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Age and growth of juvenile ladyfish (*Elops* sp) in Tampa Bay, Florida, USA

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Abstract
The age and growth of juvenile ladyfish (*Elops* sp) in Tampa Bay, Florida (USA) was examined using two cost-effective age and growth methods: length-frequency analysis (LFA) and captive rearing. The progression of monthly ladyfish size significantly increased from the beginning (i.e., when many young and small individuals were collected) to the end (i.e., when fewer older and larger individuals were collected) of the recruitment period. In most years, ladyfish growth (i.e., mean length) in Tampa Bay increased consistently from March to July. Juvenile ladyfish growth calculated by the LFA approach ranged from 0.30 to 1.3 mm day^{-1}, whereas captive reared ladyfish grew between 0.60 and 0.70 mm day^{-1}. Captive rearing data, together with length-frequency data, suggests that juvenile ladyfish reach between 212 and 297 mm SL by age-1. Individuals raised in tanks grew faster than those in the natural environment during the first 90 days, but slower after 90 days.

Keywords: Captive rearing; Conservation; Length-frequency; Life-history; Management

1. Introduction

Life-history information is essential for fishery managers charged with managing, conserving, and protecting fishery resources [1]. This type of biological information (e.g., recruitment, mortality, age, and growth) helps fishery managers understand a species' relationship with its natural environment. One of the most important life-history characteristics for fishery managers to recognize is a species' age and growth characteristics; these traits are necessary for making informed fishery management decisions. Furthermore, fish survival is often linked to early life-stage growth [2], which ultimately influences recruitment and year class strength [3]. One of the best ways to gather fisheries life-history information is through standardized fisheries-independent monitoring (FIM) programs.

Data collected through long-term FIM programs can be used to examine age and estimate growth rates for a broad spectrum of species. The Fish and Wildlife Research Institute (FWRI), a division of the Florida Fish and Wildlife Conservation Commission (FWC), established one of the first standardized fisheries monitoring programs in the United States [4]. Over time, data collected through the FWRI's FIM program has been used to elucidate life-history information for a variety of fish (e.g., red drum (*Sciaenops ocellatus*): [5]; spotted seatrout (*Cynoscion nebulosus*): [6]; permit (*Trachinotus falcatus*): [7]. Because researchers often concentrate their research efforts on the most economically valuable species (e.g., tarpon [*Megalops atlanticus*], snook [*Centropomus undecimalis*], and seatrout) of a region, the less economically valuable species are given less research attention even though they still provide social and ecological value [8].

According to Levesque [8], one prime example of a species receiving less research attention is the ladyfish (*Elops* sp). Ladyfish are a coastal nearshore species that have a worldwide distribution [9-11]. In the United States, at least two species (*Elops saurus* and *Elops smithi*) are now recognized as having sympatric distributions in the Gulf of Mexico and southeastern North Atlantic Ocean [11-13]. Notably, the ladyfish life-cycle includes a specialized leptocephalus larval stage [14], a trait shared by as few as 800 fish species worldwide [13, 15]. While not an unheard-of characteristic, this life-stage is shared by the ladyfishes' closest relatives, tarpon and bonefish (*Albula vulpes*), both are among the most prized recreational fisheries in the world [16, 17]. In Florida (USA), ladyfish are a relatively valuable recreational

and commercial species. Recreational catch rates in Florida are between two and three ladyfish per fishing trip [18, 19], and their preliminary commercial value in 2013 was around US $300,000 [20]. Despite their economic, social, and ecological worth, little biological information on ladyfish is available to fishery managers for making informed decisions, including age and growth information.

Today, the most widely accepted and applied method for estimating fish growth involves extracting and examining otoliths [21]. Depending on the species (e.g., tarpon and bonefish), procedures for preparing, processing, and interpreting otoliths can be labor intensive; it can also require a high-degree of skill [22]. Thus, with the never-ending limitation on available research funds, it is important that researchers consider less cost prohibitive methods for deriving and validating age and growth estimates. Fortunately, there are several new (e.g., habitat suitability models: [23] and traditional cost-effective (e.g., length-frequency analysis (LFA) and direct [captive rearing]) age and growth methods available to researchers [24, 25]. Given the lack of age and growth information for ladyfish, the main objective of this study was to investigate, for the first time, juvenile ladyfish age and growth in Tampa Bay, Florida (USA) using LFA and captive rearing.

2. Materials and methods

2.1. Study Area

Field-collections were made throughout the Tampa Bay region, USA (Fig. 1). Field sampling was conducted by FWC's FIM personnel at 28 (seines [18 sites] and trawls [10 sites]) pre-determined stations (i.e., fixed stations); fixed stations were stratified by geographical location, habitat, and depth [4]. Further details on field sampling procedures and site descriptions are provided by [5, 26].

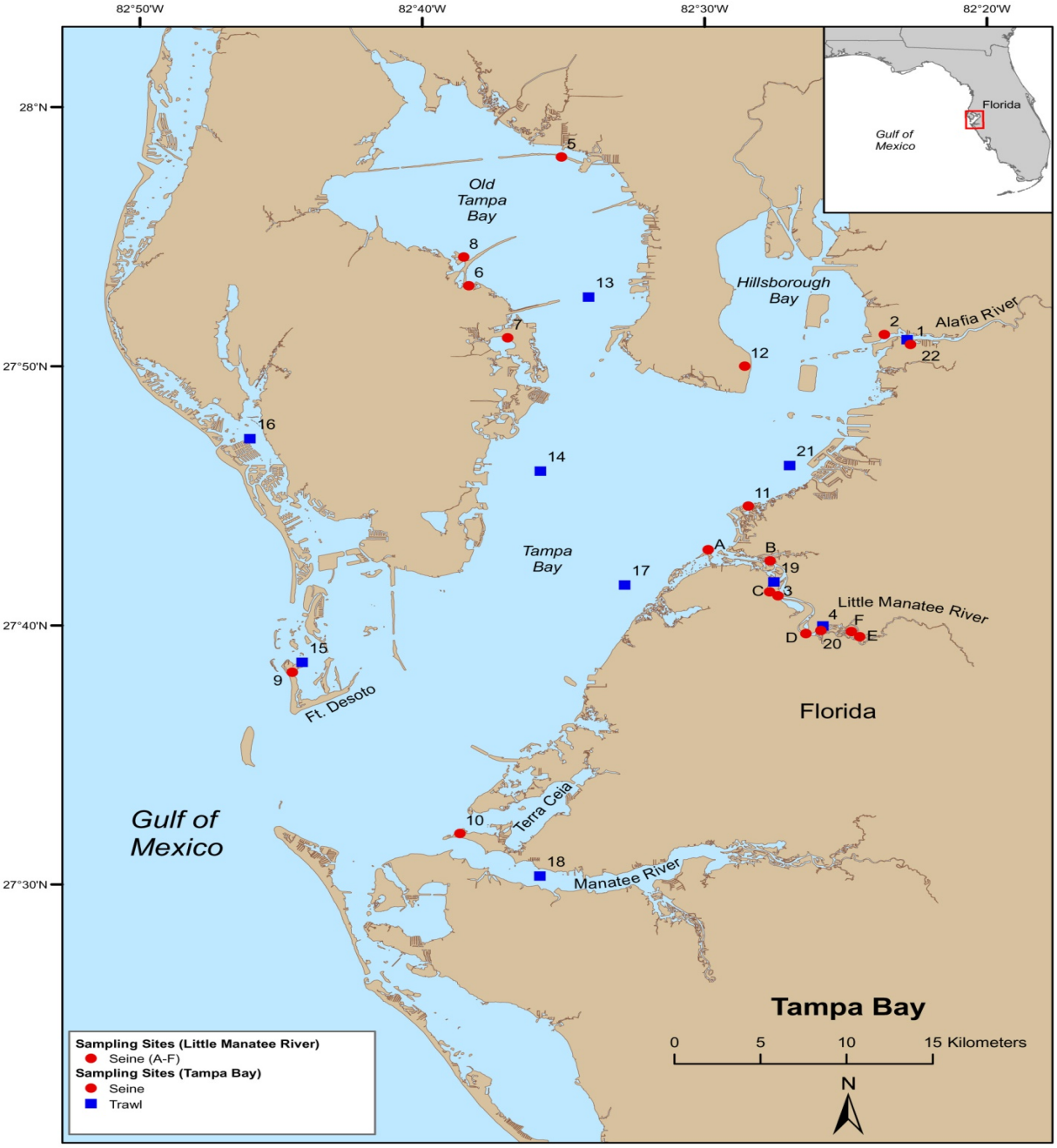

Fig 1: Map of Tampa Bay fixed-station field sampling sites during September 1987 through December 1995.

2.2. Sampling Methodology

Fixed station field sampling was conducted once a month during daylight hours (i.e., the period between one hour after sunrise and one hour before sunset). In the Little Manatee River, field collections occurred during January 1988 through 1991, and in Tampa Bay field collections occurred from September 1987 to 1995. Three haul repetitions were made at each sampling station with a center-bag seine (21.3 m long by 1.8 m high; center bag constructed of 3.2 mm #35 knotless nylon Delta mesh). Based on the profile of the beach (i.e., bank) and water depth, one of three deployment methods (beach, boat, or offshore) were used to deploy the center-bag seine (i.e., seine) at each sampling station [4]. The first deployment technique was the beach method. A beach deployment method was used when the water depth was shallow and the bank had a gradual slope. The beach deployment method consisted of the seine being pulled parallel to shore by two biologists for a total distance of 9.1 m; a 15.5 m line stretched between each seine pole was used to assure the net was being pulled the same inner-pole distance for every haul. The second deployment technique was the boat deployment method. A boat deployment method was used when the water was either to deep (water depth 0.7−1.2 m) or the bank was too steep to use a beach deployment. The boat deployment method consisted of deploying the seine from the stern in a semi-circular pattern along the bank. Once the seine was fully deployed, two biologists would pull the seine toward shore. The third and final deployment method was the offshore deployment method. An offshore deployment was used when there was either no available beach or it was too shallow to reach the beach/ bank by boat. The offshore deployment followed the same procedures as the beach deployment with one minor difference; at the end of the 9.1 m distance, two biologists worked the seine using a stationary pivot pole to ensure the catch did not escape [4].

2.3. Data

The FWC used two experimental field sampling approaches in the 1990s to survey fish throughout Florida [4]: monthly fixed station (FS) and year-round stratified random sampling (SRS). For these analyses, data was restricted to monthly FS collections because preliminary analyses of SRS data showed that fewer ladyfish were collected using the SRS approach; so pooling the datasets (SRS and FS) would not have benefited this investigation. Also, most of the individuals collected by SRS were larger and older than the selected maximum cut-off length of 100 mm SL. A maximum cut-off length of 100 mm SL was chosen because previous work by Levesque (unpubl) suggested that ladyfish larger than 100 mm SL can avoid some types of field sampling gear (i.e., small-mesh center-bag seines). Consequently, I was concerned that inclusion of the SRS-derived data could have bias the analyses by under- or over-estimating size-at-age. Therefore, I determined that pooling SRS-derived with the FS-derived datasets would not have benefited this study given that the primary objective was to validate the use of LFA against captive rearing.

After every haul, ladyfish were sorted, enumerated, and measured (20 individuals). Ladyfish were measured to the nearest 1 mm standard length (SL); however, a few ladyfish collected from the Little Manatee River were measured to the nearest 1 mm total length (TL) and weighed to nearest 0.1 gram using a digital scale. The morphometric conversion between SL and TL was estimated by simple linear regression ($y = \acute{\alpha} + \beta X_i$), and the length-to-weight conversion was calculated using an exponential regression:

$$W = a\,SL^b \qquad (1)$$

Where,

W = whole weight (grams); SL = standard length (mm).

2.4 Length-Frequency Analysis

Ladyfish age and growth estimates were derived using two approaches: (1) time dependent LFA and (2) direct measurements of growth through captive rearing. To estimate ladyfish growth by the LFA approach, monthly field collections of cohort lengths were categorized into 5 mm SL size classes, graphed, and evaluated. Descriptive statistics (e.g., mean, standard deviation, variance, standard error) were derived and cohorts identified using modal progression analysis (MPA); MPA consisted of plotting the mean SL and the collection date. Annual ladyfish growth was estimated by regression analyses of the monthly geometric mean SL on capture date. Growth was described by linear (SL = slope [age] + y-intercept) and nonlinear regression. The coefficient of determination value was used to choose the most parsimonious (i.e., the model that best fit the data) growth model. Exponential growth regression was described with the following equation:

$$SL = L_o\, e^{Gt} \qquad (2)$$

Where,

SL = standard length (mm); G = instantaneous growth coefficient (per month); L_o = initial SL (mm) size at first capture; t = the time (per month) for the average individual in the length-class to achieve the indicated size.

The relative instantaneous growth coefficient (G) was estimated by calculating the average time individuals in a year-class attained a certain length [27]. The instantaneous growth coefficient was used to represent the average growth of the population during the time period [28]. The absolute daily growth rate was estimated by the following equation:

$$G = \Delta l\,(l_2 - l_1) / \Delta t\,(t_2 - t_1) \qquad (3)$$

Where,

l_2 = SL (mm) at the end of a unit of time; l_1 = initial SL (mm) at time 0;t_2 = at the end of a unit of time (days); t_1 = initial time 0 (days).

After regressions were fitted to the dataset, comparisons of annual growth were performed using Analysis of Covariance (ANCOVA). Prior to each ANCOVA test, a preliminary model (interaction regression) was used to determine if the slopes of the regression lines differed (homogeneity of slopes assumption); significance (homogeneity of y-intercepts and coincidental slopes and intercepts of the regression lines) was achieved when the parallelism of slopes assumption was met. If annual growth rates were equal, then data were pooled (i.e., all years combined).

For the purpose of these analyses, the Ricker [28] criteria were assumed: (1) the population sampled had a normal distribution; (2) the size classes (captured) were not

influenced by gear or sampling methods; (3) mortality was the only natural population influence; and (4) the population was resident to the sampling location (i.e., lack of immigration or emigration). Based on field experience, these assumptions seemed reasonable because the data was limited to seine gear, and most of the sampling stations were suitable for collecting juvenile ladyfish.

2.5 Captive Rearing

The second approach used to derive juvenile ladyfish age and growth estimates, and validate length-frequency modal progression was the direct measurement of growth through captive rearing. Numerous juvenile ladyfish were collected from the Little Manatee River (Tampa, FL), during initial recruitment (April and May 1995). After specimens were collected, they were temporarily maintained in live-tanks and then transported to a grow-out facility. Upon arrival, the specimens were immediately transferred to outdoor square aquariums (76-liter) for the duration of the experiment. To alleviate any growth bias, ladyfish were divided into equal groups and reared in separate aquariums; each group consisted of three to five individuals per aquarium. Because ladyfish were cannibalistic, additional specimens had to be occasionally added during the first 30 to 60 days of the experiment to maintain a consistent group size.

To maintain natural water conditions, and alleviate any potential negative water quality effects on growth, monthly water changes were performed using water collected from the Little Manatee River. Water clarity was maintained by internal and external filtration filters and pumps operating at approximately 1−10 ml/s. To simulate natural conditions, each aquarium was maintained outdoors; water temperatures fluctuated with ambient conditions, Diet was based on information obtained from the scientific literature [14, 29, 30]. Initially, ladyfish were fed brine shrimp (*Artemia* sp), but once they reached ~ 40−130 mm SL, their diet was changed to Gulf menhaden (*Brevoortia patronus*) and tidewater silversides (*Menidia peninsulae*). In Louisiana, Gulf menhaden is the primary forage species (72% of the diet) of juvenile ladyfish [30, 31]. Ladyfish were fed individuals that were slightly smaller (20−40 mm SL) than the captive specimens. Because it was difficult to speculate the proper ration size (% of the body weight daily) that would prevent any growth bias caused from over or under feeding, captive ladyfish were pulse fed twice a day (after sunrise and before sunset) until satiation (i.e., determined by the presence of excess food-items after ~10 minutes of feeding). The feeding duration was defined through visual observation, which showed ladyfish usually stopped feeding after 10 minutes. Visual observations also showed that ladyfish were disinterested in feeding off the bottom of the tank. In fact, they preferred instead to attack prey (i.e., hand dropped whole Gulf menhaden) as it drifted toward the bottom during feeding sessions. During each feeding session, an attempt was made to individually feed each ladyfish specimen. Any uneaten food-items were immediately removed from the tank to alleviate any growth-dominance bias among specimens.

To measure growth, ladyfish were initially measured and weighed daily. However, due to high mortality rates resulting from handling stress, measurements were changed to weekly increments. Similar to the LFA approach, juvenile ladyfish daily growth rates were estimated for each tank by the regression of the geometric mean length over time (days in captivity). Growth was examined using linear and nonlinear regression to evaluate which model best fit the data. Two independent Student *t*-tests were used to investigate differences in mean length and growth between tanks; the experiment was completed with an equal number of specimens in two tanks. Ladyfish growth for each tank was calculated by subtracting the mean size of the group at the start ($t = 0$) of the experiment from the mean size at the end. If no significant difference was detected in mean length or growth between tanks, then the dataset was pooled. Ladyfish growth was evaluated between the tanks using ANCOVA. Prior to each ANCOVA test, a preliminary model (interaction regression) was tested to determine if the slopes of the regression lines differed (homogeneity of slopes assumption); ANCOVA significance (homogeneity of y-intercepts and coincidental slopes and intercepts of the regression lines) was achieved when the parallelism of slopes assumption was met. Overall juvenile ladyfish age and growth was evaluated by comparing the differences in the slopes and intercepts between monthly cohort modal progressions and captive rear data using an ANCOVA test and the criteria stated above.

3. Results

3.1. Length-frequency analyses: recruitment

In total, 612 juvenile ladyfish ranging in length from 20 to 100 mm SL ($\bar{x}$ = 47.9 mm SL, S.D. ± 19.3 mm) were collected in Tampa Bay during 1987 through 1995. Annual monthly length-frequency distributions demonstrated that ladyfish size increased from spring to summer (Fig. 2). The smallest ladyfish ($\bar{x}$ = 27.5 mm SL, S.D. ± 1.73 mm, $n = 4$) were collected in March and the largest ($\bar{x}$ = 91 mm SL, S.D. ± 8.72, $n = 8$) in July [F (5, 600) = 101.43, $P < 0.001$; Fig. 2]. Three separate one-way ANOVAs showed the mean size in April [F (4, 114) = 3.6, $P < 0.01$], May [F (6, 384) = 18.94, $P < 0.001$], and June [F (6, 76) = 2.38, $P < 0.04$] was significantly different among sampling years. The smallest ladyfish ($\bar{x}$ = 26.0 mm SL, S.D. ± 2.92 mm, $n = 5$) captured in April was in 1989 and the largest ($\bar{x}$ = 37.2 mm SL, S.D. ± 6.42 mm, $n = 23$) in 1994. In May, the smallest ladyfish ($\bar{x}$ = 35.4 mm SL, S.D. ± 5.49, $n = 87$) captured was in 1992 and the largest ($\bar{x}$ = 37.2 mm SL, S.D. ± 6.42 mm, $n = 23$) in 1989. The smallest ladyfish ($\bar{x}$ = 59.0 mm SL, S.D. ± 7.02 mm, $n = 7$) captured in June was in 1991 and the largest ($\bar{x}$ = 84.25 mm SL, S.D. ± 8.02 mm, $n = 4$) in 1994.

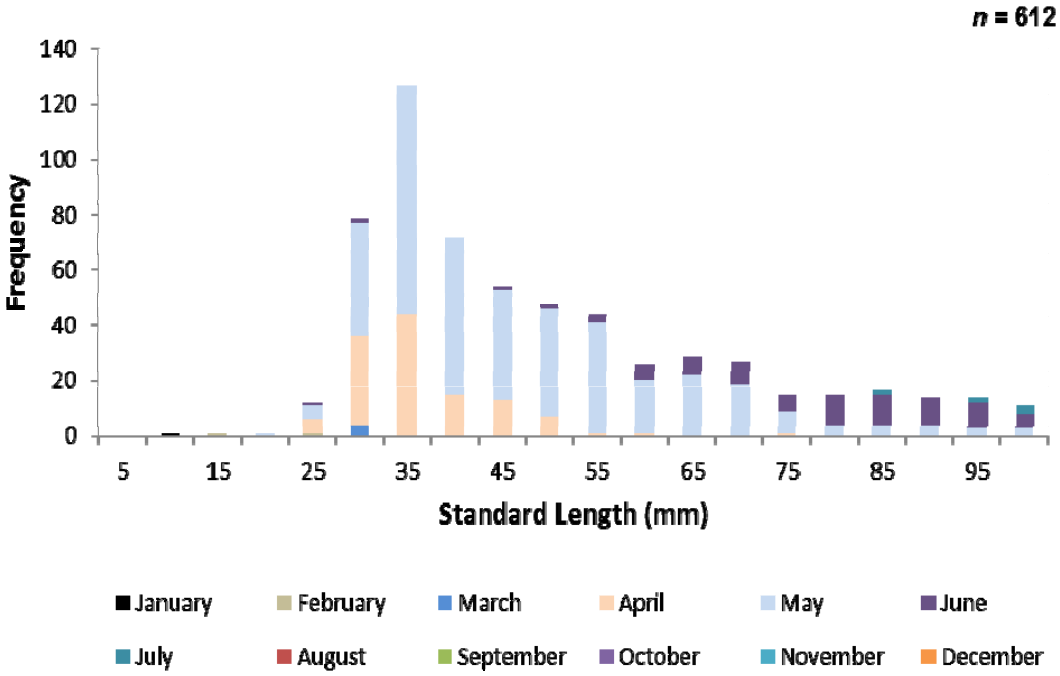

Fig 2: Cumulative monthly length-frequency distribution plots of juvenile ladyfish (*Elops* sp); The total number and size of ladyfish collected and measured in Tampa Bay. *n* = the number of ladyfish collected.

One hundred and nine juvenile ladyfish ranging in length from 1 to 94 mm SL ($\bar{X}$ = 50.2 mm SL, S.D. ± 22.64 mm) were collected in the Little Manatee River during 1988 through 1990. Annual monthly length-frequency distributions demonstrated that ladyfish size increased from spring to summer (Fig. 3). The smallest ladyfish ($\bar{X}$ = 35.5 mm SL, S.D. ± 0.71 mm, *n* = 2) were collected in April and the largest ($\bar{X}$ = 54.5 mm SL, S.D. ± 21.93 mm, *n* = 30) in June [*F* (5, 39) = 1.92, *P* = 0.11; Fig. 3]. In April and May, there were so few ladyfish collected (i.e., individuals that were measured) to permit comparisons among sampling years, but a one-way ANOVA showed the mean size in June was not significantly different among sampling years [*F* (3, 50) = 2.35, *P* = 0.08].

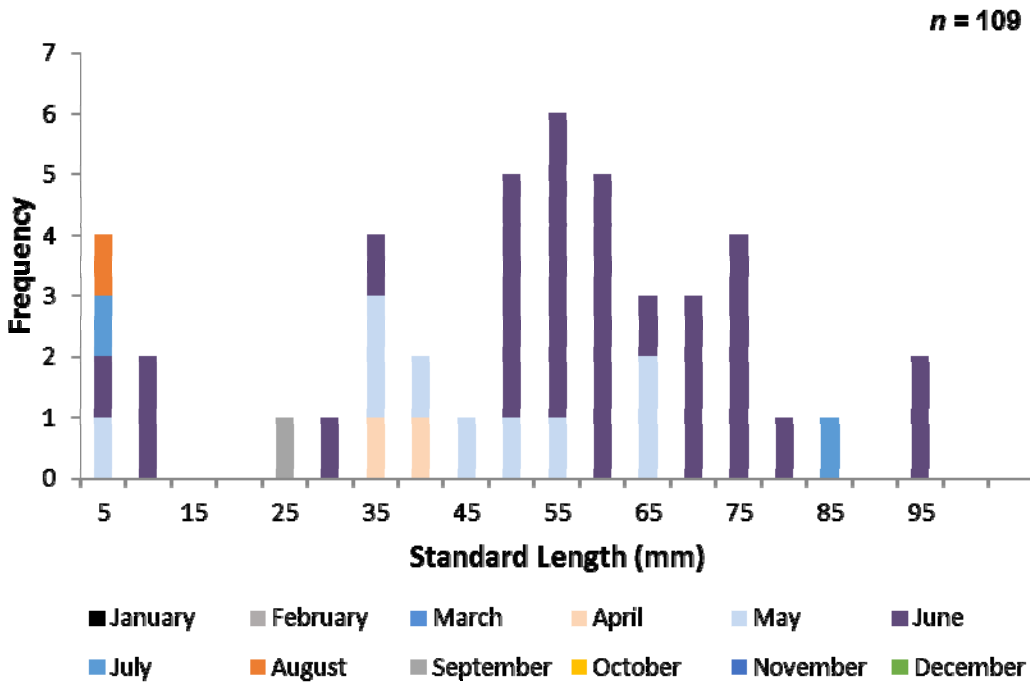

Fig 3: Cumulative monthly length-frequency distribution plots of juvenile ladyfish (*Elops* sp); The total number and size of ladyfish collected and measured in the Little Manatee River. *n* = the number of ladyfish collected.

3.2. Age and growth

3.2.1. Indirect method: length-frequency progressions

Despite the complexity in juvenile ladyfish recruitment, monthly collections exhibited seasonal patterns in Tampa Bay. In general, juvenile ladyfish growth occurred from spring to summer. The progression of monthly ladyfish size significantly increased from the beginning (i.e., when many young and small individuals were collected) to the end (i.e., when fewer older and larger individuals were collected) of the recruitment period (March-July). In most years, ladyfish growth (i.e., mean length) in Tampa Bay increased consistently from March to July. The monthly instantaneous growth coefficient ranged from 0.2223 in 1992 to 0.6795 per month in 1993. Absolute daily growth ranged from 0.4333 in 1991 to 1.2 mm day^{-1} in 1993. On average, absolute growth was 62 mm in 150 days or 0.4133 mm day^{-1}. Cohort-specific daily growth rates, elevations, and coincidentals were similar among sampling years [F (5, 11) = 0.3818, P = 0.4486]; [F (5, 16) = 1.9843, P = 0.1505]; [F (10, 11) = 0.9913, P = 0.3586], respectively. The mean daily growth rate ranged from 1.75 in 1991 to 1.97 mm in 1992 ($\bar{x}$ = 1.87 mm, S.D. ± 0.09). Compensating for the masking effect of recruitment (i.e., influx of small individuals) on growth rates, changes in growth rate was best (i.e., goodness of fit) described by an exponential regression having the formula: SL = 18.81 $^{0.2555}$ $^{(age)}$; r^2 = 0.9576 (Fig. 4). If the exponential trajectory rate was maintained over 365 days, ladyfish would reach a standard length of 403.6 mm corresponding to an estimated growth rate of 1.10 mm day^{-1}. The corrected exponential growth equation yielded a size-at-age 1 of 332.2 mm SL corresponding to an estimated growth rate of 0.9101 mm day^{-1}.

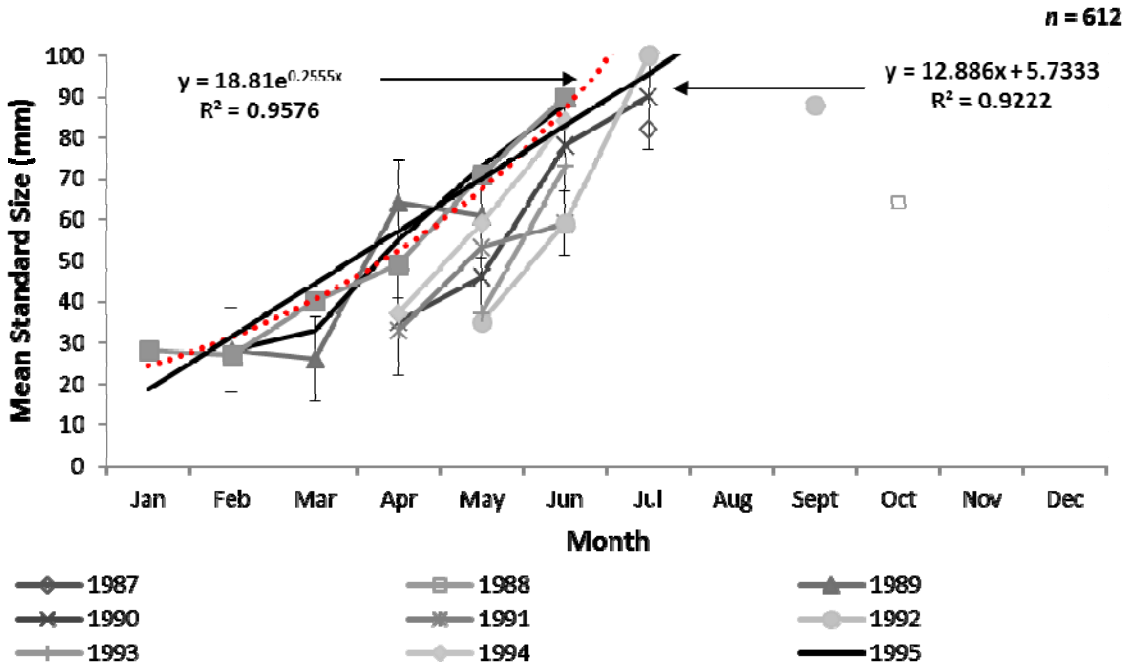

Fig 4: Annual age and growth curves of juvenile ladyfish (*Elops* sp) in Tampa Bay derived by the monthly geometric mean standard length (mm) on capture date. For comparison, the dash (exponential) and solid (linear) lines depict the mean regression trend between mean standard length (mm) and age (days).

Estimating juvenile ladyfish growth in the Little Manatee River was problematic due to the continual recruitment of small individuals. It was also problematic because of the variation in estimated growth among sampling years. To compensate for the influx of small recruits in the Little Manatee River, growth evaluations were limited to catches occurring from April to June (i.e., recruitment period). Because of limited and inconsistent data, the monthly instantaneous growth coefficient ranged from - 1.0741 in 1988 to 0.4745 in 1989. Absolute growth ranged from 0.70 in 1988 to 0.95 mm day^{-1} in 1989. On average, the absolute growth rate was 30 mm in 60 days or 0.5 mm day^{-1}. Cohort-specific daily growth rates, elevations, and coincidentals were similar among sampling years [F (2, 5) = 2.0356, P = 0.2356]; [F (2, 7) = 0.7291, P = 0.3434]; [F (4, 5) = 1.4902, P = 0.2868], respectively. Cohort-specific growth rates ranged from 1.6817 in 1988 to 1.9425 mm day^{-1} in 1989 ($\bar{x}$ = 1.7964 mm day^{-1}, S.D. ± 0.1331 mm day^{-1}). Overall growth was best (i.e., goodness of fit) described by an exponential regression having the formula: SL = 10.028 $^{0.3031}$ $^{(age)}$; r^2 = 0.8758 (Fig. 5). If the exponential trajectory rate was maintained over 365 days, ladyfish would attain a size of 380.9 mm SL corresponding to an estimated growth rate of 1.04 mm day^{-1}. The corrected exponential growth equation yielded a size-at-age 1 of 141.7 mm SL corresponding to an estimated growth rate of 0.3882 mm day^{-1}.

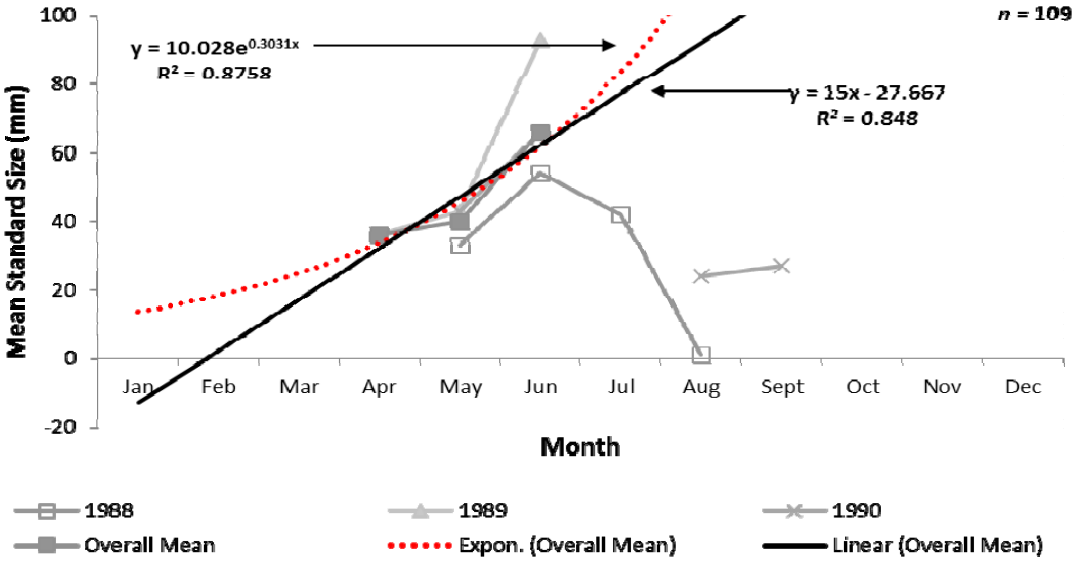

Fig 5: Annual age and growth curves of juvenile ladyfish (*Elops* sp) in the Little Manatee River derived by the monthly geometric mean standard length (mm) on capture date. For comparison, the dash (exponential) and solid (linear) lines depict the mean regression trend between mean standard length (mm) and age (days).

3.2.2. Direct method: Captive rearing

3.2.2.1. Behavioral Observations

Rearing juvenile ladyfish was problematic due to the selective feeding and cannibalistic behavior; however, the ability to assess growth in a controlled setting was largely successful (30−40% survival rate). Visual observations revealed that food-items were always consumed headfirst and ladyfish swallowed one or two prey fish (i.e., Gulf menhaden or tidewater silversides) whole per feeding session. Visual observations also showed that if the food-item was too large, then juvenile ladyfish would only make one or two attempts to swallow the food item before losing interest. In addition, visual observations showed ladyfish would abandon pursuit of a food-item if it drifted to the bottom of the tank before an individual attempted to swallow it; ladyfish did not feed off the bottom of the tank. The time required to "train" ladyfish to feed in the tank was found to be important factor in rearing specimens. Observations found that the time required for ladyfish to become familiar with feeding in the tank and prevent cannibalistic behavior was only between 1 and 2 days. Training consisted of dropping food-items in front of, and as close as possible to, an individual ladyfish without hitting them until they fed. Based on observations, ladyfish were attracted to movement (i.e., falling food-items); ladyfish used their large eyes and swift swimming movements to feed. In general, ladyfish were selective feeders, but were reasonably trainable.

3.2.2.2. Growth

Juvenile ladyfish growth was allometric (i.e., b > 3) and the morphometric conversion between weight and length was best described by power regression [$W = 0.000004\ (SL)^{3.2055}$; $r^2 = 0.9957$; $n = 29$; Fig. 6], and the length-length conversion was described by linear regression [$TL = 1.2914\ (SL) - 2.7785$; $r^2 = 0.9988$; $n = 29$; Fig. 7].

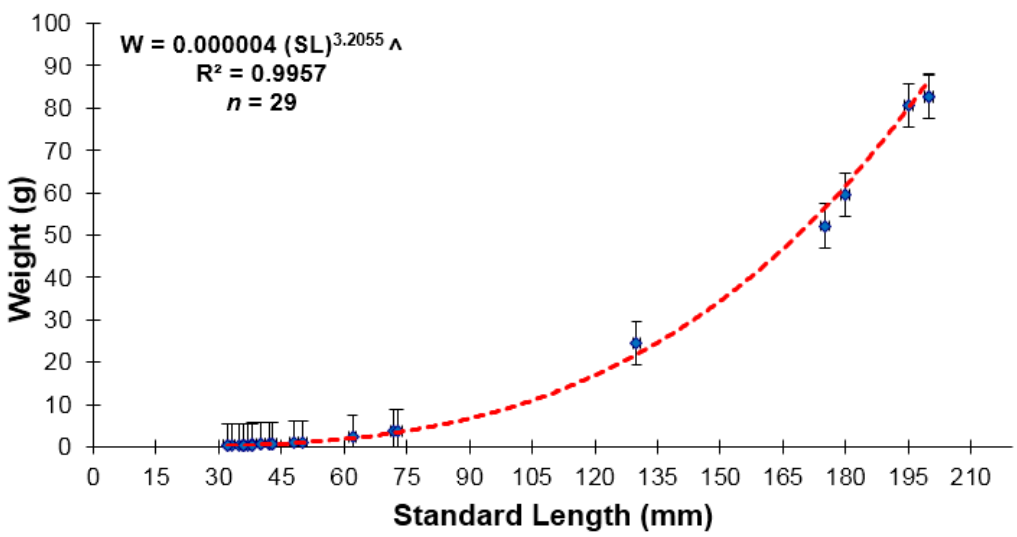

Fig 6: The association between standard length (mm) and weight (g) for juvenile ladyfish (*Elops* sp) in Tampa Bay, Florida (USA). The dash line depicts the power regression and the vertical bars represent standard error (± 1 S.E). *n* = the number of ladyfish measured.

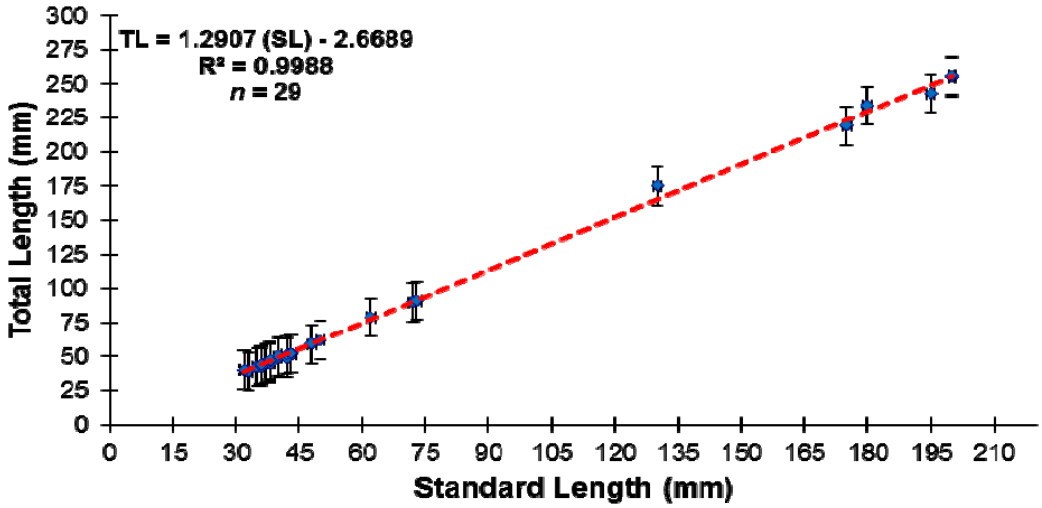

Fig 7: The association between standard length (mm) and total length (mm) for juvenile ladyfish (*Elops* sp) in Tampa Bay, Florida (USA). The dash line depicts the linear regression and the vertical bars represent standard error (± 1 S.E). *n* = the number of ladyfish measured.

To validate age and growth, an attempt was made to estimate otolith daily ring formation. Following the procedures described by Morales-Nin [32], otoliths were dissected, cleaned, and embedded in resin block. To reveal daily rings, otoliths were then cross-sectioned with a low speed diamond-blade saw and polished with various sandpaper grits. In addition, a few otoliths were individually mounted onto glass slides and polished. Despite these labor intensive efforts, thin-sections were fragile, difficult to polish, and unreadable (n = 10). Unfortunately, during the polishing process, every nucleus and corresponding otolith edge was over-polished, and eventually fractured.

Although age determination via otolith analysis proved unsuccessful, ladyfish age and growth estimates were successfully validated by directly measuring growth through captive rearing. In total, 39 ladyfish were reared in two separate tanks over a 110 day period. Over the duration of the experiment, ladyfish grew 75.6 mm SL (S.D. ± 14.5 mm; n = 25) in tank 1 and 46.7 mm SL (S.D. ± 10.6 mm; n = 14) in tank 2. Pooling the data, the overall mean growth was 61.15 mm over 110 days or 0.5559 mm day^{-1} (n = 39). Mean ladyfish size by the end of the experiment was 80.0 mm SL (S.D. ± 26.4 mm) in tank 1 and 73.8 mm SL (S.D. ± 16.9 mm) in tank 2. An unequal variance Student t-test showed the difference in mean size between tanks was weakly similar [t (168.3) = 1.98, P = 0.049]. Nonetheless, cohort-specific daily growth rates, elevations, and coincidentals were statistically similar between tanks [F (1, 13) = 4.2292, P = 0.0644]; [F (1, 14) = 1.0862, P = 0.2820]; [F (2, 13) = 2.7893, P = 0.0989], respectively. The mean ladyfish growth rate for tank 1 and tank 2 was 0.6872 and 0.4245 mm day^{-1}, respectively; growth rates were similar [t (37) = 6.54, P < 0.001]. Overall, the mean juvenile ladyfish growth rate was 0.5558 mm day^{-1}. Examination of the linear and nonlinear models (coefficient of determination value) indicated that growth was better described by linear regression (Fig. 8).

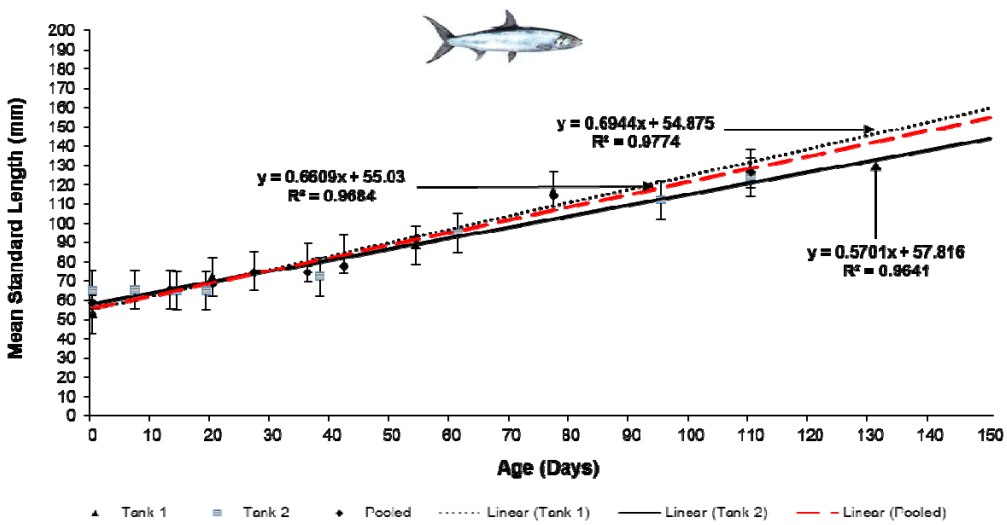

Fig 8: Somatic growth of juvenile ladyfish (*Elops* sp) in captivity (Tank 1 [n = 25]; Tank 2 [n = 14]). The dash and solid lines depict the association between mean standard size (mm) and age (days in captivity) by grow-out tank. The solid and dash lines depict the linear regression and the vertical bars represent standard error (± 1 S.E). *n* = the number of ladyfish reared.

Mean standard length regressed across age (days in captivity) showed that linear regression formulas best described growth in tank 1 (SL = 0.6944 [age] + 54.875; r^2 = 0.9774; n = 25) and in tank 2 (SL = 0.5701 [age] + 57.816; r^2 = 0.9641; n = 14). The mean ladyfish growth (data pooled) was likewise best (i.e., goodness of fit) described by a linear regression having the formula: SL = 0.6609 (age) + 55.69; r^2 = 0.9684; n = 39. If the linear trajectory rate was maintained over 365 days, then ladyfish would attain a standard length of 296.9 mm corresponding to an estimated growth rate of 0.8134 mm day^{-1}. Pooling the data, age-specific growth was between 0.04385 and 0.4994% (mm SL day^{-1}) at captivity age 30 to 40 days. However, growth increased from 0.0741 to 0.0876% (mm SL day^{-1}) at captivity age 41 to 80 day and then decreased to 0.0202% (mm SL day^{-1}) from 81 to 110 days.

The estimates of growth derived through captive rearing were comparable to those derived from LFA. Overall, growth rates were similar between ageing methods [F (1, 39) = 0.3241, P = 0.3552]; however, elevations and coincidentals were significantly different [F (1, 39) = 73.2, P = < 0.001]; [F (2, 39) = 36.1, P < 0.001], respectively. In general, there was good correspondence between the two approaches with LFA predicting a slightly faster growth rate than the direct method when an exponential regression model was applied to the data. However, if growth was modeled by linear regression, then the direct method (all data pooled) predicted a faster (35%) growth rate (**Fig. 9**). Using linear regression, growth predicted from the direct method was explained by SL = 0.6609 (age) + 55.691, while LFA was explained better by SL = 0.4295 (age) + 18.619. If both trajectories were extrapolated to 365 days, then ladyfish would attain a standard length that was 41% longer under the direct method. Using linear regression, ladyfish would attain 296.9 mm SL under the direct method and 175 mm SL under the LFA method by age-1. However, if ladyfish growth in Tampa Bay was modeled using length-frequency data collections occurring only from April to July (where mean sizes were similar between monthly collections and reared specimens), then respective growth models for each method was more consistent. Using this approach, the progression of growth was explained by the following linear regression: SL = 0.5733 (age) + 2.3 (r^2 = 0.9751) and the projected growth at age-1 would be 212 mm SL; 29% smaller than captive rearing estimates.

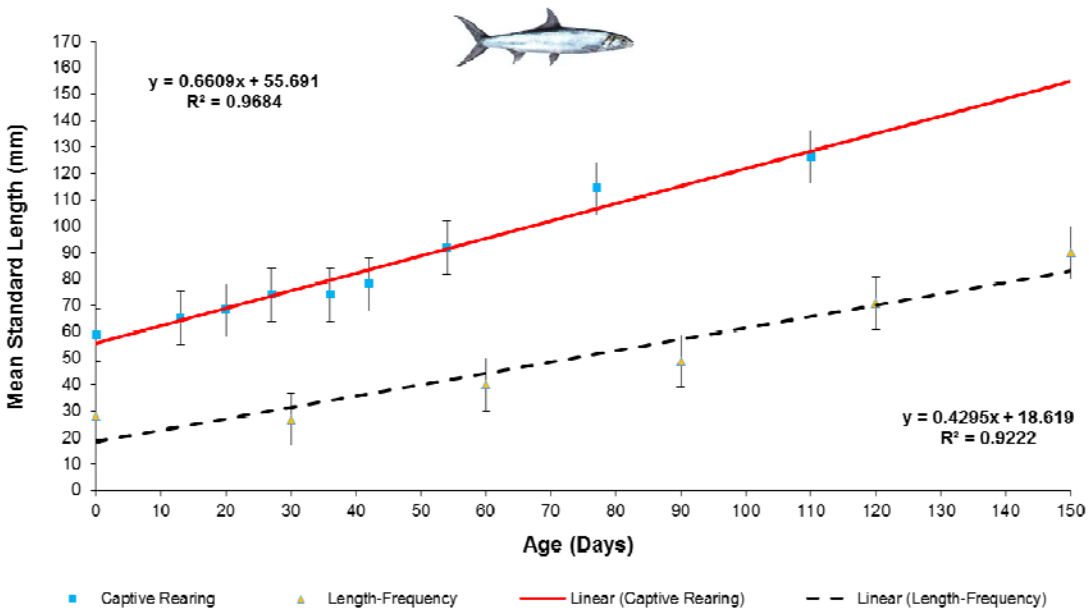

Fig 9: Age and growth curve comparison between the indirect (length-frequency analysis) and direct (captive rearing; n = 39) methods for juvenile ladyfish (*Elops* sp) in Tampa Bay (USA). The dash and solid lines depict the association between mean standard size (mm) and age (days) by method. Age (days) for length-frequency represents the monthly geometric mean standard length (mm) on capture date, while age (days) for captive rearing represents the mean standard length (mm) by the number of days in captivity. The solid and dash lines depict the linear regression and the vertical bars represent standard error (± 1 S.E).

Captive rearing information, together with LFA data, suggest that juvenile ladyfish size at age-1 in Tampa Bay waters is between 212 and 297 mm SL. Comparing percent daily growth (percent of length) between both methods showed that the direct method yielded a slightly faster growth rate for the first 90 days, but growth was faster for individuals collected from the natural environment after 90 days.

4. Discussion

Age and growth estimates are essential for managing recreational and commercial fisheries. Most researchers age fish by sectioning hard parts (e.g., otoliths, fin rays, and bones) and counting annuli rings. Once annuli have been read and interpreted, researchers apply regression analysis to estimate growth over time. Unfortunately, estimating age and growth for many species using this technique is labor intensive, time consuming, and costly. In general, growth for most fish can be described as a series of multiple sigmoid or linear growth curves; however, growth over a species' lifespan is difficult to model using a linear approach [33]. Depending on the life-stage, fish growth is usually influenced by various environmental or biological factors, including recruitment, emigration, mortality, diet, and temperature [34]. Consequently, growth rates are highly variable from one year to the next. Age and growth estimates have been derived for various economically and socially valuable species [5, 6, 35],

but few researchers have investigated lower valued species (e.g., ladyfish).

In this study, age and growth was estimated for juvenile ladyfish using two methods: LFA and captive rearing. Laslett *et al*. [36] stated that "valuable information about the growth of fish can often be extracted from length data collected regularly over an extended period." However, evaluating changes in fish length or weight through time can only be used to estimate growth under certain conditions [36, 37]. Growth estimated from length-frequency data is accurate and comparable to validated ageing methods only when biological and environmental factors (e.g., temperature, recruitment, and habitat) are stable and predictable. In general, growth estimated from length-frequency progressions is successfully applied on species that display a short recruitment period and have fast growth rates [37].

The progression of ladyfish cohort growth was predictable and modeled in this study, but various field sampling, environmental, and biological factors were considered in these analyses; applying length-frequency data to estimate fish growth is not always straightforward [36]. In fact, Iversen [38] stated there are various considerations for using length-frequency methods to estimate age, such as the following: (1) length-frequency should be used for fishes with a relatively short spawning season; (2) the technique requires a large sample size, with a wide size range; and (3) age-at-first-capture should be known so you can detect the age of the first modal group. In this study, all of these criteria were considered and adjusted accordingly, which helped standardize the analytical process and obtain better results. Though realistic age and growth estimates were calculated for juvenile ladyfish using length-frequency data, differences in ladyfish recruitment among sampling years and locations were evident in this study. As such, the interpretation and discussion of these results are reported with some reservation, especially since there is evidence of two species of ladyfish occurring in Tampa Bay [11-13]. Also, field sampling could have bias the data. For example, since FWC did not conduct any nighttime field sampling, it is possible that the data could have been bias because of gear avoidance (daytime sampling), which in turn could have affected growth predictions under the LFA approach [39]. Although this was possible, validation of the age and growth estimates through captive rearing showed that the estimates derived by LFA were probably realistic. The data also showed that ladyfish recruitment was variable from year to year. In some years, recruitment lasted longer; thus, the analyses had to be adjusted accordingly. Laslett *et al*. [36] stated that variability in annual growth needs to be considered during data analyses since environmental conditions might be more favorable in some years than others. Nonetheless, regression analysis showed there was no significant difference in growth among sampling years, so growth was easily compared over the time-series.

Growth rates for fish can sometimes change from one year to the next given the fluctuating environmental conditions. As such, numerous researchers have reported the effect of environmental conditions on growth for a variety of species (e.g., spot [*Leiostomus xanthurus*]: [34]; Greater amberjack [*Seriola dumerili*]: [40]; bonefish: [41]. Until now, only McBride *et al*. [42] have previously investigated ladyfish age and growth in any detail. Although McBride *et al*. [42] indicated that ladyfish growth might be affected by salinity or temperature; they did not consider these or any other environmental factors in their analyses. Interestingly, they reported that ladyfish reached similar age-1 sizes in Tampa Bay (200−300 mm SL) and the Indian River Lagoon (250−270 mm SL) even though these regions have somewhat distinctly different environmental conditions. Overall, the findings by McBride *et al*. [42] suggested that ladyfish could tolerate fluctuating environmental conditions without affecting growth; growth was less likely to be affected by minor changes in water temperature or other environmental conditions.

Similarly, this present study did not evaluate the effects of environmental conditions on ladyfish growth, which could explain some of the variability in annual monthly size. Regardless, juvenile ladyfish growth was reasonably modeled using length-frequency data. The findings confirm the applicability of length-frequency data for estimating juvenile ladyfish annual growth within Tampa Bay. Based on these findings, the projected length for age-1 ladyfish using LFA data was around 404 mm SL. However, when growth rates were corrected (y-intercept) to compensate for the unrealistic smaller predicted recruitment size and larger projected age-1 size, age-1 size was around 332 mm SL. Overall, this present study derived a different estimated ladyfish age-1 size than the size derived by McBride *et al*. [42], which demonstrates how small differences in data treatment can sometimes affect the outcome. For instance, McBride *et al*. [42] chose to evaluate ladyfish length-frequency data collected with a variety of gears and larger individuals since they were interested in all life-stages. In this study, I elected to only evaluate ladyfish collected with a center-bag seine since the objective was to investigate juvenile ladyfish (< 100 mm SL). It should be noted that the objectives for each study were slightly different, which explains the reason why the data was evaluated differently.

The findings demonstrated that growth models were data sensitive (i.e., changes in the slope of the growth curve); however, monthly length-frequency data could be still be used to describe realistic juvenile ladyfish growth rates. This study also reiterates how important it is to use an extended time-series when estimating growth from length-frequency data. Although it is difficult to speculate how long a time-series is necessary for a given species since it depends on local variability, it is probable that researchers should consider evaluating at least a 2−4 year time-series to resolve inter-annual trends. Furthermore, researchers must also consider the geographical location, sampling gear, habitat (e.g., beach profile, depth, and bottom sediment), species, size-class, and the number of replicates (hauls) when designing an experiment, especially when the objective is to understand recruitment, age, and growth.

To the author's knowledge, other than two previous studies [14, 29], this study is the first to report juvenile ladyfish age and growth using an extended captive rearing approach. In general, captive rearing was challenging because juvenile ladyfish were cannibalistic, choosy eaters, and sensitive to handling. Despite these traits and a small sample size (n = 39), biologically realistic growth rates were successfully derived from captive rearing. Overall, there was a strong agreement between captive rearing and length-frequency derived age-1 size estimates, which provides an interesting insight into juvenile ladyfish growth in Tampa Bay. The predicted age-1 size obtained through captive rearing was similar to that observed by Gehringer [14] and Alikunhi and Rao [29]. Although my findings were relatively similar,

ladyfish specimens for the previous two studies were collected from distinctly different regions and oceans. The morphometric regression association (weight to length) in this study was similar to that reported for ladyfish in other geographical locations [30, 43]. However, the SL to TL association in my study predicted a greater conversion length than reported by McBride *et al*. [42]. Although both association models (SL-TL) showed high correlation coefficient values, each study used a different size range, which explains the small difference in the conversion factor. McBride *et al*. [42] derived their model using 75 specimens ranging in length from 39 to 475 mm SL, whereas I calculated the SL-TL conversion using 29 specimens ranging in length from 32 to 200 mm SL. The difference in predicted length might be explained because growth [rate] typically declines with age [37] and morphometric growth rates vary between juveniles and adults. I believe that the McBride *et al*. [42] model predicted a slightly smaller (TL) individual than my model because their model was based on much larger individuals (i.e., adults) having much slower growth rates than juveniles. The morphometric weight-length model from this study was similar to the Sekavec [30] model for juvenile ladyfish collected in Louisiana waters; the size range of ladyfish specimens was similar between both studies.

Estimates of juvenile ladyfish age and growth in Tampa Bay waters using LFA and captive rearing proved to be satisfactory approach. The association between juvenile ladyfish size and age was best described by power regression for length-frequency data, whereas linear regression best fit the captive rearing data. It is difficult to understand for certainty why there were some differences in growth rates between the two approaches since both growth methods evaluated ladyfish of similar sizes and the duration (110 days) of the experiment was similar to that of field data (90−120 days). Nonetheless, no statistical differences were detected between ageing methods. There were small discrepancies in derived growth rates, but this study proved that indirect and direct growth methods can yield reliable biological growth rate predictors that are comparable to other published studies. Despite these conclusive findings, I suspect that ladyfish in the wild are able to reach a much larger age-1 size than was estimated in this study since ladyfish in the wild are not limited by feeding schedules, ration size, or other compounding factors. This notion is supported by the fact that ladyfish exhibited a slower growth rate in captivity (% of length per day) after 90 days than was evidenced by field-collected individuals. Again, one possible explanation for the difference in growth was that captive reared ladyfish were only fed twice per day; this feeding regimen would have certainly had an impact on growth after 90 days given the diet of most fish changes through ontogeny [44]. Interestingly, I noticed that captive reared specimens did not feed as aggressively as they did when they were smaller and younger; suggesting their diet changes with size. Perhaps ladyfish need to feed on live prey as they grow? If so, then this would offer a potential explanation as to why growth for field-collected ladyfish was better represented by the exponential rather than the linear model; the linear model better described growth for captive reared specimens.

Few researchers have reported age and growth estimates for ladyfish, so it is difficult to compare my findings to others. Even so, growth estimates derived by this study were relatively similar to those reported for ladyfish in other geographical locations. In Cuba, Carles [45] estimated ladyfish growth from scale annuli as 130 mm SL (age-1), 195 mm SL (age-2), and 247 mm SL (age-3). Blake and Blake [46] reported ladyfish (*E. affinis*) growth from Mexican waters by scale interpretation as linear (length = 57.4 + 129.2 [age]); assuming scale ring counts reflect age, they estimated ladyfish (*E. affinis*) can reach 103 mm (age-1), 161 mm (age-2), 220 mm (age-3), and 282 mm (age-4). In Nigeria (South Africa), Ugwumba [9] reported, through modal LFA, that age-1 ladyfish (*E. lacerta*) can reach 58−153 mm SL and 62−151 mm SL at two distinct lagoons. Ugwumba [9] estimated that age-1, age-2, and age-3 ladyfish reached 152, 242−255, and 351 mm SL, respectively. Ladyfish (*E. lacerta*) growth was nearly isometric and growth rates were estimated as linear, which was different than the findings in my study (exponential growth curve). Different species of ladyfish seem to grow a little differently, but it seems reasonable to infer that ladyfish (*Elops* sp) found in the western North Atlantic Ocean [42] grow faster than ladyfish (e.g., *E. affinis* and *E. lacerta*) found in other geographical regions.

5. Conclusions

Fishery managers rely upon having age and growth estimates for making informed decisions. As we progress toward ecosystem-based management, fishery managers will need life-history information for other species considered less economically or socially valuable. This study's findings offer insight into juvenile ladyfish growth, and demonstrate the usefulness of two cost-effective methods for estimating age and growth. Additionally, these findings show that growth can be reasonably modeled through indirect methods (i.e., length-frequency progression), but results should be viewed with caution, particularly if researchers do not have a thorough understanding of the data. Understanding the factors that impact year-class strength is a fundamental problem in fishery research [47]. Annual variability in mean length during the recruitment period (within and among locations) can sometimes skew results. Therefore, it is recommended that future studies attempt to correlate environmental or habitat factors with growth. These results demonstrated that derived growth rates were sensitive to analyses, so it is recommended that researchers also use long-term datasets when attempting to estimate growth from alternative methods. As single-species management evolves toward multi-species or ecosystem management, it is recommended that future age and growth studies pursue the effects of interactions among species (i.e., predator-prey interactions) on growth even if these species are considered less economically important.

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