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**EMERALD BOWFIN *AMIA OCELLICAUDA* ECOLOGY IN THREE  
MINNESOTA LAKES: ABUNDANCE, AGE ANALYSIS, DIET  
COMPOSITION, AND STABLE ISOTOPE FOOD WEB**

by

**Griffin Blegen**

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For the Degree of

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## STATEMENT BY THE AUTHOR

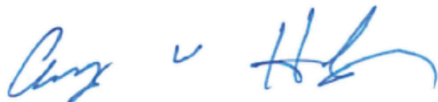
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MINNESOTA LAKES: ABUNDANCE, AGE ANALYSIS, DIET COMPOSITION,  
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Griffin Blegen

The Emerald Bowfin *Amia ocellicauda* is a predatory fish species native to Minnesota that has often been discriminated against. This research expands ecological knowledge of Bowfin in Minnesota and provides population data to guide future management. Bowfin were sampled in the spring of 2024 and 2025 and a multi-census mark-recapture model was used to estimate abundance in three lakes. Estimated populations were 196 individuals in Little Toad Lake (95% CI: 116, 242) or 4.4 fish/littoral ha (95% CI: 2.7, 5.7), 657 in Lake Sarah (95% CI: 436, 1014) or 4.2 fish/littoral ha (95% CI: 3.0, 6.7), and 612 in Gun Lake (95% CI: 368, 861) or 5.2 fish/littoral ha (95% CI: 3.2, 7.2). A subsample of 146 Bowfin was collected for age, growth, diet, and stable isotope analysis. Lapillus otoliths indicated ages ranging from 2 to 33 years. All von Bertalanffy growth parameters differed by sex, with asymptotic lengths of 702 mm for females and 561 mm for males, and growth coefficients of 0.218 and 0.633. Annual mortality (2.5-6.5%) and recruitment (RCD = 0.02 – 0.30) were low across systems. Diet analysis showed Bluegill *Lepomis macrochirus* as the dominant prey item (%IRI = 34.7-78.2%). Bowfin (TPscaled = 5.5-5.9) and Northern Pike *Esox lucius* (TPscaled = 5.4-5.7) occupied lower trophic positions than Walleye *Sander vitreus* and Largemouth Bass *Micropterus nigricans* (both TPscaled = 6.2-6.6). Bowfin displayed the broadest isotopic niche (SEAc = 1.3-3.3), and niche overlap was greatest between Bowfin and Northern Pike (58.2-100%). Together, these patterns suggest Bowfin are a broad-impact predator that regulates forage communities and contribute to ecosystem balance.

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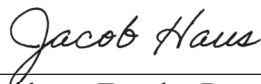
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## **Emerald Bowfin *Amia ocellicauda* Ecology in Three Minnesota Lakes: Abundance Estimates, Age Analysis, Diet Composition, and Stable Isotope Food Web**

*Abstract* - The Emerald Bowfin *Amia ocellicauda* is a predatory fish species native to Minnesota that has often been discriminated against. This research expands ecological knowledge of Bowfin in Minnesota and provides population data to guide future management. Bowfin were sampled in the spring of 2024 and 2025 and a multi-census mark–recapture model was used to estimate abundance in three lakes. Estimated populations were 196 individuals in Little Toad Lake (95% CI: 116, 242) or 4.4 fish/littoral ha (95% CI: 2.7, 5.7), 657 in Lake Sarah (95% CI: 436, 1014) or 4.2 fish/littoral ha (95% CI: 3.0, 6.7), and 612 in Gun Lake (95% CI: 368, 861) or 5.2 fish/littoral ha (95% CI: 3.2, 7.2). A subsample of 146 Bowfin was collected for age, growth, diet, and stable isotope analysis. Lapillus otoliths indicated ages ranging from 2 to 33 years. All von Bertalanffy growth parameters differed by sex, with asymptotic lengths of 702 mm for females and 561 mm for males, and growth coefficients of 0.218 and 0.633. Annual mortality (2.5-6.5%) and recruitment (RCD = 0.02 – 0.30) were low across systems. Diet analysis showed Bluegill *Lepomis macrochirus* as the dominant prey item (%IRI = 34.7-78.2%). Bowfin (TPscaled = 5.5-5.9) and Northern Pike *Esox lucius* (TPscaled = 5.4-5.7) occupied lower trophic positions than Walleye *Sander vitreus* and Largemouth Bass *Micropterus nigricans* (both TPscaled = 6.2-6.6). Bowfin displayed the broadest isotopic niche (SEAc = 1.3-3.3), and niche overlap was greatest between Bowfin and Northern Pike (58.2-100%). Together, these patterns suggest Bowfin are a broad-impact predator that regulates forage communities and contribute to ecosystem balance.

## Introduction

Bowfin, *Amia* spp., have long been viewed as a rough fish and undesirable to most anglers (Hausmann 1998; Rypel et al. 2021; Lackmann et al. 2022). This classification often leads to repeated wasted harvest by anglers and bowfishers alike (Mundahl et al. 1998). Originally, the genus *Amia* had only one member; Bowfin, *Amia calva*. Brownstein et al. (2022) split the *Amia* genus into two species: the Ruddy Bowfin, *A. calva*, and the Emerald Bowfin, *A. ocellicauda*. Although Brownstein et al. (2022) recommended Eytail Bowfin as the common name for *A. ocellicauda*, the more widely accepted common name as described by Wright et al. (2022) is Emerald Bowfin. The Ruddy Bowfin range starts near the border of Louisiana and Mississippi and extends east throughout the entirety of the Gulf and Atlantic coast basins, ending in Virginia (Brownstein et al. 2022). In comparison, the Emerald Bowfin range includes the Mississippi River, Great Lakes, and St. Lawrence River basins, that stretch from Minnesota, south along all the Mississippi River states to the Gulf of Mexico, and east throughout the Great Lake states, southern Canada, and ending in New Jersey (Brownstein et al. 2022).

Both Bowfin species can be found in a wide range of aquatic habitats and water quality regimes, including lakes, oxbows, sluggish rivers and streams, backwaters, floodplains, artificial ponds, ditches, and brackish estuaries (Burr & Bennett 2014; Clark 2015; Midwood et al. 2018; McNeese 2020). Within these various water bodies, Bowfin prefer areas with dense and extensive macrophyte beds along with a generally hard bottom substrate, and clear waters (Burr & Bennett 2014; McNeese 2020). Interestingly, they do not require a hard substrate or clear waters, only prefer them when available.

Bowfin are an extremely tolerant species that can gulp air from the surface using a highly vascularized swim bladder that acts as a lung (Daxboeck et al. 1981). The ability to be facultative air breathers allows Bowfin to live in areas of low oxygen, low pH, and high water temperatures (Burr & Bennett 2014).

Bowfin were originally thought to be a destructive, piscivorous predator with diets consisting of gamefish and forage fish alike (Eddy & Surber 1943). This assumption and others like it, is the principal reason for their repeated persecution (Scarnecchia 1992; Hausmann 1998; Midwood et al. 2018). Although they are piscivorous, adult Bowfin diets have been shown to consist primarily of crayfish, followed by fish (Hausmann 1998; Ashley & Rachels 1999; Nawrocki et al. 2016). When fish are consumed, the species present often consist of Leuciscidae and *Lepomis* spp. due to their generally small size and high abundance (Ashley & Rachels 1999; Nawrocki et al. 2016). However, Bowfin exhibit generalist feeding behaviors, having been known to cannibalize as well as eat frogs, snakes, aquatic birds, and terrestrial insects (Burr & Bennett 2014). Evidence of this generalist feeding behavior from Nawrocki et al. (2016) showed Bowfin isotopic niche sizes were two to four times larger than Largemouth Bass *Micropterus nigricans*, Northern Pike *Esox lucius*, Walleye *Sander vitreus*, Muskellunge *Esox masquinongy*, and Longnose Gar *Lepisosteus osseus*. Additionally, Bowfin occupied a lower trophic position than Largemouth Bass and Longnose Gar (Nawrocki et al. 2016). Given the trophic position and isotopic niche size shown in previous studies, Bowfin are hypothesized to assume the role of an upper-level predator, while maintaining a wide variety of prey options within a system.

Few studies exist regarding juvenile Bowfin diets. However, Schneberger (1937) showed diets did change with body size of juveniles. Stomachs of juvenile Bowfin greater than 5 cm contained damselfly nymphs, scuds, and chironomid larvae. Smaller Bowfin (< 5 cm) contained smaller prey items, including planktonic crustaceans like *Ceriodaphnia*, *Simocephalus*, *Polyphemus*, *Cyclops*, *Sida*, ostracods, and diatoms. All the small-sized juveniles also had filamentous algae in their stomachs. Similarly, juvenile Bowfin studied by Frazer et al. (1989) were shown to have larger prey items present in larger individuals, and smaller prey in smaller individuals. Their results were like Schneberger (1937), in the sense that juveniles fed on planktonic crustacean species and various aquatic macroinvertebrate species within Cladocera, Copepoda, Isopoda, and Coleoptera.

Complete population demographics of Bowfin are largely unknown, but some aspects have been studied. Mundahl et al. (1998) conducted a mark-recapture study on Lake Winona in southeastern Minnesota and found an abundance of 3.17 fish/ha; 95% CI: [1.97, 8.14]. Juvenile growth rates have been shown to be variable between different studies; some juveniles reaching >50 mm in length in the first month, and others reaching 203 to 324 mm within the first year of life (Becker 1983; Hausmann 1998; Burr & Bennett 2014). A recent Minnesota study showed, via otolith aging, that Bowfin grew to between 400 to 500 mm in their first 2 to 3 years of life (Lackmann et al. 2022). Sexual maturity is hypothesized to be between 3 and 5 years of age for both sexes, but may be closer to the 2-year mark (Hausmann 1998; Burr & Bennett 2014). The decrease in approximate age at sexual maturity may be due to the rapid growth rates shown in select studies mentioned previously. Additionally, the maximum age of Bowfin was thought to

average around a decade (Mundahl et al. 1998; for review see Table 1 in Lackmann et al. 2022). In comparison, there have been three instances of captive specimens living between the ages of 20 and 30 years old (Carlander 1969). Lackmann et al. (2022) showed maximum ages of Bowfin in the wild could be nearly three times longer than previously thought, identifying individuals that could be as much as 33 years old. This finding, in conjunction with the reported ages of select captive fish, suggests Bowfin can live decades longer than once thought possible.

Across the Bowfin range, population dynamics are relatively unknown, and their ecological importance has yet to be widely understood. Bowfin classification as “rough fish” in Minnesota has perpetuated the notion that an unlimited number of individuals can be harvested year-round. Fortunately, a sharp growth in the interest of Minnesota’s native fishes has resulted in a push to learn more about, protect, and reclassify “rough fish” species like the Bowfin (Rypel et al. 2021; Winter 2024). This research is being done to help understand Bowfin population vulnerability, and implications for fisheries management. The purpose of this study is to gain a better understanding of Emerald Bowfin population numbers and to secure valuable ecological information such as age and growth estimates, diet composition, and trophic positions in aquatic systems. From this point forward in this study, Bowfin shall mean Emerald Bowfin.

This research has five objectives to be completed within each of three study lakes; (1) to determine Bowfin population sizes using multi-census mark-recapture surveys, (2) to accurately age Bowfin from lapillus otoliths and determine if there are significant growth differences among the study lakes, (3) to quantify Bowfin recruitment and mortality, (4) to quantify Bowfin diet composition by analyzing stomach contents, and

(5) to conduct stable isotope analyses to determine Bowfin trophic position in relation to other predator and prey species.

## Methods

*Study Area* - The three lakes selected for this study ranged in locations from west-central, east-central, and southeastern Minnesota to investigate variation in Bowfin ecology across the state (Fig. 1). Study lakes needed to consist of a closed system, have documented presence of a Bowfin population, and be of a suitable size so sampling could be done by a single crew (<325 ha).

Little Toad Lake was sampled from 28 April 2024 to 20 May 2024 with a total of 192 net nights, is located about 16 km east of Detroit Lakes in Becker County, and supports a healthy fishery of Bluegill *Lepomis macrochirus*, Black Crappie *Pomoxis nigromaculatus*, Northern Pike, and Largemouth Bass. Walleye adults, fingerling, and fry have been stocked for the last decade to support a Walleye fishery. The lake has a total area of 165 ha, with 43 ha being littoral (26%; Table 1). It has a maximum depth of 20 m, Secchi depth reading of 4.1 m, and is largely dominated by pondweed *Potamogeton* spp., Wild Rice *Zizania palustris*, and Bulrush *Schoenoplectus* spp. (MNDNR 2003). The shoreline is moderately developed with less than half of the perimeter being developed via houses, cabins, agriculture, and one campground.

Lake Sarah was sampled from 16 April 2025 to 1 May 2025 with a total of 136 net nights, is located 35 km northwest of Minneapolis in Hennepin County, and has abundant shoreline development, with over half of the lake's perimeter being developed with residential houses and cabins. Largemouth Bass and Northern Pike are abundant within this system and the main targets for anglers, while Bluegill, Black Crappie, and

Walleye are secondary targets (MNDNR 2025). Lake Sarah is also stocked with Walleye to promote a viable Walleye fishery. Lake Sarah has a total area of 225 ha with 151 ha being littoral (67%), a maximum depth of 18 m, and a Secchi depth reading of 0.8 m (Table 1). Eurasian Watermilfoil *Myriophyllum spicatum* (MNDNR 2025) and Banded Mystery Snails *Callinina georgiana* (MNDNR personal communication 2025) are two confirmed aquatic invasive species present within Lake Sarah.

Gun Lake was sampled in from 5 May 2025 to 10 May 2025 for a total of 105 net nights, is located 19 km northeast of Aitkin in Aitkin County, and has limited shoreline development via houses, cabins, and a single campground. The remaining shoreline is either forested or wetlands. Bluegill and Black Crappie are primarily angled on Gun Lake, while Largemouth Bass, Northern Pike, and Walleye are secondary targets for anglers. Additionally, the stocking of various sizes and quantities of Walleye has been done since the 1960s in hopes of establishing a naturally reproducing population, with limited success. Gun Lake has a total area of 288 ha, with 118 ha being littoral (41%), a maximum depth of 13.4 m, a Secchi depth reading of 1.9 m, and has a diverse community of macrophytes and other emergent vegetation (Table 1). Two invasive species are present in Gun Lake: Curly-leaf Pondweed *Potamogeton crispus* (MNDNR 1996) and Chinese Mystery Snails *Cipangopaludina chinensis* (personal observation 2025)

*Sampling Design* - A multiple-event mark-recapture study was conducted to estimate Bowfin population numbers in each lake. Double-frame fyke nets (0.9 m x 1.8 m) with a 15.2 m lead length and 2.5 cm mesh size were used to capture Bowfin. We used the maximum number of nets possible based off a few factors such as the overall lake size, amount of probable Bowfin habitat, and distance of travel to each study site.

Fyke nets were set and checked every 24 hours starting approximately three weeks after ice-out, weather depending. Additionally, we attempted to night electrofish to determine which method of capture was more effective. Captured Bowfin were measured for total length to the nearest millimeter and marked with a clearly identifiable fin punch (Fig. 2). A specific fin punch location was utilized to mark each Bowfin (left and right pectoral, left and right pelvic, etc.) to represent different sampling days to identify the date of capture of a previously marked fish. This was done to ensure Bowfin were not being captured in the same nets on consecutive days. After being processed, Bowfin were moved away from the net location and released. The exact distance of release varied as we chose to move the fish out and away from the shoreline to the furthest extent that vegetation was visible below the boat. This ensured that the released Bowfin remained in the littoral portion of the lake and had immediate access to cover to rest after being handled, while being moved from the immediate netting location to mitigate recapturing the same individuals consecutively.

Up to 50 Bowfin caught by electrofishing and fyke netting at each lake were stored in a cooler with ice to stop further stomach content digestion and transported back to the Bemidji State University laboratory. Once there, euthanasia was done by using a clove oil and ethanol mixture added to a tub of water with the Bowfin fully submerged. After all fish were confirmed to be deceased, they were measured to the nearest millimeter and weighed to the nearest gram. After all fish were measured, they were placed into individually labeled bags and frozen to prevent further digestion and to keep fresh for later dissections. Dissections consisted of extracting stomachs for diet

composition, otoliths to use for aging and growth analysis, and dorsal white muscle tissue samples for stable isotope analysis.

*Population Estimate* - A closed population, multi-census estimate model was used to estimate population sizes. The Schnabel model is similar to the traditional Lincoln-Peterson model where there are two distinct phases of the study: marking and recapture. How the Schnabel model differs is that both of these phases occur each sampling day instead of separated across a period of time. This means that both the marking of captured fish and recording of recaptures was done during each sampling day. The Schnabel model and more specifically, the Overton modification of the Schnabel model, was used because it consists of a series of measures on marked and recaptured fish and also includes an estimator factor to allow for known harvest of individuals during capture (Overton 1965; Seber 1982):

$$N = N^{(0)} + A$$

$$A^{(1)} = \frac{\sum_{i=1}^k Z_i n_i M_i}{\sum_{i=1}^k n_i M_i}$$

Where  $N$  is the estimated population size,  $N^{(0)}$  is the conventional Schnabel estimate,  $A$  is calculated by an iterative scheme, and  $A^{(1)}$  is the first approximation of  $A$ . To calculate  $A^{(1)}$ , let  $Z_i$  represent the total number of animals removed from the population prior to the  $i^{th}$  occasion, let  $n_i$  represent the number of animals captured on the  $i^{th}$  occasion, and let  $M_i$  represent the number of marked animals available to capture on the  $i^{th}$  occasion. Assumptions of this model are as follows: the population is closed, all fish have the same chance of capture, there is no tag/mark loss between samples, and all marks are reported during the recapture period (Krebs 1998). The period between the marking and recapturing events was short enough to assume that births, immigration, emigration, and

deaths could be nullified during the calculation. There was no issue with tag retention or loss as fin punches were used as to avoid the potential for plastic tag. Additionally, marked individuals were easily discernable from unmarked ones, which led to all marks being reported. The conclusion of netting occurred when one of two scenarios happened:

- 1) the upper and lower confidence intervals are both within  $n$  amount of the given population estimate, or
- 2) the captured Bowfin are expelling eggs or milt.

The timing of netting had coincided with the pre-spawn activity of Bowfin when the majority of the population was assumed to be in the shallow near-shore areas of the lake. If the netting had continued throughout the duration of the spawn, the capture and subsequent recapture of mating fish and guarding males might have occurred. This could have led to a potentially biased population estimate by capturing the same fish repeatedly, as well as the disruption of mating and guarding Bowfin. This is why netting concluded if the presence of eggs, milt, or nesting Bowfin was encountered.

*Age and Growth Analysis* - Approximate age at harvest was estimated using otoliths. Lackmann et al. (2022) removed all three sets of otoliths from Bowfin and compared them to determine which provided the most consistent and readable age estimates. The study found the smallest set, the lapillus otoliths, provided the best results with 100% being readable, followed by 90% of asteriscus otoliths, and 60% of sagittal otoliths processed being readable, respectively (Lackmann et al. 2022). Following these results, age analysis was done primarily through lapillus otoliths. If a lapillus otolith wasn't conducive to age scoring, an asteriscus otolith was used instead.

Following methods used by Lackmann et al. (2022), all extracted otoliths were cleaned of residual tissue and photographed whole submerged in water under a dissecting microscope. Lapillus otoliths were then dried, and otolith mass was measured ( $\pm 0.1$  mg). Otoliths were then set in Buehler epoxy to be thin-sectioned using a Buehler IsoMet™ 1000 low-speed saw with twin diamond embedded blades to produce the thin-sections. The whole otolith photos were used as a reference if otolith cores were not legible to the naked eye during sectioning. Otolith thin sections were then placed in mineral oil and mounted on a glass slide to be photographed under a compound microscope. Following the age scoring protocol from Lackmann et al. (2019), two independent readers (G. Blegen and A. Lackmann) age scored otoliths using digital marks on the thin-section photographs (Fig. 3). To settle on a single age for fish that had differing age scores, the scored photographs were compared, and an age was agreed upon between readers for each fish. Examining precision between the age reader scores was completed using the coefficient of variation (CV) following Campana et al. (1995). From the otolith ages and total length data, 20 von Bertalanffy growth models (von Bertalanffy 1938) were created using combinations of the von Bertalanffy growth parameters  $L_{\infty}$ ,  $k$ , and  $t_0$  as well as sex and study site. Akaike's Information Criterion (AIC) was used to determine the highest-ranking model for predicting size at age of Bowfin (Akaike 1998). Year classes were also calculated for all otolith-aged individuals for each of the three study lakes. From these year classes, recruitment was estimated using catch-curve analysis (Chapman & Robson 1960). Annual mortality was estimated using the following equation where  $Z$  is the instantaneous mortality or the slope of the catch-curve linear regression, and  $A$  is annual mortality (Ogle 2016):

$$A = 1 - e^{-Z}$$

Two exclusionary age ranges were used for the recruitment and mortality estimates: the first set at 2-years old and the second set at the peak year class before the descending limb for each system (Smith et al. 2012). The two age ranges were chosen to cover the age at which fish recruited to the gear, and the age at which the first modal year class was evident in a given population. Recruitment was quantified by using the recruitment coefficient of determination (RCD) described by Isermann et al. (2002). RCD is derived from the  $r^2$  value of the linear regression line used in the catch-curve analysis (Isermann et al. 2002). RCD values were then bootstrapped to obtain 95% confidence intervals (Canty et al. 2024).

*Diet Analysis* - Bowfin stomachs were thawed and dissected to study diet composition. Due to fyke nets being used for capture, there was a possibility for extremely fresh prey in Bowfin stomachs due to the Bowfin consuming prey species while trapped in the net. If fresh prey items were present, they were eliminated from the diet analysis to reduce potential trap net bias on prey composition. Prey specimens were identified to the lowest taxonomic level possible. Unidentifiable stomach contents were viewed with a dissecting scope to help determine a possible species or taxonomic grouping. If no conclusion could be made on the identification or count, they were put into categories of “unidentified fish remains” and “unidentified invertebrate remains” for the composition calculation. Percent frequency of occurrence (%F), percent number (%N), and percent weight (%W) were all calculated to quantify the Bowfin diets. Prey species %F was calculated by dividing the total occurrences of prey species x, by the total occurrences of a prey species across all stomachs within each study lake. Similarly, %N

and %W were calculated by dividing a single number or weight of prey species by all numbers or all weights across all stomachs, separated by study lake (Hausmann 1998; Ashley & Rachels 1999; Nawrocki et al. 2016). From these calculations of %F, %N, %W, the Index of Relative Importance (IRI) and percent IRI (%IRI) was calculated for each prey species using these two equations (Nawrocki et al. 2016):

$$IRI = (%N \times \%W) + \%F$$

$$\%IRI_i = \frac{100IRI_i}{\sum_{i=1}^n IRI_i}$$

Using the boot package, bootstrapping techniques were used to calculate 95% confidence intervals for each prey species' %IRI value (Canty et al. 2024).

*Stable Isotope Analysis* - To get a holistic view of the relationships between Bowfin and other species present in the ecosystem, samples from ten different predators, prey, and a baseline snail group were collected to construct a stable isotope food web. A baseline group is needed due to the high variability of isotopic signatures across systems (Cabana & Rasmussen 1996). Therefore, the isotopic signatures of the predator and prey species can be measured relative to each system's baseline snail group isotopic signatures.

The following methods, described by Garvey and Chipps (2012), were utilized for the stable isotope analyses of all fish species included in this study. Each tissue sample must be at least 1.0 g in wet weight, dried at 70 °C for 24 to 48 h, homogenized with a mortar and pestle into a fine powder, packaged into Eppendorf tubes, and uniquely labeled. Once all tissue samples were ground and packaged, they were then weighed to approximately 1.0 mg (0.8-2.0 mg) and encapsulated in 6 mm x 4 mm tin capsules. These samples were then sent to the Cornell Stable Isotope Laboratory for analysis. A Thermo

Scientific Delta V Advantage IRMS coupled with a Carlo Erba NC2500 element analyzer was used to read and determine  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values for each sample. The  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values were compared against the International Atomic Energy Agency standards, which is atmospheric nitrogen for  $\delta^{15}\text{N}$  and Vienna Pee-Dee Belemnite for  $\delta^{13}\text{C}$  (Fincel et al. 2012; Maitland & Rahel 2020; Fredrickson et al. 2022). Using the harvested Bowfin, 1 cm<sup>3</sup> of white muscle tissue was collected from near the anterior end of the dorsal fin. Other predator tissue samples were taken during fyke netting using a 4 mm dermal punch tool for dorsal white muscle tissues. Skin was removed from the muscle plugs before processing. Abundant prey species (e.g. Bluegill) were collected during fyke netting based on their high occurrence in the fyke nets and the assumption that they represent a majority of forage fish in the lake and therefore stomachs (Hausmann 1998). Additional prey species were identified through stomach content analysis of Bowfin, with additional samples collected post stomach content analysis to represent the most frequently consumed prey in each lake. When analyzing stable isotope signatures, the presence of lipid-depleted  $\delta^{13}\text{C}$  samples were present which can bias further  $\delta^{13}\text{C}$  analyses if not corrected or normalized (Post et al. 2007). To avoid this bias, samples were normalized using this equation from Post et al. (2007):

$$\delta^{13}\text{C}_{\text{normalized}} = \delta^{13}\text{C}_{\text{untreated}} - 3.32 + 0.99 \times C:N$$

*Trophic Position Estimate* – Trophic positions were estimated using  $\delta^{15}\text{N}$  stable isotope values, due to the isotope of nitrogen enriching from prey species to predator species (Lepak et al. 2022). The following equation was used to estimate trophic positions:

$$TP_{\text{scaled}} = \frac{\log(\delta^{15}\text{N}_{\text{lim}} - \delta^{15}\text{N}_{\text{baseline}}) - \log(\delta^{15}\text{N}_{\text{lim}} - \delta^{15}\text{N}_{\text{consumer}})}{k} + TP_{\text{baseline}}$$

This equation was chosen due to the findings from Hussey et al. (2014). They found the traditional method of assuming a constant value of 3.4‰ for  $\Delta^{15}\text{N}$  as trophic levels increased, underestimated the true trophic position of upper-level predators. Instead, they tested and determined consumer discrimination is not fixed at 3.4‰ but narrows with increasing dietary  $\delta^{15}\text{N}$ . This negative linear relationship between  $\Delta^{15}\text{N}$  and dietary  $\delta^{15}\text{N}$  proved that a scaled approach to estimating trophic positions was necessary.

*Isotopic Niche Area and Overlap* – Isotopic niche size and niche overlap was estimated by using both  $\delta^{13}\text{C}_{\text{normalized}}$  and  $\delta^{15}\text{N}$  stable isotope values in combination with the SIBER (Stable Isotope Bayesian Ellipses in R) analysis package (Jackson & Parnell 2023). SIBER generates standard ellipse areas ( $SEA_C$ ) that represent the core 40% of data points for each species group, this represents the isotopic niche (Jackson et al. 2011). For plotting and overlap estimation, 95% confidence ellipses were chosen instead of 40% standard ellipses. Pairwise comparisons were used to estimate overlap between “Species A” and “Species B”, leading to a percentage of overlap between the selected species, essentially estimating the isotopic niche overlap between the two (Jackson et al. 2011).

## Results

*Population Estimate* – A total of 115 total Bowfin were captured in Little Toad Lake, including 28 recaptures. The recapture-to-capture ratio during the 2024 season was 24.3%. Little Toad Lake had an estimated abundance of 196 individuals; 95% CI: [116, 242], or 4.4 fish/littoral ha; 95% CI: [2.7, 5.7]. A total of 175 total Bowfin were caught in Lake Sarah with 24 recaptures, resulting in a recapture-to-capture ratio of 13.7%. Lake Sarah had an estimated abundance of 657 individuals; 95% CI: [436, 1014], or 4.2

fish/littoral ha; 95% CI: [3.0, 6.7]. A total of 161 total Bowfin were caught at Gun Lake with 20 recaptures, resulting in a recapture-to-capture ratio of 12.4%. Gun Lake had an estimated abundance of 612 individuals; 95% CI: [368, 861], or 5.2 fish/littoral ha; 95% CI: [3.2, 7.2].

*Age and Growth* - Ages of the 146 harvested Bowfin ranged from 2 to 33 years old. Total length of individuals ranged from 313 to 743 mm (Fig. 4), while body masses of individuals ranged from 243 to 3697 g. Between the primary and secondary reader scores, precision was measured by the coefficient of variation and was 4.2% (CV; Campana et al. 1995). Agreement between both age scorers using the Pearson correlation coefficient was 0.99. Analyzing the age scores further, the same age score (exact agreement) was assigned in 61% of cases across all otolith sections, agreement within 1 year was 92%, and the remaining 8% differed by 2 (n = 7), 3 (n = 3), or 4 (n = 1) years.

Bowfin exhibit sexual dimorphism in body size (Burr & Bennett 2014; Lackmann et al. 2022) and this was found to be true in each of these three systems as well (Fig. 5). The highest ranking von Bertalanffy growth model showed that  $L_{\infty}$  and k were both sex-specific and had an un-fixed  $t_0$ , while site-specificity was not a factor (Table 2). Therefore, all lakes were pooled together for the growth analysis. From this model, asymptotic length ( $L_{\infty}$ ) for females was 702 mm, while males had an  $L_{\infty}$  of 561 mm. Instantaneous growth rate (k) also differed between sexes; females: k = 0.218 and males: k = 0.633. Age at zero length ( $t_0$ ) was estimated at 0.191 for males and -2.605 for females.

*Recruitment and Mortality* - The assignment of year-classes showed variable recruitment among study lakes based on the recruitment coefficient of determination. For

Little Toad Lake, the RCD was 0.02; 95% CI: [ $<0.001$ , 0.51] at a recruitment age of 2 years, and 0.04; 95% CI: [ $<0.001$ , 0.73] at a recruitment age of 10 years. Both recruitment values classify as ‘variable’ as described by Isermann et al. (2002). For example, the year-classes of 2014 and 2015 made up over half of all caught fish ( $n = 25$ ; 54%; Fig. 6). The next most numerous year class was the 1997 class which had five total fish and accounted for roughly 11% of the collected fish. All other year-classes with represented fish had 3 or fewer individuals within them (Fig. 6). Additionally, there were 11 different year-classes (42%) between the earliest and latest classes having no representative fish within them.

The RCD for Lake Sarah was 0.27; 95% CI: [0.01, 0.66] at a recruitment age of 2 years, and 0.24; 95% CI: [0.002, 0.69] at a recruitment age of 7 years. Isermann et al. (2002) classifies the RCD value of the 2 year age minimum as ‘moderately variable’ recruitment, and ‘variable’ for the 7 year age minimum. Only two year classes were not represented between the youngest and oldest fish collected. No incredibly abundant year-classes were present in Lake Sarah, unlike in Little Toad Lake. The year-classes of 2018 and 2023 each had 8 total fish in them, while all other classes had 4 or fewer fish (Fig. 6).

The RCD for Gun Lake was 0.12; 95% CI: [0.001, 0.48] at a recruitment age of 2 years, and 0.30; 95% CI: [0.03, 0.68] at a recruitment age of 4 years. Recruitment as classified by Iserman et al. (2002) was ‘variable’ for the younger recruitment-age threshold, and ‘moderately variable’ for the older recruitment-age threshold. While Gun Lake did have 11 empty year-classes from the youngest to oldest collected fish, similar to Little Toad Lake, the differences were less extreme. The year-classes of 2011 and 2021

were the most abundant and collectively comprised 15 total fish (30%), while all other year-classes had 4 or fewer fish (Fig. 6).

Annual mortality for Little Toad Lake could not be estimated for the 2-year recruitment-age threshold due to cohort-based bias that resulted in a positive catch curve slope. Using 10 years of age as the secondary range resulted in an annual mortality rate of 2.9%. Annual mortality for Lake Sarah was 5.5% if fish recruit at 2 years, and 6.5% if they recruit at 7 years. Gun Lake had an annual mortality rate of 2.5% if the recruitment threshold was 2 years, and 4.2% if fish recruit at 4 years.

*Diets* - A total of 146 Bowfin stomachs were removed and analyzed for species composition from the three study lakes. No extremely fresh prey items were found in stomachs, so none were removed from the analysis. Prey items consisting of twenty different categories were found in Bowfin stomachs (Table 3). Of the 146 stomachs dissected, 21 were empty (14%). Among each of the three study lakes, the most important prey item (%IRI) was Bluegill (Little Toad = 34.7%; Sarah = 78.2%; Gun = 53.3%; Table 4). Additionally, dragonfly nymphs and unidentified fish remains were among the top four most important prey items (%IRI) across each study lake (Fig. 7). Evidence of cannibalism was found only in Lake Sarah with three instances of Bowfin remains being found in the stomachs of harvested Bowfin. Two of which consisted of approximately one-year-old (165 mm and 172 mm) Bowfin that were found whole in two separate Bowfin stomachs. Another noteworthy finding came from Gun Lake where we found crushed Chinese Mystery Snail shells with tissue still attached to the operculum in the stomachs of 11 Bowfin. One fish contained a total of seven opercula, suggesting some individuals were targeting this non-native aquatic species.

*Trophic Position* – Assessing the trophic position estimates for the four predator species showed consistent trophic structuring across systems. Walleye and Largemouth Bass both occupied a higher trophic position than Northern Pike and Bowfin (Table 5). Largemouth Bass (LMB) and Walleye (WAE) occupied nearly identical trophic positions in the food web (LMB:  $TP_{scaled} = 6.2-6.6$ ; WAE:  $TP_{scaled} = 6.2-6.6$ ; Table 5). Bowfin (BOF) were slightly higher in trophic position than Northern Pike (NOP), but both were situated lower than Largemouth Bass and Walleye (BOF:  $TP_{scaled} = 5.5-5.9$ ; NOP:  $TP_{scaled} = 5.4-5.7$ ; Table 5).

*Isotopic Niche Size and Overlap* – Bowfin niche overlap among predators varied across system, with the lowest amount of overlap coming from Little Toad Lake, and the highest amount from Lake Sarah (Fig. 8). Across each system, Bowfin had the largest niche size of the predator species ( $SEAc = 1.3-3.3$ ; Table 6). The Bowfin isotopic niches were roughly two to three times larger than those for Largemouth Bass ( $SEAc = 0.6-1.0$ ; Table 6), Northern Pike ( $SEAc = 0.6-1.0$ ; Table 6), and Walleye ( $SEAc = 0.5-1.0$ ; Table 6). Using Bowfin as “Species A”, the percent overlap of isotopic niches was highest with Northern Pike across each study site (58.2-100%; Table 6). Largemouth Bass and Walleye had less overall overlap compared to Northern Pike, but this varied among systems as to which was lowest between the two species. In Lake Sarah, Walleye had the second highest overlap (98.5%; Table 6) with Bowfin, while Largemouth Bass had slightly less (93.0%; Table 6). In comparison, Gun Lake showed Largemouth Bass had the second highest overlap (70.2%; Table 6) with Bowfin, compared to Walleye (60.8%; Table 6).

## Discussion

*Population Estimate* – Bowfin abundance was relatively low compared to other predatory species and appeared closely linked to littoral habitat. This is consistent with their preference for vegetated and shallow areas of aquatic systems (Burr & Bennett 2014). After altering overall Bowfin abundance estimates to reflect the littoral area in each study lake, similarities in abundance became more apparent among systems. Little Toad Lake had 4.4 fish/littoral ha, Lake Sarah had 4.2 fish/littoral ha, and Gun Lake had 5.2 fish/littoral ha. These results are similar to the only previously published paper where mark-recapture methods were used to estimate a Bowfin population; Mundahl et al. (1998) showed an abundance of 3.17 fish/ha. Although this estimate does not specifically reference littoral area, the lake used by Mundahl et al. (1998) is roughly 85% littoral, meaning this estimate may bear some resemblance to our findings. However, it should be mentioned that Mundahl et al. (1998) were stocking Bowfin in their study lake previous to the population estimation to try and combat an undersized Bluegill population. Published densities of the other predator species show vast ranges, likely due to differences in lake morphology, but almost all being multitudes higher than the Bowfin densities shown in this study. Average Northern Pike densities from various studies range from 16.1 to 26.0 fish/ha, with extreme ranges of 2.8 to 59 fish/ha (Margenau et al. 1998; Pierce & Tomcko 2005; Kempe 2018). Largemouth Bass densities ranged from 6.5 to 48.3 fish/ha, with an average of 26.0 fish/ha across 12 Minnesota lakes (McInerney & Cross 2000). Average Walleye densities from two Wisconsin studies were 4.2 to 29.2 fish/ha (Beard et al. 1997; Nate et al. 2000). Additionally, a study from New York showed average Walleye densities of 5.0 to 29.0 fish/ha (Nate et al. 2011). Interestingly, Muskellunge densities show the greatest similarities to the Bowfin densities from this

study, with averages ranging from 0.2 to 1.5 fish/ha (Hanson 1986; Miller, Ward, & Schultz 2015), and from a unique population of high density Muskellunge, 4.8 to 9.0 fish/ha (Frohnauer et al. 2007).

Our results do show some consistency of Bowfin abundance and its relation to littoral areas of lakes, though continued testing of this trend is needed. The overall littoral hectare density reported here could serve as a useful tool when estimating the potential number of Bowfin in other Minnesota lakes. However, the study lakes were specifically chosen due to known presence of Bowfin with relatively high sampling catch rates. Therefore, lakes with lower reported catches could have even lower abundances of Bowfin than found in this study. Further population estimation should be done on these lakes with known Bowfin presence, but low reported catches from MNDNR standard surveys to reveal possible abundance estimates for smaller populations. An adjustment to the methods provided here to produce better population estimates would be to start earlier in the spring. We chose to start netting approximately 3-weeks after ice-out in all systems. While this worked on lakes Little Toad and Sarah, a highly abnormal warm period in early May 2025 ended netting on Gun Lake prematurely due to the presence of spawning Bowfin. If possible, netting should begin as close to ice-out as possible, and run until Bowfin are observed spawning, or adequate confidence intervals are met.

*Age and Growth* – Bowfin in this study frequently reached 20 years of age, even surpassing 30 years. The oldest Bowfin was a male from Gun Lake that was 33 years old, which is the same as the observed maximum age found in Lackmann et al. (2022) from a similar latitude in Minnesota. Lapillus otoliths provided consistent readability throughout almost all the fish that were aged. Four Bowfin from Gun Lake required the use of the

asteriscus otolith due to more challenging readability in a lapillus otolith. Each of these fish were over 24 years old, including the 33-year-old mentioned previously, suggesting that the asteriscus otolith may provide more clarity in aging older individuals. Bowfin grow rapidly early in life, with males reaching about 95% of their asymptotic length by an age of 5 years and females doing so by approximately 11 years. Overall, our data lacked young females, with only eight individuals age five or younger compared to 20 males. This discrepancy likely contributed to the slower apparent growth rates for females in this study.

*Mortality and Recruitment* – Annual mortality and recruitment were consistently low across all three systems, highlighting similar population dynamics among them. Annual mortality ranged from 2.5% to 6.5% across all study sites and were similar to the 5-7% annual mortality estimated in Lackmann et al. (2022) from otoliths. Other than that, mortality estimates of Bowfin varied extensively compared to the annual mortality rates of 34% and 37% estimated from pectoral fin rays in Koch et al. (2009), and 86% estimated from gular plates in Davis (2006). A likely explanation for the large discrepancies in mortality estimates compared to the latter two studies is the difference in the age structure used from the sampled populations. Davis (2006) and Koch et al. (2009) examined gular plates and pectoral fin rays, respectively, and presumed much younger populations of Bowfin, whereas both this study and Lackmann et al. (2022) documented much older age distributions from otoliths. Because younger fish generally experience higher natural mortality than older individuals (Lorenzen 2022), studies dominated by younger age classes estimated by non-otolith structures are expected to produce higher mortality estimates. The recruitment estimates of RCD from 0.02 to 0.30 were lower than

Lackmann et al. (2022) where they showed RCD values from 0.34 to 0.49 and Bowfin were pooled across sites to gain an initial glimpse into otolith-derived population dynamics. In Little Toad Lake specifically, the oldest year class (1997) was the third most abundant year class present in the sample. This is a true testament to the variability of Bowfin recruitment. Nonetheless, the variable recruitment and low mortality rate estimates in this study using standardized fisheries independent gear were comparable to Lackmann et al. (2022). The overall instability in recruitment shown in our study is concerning given there are currently no bag or season limits on the harvest of Bowfin in Minnesota, despite growing sport fisheries that target this species (Rypel et al. 2021; Lackmann et al. 2022). Further research regarding Bowfin recruitment and mortality, derived from otolith thin sections, is needed statewide and across their range in North America.

*Diets* – Bowfin diets were highly varied, but major prey contributors remained consistent among systems. This is fitting with previous literature that suggests Bowfin exhibit a generalist feeding behavior (Hausman et al. 1998; Burr & Bennett 2014; Nawrocki et al. 2016; Valentine & Whitledge 2024). Generalist feeding allows Bowfin to become resistant to changes in forage composition, thus being less susceptible to dietary stressors like competition and changing prey abundances (Nawrocki et al. 2016). We found Bowfin across the study sites heavily favored fish in comparison with most other prey types. The similarities in prey importance among study lakes suggests there is at least some spatial consistency in diets of Minnesota Bowfin, at least within lakes of similar forage bases. These results are similar to findings in previous studies in which abundant forage within systems often make up the majority of upper-level predator diets.

(Hausman 1998; Glade 2021; Slagle 2025). Therefore, we can assume Bowfin aren't specialized Bluegill predators, but more likely taking advantage of the already abundant prey available. Because we only collected Bowfin for one week within each field season, this diet analysis is a snapshot of the entirety of Bowfin diet composition. This needs to be noted and acknowledged as further diversification of Bowfin diets is entirely possible during different times of the year. Future studies on Bowfin diets should investigate possible seasonal changes in diet composition. Our results mirror previous studies that show Bowfin consume a wide variety of prey species, with major contributions consisting of the abundantly available forage species present.

*Stable Isotope Analysis* – Trophic positions of the four predators remained consistent among systems, even though isotopic niche size and niche overlap varied. Across all study sites, Walleye and Largemouth Bass occupied higher trophic positions than Bowfin and Northern Pike, a pattern that aligns with previous research documenting similar predator hierarchies (Nawrocki et al. 2016; Herwig et al. 2021; Rojas et al. 2025). The comparable trophic positions of Northern Pike and Bowfin likely reflect their shared reliance on littoral prey resources. Herwig et al. (2021) showed Northern Pike diets were strongly littoral focused, with a large portion of their diets consisting of macroinvertebrates and smaller forage fishes, resembling our findings of Bowfin diets. Compared to the other piscivores present, Bowfin exhibited the largest isotopic niche size in each system; two to three times larger than all other predators sampled. This resembles previous research done by Nawrocki et al. (2016) in which they found Bowfin exhibited isotopic niche sizes two to four times larger than other predatory species present. Bowfin also displayed the widest range of niche sizes across systems ( $SEAc = 1.3-3.3$ ),

suggesting a high degree of dietary flexibility. These large areas and ranges suggest that Bowfin possess the ability to be extremely tolerant of changing forage bases, either during yearly shifts in prey composition, or long-term prey abundance fluctuations. This adaptability may allow Bowfin to maintain stable populations even in systems where prey communities are dynamic or periodically resource-limited.

Isotopic niche overlap was consistently highest between Bowfin and Northern Pike across all systems, indicating again that these predators rely on similar prey and occupy comparable ecological roles. In contrast, Bowfin's overlap with Largemouth Bass and Walleye varied substantially among lakes. In Little Toad Lake, overlap with both species remained below 40%, whereas in Lake Sarah and Gun Lake it exceeded 60%. This sharp contrast aligns with differences in littoral habitat: the lakes with more extensive littoral zones supported substantially greater overlap between Bowfin and the other predators than the lake with less littoral area, Little Toad. This pattern suggests that as littoral area increases, so does the availability of shared prey resources, that may intensify niche overlap and potentially increase competition. These results highlight that while trophic hierarchies among these predators remain stable across systems, the size and overlap of their isotopic niches are more sensitive to system-level characteristics. This pattern is consistent with prey base differences among lakes. Glade et al. (2023) showed the importance of Bluegill in predator diets increased along with the increase in the littoral area of a lake. Bluegill often have stronger year classes in lakes with large littoral zones, rather than in larger, deeper lakes (Theiling 1990; Tomcko & Pierce 2005). This higher abundance of Bluegill in shallower, more productive systems likely causes higher rates of dietary convergence among top predators due to them sharing this

abundant littoral based prey. Therefore, the extent of littoral habitat appears to be a key driver of whether predator communities converge on shared prey or partition resources.

Here we present the first large-scale, absolute abundance estimates for Emerald Bowfin in the state of Minnesota, and potentially across the full range of the *Amia* genus. These results reveal that Bowfin persist at low densities and exhibit long lifespans, low annual mortality, and limited recruitment, a combination that emphasizes their possible vulnerability in systems where they currently receive no formal protection. When paired with the diet data and stable isotope analysis these findings directly challenge long-standing misconceptions about Bowfin as ecological nuisances. Instead, these results demonstrate that Bowfin function as important native predators that contribute to the stability of prey communities and overall ecosystem balance (Scarnecchia 1992; Burr & Bennett 2014). As such, Bowfin should be recognized and managed as a valuable component of freshwater biodiversity. Moving forward, these abundance estimates provide a critical baseline for future monitoring and management of this species. These findings highlight the need for more informed conservation and management strategies that reflect the Bowfin's true ecological role as a low-density, long-lived, generalist predator.

### **Management Implications**

Given the population dynamics of Bowfin demonstrated in this study and in Lackmann et al. (2022), the results have clear and immediate relevance for fisheries management in Minnesota. Protection of Bowfin is strongly recommended, and the proposed statewide daily limit of six Bowfin per angler (MNDNR 2026) represents an appropriate first step toward ensuring sustainable harvest and maintaining long-term

population stability across all forms of take, including bowfishing, angling, and spearfishing. An additional future step in managing Bowfin in Minnesota is to implement monitoring of bowfishing tournaments, which often do not require permits and consequently provide no data on harvest numbers (Scarnecchia & Schooley 2020). By combining density estimates across lakes, we calculated an approximate abundance of 4.6 Bowfin per littoral hectare, providing managers with a practical tool for assessing population sizes in other systems and establishing a critical baseline for future research and long-term monitoring efforts. This estimate also strengthens the scientific foundation underlying the proposed bag-limit recommendations. Given the growing interest in Bowfin among diverse stakeholder groups, proactive management is essential to ensure that healthy Bowfin populations persist for future generations.

The successful management of fish populations requires the knowledge of a few core principles, including recruitment, mortality, abundance, and growth (Camp et al. 2020; Lorenzon 2022). This study vastly improved our understanding of these principles for Bowfin, but more information is needed. The fundamental next steps are to address these knowledge gaps by (1) estimating populations in systems with low reported Bowfin catches that may indicate smaller populations, (2) conducting further research on Bowfin recruitment and mortality using otolith thin sections, (3) examining potential seasonal changes in diet composition through monthly diet studies, and (4) quantifying Bowfin harvest from angling, bowfishing, and spearfishing.

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**Tables:**

**Table 1:** County, surface area (ha), littoral area (ha), maximum depth (m), Secchi depth (m), number of fyke nets used, and Emerald Bowfin *Amia ocellicauda* population estimates for Little Toad, Sarah, and Gun lakes in Minnesota, April and May 2024-2025.

<b>Lake</b>	<b>County</b>	<b>Area (ha)</b>	<b>Littoral Area (ha)</b>	<b>Maximum Depth</b>	<b>Secchi Depth</b>	<b># of Nets Used</b>	<b>Population Estimate</b>
Little Toad	Becker	164	43 (26%)	20 m	5.2 m	16	196
Sarah	Hennepin	225	151 (67%)	18 m	0.8 m	17	657
Gun	Aitkin	288	118 (41%)	13 m	1.9 m	21	612

**Table 2:** Model selection statistics for all candidate von Bertalanffy growth models for TL vs. Age of Emerald Bowfin *Amia ocellicauda* from Little Toad, Sarah, and Gun lakes in Minnesota, April and May 2024-2025.

<b>Model</b>	<b><math>t_0</math></b>	<b>df</b>	<b>AIC</b>	<b><math>\Delta</math> AIC</b>
L-inf and k sex-specific	Un-fixed	7	1431.3	0.0
L-inf and k sex and system-specific	Fixed	13	1439.1	7.8
L-inf and k sex and system-specific	Un-fixed	15	1439.6	8.4
L-inf and k sex-specific	Fixed	5	1441.8	10.6
L-inf is sex and system-specific, k is constant	Un-fixed	10	1449.9	18.6
L-inf is sex-specific, k is constant	Un-fixed	6	1451.5	20.2
L-inf is sex-specific, k is constant	Fixed	4	1471.5	40.2
L-inf is sex and system-specific, k is constant	Fixed	8	1474.6	43.3
L-inf is constant, k is sex and system-specific	Un-fixed	10	1514.9	83.6
L-inf is constant, k is sex-specific	Un-fixed	6	1516.2	84.9
L-inf is constant, k is system-specific	Un-fixed	7	1556.3	125.0
L-inf system-specific, k is constant	Un-fixed	7	1557.2	125.9
L-inf and k is constant - Null	Un-fixed	5	1558.6	127.3
L-inf and k system-specific	Un-fixed	9	1559.8	128.5
L-inf and k system-specific	Fixed	7	1579.3	148.0
L-inf system-specific, k is constant	Fixed	5	1583.7	152.4
L-inf is constant, k is sex-specific	Fixed	4	1594.0	162.7
L-inf and k is constant - Null	Fixed	3	1598.1	166.8
L-inf is constant, k is sex and system-specific	Fixed	8	1601.1	169.8
L-inf is constant, k is system-specific	Fixed	5	1602.0	170.7

**Table 3:** Common names and abbreviations of prey items present in Emerald Bowfin *Amia ocellicauda* stomachs from Little Toad (April-May 2024), Sarah (April-May 2025), and Gun (May 2025) lakes in Minnesota.

<b>Prey Species</b>	<b>Abbreviation</b>
Black Crappie	BLC
Bluegill	BLG
Bullhead spp.	BLH
Bowfin	BOF
Caddisfly Nymph	CAD
Centrarchid spp.	CEN
Central Mudminnow	CNM
Crayfish	CRAY
Damselfly Nymph	DAM
Dragonfly Nymph	DRA
Green Sunfish	GRS
Inorganic Matter	IGM
Northern Pike	NOP
Organic Matter	OGM
Predaceous Diving Beetle	PDB
Snail spp.	SNL
<i>Belostoma</i> spp.	TOB
Unidentified Fish Remains	UNKF
Unidentified Invert Remains	UNKI
Water Boatman	WBM



**Table 5:** Mean and standard deviation of total length,  $\delta^{15}\text{N}$ ,  $\delta^{13}\text{C}_{\text{normalized}}$ , and TPscaled from all species used for stable isotope analysis from Little Toad Lake (April-May 2024), Lake Sarah (April-May 2025), and Gun Lake (May 2025), Minnesota.

Lake	Species	$n$	Length (mm)	$\delta^{15}\text{N}$	$\delta^{13}\text{C}_{\text{normalized}}$	TPscaled
<b>Little Toad</b>	BOF	46	621 ± 71	11.6 ± 0.8	-27.0 ± 0.5	5.5 ± 0.5
	LMB	18	429 ± 31	13.1 ± 0.3	-27.9 ± 0.7	6.6 ± 0.2
	NOP	17	549 ± 91	11.5 ± 0.5	-28.1 ± 0.5	5.4 ± 0.3
	WAE	8	642 ± 55	13.1 ± 0.4	-27.9 ± 0.7	6.6 ± 0.3
	BLG	29	146 ± 38	9.6 ± 0.5	-28.0 ± 1.6	NA
	YEP	15	127 ± 9	9.5 ± 0.2	-30.3 ± 1.5	NA
	SPO	15	NA	9.1 ± 0.3	-30.4 ± 0.3	NA
	DRA	9	NA	4.6 ± 1.0	-28.3 ± 1.0	NA
	SNL	15	NA	5.1 ± 0.3	-26.9 ± 0.8	NA
<b>Sarah</b>	BOF	50	537 ± 90	11.3 ± 1.1	-24.2 ± 1.2	5.8 ± 0.7
	LMB	22	408 ± 69	12.1 ± 0.5	-24.7 ± 0.9	6.2 ± 0.3
	NOP	25	621 ± 105	11.2 ± 0.5	-24.5 ± 0.4	5.6 ± 0.3
	WAE	23	593 ± 63	12.1 ± 0.4	-24.4 ± 0.5	6.2 ± 0.3
	BLG	26	140 ± 42	8.7 ± 0.7	-26.2 ± 1.1	NA
	YEP	12	152 ± 28	9.4 ± 0.4	-24.8 ± 1.6	NA
	GOS	7	155 ± 29	9.6 ± 0.1	-26.7 ± 0.7	NA
	DRA	10	NA	3.7 ± 0.6	-27.1 ± 2.1	NA
	SNL	5	NA	4.1 ± 0.4	-25.3 ± 0.6	NA
<b>Gun</b>	BOF	50	615 ± 81	12.2 ± 1.1	-29.1 ± 0.3	5.9 ± 0.8
	LMB	29	440 ± 41	12.9 ± 0.7	-28.9 ± 0.5	6.5 ± 0.5
	NOP	30	604 ± 105	11.8 ± 0.7	-29.0 ± 0.5	5.7 ± 0.5
	WAE	7	553 ± 113	13.1 ± 0.9	-29.5 ± 0.3	6.6 ± 0.8
	BLC	19	142 ± 5	10.6 ± 0.5	-32.1 ± 0.4	NA
	BLG	17	123 ± 9	9.6 ± 0.6	-30.2 ± 1.5	NA
	SNL	17	NA	5.2 ± 0.4	-29.2 ± 1.1	NA

**Table 6:** Percent species A isotopic niche overlaps with species B isotopic niche using 95% confidence interval ellipses. TA represents total area of the convex hull or the total area of all points from a species. SEAc represents the basic standard ellipse area corrected for small sample sizes (Jackson et al. 2011). Collected from Little Toad Lake (April-May 2024), Lake Sarah (April-May 2025), and Gun Lake (May 2025), Minnesota.

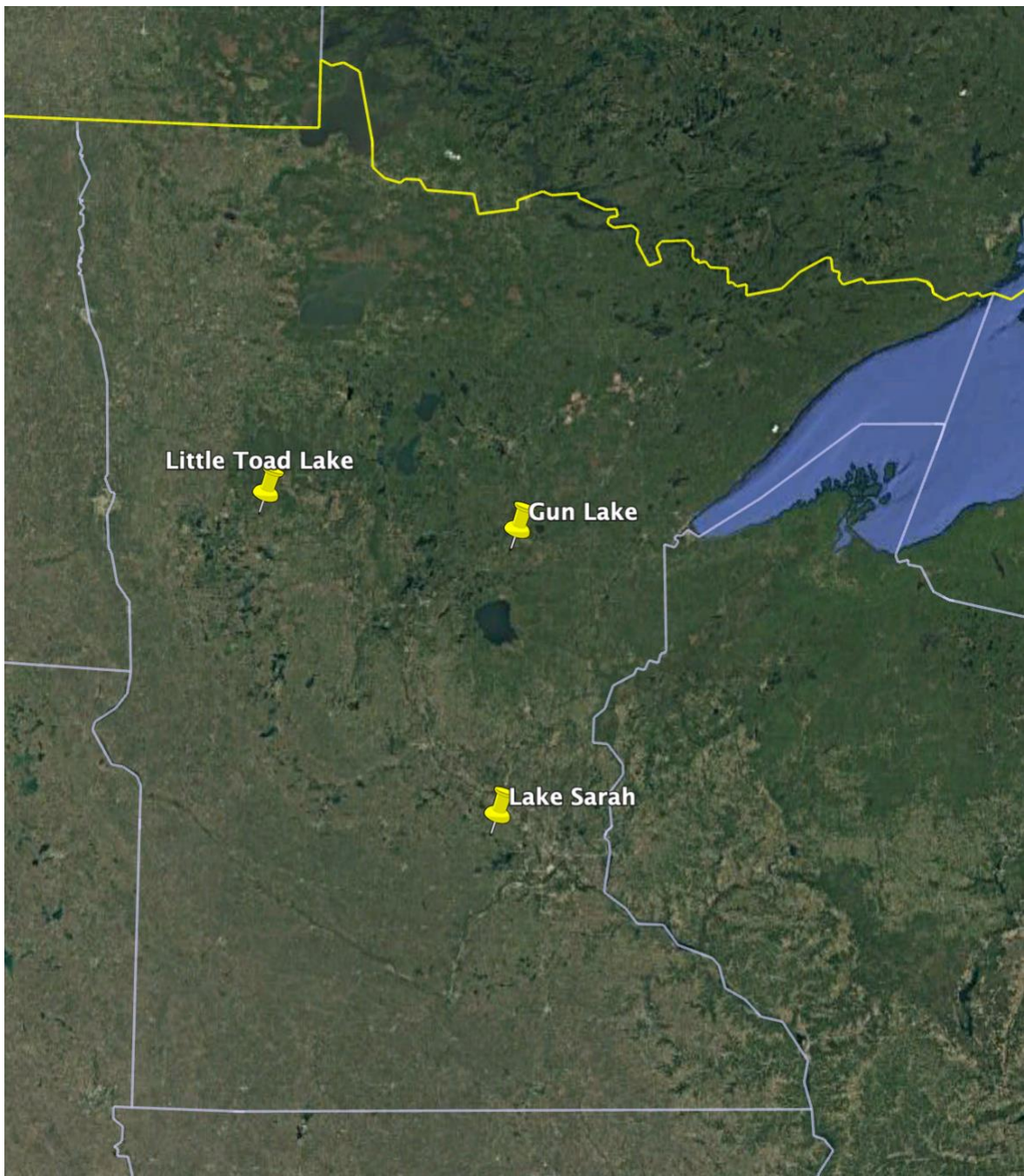
<b>Little Toad</b>							
<b>Species Code</b>		<b>Species B</b>				<b>TA</b>	<b>SEAc</b>
		<b>BOF</b>	<b>LMB</b>	<b>NOP</b>	<b>WAE</b>		
<b>Species A</b>	<b>BOF</b>	N/A	39.6	58.2	33.0	7.8	1.3
	<b>LMB</b>	18.6	N/A	4.9	60.5	1.6	0.6
	<b>NOP</b>	30.2	5.4	N/A	12.8	2.0	0.7
	<b>WAE</b>	25.7	100.0	19.1	N/A	1.4	1.0

<b>Sarah</b>							
<b>Species Code</b>		<b>Species B</b>				<b>TA</b>	<b>SEAc</b>
		<b>BOF</b>	<b>LMB</b>	<b>NOP</b>	<b>WAE</b>		
<b>Species A</b>	<b>BOF</b>	N/A	93.0	100.0	98.5	12.9	3.3
	<b>LMB</b>	25.7	N/A	61.6	99.8	3.4	0.9
	<b>NOP</b>	16.9	37.6	N/A	50.5	1.7	0.6
	<b>WAE</b>	15.0	55.0	45.5	N/A	1.4	0.5

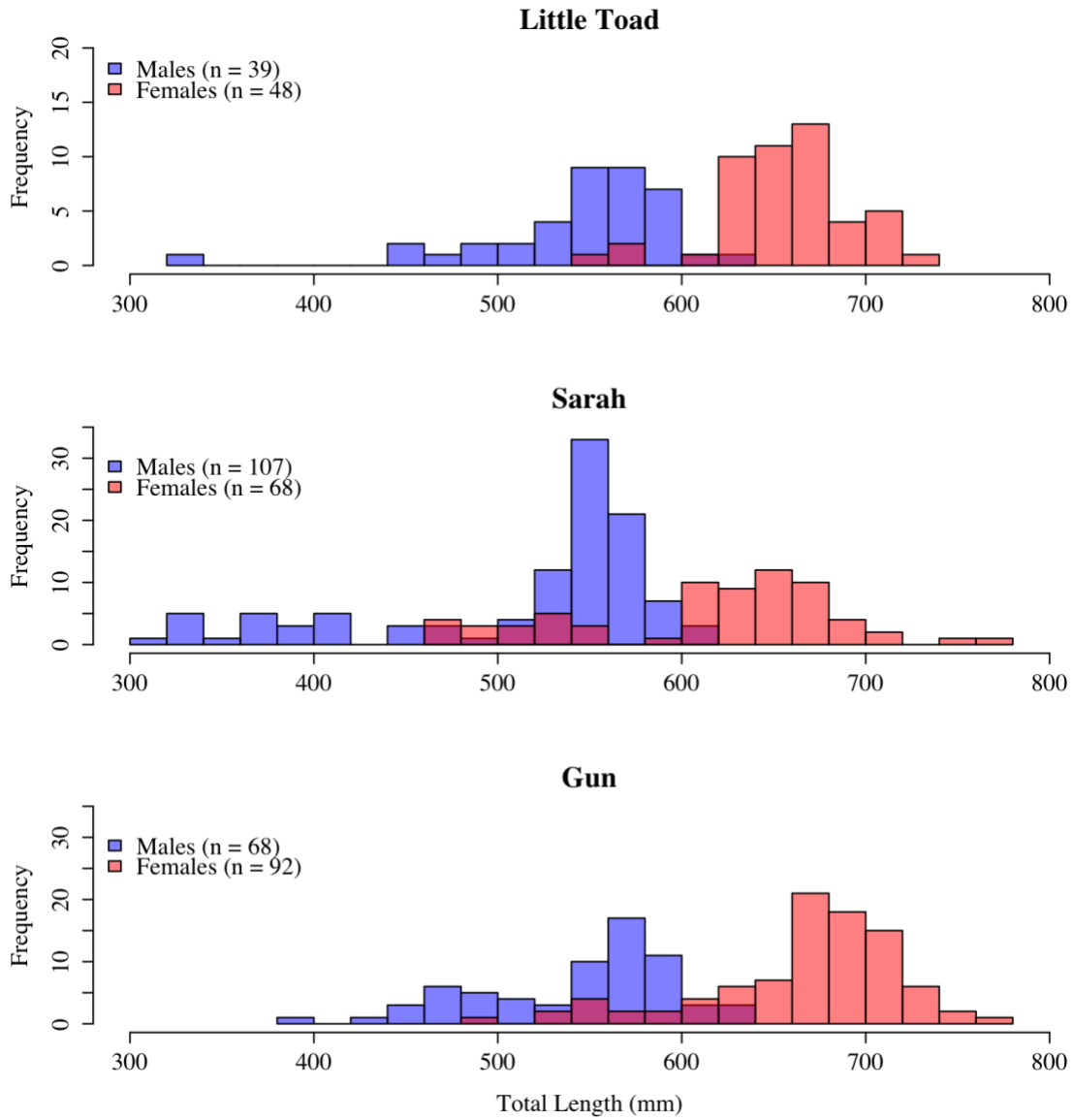
<b>Gun</b>							
<b>Species Code</b>		<b>Species B</b>				<b>TA</b>	<b>SEAc</b>
		<b>BOF</b>	<b>LMB</b>	<b>NOP</b>	<b>WAE</b>		
<b>Species A</b>	<b>BOF</b>	N/A	70.2	76.5	60.8	5.8	1.3
	<b>LMB</b>	52.6	N/A	50.9	60.8	3.3	1.0
	<b>NOP</b>	61.0	54.1	N/A	57.7	3.3	1.0
	<b>WAE</b>	38.3	51.1	45.6	N/A	0.9	0.8

**Figures:**

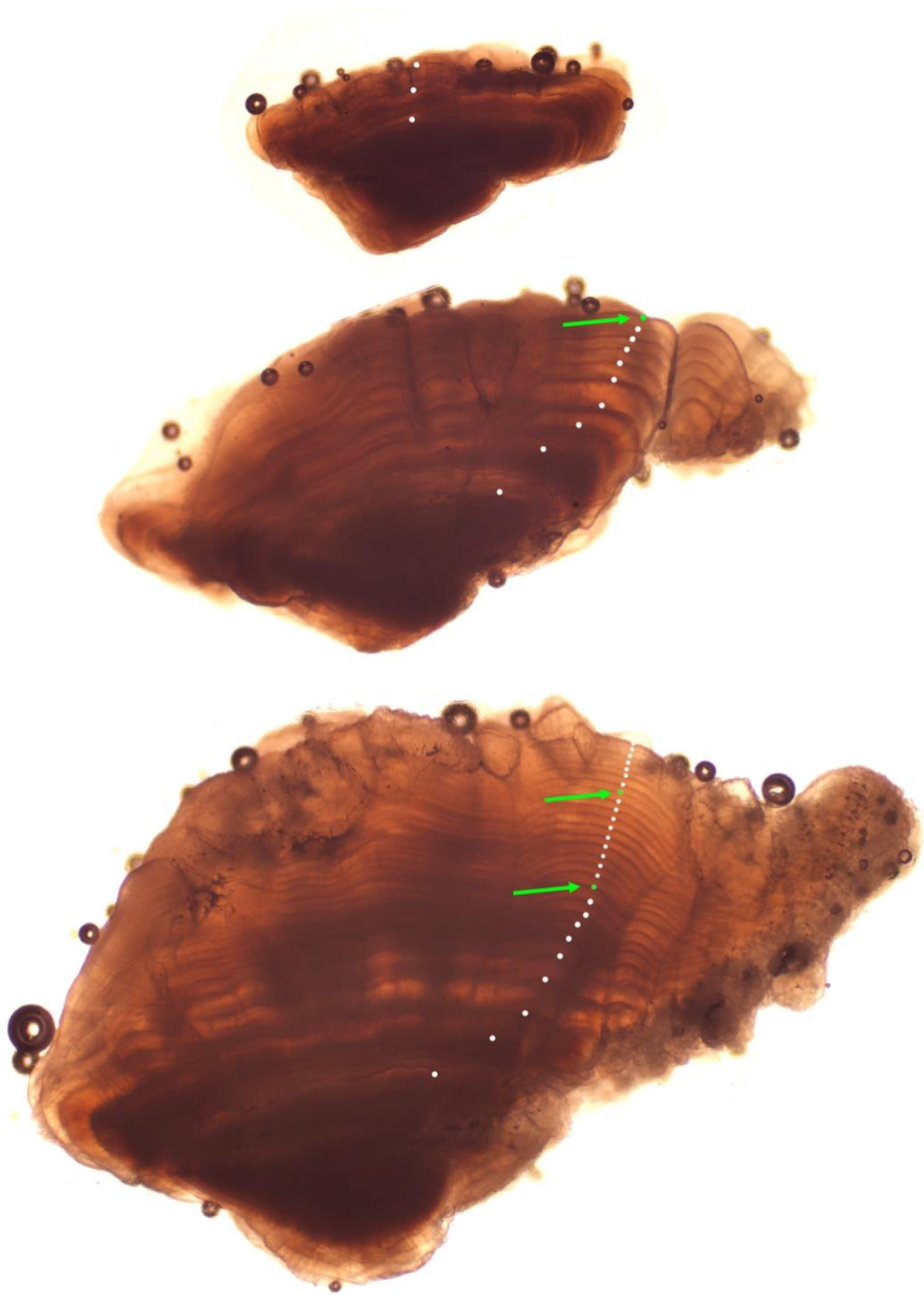
**Figure 1:** Locations of the three study lakes; Little Toad Lake (April-May 2024), Lake Sarah (April-May 2025), and Gun Lake (May 2025) set within a map of Minnesota.



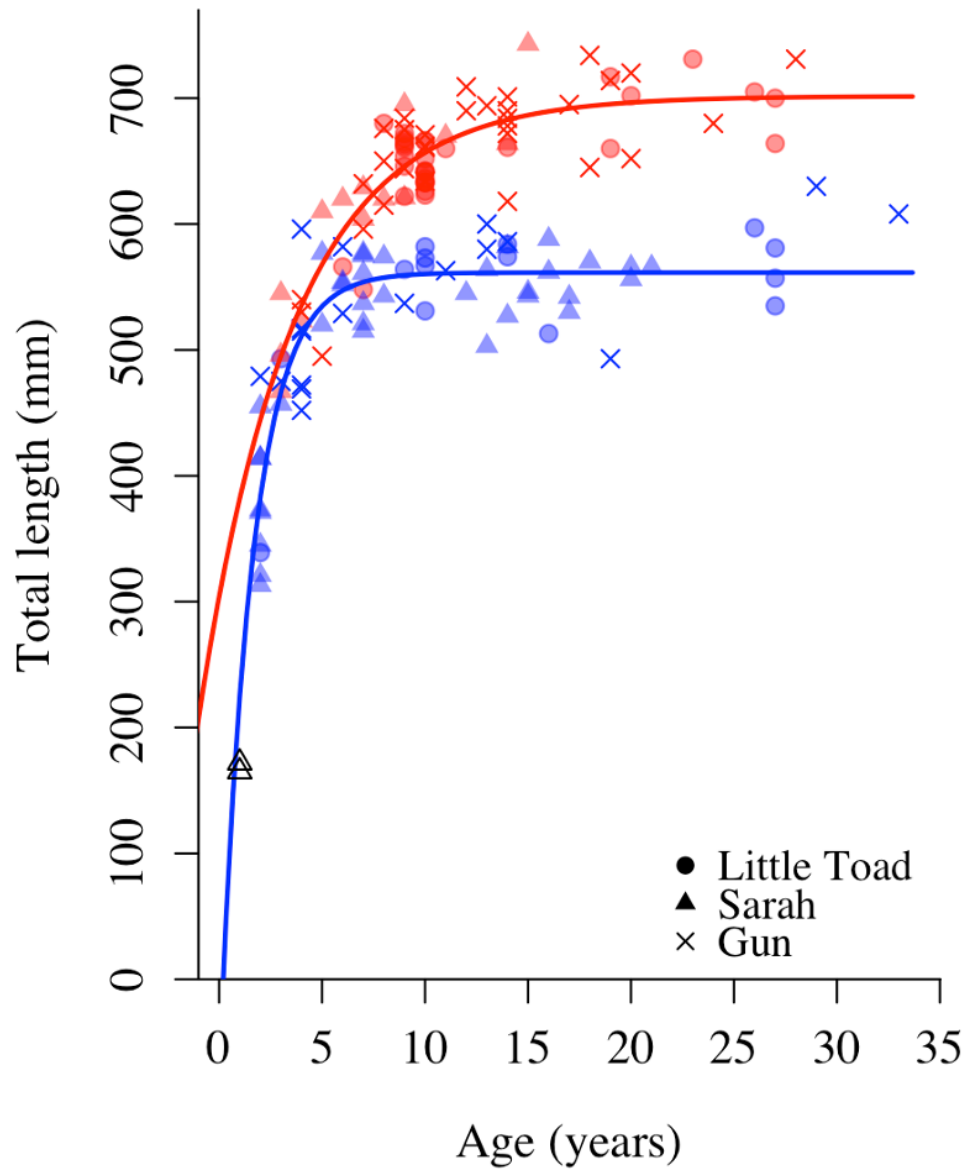
**Figure 2:** Example of fin punch used for marking Emerald Bowfin *Amia ocellicauda* during the mark-recapture population estimation.



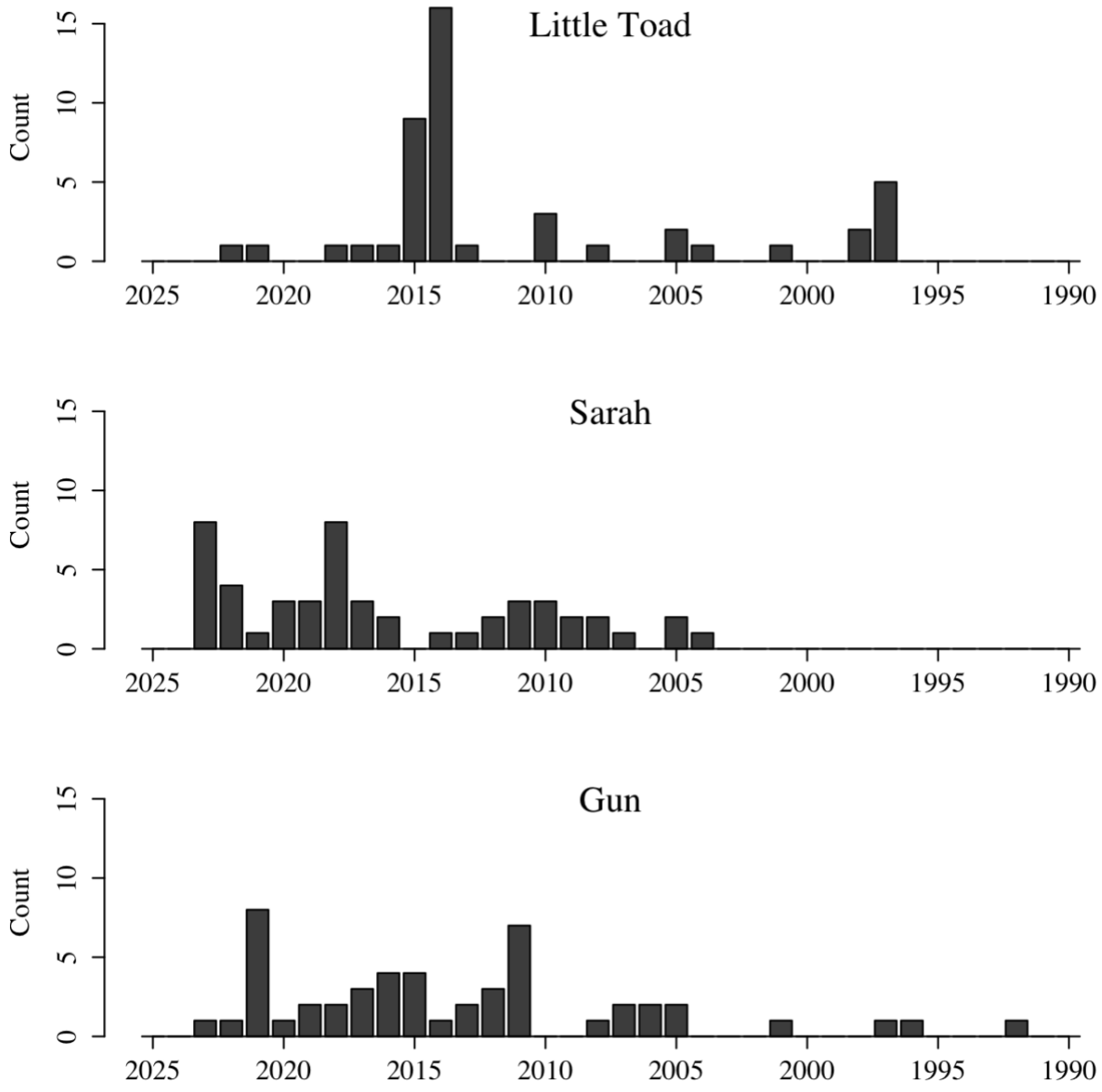
**Figure 3:** Length-frequency histogram of all Emerald Bowfin *Amia ocellicauda* caught through the duration of the study. Males (blue) and females (red) collected from Little Toad Lake (April-May 2024), Lake Sarah (April-May 2025), and Gun Lake (May 2025), Minnesota.



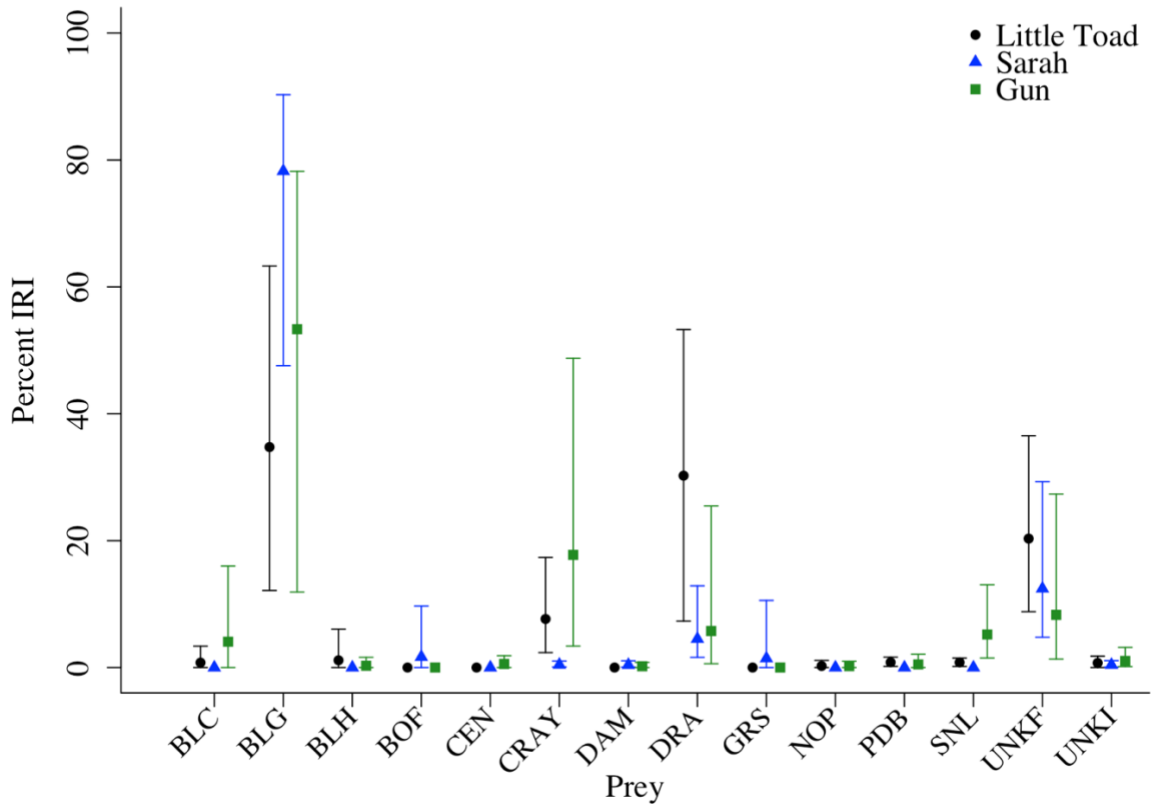
**Figure 4:** Example lapillus otolith thin sections from Little Toad Lake, Minnesota Emerald Bowfin *Amia ocellicauda*, May 2024. Green arrows and dots denote decadal annuli. Ages from top to bottom: 3 years, 10 years, 27 years.



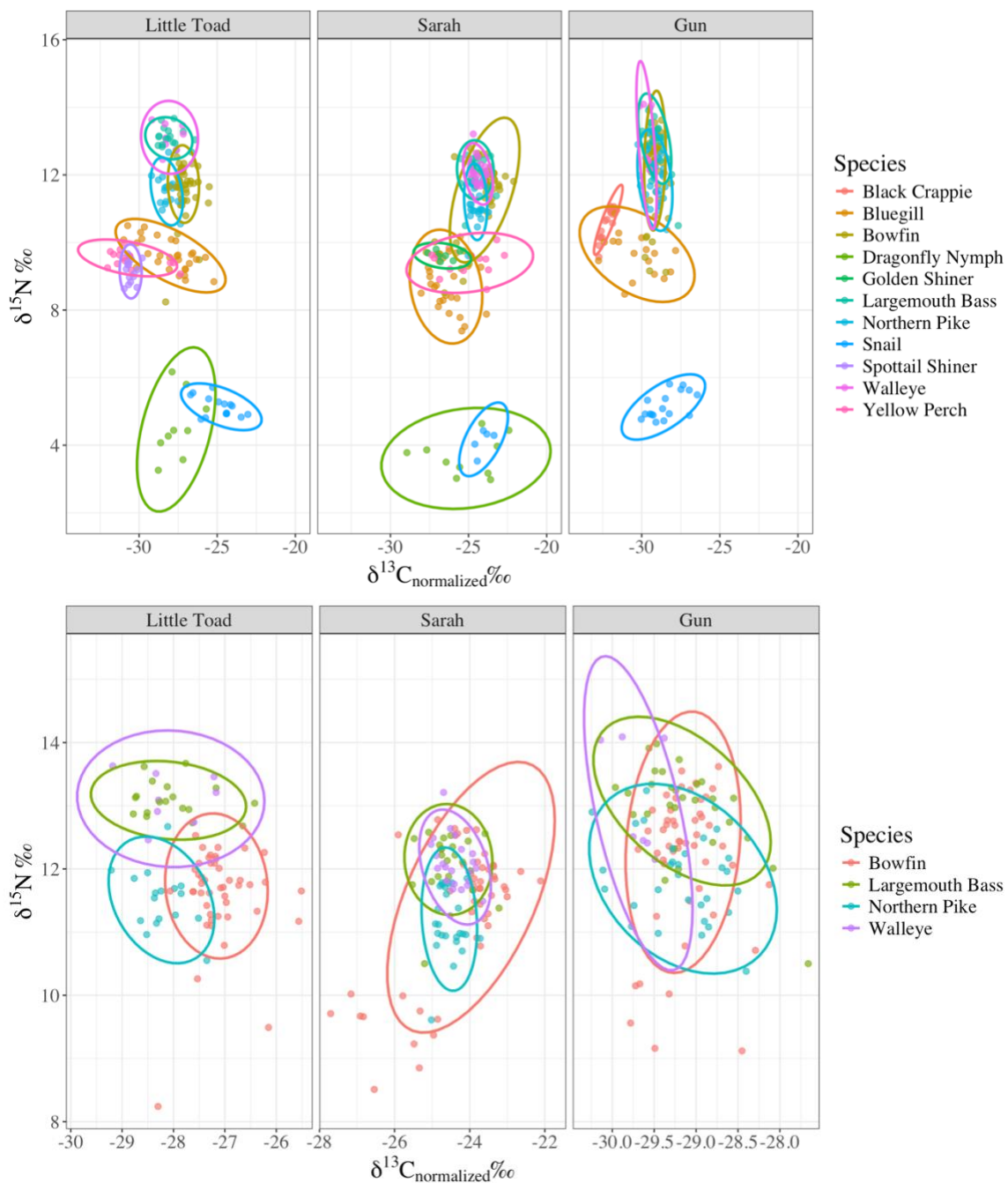
**Figure 5:** Total length (mm) versus age (years) for Emerald Bowfin *Amia ocellicauda*. Males (blue) and females (red) collected from Little Toad Lake ( $n = 46$ ), Lake Sarah ( $n = 50$ ), and Gun Lake ( $n = 50$ ) as modeled by the highest-ranked von Bertalanffy growth function (pooling sites; see Table 4). Two consumed unsexed Bowfin from Lake Sarah denoted as black triangles, not used in the analysis but included for reference. Collected from Little Toad Lake (April-May 2024), Lake Sarah (April-May 2025), and Gun Lake (May 2025), Minnesota.



**Figure 6:** Assigned year classes of Emerald Bowfin *Amia ocellicauda* from Little Toad Lake ( $n = 46$ ), Lake Sarah ( $n = 50$ ), and Gun Lake ( $n = 50$ ), that were collected during April-May 2024 (Little Toad), April-May 2025 (Sarah), and May 2025 (Gun), Minnesota.



**Figure 7:** Percent Index of Relative Importance (%IRI) values of prey specimens collected from Emerald Bowfin *Amia ocellicauda* stomachs during April-May 2024 (Little Toad), April-May 2025 (Sarah), and May 2025 (Gun), Minnesota. Error bars represent 95% confidence intervals using bootstrapping methods. See Table 2 for full names of prey species.



**Figure 8:** Isotopic niche plot of predators and prey (top) and predators only (bottom) for each system. Solid dots represent individual fish or invertebrates and colors represent species. Lines denote the 95% confidence ellipses around species centroids. Samples collected during April-May 2024 (Little Toad), April-May 2025 (Sarah), and May 2025 (Gun), Minnesota.