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Early Life of the Mink Frog (*Rana septentrionalis*): From Fertilization to Metamorphosis

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Mink Frogs (*Rana septentrionalis*) are a unique ranid species restricted to Canada and the northern edge of the United States, from northern Minnesota to northern Maine. They are a member of the *Aquarana* clade that includes Green Frogs (*R. clamitans*), American Bullfrogs (*R. catesbeiana*), and four other species. Despite being relatively common where present, the biology of this species has been poorly studied and little in particular is known about its breeding and development from fertilization through overwintering as larvae. Critically, the species' representation in museum collections is limited in general, but particularly at early life stages. Here we report on our initial efforts to describe larval Mink Frog development by inducing breeding of wild-caught adults in the laboratory, then sampling tadpoles from fertilization until the subsequent spring. Specimens, including tissue samples, adult specimens of both sexes, an entire laboratory-induced egg mass, and a captive-bred larval series are available in the Yale Peabody Museum of Natural History. Our approach here demonstrates that Mink Frogs can be captive bred for use in laboratory experiments, and our work provides a novel larval series from egg mass to metamorphosis for this secretive, understudied species.

ANURAN amphibians exhibit an impressive array of reproductive modes. Those that lay aquatic eggs that hatch into aquatic tadpoles (Mode 1 *sensu* Haddad and Prado, 2005, or Mode 3 *sensu* Nunes-de-Almeida et al., 2021) include species in the family Ranidae. Even within these modes, species lay eggs in different kinds of standing water, in clutches of different sizes and configurations, and in different places within a pond or lake (Wells, 2007). It is important to recognize this variation and ensure example specimens are available to use for taxonomic evaluations and to better understand the role of abiotic variables on development of these different forms. Taxonomic identification of tadpoles at different stages is also important and often challenging given similarities in morphology among syntopic species (Altig and McDiarmid, 2015).

Ranid frogs in temperate regions, including members of the genus *Rana,* that lay eggs in colder water typically form compact masses and lay them either communally, as in Wood Frogs (*R. sylvatica)* and Northern Leopard Frogs (*R. pipiens*; Dickerson, 1969), or attach these to submerged vegetation, as in Carpenter Frogs (*R. virgatipes*; Gosner and Black, 1968) and Mink Frogs (Dickerson, 1969; Hedeen, 1977). Communal masses help reduce the vulnerability of eggs to late season frosts because submerged egg masses are less vulnerable to both freezing and drying out under conditions when water levels drop while still allowing sufficient oxygenation in cool water (Wells, 2007). In contrast, Green Frogs and American Bullfrogs lay eggs in films at the surface of the water, which may be an adaptation to the low oxygen of warm water during summer breeding months (Moore, 1940; Wells, 2007). Note that we refrain from using *Lithobates* given that prior work that proposed splitting North American ranids into two genera, *Rana* and *Lithobates* (Frost et al., 2006, 2008), promoted taxonomic instability and results in paraphyly (Pauly et al., 2009; Yuan et al., 2016).

Mink Frog embryonic and larval development is poorly documented and understood. One reason for this may be confusing larval identification with co-occurring species and a lack of accurate reference material across developmental stages for comparison. Mink Frogs are sympatric with other ranid frogs, including Green Frogs, American Bullfrogs, Wood Frogs, Northern Leopard Frogs, and Pickerel Frogs (*R. palustris),* and share a breeding season primarily with two of these (American Bullfrogs and Green Frogs). In Maine, Wood Frogs finish breeding by late April to early May, just when Northern Leopard Frogs and Pickerel Frogs begin forming choruses (Hunter et al., 1999). Eggs of these species are all laid in clumps, like those of the Mink Frog, and are typically laid communally in vegetated shallow water (*R. pipiens, R. sylvaticus*) or individually attached to submerged vegetation (*R. palustris*; Hunter et al., 1999). Despite having similar clump-shaped egg masses, Mink Frog egg masses are unlikely to be confused with those other ranid taxa because the breeding seasons do not overlap.

However, Mink Frog larvae may be challenging to distinguish from other co-occurring ranids. By mid to late May, adult Green Frogs and American Bullfrogs have emerged and can be found feeding and establishing territories in permanent ponds. Mink Frogs emerge by late May or early June, and males of all three species can be heard in their respective choruses at night from June through early August. Mate choice and oviposition behavior of female Mink Frogs in the field has only rarely been observed (Patrick et al., 2012; Bevier and Persons, pers. obs.), which is not surprising given their brief attendance to breeding sites (Hedeen, 1972). Based

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on these sparse observations, we speculate that females likely approach a calling male, enter into amplexus, and carry the male to a preferred egg-laying location. Females then attach a single globular egg mass to submerged vegetation (Wright and Wright, 1933; Hedeen, 1972; Patrick et al., 2012; Bevier, pers. obs.).

Although egg masses of Mink Frog, Green Frog, and American Bullfrog are readily distinguishable, the later embryonic and larval stages are challenging to distinguish, and their comparative larval ecology is virtually unstudied. Documentation and museum specimens of egg and tadpole development for Mink Frogs are nearly absent but would provide important reference for investigations that focus on monitoring species distribution and abundance, disease dynamics, and habitat conservation. The online database VertNet (queried on 26 August 2021) lists 824 specimens identified as *Rana septentrionalis;* of those, only 86 were identified as larval or egg. Our contribution here can be used to better understand the current distribution of the Mink Frog by comparing our specimens to field-collected specimens elsewhere in the range. Extensive information on reproduction and development for Green Frogs and American Bullfrogs, which are syntopic with Mink Frogs over much of its range, are already available from which comparisons could be drawn (Courtois et al., 1995; Wells, 2007; Dodd, 2013).

Overall, our goal was to captive breed Mink Frogs to obtain preliminary information on egg mass production and deposition and larval development, and to obtain a series of larval specimens through development, from fertilization to metamorphosis, that can be used for future taxonomic comparisons. We note that our aim here was neither to formally test the efficacy of captive breeding of this species nor to experimentally manipulate larval development, but to document new natural history information for this species to facilitate future research.

MATERIALS AND METHODS

Study site and collections.—We collected adult ($n = 48$ total) and metamorphosing ($n = 6$) *R. septentrionalis* from Mercer, Somerset County, Maine on 11 July 2015. Water temperatures recorded on 34 nights in 2000 and 48 nights in 2001 were 19.2±0.2°C on average (range = 18.4–20.1°C; Bevier et al., 2004). A series of adults ($n = 35$) and all metamorphosing individuals were euthanized for a separate morphological study. We kept 13 adult frogs in 38 L plastic buckets and transported them to Greeley Memorial Lab, New Haven, Connecticut. We then transferred and maintained all frogs in three separate plastic sweater boxes (60 cm x 30 cm x 40 cm) containing half volume of reconstituted deionized water at about 18°C. We housed four or five individuals together in each container (one or two males and three females) that also had pieces of floating foam board insulation (2.5 cm thick) on which frogs could sit (Fig. 1A). We used binder clips to attach strips of fiberglass window screening to each piece of foam. These strips were suspended vertically down the water column to mimic vegetation that *R. septentrionalis* uses to support egg masses. We fed frogs crickets *ad libitum* and changed water every 72 hours.

Breeding.—On 13 July 2015, the day after adult frogs were placed in plastic sweater boxes, one egg mass in Group A was produced by natural breeding. This original egg mass predominantly failed (see below) and so we chose to artificially induce breeding in all three groups and raise larvae again. To induce breeding in *R. septentrionalis* in the laboratory, we used AMPHIPLEX, a mixture of a gonadotropin-releasing hormone agonist (GnRH-A; des-Gly10, D-Ala6, Pro-NHEt9-GnRH) and a dopamine antagonist (metoclopramide hydrochloride; MET) dissolved in saline, following Trudeau et al. (2010, 2013). We injected both adult male and female frogs with AMPHIPLEX intraperitoneally, following published protocols, on 31 July 2015. One egg mass was present the next day in each of two containers.

Larval rearing.—We maintained embryos from each group in a separate 5 L plexiglass aquaria. Without bubblers, Group A's egg mass dissolved and most embryos perished within a day. With egg masses produced in Groups B and C by artificial breeding, we added bubblers to increase dissolved oxygen, predicting that a lack of oxygen may have killed Group A's naturally produced clutch. Dissolved oxygen measurements from the source pond are relatively high (32–64% at 30 cm below the surface; Bevier, unpubl.) suggesting that embryos of *R. septentrionalis* require high oxygen levels. The addition of bubblers appeared to have helped Group B and C egg masses survive and maintain structure.

Once hatched and at free-feeding stage (Gosner 25), we fed larvae a mixture of rabbit chow and fish flakes (Lambert, 2015). As larvae grew, we haphazardly split clutches into two or more 5 L aquaria, each with a bubbler, to reduce larval densities. Because we could not predict *a priori* what larval densities would promote or inhibit development and survival, our attempts to split clutches to reduce densities were not systematic. In mid-April 2016, we moved all remaining larvae to outdoor mesocosms at Greeley Memorial Lab following methods from Skelly (2002), and allowed larvae to develop outdoors.

We sampled larvae from each of the three groups over the year to obtain representative individuals and variation at different developmental stages (Supplemental Table 1; see Data Accessibility). We euthanized larvae in an overdose of MS-222 and fixed them in 10% buffered formalin. Specimens were deposited at Yale Peabody Museum of Natural History and later imaged and analyzed. Snout–vent (SVL) and total length (TL) were measured from digital photos in ImageJ. For hatchlings, images were acquired using a Zeiss Stemi 2000 macroscope with a Q-Imaging Micropublisher 5.0 digital camera. Capture control software (Q-Capture 7) was used to capture multiple images at ascending focus levels (Z-stack) and embed a calibrated scale bar. Images of small larvae were acquired using a Canon 6D DSLR camera mounted on a Leica MZ75 macroscope. Images of large larvae and metamorphs were acquired with a Nikon D90 DSLR and Nikon 60 mm f2.8 macro lens. For DSLR images, Z-stacks were captured with manual focus and merged in Photoshop. Images of scale bars were captured concurrently for calibration. We categorized each tadpole measured to the appropriate Gosner stage (Gosner, 1960; Watkins-Colwell and Leenders, 2004) and then grouped tadpoles of similar stages into one of seven qualitative developmental categories. We present variation in SVL and TL across developmental categories using ggplot2 in R (Wickham, 2016) and use these values, including the proportion of tail length to body length (SVL), to compare to

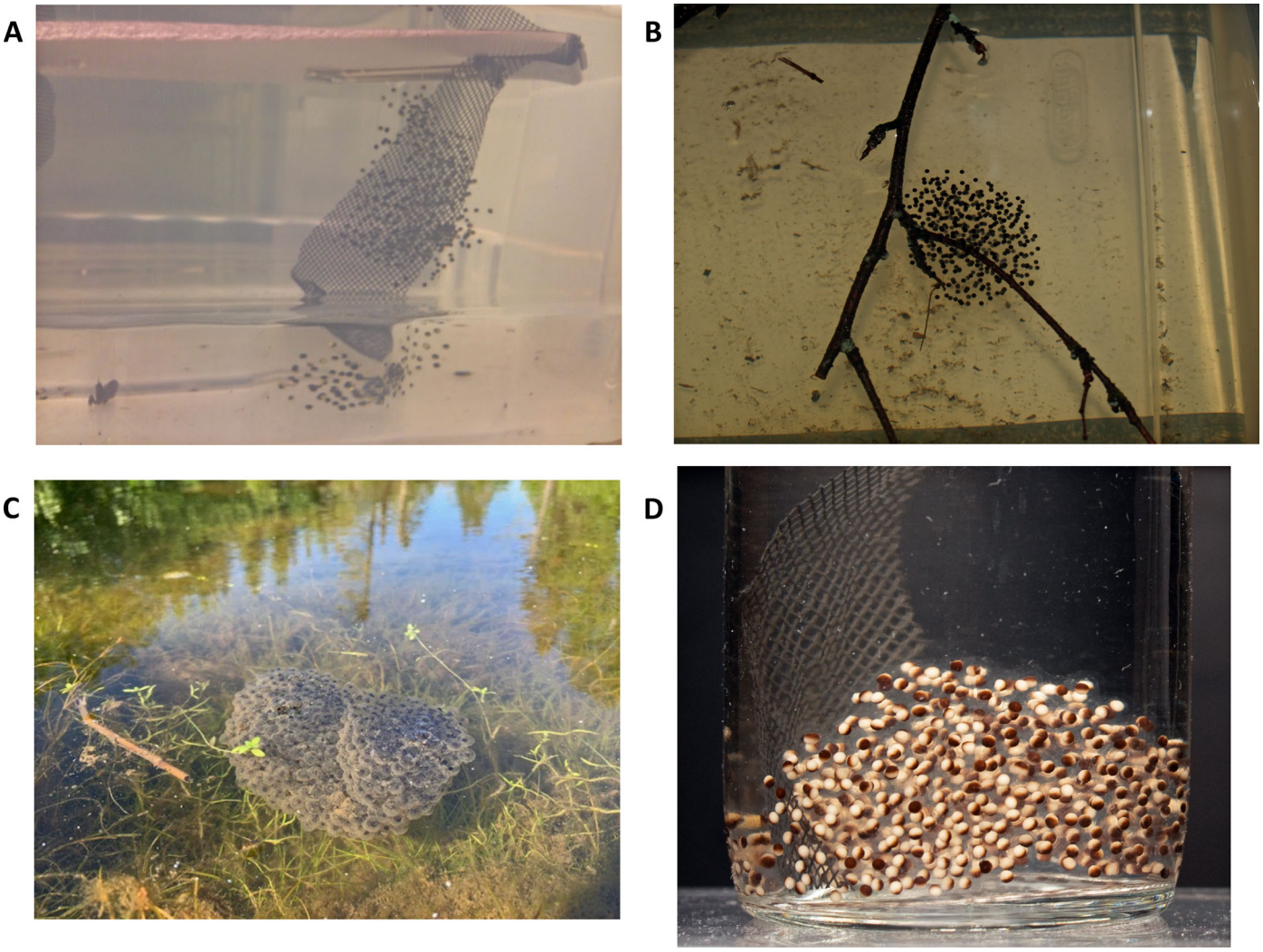

Fig. 1. (A–D) Egg masses of *Rana septentrionalis*. (A) Aquarium breeding set-up showing foam board and screening with a newly deposited egg mass (photo by G. Watkins-Colwell). (B) Egg mass of *Rana septentrionalis* in a plastic container (photo copyright D. Patrick). (C) Egg mass of *Rana septentrionalis in situ* in Aroostook County, Maine (photo by T. Persons). (D) Egg mass from captive-bred Group B (YPM HERA 019717, photo by A. Arietta courtesy of Yale Peabody Museum).

published data from Hedeen (1971) and Altig and McDiarmid (2015).

RESULTS

Egg masses.—Several Mink Frogs were observed in amplexus in transit from Maine to Connecticut, and within 24 hours of arriving in the laboratory *R. septentrionalis* successfully produced one egg mass without intervention (Fig. 1A). This first egg mass was similar in appearance to one collected in the field and photographed (Fig. 1B) and can be compared to egg masses documented in the field (Fig. 1C) as described below. The mass deposited in the lab, however, dissolved and most embryos died within 24 h of oviposition; we hypothesize this was likely due to low dissolved oxygen in laboratory conditions.

AMPHIPLEX injections resulted in three induced egg masses within 24 h, including two masses in Group B and one mass in Group C. We had no negative control treatments for comparison, nor sham controls, so we note that oviposition could have been coincident with AMPHIPLEX injections rather than a result of the injections. Regardless, no oviposition had occurred for about two weeks, between the arrival of *R. septentrionalis* to the lab and when AMPHIPLEX injections were given, suggesting the injections successfully encouraged both amplexus and ovulation.

All three egg masses produced were oviposited 10–15 cm below the water surface on strips of window screening 3 cm in width and weighted at each end. One egg mass from Group B was fixed in formalin as a morphological specimen and deposited in the Yale Peabody Museum (YPM HERA 019717, Fig. 1D). The other two egg masses were maintained in separate aquaria with bubblers. The addition of bubblers to the aquaria appeared to have enhanced embryo survival and maintained the egg mass structural integrity.

Larvae.—We observed high survival rates under laboratory conditions when bubblers were included in the aquarium set-up. Larvae appeared to grow slowly under initial densities (several hundred animals per 5 L aquarium), so we split each clutch into at least two aquaria to reduce densities to about 200 animals per aquarium. Once they were transferred to mesocosms in March 2016, larvae grew more rapidly. We

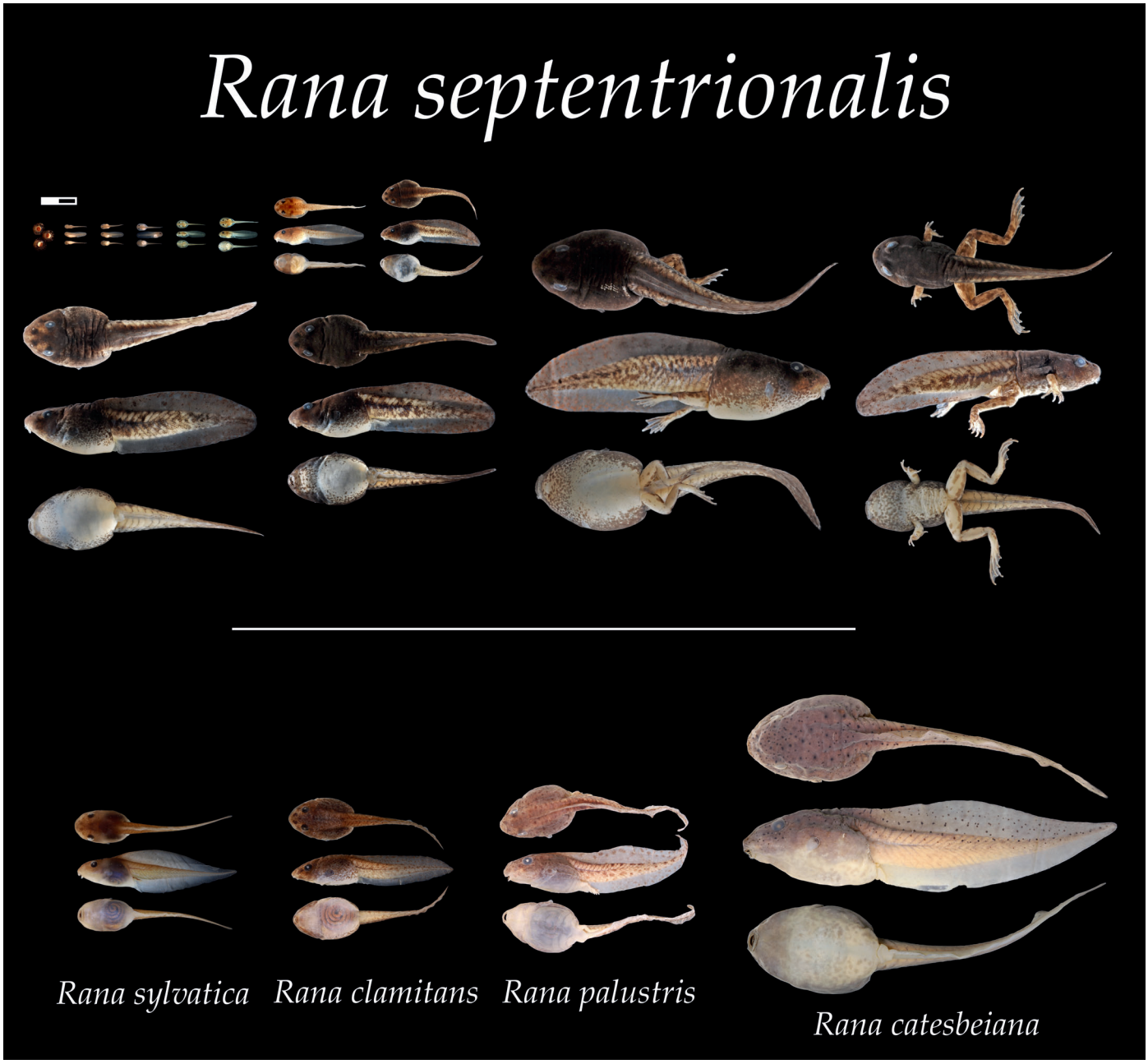

Fig. 2. Images of preserved specimens of *Rana septentrionalis* (YPM HERA 19716, 19699, 19701, 19704, 19711, 19712, 19694, 19696, 19718 [last four, part of a composite lot]) developmental series (top) from embryos to Gosner stage 42 and co-occurring ranid larvae (bottom, left to right) of *Rana sylvatica* (YPM HERA 10322), *Rana clamitans* (YPM HERA 10681), *Rana palustris* (YPM HERA 11412), and *Rana catesbeiana* (YPM HERA 13053). The scale bar is 1 cm. Large images of specimens of *R. septentrionalis* are provided in the Supplemental Materials (see Data Accessibility). Photos by A. Arietta courtesy of Yale Peabody Museum.

obtained late stage larvae, including metamorphs, by mid-July 2016 (Supplemental Table 1; see Data Accessibility).

We visually analyzed larvae (Fig. 2, Supplemental Figs. S1–S12; see Data Accessibility), differentiated seven developmental stages across the samples, and plotted these against SVL for each individual (Fig. 3). These different stages are also represented in Figure 4, in which we present TL and plot our lab-reared data in comparison to TL from Hedeen's (1971) field-collected larvae in Minnesota. The proportion of tail length to body length (SVL) is included as a trait for identification of Mink Frogs in Altig and McDiarmid (2015); Figure 5 reflects data collected on the tadpole specimens in our collection to that ratio of 1.6.

DISCUSSION

Our success in rearing larvae of Mink Frogs in captivity from egg stage through metamorphosis provides important specimens for future study and suggestions for successful husbandry of this species. The egg masses laid in captivity (Fig. 1A, D) are comparable to those seen or photographed under more natural conditions (Fig. 1B, C) and described by Aronson (1943) as a "solid mass or plinth below the surface

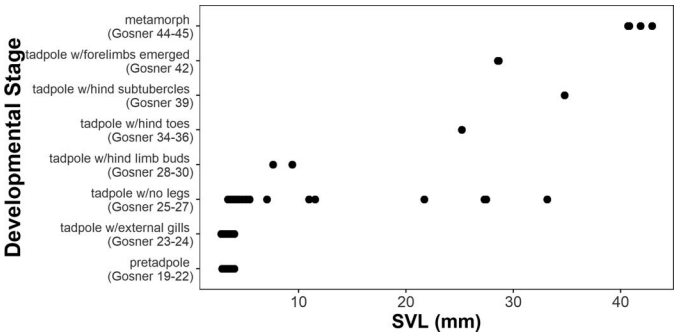

Fig. 3. Snout–vent length of specimens of *R. septentrionalis* that were captive reared, raised indoors in aquaria at early larval stages, and overwintered in outdoor mesocosms. Note that larval densities and conditions fluctuated throughout development because we adaptively managed our stock to ensure we had representative specimens across ontogeny.

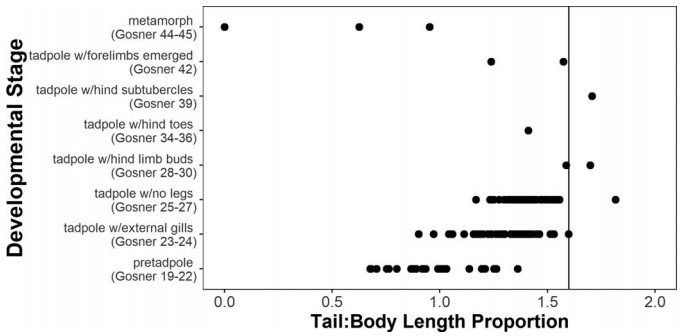

Fig. 5. Proportion of tail length to body length (SVL) across larval stages. The vertical line represents the 1.6 tail length: body length proportion reported by Altig and McDiarmid (2015) for this species.

of the water." Wright and Wright (1933) include descriptions of egg masses observed attached to vegetation from 20–47 cm (8–18 inches) below the surface of the water. In the field, the egg mass of Mink Frogs consists of 500–4000 black ova with two jelly layers, measuring 75–125 mm in diameter (Altig and McDiarmid, 2015). A mass is attached underwater to vegetation but soon after swells and falls to the bottom of the water body (Hunter et al., 1999). The colder water is likely more oxygenated than the surface water, so it is not surprising that survival of larvae in captivity hinges on highly oxygenated water produced using a bubbler. As Hedeen (1986) suggests, this need for sufficient oxygen to support developing embryos in submerged egg masses, along with low tolerance for desiccation and, possibly, avoidance of predaceous American Bullfrogs where they overlap at the bullfrog's northern range limit, may explain why the Mink Frog exhibits a southern limit to its distribution at 43°N.

Our protocols were far from standardized, but we did our best to provide adequate environments for all life stages. Density, for example, was likely reflected in the range of variation in SVL and developmental stage for larvae from the same clutch sampled at the same time. For example, larvae from Group B removed on 14 and 15 July 2016 exhibited dramatic variation in development (Gosner 25–27 compared to Gosner 42, Supplemental Table 1; see Data Accessibility) despite their kinship. This variation may be an adaptive strategy for variable environmental conditions. For example, if larvae are developing in colder less oxygenated water, or in

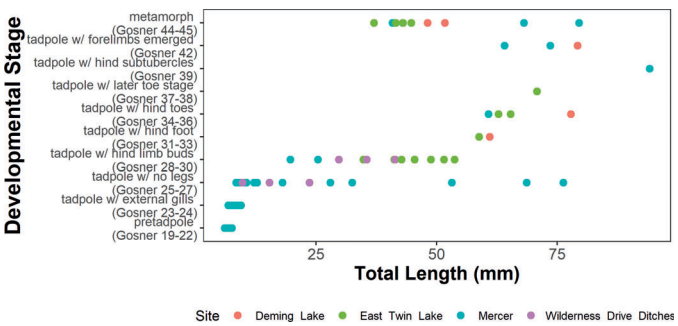

Fig. 4. Total length of Mink Frog larvae reared in our current study (Mercer origin) and from published data from Hedeen (1971) in Minnesota (Deming Lake, East Twin Lake, Wilderness Drive Ditches).

dense populations, some may overwinter twice as seen in American Bullfrogs (Dodd, 2013). Indeed, larvae of American Bullfrog have extremely variable larval periods and metamorphose in as little as three months for populations in Arizona (Dowe, 1979) or as long as three years in more northern latitudes (Oliver and Bailey, 1939; Bruneau and Magnin, 1980). This results in a range of body sizes at metamorphosis as reported in studies like that of Seale (1980). Berven et al. (1979) report similar variation in Green Frog larval periods, which may extend from 300–670 days in populations at high elevation in Virginia compared to 90–300 days for lowland populations in Virginia and Maryland. We have also observed that larvae may reach only Gosner 25 over a year in a mesocosm (Lambert, pers. obs.). Wilbur and Collins (1973) suggest this variation is consistent for ranid frogs that develop in stable, permanent habitats to ensure larvae reach optimum size for metamorphosis.

Larvae of Mink Frogs are reported to hatch in 5–13 days and grow up to 100 mm TL in 12–15 months (Altig and McDiarmid, 2015). In this study, we collected the first hatched larvae, typically staged 17–20 (Gosner, 1960) at 11 days (Supplemental Table 1; see Data Accessibility). The captive larvae then proceeded through development. Altig and McDiarmid (2015) document that larvae metamorphose at about 42 mm if within the first year of hatching, or 72 mm if they overwinter. We can compare the total lengths and developmental stages of the larvae sampled in this study to those collected from ponds in Minnesota over a year (Hedeen, 1971). Sizes at Gosner stages and the variation seen in both sets of samples are similar (Fig. 4). Mink Frog larvae at different developmental stages are featured in images that show both lateral and overhead views (Fig. 2, Supplemental Figs. S1–S12; see Data Accessibility).

These images augment field guide descriptions, including that from Altig and McDiarmid (2015), which describes mature larvae as having a body with a greenish dorsal surface with brown or black mottling, a medium-sized dorsal fin sometimes with pinkish spots, and a labial tooth row formula (LTRF) of 2/3. There may also be contrasting black marks on the posterior third of the tail at later larval stages (Altig and McDiarmid, 2015). This description also includes the ratio of tail length to body length, which for Mink Frog tadpoles is said to be about 1.6. When we plot this metric for the Mink Frog tadpoles in this study, there is substantial variation both within and between Gosner stages, and only a few individuals even reach this ratio value (Fig. 5). This difference may be the result of comparing our captive-reared tadpoles to

those collected and measured from wild populations, and may reflect the various environmental influences on differential growth between body and tail. It is also not clear how this ratio was generated, and to what population(s) of Mink Frogs it is attributed. This trait may be challenging to use to differentiate among sympatric species, but perhaps more investigation would reveal its value. As hind limbs develop in the Mink Frog, it's notable that the third toe is much shorter than the first toe (Altig and McDiarmid, 2015), and webbing extends to the toe tips of the third and fifth toes and to the last joint of the fourth toe. This pattern of webbing is one way to distinguish Mink Frog metamorphs and adults from those of American Bullfrog and Green Frog.

The series of Mink Frog tadpoles we have now documented and analyzed, combined with those for Green Frog and American Bullfrog, contribute a valuable resource to help identify larval stages in the field or in specimen collections. Larval series, including specimens ranging from fertilized egg masses through metamorphs, are relatively scarce, at least in North American museum collections (Altig and McDiarmid, 2015). These series provide rich avenues of research, including opportunities to further investigate potential effects of climate change. Mink Frog occurrence depends largely on water temperature because of the species' sensitivity to thermal conditions at each life stage (Moore, 1952; Hedeen, 1986; Popescu and Gibbs, 2009). Mink Frogs could serve well as an indicator species of climate change, particularly at the southern edge of their range, as conservation biologists are frequently interested in identifying species whose distributional patterns are vulnerable to significant environmental change (Popescu and Gibbs, 2008). There has been extensive research on the influence of climate change on various aspects of the phenology of breeding and activity in the Wood Frog (e.g., Sheridan et al., 2018; Arietta et al., 2020; Larsen et al., 2021). With the reference collection of tadpoles and guidelines for husbandry, the Mink Frog can serve as a different model for studies of climate change on species with more boreal distributions. While Mink Frogs have not generally been considered to be of conservation concern (Casper, 2005; Dodd, 2013), there is growing awareness that a warming climate could impact the species in the southern portions of its range (Popescu and Gibbs, 2009; Patrick et al., 2012). For example, the species is listed as a Species of Greatest Conservation Need in both Maine and New Hampshire's State Wildlife Action Plans. We hope that our descriptions and illustrations of larval Mink Frogs, as well as methodology for their lab rearing, can aid future studies on the species.

DATA ACCESSIBILITY

Supplemental material is available at https://www.ichthyologyandherpetology.org/h2021133. Unless an alternative copyright or statement noting that a figure is reprinted from a previous source is noted in a figure caption, the published images and illustrations in this article are licensed by the American Society of Ichthyologists and Herpetologists for use if the use includes a citation to the original source (American Society of Ichthyologists and Herpetologists, the DOI of the *Ichthyology & Herpetology* article, and any individual image credits listed in the figure caption) in accordance with the Creative Commons Attribution CC BY License.

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