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Long-Term Mark–Recapture Data to Assess Muskellunge Population Characteristics: Application to Two Illinois Reservoirs

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Long-term mark-recapture data to assess Muskellunge population characteristics: application to two Illinois reservoirs

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Abstract

Accurate estimates of growth and mortality are important for management of recreational fisheries. Accurate age estimates often require the sacrifice of fish, thus assessments of growth and mortality rates of trophy fishes such as Muskellunge *Esox masquinongy* often lack sufficient data. Mark-recapture history can be used as a non-lethal alternative to estimate growth and mortality in fishes. To determine the utility of this approach, we used data from a 17-year Muskellunge mark-recapture program conducted on two Illinois reservoirs (Kinkaid Lake and North Spring Lake). von Bertalanffy parameter estimates by sex, lake, and tag type (passive integrated transponder, and T-bar anchor tags) were obtained using a novel modification of the Fabens growth model and compared to von Bertalanffy growth estimates using known- or scale-aged fish. Mortality was calculated using both age- and length-based methods. Fabens growth model estimates of asymptotic length (L_∞) and growth coefficient (K) were within 6% (≤ 62 mm) and 23% (≤ 0.11) of corresponding von Bertalanffy growth model parameter estimates from known- or scale-aged fish by lake and sex. Provided that all sizes of fish are sampled, four years of mark-recapture data with > 100 recaptures were found to be sufficient to produce reliable parameter estimates. Growth parameters differed between male fish tagged with passive integrated transponder or T-bar anchor tags, but did not differ by tag type for females. Differences in Muskellunge growth and mortality rates between the two study lakes suggest that changing from a regionally-applied minimum length limit to lake-specific minimum length limits may be warranted. Our results highlight the feasibility of mark-recapture data as a non-lethal technique to estimate population-specific growth and mortality rates for Muskellunge and the potential value of this approach in facilitating lake-specific Muskellunge management.

Understanding population characteristics, such as growth and mortality, and the factors that influence them are important for the management and conservation of fish populations (Beverton and Holt 1957). In particular, accurate estimates of these vital rates are required to set biologically sound fisheries regulations, and reliably assess population responses to exploitation (Beverton and Holt 1957; Casselman 2007; Pardo et al. 2013) and environmental conditions (Munkittrick and Dixon 1989). Sparse or inaccurate length-at-age data may lead to spurious estimates of growth and mortality (DeVries and Frie 1996; Pardo et al. 2013). Obtaining accurate age data often requires sacrificing individuals and excising calcified structures for age estimation (e.g., otoliths, vertebrae, cleithra; Campana and Neilson 1985; Casselman 1990; DeVries and Frie 1996; Maceina et al. 2007). However, sacrificing individuals may be problematic for species with low population densities such as imperiled or trophy species where harvest of individuals (for science or recreation) can be detrimental to the population (Allan et al. 2005; Dunton et al. 2016). These scenarios often leave biologists and managers tasked with managing fish populations in data-limited situations (Pikitch et al. 2004; Dunton et al. 2016).

Management decisions for populations of Muskellunge *Esox masquinongy* are frequently data-limited because the species is difficult to sample, typically occurs at low densities, and is long-lived (Graff 1986; Strand 1986; Casselman et al. 1999). Despite inherent limitations for estimating Muskellunge population characteristics, some Muskellunge age and growth studies have been published (Casselman and Crossman 1986; Casselman et al. 1999; Faust et al. 2015); these studies used cleithra to estimate age and von Bertalanffy growth parameters (asymptotic length (L_∞), growth coefficient (K), and theoretical time at length zero (t_0)), using back calculated estimates of length-at-age. However, while cleithra age estimates are assumed to provide the most accurate and precise age estimates for Muskellunge, they have not been validated as an ageing structure (Harrison and Hadley 1979; Casselman and Crossman 1986; Casselman 1990). Furthermore, removal of the cleithra requires sacrificing fish, which is problematic because sacrificing a sufficient number of individuals within a water body to estimate growth and mortality rates is inconsistent with the strong catch-and-release ethic of Muskellunge anglers and trophy-fishery status (Margenau and Petchenik 2004; Brenden et al. 2006a; Faust et al. 2015). To combat these issues, cleithra used in these studies were archived across multiple years from angler-caught trophy individuals (often from taxidermists) and agency survey mortalities (Casselman and Crossman 1986; Casselman et al. 1999; Faust et al. 2015). Cleithra samples obtained in this manner may not represent the growth rate of the majority of fish in a population because they are trophy individuals, and anglers may preferentially harvest large individuals (Faust et al. 2015). Furthermore, previous research indicates growth rate of Northern Pike *Esox lucius*, which are closely related to Muskellunge, caught by anglers differs from fish sampled during electrofishing surveys (Crane et al. 2015). Due to the small number of cleithra typically archived from a given water body, growth is often estimated at coarser spatial (lake-district or regional) scales (Casselman and Crossman 1986; Faust et al. 2015). Consequently, archived cleithra studies rarely provide estimates of mortality rates for Muskellunge from a specific water body due to sample size constraints and because samples are archived across multiple years. Thus, lake-specific assessment of how changing environmental conditions, catch and release mortality, angler harvest attitudes, or other factors that may affect a particular Muskellunge population typically is not possible.

Limited data on Muskellunge growth and mortality rates at a water-body specific scale has often lead to management strategies at a regional or statewide scale. One approach to combat uncertainties in water-body specific growth and mortality rates is to enforce a high minimum length limit at a regional scale. While this management strategy limits harvest of a large proportion of individuals in the waterbodies throughout the region and helps ensure higher survival rates to sexual maturity and trophy sizes (Casselman 2007), it could potentially result in reduced growth rates due to increased density (Lorenzen and Enberg 2002; Gilbert and Sass 2016). Muskellunge anglers typically support these regulations because of their tendency to practice catch-and-release fishing, even when exceptional trophies are caught (Margenau and Petchenik 2004). However, some anglers may want the opportunity to harvest a trophy individual (Margenau and Petchenik 2004), but cannot in lakes where minimum length limits exceed Muskellunge growth potential. Therefore, there is a need for methods to non-lethally obtain growth and mortality estimates that are water-body specific to tailor management to each water body's Muskellunge population.

Non-lethal ageing structures (e.g., scales and fin rays) have been investigated as an alternative to cleithra for age estimation in Muskellunge to develop growth models for populations at a water-body specific scale because significantly more age data can be obtained (Johnson 1971; Harrison and Hadley 1979; Fitzgerald et al. 1997; Brenden et al. 2006a; Brenden et al. 2006b). However, multiple studies caution the use of scales or fin rays to age Muskellunge due to their tendency to be inaccurate, especially with increasing fish age (Johnson 1971; Brenden et al. 2006a). Specifically, scale age estimates may only be reliable up to age-4 in many Muskellunge populations (Fitzgerald et al. 1997), and fin rays up to age-10 (Johnson 1971; Brenden et al. 2006a), but ongoing research suggests that modern viewing techniques may improve precision and accuracy of fin ray age estimates for fish > age-10 (D.P. Crane, unpublished data). Thus, use of non-lethal ageing structures does not eliminate the need to sacrifice large, old individuals to obtain reliable estimates of growth and mortality rates (Brenden et al. 2006a).

Marking and recapturing stocked individuals is another non-lethal technique to estimate fish growth and mortality rates, but has rarely been applied to Muskellunge. Marking individuals with fin clips or physical tags (e.g., T-bar anchor tags) have been used in many fish species to estimate population size (Frohnauer et al. 2007), exploitation (Pierce et al. 1995), fish movement (Diana et al. 1977), growth (Paragamian and Beamesderfer 2003; Hamel et al. 2014a; Hamel et al. 2014b), and mortality (Pine et al. 2003). Fin clipping, along with other physical markings, have been used to evaluate age estimates derived from bony structures and assess growth rate of recaptured fish and individuals belonging to the same year class (Johnson 1971). However, estimating growth rates with these methods is limited because distinguishing these marks can be problematic in old fish due to regeneration resulting in loss of the mark or decreased confidence in distinguishing a mark (McNeil and Crossman 1979; Nielsen 1992), and naturally reproduced individuals are often not represented as these marks are typically applied to individuals at the time of stocking. Physical tags such as individually numbered T-bar anchor tags or passive integrated transponder (PIT) tags can be applied to both stocked and naturally reproduced individuals (Nielsen 1992), allowing identification of individual fish, and having sufficient short- and long-term retention rates in juvenile and adult Muskellunge (Younk et al. 2010; Rude et al. 2011). Numerous studies have used PIT and T-bar tags to evaluate population sizes of Muskellunge (Wahl and Stein 1993; Frohnauer et al. 2007). However, growth rate estimates have been limited to annual growth rates of a fish over the course of a study, rather than over the lifespan of a fish in a population (Frohnauer et al. 2007).

Measures of growth over longer time periods, such as von Bertalanffy growth parameters (L_∞, and K), are important to obtain for Muskellunge management because they are used for setting minimum length limits (L_∞; Casselman 2007) and may aid in estimating specific components of mortality (both L_∞, and K; Beverton and Holt 1956; Pauly 1980). von Bertalanffy growth parameters can be obtained with the Fabens growth model (FGM) using only mark-recapture data even when age is unknown (Fabens 1965). Despite the potential utility of the FGM, it remains under-utilized by fisheries scientists; most applications of the FGM have been for marine invertebrates (Frazer et al. 1990), and testudines (Kennett 1996; Schmid and Witzell 1997). Recently, the FGM has been demonstrated to be a powerful approach for using mark-recapture data to elucidate population characteristics of imperiled fish species such as sturgeons (Paragamian and Beamesderfer 2003; Hamel et al. 2014a; Hamel et al. 2014b) for which limited population demographic data hinders informed management. These studies used the FGM to assess growth of Shovelnose Sturgeon *Scaphirhynchus platorynchus* (Hamel et al. 2014b) and to evaluate age estimates derived from multiple hard-part structures in Shovelnose Sturgeon and White Sturgeon *Acipenser transmontanus* (Paragamian and Beamesderfer 2003; Hamel et al. 2014a). However, despite the common practice of biologists and managers in marking and recapturing Muskellunge, we are unaware of any published studies that have applied the FGM to mark-recapture datasets to evaluate Muskellunge population characteristics.

The primary objective of this study was to assess the accuracy and precision of von Bertalanffy growth model parameters estimated by the FGM using long-term mark-recapture datasets for Muskellunge from two Illinois, USA reservoirs with distinct environmental characteristics (Kinkaid Lake and North Spring Lake). Model estimates of L_∞, and K were compared with corresponding parameter estimates derived from von Bertalanffy growth models developed using known-age and scale-aged fish. We also sought to estimate the number of recapture events and years of mark-recapture data needed to precisely estimate von Bertalanffy growth model parameters for these populations. Furthermore, to illustrate how lake-specific mark-recapture data may inform management of Muskellunge populations, we estimated mortality using von Bertalanffy estimates derived from the FGM and its predicted ages of marked and recaptured individuals and assessed differences in growth and mortality rates between sexes within each reservoir and within sexes between the two lakes. Our results highlight the feasibility of mark-recapture data as a non-lethal technique to estimate population-specific growth and mortality characteristics for Muskellunge and the potential value of this approach in facilitating lake-specific Muskellunge management.

Methods

Study Sites

Kinkaid Lake (KL) is a 1113-ha reservoir located in Jackson County in southern Illinois (37°47′50″N, 89°25′55″W) and was created in 1968 by impoundment of Kinkaid Creek. Kinkaid Lake has an average depth of 12 m and maximum depth of 24 m. North Spring Lake (NSL) is a 234-ha spring-fed, formerly connected floodplain lake of the Illinois River and is located in Tazewell County in central Illinois (40°28′13″N, 89°51′46″W). North Spring Lake was isolated from the Illinois River by construction of levees in 1916 and has an average depth of 0.88 m and maximum depth of 3 m. Both lakes are important Muskellunge fisheries in Illinois, as evidenced by the proportion of the total annual statewide catch of Muskellunge determined from angler creel reports (21% and 6% of reported Muskellunge catch statewide occurs in KL and NSL, respectively; Illinois Department of Natural Resources 2010). North

Spring Lake also serves as the brood stock lake for Illinois' Muskellunge rearing and stocking program. Recreational fishing regulations for Muskellunge in both lakes consist of a 1219 mm (48 in) minimum length limit with a bag and possession limit of one fish. The lakes receive supplemental stocking of juvenile Muskellunge (~275 mm total length) on an annual basis (KL; 2000 individuals) or every third year (NSL; 1700 individuals). Natural reproduction may contribute a small proportion to the population in each lake (Rude et al. 2014).

Field Methods

Muskellunge were collected annually from 1999-2016 during a 1-2 week period each spring (late February to mid-April depending on lake-specific water temperatures) using 1.22 m x 1.83 m frame trap nets (15.24-m lead, 25.4-mm mesh bar measure). Nets were set at 12-18 fixed locations throughout each lake during each year. All fish were removed from nets daily. Total length of each captured Muskellunge was measured (nearest mm) and sex was determined for each fish based on the shape of the urogenital papilla (Lebeau and Pageau 1989; Rude et al. 2011; Rude et al. 2014). Upon initial capture, each fish was implanted with a DESTRON 125-kHz PIT tag (12.0 x 2.1 mm; Destron Fearing, South St. Paul, Minnesota) in the dorsal musculature (below the dorsal fin). Age-0 Muskellunge stocked into KL during 2004 and 2005 were implanted with a PIT tag immediately prior to stocking and thus represented known-age individuals. Fish captured in KL were also tagged with an algicide-treated, individually numbered, 76-mm T-bar anchor tag (Floy Tag and Manufacturing, Inc., Seattle, Washington; product FD-68B) affixed through the dorsal pterygiophores. A scale was removed from individuals collected in NSL for ageing. Successful implantation of a functional PIT tag was confirmed in the field by scanning the fish with a portable handheld tag reader before fish were released. Individuals captured during 2000–2016 were scanned to determine presence or absence of a functioning PIT tag. Fish bearing neither a PIT tag nor a T-bar anchor tag were tagged as described above and released, and T-bar anchor tag and PIT tag numbers were recorded for recaptured individuals. Recapture histories were compiled for individual fish for the duration of the study in each lake. T-bar anchor tags and PIT tags were used to identify recaptured individuals in KL, whereas only PIT tags were used for this purpose in NSL (T-bar anchor tags were not applied to fish in NSL). Recapture histories included sex and length at each encounter, and any fish exhibiting negative growth between recapture events (likely due to small errors in length measurements) were assumed to have not changed in length.

Growth Estimation

Growth of Muskellunge was assessed by developing von Bertalanffy models using long-term mark-recapture data with the FGM that was modified to incorporate the effect of a given variable (lake, sex, and tag type) on von Bertalanffy growth parameters (Kimura 2008). Tag type was included as a variable in the FGM comparisons because previous research by Rude et al. (2011) indicated that retention rates of PIT and T-bar tags differ in adult Muskellunge. Tag-specific retention rates may affect FGM parameter estimates because time between recapture events is an integral component of the FGM. The modified Fabens model was:

$$R_{ij} = M_{ij} + (L_{\infty(j)} - M_{ij})(1 - e^{-K_j \Delta t_{ij}})$$

where R_{ij} is the length-at-recapture of the ith individual of the jth variable, M_{ij} is the length of the ith individual of the jth variable at the previous time of capture, $L_{\infty(j)}$ is the maximum length of the average fish of the jth variable, K_j is the growth coefficient of the jth variable, and Δt_{ij} is the time between marking and recapture events for the *i*th fish of the *j*th variable. Incorporation of the effects of a given variable on von Bertalanffy growth parameters was achieved by using:

$$L_{\infty(j)} = L_{\infty(0)} + variable \cdot \Delta L_{\infty(1)}$$

$$K_j = K_0 + variable \cdot \Delta K_{(1)}$$

where *variable* is a "dummy variable" as used in Draper and Smith (1981) and Kimura (2008) in which 0 defines the set of von Bertalanffy growth parameters, and 1 defines the change in the set of von Bertalanffy growth parameters (e.g., 0 for male, 1 for female). A nonlinear mixed-effects model (Lindstrom and Bates 1990) was used to derive maximum likelihood estimates of each parameter and to test whether differences in von Bertalanffy growth parameters due to a given variable were significantly different from zero. Each recaptured individual was represented as an independent observation, and dependence among measurements from individuals recaptured multiple times were accounted for by specifying each fish as a normally distributed random effect.

To determine if the FGM can provide reliable estimates of growth of mark-recaptured fish, data from known-age (PIT tagged at stocking) individuals from KL were used to estimate growth parameters from a traditional von Bertalanffy growth model:

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

where L_t is Muskellunge length at age *t*, L_∞ is the asymptotic length, *K* is the instantaneous rate at which L_t approaches L_∞, and t_0 is the hypothetical age of Muskellunge at zero length (Ricker 1975). Because known age fish were not available for NSL, parameter estimates for the traditional von Bertalanffy growth model were estimated using a combination of information based on scale-based age estimates for young fish and the subsequent recapture history of those fish. If an individual was aged with a scale and subsequently recaptured in future years, an age was assigned based on its time at large and scale age. For example, if a fish was collected and tagged in 2003 and estimated to be age-3 during that year based on scale annuli counts and was later recaptured in 2010, it was assigned as age-10 upon recapture. Scale ages of individuals only up to age-4 were used in this analysis because Muskellunge scale age estimates decline in accuracy after age-4 (Fitzgerald et al. 1997; Brenden et al. 2006a), the low sample size of age 5-8 fish, and no fish > 9 were aged solely from viewing scale annuli. Therefore, if an individual was aged with a scale and subsequently recaptured in future years, an age was assigned based on its time at large and scale age. For example, if a fish was collected and tagged in 2003 and estimated to be age-3 during that year based on scale annuli counts and was later recaptured in 2010, it was assigned as age-10 upon recapture. Similar to the FGM, a non-linear mixed-effects model (Lindstrom and Bates 1990) was used to derive maximum likelihood estimates of each parameter, and each scale-aged individual was represented as an independent observation, and dependence among measurements from individuals used multiple times were accounted for by specifying each fish as a normally distributed random effect. Statistical comparisons of parameter estimates between the FGM and von Bertalanffy models were not obtained; however, 95% confidence intervals were provided as a baseline to determine if differences existed.

To illustrate the potential importance of lake-specific population characteristics for Muskellunge management, the aforementioned FGM methods were used to determine whether growth (parameter estimates) differed between sexes within each lake, and between lakes within a given sex. Furthermore, the models were run by tag type for each sex (PIT or T-bar; KL fish only) to assess the potential influence of differing retention rates between tag types on FGM parameter estimates. Additionally, annual FGM were run with each year of mark-recapture data consecutively from first year of mark-recapture data to the final year of study (17 years) for each lake and by sex (and both tag types for KL fish only) to estimate of number of marked and recaptured individuals and the number of years of mark-recapture data needed to provide stable estimates of K and L_∞ (within two standard errors of parameter estimates from the final model that was developed using data from all years). A P-value of ≤ 0.05 was considered significant for all statistical tests, and all statistical analyses were performed using SAS 9.2 (SAS Institute, Inc. Cary, NC).

Mortality Estimation

Weighted catch curves were developed to estimate instantaneous and annual mortality rates using predicted ages derived from the FGM for fish from each lake (Robson and Chapman 1961). The FGM does not include an estimate of t_0 needed to predict an age for an individual fish. Therefore, t_0 was derived in SAS by using the high correlation among von Bertalanffy parameters to predict t_0 (Pilling et al. 2002). Then, age (t) of a fish of a given size was predicted through reformulation of the von Bertalanffy equation (Kirkwood 1983):

$$t = t_0 - \log_e[(1 - L_t/L_\infty)/K]$$

An age was derived for all recapture events throughout a fish's life, and any fractional predicted ages were rounded to the nearest integer. An instantaneous mortality rate was calculated for the entire duration of the study for each lake by sex. Differences in instantaneous mortality rates were compared by sex within each lake and within sexes between lakes using a homogeneity of slopes test (test for interaction with ANCOVA). A P-value of ≤ 0.05 was considered significant for all statistical tests.

In addition to using predicted ages of fish for estimating mortality, von Bertalanffy parameters from the FGM were used to estimate annual mortality using the (Beverton and Holt 1956) length-based mortality equation:

$$Z = \frac{K(L_\infty - \bar{L})}{(\bar{L} - L_c)}$$

where K and L_∞ are von Bertalanffy parameters derived from the FGM, L_c is the smallest size at which fish are fully vulnerable to the gear, and $\bar{L}$ is the mean length of fish greater than L_c. Length frequency distributions were calculated and used to estimate L_c and $\bar{L}$ values within each lake. The Beverton-Holt length-based mortality equation was applied to both sexes in each lake using all years of data. Beverton-Holt mortality rate estimates were compared qualitatively between sexes and lakes and to mortality rates among models derived from weighted catch curves.

Results

A total of 1762 male and 1012 female Muskellunge were collected from Kinkaid Lake, and a total of 2674 male and 1330 female were collected from North Spring Lake. A total of 355 male, and 199 female fish were recaptured in KL, resulting in 554 male and 260 female recapture events (some fish were recaptured multiple times). A total of 313 male, and 171 female fish were recaptured in NSL, resulting in 807 male and 294 female fish recapture events (Table 1). Mean total lengths of male and female fish from KL were 872 and 972 mm, and ranged from 415-1082 mm and 413-1269 mm, respectively. Mean total lengths of male and female fish from NSL were 790 and 859 mm, and ranged from 448-1044 mm and 451-1168 mm, respectively (Figure 1).

von Bertlalanffy parameter estimates from the FGM developed from mark-recapture histories of fish from KL and NSL were similar to parameter estimates from von Bertalanffy growth models developed using known-age individuals from KL and scale-aged individuals from NSL (Table 1, Figure 2). Estimates of L_∞ from mark-recapture data and known- and scale-aged fish were within the 95% confidence intervals for L_∞ estimated using FGM, except for NSL female fish. Estimates of L_∞ derived from FGM were $\leq$ 6% ($\leq$ 62 mm) greater than corresponding estimates of L_∞ from known-age or scale-aged fish. Estimates of K from known- and scale-aged fish were within the 95% confidence intervals for FGM estimates of K for males from both lakes, but not for females. Estimates of K from FGM were $\leq$ 14% ($\leq$ 0.09) less for male fish and $\leq$ 23% ($\leq$ 0.11) less for females compared to estimates of K for known-age or scale-aged fish (Table 1). Graphical representations of both model types indicated similar growth curves between models for both males and females collected from KL (Figure 2). However, ages of young Muskellunge from NSL were systematically overestimated by the FGM compared to scale-based von Bertalanffy models (Figure 2).

Fabens growth model parameter estimates for KL fish differed between sexes (L_∞: $t_{552} = 26.04$, $P < 0.0001$; K: $t_{552} = 6.87$, $P < 0.0001$); females had greater L_∞ and lower K estimates compared to males (Table 1, Figure 2). Similarly, growth model parameters differed between sexes for fish from NSL (L_∞: $t_{482} = 18.49$, $P < 0.0001$; K: $t_{482} = 4.69$, $P < 0.0001$; Table 1, Figure 2). Significant differences in FGM parameter estimates were detected between lakes for male fish (L_∞: $t_{663} = 12.38$, $P < 0.0001$; K: $t_{663} = 8.13$, $P < 0.0001$); L_∞ and K were greater for fish from KL compared to NSL. Estimated K was significantly higher for female fish from KL compared to NSL, whereas estimated L_∞ for females did not differ between lakes (L_∞: $t_{370} = 1.00$, $P = 0.3179$; K: $t_{370} = 5.45$, $P < 0.0001$; Table 1, Figure 2). Estimates of L_∞ for male fish from KL did not differ based on tag type (PIT: 949.7, T-bar anchor: 957.2; $t_{654} = 1.75$, $P = 0.0814$); however, estimated K values for males differed by tag type (PIT: 0.5086, T-bar anchor: 0.4639; $t_{654} = 2.02$, $P = 0.0442$; Figure 3). Both L_∞ (PIT: 1090.5, T-bar anchor: 1122.5; $t_{369} = 2.32$, $P = 0.0208$) and K (PIT: 0.3753, T-bar anchor: 0.2989; $t_{369} = 2.80$, $P = 0.0054$) estimates for female fish from KL differed based on tag type (Figure 3). Parameter estimates of K and L_∞ for males from KL fell within two standard errors of the final model (all years) parameters after 4 years and 134 and 126 recapture events for PIT and T-bar tags, respectively (Figure 4). Similarly, parameter estimates of K and L_∞ for females from KL fell within two standard errors of the final model parameters after 4 years and 67 and 56 recapture events for PIT and T-bar tags, respectively (Figure 5). Parameter estimates for both male and female fish from NSL were within two standard errors of the final model parameters at 7 years and 573 and 227 recapture events for males and females, respectively (Figure 6).

Predicted ages from the FGM applied to KL fish ranged from age 1-16 for males, and 1-18 for females. Predicted ages from the FGM for NSL ranged from 2-26 for males, and 2-16 for females. Muskellunge fully recruited to the gear at age-5 for both sexes in KL, and fully recruited to the gear at age-7 for males and age-6 for females in NSL. Instantaneous mortality rates derived from weighted catch curves for male and female fish from KL were 0.456 and 0.367, respectively (annual mortality rate of 36.6% and 30.7%) and did not differ between sexes (F = 0.86, $P = 0.3631$; Figure 7). Instantaneous mortality rates differed between sexes in NSL (F = 21.57, $P < 0.0001$; male: 0.302, female: 0.471; annual mortality 26.1% and 37.6%; Figure 7). Instantaneous mortality rates differed between lakes for male (F = 26.65, $P < 0.0001$), but not female fish (F = 0.66, $P = 0.4257$), with lower estimated mortality rates in male fish from NSL (Figure 7). The Beverton-Holt length-based mortality equation required an estimate of the smallest size at which fish were fully vulnerable to the gear (L_c), and the mean size of fish greater than L_c ($\bar{L}$ value). In KL L_c values were determined as 750 mm for males and 800 mm for females, and in NSL, L_c values were determined as 650 mm for males and 700 mm for females. The mean lengths of fish greater than L_c ($\bar{L}$ values) in KL were 882 mm for males and 984 mm for females; NSL fish $\bar{L}$ values were 798 mm for males and 872 mm for females. Instantaneous mortality rates derived from the Beverton-Holt length-based equation were 0.259, and 0.230 (annual mortality 22.9% and 20.3%) for male and female fish from KL. Instantaneous mortality rates for male and female fish from NSL were 0.256 and 0.335 (annual mortality 22.5% and 28.5%), respectively.

Discussion

The FGM incorporating mark-recapture data for Muskellunge produced similar growth curves and parameter estimates to von Bertalanffy growth models developed for known-age and scale-aged fish. Parameter estimates from the FGM for KL fish were nearly identical to known-age von Bertalanffy parameter estimates, which is consistent with previous research examining the utility of the FGM compared to traditional von Bertalanffy growth models (Wang 1998). Consistency of FGM growth parameter estimates with those obtained from traditional von Bertalanffy growth models for known-age fish from KL demonstrates that mark-recapture data can be used to generate accurate predictions of length-at-age for Muskellunge populations. However, the FGM for male and female fish from NSL resulted in apparent underestimation of length for fish ages 2-5. Lack of tagging small individuals < age-3 in NSL may have led to reduced model accuracy for young fish from this lake. In contrast, the KL FGM included mark-recapture data from known-age individuals (< age-4) which likely improved model estimates of growth for fish < age-4 in this lake (Frazer et al. 1990; Wang 1998). Removal of small or large individuals within a mark-recapture dataset can result in changes in parameter estimates (Frazer et al. 1990). Our results highlight the importance of tagging and recapturing a broad range of fish sizes and ages (potentially including some age-0 at stocking) to obtain accurate and precise growth parameter estimates.

Muskellunge growth was sexually dimorphic in each lake with males approaching their estimated lake-specific asymptotic lengths at a faster rate and having a smaller asymptotic length relative to females, which is consistent with previous research on Muskellunge populations throughout their geographic range (Casselman and Crossman 1986; Casselman et al. 1999; Brenden et al. 2006a; Kapuscinski et al. 2007; Faust et al. 2015). Furthermore, estimates of growth coefficients for Muskellunge in this study were greater than reported for populations from northern waters of Muskellunge range (Canada and upper Midwest and northeast, USA; K values < 0.25 for both sexes (Casselman and Crossman 1986; Casselman 2007; Kapuscinski et al. 2007; Faust et al. 2015), but similar to populations (Virginia, USA) from similar latitudes (K values 0.30-0.50 for both sexes (Brenden et al. 2006a). Conversely, estimated asymptotic length of male and female fish in both northern and southern populations are substantially higher than our study (Johnson 1971; Brewer 1980; Casselman and Crossman 1986; Casselman et al. 1999; Brenden et al. 2006a; Kapuscinski et al. 2007; Faust et al. 2015). Reduced asymptotic length and growth potential in our fish compared to other populations may be attributed to multiple factors such as genetic strain performance at differing temperatures and latitudinal differences in temperature and length of growing season, or differences in prey base (Clapp and Wahl 1996), as these factors are some of the most important factors driving differences in individual growth rates among populations (Fry 1971). Previous research by both Younk and Strand (1992) and

Wolter et al. (2012) revealed that different genetic strains of Muskellunge exhibited different growth rates within the same lakes.

Similar to our FGM methods to evaluate growth, our age- and length-based methods to estimate mortality provided the opportunity to evaluate differences in mortality between populations and lakes. Similarity between FGM and known-age von Bertalanffy growth curves for KL fish suggest that our assigned predicted ages and subsequent weighted catch curve mortality estimates were plausible. However, both mortality estimators may have been biased to some degree. Using predicted ages from the FGM due to limited availability (in KL) or lack (in NSL) of known-age fish may have led to potential error in mortality rate estimates. Probable overestimation of age for young individuals using the FGM for fish from NSL was likely responsible for predicted age ranges of fish extending beyond typical maximum age for Muskellunge at latitudes comparable to Illinois (Brenden et al. 2006a). Inaccuracy of length-based age estimates derived from the FGM may have affected mortality rate estimates. Bias in estimated mortality rates using predicted ages from the FGM may have been particularly prominent in male fish from NSL due to inherent uncertainty of length-based age predictions for fish at or near L_∞. Our results highlight the importance of tagging a broad size range of individuals to reduce bias in estimates of mortality rate derived from length-based age estimation from FGM. Beverton-Holt length-based mortality estimates may also have been biased; this estimator is particularly sensitive to the size of fish that are first fully vulnerable to sampling gear (L_c). Error in estimated L_c can result in mortality rate errors (Pauly and Morgan 1987; Ehrhardt and Ault 1992). Potential biases aside, mortality estimates were similar in KL compared to NSL using both methods; an average mortality rate combining both methods resulted in annual mortality estimates of approximately 25-30% in KL and 25-35% in NSL (Beverton-Holt annual mortality estimates were approximately two thirds of that of the catch curve method). Annual mortality rates estimated from scale-aged fish from NSL were 44.9% for male and 44.2% for female fish. Although estimates of mortality are limited for Muskellunge populations, Casselman et al. (1996) estimated annual mortality at 8-22% in waters of Canada, Minnesota and Wisconsin, and Brenden et al. (2006b) estimated annual mortality in the New River, Virginia to be 32%.

Differences in estimated von Bertalanffy growth parameters and mortality rates between KL and NSL Muskellunge populations illustrate the potential utility of the Fabens approach for revealing differences between water-bodies that would likely be undetected using cleithra obtained from a limited number of fish sampled at a regional scale. A combination of lake-specific abiotic and biotic factors likely influenced the differences in growth and mortality rates between KL and NSL. Differences in genetic stocks are not the underlying cause for observed differences in growth and mortality rates between lakes because Muskellunge in each lake are of the same genetic stock (NSL serves as the brood stock lake for Illinois' Muskellunge rearing and stocking program). Numerous abiotic factors, such as lake depth and surface area, can result in differences in growth rates among populations (Simonson 2008; Griffiths 2013). Differences in water temperature regimes, extent of optimal thermal habitat for Muskellunge growth, or differences in forage fish base between KL and NSL may also have contributed to differences in growth and mortality rate estimates between these two lakes (W.E. Herndon and S.C. Hirst, Illinois Department of Natural Resources, unpublished data). Differences in Muskellunge density between KL and NSL may also have contributed to differences in growth and mortality rate estimates between these populations. High density may limit individual growth rate in fish (Lorenzen and Enberg 2002), and density-dependent growth has been suggested for Muskellunge

(Gilbert and Sass 2016) and Northern Pike (Margenau et al. 1998) populations. Although precise Muskellunge density estimates in each lake are unknown, results from netting data (fish/net night) and angler creel surveys (fish/angler hour) suggest that Muskellunge density may be higher in NSL than in KL (Illinois Department of Natural Resources 2010; W.E. Herndon, and S.C. Hirst, Illinois Department of Natural Resources, unpublished data), although net or angler catch rate data have not been validated as an index of Muskellunge density.

Management Implications

This study provides new techniques to evaluate population characteristics of Muskellunge using mark-recapture data. Application of the FGM and its parameter estimates and predicted ages facilitated lake-specific growth and mortality estimates to determine if populations differed between lakes. More specifically, the FGM produced estimates of von Bertalanffy parameters comparable to fish of known-age (and scale-aged), facilitating use of the FGM to compare growth between populations. Both age- and length-based methods also produced estimates of mortality that could be compared among populations. However, we acknowledge that potential errors and biases associated with these methods may exist, but use of non-lethal mark-recapture data instead of methods that require sacrificing individuals may preclude some of the associated biases with the provided techniques in this paper. Potential biases and errors aside, these methods provide a potential ‘tool kit’ for Muskellunge biologists to facilitate analyses of Muskellunge population characteristics using mark-recapture datasets.

Using mark-recapture data and these methods as a ‘tool kit’ to estimate population characteristics may be more advantageous than traditional methods because substantially larger sample sizes can be obtained, and they do not require sacrificing individuals for age estimation.

Muskellunge of all sizes can be tagged (Younk et al. 2010; Rude et al. 2011), and subsequently the entire population can be represented with mark-recapture data; whereas, growth estimates from cleithra may only represent trophy individuals (Faust et al. 2015). We also acknowledge that mark-recapture datasets used in this study are likely unique in sample size and duration (years) compared to many other Muskellunge mark-recapture datasets. However, we found that smaller sample sizes and years of mark-recapture data can be used to derive similar parameter estimates. Sample sizes of < 100 fish and 4 years of mark-recapture data may be sufficient to produce reliable growth parameter estimates in situations similar to the KL dataset where a broad range of fish sizes were tagged and recaptured. Conversely, increased sample sizes (> 500) and years of mark-recapture data (7) may be required in situations similar to the NSL dataset where only adult Muskellunge were tagged, because under-represented or missing length groups may influence FGM parameter estimates (Frazer et al. 1990; Wang 1998). Thus, our results highlight the importance of marking and recapturing a broad range of fish sizes when using this technique to estimate growth parameters. Individually numbered T-bar anchor tags may also be used to estimate growth parameters as we found little difference in FGM parameter estimates derived from PIT tag and T-bar anchor tag datasets. However, we caution the use of only T-bar anchor tags because long-term data may be reduced as a result of decreased retention rates over time (Rude et al. 2011), but in data-poor situations T-bar anchor tags facilitate the use of angler-recorded data.

For Muskellunge management, using mark-recapture data may reduce data-limited situations when managing a population. Estimates of L_∞ from the FGM may be useful for setting minimum length limits tailored to differences in Muskellunge growth potential among lakes (Casselman 2007), along with providing required information for estimating annual mortality using length-based methods (Beverton and Holt 1956; Pauly 1980; Pauly and Morgan 1987; Ehrhardt and Ault 1992). For example, results of the FGM applied to Muskellunge populations in NSL and KL suggest that the current 1219 mm (48 in) minimum length limit may exceed the biological growth potential of Muskellunge in NSL but not in KL; no fish > 1219 mm were collected during this study and anglers have only caught two fish > 1143 mm (45 in) in NSL from 1989-2010, whereas numerous fish > 1219 mm were sampled in this study and have been caught by anglers from 1992-2010 in KL (Illinois Department of Natural Resources 2010). Based on Casselman (2007), using the lower 99% confidence interval bound of L_∞, to set the minimum length limit would result in a 1016 mm (40 in) length limit for NSL, which should increase the opportunity for anglers to potentially harvest a trophy individual. Even if harvest of trophy fish did not substantially increase under a reduced minimum length limit due to the catch and release ethic of many Muskellunge anglers (Margenau and Petchenik 2004), setting minimum length limits in accordance with lake-specific Muskellunge growth potential could be used to provide anglers with an indication of a total length that could be considered representative of a trophy fish for a particular lake or set of lakes.

In addition to the methods described in this study, mark-recapture data can also be used to determine population size and provide estimates of mortality (Pine et al. 2003). Therefore, Muskellunge biologists can design mark-recapture studies that may allow them to estimate growth using the FGM, estimate mortality using a catch-curve approach incorporating predicted ages, length-based methods, and mark-recapture models, while also incorporating fish population size estimates. These data may provide Muskellunge biologists with lake-specific population characteristics needed to set effective length regulations based on individual lake growth potential (Casselman 2007; Faust et al. 2015). Furthermore, these data may provide the ability to assess changes in the population in respect to changes in angler attitude (i.e., fishing pressure), catch and release mortality, exploitation, fish density, and environmental conditions (Beverton and Holt 1957; Munkittrick and Dixon 1989; Casselman et al. 1996; Margenau and Petchenik 2004; Margenau 2007; Gilbert and Sass 2016). Therefore, application of the mark-recapture data and the techniques described in this study ultimately may lead to improved management of Muskellunge fisheries.

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Table 1. Summary of von Bertalanffy parameter estimates of asymptotic length (L_∞), growth coefficient (K) and theoretical time at length zero (t_0) derived from the Fabens growth model using mark-recapture data, and from known-age fish from Kinkaid Lake (KL) and scale-aged fish from North Spring Lake (NSL) by sex. Values associated with parameter estimates are the range of upper and lower 95% confidence intervals. Sample size (n) is the number of recapture events used in a given model. Note (t_0) is not calculated in the Fabens growth model and is assumed to be zero.

	Fabens			von Bertalanffy			
Model	n	L_∞	K	n	L_∞	K	t_0
KL Male	554	948.3 ± 5.7	0.5189 ± 0.03	73	937.7 ± 18.6	0.6004 ± 0.06	0.059 ± 0.05
KL Female	260	1088.8 ± 9.2	0.3974 ± 0.02	48	1043.9 ± 34.3	0.5001 ± 0.06	0.029 ± 0.07
NSL Male	807	903.7 ± 6.7	0.3599 ± 0.03	1399	900.5 ± 5.4	0.3867 ± 0.01	-0.507 ± 0.10
NSL Female	294	1080.3 ± 17.6	0.2771 ± 0.02	583	1018.7 ± 11.5	0.3601 ± 0.02	-0.436 ± 0.10

Figure 1. Length frequency distributions of Muskellunge collected from 1999-2016 for each lake: male fish from Kinkaid Lake (A), and North Spring Lake (C), and female fish from Kinkaid Lake (B) and North Spring Lake (D).

Figure 2. Fabens growth model and von Bertalanffy growth model curves from (**A**) Kinkaid Lake and (**B**) North Spring Lake. Solid lines represent the Fabens growth models, and dashed lines represent the von Bertalanffy growth function. Black lines and gray lines represent male and female fish, respectively. Black and gray dots represent length-at-age and standard deviation of known-age individuals by sex from (**A**) Kinkaid Lake, and black and gray dots represent length-at-age and standard deviation of scale-aged individuals by sex from (**B**) North Spring Lake.

Figure 3. Fabens growth model growth curves from Kinkaid Lake fish by tag type and sex. Black and gray lines represent male and female fish, respectively. Solid and dashed lines represent PIT tagged and T-bar anchor tagged individuals, respectively.

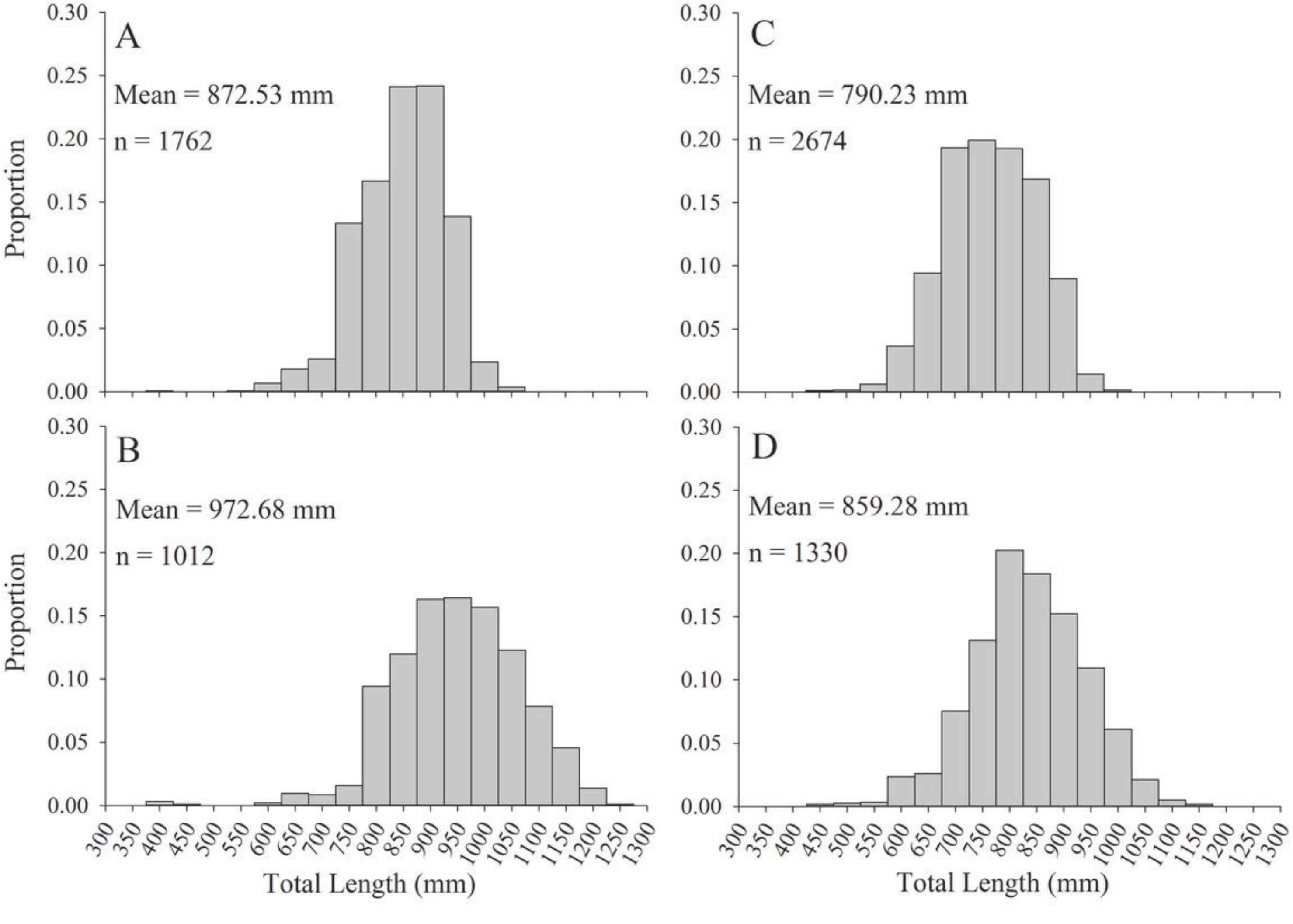
Figure 4. Annual von Bertalanffy parameter estimates of the growth coefficient (K) (**A**), and asymptotic length (L_∞) (**B**) derived from the Fabens growth model for male fish from Kinkaid Lake by tag type with each successive year of mark-recapture data. Black and gray dots represent PIT tagged and T-bar anchor tagged individuals, respectively. Error bars represent

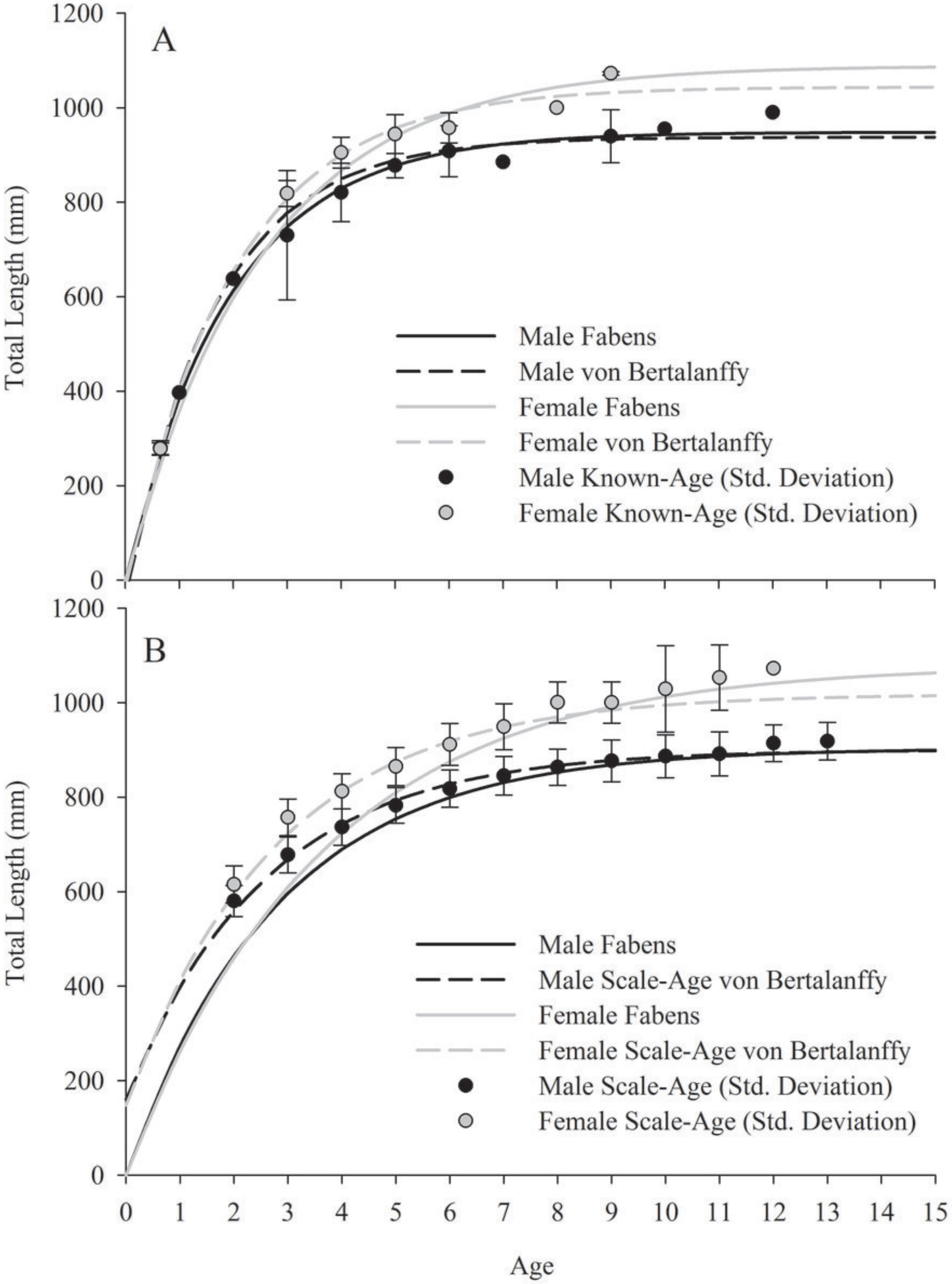
standard errors of parameter estimates. Black and gray numbers (by tag type) above each year represent the number of total recapture events used to estimate parameters.

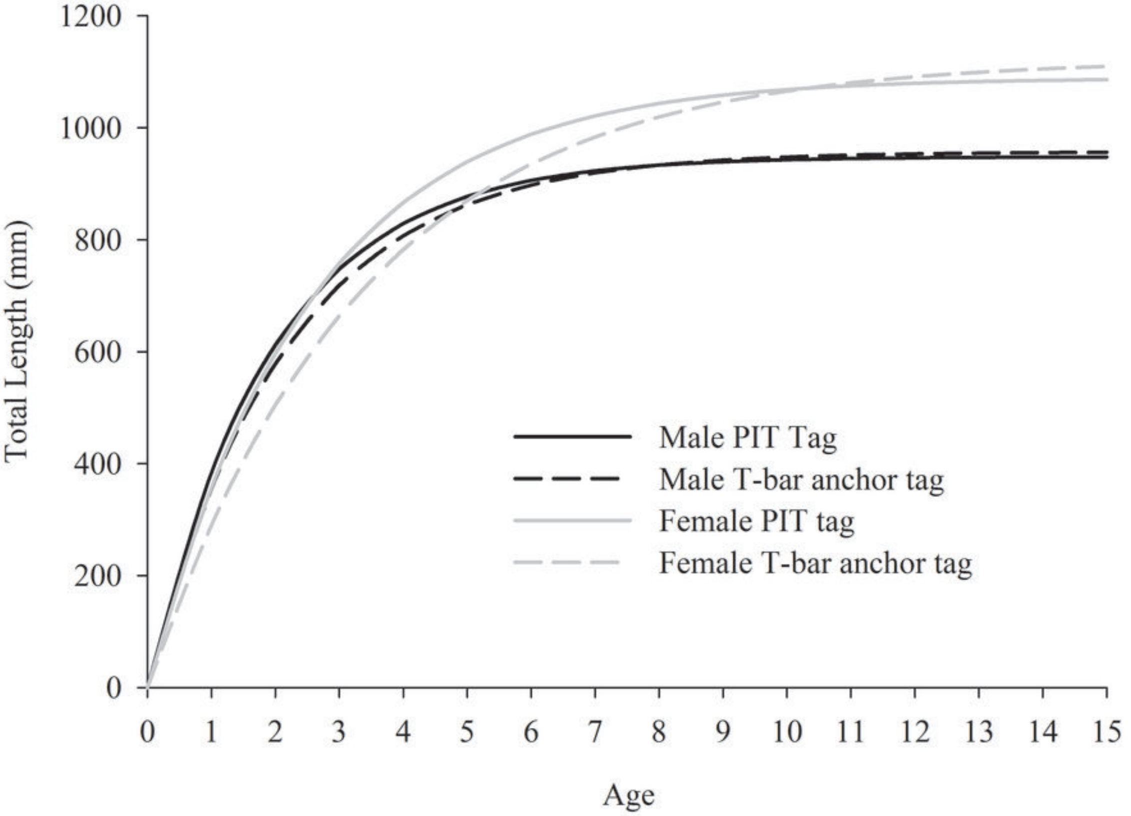
Figure 5. Annual von Bertalanffy parameter estimates of the growth coefficient (*K*) (**A**), and asymptotic length (L_∞) (**B**) derived from the Fabens growth model for female fish from Kinkaid Lake by tag type with each successive year of mark-recapture data. Black and gray dots represent PIT tagged and T-bar anchor tagged individuals, respectively. Error bars represent standard errors of parameter estimates. Black and gray numbers (by tag type) above each year represent the number of total recapture events used to estimate parameters.

Figure 6. Annual von Bertalanffy parameter estimates of the growth coefficient (*K*) (**A**), and asymptotic length (L_∞) (**B**) derived from the Fabens growth model for fish from North Spring Lake by sex with each successive year of mark-recapture data. Black and gray dots represent male and female fish, respectively. Error bars represent standard errors of parameter estimates. Black and gray numbers (by sex) above each year represent the number of total recapture events used to estimate parameters.

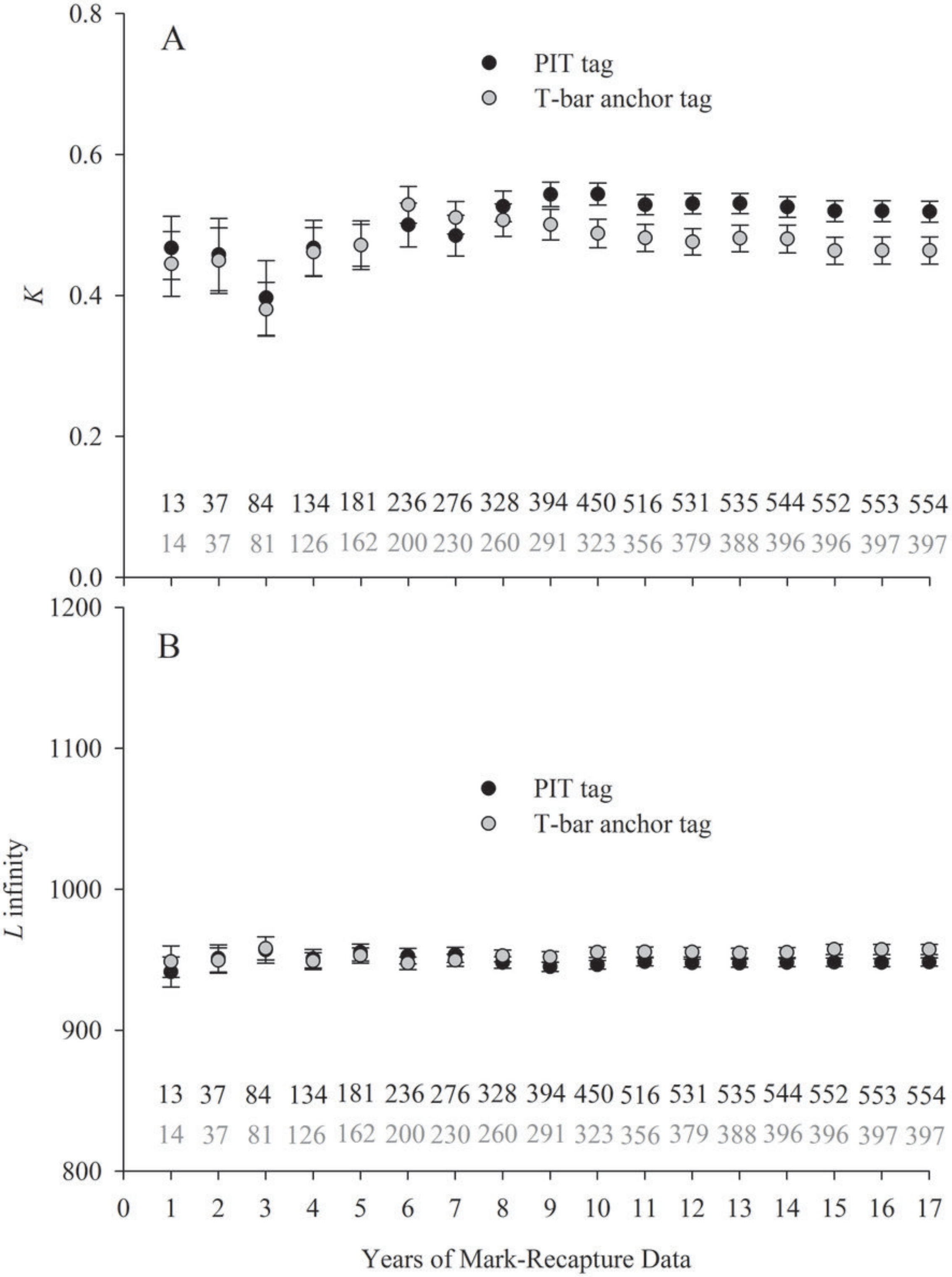
Figure 7. Weighted catch curves of male (**A, C**) fish from Kinkaid Lake and North Spring Lake, and female fish (**B**, **D**) fish from each lake, respectively. The natural log of the number of predicted age fish derived from the Fabens growth model were plotted as a function of age for Kinkaid Lake, and North Spring Lake fish. Note x-axis range differs among figures.

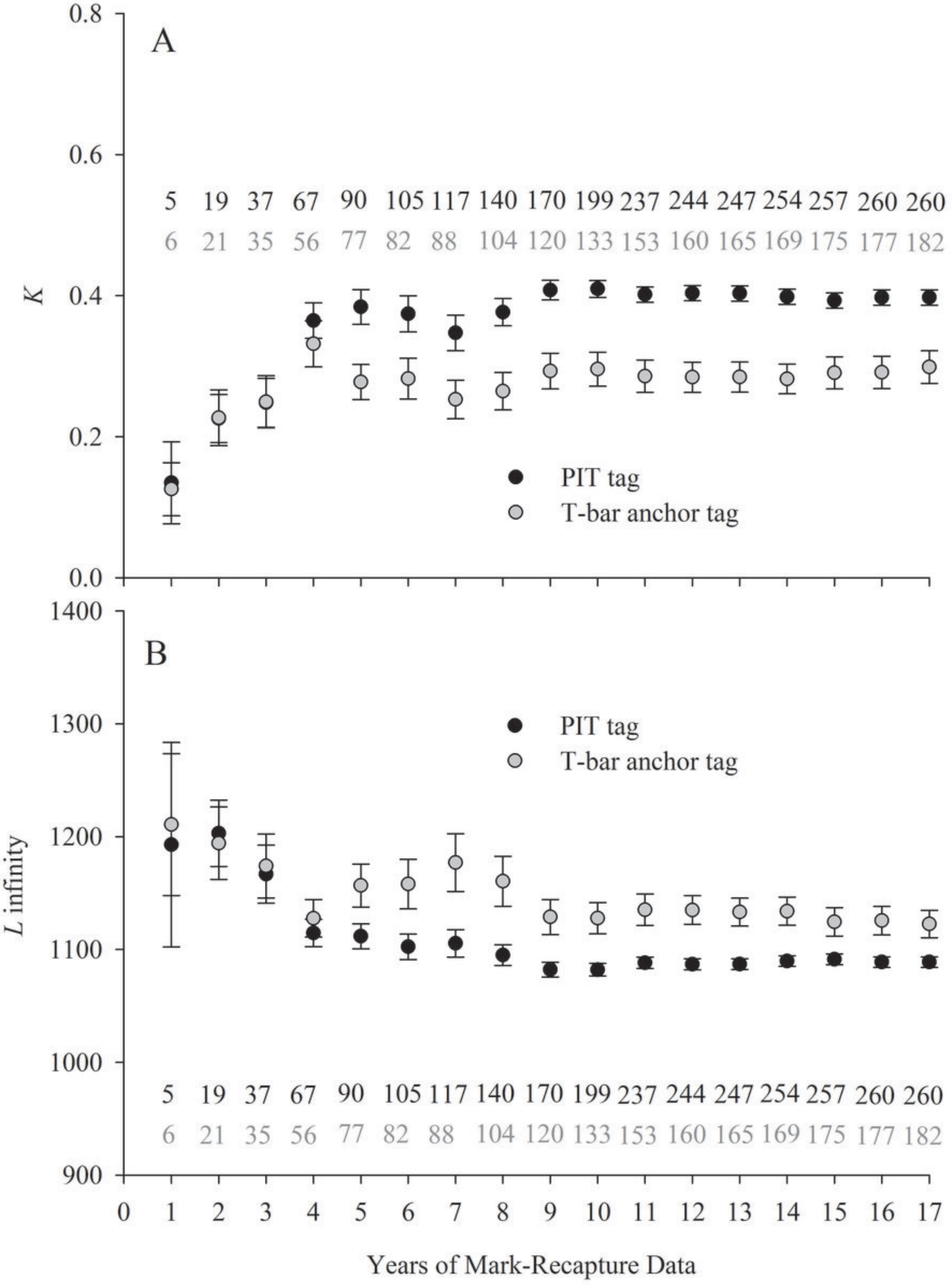

A
Mean = 872.53 mm
n = 1762
B
Mean = 972.68 mm
n = 1012
C
Mean = 790.23 mm
n = 2674
D
Mean = 859.28 mm
n = 1330
Proportion
0.00
0.05
0.10
0.15
0.20
0.25
0.30
Total Length (mm)
300
350
400
450
500
550
600
650
700
750
800
850
900
950
1000
1050
1100
1150
1200
1250
1300


A
B
Total Length (mm)
Total Length (mm)
Age
0
200
400
600
800
1000
1200
0
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
Male Fabens
Male von Bertalanffy
Female Fabens
Female von Bertalanffy
Male Known-Age (Std. Deviation)
Female Known-Age (Std. Deviation)
Male Fabens
Male Scale-Age von Bertalanffy
Female Fabens
Female Scale-Age von Bertalanffy
Male Scale-Age (Std. Deviation)
Female Scale-Age (Std. Deviation)

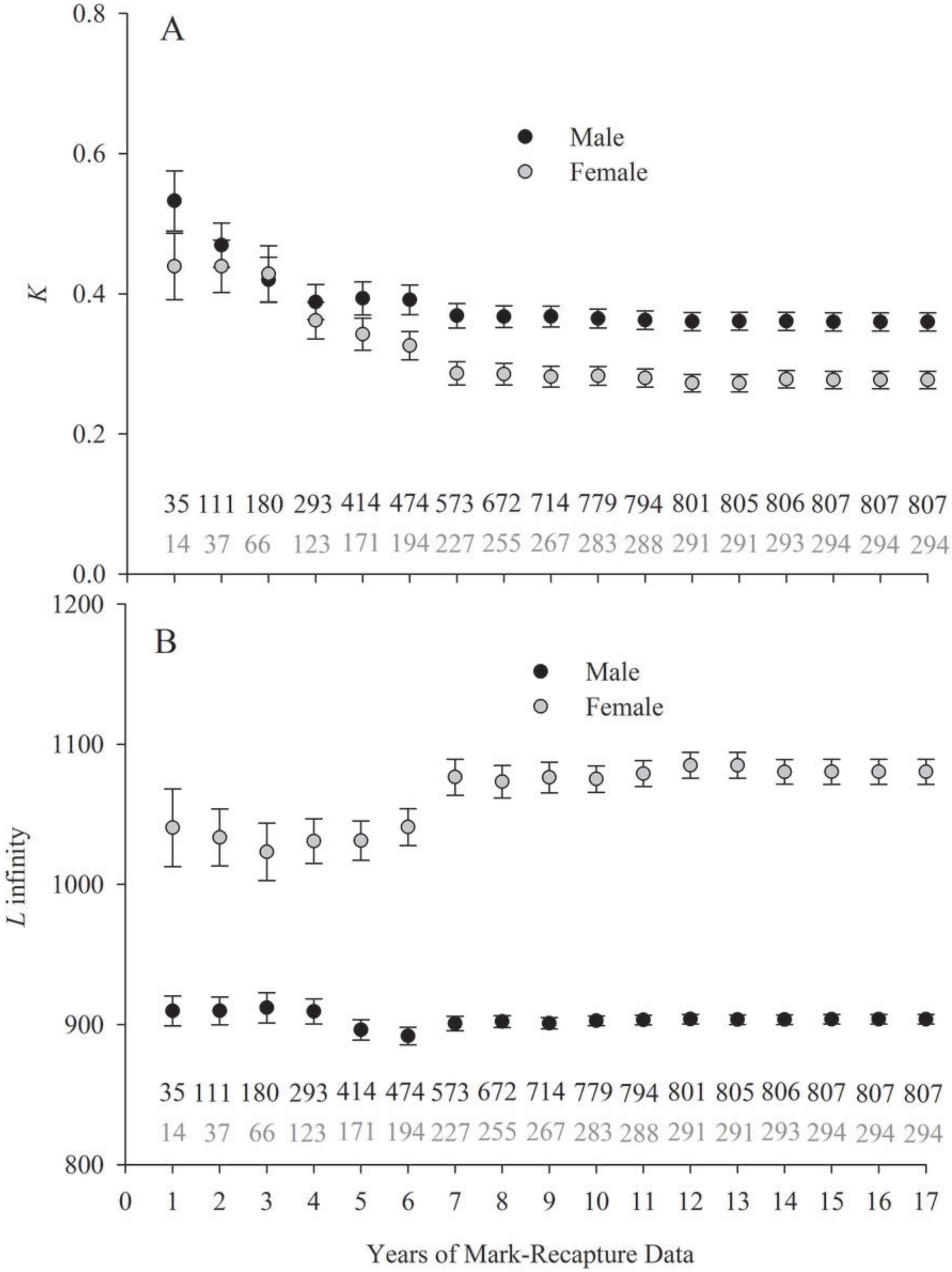


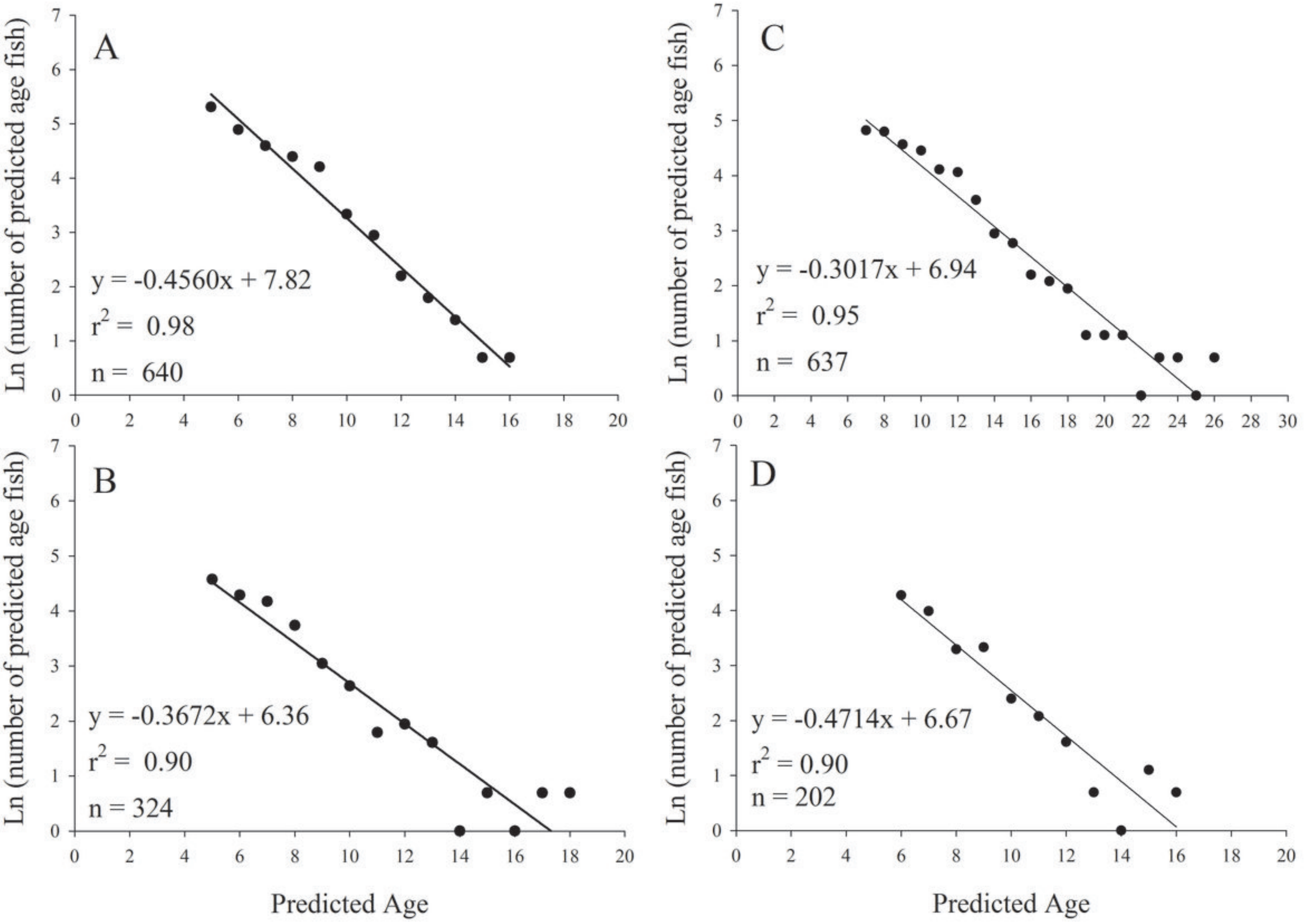
Total Length (mm)
1200
1000
800
600
400
200
0
0
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
Age
Male PIT Tag
Male T-bar anchor tag
Female PIT tag
Female T-bar anchor tag


A
PIT tag
T-bar anchor tag
K
0.0
0.2
0.4
0.6
0.8
13 37 84 134 181 236 276 328 394 450 516 531 535 544 552 553 554
14 37 81 126 162 200 230 260 291 323 356 379 388 396 396 397 397
B
PIT tag
T-bar anchor tag
L infinity
800
900
1000
1100
1200
13 37 84 134 181 236 276 328 394 450 516 531 535 544 552 553 554
14 37 81 126 162 200 230 260 291 323 356 379 388 396 396 397 397
0 1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17
Years of Mark-Recapture Data



A
K
0.0
0.2
0.4
0.6
0.8
5 19 37 67 90 105 117 140 170 199 237 244 247 254 257 260 260
6 21 35 56 77 82 88 104 120 133 153 160 165 169 175 177 182
● PIT tag
○ T-bar anchor tag
B
L infinity
900
1000
1100
1200
1300
1400
● PIT tag
○ T-bar anchor tag
5 19 37 67 90 105 117 140 170 199 237 244 247 254 257 260 260
6 21 35 56 77 82 88 104 120 133 153 160 165 169 175 177 182
0 1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17
Years of Mark-Recapture Data


A
0.8
0.6
0.4
0.2
0.0
K
● Male
○ Female
35 111 180 293 414 474 573 672 714 779 794 801 805 806 807 807 807
14 37 66 123 171 194 227 255 267 283 288 291 291 293 294 294 294
B
1200
1100
1000
900
800
L infinity
● Male
○ Female
35 111 180 293 414 474 573 672 714 779 794 801 805 806 807 807 807
14 37 66 123 171 194 227 255 267 283 288 291 291 293 294 294 294
0 1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17
Years of Mark-Recapture Data


A
y = -0.4560x + 7.82
r^2 = 0.98
n = 640
B
y = -0.3672x + 6.36
r^2 = 0.90
n = 324
C
y = -0.3017x + 6.94
r^2 = 0.95
n = 637
D
y = -0.4714x + 6.67
r^2 = 0.90
n = 202
Ln (number of predicted age fish)
Predicted Age
0
1
2
3
4
5
6
7
0
2
4
6
8
10
12
14
16
18
20
22
24
26
28
30