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Estimating Mudpuppy (*Necturus maculosus*) Abundance in the Lamoille River, Vermont, USA

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Abstract*.—The Mudpuppy (*Necturus maculosus*) is classified as a Species of Greatest Conservation Need by the state of Vermont. There is concern regarding status of populations in the Lake Champlain basin because of habitat alteration and potential effects of 3-trifluromethyl-4-nitrophenol (TFM), a chemical used to control Sea Lamprey (*Petromyzon marinus*). The purpose of our research was to assess Mudpuppy capture methods and abundance in the Lamoille River, Vermont, USA. We sampled Mudpuppies under a mark-recapture framework, using modified, baited minnow traps set during two winter-spring periods. We marked each Mudpuppy with a passive integrated transponder (PIT) tag and released individuals after collecting morphological measurements. We collected 80 individuals during 2,581 trap days in 2008–2009 (year 1), and 81 individuals during 3,072 trap days in 2009–2010 (year 2). We estimated abundance from spring trapping periods in 2009 and 2010, during which capture rates were sufficient for analysis. Capture probability was low (< 0.04), but highest following precipitation events in spring, during periods of higher river flow, when water temperatures were approximately 3 to 6° C. During October 2009, management agencies treated the Lamoille River with TFM. Surveyors recovered more than 500 dead Mudpuppies during the post-treatment assessment. Overall, Mudpuppy captures did not change between sampling periods; however, we captured fewer females during year 2 compared to year 1, and the sex ratio changed from 0.79:1 (M:F) during year 1 to 3:1 (M:F) during year 2. Our data may help wildlife managers assess population status of Mudpuppies in conjunction with fisheries management techniques.

Key Words.—amphibian; detection probability; fisheries management; lampricide; mark-recapture; non-target; salamander

Introduction

Amphibian population declines have been attributed to many complex processes, often expected to be acting concurrently, including habitat loss, disease, and invasive species (Blaustein and Kiesecker 2002; Collins and Storfer 2003; Beebee and Griffiths 2005). Additionally, amphibian populations can be deleteriously affected by pesticides and herbicides (Matson 1990; Bonin et al. 1995; Hayes et al. 2010). Given multiple perturbations and potentially interacting stressors, better understanding of amphibian population status and trends will be crucial for making informed management decisions and improving conservation actions (Grant et al. 2016).

Historically, most studies investigating amphibian populations estimated demographic parameters and abundance through analysis of raw data such as direct counts from visual encounter surveys (Mazerolle et al. 2007). Unfortunately, raw counts assume that all individuals are present and available for capture on every survey occasion, and do not address imperfect detection resulting from heterogeneity in the encounter rate of individuals (Mazerolle et al. 2007). Without adjusting estimates for detection probability, demographic parameter estimates can be biased, which may lead to incorrect inferences and management actions (Kroll et al. 2009).

Capture-mark-recapture (CMR) methods can help limit the confounding factors and biases associated with traditional count methods (Williams et al. 2002). A well-designed CMR study can provide unbiased estimates of survivorship, recruitment, and abundance (Willson et al. 2011; Cecala et al. 2013). However, in any wildlife study, capture and recapture probabilities are never perfect and are rarely constant (Pollock et al. 1990). Many factors cause these probabilities to vary, including the behavior of the target species, observer bias, and sampling method (Mazerolle et al. 2007). Therefore, estimators incorporating the effects of these covariates are needed to derive population parameters with confidence.

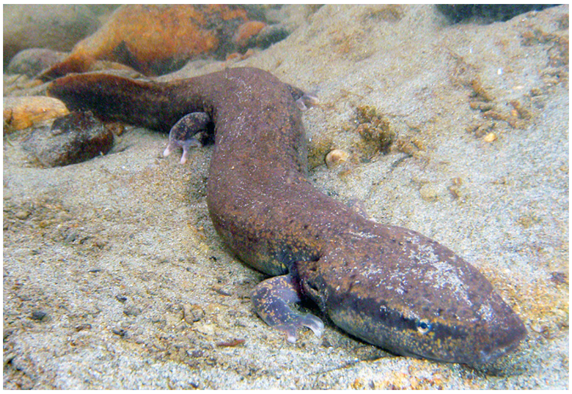

Figure 1. Mudpuppy (*Necturus maculosus*) from the Lamoille River, Vermont, USA. (Photographed by Isaac Chellman).

In this study, we used CMR techniques to estimate abundance and effect of environmental covariates on capture probabilities of the Mudpuppy (*Necturus maculosus*). Mudpuppies (Fig. 1) are habitat generalists (Harris 1959a) that feed on a variety of prey, including various aquatic invertebrates and minnows (Harris 1959b). Breeding occurs during late fall, and additional breeding may also occur during spring (Bishop 1941). Nesting, in which eggs are attached to the underside of cover, occurs during late spring (Eycleshymer 1906; Bishop 1941). Mudpuppies have a wide geographic range, which extends from southeastern Manitoba and southern Quebec, Canada, south to northern Louisiana, Mississippi, Alabama, and Georgia in the USA (Petranka 1998). Vermont represents the eastern edge of the historic range of Mudpuppies in the United States (Bishop 1941; Crocker 1960).

Although common in parts of its range (Gendron 1999), the Mudpuppy is currently listed as a rare, high-priority Species of Greatest Conservation Need in Vermont (Vermont Wildlife Action Plan Team 2015). Unbiased estimates of Mudpuppy demographics are lacking, partly because of low recapture rates (McDaniel et al. 2009). Parameter estimates have been derived for Mudpuppy populations based on count statistics (Matson 1990; McDaniel et al. 2009). However, more robust estimates are needed to better understand population dynamics of Mudpuppy populations. Given the lack of knowledge about Mudpuppy populations in Vermont (e.g., abundance in tributaries, genetic diversity, and importance of their role in the aquatic ecosystem), this study was developed to begin the process of better informing natural resource managers about these native amphibians.

Our objectives were to: (1) determine methods for successfully capturing Mudpuppies in Vermont rivers; (2) estimate live capture probability and factors influencing capture probability; and (3) estimate the population size of Mudpuppies with closed-capture models (Huggins 1991). We sampled Mudpuppies during two winter-spring periods on only one river. Furthermore, during October 2009, state and federal biologists treated the Lamoille River with 3-trifluromethyl-4-nitrophenol (TFM), a chemical used to control Sea Lamprey (*Petromyzon marinus*). The TFM treatment was not part of this study, but we assisted with the post-treatment assessment.

Materials and Methods

Study area.—We conducted our study from 2008 to 2010 in the Lamoille River, a tributary of Lake Champlain, Vermont, USA (Fig. 2). The Lamoille River is 135 km long and drains a watershed of more than 1,800 km^2. Our study area was a 1-km reach of the Lamoille River that extended from just downstream of Bear Trap Road upstream to an area below Peterson Dam (Fig. 2). Peterson Dam is 15.5-m high and located 9 km upstream from the mouth of Lake Champlain, and it is the first anthropogenic barrier encountered when navigating upstream from the lake. Bedrock, boulder, and cobble dominated the river substrate within about 500 m of the Peterson Dam. Substrate composition changed to primarily sand, silt, and organic matter through the rest of the study reach. Average width of the river in the study reach was 115 m. Water depth within the trapping area ranged between 0.5 and 2.5 m. During the two study periods, air temperature ranged from -15 to 25° C and water temperature ranged from 0.5 to 16° C.

Field sampling.—During both periods of the study, we used modified minnow traps to sample adult Mudpuppies and obtain encounter (live capture) histories in a mark-recapture framework. One of our initial goals was effectively capturing Mudpuppies to better allow: (1) current and future study; (2) estimation of demographic parameters; and (3) managers the ability to monitor population status over time. Therefore, we set traps non-randomly in three clustered arrays, which encompassed areas with known rocky cover. Additionally, to maintain safety while working on a large river during winter, we placed traps parallel to the shoreline, within approximately 10 m of the bank. The Lamoille River frequently freezes near the shoreline, but mid-river often remains open water throughout the winter. During this study, enough ice was present to prevent safe boating, but mid-channel ice was not thick enough to bear the weight of a person. Therefore, we did not set traps throughout the full width of the river.

Our trap arrays were 140 m long and contained eight traps, which we set 20 m apart. Because of restricted access, we placed all traps along the southern bank (Fig. 2). River substrate within the upstream trap array near Peterson Dam was predominantly cobble, silt, and

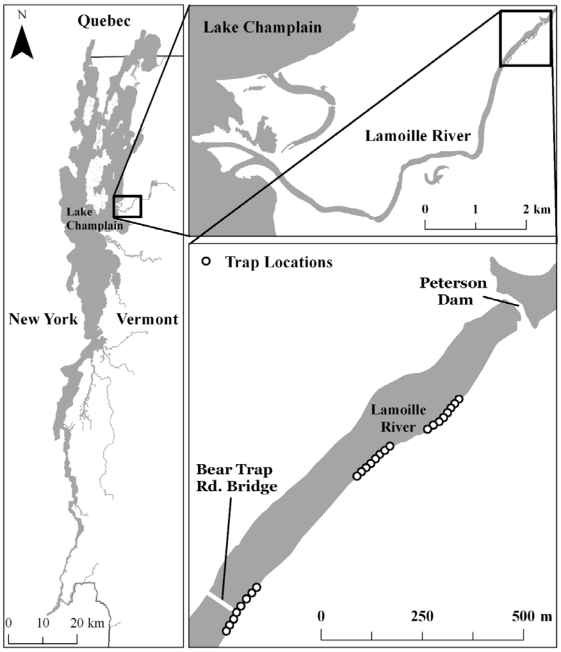

FIGURE 2. The Lake Champlain basin (left), lower Lamoille River, Vermont, USA (top right), and Mudpuppy (*Necturus maculosus*) trapping arrays during December 2008 to May 2009 (year 1) and December 2009 to May 2010 (year 2) between Bear Trap Road and the Peterson Dam, Milton, Vermont, USA (lower right).

scattered boulders. Within the middle and downstream trap arrays, the substrate was predominantly silt. Cobble and boulder used for bank stabilization of the adjacent road and Bear Trap Road bridge dominated the river substrate within about 2 m of shoreline.

Minnow traps were cylindrical and made of wire mesh with an inward-facing conical entrance on each end (Frabill, Plano, Illinois, USA; Fig. 3A). To allow adult Mudpuppies passage, we expanded trap entrances as described by Gendron et al. (1997) and fit each end with a 3.5 cm or 5 cm electrical box adapter using methods adapted from Rodda et al. (1999), which maintained trap entrance shape and created a smooth surface over which Mudpuppies could pass (Figs. 3B and 3C). We placed roofing slate inside traps to provide cover and weight for anchoring traps on the substrate (Fig. 3B). We baited traps with frozen, pathogen-free Golden Shiners (*Notemigonus crysoleucas*; purchased from a certified dealer for bait) placed in porous containers attached inside the trap with zip ties. To limit trap loss, we either attached traps to shore with a small (#3) chain or through the ice using the methods of Gendron et al. (1997), as modified by Robert Foster et al. (unpubl. report), to limit refreezing of holes in the ice. We checked traps at least every 48 h.

We set 24 traps during 121 days from December 2008 to May 2009 (year 1) and 24 traps during 142 days from December 2009 to May 2010 (year 2). We set traps in the same locations during both years. At the onset of trapping, we visually recorded (1) water depth categories (< 1 m or > 1 m); (2) primary (most abundant) substrate type (e.g., boulder, cobble, sand, silt, etc.) and (3) secondary (second most abundant) substrate type in the area within 5 meters of each trap location. We accumulated 5,653 trap days during our two winter to spring sampling periods. We did not set traps from mid-May through November because trapping Mudpuppies has been ineffective during the warmer periods of late spring through early fall (Gendron 1999; McDaniel et al. 2009). We obtained coarse estimates of Mudpuppy movement by measuring the distance (nearest m) between trap location of initial capture and trap location of recapture.

We weighed Mudpuppies to the nearest gram and briefly secured individuals in plastic bags to measure total length (TL) and snout-vent length (SVL) to the nearest 5 mm. We determined sex of adult Mudpuppies by inspecting the cloaca (in males, the cloaca is conspicuously swollen and contains paired papillae at the posterior end through winter and early spring; in females, the cloaca has no evident swelling or papillae; Bishop 1926; Gendron 1999). To provide a unique

FIGURE 3. Sampling gear used to capture adult Mudpuppies (*Necturus maculosus*) in the Lamoille River, Vermont, USA. (A) Stacks of modified minnow traps ready for deployment. (B) close up view of modified trap entrance from the inside (showing the electrical box adapter inserted and glued into the opening), roofing slate cover object, and a captured Mudpuppy. (C) A trap with two captured Mudpuppies showing a profile view of the opening fitted with an electrical box adapter. (Photographed by Isaac Chellman).

identifier, we injected a 125-kHz passive integrated transponder (PIT) tag (Biomark, Boise, Idaho, USA) laterally into the tail base of Mudpuppies > 150 mm SVL. After processing, we treated PIT tag injection points with a fine coating of liquid bandage to facilitate healing. We held Mudpuppies briefly in cold, aerated water before release back to their point of capture.

On 1 October 2009, between years 1 and 2 of this study, state and federal biologists treated a 9-km reach of the Lamoille River between the Peterson Dam and Lake Champlain with TFM, which was dispensed at the Peterson Dam pump house during a 12-h period (Vermont Fish and Wildlife Department, unpubl. report). Our entire study area was within the TFM treatment reach. We assisted with collecting Mudpuppy mortalities during the post-treatment assessment that occurred on 2 and 3 October 2009. During the post-treatment assessment, four teams of two biologists surveyed for fish and amphibians throughout the entire treated portion of river, including banks, shallows, and other areas where the bottom was visible. We collected all dead Mudpuppies observed to preserve specimens and scan adults for PIT tags. We recorded TL of all Mudpuppies to the nearest mm. We did not record sex of dead adult Mudpuppies because our method for determining sex of adults was unreliable for partially degraded carcasses.

Capture probability and abundance estimates.—To obtain estimates of capture probability (p; the probability that an unmarked animal would be captured), recapture probability (c; the probability that a previously marked animal would be recaptured), and abundance (N), we analyzed Mudpuppy capture histories using Huggins' closed capture model (Huggins 1991). This model uses capture histories as inputs, and then finds maximum likelihood estimates of p and c, and the covariates affecting those probabilities. With rigorous estimates of p and c, population size can be estimated as the number of captured animals, plus the number of animals that failed to be captured ($1-p$), across the entire sampling period (Huggins 1991).

Closed capture models assume that the population under study is effectively closed to birth, immigration, death, and emigration. To help meet these assumptions, we estimated population size for a period of approximately one month in the early spring of each sampling period (spring 2009 and spring 2010), beginning when water temperature and river flows started increasing, and continuing until we did not catch Mudpuppies for at least one week. During this interval, capture and recapture rates were sufficient to provide estimates. Captures and recaptures during other intervals in our study were insufficient for population estimation. The spring 2009 sampling period began on 23 March and ended on 22 April. The spring 2010 sampling period began on 14 March and ended on 18 April.

Mudpuppies exhibit seasonal changes in activity and movement (Shoop and Gunning 1967; Harris 1959a; Gendron 1999). In general, Mudpuppies exhibit site fidelity and limited home ranges (Shoop and Gunning 1967; Sajdak 1982), particularly during the late spring nesting period when females may guard eggs (Bishop 1941; Gendron 1999). Given the presence of suitable nesting habitat (e.g., large natural rocks and installed riprap) in our study area, we assumed Mudpuppies remained within the study area during each month-long period as they engaged in potential courtship and breeding. We estimated early spring abundance and standard error (SE) separately for each period.

Mudpuppy capture probability may be influenced by breeding season, photoperiod, water temperature, rainfall, or other unknown factors (Hutchison and Ritchart 1989; Gendron 1999). For estimates of population size each spring, we ran a suite of *a priori* models incorporating combinations of environmental covariates that we hypothesized may influence Mudpuppy p and c. Because of the low number of recaptures (see Results), we assumed that capture and recaptures were similarly influenced by the environmental covariates, and hereafter refer to capture and recapture events as captures. In all models, sexes were analyzed separately as a group effect. A small number of juvenile Mudpuppies were captured during each spring trapping period. Therefore, we removed two juveniles from the spring 2009 data set and one juvenile from the spring 2010 data set from analyses because sex could not be determined.

For the Huggins' (1991) analysis, we investigated a set of environmental covariates that may have affected Mudpuppy activity and capture probability during early spring. The covariates we chose were informed by potential environmental cues present during successful late winter-early spring trapping efforts in other systems (Bonin et al. 1995; Gendron et al. 1997; McDaniel et al. 2009). The heightened Mudpuppy activity and increased trapping success in early spring may be initiated by, or related to, the corresponding changes in closely interrelated environmental variables, including increasing ambient temperatures, early season snowmelt, and the onset of precipitation in the form of rain, all of which increase water temperatures and river discharge rates. Because we planned to investigate the possible relationship of environmental covariates in a general way, we made several covariates binary to represent thresholds above or below which the covariate may have affected capture probability (e.g., water temperature below a certain level, river flows above a selected rate, etc.).

Table 1. Sampling effort (traps [n] × days deployed) and number of individual Mudpuppies (*Necturus maculosus*) collected in the Lamoille River, Vermont, USA, from December 2008 to May 2009 (Year 1) and December 2009 to May 2010 (Year 2) trapping. Captures (n) include new captures for the year (i.e., no same year recaptures). Recaptures (n) include only the initial recapture occasion of new Mudpuppies for the year.

	Year 1			Year 2		
Dates Deployed	6–21 December	16 Jan. to 7 May	Total	1–21 December	5 Jan. to 7 May	Total
Days Deployed (n)	15	106	121	20	122	142
Effort (trap days)	342	2,239	2,581	462	2,610	3,072
Mudpuppies (n)						
Captures	*7	73	80	24	57	81
Recaptures	1	11	12	5	12	17

*Includes one incidental juvenile captured by hand while checking traps.

We considered the effect of water temperature on capture and recapture rates (T and T^2). Additionally, because there has been limited success capturing Mudpuppies during warmer times of year (Gendron 1999), we suspected that Mudpuppy activity (and, correspondingly, capture probability) would likely decrease as water temperatures increased above a certain threshold. Therefore, we investigated whether capture probability was higher during the period when water temperatures just began climbing (between 3° and 6° C; represented by the binary covariate TT).

The covariate P represents total precipitation on the day we checked traps. We further dichotomized this covariate as PT, indicating whether precipitation on the day traps were checked exceeded 2.5 mm (which we estimated may be enough to potentially affect stream conditions that day). Because we normally checked traps every other day, we were interested in learning if precipitation events prior to the day of trap checking possibly affected capture probability. Correspondingly, river flow rates on the day of capture may be affected by rainfall events on previous days. Therefore, we were also interested in whether precipitation events one and two days prior to trap check days affected Mudpuppy capture probability. To model these possible effects, we investigated the binary covariate YP, indicating whether precipitation on the day before we checked traps exceeded 2.5 mm, and the binary covariate PP, indicating whether precipitation two days before we checked traps exceeded 6 mm (a heavier precipitation event that may alter stream conditions for a more than one day).

Streamflow conditions are often related to precipitation events, and may affect the probability of capture (Crocker et al. 2007). We hypothesized that Mudpuppy activity may decrease with flow extremes because the lowest flow rates usually occur in summer (during known periods of decreased trapping success), and very high flow events may prevent Mudpuppies from successfully foraging, breeding, and nesting. The covariate F represents river flow (in cubic feet per second; cfs). We additionally considered the binary covariate FT as flows that exceeded 3,000 cfs on the day we checked traps; whereas, the binary covariate PF indicates flows that exceeded 3,000 cfs on the day before we checked traps.

Because of the low number of total captures, we considered models with one to four covariates, and evaluated all combinations of variables within those limits. That is, the model set only incorporated combinations of up to three covariates plus the intercept, which represented overall capture probability. We excluded redundant combinations from the model set, including temperature + temperature thresholds, flow + flow thresholds, and precipitation + precipitation thresholds. We ran 85 models for each trapping season.

We ran the Huggins' closed capture analyses in program MARK (White and Burnham 1999) and used model selection procedures (Burnham and Anderson 2002) to compare the strength of evidence among models. For all models, we used the alternative optimization method because some models failed to converge under the default method. We used model averaging to draw inferences on the estimated parameters and estimated population size (Burnham and Anderson 2002).

Results

We captured 160 live Mudpuppies (with an additional 29 recapture events) during 5,653 trap days and one live juvenile Mudpuppy incidentally (Table 1). Incidental trap captures included numerous crayfish, small fish, and several adult Northern Leopard Frogs (*Rana pipiens*). Although substrate type varied at the trap locations, we captured at least one Mudpuppy from every trap set during the course of the study. The substrate types we observed included boulder, cobble, pebble, sand, and silt. Anecdotally, we observed that traps with the highest number of Mudpuppy captures were in close proximity to large cobble and boulders. Traps resulting in the lowest captures were generally in locations without many large cover objects and substrate composed primarily of silt and sand.

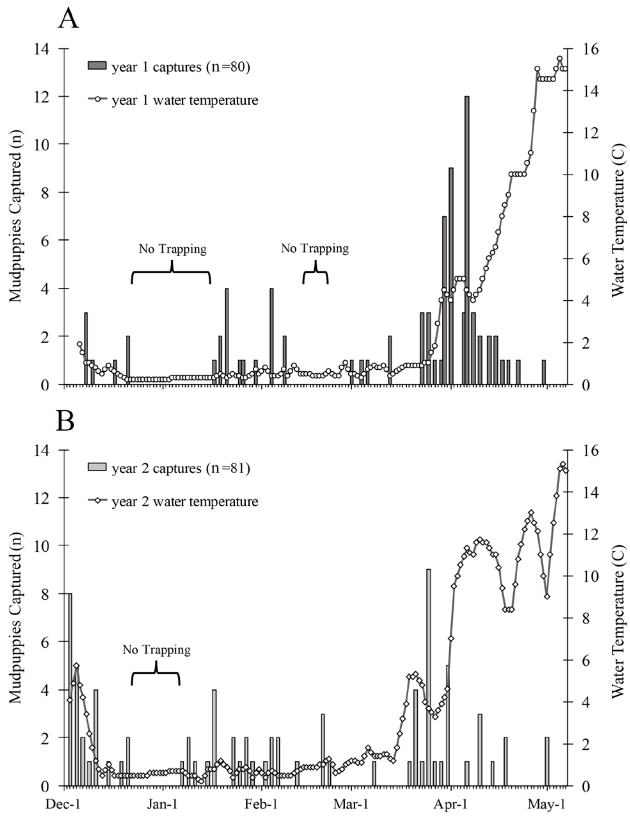

Figure 4. Water temperature and number of Mudpuppies (*Necturus maculosus*) captured from traps set in the Lamoille River, Vermont, USA, during (A) December 2008 to May 2009 (year 1) and (B) December 2009 to May 2010 (year 2). Mudpuppy captures do not include same year recaptures. Time periods when traps were not deployed are shown. Water temperature is the daily mean.

Mudpuppies moved an average distance of 81.8 m ± 21.3 (SD; range = 60.5–103.1 m) between captures. Males moved 87.5 m ± 30.1 (range = 57.4–117.6 m) on average and females moved 71.7 m ± 25.8 (range = 45.9–97.5 m) on average. The maximum distance moved was 780 m for a male and 440 m for a female. The largest movements (> 150 m) were in an upstream direction during early spring.

Sex ratio of newly captured, live adult individuals differed between the two years. In year 1, 44% of new adult captures were male and 56% were female, which was not different from an even sex ratio ($\chi^2 = 0.853$, df = 1, $P = 0.356$). In year 2, 75% of new adult captures were male and 25% were female (3M:1F), which differed significantly from a 1:1 sex ratio ($\chi^2 = 19.0$, df = 1, $P < 0.001$). Sex ratios for recaptured adult Mudpuppies were not different from 1:1 in either year (year 1: $\chi^2 = 0.333$, df = 1, $P = 0.564$; or year 2: $\chi^2 = 2.25$, df = 1, $P = 0.134$).

Changes in Mudpuppy capture rates appeared to be related to water temperature (Fig. 4). In year 1, more than half the total captures (53%) occurred during spring when water temperatures ranged between approximately 3° and 6° C. However, as water temperatures increased to 10° C, captures quickly declined. When the water temperature was > 10° C, capture rates dropped to nearly zero (Fig. 4A). We observed a similar association of capture rates and water temperature during year 2. However, unlike year 1, the spike in captures during year 2 occurred during both late fall and early spring. Water temperatures during both periods of higher capture rates during year 2 (early December and early spring) were around 3° to 6° C (Fig. 4B).

With the exception of three juveniles captured during year 1 and four juveniles captured during year 2, live trapped Mudpuppies were adults. During year 1, we captured live Mudpuppies ranging between 170 and 350 mm TL ($\bar{x}$ = 302.7 mm, Standard Deviation (SD) = 28.8 mm; Fig. 5A). During year 2, we captured live Mudpuppies ranging between 210 and 360 mm TL ($\bar{x}$ = 290.5 mm, SD = 31.7 mm; Fig. 5B). The change in TL between years was significant ($t = 2.497$, df = 154, $P = 0.014$). The weight range of live captured Mudpuppies was between 20 and 280 g ($\bar{x}$ = 147.9 g, SD = 44.5 g), but precise weights of Mudpuppies > 200 g during year 1 were not determined.

During the post-TFM treatment assessment, we recovered 528 dead Mudpuppies, ranging in total length from 25 to 360 mm ($\bar{x}$ = 150.6 mm, SD = 64.9 mm; Fig. 6). Using the aging method based on TL modal peaks

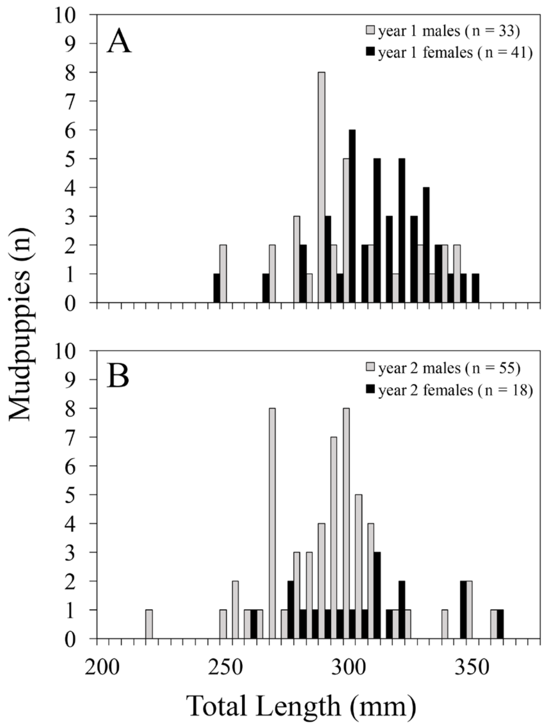

FIGURE 5. Total length frequency histogram of male and female adult Mudpuppies (*Necturus maculosus*) collected in the Lamoille River, Vermont, USA, from (A) December 2008 to May 2009 trapping (year 1) and (B) December 2009 to May 2010 trapping (year 2). Data on captured juveniles (year 1, n = 3; year 2, n = 4) and adults (year 1, n = 2; year 2, n = 4) with no length and/or sex recorded are not shown.

(Richmond 1999), juveniles comprised more than 70% of Mudpuppy mortalities. None of the adult Mudpuppy mortalities collected contained PIT tags.

Capture probability and abundance estimates.— Because of the low number of captures, there was model uncertainty from the analyses of both spring trapping periods. For the spring 2009 full model set, 90% of the AIC_c weight was distributed among the top 19 models (Table 2), while the spring 2010 model set included 90% of the AIC_c weight distributed among the top 11 models (Table 3). Capture and recapture probabilities were extremely low, usually less than 0.04. The top models for spring 2009 and 2010 included various combinations of the environmental covariates analyzed (Appendix). However, all top models with AIC weights of at least 0.01 in both spring periods included > 6 mm precipitation two days prior to the trapping day (PP), which increased the probability of capture. During spring 2009, flows that exceeded 3,000 cfs within one day of checking a trap were also associated with increased capture probability. During spring 2010, capture probabilities were significantly higher when stream temperatures were between 3 and 6° C (TT).

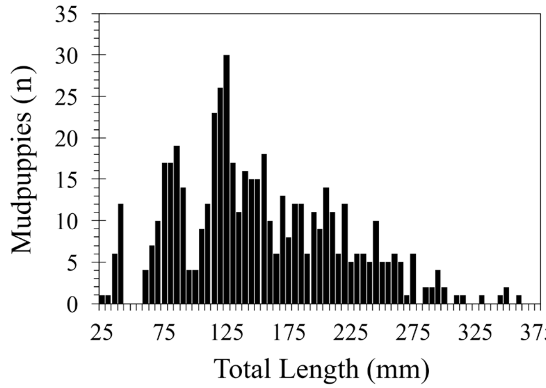

FIGURE 6. Total lengths of Mudpuppies (*Necturus maculosus*; n = 515) recovered in the Lamoille River, Vermont, USA, during two days (2–3 October 2009) of post-TFM treatment assessment. We did not measure 13 salamanders because of deterioration.

Although the beta coefficients had high uncertainty because of small sample sizes, these results suggest that Mudpuppy capture probabilities may be doubled by sampling on days that follow larger precipitation events that result in high stream flow. For example, the top ranking 2009 model indicates that baseline capture probability is (exp(5.348)/(1+exp(5.348)) = 0.005. Following a significant precipitation event, the capture probability increased to 0.013, and with stream flow > 3,000 cfs, capture probability increased to 0.035.

Between 23 March and 22 April of spring 2009, the model averaged *N* for adult Mudpuppies was 300 adults, consisting of 141 males (SE = 68.72) and 159 females (SE = 77.08; Fig. 7). Between 14 March and 18 April of spring 2010, *N* for adult Mudpuppies was 123 adults, consisting of 109 males (SE = 57.96) and 14 females (SE = 9.75; Fig. 7). Low capture probability of Mudpuppies resulted in few recaptures and large confidence intervals in our model-averaged abundance estimates. Therefore, we could not detect a change in *N* between years for male Mudpuppies. However, we detected a decline in *N* for female Mudpuppies. Although we had few recaptures, the confidence intervals for female Mudpuppies did not overlap, which suggests that female abundance declined between years.

DISCUSSION

Incorporating heterogeneity in capture probability reduced the bias of our parameter estimates; however, our capture methods were adult-biased, and the precision of our abundance estimates was reduced by low recapture rates. Because the study was conducted during two years on only one river, we do not know if observed differences in demographic parameters (or, in some instances, apparent lack thereof) are related to any particular source (e.g., differences in water temperature, river discharge, precipitation events, sex-biased trap

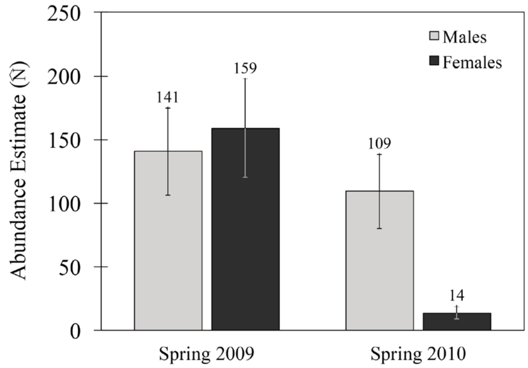

Figure 7. Model averaged abundance estimates ($\hat{N}$) ± standard error of adult male and female Mudpuppies (*Necturus maculosus*) within the area where traps were deployed in the Lamoille River, Vermont, USA, during spring 2009 (23 March to 22 April) and spring 2010 (14 March to 18 April). We used the Huggins closed capture model framework in program MARK to estimate abundances.

response, or TFM treatment). The changes we observed may represent changes in Mudpuppy availability for capture during sampling or an actual change in population structure.

Mudpuppies have limited home range sizes (Shoop and Gunning 1967; Sajdak 1982; Matson 1998), and movements between capture events in this study were similar to those found in Louisiana (Shoop and Gunning 1967). The largest documented movement of a Mudpuppy was 1 km in 24 h by a radio-tagged female during a study on the Mukwonago River, Wisconsin, USA (Sajdak 1982). However, all other radio-tagged and recaptured Mudpuppies in the Wisconsin study had movements over smaller distances and longer periods of time (Sajdak 1982). Based on our trapping data and other published movement data, Mudpuppies appear to be fairly sedentary, and at least a portion of populations exhibit site fidelity (Shoop and Gunning 1967; Sajdak 1982; Matson 1998). More research on direct movements (e.g., radio tracking) is needed to determine if Mudpuppy populations engage in longer distance movements, such as potential seasonal migrations, which have been hypothesized, but for which definitive evidence is currently lacking (Gendron 1999).

We were not able to estimate the age structure of Mudpuppies in either year of our study. Our live-capture methods were adult-biased (Gendron 1999; McDaniel et al. 2009). With few exceptions (three captures in year 1

Table 2. Top 19 models from Huggins closed capture abundance estimates of Mudpuppies (*Necturus maculosus*) captured in the Lamoille River, Vermont, USA, during 23 March to 22 April 2009 (spring 2009) trapping. Because of low recaptures, capture and recapture probability have the same intercept, indicating that trapping effect was not considered. In all models, sex was a group effect and thus the effect of each covariate was estimated separately for males and females. Model parameters are F = river flow in cubic feet/second (cfs); T = water temperature and water temperature^2; FT = binary variable for river flows that exceeded 3,000 cfs on the day of trap checking; PF = binary variable for flows that exceeded 3,000 cfs on the day before trap checking; PP = binary variable for precipitation > 6 mm two days before trap checking; PT = binary variable for precipitation > 2.5 mm on the day of trap checking; TT = binary variable for water temps between 3° and 6° C; YP = binary variable for precipitation > 2.5 mm on the day prior to trap checking.

Model	AIC_c	Delta AIC_c	AIC_c Weights	Model Likelihood	# Par.	Deviance
Intercept + PP + PF	298.27	0.00	0.20	1.00	3	292.24
Intercept + PP + TT + PF	299.50	1.23	0.11	0.54	4	291.46
Intercept + YP + PP + PF	299.85	1.58	0.09	0.45	4	291.80
Intercept + YP + PP	300.10	1.84	0.08	0.40	3	294.08
Intercept + PT + PP + PF	300.21	1.94	0.07	0.38	4	292.16
Intercept + T + PP + PF	300.21	1.94	0.07	0.38	5	290.14
Intercept + PP + FT + PF	300.29	2.02	0.07	0.36	4	292.24
Intercept + YP + PP + TT	301.98	3.71	0.03	0.16	4	293.93
Intercept + PT + YP + PP	302.03	3.76	0.03	0.15	4	293.98
Intercept + YP + PP + FT	302.07	3.80	0.03	0.15	4	294.03
Intercept + F + YP + PP	302.11	3.84	0.03	0.15	4	294.07
Intercept + F + PP	302.60	4.33	0.02	0.11	3	296.57
Intercept + PP + FT	303.25	4.98	0.02	0.08	3	297.22
Intercept + T + YP + PP	303.36	5.09	0.02	0.08	5	293.29
Intercept + PP	303.44	5.17	0.01	0.08	2	299.43
Intercept + PP + TT	304.32	6.05	0.01	0.05	3	298.29
Intercept + T + F + PP	304.55	6.28	0.01	0.04	5	294.48
Intercept + T + PP	304.57	6.31	0.01	0.04	4	296.53
Intercept + F + PP + TT	304.62	6.35	0.01	0.04	4	296.57

Table 3. Top 11 models from Huggins closed capture abundance estimates of Mudpuppies (*Necturus maculosus*) captured in the Lamoille River, Vermont, USA, from 14 March to 18 April 2010 (spring 2010) trapping. Because of the small number of recaptures, capture and recapture probability have the same intercept, indicating that recapture effect was not considered. In all models, sex was a group effect and thus the effect of each covariate was separately estimated for males and females. Model parameters are F = river flow in cubic feet/second (cfs); P = total daily precipitation on the day of trap checking; FT = binary variable for river flows that exceeded 3,000 cfs on the day of trap checking; PF = binary variable for flows that exceeded 3,000 cfs on the day before trap checking; PP = binary variable for precipitation > 6 mm two days before trap checking; PT = binary variable for precipitation > 2.5 mm on the day of trap checking; TT = binary variable for water temperatures between 3° and 6° C; YP = binary variable for precipitation > 2.5 mm on the day prior to trap checking.

Model	AIC_c	Delta AIC_c	AIC_c Weights	Model Likelihood	# Par.	Deviance
Intercept + PP + TT	166.75	0.00	0.25	1.00	3	160.70
Intercept + PP + TT + FT	167.43	0.68	0.18	0.71	4	159.35
Intercept + PT + PP + TT	168.07	1.32	0.13	0.52	4	159.99
Intercept + F + PP + TT	168.53	1.78	0.10	0.41	4	160.45
Intercept + PP + TT + PF	168.66	1.90	0.10	0.39	4	160.58
Intercept + YP + PP + TT	168.75	2.00	0.09	0.37	4	160.67
Intercept + F + P + TT	172.55	5.80	0.01	0.06	4	164.47
Intercept + PP	172.65	5.90	0.01	0.05	2	168.63
Intercept + PT + PP	172.99	6.24	0.01	0.04	3	166.94
Intercept + PP + FT	173.13	6.38	0.01	0.04	3	167.08
Intercept + P + TT + FT	173.61	6.86	0.01	0.03	4	165.53

and four captures in year 2), Mudpuppies captured in this study were probably sexually mature individuals more than six years old. Younger age classes were present in the population as evidenced by the sizes of Mudpuppies recovered in the post-TFM treatment assessment. We do not know the precise number of age classes because determining age with this method is inaccurate for older individuals (McDaniel et al. 2009); however, we collected larvae (i.e., young of the year individuals < 60 mm; Bishop 1926), juveniles, and adults following the TFM treatment. The age class distribution of Mudpuppies recovered following TFM treatment was similar to the distributions obtained by seining and rock flipping in the Grand River, Ohio (Matson 1990). However, seining is highly biased to capturing larval and juvenile Mudpuppies, whereas rock flipping is biased to capturing adults (Matson 1990). Rock flipping is not feasible in the lower Lamoille River because of water depth (> 2 m throughout most of the river channel) and frequent turbidity (i.e., poor visibility). Seining is not practical because of deep water and presence of rocky substrate that would impede the nets.

Our low capture probabilities are similar to those estimated for salamanders in other systems (Jung et al. 2000; Bailey et al. 2004b; Cecala et al. 2013). Our study and others in northern river systems reveal similar seasonal trends in capture rates (Matson 1990; Gendron et al. 1997; McDaniel et al. 2009; Craig et al. 2015). Mudpuppies may not be available for capture during the warmer months because of many possible factors, including affinity for remaining in cooler water of deeper crevices, predator avoidance, seasonal changes in foraging behavior, and parental care during late spring and early summer (Gendron 1999). Based on our data, early spring is the most efficient sampling time and yields the greatest number of captured Mudpuppies.

Sex ratios of Mudpuppies captured during year 1 were not statistically different from 1:1, but were highly male-biased during year 2. Biased Mudpuppy sex ratios have been observed in other studies, which varied in method, time of year, and location. Mudpuppies collected by set lines and dip net in some studies have not differed significantly from a 1:1 sex ratio (Cagle 1954; Gibbons and Nelson 1968; Sajdak 1982), but a study in Louisiana found Mudpuppies caught on set lines had a M:F sex ratio of exactly 0.5:1 (Shoop 1965). However, another study using set lines in the same area found an even sex ratio (Cagle 1954). A study using set lines between November and February in Louisiana also found a highly female-biased sex ratio of 0.47:1 (52 males and 110 females; Shoop and Gunning 1967). A noxious fish control effort (where Mudpuppies were speared from boats) in Evans Lake, Michigan, USA, observed a male-biased sex ratio of 1.6:1 (66 males and 41 females; Lagler and Goellner 1941). Mudpuppy sampling in Ontario, Canada, using modified minnow traps yielded overall female-biased sex ratios (McDaniel et al. 2009). The large variability in sex ratio among studies complicates interpretation of the sex ratios we observed. However, the large reduction in female captures from year 1 to year 2, and the non-overlapping confidence intervals in our model-averaged female abundance estimates for the spring periods, suggests that some factor or factors reduced the number of females, or resulted in fewer females being available for capture.

Mudpuppy females may select different preferred temperatures than males during the spring breeding period. For example, females may select colder water in crevices or greater depths than males. Laboratory work has demonstrated changes in Mudpuppy preferred temperatures following acclimation to different temperatures (Hutchison and Hill 1976). However, we are not aware of any field studies investigating possible behavioral differences between Mudpuppy sexes related to water temperature or river flows. Alternatively, female Mudpuppies may exhibit greater trap-shyness than males through a learned response to stress during initial capture (Bailey et al. 2004a; Cecala et al. 2013). When compared with males, female Mudpuppies in eastern Canada exhibit significantly higher levels of the stress response hormone corticosterone following trapping and confinement (Gendron et al. 1997). Fewer female captures in the second year may have also resulted from more general trap avoidance, which could be caused by factors such as neophobia (i.e., evading new habitat that may contain predators; Gall and Mathis 2010; Mathis and Unger 2012), or preference for more familiar habitat types (Mushinsky 1976).

Breeding behavior of females may have been different between year 1 and year 2. For example, because of physiological constraints or environmental influences, some females may not breed every year (Gendron 1999), which would alter their movement patterns and potentially lower capture probability. However, we expect that variation in reproductive schedules and breeding condition among females within the population would mask differences in capture rates between years. Therefore, different breeding cycles within the population is an unlikely explanation for the reduced number of females sampled during year 2. Finally, adult females may be more susceptible than adult males to TFM-induced mortality.

We do not know if treating the Lamoille River with TFM during October 2009 will have long-term effects on the Mudpuppy population. Adult Mudpuppies in a laboratory study showed no effects from exposure to TFM at concentrations 1.6 times the minimum lethal concentration for larval Sea Lamprey (Boogaard et al. 2003). However, Mudpuppy mortalities observed following TFM treatments in several river systems have been composed primarily of juveniles (Boogaard et al. 2003; Al Breisch, unpubl. data). In the Lamoille River, we recovered carcasses of larvae, juveniles, and adults during the post-treatment assessment, but more than 70% of observed mortalities were juveniles. If adults are less affected by TFM than juveniles, a larger sample size, higher recapture rates, and several collection methods that target all life stages are needed to detect possible declines in Mudpuppy abundance following treatments.

Inferences on the change in female Mudpuppy abundance we observed in this study are limited by the short duration and our sampling methodology. Implementing a method, or multiple methods, to collect all life stages (eggs, larvae, juveniles, and adults) would be difficult in a deep river system with limited visibility. However, long life spans (Gendron 1999; McDaniel et al. 2009) and evidence for limited movement (Shoop and Gunning 1967; Matson 1998) suggest that a large subset of the population could be marked and recaptured during long-term monitoring, which would improve the reliability of demographic parameter estimates. Long-term studies would better detect changes in population structure and abundance.

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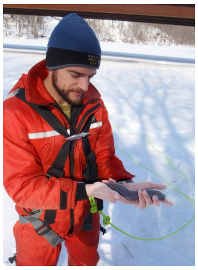
Appendix. Beta estimates (and standard errors) from models carrying at least 5% of the AIC_c weight in Huggins closed capture abundance estimate modeling of Mudpuppies (*Necturus maculosus*) captured in the Lamoille River, Vermont, USA, from 23 March to 22 April 2009 (spring 2009) and 14 March to 18 April 2010 (spring 2010) trapping. In all models, sex was a group effect and thus the effect of each covariate was separately estimated for males and females. Model parameters are T = water temperature and water temperature^2; F = river flow in cubic feet/second (cfs); FT = binary variable for river flows that exceeded 3,000 cfs on the day of trap checking; PF = binary variable for flows that exceeded 3,000 cfs on the day before trap checking; PP = binary variable for precipitation > 6 mm two days before trap checking; PT = binary variable for precipitation > 2.5 mm on the day of trap checking; TT = binary variable for water temperatures between 3° and 6° C; YP = binary variable for precipitation > 2.5 mm on the day prior to trap checking.

Spring	Model	Weight	Intercept	PP	PF	TT	YP	PT	T	T^2	FT
2009	Int. + PP + PF	0.195	-5.35 (0.53)	1.05 (0.34)	0.98 (0.36)	–	–	–	–	–	–
2009	Int. + PP + TT + PF	0.105	-5.21 (0.55)	1.05 (0.34)	1.33 (0.56)	-0.49 (0.57)	–	–	–	–	–
2009	Int. + YP + PP + PF	0.089	-5.38 (0.53)	1.31 (0.53)	0.76 (0.5)	–	0.33 (0.5)	–	–	–	–
2009	Int. + YP + PP	0.078	-5.29 (0.53)	1.98 (0.32)	–	–	0.85 (0.36)	–	–	–	–
2009	Int. + PT + PP + PF	0.074	-5.36 (0.53)	1.03 (0.35)	0.97 (0.36)	–	–	0.09 (0.31)	–	–	–
2009	Int. + T + PP + PF	0.074	-4.51 (0.77)	1.02 (0.34)	1.14 (0.47)	–	–	–	-0.32 (0.31)	0.02 (0.03)	–
2009	Int. + PP + FT + PF	0.071	-5.35 (0.53)	1.06 (0.36)	0.99 (0.44)	–	–	–	–	–	-0.02 (0.44)
2010	Int. + PP + TT	0.251	-5.54 (0.66)	1.55 (0.38)	–	1.17 (0.45)	–	–	–	–	–
2010	Int. + PP + TT + FT	0.179	-5.41 (0.66)	2.47 (1.04)	–	1.16 (0.45)	–	–	–	–	-1.04 (1.04)
2010	Int. + PT + PP + TT	0.130	-5.43 (0.67)	1.65 (0.41)	–	1.14 (0.46)	–	-0.34 (0.4)	–	–	–
2010	Int. + F + PP + TT	0.103	-5.35 (0.76)	1.74 (0.57)	–	1.27 (0.48)	–	–	–	–	–
2010	Int. + PP + TT + PF	0.097	-5.5 (0.67)	1.77 (0.76)	-0.26 (0.77)	1.17 (0.45)	–	–	–	–	–
2010	Int. + YP + PP + TT	0.092	-5.57 (0.67)	1.52 (0.42)	–	1.19 (0.46)	0.07 (0.42)	–	–	–	–



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