



Age, differential growth and mortality rates in unexploited populations of Florida gar, an apex predator in the Florida Everglades

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Abstract Florida gar, *Lepisosteus platyrhincus* DeKay, were sampled in two canal systems in south Florida during 2000–2001 to estimate age, growth and mortality as part of the Everglades ecosystem-restoration effort. Tamiami (C-4) and L-31W canal systems had direct connections to natural wetlands of the Everglades and harboured large Florida gar populations. Of 476 fish aged, maximum ages were 19 and 10 years for females and males, respectively. Maximum sizes were also larger for females compared with males (817 vs 602 mm total length). Overall, female Florida gar from both Tamiami and L-31W were larger at age than males from L-31W that, in turn, were larger at any given age than males from Tamiami. Females also had lower rates of annual mortality ($Z = 0.21$) than males from L-31W ($Z = 0.31$) or males from Tamiami ($Z = 0.54$). As a large and long-lived apex predator in the Everglades, Florida gar may structure lower trophic levels. Regional- and sex-specific population parameters for Florida gar will contribute to the simulation models designed to evaluate Everglades restoration alternatives.

KEYWORDS: age validation, branchiostegal ray, *Lepisosteus platyrhincus*, sexual dimorphism.

Introduction

Population dynamics of fishes, including traits such as age and growth, are essential to understand responses to altered abiotic and biotic regimes. Seasonal hydrological fluctuations in the Everglades of south Florida, USA strongly influence the population dynamics of wetland fish communities (Loftus & Kushlan 1987; Trexler, Loftus & Perry 2005). The Everglades is the

largest wetland in the United States, covering approximately 6200 km² (Sutula, Perez, Reyes, Childers, Davis, Day, Rudnick & Sklar 2003). Because of its low and flat landscape, relatively small differences in mean water level amplify into large differences in amount of wetted area and flooding duration. Such conditions create a close but poorly understood relationship between hydrology and fish populations. Over the last century, human modifications to the

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south Florida landscape, especially the excavation of vast networks of interconnected drainage canals, have greatly altered the region's hydrology. One result has been a change in the duration that Everglade wetlands are covered by water, an effect that has, in turn, changed the structure of local fish communities (Trexler et al. 2005).

In an attempt to reverse human-induced changes in the region's hydrology, major ecosystem restoration is underway (DeAngelis, Trexler & Loftus 2005). One goal of the restoration effort is recovery of historic fish community and abundance patterns (Ogden, Davis & Brandt 2003). Consequently, fishes are considered key indicators for measuring restoration success, especially because of their roles as prey and predators in wetland food webs (Gunderson & Loftus 1993; Trexler, Loftus, Jordan, Chick, Kandl, McElroy & Bass 2001; Williams & Trexler 2006). However, much of the population and life-history information incorporated into existing simulation models has been drawn from other ecosystems and related species because local empirical data are lacking. This shortage of basic life-history information is a concern because fish growth and mortality data are needed to parameterise ecological models used to compare and predict the effects of Everglades restoration under different management alternatives.

One of the most widespread and abundant large fish in the Everglades is the Florida gar, *Lepisosteus platyrhincus* DeKay (Hunt 1953; Loftus & Kushlan 1987). It is considered an apex or top-level predator in the aquatic ecosystems of the Everglades (Gunderson & Loftus 1993; Loftus 2000), where it consumes a wide variety of fishes, insects, amphibians and crustaceans (Hunt 1953; Holloway 1954; Crumpton 1971; Loftus 2000). Despite its recognition as an apex predator and its overall ecological importance within the Everglades ecosystem, there are few published studies on the biology and life history of Florida gar. In particular, there is no information about growth and mortality of Florida gar. As these life-history parameters rely on accurate age estimates, it is also important that the ageing method for Florida gar be validated for accuracy and its precision estimated. The goals of this study were, therefore, to determine the age of Florida gar using an accurate and precise ageing method, to model comparative growth between females and males and to estimate mortality rates.

Methods

Florida gar were collected from reaches of two major Everglades canal systems: (1) within the 137-km long

Tamiami Canal (C-4) (near 25°46' N and 80°42' W); and (2) within the 8-km long Canal L-31W (near 25°23' N and 80°34' W), which is a major part of the extensive L-31N Canal system. The two canals were excavated through the interior of southern Everglades wetlands, the Tamiami in the 1920s and L-31W ca. 1971, and are similar in width (20–30 m), depth (6–8 m) and cross-section (box cut) to other major canals in the Everglades. Both canals are directly connected seasonally to adjacent freshwater marshes.

Florida gar were sampled from both canal systems in January, April, June, July and October 2000, and in January 2001. Fish were collected during daytime by boat electric fishing using Smith-Root® GPP 9.0 (Vancouver, WA, USA), 30–60 Hz, 250–500 V pulsed-DC, with a power output of ~1500 W. On each sampling date, a 1-km reach of canal was electric fished (totalling 4 km in each canal over the study period). Fish were measured for total length (TL, mm), weighed, sexed by macroscopic examination of gonads and otoliths and branchiostegal rays were removed for ageing.

Ferrara (2001) detected presumptive annuli in whole views of otoliths from spotted gar, *Lepisosteus oculatus* Winchell, longnose gar, *Lepisosteus osseus* L., and alligator gar, *Atractosteus spatula* (Lacepède). However, patterns potentially useful for ageing were not visible in whole or sectioned otoliths of Florida gar collected in this study. Therefore, branchiostegal rays, which have been used to age a variety of gar species (Netsch & Witt 1962; Redmond 1964; Johnson & Noltie 1997; Love 2004), were used in this study.

Branchiostegal rays were removed and cleaned by immersing them in simmering water (~95 °C), using forceps to remove any remaining skin (as opposed to boiling them in a weak solution of potassium hydroxide, known to degrade the most recent growth at the edge of the structure) (Netsch & Witt 1962). Cleaned rays were then stored dry until aged. For ageing, both branchiostegal rays were immersed whole in freshwater and viewed using transmitted light with a stereomicroscope at 5–50× magnification. Opaque annuli on the surface of the rays were counted to age gar (Bulkley 1960; Netsch & Witt 1962). Incomplete opaque bands or 'checks' identified following the criteria of Bulkley (1960) and Netsch & Witt (1962) were not counted as annuli. Rays that were entirely opaque or translucent, or eroded and broken along the margins, were considered unreadable. The amount of translucent growth on the edge of the ray relative to the previously completed growth increment was also coded and ranged from 0 (no growth) to 3 (> 2/3 of the previously

completed increment). Age was estimated by assigning an age (annulus) class based on a birthdate of 1 January (Chilton & Beamish 1982), taking into account the amount of translucent growth at the margin of the ray to ensure that fish in the same cohort would be assigned the same age (Murie & Parkyn 2002, 2005).

A subsample of 100 rays was aged independently by an experienced second reader to estimate precision of ages between readers to determine the reliability in using branchiostegal rays to age Florida gar. Ageing precision was estimated by calculating the percent agreement between two independent readers based on the average percent error (APE) (Chilton & Beamish 1982) and the coefficient of variation (CV) (Kimura & Lyons 1991). The concordance correlation coefficient (Lin 1989, 2000; Murie & Parkyn 2005) was also estimated to determine the deviation of paired ages from a 1:1 relationship.

The potential existed for fish to deposit more than one annulus each year in the subtropical temperature and rainfall regimes of the Everglades (Brothers 1979; Bwanika, Murie & Chapman 2007). It was therefore necessary to validate the assumption that Florida gar in south Florida deposit only one annulus in a 12-month period. Timing and periodicity of annulus formation in branchiostegal rays were examined by measuring the relative amount of marginal increment (growth) in the rays over the year, calculated as the index of completion (Tanaka, Mugiya & Yamada 1981; Murie & Parkyn 2005): $C = W_n/W_{n-1}$, where W_n = width of the marginal increment and W_{n-1} = width of previously complete increment. All distances were measured along the median curvature of the ray (Fig. 1), following techniques used by Netsch & Witt (1962) as modified by Redmond (1964). The index of completion was plotted as a function of the month of collection for one complete year for fish aged ≥ 1 year and when sample size was ≥ 5 . A single minimum in the measured index of completion would suggest the formation of one annulus each year, whereas two minima would indicate deposition of two annuli per year.

Length frequencies of Florida gar between genders and collection sites were compared using a Kolmogorov–Smirnov D statistic (Ferrara 2001). Weight–length relationships were determined for logarithmically transformed weight and length data, and differences between genders and collection sites were tested by ANCOVA ($\alpha = 0.05$).

Back-calculated length at the most recently formed annulus was determined using the body proportional equation of Francis (1990):

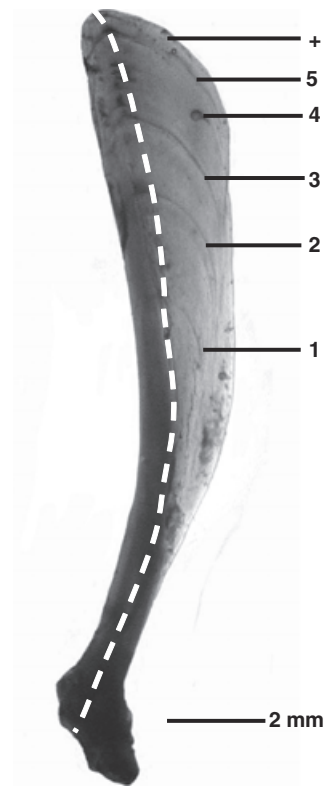


Figure 1. Branchiostegal ray of a 5-year-old Florida gar showing five opaque annuli with a translucent growth zone at the ray margin. Branchiostegal ray length was measured on the medial curvature of the ray (dashed line). Scale bar = 2 mm.

$$L_A = [(a + b \cdot R_A)/(a + b \cdot R_C)]L_C$$

where L_A = back-calculated length to annulus A, a = intercept from the linear regression of total length as a function of branchiostegal ray length, b = slope from the linear regression of total length as a function of branchiostegal ray length, R_A = branchiostegal ray length to annulus A, R_C = branchiostegal ray length at time of capture and L_C = fish total length at time of capture. Differences among regressions of TL as a function of branchiostegal ray length were compared simultaneously among males and females from both canals using an ANCOVA and pooled if non-significant. Mean ($\pm 1SE$) back-calculated length at age was determined for the most recently formed annulus for all ages > 0 .

A von Bertalanffy growth equation (Beverton 1994) was used to model back-calculated TL at age using non-linear regression analysis (SAS Institute Inc., 1999):

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

where L_t is the back-calculated TL (mm) at time t (age, in years), L_∞ is the estimate of average maximum length (asymptotic length, mm), k is the growth coefficient and t_0 is the theoretical age (years) when fish length would be 0. Differences in von Bertalanffy growth curves between males and females from L-31W and Tamiami were determined using likelihood ratio tests (LRT) (Kimura 1980; Cerrato 1990; Haddon 2001).

Catch curves plotting the \log_e of the catch in numbers against age (Ricker 1975) were constructed separately for males and females from L-31W and Tamiami to estimate total mortality of Florida gar. Total instantaneous mortality (Z) was estimated by the slope of a linear regression fit to the descending right limb of the catch-curve (Ricker 1975). Regressions excluded fish in older age classes that were preceded by two consecutive zero frequencies (Williams, Davies, Mapstone & Russ 2003). Differences in Z between females and between males from L-31W and Tamiami were tested using ANCOVA (Zar 1996), and data were pooled when not significantly different. All statistical tests were conducted with $\alpha = 0.05$.

Results

Fish collections

In total, 253 and 223 Florida gar with sex-specific data and intact branchiostegal rays were collected from L-31W and Tamiami, respectively. Florida gar collected from L-31W ranged in size from 253–694 mm TL and all individuals > 557 mm were females (Fig. 2). In Tamiami, Florida gar ranged from 244–817 mm TL and all individuals > 453 mm were females. Length-frequency distributions of Florida gar from L-31W and Tamiami were significantly different for both females (Kolmogorov–Smirnov Test: $D = 0.367, P < 0.0001$) and males ($D = 0.409, P < 0.0001$) and were skewed towards smaller individuals in Tamiami.

Male and female Florida gar from L-31W and Tamiami did not differ significantly in their \log_{10} Weight (WT) vs \log_{10} TL relationship (ANCOVA: $F_{3,472} = 1.64$, slope $P = 0.18$, intercept $P = 0.12$). The pooled regression describing the relationship between weight and total length of Florida gar was $WT = 6.165 \times 10^{-7} TL^{3.313}$ ($r^2 = 0.98, n = 476, P < 0.01$).

Index of completion of marginal increment

A total of 438 branchiostegal rays was measured from fish > 0 years of age to calculate the index of

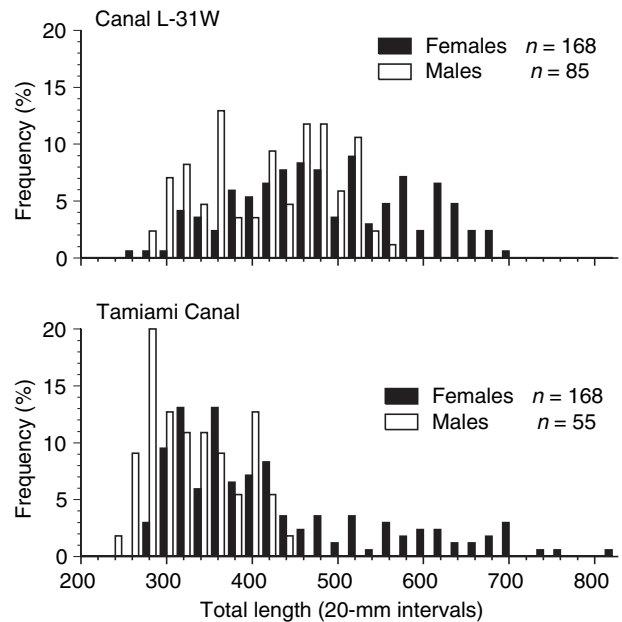


Figure 2. Length distributions of Florida gar collected from Canal L-31W and Tamiami Canal.

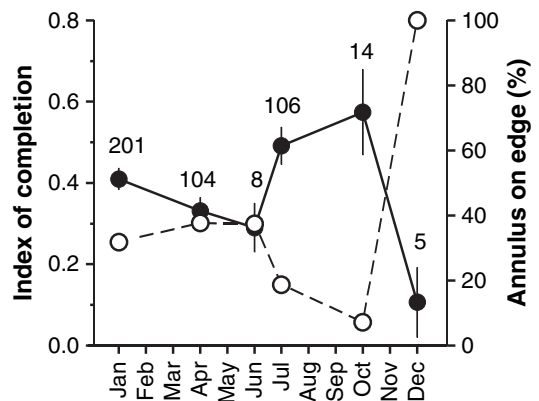


Figure 3. Marginal-increment analysis for Florida gar showing mean (\pm SE) index of completion (●) and percentage of branchiostegal rays with the annulus on the edge (○) in relation to month of collection. Number above filled symbols is the sample size.

completion to determine the periodicity in the marginal increment. The index of completion plotted over a 12-month period for all months was unimodal (Fig. 3), suggesting that gar were depositing only one annulus per year. The greatest marginal increment was apparent in Florida gar during July through October. The index of completion was lowest in December through June indicating that the opaque zone was initiated sometime around December and deposited throughout the December to June time period by

different individual fish. This observation was supported by the opaque zone appearing on the edge of the rays in the majority of fish during or just prior to December.

Age estimates

Of 476 branchiostegal rays aged from Florida gar, <2% ($n = 8$) were unreadable and excluded from analyses. Florida gar from L-31W ranged in age from 0 to 17 years for females and 0 to 10 years for males. Females collected from Tamiami ranged from 0 to 19 years of age and males from 0 to 5 years of age. Among 100 fish aged, 64% of two independent age readings were assigned the same age and 94% agreed within ± 1 annulus. All other readings differed by ± 2 or ± 3 years (6%). Average percent error (6.4%) and

CV (9.0%) were low, substantiating high precision in detecting annuli. Lin's concordance correlation (0.96) was also high, indicating that the difference between the two independent readings did not systematically increase with age.

Growth of Florida gar

The total length (TL)–branchiostegal ray length (RL) relationships did not differ between females and males from L-31W or Tamiami (ANCOVA: $F_{3,389} = 0.74$, slope $P = 0.30$, intercept $P = 0.41$). A pooled regression equation was, therefore, fitted to all data and used to back-calculate length at age for gar from both sites: $TL = 20.190 + 27.187RL$ ($r^2 = 0.92$, $P < 0.01$).

Growth of female and male Florida gar was similar for the first 2–3 years of age (Fig. 4). Based on von Bertalanffy growth models (Table 1), however, females were larger than males at ages >3 years (LRTs: $\chi^2 = 16.47$, d.f. = 3, $P < 0.01$ for L-31W; $\chi^2 = 21.78$, d.f. = 3, $P < 0.01$ for Tamiami). In addition, small-scale regional differences in growth were evident, with females from Tamiami larger at age than females from L-31W (LRT: $\chi^2 = 56.39$, d.f. = 3, $P < 0.01$) and males from L-31W larger at age than males from Tamiami (LRT: $\chi^2 = 28.34$, d.f. = 3, $P < 0.01$).

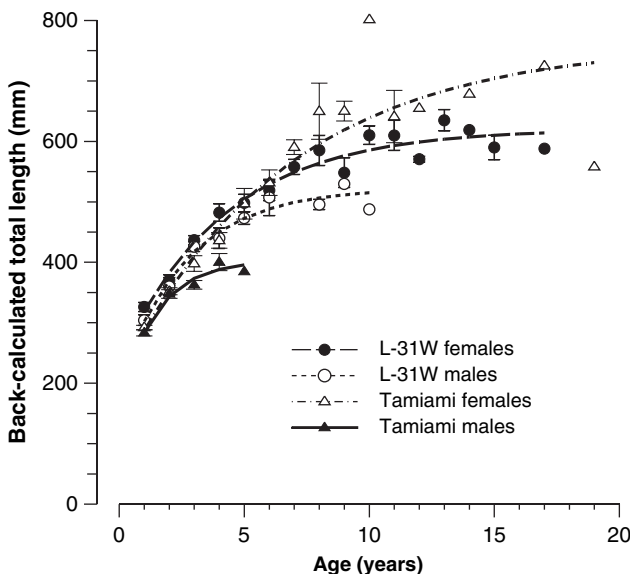


Figure 4. Mean back-calculated total length (\pm SE) at age for female and male gar from Canal L-31W and Tamiami Canal. Lines represent modelled von Bertalanffy growth curves.

Total mortality

Total mortality rates were not different for female Florida gar from Tamiami and L-31W (ANCOVA: $F_{1,23} = 0.02$, $P = 0.88$) and the pooled mortality estimate for females overall was 0.209 ($r^2 = 0.94$) (Fig. 5). By contrast, mortality rates for male Florida gar between the two canal systems were different (ANCOVA: $F_{1,6} = 7.66$, $P = 0.032$) and were estimated to be 0.314 ($r^2 = 0.80$) for L-31W and 0.54 ($r^2 = 0.94$) for Tamiami. Mortality rate for females (pooled) was significantly lower than the mortality rate of males from either L-31W (ANCOVA: $F_{1,12} = 5.84$, $P = 0.033$) or Tamiami (ANCOVA: $F_{1,7} = 19.01$, $P = 0.003$).

Table 1. Von Bertalanffy parameters (\pm 1SE) fitted to back-calculated total length (TL) at age for Florida gar from two canal systems in the Everglades of southern Florida

Site	Sex	L_{∞} (mm)	k	t_0 (years)	n	Range (years)
Canal L-31W	Male	523 \pm 24	0.37 \pm 0.09	-1.33 \pm 0.45	74	1–10
Canal L-31W	Female	620 \pm 17	0.24 \pm 0.03	-2.01 \pm 0.41	158	1–17
Tamiami Canal	Male	403 \pm 20	0.70 \pm 0.25	-0.74 \pm 0.50	45	1–5
Tamiami Canal	Female	762 \pm 38	0.15 \pm 0.02	-2.16 \pm 0.30	151	1–19

L_{∞} , asymptotic length; k , growth coefficient; t_0 , is the theoretical age when fish length is zero and range is the observed minimum and maximum ages.

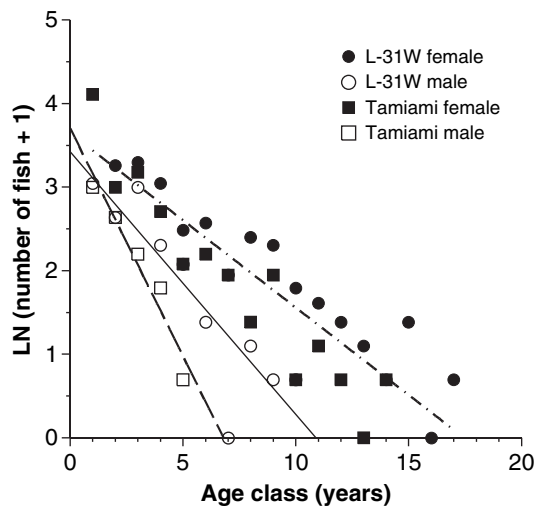


Figure 5. Catch curve regressions of $\ln(\text{catch} + 1)$ as a function of age of Florida gar. Solid line is for males from Canal L-31W ($r^2 = 0.80$), dashed line is for males from Tamiami Canal ($r^2 = 0.94$) and dot-dashed line is for females pooled from both sites ($r^2 = 0.83$).

Discussion

Florida gar from the Everglades were relatively long-lived and sexually dimorphic, and overall females were larger at age and older than males in both Tamiami and L-31W canal systems. Growth trajectories among females from Tamiami and L-31W, and males from L-31W diverged markedly after 4–5 yr, whereas growth of males from Tamiami was markedly less than all other gar after their first 2 yr. Sexual dimorphism, with females larger than males, has been previously noted in other gar species from the southeastern USA, including longnose gar (Netsch & Witt 1962), spotted gar (Redmond 1964; Love 2002, 2004) and alligator gar (Ferrara 2001).

As this was the first study on age and growth of Florida gar, conspecific comparisons were not possible. It was therefore hypothesised that age and growth of Florida gar would be most similar to its closest congener, the spotted gar (Suttkus 1963; Wiley 1976), especially as gene interchange appears to occur where the ranges of the two species meet (Lee, Gilbert, Hocutt, Jenkins, McAllister & Stauffer 1980). Back-calculated length at age of spotted gar (Redmond 1964; Ferrara 2001; assuming $t_0 = 0$) was similar to female Florida gar from the present study, but appeared to be greater than male Florida gar after 3–5 yr (Fig. 6). Redmond (1964) reported a maximum age of 8 yr for spotted gar from southeastern Missouri, USA, but noted that larger female spotted gar in his study could not be aged adequately; this was apparent from

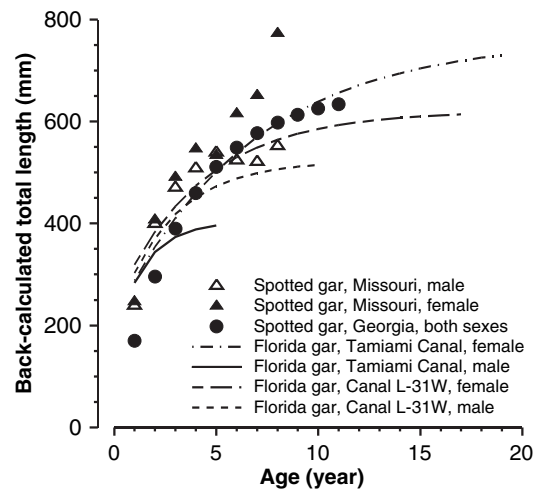


Figure 6. Total length at age for female and male Florida gar from Canal L-31W and Tamiami Canal in the Everglades and for spotted gar from Missouri (Redmond 1964) and Georgia (Ferrara 2001).

females in his study that were aged as 8 yr olds that were > 750 mm TL (see Fig. 6). Spotted gar from Lake Seminole, Georgia, USA and Lake Pontchartrain, Louisiana, USA also had maximum ages between 8 and 10 yr (Ferrara 2001; Love 2004). Although male Florida gar from L-31W had a similar maximum age, males from Tamiami were much younger. In contrast, female Florida gar attained a maximum age almost double that of spotted gar females (19 vs 10 yr).

In addition to growth, mortality rates are essential to understand the production dynamics of populations and their response to restoration alternatives. Mortality has not been estimated previously for Florida gar and these Everglades populations that receive little or no fishing exploitation (W.F. Loftus and J. Fury, personal communications), provide valuable opportunities to directly estimate natural mortality of a high trophic-level predator. Lower natural mortality for female gar than male gar, especially males from Tamiami, may occur for a variety of reasons. Females may have increased foraging success (Love 2002) and with faster growth rates may reduce their vulnerability to predators. Males may also be more active than females during courtship and spawning (e.g. as for spotted gar; Tyler & Granger 1984; Love 2004) and therefore exposed to a higher risk of predation.

Canal habitats are recent constructs within the Everglades landscape; the historic natural system had only small areas of deeper water, such as pits excavated by alligators, *Alligator mississippiensis* Daudin,

('alligator holes'), which provided refuge for fishes from dry-season conditions. Today, the extensive canal system offers many kilometres of continuous deep-water habitat for Florida gar (Loftus & Kushlan 1987; L. Nico, unpublished data). Both L-31W and Tamiami canal systems, as with other Everglades canals, were excavated for roadbed fill and drainage through natural wetlands and thereby allow large predators, such as Florida gar and alligators, to move between canals and adjacent marsh habitat. Wetlands have emergent vegetation, which provides both refuge and habitat for prey, ambush sites for predatory gar and egg-deposition sites for gar. This is in contrast with other canal systems (e.g. eastern reaches of Snake Creek Canal or C-9) that drain urban areas that have no adjacent wetland connection and very few Florida gar (L. Nico and W. Loftus, personal observations). Restoration plans call for some Everglades canals to be back-filled, thereby reducing canal habitat available to gar. If this reduction of deep-water canal habitats occurs simultaneously with the redistribution of water to restore sheet flow and rehydrate wetlands, it may enhance habitat connectivity and benefit gar populations. Future studies aimed at quantifying the effect of major environmental variables (such as water level and duration), as well as biotic variables (i.e. prey resources and intensity of predation), will be instrumental in providing a more comprehensive overview of the influences structuring the variable growth and mortality of this important, abundant and widely distributed apex predator in the Everglades.

Acknowledgments

Many individuals provided assistance with this project. We are especially grateful to G. R. Best, M. Brown, C. Diel, D. Elswick, P. George, G. Hill, H. Jelks, E. Leonard, R. Lewis, M. Perry and A. Torres. Others helping with field work included L. Albert, F. Aranzamendi, A. Benson, J. Curnutt, D. Doroshef, K. Fitzpatrick, N. Flavin, T. L. Fullbright, P. Fuller, G. Hogue, S. Howarter, J. Kline, A. Martin, M. Raley, E. Rolla, W. Starnes, R. Taylor, J. Williams and S. Vincent. S. Bostick assisted in formatting the manuscript. Funding and administration for this study was provided by G. Ronnie Best through the US Geological Survey's South Florida Place-based Science Program, the US Geological Survey-Florida Integrated Science Center and the Department of Fisheries and Aquatic Sciences, IFAS, University of Florida. Any use of trade, product or firm names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

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