oreas*. On two occasions, a male *L. chrysocephalus* periodically moved into and out of the trough during platform construction by a male *N. platyrhynchus*. Nest associates did not congregate over the nest until after a nest-building male *N. platyrhynchus* began to more frequently fan the trough during latter stages of mound construction. Similarly, *L. cornutus* and other nest associates did not congregate over nests of *N. raneyi* until a nest-building male fanned the spawning trough with his anal fin.

TABLE 4. Average electivity value per size class of pebbles in nests of *Nocomis micropogon*, *Nocomis platyrhynchus*, and *Nocomis raneyi*. Underscored means do not differ significantly.

Species	Electivity per pebble size class (mm)					
<i>N. micropogon</i>	<0.8	0.8	2.5	23.0	6.0	11.3
\bar{x}	<u>-0.99</u>	<u>-0.94</u>	<u>-0.81</u>	<u>-0.52</u>	<u>0.19</u>	<u>0.60</u>
F=59.24; p=0.0001; df=5						
<i>N. platyrhynchus</i>	<0.8	0.8	23.0	2.5	6.0	11.3
\bar{x}	<u>-0.64</u>	<u>-0.56</u>	<u>-0.53</u>	<u>-0.37</u>	<u>-0.06</u>	<u>0.57</u>
F=5.26; p=0.038; df=3						
<i>N. raneyi</i>	<0.8	0.8	2.5	23.0	6.0	11.3
\bar{x}	<u>-0.94</u>	<u>-0.86</u>	<u>-0.80</u>	<u>-0.63</u>	<u>0.42</u>	<u>0.68</u>
F=56.54; p=0.0001; df=3						

TABLE 5. Average water current (cm/sec) 0.5 m upstream and downstream of nests, nest crest, and spawning trough on upstream slope of pebble nests of *Nocomis micropogon*, *Nocomis platyrhynchus*, and *Nocomis raneyi*. Underscored means do not differ significantly.

Species	Water current (cm/sec)			
<i>N. micropogon</i>	trough	downstream	crest	upstream
\bar{x}	0.06	<u>0.26</u>	<u>0.28</u>	<u>0.32</u>
F=4.76; p=0.0084; df=5				
<i>N. platyrhynchus</i>	trough	downstream	upstream	crest
\bar{x}	0.01	<u>0.30</u>	<u>0.30</u>	<u>0.33</u>
F=14.22; p=0.0001; df=3				
<i>N. raneyi</i>	trough	downstream	upstream	crest
\bar{x}	0.02	<u>0.26</u>	<u>0.27</u>	<u>0.28</u>
F=27.93; p=0.0001; df=3				

Six aggressive behaviors (non-contact head displacement, non-contact body displacement, chase, circle swim, head/body butt and lateral swim/head bobbing) were observed between conspecific nest-building and intruder males of each species with one exception. Lateral swim/head bobbing was not observed in *N. platyrhynchus*. One satellite male *N. platyrhynchus* was observed over each of two of five nests observed. In *N. raneyi*, one satellite male occurred over one of five nests observed. Satellite males in both species were not observed to spawn in nests of conspecific resident males.

Spawning analysis: As the chronological categories reflecting the sequence of male-female interactions characteristic of a successful spawn were similar between the

two species, those of *N. raneyi* are presented with annotations of variations observed in *N. platyrhynchus*.

Interim: A male *N. raneyi* postured over his spawning trough. Aligned parallel to the water current, a male (with paired and dorsal fins extended) maintained a position at the downstream end of the spawning trough.

A male *N. raneyi* routinely reshaped and fanned the spawning trough during interim. A male reshaped the trough with his jaws by moving pebbles from the floor to lateral margins of the trough. Trough fanning occurred when an interim male moved forward, dipped his anal fin into the trough, and swam forward while quivering his tail. He vibrated his extended anal fin for about two sec in the upstream end of the trough. After these activities, a male usually drifted tail first to the crest of the nest and then resumed trough posture.

Approach: A female *N. raneyi* approached an interim male from a downstream position. In *N. platyrhynchus*, a female often approached an interim male from lateral margins of the nest. A female swam upstream either directly towards or to one side of the caudal fin of a posturing interim male. Then she moved into the trough aside or beneath the male's caudal region. A female usually delayed trough entry until the interim male was postured in the trough.

Alignment: A female *N. raneyi* aligned parallel either beneath or aside the postured male. During alignment, the male tilted and pressed his body laterally against the female while extending his pectoral fin beneath her head or breast.

Run: A female *N. raneyi* swam upstream in the trough (=run) with quick beats of her caudal fin. The tilted male usually responded immediately by matching the female's forward movement. The male remained slightly ahead (i.e., his eye or posterior margin of opercle even with female's snout) as the aligned pair moved upstream. The female followed the contour of the trough's substrate until she reached the upstream rim of the trough. Here, she pitched her snout upwards into the water column while her vent and ventral surface of her caudal peduncle pressed the upstream rim of the trough (=retroflexure). At the height of retroflexure, the anterior portion (i.e., from snout to pelvic girdle) of the female's body approximated a 30 degree angle with her caudal peduncle. In *N. platyrhynchus*, small females arched nearly 90 degrees during retroflexure.

Clasp: A male *N. raneyi* initiated the clasp as a female retroflexed. First, a male turned his head towards the female and sagittally arched his body over her back. His posterior flank crossed over the tail and then caudal peduncle of the female, appearing to anchor her to the substrate. At the height of female retroflexure, the male then flexed his posterior flank into the female's epaxial body region just posterior to the dorsal. Her vent was pressed to the upstream slope of the trough as the male's vent was slightly to one side. In this position the male's body formed a crescent from snout to anal fin during the clasp.

Dissociation: A male and female *N. raneyi* quickly separated after the clasp. The male's body relaxed parallel to the current as he drifted tail first downstream to resume interim activities. After rising into the water column, the female regained a horizontal position. She swam downstream of the nest or returned to the downstream slope of the nest to initiate another approach.

DISCUSSION

The three-stage sequential process of nest construction [i.e., excavating a concavity with a central channel parallel to water current; constructing a platform (with central upstream channel) with stones from lateral margins of the concavity; and building a mound (with a spawning trough on the upstream slope of the nest) over the platform with pebbles from the streambed] in *N. platyrhynchus* and *N. raneyi* was like that reported in *N. micropogon* by Maurakis et al. (1991) and Sabaj (1992). Lobb and Orth (1988) reported active mounds of *N. platyrhynchus* at water temperatures between 15-25 C. Water temperatures in *N. platyrhynchus* (range=19-20 C) and in *N. raneyi* (range=16-19.5 C) when nest-building and spawning were observed in the two species are comparable to those (range=17-26.7 C, \bar{x} =21.2 C) in upper Tennessee drainage streams in Virginia reported by Jenkins and Burkhead (1994) and those (17.5-19 C) in Catoctin Creek (Potomac River drainage, Virginia) by Maurakis et al. (1991) for *N. micropogon*. Nests of each species at these water temperatures were in various stages of construction (i.e., concavity, platform, and mound) and spawning activity. Regardless of the preponderance of 23 mm or larger stones in substrates near nests of each species, stones in the 11.3 mm size class in completed mound nests of *N. platyrhynchus* and the 11.3 and 6.0 mm size classes in those of *N. raneyi* were preferentially selected more than other stone size classes. These results are similar to those reported for *N. micropogon* where males selected 11.3 mm size class stones for nest construction (Maurakis et al., 1991). Comparisons of substrate composition of nests examined in this study were not made with those reported for *N. platyrhynchus* by Lobb and Orth (1988) as their visual determinations of dominate and subordinate substrate types were classified subjectively.

In a study of microhabitat use by *N. platyrhynchus* in New River, West Virginia, Lobb and Orth (1988) reported water current velocities upstream and to the sides of mounds of *N. platyrhynchus* ranged from 0.07-0.69 m/sec. They did not, however, specify water current velocities over different parts (e.g. trough) of nests. In our study, water current was lowest (\bar{x} range=0.01-0.06 cm/sec) in spawning troughs in nests of all three species. Reduced water current velocities in troughs (where female retroflexure and male clasping occur) in *N. platyrhynchus*, *N. raneyi*, and *N. micropogon* are a result of the physical construction and form of nests. These reduced velocities, like those in pits of nests of *Nocomis leptcephalus* (Maurakis et al., 1992), facilitate sinking of demersal gametes as fertilized eggs of these species were collected from troughs of nests in each species.

Aggressive behaviors observed between conspecific male *N. platyrhynchus* and *N. raneyi* were like those described between male *N. micropogon* by Maurakis et al. (1997) with one exception. Lateral swim/head bobbing between male *N. raneyi*, also occurring in *N. micropogon*, was not observed in *N. platyrhynchus*; however, future studies may reveal the behavior in the species.

Specific spawning actions and sequences of behaviors exhibited by conspecific males and females of *N. platyrhynchus* and *N. raneyi* were like those described in mating pairs of *N. micropogon* by Sabaj (1992). Interim males of both *N. platyrhynchus* and *N. raneyi* engaged in mound building, trough digging and reshaping, trough fanning, and trough posturing, behaviors comparable to those of breeding male *N. micropogon* described by Maurakis et al. (1991) and Sabaj (1992).

Lobb and Orth (1988) reported *C. anomalum* and *L. chrysocephalus* spawning and/or feeding in nests of *N. platyrhynchus*. In the present study, these two species plus *L. ardens*, *N. rubellus*, and *P. oreas* congregated over nests of *N. platyrhynchus*, but none were observed spawning over the nest.

ACKNOWLEDGEMENTS

This paper is dedicated to longtime colleague and friend, William S. Woolcott, retired D.A. Kyuk Professor of Biology at University of Richmond, who died a week before funding for the study was awarded by the Virginia Academy of Science. Mark Sabaj critically reviewed the manuscript and made significant suggestions for its improvement. Especial thanks to Bob Jenkins for locality information of *Nocomis platyrhynchus*. The study was funded the Virginia Academy of Science, Science Museum of Virginia, and University of Richmond.

LITERATURE CITED

- Gross, M. R. 1984. Sneakers, satellites, and parentals: polymorphic mating strategies in North American sunfishes. *Zeitschrift fuer Tierpsychologie* 60:1-26.
- Ivlev, V. S. 1961. *Experimental Ecology of the Feeding of Fishes*. Yale Univ. Press. New Haven, CT. 302 p.
- Jenkins, R. E. and N. M. Burkhead. 1994. *Freshwater Fishes of Virginia*. Amer. Fish. Soc. Bethesda, MD. 1079 p.
- Lachner, E. A. and R. E. Jenkins. 1971. Systematics, distribution, and evolution of the *Nocomis biguttatus* species group (Family Cyprinidae: Pisces) with a description of a new species from the Ozark Upland. *Smithsonian Contributions to Zoology*. 91:1-28.
- Lobb, M. D. and D. J. Orth. 1988. Microhabitat use by the Bigmouth chub *Nocomis platyrhynchus* in the New River, West Virginia. *Am. Midl. Nat.* 120(1):32-40.
- Maurakis, E. G. and W. S. Woolcott. 1993. Spawning behaviors in *Luxilus albeolus* and *Luxilus cerasinus* (Cyprinidae). *Va. J. Sci.* 44(3):275-278.
- Maurakis, E. G. and W. S. Woolcott. 1995. Techniques of videotaping fishes from above the surface of the water. *Southeastern Fishes Council Proceedings* 31:4-5.
- Maurakis, E. G., W. S. Woolcott, and E. S. Perry. 1997. Descriptions of agonistic behaviors in two species of *Nocomis* (Pisces: Cyprinidae). *Va. J. Sci.* 48(3):195-202.
- Maurakis, E. G., W. S. Woolcott, and M. H. Sabaj. 1991. Reproductive-behavioral phylogenetics of *Nocomis* species-groups. *Am. Midl. Nat.* 126:103-110.
- Maurakis, E. G., W. S. Woolcott, and M. H. Sabaj. 1992. Water currents in spawning areas of pebble nests of *Nocomis leptcephalus* (Pisces: Cyprinidae). *Southeastern Fishes Council Proceedings* 25:1-3.
- Reighard, J. 1943. The breeding habits of the river chub, *Nocomis micropogon* (Cope). *Pap. Mich. Acad. Sci. Arts Lett.*, 24:397-423.
- Sabaj, M. H. 1992. Spawning clasps and gamete deposition in pebble nest-building minnows (Pisces: Cyprinidae). Unpubl. Masters Thesis, Univ. Richmond, Virginia. 85 p.
- SAS. 1985. *SAS user's guide: statistics, version 5*. SAS Inst., Inc., Cary, NC. 956 p.

Vives, S. P. 1990. Nesting ecology and behavior of hornyhead chub *Nocomis biguttatus*, a keystone species in Allequash Creek, Wisconsin. *Am. Midl. Nat.* 124:46-56.