Spawning Behavior of Lenok, *Brachymystax lenok* (Salmoniformes) from the Uur River, Northern Mongolia¹

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Received May 21, 2008

Abstract—Video cameras inside underwater housings were used to record the spawning activities of lenok (sharp snout type) in the Uur River, Hovsgol Province (Northern Mongolia). This study constitutes the first underwater video recordings of lenok spawning in the wild. A qualitative description of spawning behavior is presented based on observations taken from five females. Our observations indicate that a previously reported lenok-specific behavior, the presence of satellite females, may have been based on a misidentification of female-mimicking males. Immediately after spawning, lenok females rest before covering their eggs. They share this unusual trait with *Hucho taimen*, although we cannot determine the pattern of "resting" evolution until we have a more robust phylogeny for the Salmonidae.

DOI: 10.1134/S0032945208110040

INTRODUCTION

The lenok (*Brachymystax lenok*), commonly known as Manchurian trout, is a freshwater salmonid fish inhabiting rivers and lakes throughout eastern Siberia including portions of Kazakhstan, Mongolia, China and Korea (Froufe et al., 2004). Traditionally, lenok has been recognized as a monotypic species belonging to the Brachymystax genus with two forms (sharp and blunt snout type) that vary in morphology with both sympatric and allopatric distributions (Mina, 1991; Alekseyev et al., 2003). The Brachymystax genus is thought to form the most basal clade of the entire Salmoninae subfamily (Norden, 1961; Holčík, 1982; Phillips et al., 1995, 2004) and thus studies of life history, ecology and behavior of lenok represent a key piece reconstructing the evolution of the salmonines (Esteve and McLennan, 2007).

There are very few publications written in English about this species' ecology and, of these, most are molecular studies discussing inter and intra species affinities (Shed'ko et al., 1996; Froufe et al., 2004, 2005; Xia et al., 2006). Other reports discussing some aspects of lenok spawning ecology are written in Russian language and are thus not easy accessible to the western scientific community (Misharin, 1942; Mitrofanov, 1959; Smol'yanov, 1961; Besednov and Kucherov, 1972; Kifa, 1974). There is only one English manuscript describing the actual behaviors of lenok during spawning: based on Baimukanov's (1996) observations of lenok spawning at Markakol Lake, Kazakhstan. The report by Baimukanov is intriguing because in it the author described the presence of satellite females close to the nesting female. Satellite females have not been described before in any salmonine species (reviewed by Esteve, 2005), so if they are indeed present in lenok they will be unique. Aside from this possible novelty, we do not know whether lenok exhibits any other unique behaviors, nor do we know whether it displays behaviors previously thought to be autapomorphies for other salmonid genera (e.g., sequential spawning and undulating 1 and 2 in *Salvelinus*: Fabricius and Gustafson, 1954; Esteve and McLennan, 2007).

In this paper we present the results of our underwater video recordings of 5 different lenok females spawning in the Uur River (Hovsgol Province, Northern Mongolia). We were particularly interested in: (1) delineating the sequence of spawning behaviors to identify differences and similarities with other salmonines and (2) searching for the presence of satellite females.

MATERIAL AND METHODS

Underwater recordings took place in the Uur River during May 12–14, 2006 (50.19' 16.14" N, 101.53' 32" E; 1065 m altitude). The Uur River originates from the Kheven-Saluu Mountains in north-eastern Hovsgol Province (Fig. 1) and flows south for 331 km until it meets the Eg River. The combined Eg-Uur, recognized from this point on as the Eg River, flows for another 200 km until it reaches the Selenge River, a tributary of Lake Baikal.

¹The article is published in the original.

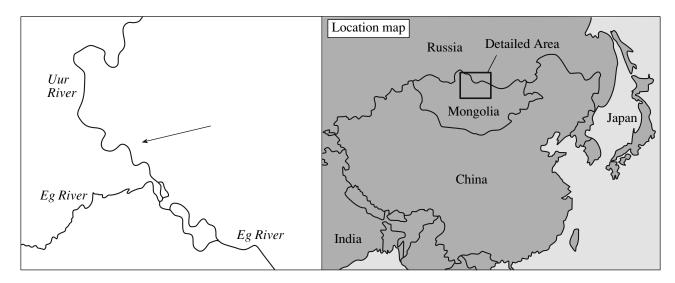


Fig. 1. Uur River in Northern Mongolia. Arrow indicates the location where the recordings took place.

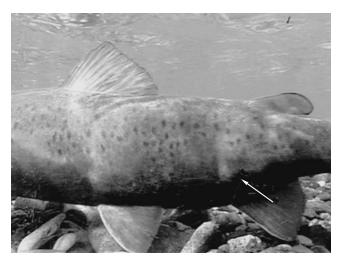


Fig. 2. Male pigmentation. Lighter areas (see arrow) are red (colour and video pictures are available at http://www.zoo.utoronto.ca/manuesteve/UTlenok.html).

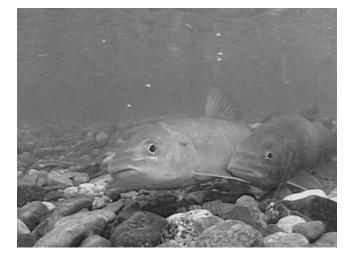


Fig. 3. Lenok male quivering a nesting female.

Underwater Video and Tape Analysis

One colour and two black and white digital video camcorders mounted inside underwater housings were used to monitor the mating activities of 5 different lenok females associated with a variable number of males. Video signals for the three cameras were transmitted via cable to digital recorders located outside the river. The area on which the cameras were located consisted of approximately 70 m² of fast moving water and shallow pools located about 20 m from the left river bank and 50 meters from the right one. Water depth ranged from 0.5–0.2 m and temperature from 2–9°C. Actual redds, areas of disturbed gravel containing the nests, consisted of elliptical areas approximately 1 meter across the long axis, located in tail pool areas with downwelling flow. Redds were located. Males and females were not noticeably sexually dimorphic but they did differ slightly in colouration, males being darker with red patches and round black spots along their bodies (Fig. 2). This difference, however, was not completely consistent, so we used behavior to identify both sexes. The fish slightly behind the other, intermittently performing quivering-typical male salmonine courtship behavior consisting of low amplitude and high frequency body vibrations from head to tail (Fig. 3)—was identified as the male; while the female was the more advanced fish regularly performing nest digging behavior (Fig. 4).

Our analysis is based on 206 min of behavioral interactions. Only one female was recorded actually spawning (egg release). We recorded the number and colour of males around each female and approximated the relative size of the nesting female and the males around her. Arctic graylings (*Thymallus arcticus*) were often present during the observations and interacted with lenok.

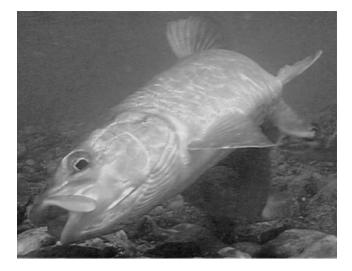


Fig. 4. Lenok female turns on her side and excavates the nest with intense beatings of her caudal fin.

RESULTS

Female behavior comprised mainly *digging*-female turns onto her side and excavates a depression in the gravel by tail beats- and *probing*-female lies over her nest and presses her anal fin into the substrate to test its suitability: Fig. 5. Male behavior consisted of quiverings, fighting displays and actual attacks towards of other males approaching the female. We recorded 178 female diggings performed by 5 different females and 140 male quiverings performed by at least 19 different males (table).

Female 1 was recorded for 19 minutes. Two males of approximately her size fought to gain access to her. A third male with female colouration (lighter with no red patches and fewer round black spots along their bodies) remained half a meter downstream of the nest and was not involved in the fights. One of the big males attacked him once, but on two other occasions, he



Fig. 5. Lenok female tests the suitability of her nest by pressing her anal fin into the gravel in a behavior known as *probing*.

approached the female, passed beneath her and quivered her even though a bigger male was present. He then returned to his position slightly downstream from the main pair. During the observation period one of the two fighting males was recorded quivering a grayling female. Recordings ended when the female lenok abandoned her nest for no apparent reason.

Female 2 was recorded for 16 minutes. She was nest probing and building when recordings started. One dominant male, similar in size, was guarding her and regularly performed quiverings. Two other subdominant males, the same size as the dominant one, were located downstream and frequently approached the female. Recordings were interrupted when a piece of floating ice hit the camera, forcing us to remove it.

Female 3 was recorded for 35 minutes. She was guarded by a slightly smaller dominant male. She did

Female	Date	Video length (min)	# males			Total	# quivers			Total	# female
			d	sd	m	10141	d	sd	m	iotai	digs
1	May 12 16:54–17:13	19	2	0	1	3	7	_	2	9	15
2	May 13 17:10–17:25	16	1	2	0	3	11	3	-	14	8
3	May 13 14:45–15:20	35	1	3	0	4	16	4	—	20	20
4	May 14 15:39–17:31	115	1	3	2	6	54	12	1	67	123
5	May 14 17:40–18:01	21	1	2	0	3	29	1	-	30	12
Total		206				19				140	178

Spawning history of five nesting lenok females in the Uur River, Mongolia, d = dominant male; sd = subdominant male; m = male mimicking a female's colour pattern

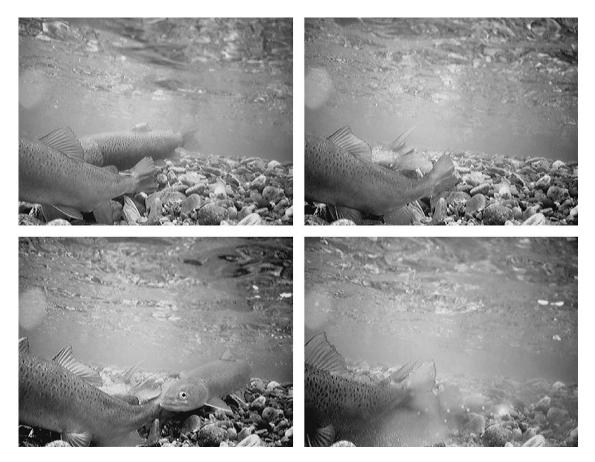


Fig. 6. Two second intervals of spawning lenok. From left top to bottom right: (1) probing female begins to tremble and the dominant male joins her; (2) the pair is spawning; (3) a subdominant male joins the pair; (4) the three fish spawning, the female is in the middle; eggs and sperm can be seen.

not perform any probing behavior indicating that she was in the initial stage of nest-building. Three other males, about the same size as the dominant one, were situated downstream and occasionally approached the female. Two grayling males located nearby approached and quivered her on two occasions. Recordings ended when the female left the area for no apparent reason.

Female 4 was recorded for 115 minutes. When observations started she appeared to be in the process of selecting the nest site, digging in two locations separated by one meter. Six males were around her. Two of them were slightly bigger than she. One of these two eventually assumed the dominant role after a series of displays and actual fights with the other male. Two other males, slightly smaller than the female, remained downstream and approached her when the others were chasing each other. In addition, two more males of even smaller size with female colouration remained passively in the nest area slightly downstream of the main pair. One of these males quivered the female on one occasion. The female was disturbed many times by grayling males. We were forced to relocate our camera following a collision with floating ice; she never returned to her nest after that interruption.

Female 5 was recorded for 21 minutes. One dominant male, approximately her size, courted and guarded her. Two subdominant males, relatively smaller than the female, were located downstream and approached her on many occasions. The female was in the last stages of nest building, probing on a regular basis. She finally spawned with the dominant male at 5:59 pm. The spawning act lasted 7 seconds, with the emission of eggs and sperm clearly displayed on our screen. One of the subdominant males joined the pair 2 s after they started to spawn, assumed the spawning position and released milt (Fig. 6). After spawning, the female remained over her nest resting. She left the area 2 min 17 sec later when we had to enter the river to correct our camera position.

DISCUSSION

Underwater video provided a useful tool to investigate and describe lenok spawning activities under natural conditions. Even though we only recorded part of each female's spawning repertoire, we can piece these fragments together to reconstruct a general picture of that repertoire. Spawning in the Uur River coincided with thawing; no fish appeared until most of the ice had broken up and floated down river. Males started to compete for spawning territories prior to the females' arrival; we observed many intra-sexual displays (e.g., lateral, frontal, head down tail beat; for a description see Esteve and McLennan, 2007) and actual attacks without any females being present. During lateral displays males were seen flexing their bodies upwards and dilating their throats. Although males did differ in size, we never observed precocious maturing parr commonly found in Salvelinus, Salmo and some Oncorhynchus species (Esteve and McLennan, 2007). When females arrived they began searching for a nest site within the territories defended by males and from there moved to nest building by *digging*. During the nest building phase three females abandoned their chosen site, probably because nest conditions were not suitable (female 1) or because they were disturbed, either by us (female 2) or by grayling males (female 4). These observations agree with data from many salmonid species, in which females have been reported to abandon their nests before completion (Barlaup et al., 1994). As a result of these false redds, female-disturbed gravel containing no nests are commonly found in spawning locations (Edo et al., 2000).

The winning male from the territorial disputes positioned himself slightly behind the female as she was building her nest. He frequently crossed over her tail in an attempt to guard her from males approaching from either side. From time to time the dominant male approached the female laterally and quivered her, combining quivering with frequent attacks towards other males approaching the area. Male dominance was, however, not always predetermined by the interactions between males during territory establishment. In some groups fighting between rival males continued while the female was nest building. We never observed the male digging behavior described for Oncorhynchus in this species. As nest building progressed the female tested the substrate's suitability by probing it with her anal fin. Once the nest was finished she assumed the spawning position; trembling, with her anal fin pressed into the gravel. The dominant male joined her then both, while trembling and gaping, emitted their gametes. At this point a subdominant male rushed in to join some pairings and release milt.

Contrary to the observations by Baimukanov (1996) no satellite females were observed during this study. We did, however, see males with female colouration close to the nesting female and many times we witnessed them courting her even in the presence of the dominant male. Baimukanov (1996) made his observations from a platform and used sexual dimorphism in colour to differentiate males from females. He did not report any quivering by the purported "satellite females", but such behavior is almost impossible to distinguish from above the water (pers. obs.). Given this, it seems likely that what he identified as "satellite females" were males adopting female colouration. A female mimic avoids attacks from the dominant male and can thus position himself in a location close to the nest, waiting to dart in and release milt at the appropriate time (Schroder, 1981; Groot, 1996). Female mimics have been reported for a variety of salmonid species including arctic charr (*Salvelinus arcticus*), pink salmon (*Oncorhynchus gorbuscha*) and chum salmon (*O. keta*), so it would not be extraordinary to find them in lenok as well.

One of the goals of this project was to identify whether lenok displays three behaviors thought to be autapomorphic for *Salvelinus*. Based on our observations the answer to this question is "no". First, none of the females performed the typical tail swinging motions *Salvelinus* females use for clearing debris and small particles from their nest site. Second, the one female we observed spawning did not perform the *probing* behavior that always precedes egg release in salmonines, which to us indicates that a second spawning act was not about to happen. We thus tentatively propose that female lenok do not lay successive batches of eggs in one nest.

Finally, we did not observe the typical 'swimming in place' behavior chair females use to ventilate and distribute their eggs over gravel crevices right after spawning. In fact, based on our single observation, lenok females share a distinct postspawning behavior with Siberian taimen (Hucho taimen): rather than immediately covering their eggs they rest for a period of time, and then proceed to egg covering. Unfortunately the observed female was disturbed soon after spawning so we could not determine the length of the rest period. Baimukanov (1996) reported egg covering in his study but did not record the time between spawning and first covering. In a previous study (Esteve et al., in press) we documented rest periods of 3 min 17 sec and 4 min 19 sec respectively from a single taimen female recorded spawning in two separate redds. Rest periods for lenok females (our one data point implies a time of at least 2 min 17 sec) are probably similar but we need further observations to confirm this assumption. "Female resting after spawning" separates lenok and taimen from species in which the females immediately cover their eggs after spawning (Salmo, Parahucho, Oncorhynchus; Esteve et al., in press) and from species that perform a distinct undulating movement after spawning (Salvelinus; Esteve and McLennan, 2007).

One unexpected result of this study was the observation that male lenok occasionally quivered grayling females, while male graylings were often seen quivering lenok females. Lenok females were generally bigger than grayling females, but lenok males were also generally bigger than grayling females so this is not a simple case of males being attracted to a supernormal stimulus. Rather, we believe these interspecific quiverings are the result of two relatively closely related species spawning in the same place at the same time. In general, unattended lenok and grayling males, like other salmonine males, are highly motivated to spawn and will try to do so with anyone in their path when certain stimuli are provided (i.e. female *probing*; pers. obs.). These mistaken quiverings, therefore, are not unexpected, nevertheless it is important to actually document them as they may have an effect in the reproduction of both species.

In conclusion, this study has expanded our knowledge of lenok spawning behavior, has demonstrated that the previous identification of satellite females was probably based on a misidentification of female-mimicking males, and has reinforced the conclusion that *Salvelinus* has three autapomorphic breeding behaviors that can be used to unambiguously identify charr. That said, we realize that this video-based study is but a preliminary foray into the spawning behavior of lenok. We hope that our work motivates other scientists to test our findings and to fill other gaps in our knowledge and build a more complete and robust database for the breeding behavior of this important species.

ACKNOWLEDGMENTS

Recordings were done with the help of Y. Davaakhuu, D. Gilroy, Kh. Badarch, and U. Nemekhbayar. We wish to thank M. Amaraa, T. Monkhnasan, P. Tsogtsaikhan and B. Ganzorig for assistance in the field. Thanks to Taimen Conservation Fund, Sweetwater Travel and Hovsgol Travel for field support and assistance. Financial support was from the Taimen Conservation Fund (Mongolia) and The National Geographic Society. Additional funds were provided by a NSERC Discovery Research Grant to DAM.

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JOURNAL OF ICHTHYOLOGY Vol. 48 No. 11 2008