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Using multi-model inference to determine the growth rates of red snapper, *Lutjanus campechanus*, through ontogeny

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ABSTRACT

Growth rates of a single cohort of F1, captive-reared red snapper, *Lutjanus campechanus*, were determined through ontogeny using a multi-model inference approach. Water temperature averaged 23.6 ± 0.13 °C based on the ambient conditions of the study location in Miami, Florida. Growth rates in length-at-age and weight-at-age were best expressed using the von Bertalanffy model with the equations $L_t = 742.6\ (1 – e^{0.001804(a\text{-}31.57)})$ and $W_t = 84720\ (1 – e^{-0.0005787(a+78.71)})^{3.304}$, respectively. The length-weight relationship was expressed by the equation $W = 0.000003158\ (L_t^{3.304})$. Red snapper grew to market-based harvest sizes of 450 g and 750 g by 318 (SGR = 1.403%/day) and 393 (SGR = 1.2%/day) days post hatch, respectively. Size at age was markedly higher than those reported in age-class studies for captive-reared red snapper and in the available wild-capture data for the species. Feed conversion ratios (1.32, cumulatively) generated in this study were commensurate with or lower than other commercially cultured snapper species. After applying the data generated by this study, recently published species selection methodology rank the red snapper within the highest priority tier for aquaculture development in the Southeastern United States and the Caribbean region.

1. Introduction

The red snapper, *Lutjanus campechanus*, is one of the most valuable and contentiously managed fisheries in the United States (Goethel and Smith, 2018; Simmons et al., 2019). High market value and the uncertain status of wild spawning stocks has led the species to receive significant attention as a candidate for commercial aquaculture for several decades (Arnold et al., 1978; Laidley et al., 2004; Phelps et al., 2000; Saillant et al., 2013). Similar to many of the other Lutjanid species, red snapper are eurythermal and euryhaline, tolerating broad ranges of temperature (15.0–29.0 °C) and salinity (2 – 36) in their native range throughout the southern US, the Gulf of Mexico, and the Caribbean region (Galkanda-Arachchige et al., 2021; Patterson et al., 2005; Szedlmayer and Lee, 2004).

Aquaculture of other snapper species has developed into a meaningful production industry in Asia and the Indo-Pacific region and forays into the culturing of certain species have expanded into Latin America in recent years (Coniza et al., 2012; FAO, 2016; Ibarra-Castro et al., 2013). Growout methods range from land-based, flow through and RAS systems to cage culture arrays and suggest a general tolerance to a wide range of culture conditions (Castillo-Vargasmachuca et al., 2013; Coniza et al., 2012; Duray et al., 1996). Published research on many of these snapper species has kept apace with industrial development, and studies encompassing topics including hatchery production, ontogenic development, and market distribution are widely available (Catacutan et al., 2001; Estrada-Godínez et al., 2015; Herrera-Ulloa et al., 2010; Ibarra-Castro et al., 2020). Generally, snapper aquaculture has been successful based on the interplay between relatively fast growth rates, low feed conversion ratios, high market demand, and a tolerance to diverse culture conditions (Benetti et al., 2002; Coniza et al., 2012; Estudillo et al., 2000; Hernández et al., 2016).

Despite continued research into the cultivation of northern red snapper, the status of the industry currently lags other snapper species that have achieved commercial relevance (Saillant et al., 2013). Recent advancements in the captive spawning, larval rearing, and fingerling production of the species have renewed interest in red snapper from private stakeholders and the public sector (Buchalla et al., 2023; McGuigan et al., 2021). These commercial interests have developed a collaborative partnership with the University of Miami Aquaculture Program and the National Oceanic and Atmospheric Administration (NOAA) which has allowed for the continued investigation of the aquaculture potential of the species and distribution of commercial quantities of fingerlings to the private sector. However, basic questions about the aquaculture performance of the species remain, including a comprehensive understanding of how red snapper grow under culture conditions throughout life-history. Existing studies have explored growth performance across narrow age-classes and have begun to document the changes induced by varying dietary compositions of

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Table 1
Summary of growth parameters used in the analysis for the growth of *L. campechanus*.

Parameter (unit)	Equation
Absolute growth (g)	$\Delta G = W_2 - W_1$
Absolute growth rate (g/day)	$AGR = (W_2 - W_1)/(t_2 - t_1)$
Instantaneous growth rate (g/day)	$g = (\ln W_2 - \ln W_1)/(t_2 - t_1)$
Specific growth rate (% body weight/day)	$SGR = 100 * (e^g - 1)$
Feed Conversion Ratio (FCR)	$FCR = \Delta W/f$
Length-weight relationship	$W = aL^b$
von Bertalanffy model	$S_t \sim S_{inf} * (1 - e\hat{}(-k * (\alpha - t_0)))$
Laird–Gompertz model	$S_t \sim S_{inf} * exp\ (-e\hat{}-k * (\alpha - t_0))$
Logistic model	$TS \sim S_{inf} * (1 + e\hat{}(-k * (\alpha - t_0)\hat{} - 1$

W_1 = initial weight
W_2 = final weight
t_1 = initial age (days post hatch)
t_2 = final age (days post hatch)
f = quantity of feed
L = length
a = intercept after logarithmic transformation
S_t = total size at age t [length (mm) or weight (g)]
S_{inf} = average asymptotic maximum size [length (mm) or weight (g)]
α = age (days)
k = growth coefficient
t_0 = age at size = 0 (days)

protein and lipids, but to date, there has been no data published describing the growth of this species in captivity throughout its life-history (Davis et al., 2005; Galkanda-Arachchige et al., 2021; Miller et al., 2005).

Typical models of fish growth explain changes in size (length or weight) as a function of age or explain changes in weight as a function of length. In many cases, the von Bertalanffy growth model is adopted as the *de facto* curve to explain growth as a function of age. However, meta-analyses have indicated that this model does not necessarily represent the most reliable estimate for growth for certain species or certain environmental conditions, and may serve as the best model in less than 50% of cases. (Barker and Link, 2015; Katsanevakis and Maravelias, 2008). As such, integrating a multi-model inference approach to account for other common growth patterns such as the Laird-Gompertz model and the logistic model is essential. When comparing the suitability of these non-linear models, the use of R^2 is an improper approach still being widely reported. Considering that R^2 assumes the total sum of squares must equal the regression sum of squares plus the residual sum of squares, which is often not the case in non-linear models, more refined methods for statistical comparison are necessary (Spiess and Neumeyer, 2010). This requires quantifying the residual sum of squares (RSS) for each model and incorporating the Aikake information criterion (AIC) to assess the suitability in each non-linear model (Akaike, 1974).

This study presents data on the growth in length and weight of red snapper reared in flow-through and semi-recirculating tanks in Miami, Florida, at ambient, seasonally dependent water temperatures. It represents the first data available for the full life-history of this ecologically and economically important species from nursery through sexual maturity and should provide reasonable approximations of growth capabilities in a variety of aquaculture contexts. Additionally, the data presented here provide insight into the stark differences in growth rates between captive-raised and wild-caught red snapper for the first time.

2. Materials and methods

2.1. Fingerling Production

All red snapper used in this analysis were F_1 generation offspring, produced by the same wild broodstock, which spawned volitionally at the University of Miami Experimental Hatchery. Larval rearing protocols followed those described by Buchalla et al. (2023) and McGuigan et al. (2021). After metamorphosis, fingerlings were split into an array of (9) 450 L fiberglass tanks that received flow-through water that was filtered to 1 µm and passed through a standard UV sterilizer. As the size of the fingerlings increased, they were moved to (12) 1000 L polyethylene tanks and received flow-through water that was filtered to 10 µm but did not received UV sterilization. As fish approached market size, a subset of individuals was randomly selected and transferred to a 4500 L and subsequently a 15,000 L fiberglass tank that received flow-through water filtered to 10 µm. A randomly selected subset of these fish was held past sexual maturity to serve as future broodstock and was housed in a 60,000 L fiberglass tank with a recirculating system and mechanical, UV, and biological filtration. Growth rates were determined by regularly sampling individual total lengths (mm) and weights (g). Although infrequent, individual mortalities were observed, at which point final measurements of length and weight were collected and a necropsy was conducted to determine sex and observe internal characteristics. All growout and handling procedures described here were carried out in accordance with the standards of the Institutional Animal Care and Use Committee (IACUC).

2.2. Growth parameters

Fish were sampled every 14 days while in the 450 L tank system (n = 90; maximum stocking density = 7.2 kg/m^3), every 21 days while in the 1000 L tank system (n = 40; maximum stocking density = 3.1 kg/m^3), and with decreasing frequency when the fish surpassed market-size (n = 11 – 79; maximum stocking density = 18.2 kg/m^3) to minimize handling stress in the potential brood cohort. Each fish was collected and measured for total length (TL), fork length (FL), and wet weight (W) during each sampling date. All fish were anaesthetized using a standard concentration of clove oil (Eugenol) prior to sampling and placed in a clean tank after receiving a prophylactic freshwater bath to assess fish health. Sex determination was accomplished through cannulation once fish reached an appropriate size. Growth in weight was analyzed both as absolute and specific growth and total-tank feed consumption was included to calculate feed conversion ratios (FCR) for fish through sampling at 262 dph. Multiple models were assessed for goodness of fit to determine the most effective techniques to model length (mm)-at-age (LA), weight (g)-at-age (WA), and weight (g)-at-length (mm;WL).

2.3. Feeding

All fish were fed with a commercially available marine grower pellet containing at least 48.0% crude protein and 14.0% fat, until being transferred to the 15,000 L system, at which point diets transitioned to natural feed items including squid, sardines, and shrimp. Pellet size began at 1 mm and progressively increased to 12 mm as the fish grew. In the 450 L and 1000 L systems, fish were fed to satiation twice daily, while in the 4500 L and 15,000 L systems, fish were fed to satiation once daily, with one day of no feeding per week. Satiation was defined as the point at which two total pellets or pieces of cut feed fell to the bottom of the tank before being eaten. Relative ad libitum feeding rates declined over time as the fish grew, beginning at approximately 5% of total biomass during the fingerling stage and reaching approximately 2% of total biomass at the conclusion of sampling. Feed conversion ratios (FCR) were determined by calculating the ratio between the total weight of food given and the total weight of the fish that were sampled. FCR assessment ceased at 262 dph when feeding transitioned from commercial feed to natural food items.

2.4. Water quality and tank maintenance

Each tank was constantly supplied with pure oxygen and aeration which were bubbled into the water using semi-porous diffusers. Dissolved oxygen concentration (mg/L) and temperature (°C) were measured in each tank daily using a YSI 550a Dissolved Oxygen Meter.

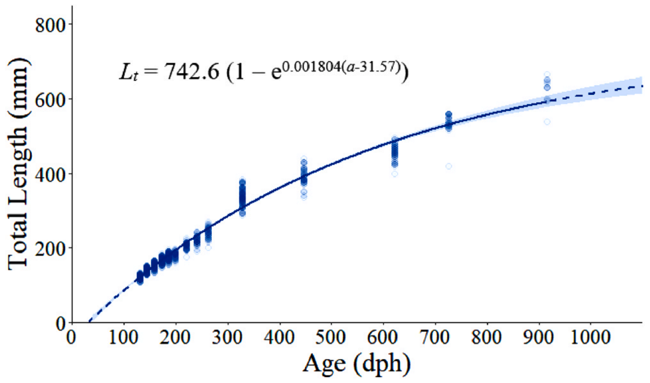


Fig. 1. The length-at-age von Bertalanffy regression model (solid line) and extrapolated predictions of length at age (dashed line) of *L. campechanus* juveniles and adults generated from individuals aging 130 – 916 days post hatch (dph). Shading represents the bootstrapped upper and lower 95% confidence intervals.

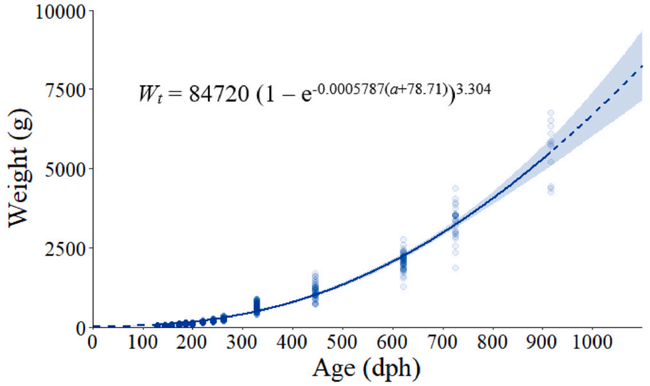


Fig. 2. The weight-at-age von Bertalanffy regression model (solid line) and extrapolated predictions of weight-at-age (dashed line) of *L. campechanus* juveniles and adults generated from individuals aging 130 – 916 days post hatch (dph). Shading represents the bootstrapped upper and lower 95% confidence intervals.

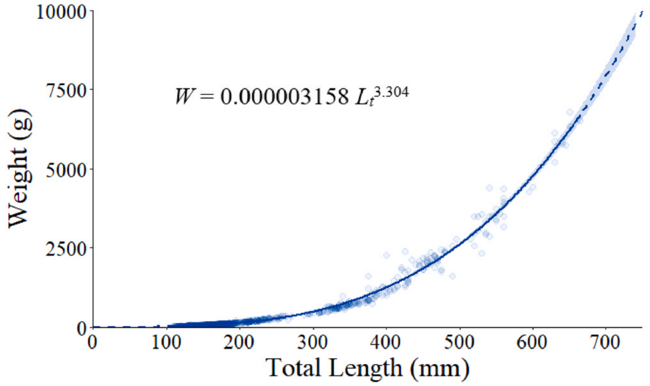


Fig. 3. The weight-at-length, exponential regression model (solid line) and extrapolated predictions of weight-at-length (dashed line) of *L. campechanus* juveniles and adults generated from individuals aging 130 – 916 days post hatch (dph). Shading represents the bootstrapped upper and lower 95% confidence intervals.

Tank bottoms were siphoned daily in the 450 and 1000 L systems and biweekly in the 4500, 15,000, and 60,000 L systems to remove waste and prevent algal buildup. Daily water exchange rates through each flow through tank system exceeded 1000%, though exact rates were changed at times to ensure optimal water quality.

Table 2
Summary of the cumulative values for relevant growth parameters at various ages. Feed conversion ratio (FCR) data was available until 262 days post hatch (dph). The WA model generated the ages of 318 dph and 393 dph for market sizes of 450 and 750 g, respectively. The full scope for sampling used in this study encompassed 916 dph.

Parameter (unit)	262 dph	318 dph	393 dph	916 dph
Average size (g)	257.8	451.75	751.9	5582.27
Average size (mm)	240.1	299.7	355.7	625
Absolute Growth (g)	225.49	419.44	719.59	5549.96
Absolute Growth Rate (g/day)	1.708	2.23	2.74	7.06
Instantaneous Growth Rate (g/day)	0.0157	0.014	0.0197	0.00655
Specific Growth Rate (%/day)	1.573	1.403	1.2	0.655
FCR	1.32	-	-	-

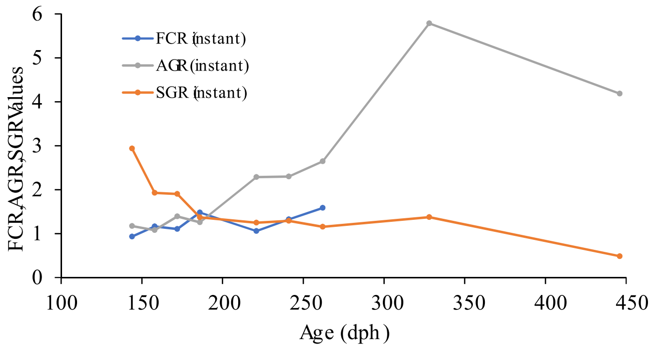


Fig. 4. The feed conversion ratio (FCR), absolute growth rate (AGR), and specific growth rate (SGR) for each sampling period through harvest size at 462 dph. FCR was calculated through 262 dph when feed transitioned from commercial pellet feed to cut natural feeds. AGR and SGR were calculated to the date at which *L. campechanus* exceeded a final harvest size of 750 g.

Table 3
Summary of the water quality parameters taken from each tank system for the duration of the trial. "dph" indicates days post hatch.

Parameter (unit)	130–199 dph	200–261 dph	262–620 dph	621–916 dph
Temperature (°C)				
Mean	23.4 ± 0.26	23.9 ± 0.25	26.2 ± 0.15	25.1 ± 0.19
Min	21.8	19.7	19	20.4
Max	25.1	26.9	29.5	29.3
Mean Dissolved Oxygen (mg/l)	11.2 ± 0.52	9.6 ± 0.26	9.6 ± 0.15	9.2 ± 0.28
Tank volume (L)	450	1000	4500–15,000	15,000–60,000
Maximum stocking density (kg/m^3)	7.2	3.1	18.2	1.37

2.5. Statistical analyses

All statistical analyses and figures were generated using RStudio 2022.02.03. Because of their broad applications and widespread use in fisheries growth studies, the von Bertalanffy, Laird-Gompertz, and logistic models (Table 1) were compared to obtain the most suitable model for predicting LA, WA, and WL. Appropriate starting values for each parameter in the LA and WA models were calculated manually by obtaining a theoretical maximum average size (S_{inf}) from the oldest size-class and performing a linear regression to generate suitable approximations of the growth coefficient (K) and age at size = 0 (t_0). A Newton Least Squares (NLS) regression was then performed to generate values

Table 4
Comparison of growth performance in various relevant aquaculture species both endemic and non-native to the Caribbean region. Feed conversion ratio is given by "FCR.".

Species	Temperature (°C)	Stocking density (kg/m^3)	Harvest size (g)	Age at harvest (months)	FCR	Growth rate (g/day)	Reference
American red snapper (*L. campechanus)*	19–29.5	3–18	450–750	10–14	1.32	2.2–2.75	current study
Spotted rose snapper (*L. guttatus*)	23–29	15–22	250–340	8–12	1.4–1.8	1.16–1.8	Hernández et al. (2015); Castillo-Vargasmachuca et al. (2018)
Mangrove red snapper (*L. argentimaculatus*)	25–33	2.5–5	250–300	8–12	2.2–6.3	0.53–0.64	Coniza et al. (2012); Muyot et al. (2021)
Mutton snapper (*L. analis*)	25–32	4–40	250–350	8–10	1.1–1.6	1.16–1.28	Benetti et al. (2002)
Pacific red snapper (*L. peru*)	25–30	1–8	400–500	10–14	2.2 – 2.6	1.0–1.4	Castillo-Vargasmachuca et al., (2012, 2013)
Barramundi (*L. calcifer*)	28–32	5–10	1000–3000	12–24	1.1–2.2	1.2–5.8	Glencross (2008)
Red drum (*S. ocellata)*	22–25	2–14	1000–3000	10–18	1.9–2.4	2.5–5	Vela et al. (2019)
European sea bass (*D. labrax*)	20–28	20	400–3000	16–24	1.1–2.6	1–4	Kousoulaki et al. (2015); Rizzo and Spagnolo (1996)
Sea bream (*Sparus aurata*)	16–22	10–25	280–2000	10–14	2.1–3	0.9–1.3	Seginer (2016)
Florida pompano (*T. carolinus*)	27–29	1.3–4	450–750	12–17	3–5.5	1.3–3.8	Weirich et al. (2006); Weirich et al. (2021)
Japanese hamachi (*S. quinqueradiata*)	13–22	2–10	3500–4000	18–24	1.4–2.1	3.1–4.5	Rotman et al. (2021); Schwebel (2017)
Cobia (*R. canadum)*	20–30	5–10	3000–10,000	12–24	1.3–2.2	8–18	Benetti et al. (2010)

Table 5
Species selection criteria from Alvarez-Lajonchère, L. & Ibarra-Castro, L. (2013) updated with information from current study. Only criteria for which changes in scoring are observed are reported here. Full descriptions of each criteria and associated values can be found in Tables A.3 & A.4 in Appendix A.

	Criteria Assessed							Priority
	Market	Juvenile Production	Juvenile Nursery Growth	Grow-out Growth	Juvenile Yield Index	Feeding	Total Score (includes all criteria)	
2013 Value	25 (9)	6 (−2)	2 (−1)	8 (−2)	3	20 (−1)	169	3
New Value	50 (9)	8 (2)	8 (3)	16 (1)	30	32	259	1
New Value Ref.	Red Snapper, Fresh, Wild, USA, Whole (Price per Pound), 2021; National Fisherman (2021)	Buchalla (2023); McGuigan et al. (2021)	Current Study	Current Study	Buchalla (2023); McGuigan et al. (2021)	Current Study		
Score Change	25	6	10	11	27	13	90	

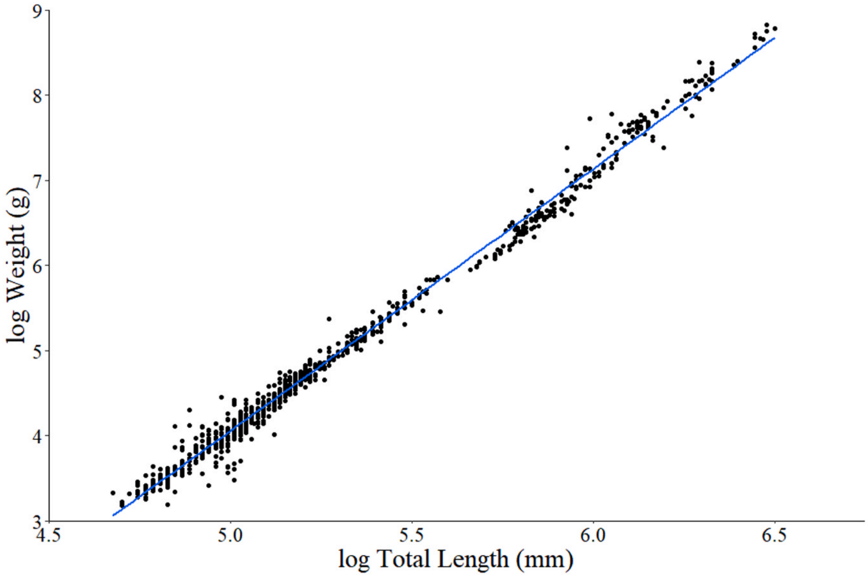


Fig. A.1. Relationship between weights and total lengths (log transformed) of captive red snapper.

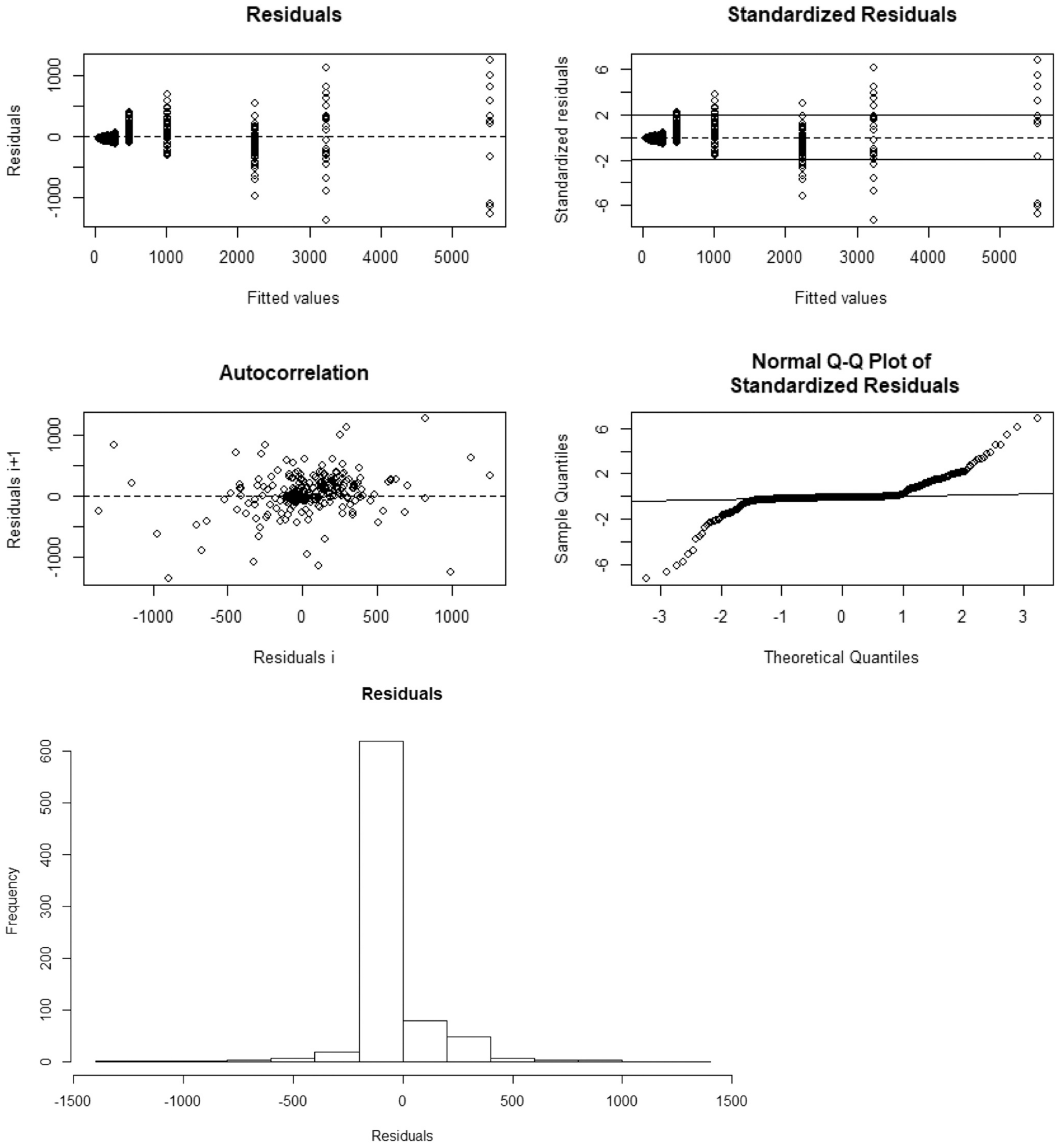


Fig. A.2. WA Residuals calculated for the von Bertalanffy model.

for S_{inf}, K, and t_0 which were used to compute bootstrapped confidence intervals within the Fisheries Stock Analysis (FSA) R Package (Ogle et al., 2022). Because R^2 values have been widely demonstrated to be insufficient measures of model-fitting for non-linear equations, Akaike information criterion (AIC) were used to compare the fit between models in this study (Kvålseth, 1985; Willett and Singer, 1988). The WL model was generated by logarithmic transformation of the standard model.

$$W = aL^{\beta}$$

to.

$$\mathrm{Log}(W) = \log(a) + \beta\log(L)\cdot$$

A linear regression was then performed to obtain starting values, at which point an NLS regression was conducted to generate values for *a* and β.

Market research has shown that 450 g and 750 g represent optimal harvest sizes for red snapper based on consumer preference (Miranda et al., 2021). As such, the WA model was used to determine the age at which individuals should reach these sizes (318 and 393 dph,

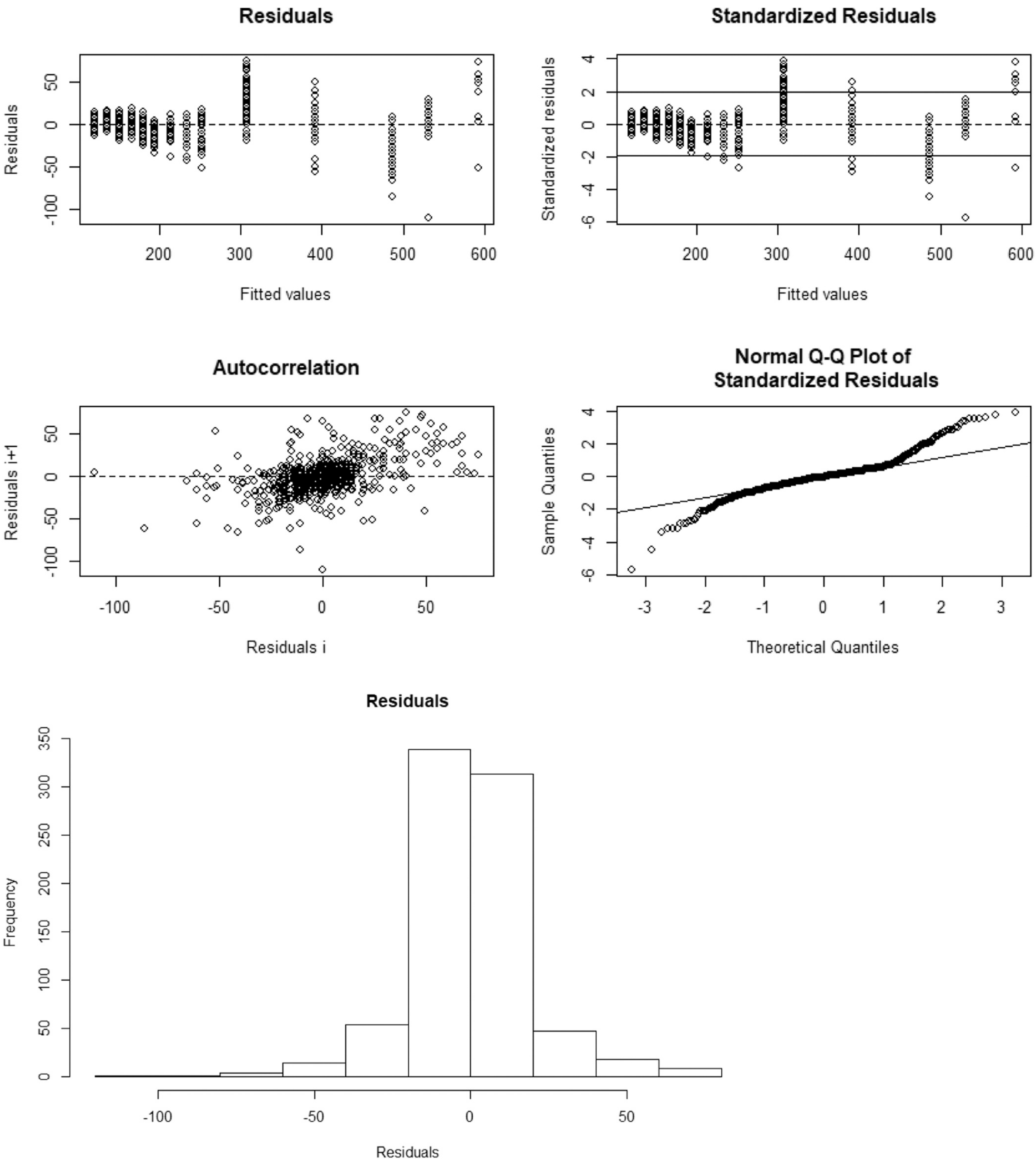


Fig. A.3. LA Residuals calculated for the von Bertalanffy model.

respectively), at which point the LA model was used to predict average length of fish at the corresponding age.

At each sampling date, all fish were measured from each tank. No outliers were excluded from the dataset. Graphical representations of residuals from each model as well as the log-transformed linear relationship between weight and length can be viewed in Appendix A.

3. Results

No statistically significant differences were observed between tanks at any of the sampling dates where fish were housed in replicated tanks (through 262 dph). As such, growth performance was calculated using pooled data aggregated from all tanks at each sampling date. No sexually dimorphic traits were observed before maturation and differences in size were insignificant between sexes after maturation; thus each growth model represents the combined performance of males and females.

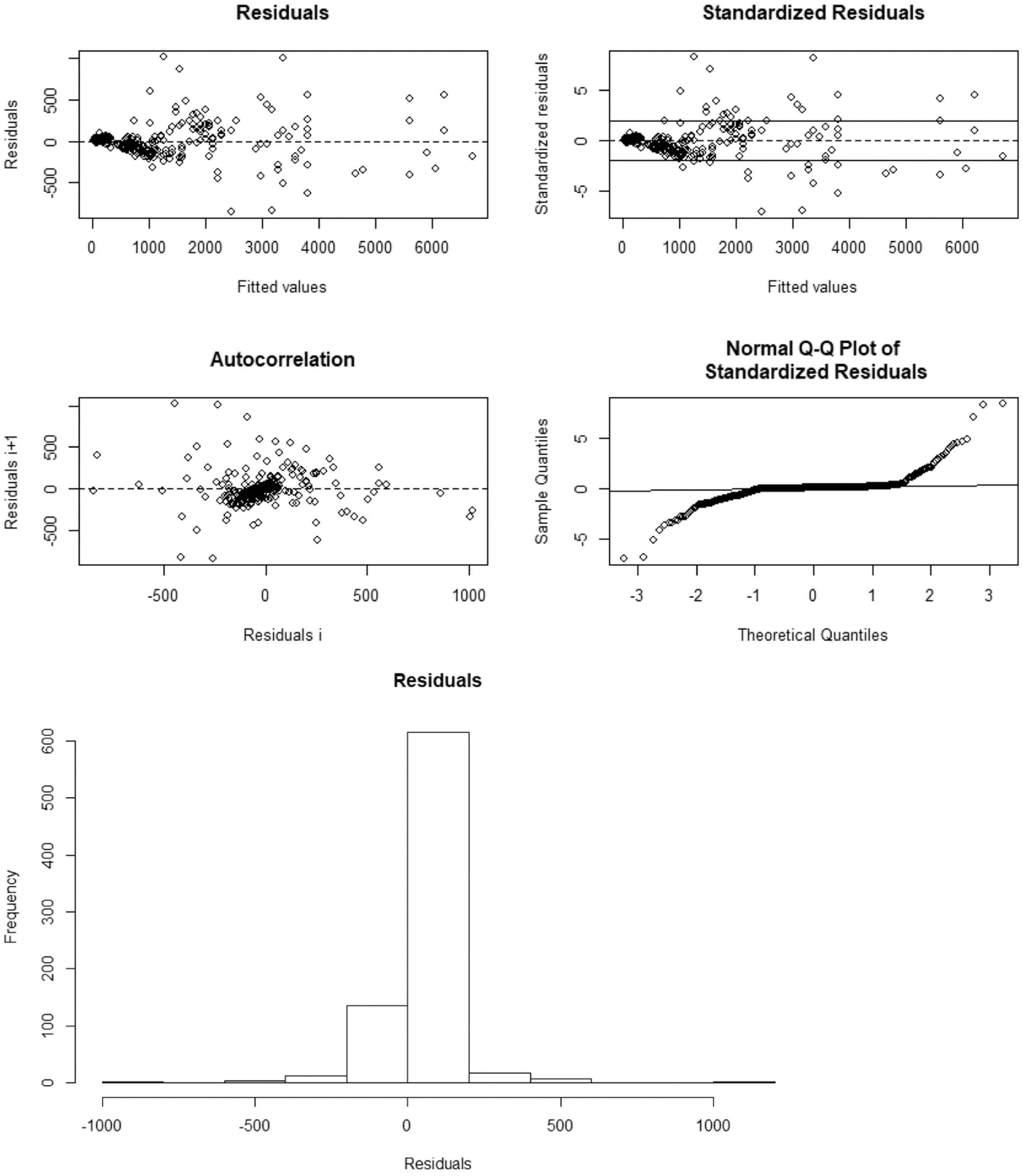


Fig. A.4. LW Relationship Residuals calculated for the von Bertalanffy model.

The AIC for the LA and WA models both indicate that the von Bertalanffy model was the most suitable for the data. Curves for the LA, WA, and WL models are presented in Figs. 1, 2, and 3, respectively. The LA relationship for captive reared northern red snapper was best described by the equation.

$$L_t = 742{\cdot}6\ (1 - e^{0{\cdot}001804(a-31{\cdot}57)})$$

while the WA relationship was best described by the equation.

$$W_t = 84720\ (1 - e^{-0{\cdot}0005787(a+78{\cdot}71)})^{3{\cdot}304}$$

The WL relationship for captive-reared northern red snapper was described by the power equation.

$$W = 0{\cdot}000003158\ L_t^{3{\cdot}304}$$

Table A.1
WA AIC Results computed for the von Bertalanffy, Gompertz, and logistic models.

	K	AICc	Delta_AICc	AICcWt	Cum.wt	LL
VBGF	4	10626.87	0	1	1	-5309.41
Gompertz	4	10673.43	46.56	0	1	-5332.69
logistic	4	10788.62	161.75	0	1	-5390.28

Table A.2
LA AIC Results computed for the von Bertalanffy, Gompertz, and logistic models.

	K	AICc	Delta_AICc	AICcWt	Cum.wt	LL
VBGF	4	7013.13	0	1	1	-3502.54
Gompertz	4	7103.61	90.48	0	1	-3547.78
logistic	4	7248.65	235.52	0	1	-3620.3

A summary of the relevant growth performance parameters observed for northern red snapper in this study is presented in Table 2. Each value represents the cumulative data through the given age. Absolute growth rate (AGR) increased with age while instantaneous growth rate (IGR) and specific growth rate (SGR) decreased with age. Fig. 4 shows the trends in AGR, SGR, and FCR within each sampling period as fish progressed through harvest-size and eventually maturation. AGR ranged from 1.08 to 5.8 g/day and increased with age, although a decline after one year post hatch may correspond with the onset of sexual maturation and gamete production. SGR ranged from 0.5% to 2.98%/day and decreased with age, while FCR values ranged from 0.93 to 1.47 and showed a modest increase with age.

Survival rates in the 450 L and 1000 L systems were 98.9% and 92.5% respectively. A summary of the water quality parameters for each of the culture systems described above is presented in Table 3.

4. Discussion

The AIC model selection results presented here indicate the broad suitability of multiple growth models for the growth of captive-reared red snapper and reinforce the need for multi-model inference to measure growth most effectively across teleost species. For the LA and WA relationships, the von Bertalanffy model was the most appropriate model based on AIC, but the equations generated for both the Gompertz and logistic models also fit the data closely. Despite reductions in sample size at later ages, confidence intervals were comparable to wild-capture data despite significantly smaller sample sizes at later ages. The power model was selected as the most appropriate for the WL data and generated the narrowest confidence intervals of any of the relationships presented here. The LA relationship showed a decrease in growth rate in later sampling dates, with total length approaching a theoretical asymptote of 742.6 mm. Because the WA relationship did not capture decreases in growth in even the latest sampling dates for this study, the theoretical asymptotic size of 84,720 g is predictably larger than any reasonable maximum size for the species. As such, the von Bertalanffy model for WA should only be used to model weight within the ages sampled here. Considering the Q_{10} physiological concept, which suggests that the metabolic rate and associated scope for growth roughly doubles with every 10 °C, the growth rates presented here may increase further with rearing practices that utilize higher, more stable temperatures (Jobling, 2002; Schmidt-Nielsen, 1983). This trend for accelerated growth rates at higher temperatures has been documented across a range of other Lutjanid species (Alcalá-Carrillo et al., 2016; Castillo-Vargasmachuca et al., 2013; Watanabe et al., 2001; Wuenschel et al., 2004).

Farmed fish generally grow more quickly in both length and weight than wild fish of the same species, but also gain more weight per unit of length than wild fish (Fleming et al., 2002). The general pattern of accelerated growth in farmed fish can be attributed to the optimization of environmental and ecological conditions within a controlled setting. This is due to an increased scope for growth resulting from lack of predation or energy needed for predator avoidance, the high availability of nutrient-dense food, and control of water quality parameters such as temperature, dissolved oxygen concentration, and laminar flow rate (Saraiva et al., 2018). Studies suggest that the allometric growth observed in farmed fish can be explained by an increased ability to form muscular and fatty tissues as opposed to the more energetically costly growth in the skeletal system that is necessary to increase total length (Lavajoo et al., 2020). The results presented here confirm the trend for accelerated growth rates in terms of length and weight in captive-raised red snapper relative to the available data for wild-caught red snapper (Saari et al., 2014; White and Palmer, 2004; Wilson and Nieland, 2001). Further, while increased rates of growth in terms of length were significant compared with wild-capture data, increased growth in terms of weight was considerably more pronounced, as has been shown across taxa (Benetti et al., 2002; Iversen and Benetti, 1995; Saari et al., 2014). The WA model predicted weights-at-age for farm raised red snapper from 3.7:1 – 4.2:1 compared with wild-caught red snapper from 0.5 to 1.5 years; by 3 years, this increase in weight at age was 5.7:1. Length-at-age for captive-reared red snapper was 1.6:1 through 1.5 years and diminished to 1.37:1 by 3 years of age (Saari et al., 2014). These findings indicate that the optimized environmental conditions available in captivity accelerate both the skeletal and muscular growth from even the youngest life-stages, but that these increases in size become more related to muscular growth as fish age. The growth rates observed in this study also surpass those found in short-term studies on captive red snapper both in the juvenile stage (1.97:1; Galkanda-Arachchige et al., 2021) and as sub-adults (2.73:1; Davis et al., 2005).

Species selection methods are critically important when considering new aquaculture ventures and incorporate a variety of criteria including the biological characteristics of the fish, the market prices and availability of wild-caught conspecifics, and the current aquaculture technologies available for the given species (Abellan and Basurco, 1999; Benetti et al., 1998; Cai et al., 2009). The growth performance of red snapper in this study was compared to available data from established, commercially relevant snapper species as well as other notable marine finfish species (Table 4). Recently, projects have sought to quantify the relative importance of these individual criteria to develop more reliable systems for species selection. One such study applied a novel, five-phase ranking system considering market criteria, performance traits including growth rate, biomass yield, and FCR, and current levels of industrial development to native species in the Caribbean to quantify the optimal species for the region. (Alvarez-Lajonchère and Ibarra-Castro, 2013). Using the available information from preliminary studies involving red snapper and supplementing unknown information with values from wild-capture literature, this system ranked red snapper in the 3rd highest-priority species class. After incorporating the growth performance, FCR, and survival rates documented in the current study into the analysis presented by Alvarez-Lajonchère and Ibarra-Castro (2013), the red snapper improved from the 3rd highest- priority endemic species class to the 2nd highest- priority endemic species class in the region. Including current wholesale prices and advances in spawning and juvenile production (Buchalla et al., 2023; McGuigan et al., 2021) into the 2013 analysis elevated the red snapper into the top priority class of endemic species in the Caribbean. A full accounting of these updated values within the five-phase ranking presented by Alvarez-Lajonchère and Ibarra-Castro (2013) can be found in Table 5. These findings reinforce the value in establishing data-based systems to conduct species selection analyses while demonstrating the importance of updating these classifications as new datasets become available. Further, based on the cross-taxa trend for captive growth rates to significantly exceed those of wild individuals, the incorporation of wild-capture data into these systems may be inappropriate.

This study provides the first estimates of food conversion, growth

Table A.3
Criteria of the evaluation point scoring system, considerations for scores assigned and the relative weight multipliers (in parentheses) are as follows (from Alvarez-Lajonchère and Ibarra-Castro (2013).

No.	Criterion/consideration	Points	Relative weight multiplier	Maximum total points
1	Species state of development of culture technologies		×3	30
1.1	Commercial-scale production on several sites/countries	10		
1.2	Commercial-scale production in one site/country	8		
1.3	Pilot-scale	5		
1.4	Experimental-scale	2		
1.5	Preliminary results based only on experimental scale or culture practices have been stopped for several years	0[a]		
	Additional points:			
	– Suitability to culture systems:			
	• Adaptation to wide range of culture systems	3		
	• Good results on large offshore cages	3		
	• Good results on recirculation systems, avoiding rough sea weather and land limitations	2		
	• Good results on intensive, semi-intensive and extensive systems	2		
	– Mortality during nursery and grow-out periods ≤ 20%	2		
	– Assessment based on ≥2 years of commercial or pilot-scale operations	1		
2	Market		×5	50
2.1	Wholesale price ≥ US$ 10/kg	10		
2.2	Wholesale price US$ 8.00–9.99/kg	8		
2.3	Wholesale price US$ 5.00–7.99/kg	5		
2.4	Wholesale price US$ 3.00–4.99/kg	2		
2.5	Wholesale price b US$ 3.00	0[a]		
	Additional points:			
	– Total aquaculture production value of species/close species			
	• > US$ 1×10^6	5		
	• US$ $0.1–1.0 \times 10^6$	4		
	• US$ $0.2–0.9 \times 10^5$	3		
	– Allowing for value-added processing industry			
	• Good filet yield (≥40%)	2		
	• Good filet price (>US$ 12.00/kg)	2		
	• Moderate filet price (US$ 8.00–12.00/kg)	1		
	• Species that can be marketed in various presentations (whole, fileted, in pre-packed cuts, fresh, salted, canned, smoked, frozen, etc.)	2		
	– Possibility of roe eating	1		
	– Possibility of live fish marketing	1		
	– Additional advantages for marketing (i.e., better lipid composition, absence of toxic substances, etc.)	1		
	– Cultured fish without certain toxic/parasites of wild fish	1		
	– Species that can be marketed in a wide range of sizes	2		
	– Species that suffered a drastic decline in wild stocks or the availability of wild fish is scarce or prohibited	2		
	– Significant price variability	−2		
3	Captive maturation and spawning control		×2	20
3.1	Voluntary spawning	10		
3.2	Induced spawning and natural fertilization	8		
3.3	Induced ovulation and artificial fertilization	4		
3.4	Wild ovulated spawners and artificial fertilization	2		
3.5	Very few practical results	0[a]		
	Additional points:			
	– Heterosexual spawners	1		
	– Batch spawners with asynchronous ovarian development	1		
4	Juvenile mass production technology development		×2	20
4.1	Commercial-scale in several sites/countries	10		
4.2	Commercial-scale in one site/country	8		
4.3	Pilot-scale	5		
4.4	Experimental-scale/wild juveniles available	3		
4.5	Preliminary results on experimental scale	0[a]		
	Additional points:			
	– Species with egg diameters bigger than 1 mm	1		
	– Total duration of larval rearing of 30–35 days or less	1		
	– Species that can be reared in fertilized ponds	1		
	– Larviculture difficulties[b]			
	• Difficulties between 1 and 3	2		
	• Difficulties between 4 and 5	1		
	• Difficulties > 5	−2		
5	Juvenile nursery growth in ≥90–120 days		×2	20
5.1	>150 g (>1.25 g/day)	10		
5.2	Between 120 and 140 g (≥1 g/day)	7		
5.3	Between 25 and 100 g (≥0.2 g/day)	4		
5.4	b25 g (b0.2 g/day)	1		
	Additional points:			
	– Data based on commercial or pilot-scale operations	1		
	– Harvest biomass			
	• ≥10 kg/m^3	2		
	• ≥5 kg/m^3	1		
	– Maximum biomass ≥ 1 kg/L/min	1		
6	Grow-out growth to commercial size		×4	40
6.1	Excellent AGR ≥ 4 kg in 12 months (≥12 g/day)	10		
6.2	Very good AGR: ~2–3.9 kg in 12 months (~6–11 g/day)	8		
6.3	Good AGR: ~1–1.9 kg in 12 months (~3–5 g/day)	6		
6.4	Moderate AGR: ~0.8–1 kg in 12–14 months (~2–2.9 g/day)	4		
6.5	Fair AGR: ~0.4–0.7 kg in 12–16 months (0.9–1.9 g/day)	2		
6.6	Poor AGR: ~0.4–0.6 kg in > 20 months (b0.9 g/day)	0[a]		
	Additional points:			
	– Maximum observed total length ≥ 140 cm	1		
	– Total length at first sexual maturity ≥ 55 cm	1		
	– Length at first maturity/commercial size ≥ 2	1		
	– Growth performance index (Φ') ≥ 3.25	1		
	– Great size dispersion (Δ Lt ≥ 100%)	−2		
7	Biomass yields		×4	40
7.1	≥40 kg/m^3 in cages/≥100 kg/m^3 in tanks	10		
7.2	~25–39 kg/m^3 in cages/~50–99 kg/m^3 in tanks	8		
7.3	≥20 t/ha/year in ponds	6		
7.4	~10–24 kg/m^3 in cages/tanks or ≥10 t/ha/year in ponds	4		
7.5	~5–9 kg/m^3 in cages/tanks or 6–9 t/ha/year in ponds	2		
	Additional points:			
	– Gregarious species	2		
	– Yield by water flow in tanks			
	• Yield > 1.5 kg/Lpm	3		
	• Yield 1.0–1.5 kg/Lpm	2		
8	Juvenile yield index		×3	30
8.1	b1000 juveniles/t/year	10		
8.2	~1000–1499 juveniles/t/year	8		
8.3	~1500–1999 juveniles/t/year	6		

(continued on next page)

Table A.3 (*continued*)

No.	Criterion/consideration	Points	Relative weight multiplier	Maximum total points
8.4	~2000–2500 juveniles/t/year	3		
8.5	>2500 juveniles/t/year	1		
9	Feeding		×4	40
9.1	FCR ≤ 1.2	10		
9.2	FCR ~ 1.3–1.6	8		
9.3	FCR ~ 1.6–2	5		
9.4	FCR > 2.1–3.0	2		
9.5	FCR > 3	1		
	Additional points:			
	– Good knowledge of nutritional requirements	2		
	– Specific feeds developments			
	• Fishmeal and fish oil in feed: b20%	3		
	• Fishmeal and fish oil in feed: 20–30%	2		
10	Tolerances		×1	10
10.1	Very tolerant to most factors	10		
10.2	Very tolerant to several factors	8		
10.3	Moderate tolerance to several factors	5		
10.4	Slightly tolerant to many factors	3		
10.5	Weakly tolerant to many factors	1		
10.6	Species prone to mass mortalities from low stress levels	0		
	Additional points:			
	– Oceanic/pelagic species adequate for offshore cages	3		
	– Social crowding	2		
	– Estuarine species suitable for poor water quality	1		
	– Species tolerant to fresh water/low salinity (3–5 ppt)	1		
	– Handling resistance	1		
	– Disease resistance	1		
	– Vulnerable to parasites and diseases	−2		
11	Bonus group: preliminary profitable analysis of culture economics and some important economic information.			
11.1	Profitable estimates of the species within the region	10		
11.2	Profitable estimates of the species on other region	8		
11.3	Profitable estimates of a close species in the region	6		
11.4	Profitable estimates of a close species in other region	4		
11.5	Net present value b 0 or profitability index b 1 or IRR less than the minimum acceptable rate of return	0[a]		
11.6	Economic failure within the region	0[a]		
11.7	Other positive financial indexes, figures or information:			
	– Initial capital investment of ≤$0.50 per dollar of annual sales revenue.	4		
	– Initial capital investment of $1.00 per dollar of annual sales revenue.	2		
	– Payback period (short, less than project's useful life)	2		
	– Profit margin ≥ $1.00/kg	4		
	– Profit margin ≥ $0.50–0.99/kg	3		
	– Cost of feed ≤ $1.50–1.70/kg fish produced	2		
	– Juvenile cost ≤ $1.00/kg	2		
	– Labor cost ≤ $2.00/kg	2		
	– Land/sea area long term lease concessions (≥75 years)	2		
	– Initial long periods free of tax payments (≥20 years)	2		
	– Species that must be reared in earthen ponds with high costs of earthmoving and construction	−2		
	– Species that must be fed with totally imported feeds	−2		
	– Species that have to depend on imported juveniles until hatchery mass production technology are ready	−2		
Total points (without including additional points)				310

Values[c] (%)	Points	Evaluation	Priority category
85–100	≥248	Excellent	1
60–84	186–247	Good	2
40–59	124–185	Marginal/poor	3
b40	b124	Not worth considering at present	4

US$ = United States dollars.

[a] Discarded.

[b] From Tucker (1998).

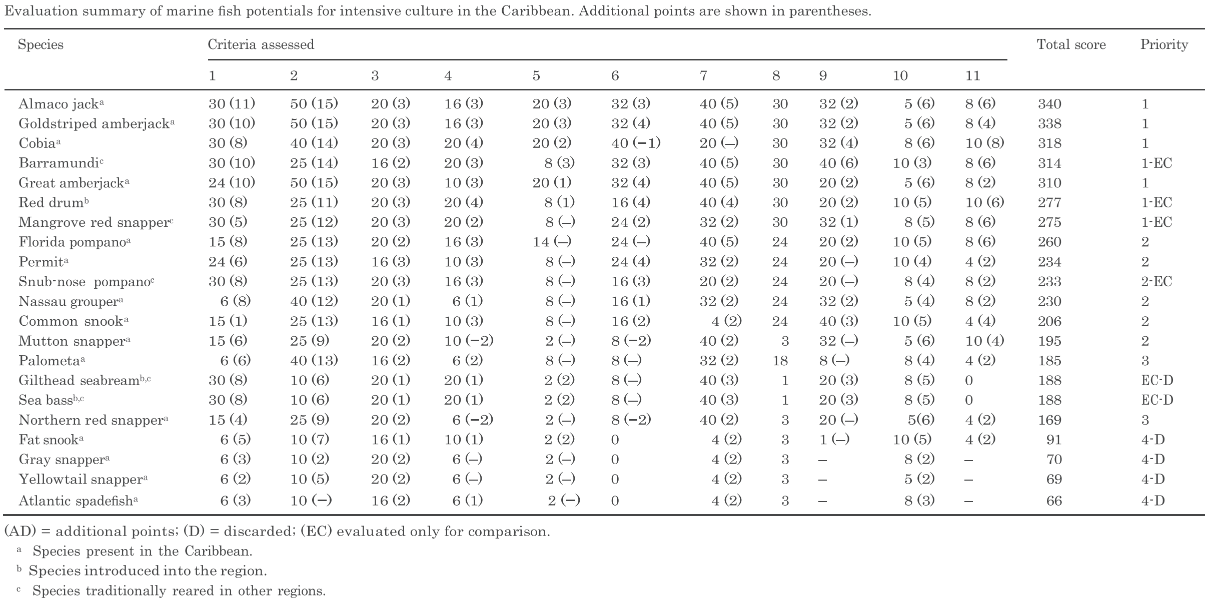
[c] Category limits can extend up to 5%.

performance and survival of captive red snapper from juveniles until sexual maturity using an innovative multi-model inference, and the results found here demonstrates the strong potential of red snapper as candidate species for marine aquaculture in the region.

CRediT authorship contribution statement

Charles McGuigan: Conceptualization, Methodology, Data Collection, Writing – original draft. **Yole Buchalla:** Conceptualization, Methodology, Data collection, Writing – review & editing. **Carlos Tudela**: Methodology, Data Collection. **Sean Starkman**: Data Collection, Investigation, Writing – review & editing. **Daniel Benetti**:

Table A.4
Evaluation summary of marine fish potentials for intensive culture in the Caribbean. Additional points are shown in parentheses (from Alvarez-Lajonchère and Ibarra-Castro (2013).



Evaluation summary of marine fish potentials for intensive culture in the Caribbean. Additional points are shown in parentheses.

Species	Criteria assessed											Total score	Priority
	1	2	3	4	5	6	7	8	9	10	11		
Almaco jack[a]	30 (11)	50 (15)	20 (3)	16 (3)	20 (3)	32 (3)	40 (5)	30	32 (2)	5 (6)	8 (6)	340	1
Goldstriped amberjack[a]	30 (10)	50 (15)	20 (3)	16 (3)	20 (3)	32 (4)	40 (5)	30	32 (2)	5 (6)	8 (4)	338	1
Cobia[a]	30 (8)	40 (14)	20 (3)	20 (4)	20 (2)	40 (−1)	20 (–)	30	32 (4)	8 (6)	10 (8)	318	1
Barramundi[c]	30 (10)	25 (14)	16 (2)	20 (3)	8 (3)	32 (3)	40 (5)	30	40 (6)	10 (3)	8 (6)	314	1-EC
Great amberjack[a]	24 (10)	50 (15)	20 (3)	10 (3)	20 (1)	32 (4)	40 (5)	30	20 (2)	5 (6)	8 (2)	310	1
Red drum[b]	30 (8)	25 (11)	20 (3)	20 (4)	8 (1)	16 (4)	40 (4)	30	20 (2)	10 (5)	10 (6)	277	1-EC
Mangrove red snapper[c]	30 (5)	25 (12)	20 (3)	20 (2)	8 (–)	24 (2)	32 (2)	30	32 (1)	8 (5)	8 (6)	275	1-EC
Florida pompano[a]	15 (8)	25 (13)	20 (2)	16 (3)	14 (–)	24 (–)	40 (5)	24	20 (2)	10 (5)	8 (6)	260	2
Permit[a]	24 (6)	25 (13)	16 (3)	10 (3)	8 (–)	24 (4)	32 (2)	24	20 (–)	10 (4)	4 (2)	234	2
Snub-nose pompano[c]	30 (8)	25 (13)	20 (3)	16 (3)	8 (–)	16 (3)	20 (2)	24	20 (–)	8 (4)	8 (2)	233	2-EC
Nassau grouper[a]	6 (8)	40 (12)	20 (1)	6 (1)	8 (–)	16 (1)	32 (2)	24	32 (2)	5 (4)	8 (2)	230	2
Common snook[a]	15 (1)	25 (13)	16 (1)	10 (3)	8 (–)	16 (2)	4 (2)	24	40 (3)	10 (5)	4 (4)	206	2
Mutton snapper[a]	15 (6)	25 (9)	20 (2)	10 (−2)	2 (–)	8 (−2)	40 (2)	3	32 (–)	5 (6)	10 (4)	195	2
Palometa[a]	6 (6)	40 (13)	16 (2)	6 (2)	8 (–)	8 (–)	32 (2)	18	8 (–)	8 (4)	4 (2)	185	3
Gilthead seabream[b,c]	30 (8)	10 (6)	20 (1)	20 (1)	2 (2)	8 (–)	40 (3)	1	20 (3)	8 (5)	0	188	EC-D
Sea bass[b,c]	30 (8)	10 (6)	20 (1)	20 (1)	2 (2)	8 (–)	40 (3)	1	20 (3)	8 (5)	0	188	EC-D
Northern red snapper[a]	15 (4)	25 (9)	20 (2)	6 (−2)	2 (–)	8 (−2)	40 (2)	3	20 (–)	5(6)	4 (2)	169	3
Fat snook[a]	6 (5)	10 (7)	16 (1)	10 (1)	2 (2)	0	4 (2)	3	1 (–)	10 (5)	4 (2)	91	4-D
Gray snapper[a]	6 (3)	10 (2)	20 (2)	6 (–)	2 (–)	0	4 (2)	3	–	8 (2)	–	70	4-D
Yellowtail snapper[a]	6 (2)	10 (5)	20 (2)	6 (–)	2 (–)	0	4 (2)	3	–	5 (2)	–	69	4-D
Atlantic spadefish[a]	6 (3)	10 (–)	16 (2)	6 (1)	2 (–)	0	4 (2)	3	–	8 (3)	–	66	4-D

(AD) = additional points; (D) = discarded; (EC) evaluated only for comparison.

[a] Species present in the Caribbean.

[b] Species introduced into the region.

[c] Species traditionally reared in other regions.

Conceptualization, Supervision, Writing – review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data Availability

Data will be made available on request.

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Appendix A

See Figs. A1–A4 and Tables A1–A4.

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