Age and growth of Niagara River Lake Sturgeon

Jonah L. Withers*, Dimitry Gorsky, Zy Biesinger, Donald Einhouse, Michael Clancy, Lori Davis, Curtis Karboski, Chris Legard, Eric Bruestle, Nicholas Markley, Robert Roth, Rich Zimar, John A. Sweka

J. Withers, L. Davis, N. Markley, J.A. Sweka
U.S. Fish & Wildlife Service, Northeast Fishery Center, P.O. Box 75, Lamar, PA 16848

D. Gorsky, Z. Biesinger, C. Karboski, E. Bruestle
U.S. Fish & Wildlife Service, Lower Great Lakes Fish & Wildlife Conservation Office, 1101 Casey Road, Basom, NY 14013

D. Einhouse, R. Zimar
New York State Department of Environmental Conservation, Lake Erie Fisheries Unit, 178 Point Drive North, Dunkirk, NY 14048

M. Clancy, R. Roth
New York State Department of Environmental Conservation, Region 9, 182 East Union Street, Suite 3, Allegany, NY 14706

C. Legard
New York State Department of Environmental Conservation, Region 6, 541 East Broadway, Cape Vincent, NY 13618

*Corresponding author: Jonah_Withers@fws.gov

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Abstract

Knowledge of the distribution of ages of fish within a stock, and subsequently individual growth rates, allows managers the ability to calculate key metrics (i.e., recruitment, mortality, and stock growth rate) that greatly improve stock assessment models. Two remnant stocks of Lake Sturgeon *Acipenser fulvescens* exist near and within the Niagara River; one primarily occupying the headwaters of the river and the other primarily occupying the mouth of the river. Though initial efforts in the late 1990s collected data on the lower Niagara River stock, a long-term, comprehensive examination of age and growth is lacking and the age structure of the stock found at the headwaters has yet to be formally described to our knowledge. To ascertain the current age structure of these two stocks we sampled Lake Sturgeon in the lower Niagara River and at the headwaters of the Niagara River between 2012 and 2017 and took a portion of the leading pectoral fin spine of captured Lake Sturgeon for age estimation. Ages ranged between 4 and 42 years with females generally being older and larger than males. The median age appeared to increase from 14 to 18 years old throughout our study in both stocks. Lengths-at-age of both stocks were larger than those reported in other systems and growth rates appear to have increased over the past decade in the lower Niagara River. Despite efforts to improve age estimation accuracy, age estimates from fish whose ages were partly-known (derived from multiple age estimates from fish that were captured multiple times) demonstrated assigned ages may have greater error than expected. Additionally, a lack of young individuals confounded growth analyses. Although there was uncertainty in the assigned ages, this study still provides evidence of consistent recruitment in both stocks and, to our knowledge, the first characterization of the age structure of the Lake Sturgeon stock occupying the headwaters of the Niagara River.

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Introduction

Lake Sturgeon *Acipenser fulvescens* are an ancient, keystone species that have suffered dramatic declines throughout their distribution (Tody 1974; Auer 1999). Since their decline throughout the Laurentian Great Lakes in the late 19th and early 20th centuries, Lake Sturgeon stock status and recovery have been difficult to assess due to their rarity and biology. As the largest and longest-lived freshwater fish species endemic to North America (Scott and Crossman 1973), Lake Sturgeon exhibit late age-at-maturity (Scott and Crossman 1973; Winemiller and Rose 1992), slow growth, and skip-spawning which predisposes them to overharvest and prolonged recovery rates (Haxton et al. 2014; Sweka et al. 2018). Like other long-lived, cartilaginous species, assigning accurate ages to Lake Sturgeon is difficult. However, age estimates of individuals within a stock greatly improve stock assessment models. As the age structure of a stock is identified, researchers and managers can begin to quantify key metrics, such as recruitment, individual growth rate, and total mortality, and how these metrics vary temporally.

Since ages of wild Lake Sturgeon are not known, researchers and managers rely on osseochronometry, or the interpretation of fast and slow calcium carbonate deposition on calcified accretions to indirectly estimate growth and assign an estimated age to a fish (Casselman 1987). The accuracy of the age estimate is predicated on the choice of calcified structure, preparation method, and interpretation and is thus subject to error (Casselman 1983). Consequently, Beamish and McFarlane (1983) and Campana (2001) strongly recommend the accuracy and precision of age estimates be validated when possible.

Lake Sturgeon are currently listed as a threatened species in New York State and are considered a priority species for recovery (NYSDEC 2018). Two known stocks of Lake Sturgeon

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exist in and around the Niagara River; one at the headwaters (HNR), upstream of Niagara Falls, and the other at the mouth of the river, downstream of Niagara Falls (LNR; Figure 1; Hughes et al. 2005; Neuenhoff et al. 2018). Though genetically similar (M. Bartron, US Fish and Wildlife Service, unpublished data), these two groups of Lake Sturgeon are spatially separated by Niagara Falls and differ demographically (present study). Given the spatial separation and demographic differences, these two groups of Lake Sturgeon are considered two distinct stocks and are managed as such (Wells and Richmond 1995; NYSDEC 2018). Describing the age composition of these stocks is important to managers because it provides a means for assessing recruitment and cohort strength over time; as well as age at sexual maturity. The New York State Lake Sturgeon recovery plan requires two criteria to be met within six of seven management units before initiating delisting: 1) evidence of at least 750 sexually mature Lake Sturgeon and 2) evidence of natural recruitment in at least three years of a five year period within the last 20 calendar years (NYSDEC 2018). The LNR and HNR stocks represent two of the seven management units and age estimates can provide managers with age at maturity as well as recruitment; contributing to assess both delisting criteria within management units. In the late 1990s, efforts were made to assess the stock age structure of Lake Sturgeon in the LNR (Hughes et al. 2005); however, no studies we are aware of have re-examined the age structure of this stock and no studies have documented the age structure of Lake Sturgeon occupying the HNR. To facilitate future stock assessment, we sought to characterize the age distributions and average individual growth rates of these two Lake Sturgeon stocks.

Methods

Study area

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The Niagara River is approximately 58 km long and is the major connecting waterway between Lake Erie and Lake Ontario (Figure 1). The river forms the international border of Canada and the United States beginning at the northeast end of Lake Erie and flowing north into the main-stem of the river. The majority of Lake Erie's discharge flows into the headwaters of the river, near Buffalo, NY and Fort Erie, ON, and begins its way through the 35 km reach of the upper Niagara River.

The Niagara River can be described by its three main sections, the upper Niagara River, and two sections in the LNR; the Niagara Gorge, and the lower portion of the Niagara River. The upper Niagara is relatively shallow (7 m) compared to the LNR and is characterized by variable water velocities depending on river width, ranging from 0.6 m/s to 3.7 m/s (INWC 2016). Once the river reaches Grand Island, it splits into two channels before reuniting at the northwestern end of Grand Island. The river then enters the Niagara Cascade for about one kilometer before dropping 57 m over Niagara Falls and entering the LNR. The first portion of the LNR, known as the Niagara Gorge, is a 7 km gorge comprised of a deep pool just below the falls followed by deep rapids with velocities measured up to 9.0 m/s (INWC 2016). After the gorge, the river slows and traverses approximately 15 kilometers before reaching the mouth where it meets Lake Ontario.

Sampling

We sampled in the HNR, proximate to documented Lake Sturgeon egg deposition (Neuenhoff et al. 2018), south-southeast of Bird Island reef and in the LNR, downstream of the gorge and around the mouth of the river. We used experimental gillnets to sample Lake Sturgeon at the HNR (see Neuenhoff et al. 2017 for sampling method specifics) throughout May and we used

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baited setlines in the LNR (see Bruestle et al. 2018 for sampling method specifics) between March and October from 2012 to 2017. We measured and tagged captured Lake Sturgeon with passive integrated transponders (PIT) and FLOY T-bar anchor tags (Floy Tag & Mfg. Inc., Seattle, Washington, USA) to identify recaptured individuals. We assigned sex when possible by gamete expression or gonad assessment via visual observation through a small incision. We took a small (1.5 to 2.5 cm) section of the left, leading pectoral fin spine roughly 5 cm from the point of articulation for age estimation. If an individual was recaptured in a later year of sampling, we removed the right leading pectoral fin spine for partial age validation. We stored spine samples in envelopes and allowed them to air-dry for a minimum of 48 hours before processing.

Processing, reader selection, and age estimation

Once dried, we took a thin (0.5 mm) transverse section from the basal end of the spine sample using a low speed, diamond-bladed sectioning saw. The transverse section was allowed to dry before fixing it to microscope slides using a two part epoxy. Once the epoxy hardened, we ground and polished the sample to preferred thicknesses (translucency).

Since age assessment is subjective, can have low reader accuracy despite high reader precision, there can be large amounts of error in age estimates. To select a reader to estimate ages, we had three individuals estimated ages of known-age Lake Sturgeon spine sections collected from Lake Winnebago provided by the Wisconsin Department of Natural Resources. Readers defined an annulus as a translucent check following opaque zonation such that the area from the distal edge of one translucent check to the distal edge of the consecutive translucent zone would denote one calendar year. Beginning at the focus, or origin, readers would identify the first annulus and progressively denote annuli while moving towards the edge of the spine.

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Though the sample size was relatively small within year classes and only contained individuals up to age 14, assessing the accuracy of each reader with this index was believed to be valuable enough to identify a single, best reader. Once we determined a single best reader from accuracy of age estimates on the known-age spines from Lake Winnebago, that individual proceeded to estimate the ages of spines collected from Lake Sturgeon from the HNR and LNR in the same manner.

Our age estimator viewed each spine section under a compound microscope (Zeiss Axioskop 2 plus) using transmitted light and a magnification between 12.5x and 100x. Our estimator identified the focus of each sample and identified each annulus, considered to be one complete opaque zone-relating to faster growth during the growing season-and one translucent zone-pertaining to the slower growth during winter months, toward the outer edge. Our estimator was given the month of capture to help determine whether marginal increment growth near the outer edge should be classified as a complete annulus. In addition to providing an age estimate, our estimator assigned a confidence rating to each section where samples with zones that were indistinct, variable in appearance, or coalesced received a lower rating. To reduce error, we removed sections that received very low confidence ratings from further analyses.

Analyses

After we removed age estimates with low confidence scores; we created annual age distributions, cohort strength, distributions of length-at-age, and growth curves for each stock of Lake Sturgeon using age estimates from their first capture. We calculated cohort strength by subtracting the estimated age from the year of capture. We used linear regressions between fork length and total length to estimate total length when measurements were not available (Lake

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Sturgeon from the HNR: $y = 0.982x - 15.429$, $r^2 = 0.953$; Lake Sturgeon from the LNR: $y = 1.0704x - 43.184$, $r^2 = 0.9859$). We fit length-at-age growth curves using the von Bertalanffy equation:

$$L_t = L_\infty(1 - e^{-K(t-t_0)})$$

where L_t is predicted length at age t, L_∞ is the asymptotic length, K is the growth rate coefficient, and t_0 is the age when length is zero; the Gompertz equation:

$$L_t = L_\infty e^{e^{-K(t-I)}}$$

where I is the age at the inflection point; and the Logistic equation:

$$L_t = \frac{L_\infty}{1 + e^{-g_\infty(t-I)}}$$

where g_∞ is the instantaneous growth rate at infinity.

We compared stock age structures and lengths between stocks using a Mann Whitney U test since data were not normally distributed (using Shapiro-Wilk tests on LNR ages: $W = 0.98$ $p < 0.001$, LNR total lengths: $W = 0.99$ $p < 0.001$, HNR ages: $W = 0.81$ $p < 0.001$, and HNR total lengths: $W = 0.96$ $p < 0.001$). We also compared differences in lengths and age structure between sexes within and between stocks using Mann Whitney U tests. Finally, we used a Kruskal-Wallis test to test for differences in age by year within each stock.

We examined recaptured Lake Sturgeon spines as a form of partial age validation. We took the age estimate from the first capture as the “true” age. Our expected age at time of recapture was calculated as the “true” age estimate from the time of first capture plus time at liberty. We then compared this expected age estimate to the age estimate assigned to the spine taken during recapture.

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Results

Of the 668 Lake Sturgeon we captured in the LNR between 2012 and 2017, we deemed 618 had age estimates we considered trustworthy. Of the 186 Lake Sturgeon we captured in the HNR between 2012 and 2017, we deemed 164 had age estimates we considered trustworthy. Age estimates ranged between 4 and 30 years old in the LNR (median = 15 years old) and 9 and 42 years old at the HNR (median = 16 years old). Lengths ranged from 81.8 to 181.9 cm in the LNR (median = 140 cm) and from 117.8 to 187.4 cm at the HNR (median = 144.7 cm).

We found age distributions and sizes differed by sex and stock. Despite the age distributions appearing similar between stocks, with the majority of captured fish having ages between 14 and 19, HNR Lake Sturgeon were older ($W = 45282$, $p = 0.035$). Overall sizes at the HNR were also slightly larger than those present in the LNR ($W = 38020$, $p < 0.001$). Female Lake Sturgeon sampled in the LNR were longer ($W = 915$, $p < 0.001$) and estimated to be older ($W = 1178$, $p < 0.001$) than males with females estimated to be 11 to 30 years old (median = 18 years old) and ranged in size from 123.1 to 181.9 cm (median = 149.4 cm) while males were estimated to be 9 to 26 years old (median = 16 years old) and ranged in size from 115.3 to 170.7 cm (median = 137.5 cm). Similarly, females at the HNR were longer ($W = 181$, $p = 0.004$) and older ($W = 176$, $p = 0.003$) than males with females estimated to be between 14 to 42 years old (median = 23 years old) and ranged in size from 131.1 to 187.4 cm (median = 165.5 cm) and males estimated to be between 10 and 33 years old (median = 16 years old) and ranged in size from 117.8 to 178.6 cm (median = 143.3 cm). Age distributions varied between years with median ages increasing from 14 in 2012 to 18 in 2017 in both stocks (Figures 2 and 3; LNR: $\chi^2 = 63.01$, $df = 5$, $p < 0.001$; HNR: $\chi^2 = 19.69$, $df = 5$, $p = 0.001$). Cohorts ranged from 1983 to 2013 in the LNR and from 1974 to 2006 at the HNR (Figure 4). The strongest year classes were 1998

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in the LNR with the majority of fish coming from 1997 to 2001 and 1999 at the HNR with the majority of fish coming from 1996 to 2000.

Our partial age validation, by comparing recaptured fish's age estimates to their age estimate at first capture, showed age estimates of recaptures generally over-estimated the expected age (Figure 5). Linear regressions of estimated age at recapture versus expected age given the assigned age at original capture showed slopes differing from 1 and intercepts differing from 0 (parameter estimate ± se; slope: 0.84 ± 0.13, intercept: 3.78 ± 2.22). This indicated that there was an inconsistent bias in age estimation: ages of younger Lake Sturgeon tended to be overestimated more than those of older Lake Sturgeon.

We calculated average individual growth rates for Lake Sturgeon captured in the LNR using a von Bertalanffy growth curve (Figure 6). We were not able to fit growth curves to the length-at-age data from those sampled at the HNR (Figure 7). We made attempts to fit a growth curve to the data by fixing t_0 and constraining L_∞ in a von Bertalanffy model as well as fitting Gomperz and Logistic models; however, an absence of young individuals likely caused data to appear more linear and prevented data from fitting these growth models. The lack of young individuals produced unrealistic length at age-0 estimates; therefore we did not pursue further considerations about the von Bertalanffy growth curve.

Discussion

We found differences in sizes and ages of Lake Sturgeon between sexes within both the LNR and the HNR stocks. Since sampling of both stocks occurred near known spawning sites during spawning seasons, when sex is more confidently assigned, individuals whose sex was assigned were more likely to be sexually mature. Given females sexually mature at older ages and larger

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sizes than males (Pikitch et al. 2005; Bruch 2008) it is not surprising that the median age of sampled females was older than males.

We also observed differences in lengths and ages between the two stocks. Observed differences could be driven by disparities in resources or habitat. Though both systems provide heavy flow and preferred spawning substrate, warmer temperatures and higher productivity in Lake Erie may facilitate faster growth and larger sizes than in Lake Ontario. Alternatively, differences may be an artifact of using different sampling gears between stocks (gill nets in HNR versus setlines in LNR).

In addition to having similar age distributions, both stocks showed a lack of young, small individuals and old, large individuals. Median ages in both stocks increased from 14 to 18 years old between 2012 and 2017 suggesting some regional effect that produced a strong year class in 1998. The lack of young, small individuals is in part due to the selectivity of the gear used to catch Lake Sturgeon. The lack of old individuals could be due to low year class strength prior to 1998 and also the filtering of age data with low reader confidence (generally spines with very high numbers of compacted growth increments or where resorption may have occurred).

We found mean lengths and lengths-at-age in the LNR and HNR were larger than those reported in most other systems while mean ages were similar to many other systems. We found mean total lengths of Lake Sturgeon from the LNR and HNR were larger than mean total lengths of Lake Sturgeon from Lake St. Clair River, St. Marys River, Lake St. Clair, Lake Huron in Michigan waters, and the North Channel and Georgian Bay of Lake Huron; comparable to mean total lengths of Lake Sturgeon from the Winnebago system; and smaller than mean total lengths of Lake Sturgeon from the Detroit River (Table 1). Mean ages of Lake Sturgeon from the LNR

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and HNR were slightly less than mean ages reported from the Winnebago system, Lake St. Clair River, and Lake St. Clair but greater than mean ages reported in Lake Huron in Michigan waters and the North Channel and Georgian Bay of Lake Huron (Table 1). Both LNR and HNR Lake Sturgeon length at age 10 were predicted to be larger than Lake Sturgeon at age 10 in the St Marys River (Table 1). Lake Sturgeon from the LNR were predicted to be larger at age 10 than the previous length-at-age prediction (Table 1).

Although gear-based size selection tended towards larger individuals, size at age appears to have increased over time. Hughes et al. (2005) captured slightly younger, smaller individuals using the same sampling methods in the late 1990s and early 2000s. The increase in mean total lengths and length-at-age in the LNR could signify a shift in growth rate over time. Jacobs et al. (2017) proposed young Lake Sturgeon may be transitioning from foraging on lower trophic prey items to higher trophic prey items, such as round goby (*Neogobius melanostomus*), whose higher energy content could result in increased Lake Sturgeon growth at younger ages. This may partly explain the faster growth rate we observed than what Hughes et al. (2005) reported.

It is important to note length-at-age, von Bertalanffy models are sensitive to age estimation error. Both the LNR and HNR lack data from young individuals that are important to developing a growth model and though we attempted to quantify estimation errors, no consistent bias was detected; therefore we could not correct data for these errors. Given many of the captured individuals were estimated to be greater than 14 years old, age estimation errors are to be expected given the nature of the spine structure used to estimate ages of these fish (Bruch et al. 2009). Future studies on the age structure of these stocks would benefit from the collection of younger (less than 14 years old) Lake Sturgeon. Furthermore, despite removing low quality spines for age estimation, our age estimates appear somewhat poor given partial age validation

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through ageing individuals captured multiple times. The lack of agreement between estimates from partially validated ages demonstrates errors likely occurred during processing or interpretation. Though we attempted to train readers on known-age spines, there was a lack of samples available within, and across, age classes. Future studies may benefit from training readers on inventoried, known-age spines ($n > 100$ of varying ages) to gain experience in interpretation before attempting to assign ages. Although we used known-age samples for reader evaluation and training, sample sizes within each cohort were limited and many ages were not present. Establishing a long-term index of known-age samples with more than five samples in each cohort would be a valued resource in age interpretation training. Additionally, the use of a fluorochrome label has been shown to assist in Lake Sturgeon pectoral fin spine interpretation by providing readers with spatial reference points in the form of fluorochrome marks within calcified structures that relate to time of previous capture (Rossiter et al. 1995).

Although we recognize that there is error in our estimates of Lake Sturgeon age, these data still aid in determining the status of the HNR and LNR stocks. One of the delisting criteria of New York State's Lake Sturgeon recovery plan (see NYSDEC 2018) is evidence of natural recruitment in at least three years of a five-year period within the last 20 calendar years. Even with the inaccuracies of ageing Lake Sturgeon spines, our data demonstrate this criterion has been met given the number of consecutive cohorts within each stock. Error in age estimates could present problems when using these data in other stock assessment models such as catch curve analysis to estimate mortality or when conducting virtual stock analysis or catch-at-age modeling. In such models, aging error can lead to inappropriate estimates of recruitment time series, yield predictions, and ultimately lead to overfishing (Tyler 1989; Bradford 1991). Thus, additional efforts to increase the accuracy of age estimation in Lake Sturgeon are warranted,

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especially if such data are used to manage a recovered fishery with some level of allowable exploitation.

Supplemental Material

Reference S1. Casselman JM. 1983. Age and growth assessment of fish from their calcified structures—techniques and tools. Pages 1-17 in Prince ED, Pulos LM, editors. Proceedings of the international workshop on age determination of oceanic pelagic fishes: tunas, billfishes, and sharks. National Oceanic Atmospheric Administration Technical Report National Marine Fisheries Service. Available: https://spo.nmfs.noaa.gov/Technical%20Report/tr8opt.pdf (June 2020).

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Data S1. Raw age and length data of captured and recaptured Lake Sturgeon *Acipenser fulvescens* collected from headwaters of the Niagara River and the lower Niagara River from spring sampling between 2012 and 2017.

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Table Captions

Table 1. Reported mean total lengths, mean ages, and lengths-at-age of Lake Sturgeon *Acipenser fulvescens* captured throughout the Great Lakes between 1995 and 2017.

Figure Captions

Figure 1. Map of the study area detailing the headwaters, the upper portion, the lower portion, and the mouth of the Niagara River between 2012 and 2017. Striped areas denote the distribution of Lake Sturgeon *Acipenser fulvescens* from the lower Niagara River while grey shaded areas denote the distribution of Lake Sturgeon from the headwaters of the Niagara River.

Figure 2. Annual age distribution of Lake Sturgeon *Acipenser fulvescens* captured in the lower Niagara River between 2012 and 2017.

Figure 3. Annual age distribution of Lake Sturgeon *Acipenser fulvescens* captured near the headwaters of the Niagara River between 2012 and 2017.

Figure 4. Cohort strength of Lake Sturgeon *Acipenser fulvescens* captured between 2012 and 2017 in the lower Niagara River (left) and the headwaters of the Niagara River (right) given estimated ages.

Figure 5. Comparison of expected age, given estimated age at first capture + years at liberty, and estimated age at time of recapture of Lake Sturgeon *Acipenser fulvescens* from the lower Niagara River and headwaters of the Niagara River captured between 2012 and 2017. Linear regression was $y = 0.836x + 3.779$ with $r^2 = 0.577$. The solid line denotes a 1 to 1 relationship, the dash line represents the linear regression between estimated age and expected age, and the grey shading represents 95% confidence intervals.

Figure 6. Length-at-age using estimated ages and total lengths of lower Niagara River Lake Sturgeons *Acipenser fulvescens* collected between 2012 and 2017. Box plots denote median and quartile length estimates for each age sampled. Black curved line denotes a fitted von Bertalanffy growth curve with L_∞, K, and t_0 values provided and grey shading represents 95% confidence intervals.

Figure 7. Length-at-age using estimated ages and total lengths of Lake Sturgeon *Acipenser fulvescens* collected at the headwaters of the Niagara River between 2012 and 2017. Box plots denote median and quartile length estimates for each age sampled.

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Table 1. Reported mean total lengths, mean ages, and lengths-at-age of Lake Sturgeon *Acipenser fulvescens* captured throughout the Great Lakes between 1995 and 2017.

System	Total Length (mean ± sd; cm)	Mean Age (Years)	Length at Age 10 (mean ± sd; cm)	Source
Detroit River	158.3	--	--	Hill & McClain 2002
Headwaters of the Niagara River	146.30 ± 11.69	17 ± 5.04	145.37	Present study
Lower Niagara River	140.64 ± 13.33	15.6 ± 3.16	123.19 ± 0.82	Present study
Lower Niagara River	--	--	115.61	Hughes et al. 2005
Winnebago System	140	20-23	--	Bruch 1999
Lake St. Clair River	123.5	20	--	Thomas & Haas 2002
St. Marys River	121.7 ± 24.23	19 ± 8.91	76.54	Hill & McClain 2002
Lake St. Clair	119.8	18.7	--	Thomas & Haas 2002
Lake Huron in Michigan waters	115	11	--	Hill & McClain 2002
North Channel & Georgian Bay of Lake Huron	107.9	11.8	--	Hill & McClain 2002

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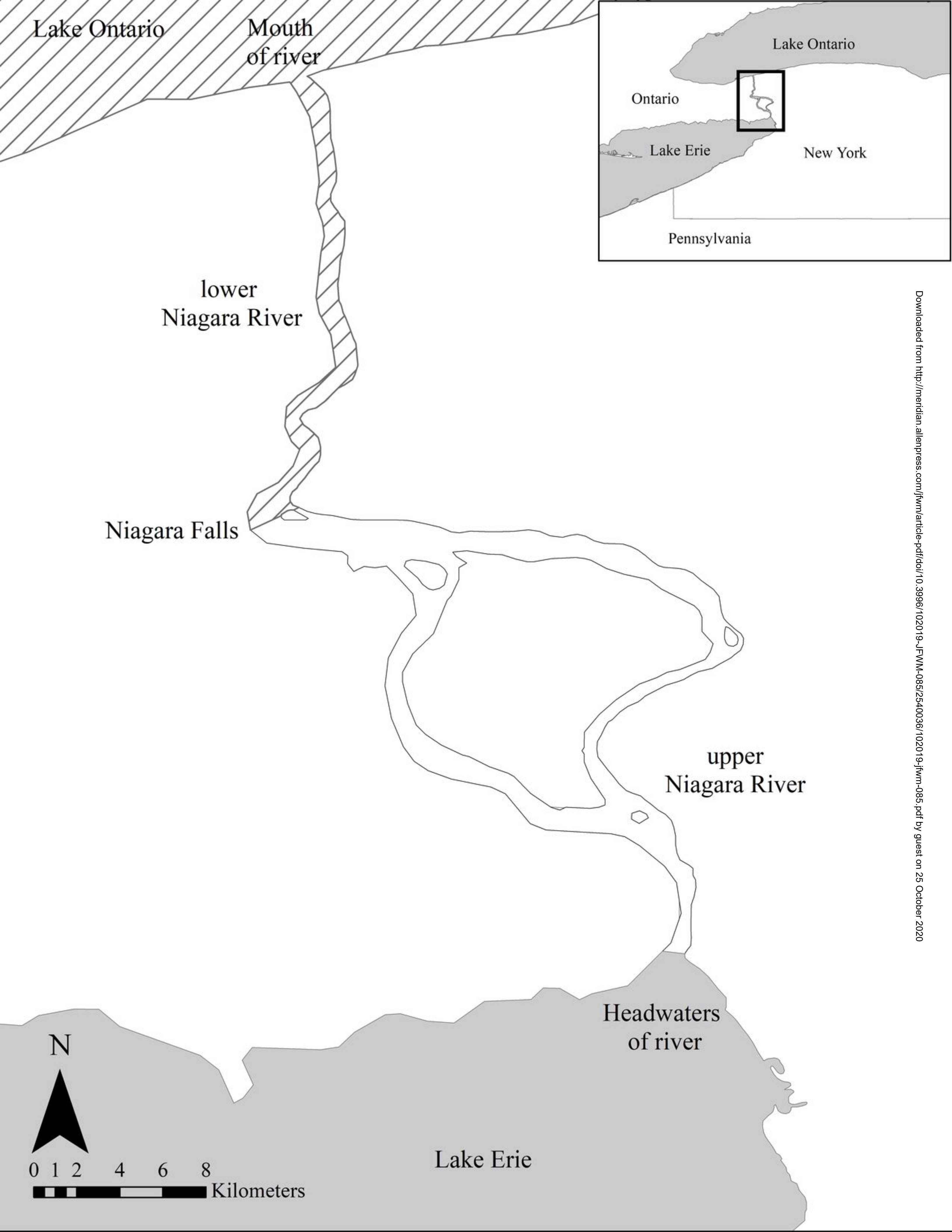

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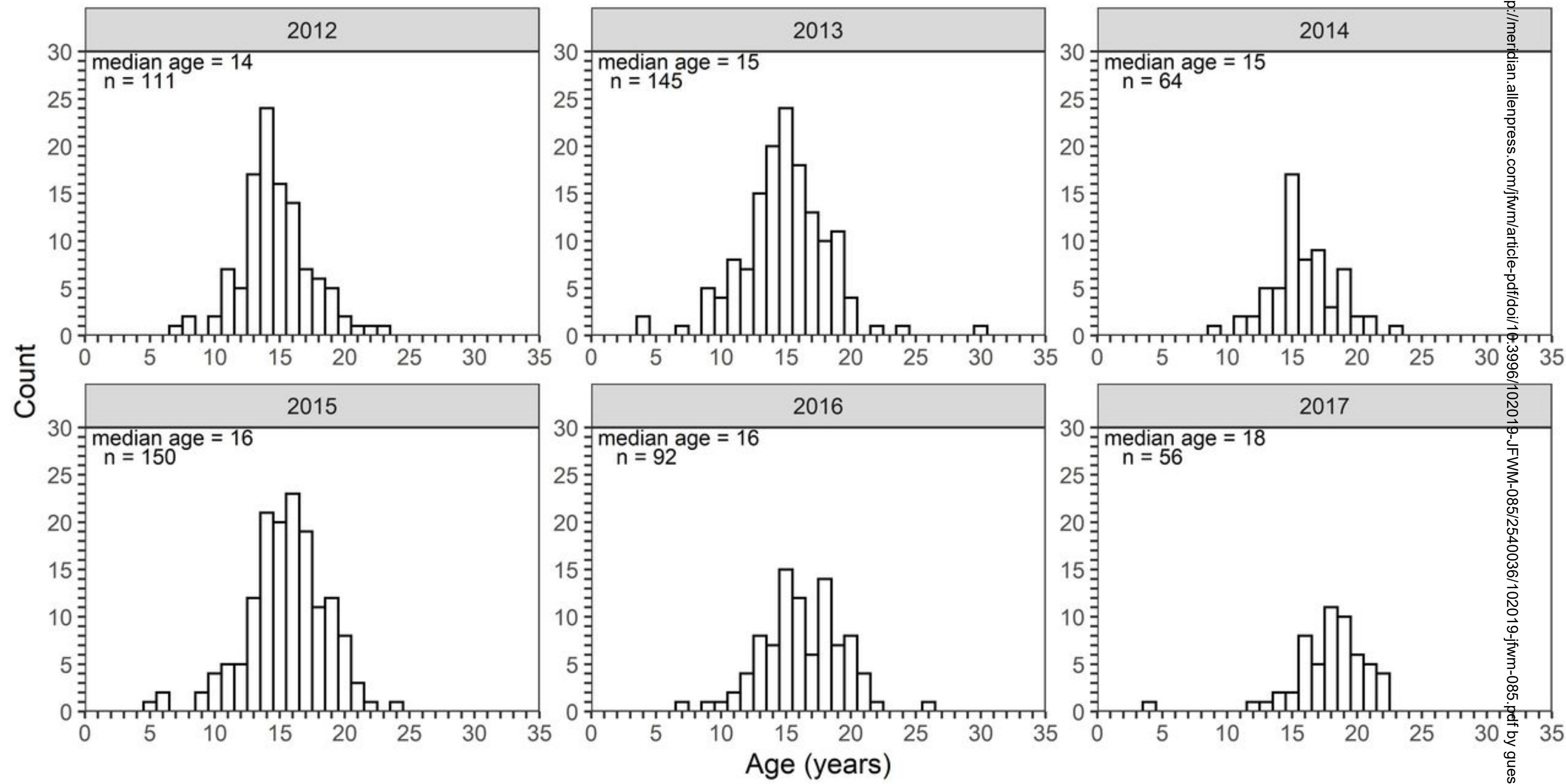

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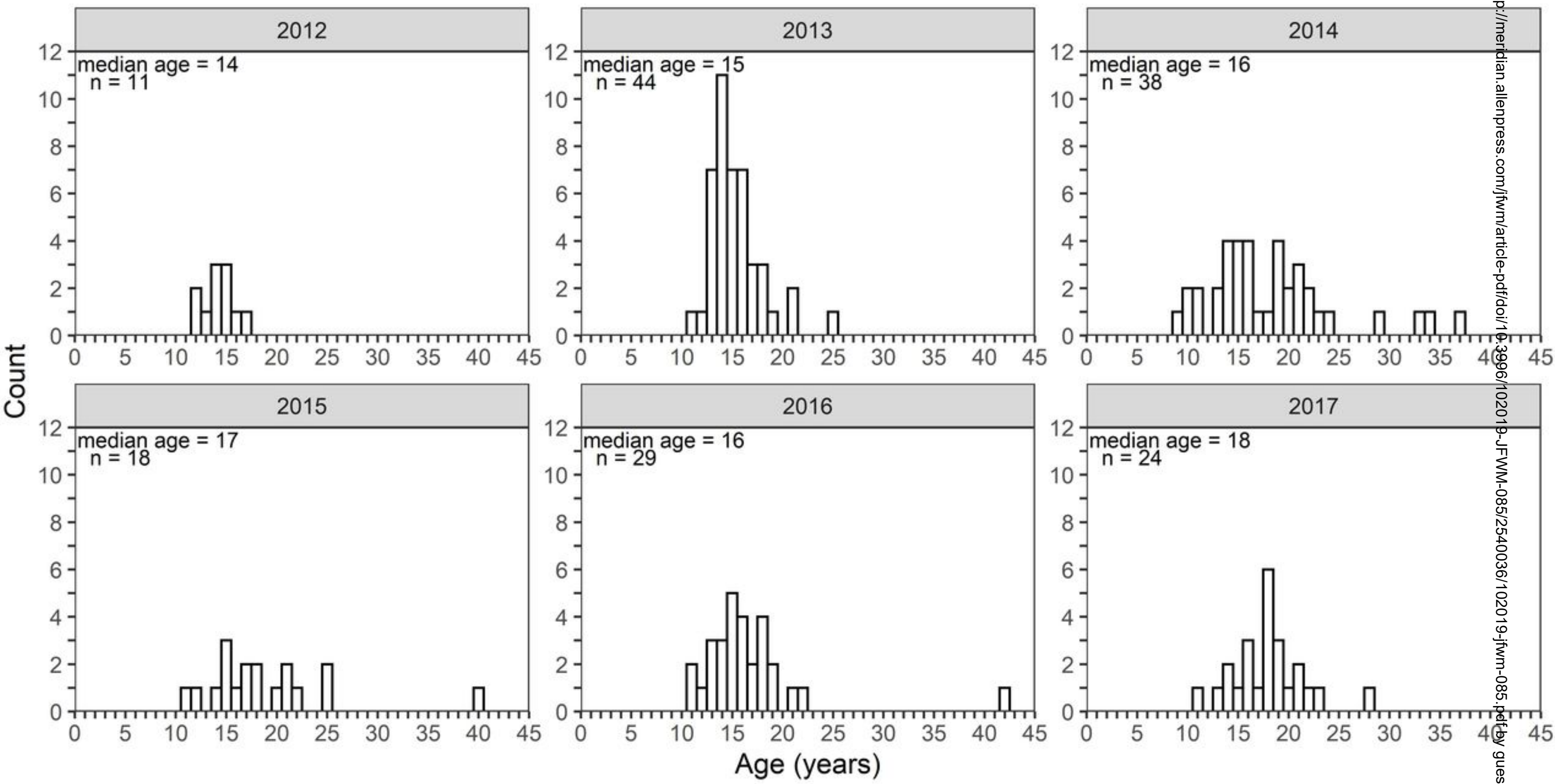

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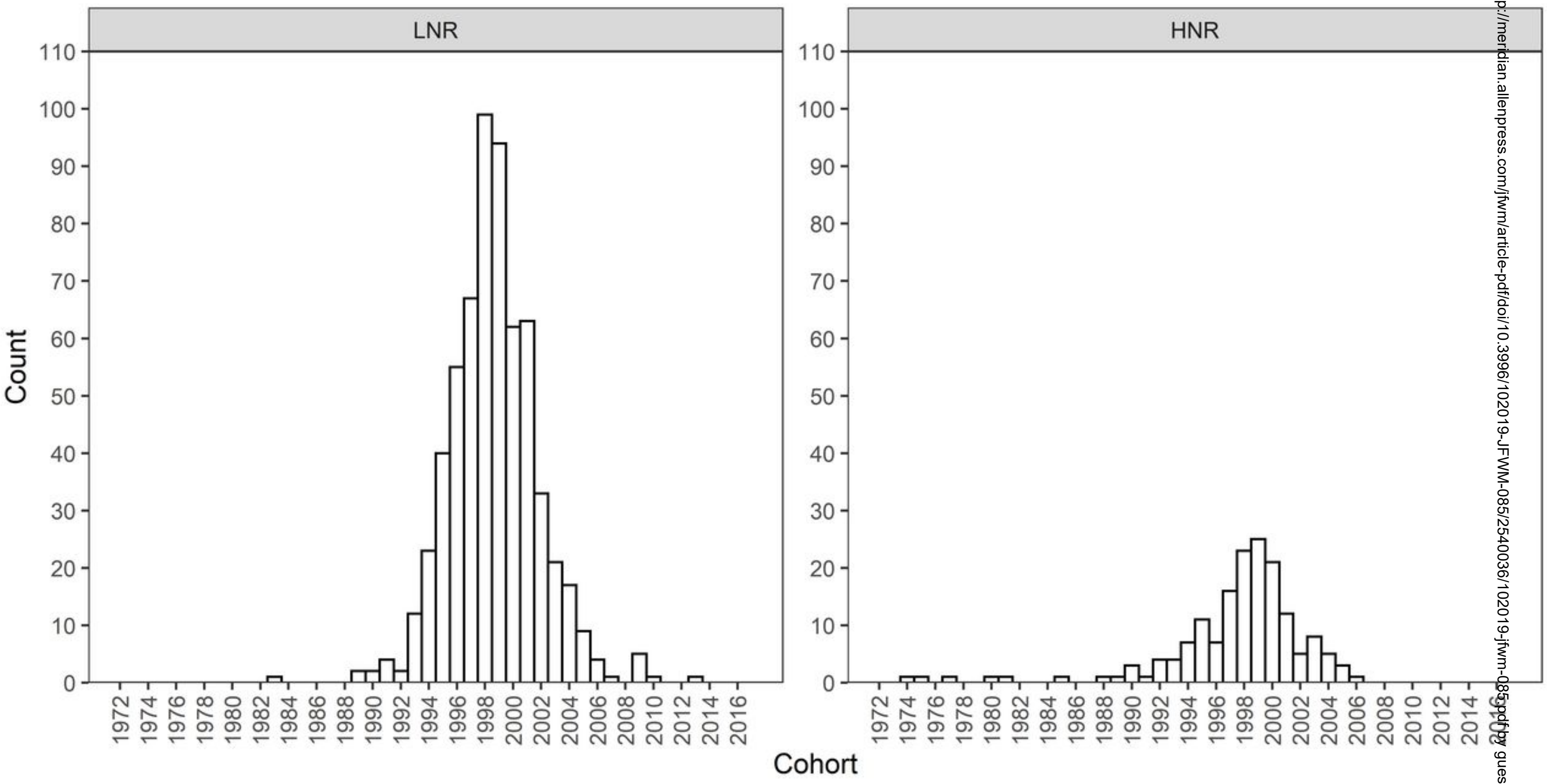

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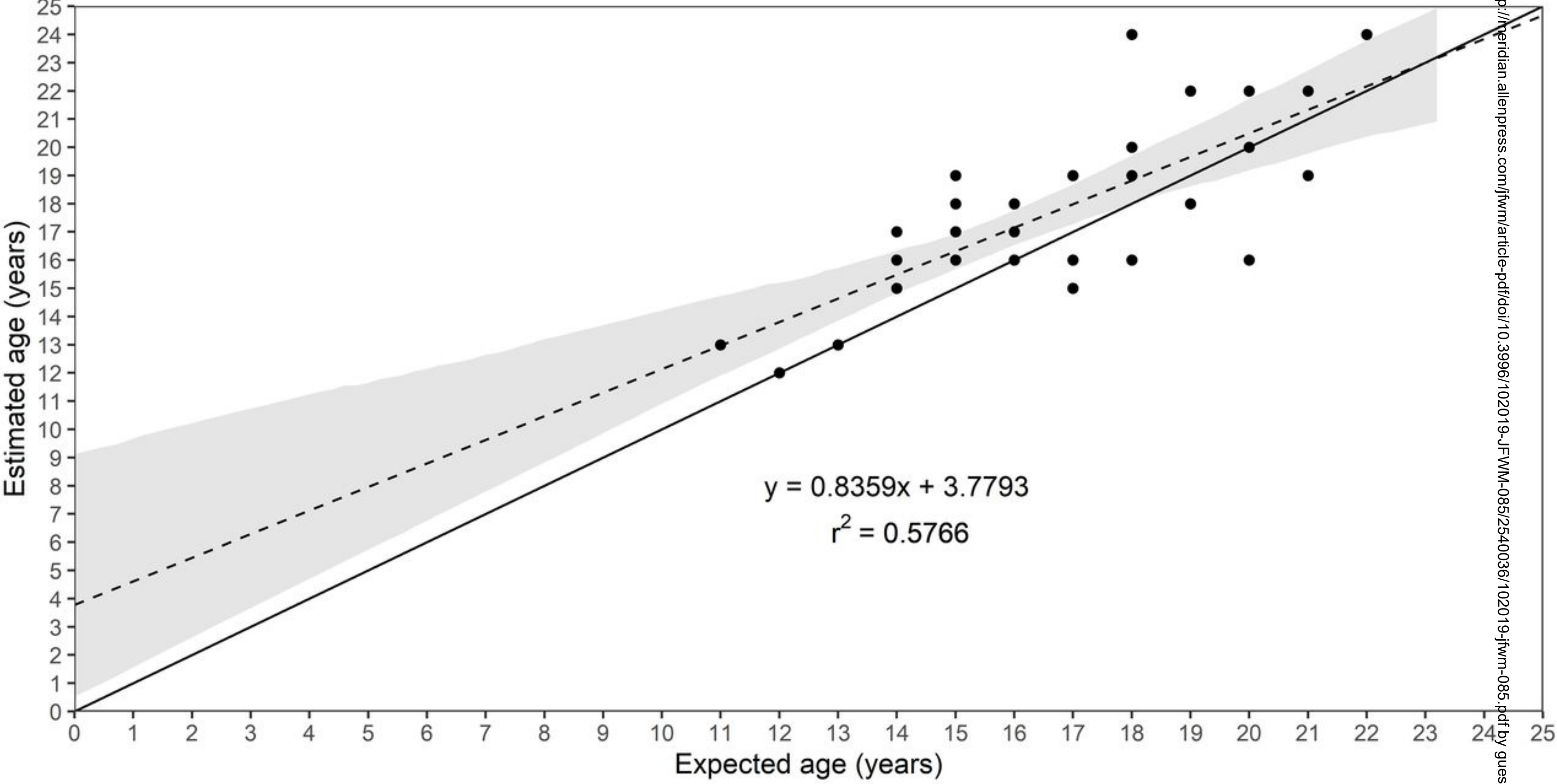

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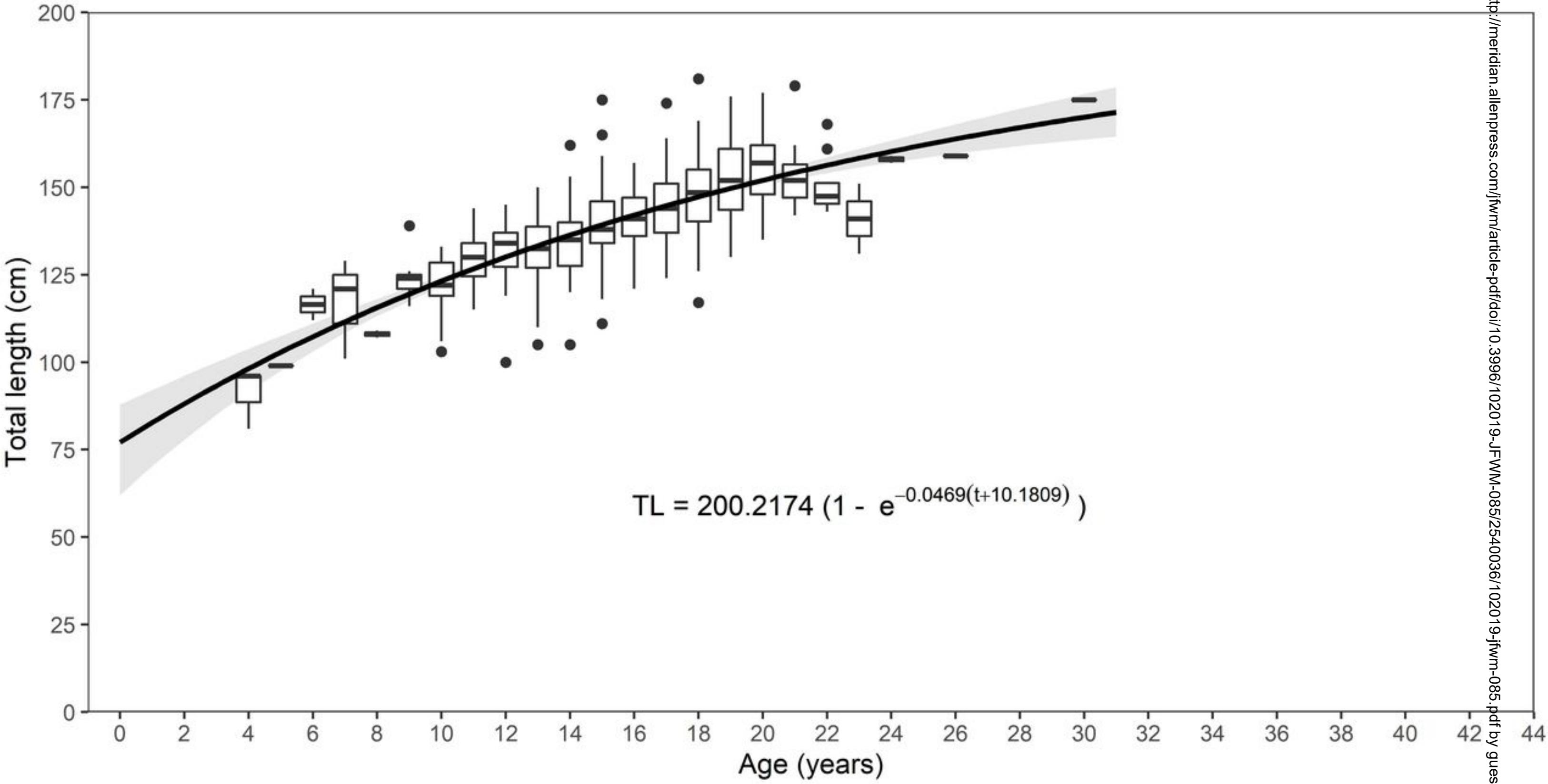

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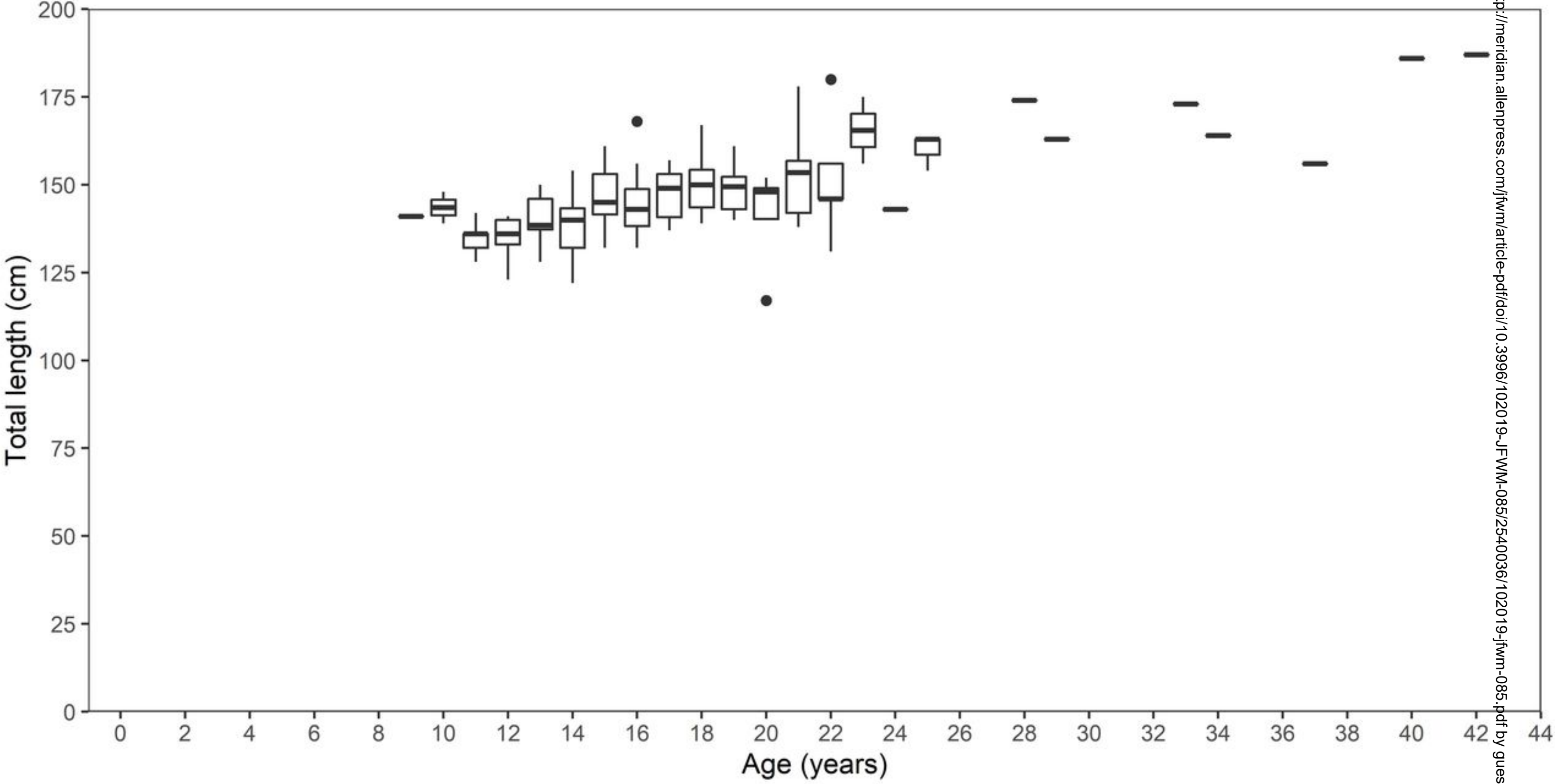

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