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Comparison of Spawning and Non-spawning Substrates in Nests of Species of *Exoglossum* and *Nocomis* (Actinopterygii: Cyprinidae)

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ABSTRACT

Percent composition of pebble size classes from spawning and non-spawning substrates of nests were used to test the hypothesis that distribution of pebble sizes is random in nests of *Exoglossum laurae*, *Exoglossum maxillingua*, *Nocomis leptocephalus*, *Nocomis micropogon*, *Nocomis platyrhynchus*, and *Nocomis raneyi* in Virginia. In nests of the two species of *Exoglossum*, spawning areas (i.e., upstream bases of nests) contain significantly greater amounts of the 6.0 mm size class, and significantly smaller amounts of the 2.5 mm size class of stones than do non-spawning areas. Spawning areas (i.e., pits) in nests of *N. leptocephalus* contain significantly more 6.0 mm pebbles than non-spawning areas, whereas spawning areas (i.e., troughs) in nests of *N. micropogon*, *N. platyrhynchus*, and *N. raneyi* are composed of significantly more 6.0 and 11.3 mm pebbles than non-spawning areas. In all *Nocomis* species, there was significant selection against the largest (23.0 mm) size class of pebbles in spawning areas. Male *Exoglossum* and *Nocomis* expend significant amounts of time reorganizing substrate material in spawning areas of their nests before and during spawning. Reorganizing pebbles results in relatively uniform sizes of substrate material at spawning areas in nests of each species. We propose that selection of 6.0 and 11.3 mm size classes for spawning areas is related to spawning behaviors and enhancement of survival of eggs and larvae in nests. Sizes larger than 11.3 mm interfere with spawning behaviors, and sizes smaller than 6.0 mm form a compacted substrate, which can crush eggs and larvae during trough or pit reshaping, and impede water flow, and consequently, aeration of eggs and larvae.

INTRODUCTION

Reighard (1943), Lobb and Orth (1988), Maurakis et al. (1991a,b; 1992a; 1998), and Vives (1990) present qualitative and quantitative information of overall composition of pebble nests constructed by males in species of *Exoglossum* (*E. laurae* and *E. maxillingua*), and *Nocomis* (*N. biguttatus*, *N. leptocephalus*, *N. micropogon*, *N. platyrhynchus*, and *N. raneyi*). However, no attention is given to composition of substrates at specific sites in nests where spawning occurs. In *Exoglossum* and *Nocomis*, a completed nest is typically a dome-shaped mound of pebbles (Van Duzer, 1939; Lachner, 1952; Maurakis, 1991b), and the spawning act is restricted to a specific site that accounts for only a small portion of the total nest substrate. In *Exoglossum*, the spawning act occurs at the upstream base of the nest (Van Duzer, 1939; Maurakis, 1991b). In *Nocomis*, spawning occurs either in a pit (*N. leptocephalus*, Maurakis et al., 1991a, Sabaj et al., 2000) or in the upstream half of a trough (*N. micropogon*, *N. platyrhynchus*, *N. raneyi*; Maurakis et al., 1991a, Maurakis, 1998; Sabaj et al., 2000) located on the upstream slope of the nest. Direct observations and reviews of video recordings of nest construction and breeding behaviors of males in *N. platyrhynchus* and *N. raneyi* in Virginia by Maurakis (1998) reveal that considerable time is spent by males in reorganizing substrate material where spawning occurs, and that apparent sizes of substrate material are smaller than those in non-spawning areas of nests.

Objectives of our study are to analyze percent composition of size classes of pebbles from spawning and non-spawning substrates to test whether the distribution of pebble sizes is random in nests of *E. laurae*, *E. maxillingua*, *N. leptocephalus*, *N. micropogon*, *N. platyrhynchus*, and *N. raneyi* in Virginia.

MATERIALS EXAMINED

The state, drainage, collection number (EGM=Eugene G. Maurakis), locality, collection date, and number of nests in parenthesis for *Exoglossum* and *Nocomis* species are:

Exoglossum laurae. Virginia: New, EGM-VA-439 B, Craig Co., Clemmons farm, Sinking Cr., St. Rt. 42, 28 May 1999, (9).

Exoglossum maxillingua. Virginia: James, EGM-VA-438, Craig Co., Johns Cr., Co. Rt. 658 at Maggie, 13 May 1999, (6); EGM-VA-440, Craig Co., Johns Cr., Co. Rt. 632, 0.3 km upstream of Maggie, 28 May 1999, (6); EGM-VA-443, Rockbridge Co., South R., Co. Rt. 608 Bridge, 3 km S of Vesuvius, 29 May 1999, (2).

Nocomis leptocephalus. Virginia: Rappahannock, EGM-VA-427, Faquier Co., Thumb Run, Co. Rt. 688, 29 May 1998, (2); James, EGM-VA-428, Albemarle Co., Stockton Cr., Co. Rt. 691, 50 m. from US 250, 3.2 km W of Yanay Mills, 3 June 1998, (5); EGM-VA-429, Albemarle Co., confluence of Mechum R. and Lickinghole Cr., US Rts. 240 and 250 Jct., 3 June 1998, (2); EGM-VA-438, Craig Co., Johns Cr., Co. Rt. 658 at Maggie, 13 May 1999, (1); EGM-VA-445, Nelsen Co., Rockfish R., Co. Rt. 612, 1 mi S. of St. Rt. 151, 29 May, 1999, (3); New, EGM-VA-437, Craig Co., Clemmons farm, Sinking Cr., St. Rt. 42, 13 May 1999, (6); EGM-VA-439 B, Craig Co., Clemmons farm, Sinking Cr., St. Rt. 42, 28 May 1999, (2).

Nocomis micropogon. Virginia: Potomac, EGM-VA-426, Loudon Co., Catoctin Cr., Co. Rt. 664 at Taylorsville, 27 May 1998, (6); James, EGM-VA-444, Albemarle Co., confluence of Mechum R. and Lickinghole Cr. at US Rts. 240 and 250 Jct., 29 May 1999, (2); EGM-VA-445, Nelsen Co., Rockfish R., Co. Rt. 612, 1.6 km S of St. Rt. 151, 29 May 1999, (1).

Nocomis platyrhynchus. Virginia: New, EGM-VA-416, Montgomery-Floyd Co. Line, Little R., St. Rt. 8 Brigde and 1 km upstream on dirt road, 16 May 1998, (2); EGM-VA-417, Montgomery Co., Little R. at Co. Rt. 693 and 613 Jct., E of Snowville about 8 km W of Riner, 16 May 1998, (2); EGM-VA-439 A, Montgomery Co., Little R. at Jct. Co. Rt. 693 and 613, about 8 km W of Riner, 13 May 1999 (4); EGM-VA-441, Montgomery-Floyd Co. Line, Little R., St. Rt. 8, under bridge and along Little Camp Rd, 28 May 1999, (4).

Nocomis raneyi. Virginia: James, EGM-VA-424, Rockbridge Co., Maury R. at US Rt. 60 at Ben Salem wayside, 23 May 1998, (4); EGM-VA-442, Rockbridge Co., Maury R. at US Rt. 60 at Ben Salem wayside, 28 May 1999, (7).

MATERIALS AND METHODS

Pebble samples of spawning and non-spawning substrates in nests of each species were collected in a 1-liter plastic beaker. Spawning and non-spawning substrate samples were air-dried and sifted through five custom-built wire sieves. Mesh sizes of sieves (23.0, 11.3, 6.0, 2.5, and 0.8 mm) were determined by commercially available prefabricated screen sizes and provide a more detailed account of nest composition than standard sieve samplers described by Hynes (1970). Material (<0.8 mm) that sifted through the smallest size mesh was collected in a pan. Weights of materials in each sieve size and pan were used to calculate the percentage of material per mesh and pan size. Percentages of size classes (based on weights) were used in electivity indices (Ivlev, 1961) to calculate the relative proportion of each pebble size class in spawning areas and non-spawning areas of nests. The equation $E = (n - p) / (n + p)$ (where E = pebble size selection, n = the percentage of a particular pebble size in the spawning area of the nest, and p = the percentage of a particular pebble size in the non-spawning area of the nest) was used to determine if selection of pebble size for the spawning area was nonrandom. Electivity index values range from 1 to − 1. Values closer to one indicate a greater selection of a particular pebble size. Percentages and electivity values were transformed to arcsin equivalents. Differences in average percentages of each size class of stones between spawning and non-spawning areas in nests of each species were tested with a *t*-test (SAS, 1996). Differences in average percentages and those of electivity values among pebble size classes of spawning and non-spawning areas in nests of each species were determined with a General Linear Model and Duncan's Multiple Range Test (SAS, 1996).

RESULTS

Exoglossum species:

At spawning substrates, percentages of 6.0 and 2.5 mm size classes ($\bar{x}$=73.91 and 21.3, respectively) in nests of *E. laurae*, and those of 6.0 and 2.5 mm size classes ($\bar{x}$=73.61 and 21.87, respectively) in nests of *E. maxillingua* were significantly greater than those of other size classes in each species (Table 1). In non-spawning substrates, percentages of 6.0 and 2.5 mm size classes of pebbles in nests of *E. laurae* ($\bar{x}$=49.48 and 40.26, respectively), and those for *E. maxillingua* ($\bar{x}$=59.79 and 34.99, respectively) were significantly higher than averages of other size classes (Table 2).

t-test values:

In nests of each species, the average amount of 6.0 mm stones in spawning areas was significantly greater than that in non-spawning areas (Table 3). Conversely, the amount of 2.5 mm stones in spawning areas was significantly lower than that in non-spawning areas in nests of each species (Table 3).

Electivity values:

Only the 6.0 mm size class of stones had positive electivity values at spawning substrates in nests of each species of *Exoglossum* (Table 4).

TABLE 1. Average percentage of material by size class in spawning areas of nests of *Exoglossum laurae*, *Exoglossum maxillingua*, *Nocomis leptocephalus*, *Nocomis micropogon*, *Nocomis platyrhynchus*, and *Nocomis raneyi*. Underscored means do not differ significantly.

Species	% spawning nest area size class (mm)					
E. laurae	23.0	<0.8	0.8	11.3	2.5	6.0
$\bar{x}$	0.00	0.33	0.63	3.81	21.30	73.91
F=126.68; p=0.0001; df=5						
E. maxillingua	23.0	<0.8	0.8	11.3	2.5	6.0
$\bar{x}$	0.00	0.10	0.27	3.17	22.87	73.61
F=718.02; p=0.0001; df=5						
N. leptocephalus	<0.8	0.8	2.5	23.0	6.0	11.3
$\bar{x}$	0.05	0.07	2.85	4.80	28.47	63.76
F=214.62; p=0.0001; df=5						
N. micropogon	<0.8	0.8	2.5	23.0	6.0	11.3
$\bar{x}$	0.13	0.15	0.67	8.57	12.03	78.46
F=168.21; p=0.0001; df=5						
N. platyrhynchus	<0.8	0.8	2.5	6.0	23.0	11.3
$\bar{x}$	0.03	0.04	0.18	7.94	22.94	68.84
F=87.69; p=0.0001; df=5						
N. raneyi	<0.8	0.8	2.5	6.0	23.0	11.3
$\bar{x}$	0.04	0.10	0.69	14.29	15.16	69.68
F=139.90; p=0.0001; df=5						

Nocomis species:

In spawning areas, percentages of the 11.3 mm size class were significantly higher than those of other size classes in nests of all species of *Nocomis* (Table 1). Although lower in proportion to the 11.3 mm size class, other size classes were significantly higher at spawning areas in nests of all species of *Nocomis*: 6.0 mm in *N. leptocephalus*; 6.0 and 23.0 mm in *N. micropogon*; 23.0 mm in *N. platyrhynchus*; and 23.0 and 6.0 mm in *N. raneyi* (Table 1). In non-spawning areas, percentages of the 11.3 and 23.0 mm size classes were significantly higher than those of other size classes in nests of each species of *Nocomis* (Table 2).

t-test values:

In *N. leptocephalus*, amounts of both 6.0 and 2.5 mm stones in spawning areas were significantly greater than those in non-spawning areas (Table 3). Conversely, amount of 23.0 mm size class of stones in spawning areas was significantly lower than that of the same size class in non-spawning areas (Table 3). In *N. micropogon, N. platyrhynchus,* and *N. raneyi,* amounts of 11.3 and 6.0 mm stones in spawning areas of nests of each species were significantly greater than those of the same size classes at non-spawning areas. As in *N. leptocephalus*, amounts of 23.0 mm size class of stones at

TABLE 2. Average percentage of material by size class in non-spawning areas of nests of *Exoglossum laurae, Exoglossum maxillingua, Nocomis leptocephalus, Nocomis micropogon, Nocomis platyrhynchus,* and *Nocomis raneyi.* Underscored means do not differ significantly.

Species	% non-spawning nest area size class (mm)					
E. laurae	23.0	<0.8	0.8	11.3	2.5	6.0
$\bar{x}$	0.00	0.37	1.43	8.47	40.26	49.48
F=49.43; p=0.0001; df=5						
E. maxillingua	23.0	<0.8	0.8	11.3	2.5	6.0
$\bar{x}$	0.00	0.54	1.73	2.94	34.99	59.79
F=406.65; p=0.0001; df=5						
N. leptocephalus	0.8	<0.8	2.5	6.0	23.0	11.3
$\bar{x}$	0.06	0.06	0.95	12.36	19.90	68.55
F=128.22 p=0.0001; df=5						
N. micropogon	0.8	<0.8	2.5	6.0	23.0	11.3
$\bar{x}$	0.13	0.14	0.35	5.84	34.92	58.62
F=37.27; p=0.0001; df=5						
N. platyrhynchus	0.8	<0.8	2.5	6.0	11.3	23.0
$\bar{x}$	0.06	0.09	0.43	2.47	31.68	65.28
F=124.24; p=0.0001; df=5						
N. raneyi	<0.8	0.8	2.5	6.0	11.3	23.0
$\bar{x}$	0.08	0.08	0.17	2.86	38.40	58.44
F=85.19; p=0.0001; df=5						

spawning areas were significantly lower than those of the same size class at non-spawning areas in nests of *N. micropogon, N. platyrhynchus,* and *N. raneyi* (Table 3).

Electivity Values:

In *N. leptocephalus*, average electivity values for 6.0 ($\bar{x}$ = 0.41)and 2.5 ($\bar{x}$ = 0.35) mm size classes were significantly higher than those of all other size classes ($\bar{x}$ range = −0.60 to 0.02) (Table 4). In *N. micropogon*, average electivity values for 6.0 ($\bar{x}$ = 0.52) and 2.5 ($\bar{x}$ = 0.39) mm size classes were significantly greater than those of other size classes ($\bar{x}$ range=−0.75to −0.14) with one exception: they did not differ from that of 11.3 mm size class ($\bar{x}$ = 0.16) (Table 4). In *N. platyrhynchus*, average electivity values for 11.3 mm size class ($\bar{x}$ = 0.40) and 6.0 mm size class ($\bar{x}$ = 0.39) were significantly higher than those of all other size classes ($\bar{x}$ range=−0.57to −0.18) with one exception: they did not differ from that of 2.5 mm size class ($\bar{x}$ = 0.08) (Table 4). In *N. raneyi*, average electivity values for 6.0 ($\bar{x}$ = 0.64), 2.5 ($\bar{x}$ = 0.38), and 11.3 ($\bar{x}$ = 0.31) mm size classes were significantly different from other size classes ($\bar{x}$ range = −0.62 to −0.12) (Table 4).

TABLE 3. Probability of substrate amount by size class in spawning areas greater than that in non-spawning areas in nests of *Exoglossum laurae, Exoglossum maxillingua, Nocomis leptocephalus, Nocomis micropogon, Nocomis platyrhynchus*, and *Nocomis raneyi*.

Species	Size class (mm)	Mean	Std Error	T	Prob>|T|
E. laurae	23.0	0	0		
	11.3	-4.6555556	3.4267782	-1.3585810	0.2113
	6.0	24.4333333	3.3591914	7.2735759	0.0001
	2.5	-18.9555556	5.6464126	-3.3570971	0.0100
	0.8	-0.8066667	0.3665757	-2.2005457	0.0589
	<0.8	-0.0400000	0.0874960	-0.4571636	0.6597
E. maxillingua	23.0	0	0	.	.
	11.3	0.2357143	0.9997036	0.2357842	0.8173
	6.0	13.8214286	1.9150411	7.2173014	0.0001
	2.5	-12.1142857	2.2246337	-5.4455192	0.0001
	0.8	-1.4600000	0.2303771	-6.3374344	0.0001
	< 0.8	-0.3721429	0.0932159	-3.9922673	0.0015
N. leptocephalus	23.0	-15.0952381	3.5144157	-4.2952340	0.0004
	11.3	-4.7952381	3.6559116	-1.3116395	0.2045
	6.0	16.1047619	2.3179165	6.9479474	0.0001
	2.5	1.9014286	0.8170837	2.3270914	0.0306
	0.8	0.0076190	0.0169720	0.4489178	0.6583
	<0.8	-0.0142857	0.0119835	-1.1921105	0.2472
N. micropogon	23.0	-26.3555556	6.0544087	-4.3531180	0.0024
	11.3	19.8333333	6.3812007	3.1080880	0.0145
	6.0	6.1888889	1.7459035	3.5448058	0.0076
	2.5	0.3177778	0.2232884	1.4231718	0.1925
	0.8	0.0200000	0.0457044	0.4375950	0.6733
	<0.8	-0.0122222	0.0438044	-0.2790180	0.7873
N. platyrhynchus	23.0	-42.3333333	3.9072453	-10.8345728	0.0001
	11.3	37.1583333	2.7921822	13.3079901	0.0001
	6.0	5.4750000	1.8429688	2.9707502	0.0127
	2.5	-0.2391667	0.3215221	-0.7438577	0.4726
	0.8	-0.0208333	0.0178995	-1.1639071	0.2691
	<0.8	-0.0600000	0.0378193	-1.5864896	0.1409
N. raneyi	23.0	-43.2818182	4.0513481	10.6833126	0.0001
	11.3	31.2818182	5.4995011	5.6881193	0.0002
	6.0	11.4272727	2.9427906	3.8831416	0.0030
	2.5	.5163636	0.2665342	1.9373258	0.0814
	0.8	0.0209091	0.0445473	0.4693682	0.6489
	<0.8	-0.0381818	0.0277265	-1.3770862	0.1985

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

Species	Electivity per pebble size class (mm)					
E. laurae	23.0	0.8	11.3	2.5	<0.8	6.0
$\bar{x}$	-0.99	-0.49	-0.37	-0.31	-0.16	0.20
F=8.69; p=0.0001; df=5						
E. maxillingua	23.0	0.8	<0.8	2.5	11.3	6.0
$\bar{x}$	0.99	-0.71	0.54	-0.21	-0.11	0.11
F=25.50; p=0.0001; df=5						
N. leptocephalus	23.0	<0.8	11.3	0.8	2.5	6.0
$\bar{x}$	-0.60	-0.15	-0.03	0.02	0.35	0.41
F=14.06; p=0.0001; df=5						
N. micropogon	23.0	<0.8	0.8	11.3	2.5	6.0
$\bar{x}$	-0.75	-0.45	-0.14	0.16	0.39	0.52
F=10.97; p=0.0001; df=5						
N. platyrhynchus	23.0	<0.8	0.8	2.5	6.0	11.3
$\bar{x}$	-0.57	-0.42	-0.18	0.08	0.39	0.40
F=10.37; p=0.0001; df=5						
N. raneyi	23.0	<0.8	0.8	11.3	2.5	6.0
$\bar{x}$	-0.62	-0.28	-0.12	0.31	0.38	0.64
F=11.79; p=0.0001; df=5						

DISCUSSION

We reject the hypothesis that pebbles are distributed randomly between spawning and non-spawning areas in nests constructed by males in *E. laurae, E. maxillingua, N. leptocephalus, N. micropogon, N. platyrhynchus*, and *N. raneyi*. In nests of the two species of *Exoglossum*, spawning areas (i.e., upstream bases of nests) contain significantly greater amounts of 6.0 mm size class of stones than non-spawning areas. In contrast, significantly smaller amounts of 2.5 mm size pebbles were present in their spawning areas. Similarly, spawning areas (i.e., pits) in nests of *N. leptocephalus* contain more 6.0 mm pebbles than non-spawning areas, whereas spawning areas (i.e., troughs) in nests of *N. micropogon, N. platyrhynchus*, and *N. raneyi* are composed of significantly more 6.0 and 11.3 mm pebbles than non-spawning areas. In all *Nocomis* species, there was significant selection against the largest (23.0 mm) size class of pebbles in spawning areas. Male *Exoglossum* and *Nocomis* expend significant amounts of time reshaping and reorganizing substrate material in spawning areas of

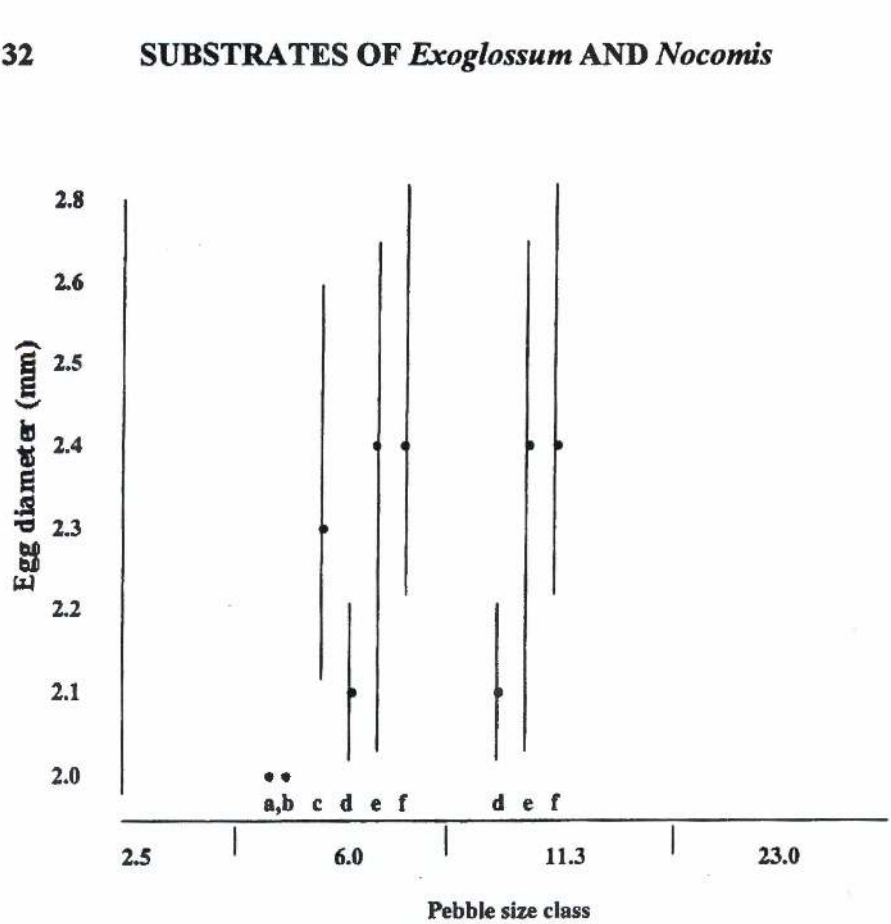

FIGURE 1. Distribution of egg diameter per size class of pebbles by species of *Exoglossum* and *Nocomis*. Key: a=*E. laurae* (Raney, 1939); b=*E. maxillingua* (Van Duzer, 1939); c=*N. leptocephalus* (pers. obs., EGM-NC-211) d=*N. platyrhynchus* (Zorman and Maurakis, 2000) e= *N. micropogon* (Fish, 1932; Cooper, 1980; Buynak and Mohr, 1980); f=*N. raneyi* (Maurakis et al., 1992b).

their nests before and during spawning (Raney, 1939; Van Duzer, 1939; Sabaj, 1992; Maurakis et al., 1991b). Reorganizing pebbles results in relatively uniform sizes of substrate material in spawning areas of nests of each species. We propose that uniform composition of substrates in spawning areas is related to spawning behaviors and enhancement of survival of eggs and larvae in nests. In *Exoglossum* and *Nocomis*, a successful spawn is the end result of a precise sequence of male-female interactions (i.e., approach, alignment, run, clasp) coordinated in part by the topography of the pebble nest (Sabaj, 1992; Maurakis, 1998; Sabaj et al., 2000). By reshaping and reorganizing the spawning substrate, the male removes obstructions (e.g. stones >11.3 mm size class) that may interfere with the sequence of spawning behaviors.

Size uniformity of pebbles and resultant interstices in spawning substrates also may afford conditions that prevent crushing and smothering of buried eggs and post-hatch larvae. Egg diameters of all species range from 2.0-2.8 mm and spawning substrates range from 6.0 – 11.3 mm. (Figure 1). Spawning substrates do not contain extremely small gravel (2.5 mm) and sand (≤ 0.8 mm). These smaller sizes form compacted substrate material, which can crush eggs and larvae during trough or pit reshaping, and impede water flow, and consequently, aeration of eggs and larvae.

Sabaj (1992) and Maurakis et al. (1992a) stated nest-building male *Exoglossum* and *Nocomis* cause reduced water current velocities for egg deposition by physically modifying an area of streambed, a result of their nest building activity. We concur with their findings, and stipulate that in modifying the substrate, males are selective in which sizes of stones they deposit in spawning areas before and during spawning.

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