

Morphometric criteria for selection of high-yield phenotypes in *Epinephelus marginatus* (Lowe, 1834) under varying farming systems

Matheus Luiz da Costa Silva¹ , Graziela Tarôco² , Caio Augusto Perazza^{3,4} , Alexandre Wagner Silva Hilsdorf⁵ , Leila de Genova Gaya^{5*} 

¹Universidade Estadual Paulista  – Faculdade de Ciências Agrárias e Veterinárias – Jaboticabal (SP), Brazil.

²Universidade Federal de Lavras  – Programa de Pós-Graduação em Zootecnia – Lavras (MG), Brazil.

³Universidade de Mogi das Cruzes  – Núcleo Integrado de Biotecnologia – Mogi das Cruzes (SP), Brazil.

⁴Universidade de São Paulo  – Instituto Oceanográfico – São Paulo (SP), Brazil.

⁵Universidade Federal de São João del-Rei  – Departamento de Zootecnia – São João del-Rei (MG), Brazil.

*Corresponding author: genova@ufs.ju.edu.br

ABSTRACT

This study evaluated morphometric traits as indirect selection criteria for high-yield phenotypes in dusky grouper (*Epinephelus marginatus*) reared under three commercial production systems: recirculating aquaculture systems (RAS), marine cages (MC), and estuarine ponds (EP). Fish (n = 55) were harvested at 730 days to assess carcass weight (CW) and meat volume (MV). Differences among systems were analyzed using analysis of variance followed by Tukey's test ($p < 0.05$). Paired morphometric traits standard length (SL), head length (HL), body height (BH), and body width (BW) were evaluated through quadrant classification, and CW and MV were compared between quadrants using Welch's t-test. SL $\times$ BH was the best-performing criterion in RAS and BH $\times$ BW in EP for CW, while no significant differences in CW were observed in MC. Overall, no significant differences in MV were detected among quadrants in any of the farming systems. Despite the limited sample size, these findings suggest that non-lethal morphometric traits may be useful for phenotypic indirect selection for a higher meat yield in dusky grouper aquaculture, depending on the production system.

Keywords: Marine aquaculture; Phenotypic selection; Indirect selection; Carcass yield; Sustainability.

Cr terios morfom tricos para sele  o de fen tipos de alto rendimento em *Epinephelus marginatus* (Lowe, 1834) criado em diferentes sistemas comerciais

RESUMO

Este estudo avaliou caracter sticas morfom tricas como cr terios de sele  o indireta para fen tipos de alto rendimento em garoupa-verdadeira (*Epinephelus marginatus*) criada em tr s sistemas comerciais de produ  o: fluxo cont nuo de  gua (FC), tanques-rede marinhos (TRM) e viveiros estuarinos (VE). Os peixes (n = 55) foram abatidos aos 730 dias para avalia  o do peso   despesca (PD) e volume de carne (VC). As diferen as de rendimento entre os sistemas foram analisadas por an lise de vari ncia seguida do teste de Tukey ($p < 0,05$). Os pares de caracter sticas morfom tricas comprimento padr o (CP), comprimento de cabe a (CC), altura corporal (AC) e largura corporal (LC) foram avaliados por classifica  o em quadrantes com base nas m dias de cada caracter stica, gerando quatro grupos: alto-alto, alto-baixo, baixo-alto e baixo-baixo. O PD e o VC foram comparados entre os quadrantes utilizando o teste t de Welch. CP $\times$ AC foi o melhor cr terio no FC e AC $\times$ LC no VE para PD, sem diferen as significativas no TRM. N o foram detectadas diferen as significativas para VC em nenhum sistema. Apesar do tamanho amostral limitado, os resultados sugerem que caracter sticas morfom tricas mensur veis em animais vivos podem ser  teis para a sele  o fenot pica indireta objetivando maior peso, dependendo do sistema de produ  o.

Palavras-chave: Aquicultura marinha; Sele  o fenot pica; Sele  o indireta; Rendimento de carca a; Sustentabilidade.

Received: October 7, 2025 | **Approved:** June 11, 2026

Section editor: Felipe Vieira 

INTRODUCTION

The dusky grouper *Epinephelus marginatus* (Lowe, 1834) is an apex predator found in the eastern Atlantic Ocean, the Mediterranean Sea, and along the western Atlantic Ocean from the southern coast of Brazil to Patagonia (Pollard et al., 2018). This species is a protogynous hermaphrodite, exhibiting strong local fidelity and characterized by late sexual maturity and slow growth rates (Concini et al., 2018). According to Begossi et al. (2019), the dusky grouper is highly valued for its meat in culinary practices and plays a significant role as a commercial species in southeastern Brazil. However, high demand has led to the depletion of this species in its natural habitat (Priolli et al., 2016). The dusky grouper is classified as “vulnerable” on the International Union for Conservation of Nature Red List (Pollard et al., 2018). This situation emphasizes that inadequate fishing management can lead to a further decline in wild stocks. Consequently, there is an urgent need for technological advancements in captive production. Investigating the growth of this species, including its morphometric traits and performance parameters, is essential for determining the optimal size and stage for harvest (Begossi et al., 2019; Concini et al., 2018; Priolli et al., 2016).

Body weight and meat yield in fish are strongly influenced by the shape and proportions of the animal's body, which are determined by a combination of anatomical, physiological, and genetic factors (Bosworth et al., 2020; Fernandes et al., 2020). In dusky groupers, for example, Tarôco et al. (2024) identified significant associations between morphometric traits and carcass yield, highlighting the potential of these traits as indicators of productive performance. The relationship between zootechnical yield and morphometry in dusky groupers (*E. marginatus*) at harvest size and raised in commercial farming environments remains poorly understood. The literature primarily addresses this type of relationship only in juveniles or in natural environments (Aride et al., 2021; Russo et al., 2009; Tosta et al., 2022).

However, the expression of morphometric and performance-related traits is not determined solely by genetic factors; it is strongly influenced by environmental conditions through phenotypic plasticity and genotype–environment interactions. Key abiotic variables, such as salinity, temperature, and water pH, can affect metabolic rates, osmoregulatory balance, endocrine regulation, and energy partitioning, thereby influencing growth dynamics and morphometric development in fish (Michel et al., 2017; Mozanzadeh et al., 2021; Quadroni et al., 2023).

For instance, suboptimal thermal conditions may reduce

feed efficiency and protein synthesis, while fluctuations in salinity can modify body depth, condition factor, and overall body conformation. Beyond their direct physiological effects, environmental factors can also modulate the expression of genes associated with growth, stress response, and skeletal development, leading to persistent phenotypic adjustments even under subsequent stable conditions (Angilletta Jr., 2009; Ghalambor et al., 2015).

Therefore, both the rearing environment and the production system must be carefully considered in phenotypic evaluations. In addition to environmental effects, genetic factors contribute substantially to phenotypic variation in fish. In marine species such as the gilthead seabream (*Sparus aurata*), estimated heritability for body weight traits and for morphometric measurements ranges from 0.18 to 0.60 (Boulton et al., 2011; Saillant et al., 2006). These findings can support the use of these traits as potential selection criteria in genetic improvement programs for dusky grouper, depending on the heritability estimates for this species (Gianola & Rosa, 2015).

In this context, when associations between morphometric traits and productive performance (such as carcass yield) are identified, indirect selection can be utilized. This method involves selecting one trait as a criterion to achieve genetic improvements in another related trait, known as the selection objective (García-Ballesteros et al., 2022). This technique is particularly recommended when it is more practical to select based on the criterion than on the objective itself. Consequently, this strategy can help increase the volume of meat in fish without the need to slaughter potential breeders for weighing and evaluating carcass yield, as morphometric assessments can be conducted on live animals (Qiu et al., 2023).

Against this background, the primary aim of this research was to evaluate the relationship between morphometric traits. The study had three specific goals: to identify morphometric profiles associated with better productive performance, to compare harvesting traits across the different farming systems, and to investigate the potential of utilizing morphometric traits for indirect selection in breeding programs.

MATERIALS AND METHODS

This study strictly followed the animal experimentation protocols set by the National Council for Animal Experimentation Control to ensure that international animal welfare standards were met in laboratory settings. The Ethics Committee on the Use of Animals at the Universidade de Mogi das Cruzes, São Paulo, Brazil approved this study under protocol #005/2020 as a result.

Data source

Data were collected from 58 dusky groupers in December 2020 at the time of harvest. The fingerlings, sourced from Redemar Marine Hatchery in Ilhabela, São Paulo, Brazil, were the result of crossings between four females and one male, ensuring no genetic relatedness. The fish were raised under standardized conditions until the nursery phase and, at 310 days, weighing 139.53 ± 36.46 g, were then transferred to different farming systems, each characterized by distinct technological setups, stocking densities, water parameters, and feeding strategies, such as:

- Recirculating aquaculture system (RAS) (Fig. 1a): This system features continuous seawater renewal and a stocking density of 50 fish/m³, equivalent to 29.2 kg/m³, based on an average final weight of 583 g. Key environmental conditions include a stable temperature of 23.7°C, an oxygen concentration of 6.1 mg/L, and a salinity of 35 ppt. The fish are fed a marine carnivore extruded diet containing 45% crude protein twice daily, at a rate of 1% of their body biomass;
- Marine cages (MC) (Fig. 1b): These are floating circular cages located near the coast with a stocking density of 8 fish/m³. The fish are fed once daily to apparent satiation with trash fish. The water conditions include a temperature of 24°C, a salinity of 35 ppt, and an oxygen level of 6.3 mg/L;
- Estuarine ponds (EP) (Fig. 1c): These lined ponds receive brackish or marine water from lagoons connected to the sea, with a stocking density of 4 fish/m³. The fish are fed an extruded diet with 45% crude protein twice daily, at a rate of 1% of their body biomass. Environmental conditions in the ponds include a temperature of 21°C, an oxygen concentration of 7 mg/L, and a salinity of 17 ppt.

The farming systems used for dusky grouper culture are presented in Fig. 1: RAS, MC, and EP.

At 730 days, the fish were harvested and weighed. The following morphometric measurements were recorded: standard length (SL), measured from the front part of the head to the end of the caudal peduncle, in centimeters; head length (HL), the distance from the front of the head to the edge of the operculum, also in centimeters; body height (BH), measured from the ventral fin insertion to the dorsal fin insertion, in centimeters; and body width (BW), measured as the distance between the ventral fin insertions, in centimeters.

The fish were eviscerated and processed into standardized cuts. First, the head was removed from the body, followed by the detachment of the dorsal, pectoral, and caudal fins. After discarding the internal organs, the carcass weight (CW)

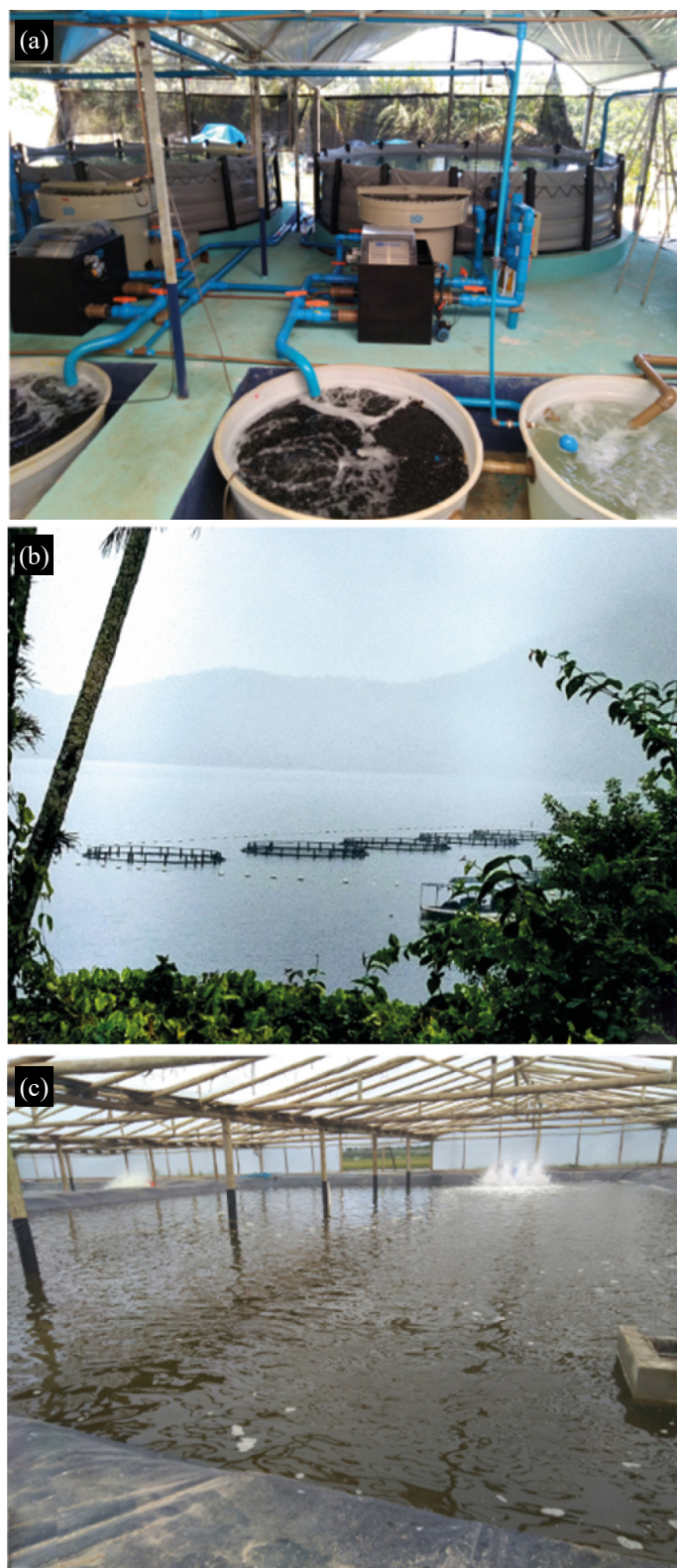


Figure 1. Schematic representation of the farming systems used in the production of dusky grouper (*Epinephelus marginatus*): (a) recirculating aquaculture system; (b) marine cage system; and (c) estuarine ponds system.

was measured in grams. To estimate meat volume (MV) and determine the number of steaks per fish, each fish was cut into transverse sections 3-cm thick. The total number of steaks was recorded, and the cross-sectional area (in cm²) of each steak was measured using ImageJ software (Schneider et al., 2012). The MV (in cm³) was calculated by multiplying the area of each steak by its thickness. The individual volumes of the steaks were then summed to obtain the total MV per fish, with a maximum of six steaks per individual.

Statistical analysis

All statistical analyses and graphical plots were conducted using R software, version 4.4.1 (R Core Team, 2016), with a statistical significance level set at 5%. The quadrants were created using the dplyr package (Wickham et al., 2023), while the graphs were plotted with the ggplot2 package (Wickham, 2016).

Descriptive statistics were calculated for the overall dataset and for each production system, with the goal of minimizing the influence of environmental factors (Oufiero & Whitlow, 2016). The normality of CW and MV within each farming system was assessed using Shapiro-Wilk's test, while the homogeneity of their variances was verified with Bartlett's test, both at a 5% significance level (Suppl. Mat. 1—<https://doi.org/10.5281/zenodo.21055728>). Based on these results, Pearson's correlation coefficients were estimated between the morphometric measures (SL, HL, BH, and BW) and the performance variables (CW and MV) for each production system, as well as for the entire dataset. Additionally, an analysis of variance (ANOVA) was conducted, followed by Tukey's test to compare the means of CW and MV among the different production systems.

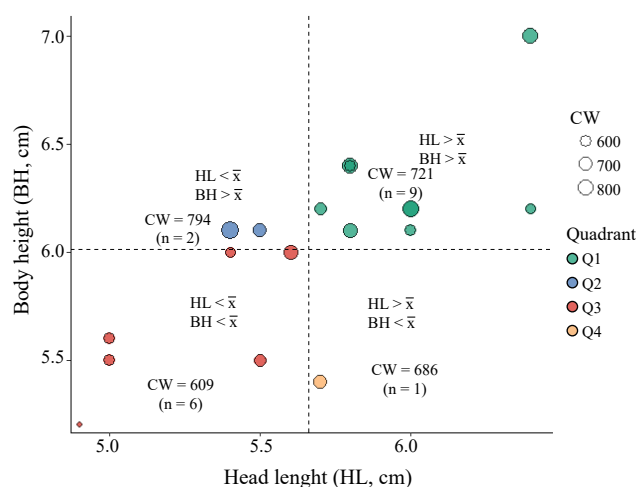
The morphometric groups were defined using combinations of ordered pairs of morphometric measurements plotted on a Cartesian plane. Each pair of traits (for instance, SL × HL) was represented on the x and y axes, respectively, and the quadrants were delineated based on the average values of these characteristics. The pairs considered included SL × HL, SL × BH, SL × BW, HL × BH, HL × BW, and BH × BW, which resulted in the data being divided into four distinct groups. These groups were classified into four quadrants:

- Animals that are larger than the mean in both axes;
- Larger in the y-axis and smaller in the x-axis;
- Smaller in both axes;
- Larger in the x-axis and smaller in the y-axis.

The animals were grouped into quadrants and classified based on ordered pairs to evaluate their zootechnical performance through various morphometric measurements. The variables CW and MV were analyzed using the ordered pair combinations

specific to each farming system. To establish the functional biological boundaries defining each morphometric group, the mean values of CW and MV were estimated for each quadrant. For the analyses within specific farming systems, the sample mean of each morphometric measure was calculated using data from each system independently. For the analysis of the pooled dataset (all systems combined), the sample mean of each measure was calculated considering all individuals.

The quadrant division served as a morphofunctional interpretation tool, with each quadrant representing a combined profile of the two analyzed traits. This approach enables the identification of biologically coherent morphometric groups that arise naturally from the interaction between the variables in their original scale, thereby preserving the intrinsic biological significance of each measurement. A graphical representation of the quadrant-based morphometric classification, exemplified by the dispersion of HL × BH within the RAS system, is shown in Fig. 2.



Dash lines indicate mean HL and BH values.

Figure 2. Scatter plot illustrates the division of individuals into quadrants based on head length (HL) × body height (BH) within the recirculating aquaculture system. The dashed lines represent the mean values used to define the quadrant boundaries. CW corresponds to carcass weight (g) means per quadrant.

To compare the means of CW and MV among different morphometric groups, we used Welch's t-test to analyze the data from all quadrants. This test was chosen due to unequal sample sizes and heterogeneous variances, as it adjusts the degrees of freedom and offers greater robustness compared to the conventional Student's t-test (Haginouchi et al., 2024; Molina-Botero et al., 2024).

RESULTS

Descriptive statistics

The dataset initially included 58 groupers, but it was reduced to 55 after removing records with questionable or incomplete data, including individuals with missing phenotypes and values that fell outside the biological boundaries of the traits.

Table 1 presents the summary statistics of the traits evaluated across the different farming systems and the overall dataset.

The coefficients of variation (CV) for CW and MV were: 12.9 and 15.8% in MC; 16 and 16% in RAS; and 19.4 and 24.7% in EP, respectively (Table 1).

Table 1. Summary statistics for the traits examined in each farming system, as well as for the overall dataset.

Fish farming system	Variable	N	Mean	Min	Max	SD	CV (%)
RAS	SL (cm)	18	18.30	16.00	20.40	1.11	6.65
	HL (cm)	18	5.66	4.90	6.40	0.43	7.60
	BH (cm)	18	6.01	5.20	7.00	0.43	7.19
	BW (cm)	18	2.92	2.30	3.70	0.35	11.83
	CW (g)	18	690.00	514.00	888.00	111.00	16.00
	MV (cm ³)	18	230.90	154.00	279.70	36.90	16.00
MC	SL (cm)	18	17.00	14.50	19.00	1.29	7.60
	HL (cm)	18	5.03	4.50	5.10	0.39	7.77
	BH (cm)	18	5.60	4.70	6.40	0.48	8.53
	BW (cm)	18	2.63	2.20	3.20	0.23	8.93
	CW (g)	18	983.00	722.00	1170.00	127.00	12.90
	MV (cm ³)	18	335.00	243.00	440.00	52.80	15.80
EP	SL (cm)	19	15.40	12.30	18.00	1.60	10.38
	HL (cm)	19	4.68	3.90	5.60	0.57	12.19
	BH (cm)	19	5.02	4.20	5.80	0.44	8.77
	BW (cm)	19	2.41	1.80	3.00	0.29	11.89
	CW (g)	19	444.50	320.00	602.00	86.20	19.40
	MV (cm ³)	19	136.00	82.10	194.00	33.60	24.70
Total	SL (cm)	55	17.00	12.30	20.40	1.80	10.60
	HL (cm)	55	5.10	3.90	6.40	0.62	12.10
	BH (cm)	55	5.50	4.20	7.00	0.61	10.60
	BW (cm)	55	2.70	1.80	3.70	0.36	13.47
	CW (g)	55	701.20	320.00	1170.00	247.30	35.27
	MV (cm ³)	55	232.00	82.10	440.00	92.00	39.64

N: number of observations; Min: minimum value; Max: maximum value; SD: standard deviation; CV: coefficient of variation; RAS: recirculating aquaculture system; MC: marine cages; EP: estuarine pond; SL: standard length; HL: head length; BH: body height; BW: body width; CW: carcass weight; MV: meat volume.

Comparison among systems

A comparison of the average zootechnical performance traits among the farming systems is provided in Table 2.

The distributions of the CW and MV variables were normally distributed across all systems ($p > 0.05$). Additionally, the Bartlett's test p -values for homogeneity of variances were above 0.05 for all systems. The precise p -values for these tests can be found in Suppl. Mat. 1 (<https://doi.org/10.5281/zenodo.2105572>). The ANOVA, along with Tukey's test, was statistically significant ($p < 0.05$) in zootechnical performance among the various farming systems (Table 2).

Table 2. Comparison of the average zootechnical performance traits across different fish farming systems.

Variable	Fish farming system	Mean*
CW (g)	RAS	689.90 ^b
	MC	983.30 ^a
	EP	444.50 ^c
MV (cm ³)	RAS	230.90 ^b
	MC	334.96 ^a
	EP	135.80 ^c

CW: carcass weight; MV: meat volume; RAS: recirculating aquaculture system; MC: marine cages; EP: estuarine pond; *means with different letters differ statistically according to Tukey's test at a 5% significance level.

Pearson's correlations

Table 3 shows the Pearson's correlation results for the characteristics of RAS, MC, and EP farming systems.

Table 3. Pearson's correlations among traits examined in recirculating aquaculture, marine cage, estuarine pond, and the overall dataset.

Fish farming system	Variable	SL	HL	BH	BW	CW
RAS	HL	0.77*				
	BH	0.87*	0.76*			
	BW	0.78*	0.77*	0.88*		
	CW	0.45 ^{NS}	0.41 ^{NS}	0.52 ^{NS}	0.44 ^{NS}	
	MV	0.44 ^{NS}	0.48 ^{NS}	0.54*	0.47 ^{NS}	0.91*
MC	HL	0.93*				
	BH	0.94*	0.88*			
	BW	0.79*	0.69*	0.81*		
	CW	0.16 ^{NS}	0.10 ^{NS}	0.25 ^{NS}	0.10 ^{NS}	
	MV	0.22 ^{NS}	0.12 ^{NS}	0.30 ^{NS}	0.16 ^{NS}	0.92*
EP	HL	0.88*				
	BH	0.77*	0.71*			
	BW	0.57*	0.56*	0.84*		
	CW	0.48 ^{NS}	0.46 ^{NS}	0.40 ^{NS}	0.30 ^{NS}	
	MV	0.42 ^{NS}	0.41 ^{NS}	0.31 ^{NS}	0.20 ^{NS}	0.91*
Total	HL	0.91*				
	BH	0.92*	0.85*			
	BW	0.80*	0.78*	0.89*		
	CW	0.45*	0.29*	0.46*	0.31*	
	MV	0.46*	0.31*	0.47*	0.32*	0.98*

SL: standard length; HL: head length; BH: body height; BW: body width; CW: carcass weight; MV: meat volume; RAS: recirculating aquaculture system; MC: marine cages; EP: estuarine pond; *statistically significant at 5%; NS: not significant.

In RAS, MV showed a significant correlation with BH ($r = 0.54$; $p < 0.05$). No other significant correlations between CW/MV and morphometric traits were detected in RAS. In MC, all correlations among morphometric traits (SL, HL, BH, BW) were significant ($p < 0.05$), with r values ranging from 0.69 to 0.94. CW and MV were significantly correlated with each other ($r = 0.92$), but not with any morphometric trait ($p > 0.05$). In EP, SL and BW were correlated at $r = 0.57$, and HL and BW at $r = 0.56$ ($p < 0.05$ for both).

In terms of significance, all correlations followed a similar pattern to those in the other systems, with positive and

significant correlations among the morphometric measurements. Additionally, the zootechnical performance variables were only correlated with one another.

t-Tests analysis

The t-test results for CW and MV are presented in Table 4 and in Suppl. Mat. 2 and 3 (Silva et al., 2026). Table 4 details CW means within the RAS and EP system, while the complete results for CW and MV across the overall dataset are provided in Suppl. Mat. 2 and 3 (Silva et al., 2026).

Table 4. Results of the t-tests comparing mean carcass weight (g) per quadrant, based on morphometric combinations, within recirculating aquaculture system and estuarine pond systems.

System	Morphometric Group	Q1	Q2	Q3	Q4	Significance
RAS	SL × HL	734	678	611	730	NS
	Ni	7	3	5	3	
	SL × BH	748	674	623	602	Q1 and Q3*
	Ni	9	2	6	1 (Si)	
	SL × BW	730	750	620	745	Q1 and Q3*
	Ni	8	1 (Si)	7	2	
	HL × BH	721	794	609	686	Q1 and Q3*
	Ni	9	2	6	1 (Si)	
	HL × BW	736	700	649	642	NS
	Ni	8	1 (Si)	7	2	
EP	BH × BW	732	743	620	0	Q1 and Q3*
	Ni	9	2	7	0	
	SL × HL	492	447	411	0	Q1 and Q3*
	Ni	7	2	10	0	
	SL × BH	485	602	389	477	Q1 and Q3*
	Ni	6	1 (Si)	9	3	
	SL × BW	485	489	391	477	Q1 and Q3*
	Ni	6	2	8	3	
	HL × BH	485	602	400	536	Q1 and Q3*
	Ni	6	1 (Si)	11	1 (Si)	
	HL × BW	485	489	402	536	Q1 and Q3*
	Ni	6	2	10	1 (Si)	
	BH × BW	502	376	414	0	Q1 and Q3*
	Ni	7	1 (Si)	11	0	

RAS: recirculating aquaculture system; EP: estuarine pond; SL: standard length; HL: head length; BH: body height; BW: body width; Ni: number of individuals; Si: insufficient individuals to perform t-test ($Ni < 2$); NS: no statistical significance was found for the tests between quadrants; Q1: individuals above the mean on both axes; Q2: below the mean on the x-axis and above on the y-axis; Q3: below the mean on both axes; Q4: above the mean on the x-axis and below on the y-axis. The value reported for each quadrant corresponds to the mean carcass weight of the individuals within that group; *statistically significant at 5%.

Significant differences in CW were observed among the morphometric groups in both the RAS and EP systems (Table 4). The CW mean varied in both systems as a function of the morphometric groups formed using the ordered pairs: SL $\times$ BH, SL $\times$ BW, HL $\times$ BH, and BH $\times$ BW. SL $\times$ HL and HL $\times$ BW were significant for mean CW only in the EP system. Among these, the measure that grouped individuals with the highest mean weight in the RAS system was SL $\times$ BH, while in the EP system it was BH $\times$ BW.

When considering the overall dataset that included all fish farming systems (Suppl. Mat. 2—<https://doi.org/10.5281/zenodo.21055728>), the difference between CW averages was significant across all morphometric groups, except for HL $\times$ BW. The significant differences in weight means were found between quadrants 1 (Q1) and 3 (Q3), except for BH $\times$ BW, in which the differences occurred between Q1 and Q2, and between Q2 and Q3. For SL $\times$ BW, there was also a significant difference between groups Q3 and Q4.

No significant differences were observed in the mean MV for the evaluated combinations across any of the farming systems ($p > 0.05$). However, these differences were detected in the analysis of the complete dataset (Suppl. Mat. 3—<https://doi.org/10.5281/zenodo.21055728>). In this case, the mean MV was statistically significant among all morphometric groups, except for HL $\times$ BH. These differences were primarily between Q1 and Q3, except for HL $\times$ BW, in which the difference was between Q1 and quadrant 4 (Q4). For SL $\times$ BW, a difference was also found between Q3 and Q4, and for BH $\times$ BW, between Q1 and Q2.

DISCUSSION

The descriptive statistics revealed notable differences in the variability of zootechnical traits among the different farming systems. Fish raised in the MC system showed lower dispersion in CW and MV, with coefficients of variation of 12.9 and 15.8%, respectively. In contrast, the RAS and EP systems exhibited higher variability for both zootechnical performance traits. The different dispersions around the mean among the different systems may be attributed to differences in environmental and management conditions, such as stocking density, salinity, temperature, dissolved oxygen, feeding protocol, and diet composition, factors known to influence phenotypic variability in aquaculture species (Gjedrem & Rye, 2018; Moses et al., 2021; Vallecillos et al., 2021).

The results of the ANOVA and Tukey's post-hoc test confirmed significant differences in zootechnical performance among the various systems, demonstrating that environmental

and management factors significantly influence both CW and MV. The MC outperformed the other systems, exhibiting not only higher average values for zootechnical traits but also greater consistency. These findings are consistent with previous studies indicating that different production systems impose distinct environmental conditions that can affect phenotypic expression (Sae-Lim et al., 2016; Vallecillos et al., 2021). Therefore, management and selection strategies tailored to specific systems are more effective than applying standardized practices across all systems (Castellano & Moroney, 2018).

The weak or non-significant correlations between morphometric traits and performance variables (CW and MV) observed in most systems suggest that environmental and biological variability may diminish the predictive power of linear morphometrics. Notably, the significant correlation detected between MV and BH in the RAS system indicates that specific trait combinations may be more responsive under certain rearing conditions. These findings are aligned with the studies conducted by Li et al. (2023) and Wang et al. (2017), which emphasize that relationships among morphometric traits are context-dependent and influenced by factors such as habitat, sex, diet, and hydrodynamic conditions.

Estimates of statistically significant correlations between all variables in the complete dataset may have been influenced by sample size, which impacts statistical significance (Table 3). Conversely, certain Pearson's correlations in specific aquaculture systems were not statistically supported, which may be due to the smaller number of animals in these groups.

T-tests comparing morphometric groupings by quadrant revealed that larger individuals consistently clustered in Q1 and exhibited higher mean values for CW, particularly in the RAS and EP systems. However, no consistent pattern was observed for MV within individual systems. The interpretation of these results, particularly the comparisons across farming systems, requires caution due to the limited sample size within each system and the potential influence of environmental variability among production conditions. The pronounced environmental differences among the MC, RAS, and EP, encompassing factors such as salinity, stocking density, and feeding regime, represent a potential confounding variable. These differences are known to influence morphometric development and zootechnical performance, complicating direct phenotypic comparisons across systems (Abaad et al., 2016).

The emergence of statistically significant patterns for both CW and MV in this aggregated analysis likely reflects the increased statistical power afforded by the larger combined

sample size. However, it may also amalgamate the distinct and possibly contradictory effects of each unique rearing environment on muscle growth and body form. Furthermore, the uneven distribution of individuals across morphometric quadrants, a consequence of both biological correlations and sample size, limited statistical power in underpopulated quadrants and increased the risk of type II errors (Cohen, 1988).

The absence of individuals in specific quadrants (Table 4, Suppl. Mat. 2 and 3—<https://doi.org/10.5281/zenodo.21055728>) may reflect an underlying biological pattern in the evaluated traits, as individuals with values below the mean for one morphometric measure also tend to exhibit below-average values for another (Russo et al., 2009). The predominance of individuals in Q1 and Q3, corresponding to organisms with values either above or below the mean for both traits, suggests the existence of a biological pattern within the studied population. This interpretation is supported by the Pearson's correlations observed among the morphometric measures (Table 4).

Furthermore, the low frequency of individuals in Q2, even after increasing the sample size via the analysis of the pooled dataset (Suppl. Mat. 2—<https://doi.org/10.5281/zenodo.21055728>) reinforces the hypothesis that this distribution is not random. However, applying this approach to larger datasets may reveal a greater representation of individuals in Q2 and Q4, which could alter the statistical significance of the tests. Such a scenario would allow for the identification of zootechnical yield patterns associated with morphometric groups that were not evident in the present study, likely due to the absence or low frequency of individuals in these quadrants.

The concentration of individuals in certain quadrants (particularly Q1 and Q3) reflects the correlational structure among morphometric traits but also limits statistical power in quadrants with few observations (Q2 and Q4). Although Welch's t-test allowed detection of differences in CW in the RAS and EP systems, results for underrepresented quadrants should be interpreted with caution due to the increased risk of type II error.

While no strong correlations were observed between morphometric traits and performance, individuals in Q1 showed higher CW and MV values, indicating a possible association between body shape and performance. However, selection decisions based solely on these traits should be approached cautiously, as body weight includes non-edible components such as viscera and fat. As reported by Souza et al. (2015), differences between whole-body weight and fillet yield can arise due to variation in tissue composition.

Selection programs may benefit from considering specific

morphometric relationships (e.g., $SL \times BH$, $HL \times BH$, and $BH \times BW$), as these were consistently associated with performance patterns within rearing systems. This pattern was especially evident in the RAS and EP systems, in which greater phenotypic variability and distinct quadrant-specific responses were observed, suggesting that body shape traits may be differentially expressed under contrasting environmental conditions. However, the application of these relationships as selection criteria should be approached with caution, given the limited sample size. Additionally, the well-documented influence of environmental effects and genotype $\times$ environment interactions on phenotypic traits in aquaculture species further supports this caution (Gjedrem & Rye, 2018; Sae-Lim et al., 2016; Wringe et al., 2016).

Although the EP system exhibited lower average performance, the presence of individuals surpassing system-level means indicates substantial untapped phenotypic potential. This finding aligns with previous studies demonstrating that suboptimal production environments may mask genetic merit, leading to an underestimation of individual performance potential (Houston et al., 2020).

Similar morphometric–performance associations have been reported in marine fish species, whose body depth and width are positively correlated with growth rate, biomass accumulation, and fillet yield (Boulton et al., 2011; Fragkouli et al., 2021; Vallecillos et al., 2023). These traits are also known to present moderate heritability coefficient, reinforcing their suitability as phenotypic indirect selection criteria in breeding programs (Antonello et al., 2009).

Although the dusky grouper population within the farming systems consisted of half and full-siblings, a potential methodological limitation, variability in morphometric and zootechnical yield phenotypes is expected, according to Houston et al. (2020).

Another important aspect to consider is the behavioral ecology. Study by Baras and Jobling (2002) indicates that factors such as social dominance and competition for food can lead to growth differences and increased cannibalism, even among genetically similar fish. These dynamics can complicate the consistency of morphometric–performance associations, which may explain why biometric indices have limited predictive power in certain systems, such as the MC system.

CONCLUSION

While morphometric traits provide valuable insights into fish body shape and relative size, they are limited as standalone predictors of carcass yield or MV. Among the systems evaluated, MC showed the highest mean values for

both CW and MV, followed by RAS and EP. Phenotypic indirect selection based on morphometric traits seemed to be ineffective in the MC. However, in the RAS and EP systems, specific combinations of traits, especially those relating to BH and BW, were linked to better CW. From a production management perspective, selected morphometric traits may serve as indirect indicators for identifying potential broodstock without the need for slaughter in specific systems, but their effectiveness appears to be system-dependent and was not observed for CW in the MC system.

The most promising morphometric combinations associated with CW gains were SL $\times$ BH in RAS and BH $\times$ BW in EP. The use of these phenotypic traits as selection criteria within each respective farming system is recommended for practical applications. However, the application of these criteria as an indirect selection tool for *E. marginatus* assumes that the heritability of both the morphometric traits and harvest weight are moderate to high (Boulton et al., 2011; Saillant et al., 2006). Furthermore, extrapolating these results to broader populations should be done with caution, as the sample size and the unequal distribution of individuals among morphometric quadrants may limit the inference of the observed effects. These findings emphasize the need for system-specific selection strategies to optimize phenotypic selection and enhance production efficiency in dusky grouper aquaculture.

The limited number of individuals used in this study ($n = 55$, distributed across three farming systems) reduces the statistical power and robustness of the estimated associations. However, given the dusky grouper's vulnerability to extinction (Pollard et al., 2018) and the incipient nature of its production in Brazil (Begossi et al., 2019), this constraint reflects inherent biological and husbandry challenges associated with data acquisition for this species. Nevertheless, as few studies have addressed broodstock selection in this species, the present work provides valuable preliminary insights to support future research involving larger sample sizes.

Future research could explore mathematical modeling to simulate individual distribution across morphometric combinations (Bianca, 2021), as well as advanced phenotyping tools such as ultrasonography and computed tomography (Rezende et al., 2023). Additionally, investigations into genotype-by-environment interactions would contribute to more robust selection strategies, provided that genetic data become available.

CONFLICT OF INTEREST

Nothing to declare.

DATA AVAILABILITY STATEMENT

Data will be made available upon request.

The supplementary material is available at Zenodo: <https://doi.org/10.5281/zenodo.21055728>

AUTHORS' CONTRIBUTIONS

Conceptualization: Gaya, L.G.; **Data curation:** Silva, M.L.C., Tarôco, G., Perazza, C.A.; **Formal Analysis:** Silva, M.L.C.; **Writing – original draft:** Silva, M.L.C.; **Investigation:** Tarôco, G.; **Resources:** Tarôco, G., Hilsdorf, A.W.S.; **Writing – review & editing:** Perazza, C.A., Hilsdorf, A.W.S., Gaya, L.G.; **Supervision:** Hilsdorf, A.W.S.; Gaya, L.G.; **Final approval:** Gaya, L.G.

FUNDING

Conselho Nacional de Desenvolvimento Científico e Tecnológico 

Grant No.: 309570/2021-2

Fundação de Amparo à Pesquisa do Estado de São Paulo 

Grant No.: 2019/07.023-2

Coordenação de Aperfeiçoamento de Pessoal de Nível Superior 

Grant No.: 88882.184482/2018-01

DECLARATION OF THE USE OF ARTIFICIAL INTELLIGENCE TOOLS

During the preparation of this work the authors used AI language tools (ChatGPT and Claude) to improve the English language. After using this tool/service, the authors reviewed and edited the content as needed and take full responsibility for the content of the publication.

ACKNOWLEDGMENTS

The authors thanks Claudia Ehlers Kerber from the Redemar Marine Hatchery for all the support during this project.

REFERENCES

- Abaad, M., Tuset, V. M., Montero, D., Lombarte, A., Otero-Ferrer, J. L., & Haroun, R. (2016). Phenotypic plasticity in wild marine fishes associated with fish-cage aquaculture. *Hydrobiologia*, 765, 343-358. <https://doi.org/10.1007/s10750-015-2428-5>
- Angilletta Jr., M. J. (2009). *Thermal adaptation: A theoretical and empirical synthesis*. Oxford University Press. <https://doi.org/10.1093/acprof:oso/9780198570875.001.1>



- Antonello, J., Massault, C., Franch, R., Haley, C. S., Pellizzari, C., Bovo, G., Patarnello, T., de Koning, D. J., & Bargelloni, L. (2009). Estimates of heritability and genetic correlation for body length and resistance to fish pasteurellosis in the gilthead sea bream (*Sparus aurata* L.). *Aquaculture*, 298(1-2), 29-35. <https://doi.org/10.1016/j.aquaculture.2009.10.022>
- Aride, P. H. R., Gomes, M. F. S., Azevedo, D. G., Sangali, G. R., Silva, A. C. F., Lavander, H. D., Souza, A. B., Polese, M. F., Mattos, D. C., Bassul, L. A., Cardoso, L. D., Oliveira, A. T., & Faggio, C. (2021). Dusky grouper *Epinephelus marginatus* growth and survival when exposed to different photoperiods. *Fishes*, 6(3), 31. <https://doi.org/10.3390/fishes6030031>
- Baras, E., & Jobling, M. (2002). Dynamics of intracohort cannibalism in cultured fish. *Aquaculture Research*, 33(7), 461-479. <https://doi.org/10.1046/j.1365-2109.2002.00732.x>
- Begossi, A., Salyvonchik, S., Glamuzina, B., Souza, S. P., Lopes, P. F. M., Priolli, R. H. G., Prado, D. O., Ramires, M., Clauzet, M., Zapelini, C., Schneider, D. T., Silva, L. T., & Silvano, R. A. M. (2019). Fishers and groupers (*Epinephelus marginatus* and *E. morio*) in the coast of Brazil: Integrating information for conservation. *Journal of Ethnobiology and Ethnomedicine*, 15, 53. <https://doi.org/10.1186/s13002-019-0331-2>
- Bianca, C. (2021). Mathematical and computational modeling of biological systems: Advances and perspectives. *AIMS Biophysics*, 8(4), 318-321. <https://doi.org/10.3934/BIOPHY.2021025>
- Bosworth, B., Waldbieser, G., Garcia, A., Tsuruta, S., & Lourenco, D. (2020). Heritability and response to selection for carcass weight and growth in the Delta Select strain of channel catfish *Ictalurus punctatus*. *Aquaculture*, 515, 734507. <https://doi.org/10.1016/j.aquaculture.2019.734507>
- Boulton, K., Massault, C., Houston, R. D., de Koning, D. J., Haley, C. S., Bovenhuis, H., Batargias, C., Canário, A. V. M., Kotoulas, G., & Tsigonopoulos, C. S. (2011). QTL affecting morphometric traits and stress response in the gilthead seabream (*Sparus aurata*). *Aquaculture*, 319(1-2), 58-66. <https://doi.org/10.1016/j.aquaculture.2011.06.044>
- Castellano, R. L., & Moroney, J. (2018). Farming adaptations in the face of climate change. *Renewable Agriculture and Food Systems*, 33(3), 206-211. <https://doi.org/10.1017/S174217051700076X>
- Cohen, J. (1988). *Statistical power analysis for the behavioral sciences* (2nd ed.). Lawrence Erlbaum Associates. <https://doi.org/10.1016/C2013-0-10517-X>
- Condini, M. V., García-Charton, J. A., & Garcia, A. M. (2018). A review of the biology, ecology, behavior and conservation status of the dusky grouper, *Epinephelus marginatus* (Lowe, 1834). *Reviews in Fish Biology and Fisheries*, 28, 301-330. <https://doi.org/10.1007/s11160-017-9502-1>
- Fernandes, A., Turra, E., Alvarenga, E., Passafaro, T., Lopes, F., Alves, G., Singh, V., & Rosa, G. M. (2020). Deep learning image segmentation for extraction of fish body measurements and prediction of body weight and carcass traits in Nile tilapia. *Computers and Electronics in Agriculture*, 170, 105274. <https://doi.org/10.1016/j.compag.2020.105274>
- Fragkoulis, S., Kerasovitis, D., Batargias, C., & Koumoundouros, G. (2021). Body-shape trajectories and their genetic variance component in gilthead seabream (*Sparus aurata* L.). *Scientific Reports*, 11(1), 16964. <https://doi.org/10.1038/s41598-021-95726-9>
- García-Ballesteros, S., Fernández, J., Kause, A., & Villanueva, B. (2022). Predicted genetic gain for carcass yield in rainbow trout from indirect and genomic selection. *Aquaculture*, 554, 738119. <https://doi.org/10.1016/j.aquaculture.2022.738119>
- Ghalambor, C. K., Hoke, K. L., Ruell, E. W., Fischer, E. K., Reznick, D. N., & Hughes, K. A. (2015). Non-adaptive plasticity potentiates rapid adaptive evolution of gene expression in nature. *Nature*, 525(7569), 372-375. <https://doi.org/10.1038/nature15256>
- Gianola, D., & Rosa, G. J. M. (2015). One hundred years of statistical developments in animal breeding. *Annual Review of Animal Biosciences*, 3, 19-56. <https://doi.org/10.1146/annurev-animal-022114-110733>
- Gjedrem, T., & Rye, M. (2018). Selection response in fish and shellfish: a review. *Reviews in Aquaculture*, 10(1), 168-179. <https://doi.org/10.1111/raq.12154>
- Haginouchi, T., Zhang, Y., Nishino, D., Phomvisith, O., & Gotoh, T. (2024). PSV-6 effect of maternal undernutrition on gene expression related to immune system in spleen of Japanese Black (Wagyu) fetuses. *Journal of Animal Science*, 102(Suppl. 3), 527-528. <https://doi.org/10.1093/jas/skae234.593>
- Houston, R. D., Bean, T. P., Macqueen, D. J., Gundappa, M. K., Jin, Y. H., Jenkins, T. L., Selly, S. L. C., Martin, S. A. M., Stevens, J. R., Santos, E. M., Davie, A., & Robledo, D. (2020). Harnessing genomics to fast-track genetic improvement in aquaculture. *Nature Reviews Genetics*, 21(7), 389-409. <https://doi.org/10.1038/s41576-020-0227-y>
- Li, Y., Feng, M., Huang, L., Zhang, P., Wang, H., Zhang, J., Tian, Y., & Xu, J. (2023). Weight-length relationship analysis revealing the impacts of multiple factors on body shape of fish in China. *Fishes*, 8(5), 269. <https://doi.org/10.3390/fishes8050269>
- Michel, M., Chien, H., Beachum, C., Bennett, M., & Knouft, J. (2017). Climate change, hydrology, and fish morphology: Predictions using phenotype-environment associations. *Climatic Change*, 140, 563-576. <https://doi.org/10.1007/s10584-016-1856-1>

- Molina-Botero, I., Villegas, D., Montoya, A., Mazabel, J., Bastidas, M., Ruden, A., Gaviria, H., Peláez, J. D., Chará, J., Murgueitio, E., Moorby, J., & Arango, J. (2024). Effect of a silvopastoral system with *Leucaena diversifolia* on enteric methane emissions, animal performance, and meat fatty acid profile of beef steers. *Agroforestry Systems*, 98, 1967-1984. <https://doi.org/10.1007/s10457-024-01046-y>
- Moses, M., Chauka, L. J., de Koning, D. J., Palaiokostas, C., & Mtolera, M. S. P. (2021). Growth performance of five different strains of Nile tilapia (*Oreochromis niloticus*) introduced to Tanzania reared in fresh and brackish waters. *Scientific Reports*, 11, 11147. <https://doi.org/10.1038/s41598-021-90505-y>
- Mozanzadeh, M. T., Safari, O., Oosooli, R., Mehrjooyan, S., Najafabadi, M. Z., Hoseini, S. J., Saghavi, H., & Monem, J. (2021). The effect of salinity on growth performance, digestive and antioxidant enzymes, humoral immunity and stress indices in two euryhaline fish species: Yellowfin seabream (*Acanthopagrus latus*) and Asian seabass (*Lates calcarifer*). *Aquaculture*, 534, 736329. <https://doi.org/10.1016/j.aquaculture.2020.736329>
- Oufiero, C., & Whitlow, K. (2016). The evolution of phenotypic plasticity in fish swimming. *Current Zoology*, 62(5), 475-488. <https://doi.org/10.1093/cz/zow084>
- Pollard, D. A., Afonso, P., Bertonicini, A. A., Fennessy, S., Francour, P., & Barreiros, J. (2018). *Epinephelus marginatus*. *The IUCN Red List of Threatened Species* 2018. <https://doi.org/10.2305/IUCN.UK.2018-2.RLTS.T7859A100467602.en>
- Priolli, R. H. G., Bajay, M. M., Silvano, R. A. M., & Begossi, A. (2016). Population genetic structure of an estuarine and a reef fish species exploited by Brazilian artisanal fishing. *Scientia Marina*, 80(4), 467-477. <https://doi.org/10.3989/scimar.04407.17A>
- Qiu, Z., Tang, Z., Ma, Y., Huang, T., Xiao, J., Chen, L., Guo, Z., Luo, Y., & Sun, Y. (2023). Correlation and path coefficient analysis between morphometric traits and body weight in *Leptobarbus hoevenii*. *Journal of Southern Agriculture*, 54(9), 2646-2653. <https://doi.org/10.3969/j.issn.2095-1191.2023.09.015>
- Quadroni, S., Santis, V., Carosi, A., Vanetti, I., Zaccara, S., & Lorenzoni, M. (2023). Past and present environmental factors differentially influence genetic and morphological traits of Italian barbels (Pisces: Cyprinidae). *Water*, 15(2), 325. <https://doi.org/10.3390/w15020325>
- R Core Team (2016). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing. Retrieved from <https://www.R-project.org/>
- Rezende, C. E. D., Perazza, C. A., Freitas, R. T. F. D., Hallerman, E., & Hilsdorf, A. W. S. (2023). Use of ultrasonographic imaging for non-invasive carcass yield prediction in Nile tilapia (*Oreochromis niloticus*). *Aquaculture International*, 31(5), 2763-2778. <https://doi.org/10.1007/s10499-023-01109-4>
- Russo, T., Pulcini, D., Bruner, E., & Cataudella, S. (2009). Shape and size variation: Growth and development of the dusky grouper (*Epinephelus marginatus* Lowe, 1834). *Journal of Morphology*, 270(1), 83-96. <https://doi.org/10.1002/jmor.10674>
- Sae-Lim, P., Gjerde, B., Nielsen, H. M., Mulder, H., & Kause, A. (2016). A review of genotype-by-environment interaction and micro-environmental sensitivity in aquaculture species. *Reviews in Aquaculture*, 8(4), 369-393. <https://doi.org/10.1111/raq.12098>
- Saillant, E., Dupont-Nivet, M., Haffray, P., & Chatain, B. (2006). Estimates of heritability and genotype-environment interactions for body weight in sea bass (*Dicentrarchus labrax* L.) raised under communal rearing conditions. *Aquaculture*, 254(1-4), 139-147. <https://doi.org/10.1016/j.aquaculture.2005.10.018>
- Schneider, C. A., Rasband, W. S., & Eliceiri, K. W. (2012). NIH Image to ImageJ: 25 years of image analysis. *Nature Methods*, 9(7), 671-675. <https://doi.org/10.1038/nmeth.2089>
- Silva, M. L. C., Tarôco, G., Perazza, C. A., Hilsdorf, A. W. S., & Gaya, L. G. (2026). Supplementary Material: Morphometric criteria for selection of high-yield phenotypes in *Epinephelus marginatus* (Lowe, 1834) under varying farming systems [Data set]. *Zenodo*. <https://doi.org/10.5281/zenodo.21055728>
- Souza, R., Viegas, E., Zuanon, J., Carvalho, M., & Goes, E. S. R. (2015). Processing yield and chemical composition of rainbow trout (*Oncorhynchus mykiss*) with regard to body weight. *Acta Scientiarum. Animal Sciences*, 37(2), 103-108. <https://doi.org/10.4025/actascianimsci.v37i2.24165>
- Tarôco, G., Perazza, C. A., Gomes, M. E. S., Kerber, C. E., Reis-Neto, R. V., & Hilsdorf, A. W. S. (2024). Assessment of body metrics, weight, and carcass yields in dusky grouper (*Epinephelus marginatus*) through correlation and path analysis: Implications for optimizing genetic breeding programs. *Aquaculture*, 590, 741100. <https://doi.org/10.1016/j.aquaculture.2024.741100>
- Tosta, G., Muramoto, C., Medeiros, S. C., Albinati, R., Olier, B. S., & Sanches, E. (2022). Skeletal anomalies in dusky grouper (*Epinephelus marginatus*) larviculture. *Latin American Journal of Aquatic Research*, 50(4), 628-632. <https://doi.org/10.3856/vol50-issue4-fulltext-2903>
- Vallecillos, A., María-Dolores, E., Villa, J., Afonso, J. M., & Armero, E. (2023). Potential use of image analysis in breeding programs for growth and yield traits in meagre (*Argyrosomus regius*). *Journal of Marine Science and Engineering*, 11(11), 2067. <https://doi.org/10.3390/jmse11112067>

- Vallecillos, A., María-Dolores, E., Villa, J., Rueda, F. M., Carrillo, J., Ramis, G., Soula, M., Afonso, J. M., & Armero, E. (2021). Phenotypic and genetic components for growth, morphology, and flesh-quality traits of meagre (*Argyrosomus regius*) reared in tank and sea cage. *Animals*, 11(11), 3285. <https://doi.org/10.3390/ani11113285>
- Wang, L., Wu, Z., Liu, M., Liu, W., Zhao, W., Liu, H., Zhang, P., & You, F. (2017). Length–weight and length–length relationships, and condition factors of black rockfish (*Sebastes schlegelii* Hilgendorf, 1880) in Lidao Bay, China. *Thalassas*, 33(1), 57-63. <https://doi.org/10.1007/s41208-017-0021-6>
- Wickham, H. (2016). *ggplot2: Elegant graphics for data analysis*. Springer. Retrieved from <https://ggplot2.tidyverse.org>
- Wickham, H., François, R., Henry, L., Müller, K., & Vaughan, D. (2023). *dplyr: A grammar of data manipulation (R package version 1.1.4)*. Retrieved from <https://CRAN.R-project.org/package=dplyr>
- Wringe, B. F., Purchase, C. F., & Fleming, I. A. (2016). In search of a “cultured fish phenotype”: a systematic review, meta-analysis and vote-counting analysis. *Reviews in Fish Biology and Fisheries*, 26, 351-373. <https://doi.org/10.1007/s11160-016-9431-4>