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Bioenergetic Approach to Describing Gulf Sturgeon (*Acipenser oxyrinchus*) Growth in Two Florida Rivers

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Abstract: Bioenergetics models are commonly used by scientist and managers to describe energy uptake and metabolism of fish species. Much data is needed to inform these models and often species specific data is unavailable or difficult to acquire, such as in the case with Gulf of Mexico sturgeon. This study applied a new method, developed by Walters and Essington (this issue), to estimate bioenergetics parameters using field observations for Gulf sturgeon populations in the Apalachicola and Suwannee Rivers, Florida, U.S.A. Bioenergetics derived growth curves were compared to growth curves developed using traditional direct aging methods. We obtained bioenergetic parameter estimates for both populations and the bioenergetic method was able to accurately simulate annual variability in Gulf sturgeon growth rates. Further, the bioenergetics growth estimates, which incorporate length-at-age and length-increment data estimated very different growth trajectories than traditional von Bertalanffy curves that used only length-at-age. This indicates that length-at-age data alone can lead to errors in growth estimates, resulting in erroneous management advice. Using field data to inform bioenergetic models should be a useful approach for fisheries researchers and managers to describe the growth and energetic characteristics of fish populations.

Keywords: Bioenergetic models, sturgeon, growth curves.

INTRODUCTION

Bioenergetics models are models used to describe energy uptake and allocation in organisms [1]. These models produce estimates of growth and food consumption based on the biology and environment of a specific organism. Bioenergetics models are used in fisheries management and are informed using data collected through both field and laboratory studies [2]. The results of these models are commonly used to make predictions and management recommendations concerning populations in the field.

Estimates of bioenergetics parameters and consumption, often obtained from laboratory studies, are not always available for a specific species, in which case they are commonly acquired from similar or related species [3, van Poorten and Walters, this issue]. An alternative approach to using laboratory studies to estimate bioenergetics parameters, using field data as much as possible, has been suggested by Walters and Essington [4]. This method uses length-at-age and incremental growth data from tag-recapture field studies to estimate feeding and metabolism parameters from which traditional von Bertalanffy growth parameters can be calculated. The Walters and Essington [4] method has the ability to describe variation in growth rates during the life of an organism, providing the ability to estimate variation in mass, without allowing loss in length, based on life history events (i.e. spawning) and environmental temperature.

Relatively little bioenergetics research has been conducted on sturgeon *Acipenser* spp. populations as evident by the late appearance in the literature of the first bioenergetics parameter estimates in 2002 for white sturgeon *A. transmontanus* [5]. Estimates of bioenergetics parameters for Gulf sturgeon *A. oxyrinchus desotoi*, a subspecies of Atlantic sturgeon *A. o. oxyrinchus* have not been made despite several interesting life history attributes from a bioenergetics perspective. Gulf sturgeon have the southernmost distribution of any North American sturgeon species [6] and are anadromous, spawning in and spending a majority of the year in freshwater environments. Gulf sturgeon are observed in these freshwater environments during the warmest period of the year and do not feed or exhibit growth, instead becoming dormant during this time and losing weight [7,8]. Similar to humpback chub *Gila cypha* in the Grand Canyon [9], Gulf sturgeon growth rates vary during their life history and describing growth using traditional, non-bioenergetic methods such as using standard von Bertalanffy growth curves, may not be optimal.

The use of incremental growth data has been suggested as a way to estimate growth model parameters [10]. Using incremental growth data from the existing Gulf sturgeon tagging studies to estimate growth has the advantages of not requiring direct age estimates of individuals, important in a case such as for Gulf sturgeon where data from direct age estimating methods such as otolith and fin-ray aging are scarce. The advantages of combining direct aging and tagging data in an analysis are that the sample size of individuals used for aging is increased, potentially including a better representation of the population, and that the effect of any

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age-assignment errors within the direct aging data is diluted by the additional tagging data.

The objective of this study was to estimate bioenergetics parameters for two Gulf sturgeon populations and evaluate the growth characteristics of these populations. The two Gulf sturgeon populations examined were from the Apalachicola and Suwannee rivers, Florida. These rivers are located on the Gulf coast of northwest Florida approximately 200 km apart and the Gulf sturgeon populations of each are believed to be closely genetically related [11]. Gulf sturgeon are unique in that they feed primarily in cooler winter months in nearshore areas of the Gulf of Mexico and spend the remaining portions of the year in river systems spawning then resting, seeking refuge from warm water temperatures in the Gulf of Mexico. They are observed not to feed or to exhibit a great deal of movement while in river systems during summer months [7,8]. Individuals from neighboring river systems have been observed to use the same foraging areas of the Gulf of Mexico during winter [12] and occasionally spend an entire summer season in a foreign river system [13]. These factors lead us to hypothesize that the bioenergetics and growth characteristics of the Apalachicola and Suwannee populations are similar because of the close proximity and similar feeding habits of these two populations.

METHODS

Study data were obtained from Gulf sturgeon monitoring programs operated primarily by U.S. federal agencies. These programs tag and recapture Gulf sturgeon generally on an annual basis during summer and fall when Gulf sturgeon are found in freshwater. Data consisted of direct length-at-age [14] and tagging data from 1978-2007 [15] for the Apalachicola River and length-at-age and tagging data from 1982-2007 for the Suwannee River [16]. A small group of hatchery reared individuals from the Suwannee River dataset were excluded from the analysis to reduce the impact of hatchery effects on predicted growth. Measurement error variance (σ^2_m) was assessed using fish captured and recaptured within seven days and calculating the root mean square difference between the two measurements. Coefficient of variation in asymptotic size, which is used to calculate the deviance variance (σ^2_R) was set at 0.2.

Bioenergetics parameters were estimated using the methods described by Walters and Essington [3]. Parameters were estimated using an MCMC routine to find the posterior probability distribution of each parameter. These posterior distributions were compared across populations for differences. Parameter correlation was also examined within each population. An assumption for this model was that maximum age for Gulf sturgeon was 50 years, which is supported by other Atlantic sturgeon studies [17, 18] and our tagging data. All model parameters and prior distributions are shown in Table **1**.

Model progression proceeds as follows. Individuals in each population are assumed to spawn on May 21 and eggs hatch on June 1. Larvae are born at a length of 8.3 mm [19]. Individuals spend their first three years in freshwater and thereafter begin annual migrations between freshwater and the Gulf of Mexico, entering the Gulf on November 1 and re-entering freshwater on March 15. When fish exceed 24 kg, they are assumed to be mature. Interspawning interval was set at four years [18]. Spawning and associated behavior results in a 15% decrease in body mass [6]. Length- and weight-at-age are evaluated every two-weeks.

Bioenergetic derived growth estimates were compared to growth estimates developed using the direct aging data in a traditional von Bertalanffy growth curve [20], representing a technique commonly used by fisheries managers. The standard von Bertalanffy growth function was used

$$L_a = L_\infty(1-e^{-k(a-t_0)}) \tag{1}$$

where L_∞ is the asymptotic length, k is the Brody metabolic parameter and L_a is the length-at-age. The maximum likelihood estimate of the theoretical age at zero-length (t_o) was estimated by assuming length-at-hatch (L_H) of 8.3 (Table **1**):

$$t_0 = \frac{\ln\left(1-\frac{L_H}{L_\infty}\right)}{k} \tag{2}$$

Equation 1 was fit to the length-at-age data only and solved using non-linear regression. Using the estimates of von Bertalanffy length-at-age estimates, weight-at-age was obtained using the formula:

$$W = aL^b \tag{3}$$

where W is weight, L is length, and a and b are weight function parameters. In this case a is unique for each population while b is a constant value of 3.0 (Table **1**). Estimates of asymptotic weight, W_∞, was also compared between bioenergetics and von Bertalanffy results.

RESULTS

Before analysis began, the tag datasets were examined to identify any obvious errors. Individuals for which the observed absolute annual growth rate between tagging and recapture was greater than 150 mm/year were removed. Additionally, any fish observed to lose more than 10mm were also removed, regardless of the time at-large. In total, 164 and 569 were removed from the tag-recapture database due to perceived misidentification from the Apalachicola and Suwannee populations, leaving 385 and 2587 tag records, respectively. Additionally, 102 and 585 individuals from the same populations had age information available and all were used in the analysis.

The median of the posterior parameter distributions are provided in Table **1**, while the posterior probability density distributions for both populations are provided in Fig. (**1**). Model parameters were generally not strongly correlated with each other, the exception being the *m* parameter which was somewhat confounded with all other parameters (Fig. **2**). Posterior distributions of bioenergetics parameters varied among both Gulf sturgeon populations with generally greater differences existing between metabolic related parameters (m, n, Q_m) than with consumption related parameters (H, d, Q_c). Posterior distributions were relatively narrow for most parameters in both populations, being tightest for the Suwannee population, largely due to the greater sample size.

Table 1. Parameters Used in the General Bioenergetics Model. Median Posterior Values of the Estimated Parameters are Shown with Prior Distributions Indicated Below

		Apalachicola	**Suwannee**	
Parameter	**Description**	**Value (Prior)**	**Value (Prior)**	**Units**
a	Intercept coefficient of length-weight relationship	6.11 e^{-6}	6.36 e^{-6}	g mm^{-b}
b	Power coefficient of length-weight relationship	3.0	3.0	–
H	Net food consumption rate per W^{-d}	38.28 $U(0,100)$	49.41 $U(0,100)$	g g^{-1} yr^{-1}
m	Standard metabolic rate per W^{-n}	5.22×10^{-2} $U(0,10)$	1.59 $U(0,10)$	g g^{-1} yr^{-1}
d	Food consumption power parameter	0.51 $U(0.5,1.0)$	0.52 $U(0.5,1.0)$	–
n	Metabolism power parameter	1.31 $U(0.5,1.5)$	0.83 $U(0.5,1.5)$	–
Q_c	Proportional increase in feeding rate per 10°C temperature increase	2.31 $U(0,20)$	1.51 $U(0,20)$	–
Q_m	Proportional increase in metabolism per 10°C temperature increase	0.40 $U(0,20)$	3.30 $U(0,20)$	–
θ	Slope parameter for decreasing allocation to structural tissue as W_s/W varies around f^*_s	0.2	0.2	–
g	Steepness parameter for decrease in feeding at high temperatures	0.5	0.5	°C^{-1}
T_m	Water temperature at which feeding drops by half	1000	1000	°C
W_{ma}	Weight-at-maturity	24	24	kg
p_{gonad}	Proportion of body weight lost to spawning	0.15	0.15	–
Sp_{int}	Spawning interval	4	4	yr
$Tmin_s$	Value at inflection point of Gulf of Mexico water temperature sine wave	22.5	22.5	°C
$Tmax_s$	Maximum of Gulf of Mexico water temperature	30.8	30.8	°C
$T\Delta_s$	Offset of Gulf of Mexico water temperature sine wave	0.65	0.65	Yr
$Tmin_f$	Value at inflection point of freshwater temperature sine wave	21.5	22.2	°C
$Tmax_f$	Maximum of freshwater temperature	29.7	27.8	°C
$T\Delta_f$	Offset of freshwater temperature sine wave	0.64	0.68	yr
CV_L	Coefficient of variation of individual maximum body lengths	0.2	0.2	mm^2
σ^2_m	Measurement variance for L_1 and L_2	31	31	mm^2

The effect of differences in parameters can be seen in the bioenergetics model predicted annual growth patterns for the Apalachicola and Suwannee river Gulf sturgeon populations (Fig. **3**). The model predicted a reduction of length growth rate and weight loss with the increase of temperatures during summer for the Apalachicola population while the Suwannee population continually increased in mass throughout summer. Ultimately the bioenergetics model predicts that the Suwannee population will reach a higher maximum weight than the Apalachicola population. This is the opposite case of our direct aging von Bertalanffy growth curves and parameter estimates (Table **2**; Fig. **3**) as the Apalachicola population was predicted to have a larger W_∞ than the Suwannee population. The difference between von Bertalanffy and bioenergetics models results is likely a result of under-representation of older, larger individuals in the Suwannee River aging sample. Bioenergetics model estimates of W_∞ were similar to those described previously for Suwannee River Gulf sturgeon [21].

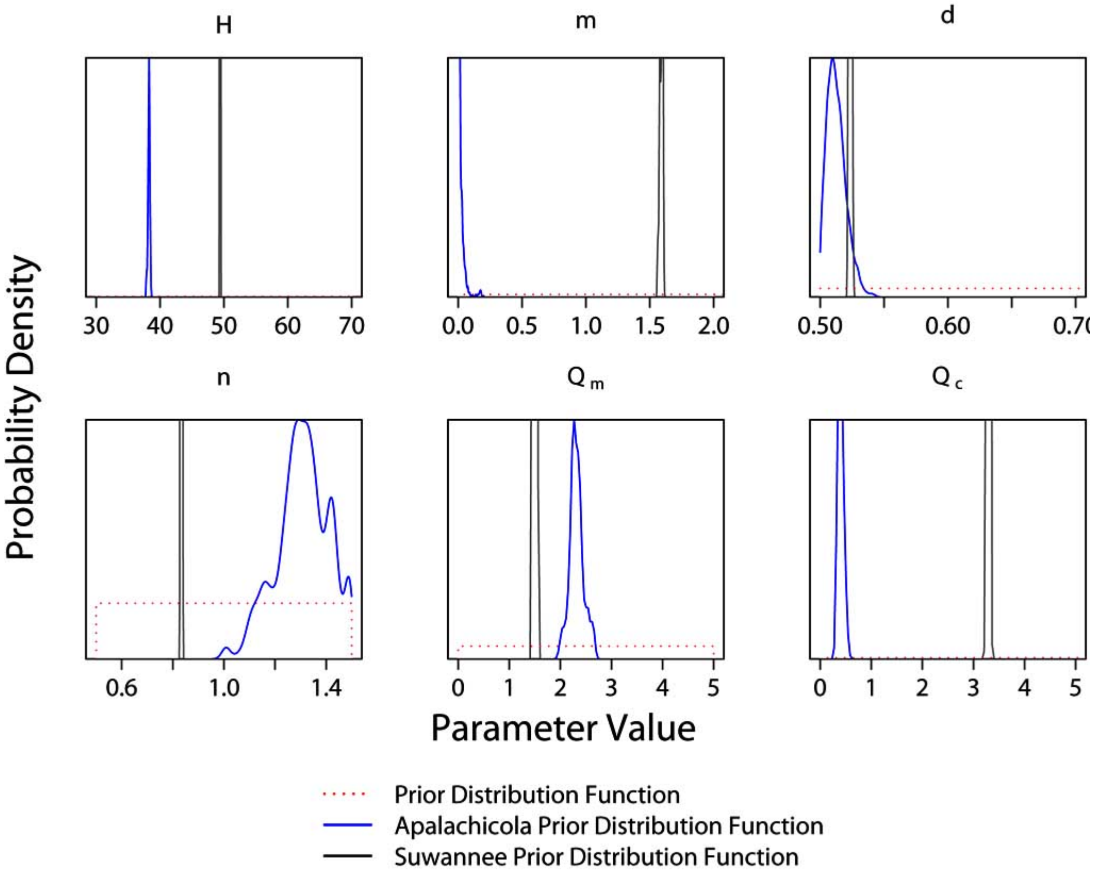

Fig. (1). Prior (dotted) and posterior (solid) probability densities for the general bioenergetics parameters for the Apalachicola River Gulf sturgeon population (blue line) and Suwannee River Gulf sturgeon population (black line).

DISCUSSION

Our bioenergetic consumption parameter estimates for Gulf sturgeon were generally similar for both the Apalachicola and Suwannee populations which would be expected since Gulf sturgeon feed on similar items along relatively homogenous nearshore estuarine areas in the Gulf of Mexico and not in more heterogeneous individual river systems [12]. One key difference between two populations predicted by the model was that the Suwannee population remains active and exhibits increases in mass during warm summer months. This observation is not supported by field observations [8] and the result may be related to data being collected in a limited annual window rather than continuously throughout the year. The majority of Apalachicola River tagging observations occurred through months from June to November, reflecting the practice in that system for sampling resting areas during summer months, while the majority of sampling in the Suwannee River occurred in the months of April and November, reflecting the practice in that system of sampling individuals when making migration runs, either incoming for spawning or outgoing for feeding. The effect would be that the Apalachicola dataset contains sufficient resolution during summer months to describe decrease in growth exhibited by the population, despite being one-sixth the total size of the Suwannee dataset. Conversely, in the Suwannee summer data may be swamped by individual incremental growth observations from mid-spring to fall resulting in the model incorrectly allocating rapid winter/spring growth throughout the entire year instead.

Our bioenergetic parameter estimates were generally similar to those found by van Poorten and McAdam [22] for white sturgeon in the Columbia River, which is notable given geographical, environmental, and behavioral differences between species. One notable difference is in estimates of the *H* parameter, representing the net food consumption rate, being greater for Gulf sturgeon than white sturgeon. This implies that white sturgeon must expend more energy per unit of food consumed than Gulf sturgeon, likely a consequence of dietary differences as white sturgeon tend to be piscivorous while Gulf sturgeon feed almost entirely on benthic invertebrates. Another major difference in parameter estimates is in the *m* value for the Suwannee River Gulf sturgeon population, which is over an order of magnitude higher than the next closest estimates. As discussed earlier, this may be a result of the sampling program failing to capture the reduction in growth rate observed during warmer summer months.

Standard von Bertalanffy growth curve estimates using only length-at-age data can be improved by using an estimation method that includes directly measured increment growth data, such as those developed by Fabens [10]. Both L_∞ and k can be solved from the bioenergetics model using the reformulation of the von Bertalanffy growth model in Essington *et al.* [23], however certain model parameters

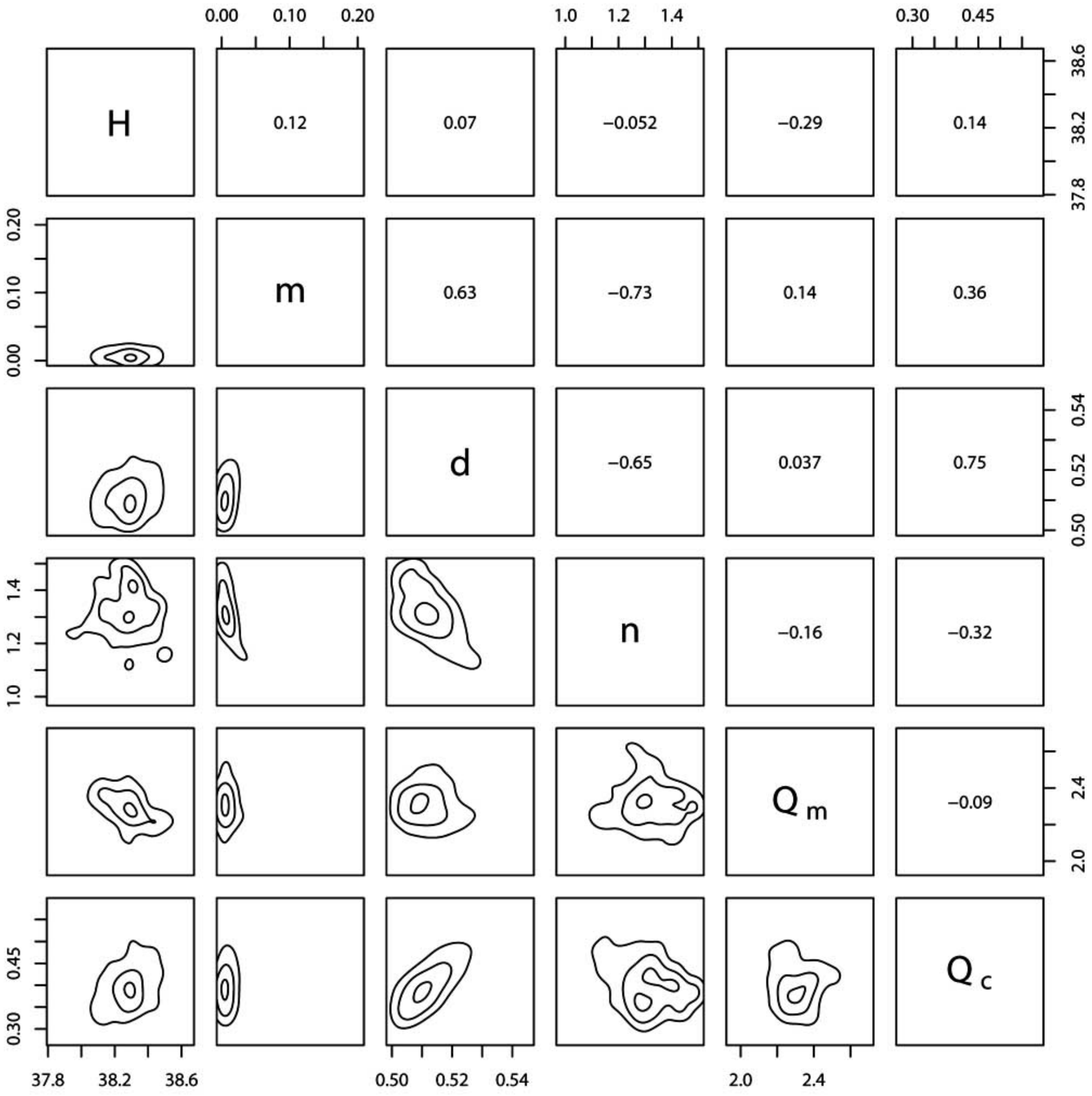

Fig. (2). Correlations between bioenergetics parameters for Apalachicola River Gulf sturgeon.

must be constrained (i.e., *n*=1.0, *d*=0.667) in order to use this method and seasonal deviation in the length-weight relationship must be ignored. While we could run the bioenergetics model while constraining these parameters this may penalize the accuracy of our predictions as energy losses attributed to reproduction could not be accounted. As a consequence we were unable to directly compare von Bertalanffy parameter estimates estimated from direct aging data and bioenergetics model.

Table 2. von Bertalanffy Parameters Estimated Through Direct Estimates Using Length-at-Age Data

	von Bertalanffy Estimate			
Population	L_∞ (mm)	W_∞ (kg)	K	t_o (mm)
Apalachicola	2168	62.3	0.13	-0.83
Suwannee	1697	31.1	0.21	-0.63

We had hoped to evaluate Gulf sturgeon growth characteristics based on sex, however sample sizes for individuals with sex data were insufficient to perform a satisfactory analysis. It is hypothesized that females attain a larger maximum size in both length and weight and information on sexually dimorphic growth would be important to resource managers in evaluating the potential for limited, highly-regulated harvest which could use maximum size limit regulations to protect large, fecund female individuals. Preliminary results suggested there may be differences between sexes, but more data is need for a complete analysis. If sexually dimorphic growth patterns do exist, our overall model results could be affected, especially if the field sampling was biased (e.g. a larger proportion of older males, with a lower L_∞ could negatively bias overall population predicted L_∞).

CONCLUSION

Our study demonstrates how bioenergetics can be used to better model variability in growth patterns observed in field

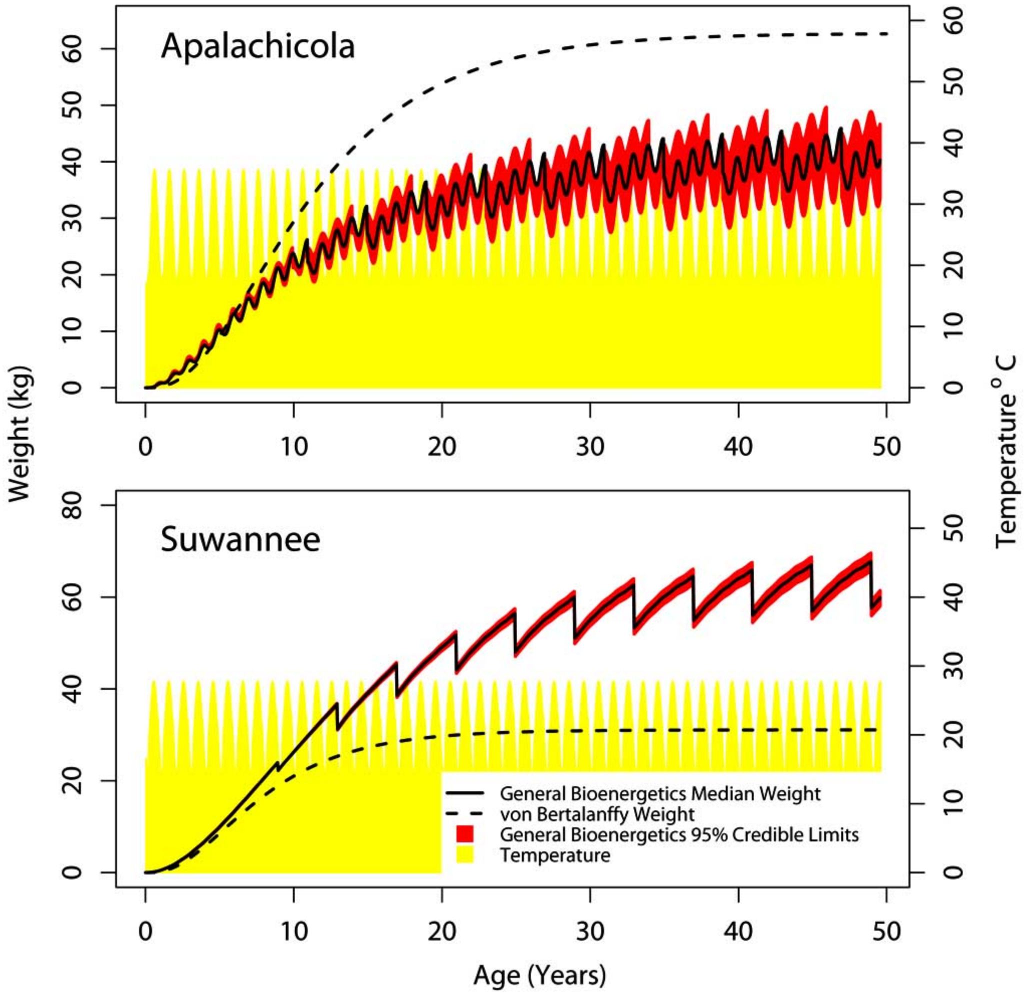

Fig. (3). Predicted weight of Gulf sturgeon from the Apalachicola (top) and Suwannee (bottom) rivers in Florida. Median growth estimate shown in black and 95% credible region filled in red. Temperatures assumed to be experienced by each population as a combination of Gulf of Mexico and riverine water temperatures are shown in yellow.

studies that may not be modeled by standard von Bertalanffy methods. Additionally, we observed that including tagging data alone cannot account for seasonal variability in growth observed for Gulf sturgeon, however, by including temperature data these changes in seasonal growth can be captured by the bioenergetics model. Using field data to inform bioenergetics models should be a valuable technique for fisheries managers since field research and monitoring programs are ongoing for many species and growth data is a common product of basic fisheries studies,. In cases where field data is available, laboratory experiments dedicated to estimating bioenergetics would be unnecessary, avoiding extra costs and difficulties, especially in the case of protected species or species that cannot be maintained in a controlled environment. As our results show, care should be taken when using field data as a given sampling regime may not be sufficient to accurately describe growth patterns observed through other methods.

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