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Morphometric relationships as proxies for reproductive maturity in the clam *Anomalocardia flexuosa* (Linnaeus, 1767)

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ABSTRACT

The objective of this study was to describe the morphometric relationships between different shell dimensions of the bivalve *Anomalocardia flexuosa*, to check the changes in the growth pattern, and to determine the adult and juvenile phases and the size of sexual maturity of the species using morphometric measurements. Considering the 52,873 specimens measured in the present study, all the allometric relationships established for *A. flexuosa* were significant, and both the relations between length × height and length × width showed positive allometry. The K means clustering separated the dataset between juveniles and adults and defined 13.20–14.60 mm shell as the interval of length for the transitional phase. The growth pattern was significantly different between juveniles and adults, in which juveniles presented isometric growth and adults had a negative allometric growth. The fit of the logistic model indicated that the shell length at sexual maturity was 13.80 mm. The *A. flexuosa* juvenile shell had a more rounded shape than the adult. Processes related to animal development and environmental characteristics may influence the shell shape. The maturity size found in the present study is according to the range of maturity proposed in the literature.

Keywords: Allometry; L50; Shell; Morphological maturity.

Relações morfométricas como indicadoras para maturidade reprodutiva no molusco *Anomalocardia flexuosa* (Linnaeus, 1767)

RESUMO

Os objetivos deste estudo foram descrever as relações morfométricas entre diferentes dimensões da concha do bivalve *Anomalocardia flexuosa*, verificar as alterações no padrão de crescimento e determinar as categorias adulto e juvenil e o tamanho da maturidade sexual da espécie utilizando medidas morfométricas. Considerando os 52.873 espécimes medidos no presente estudo, todas as relações alométricas estabelecidas para *A. flexuosa* foram significativas, e ambas as relações comprimento × altura e comprimento × largura apresentaram alometria positiva. O agrupamento *K means* separou o conjunto de dados entre juvenis e adultos e definiu 13,20–14,60 mm da concha como o intervalo de comprimento para a fase de transição. O padrão de crescimento foi significativamente diferente entre juvenis e adultos; juvenis apresentaram crescimento isométrico, e os adultos, crescimento alométrico negativo. O ajuste do modelo logístico indicou que o comprimento da concha na maturidade sexual foi de 13,80 mm. A concha juvenil de *A. flexuosa* apresentou formato mais arredondado que a adulta. Aspectos relacionados ao desenvolvimento do animal e às características ambientais podem influenciar o formato da concha. O tamanho de maturidade encontrado no presente estudo está de acordo com a faixa de maturidade proposta na literatura.

Palavras-chave: Alometria; L50; Concha; Maturidade morfológica.

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INTRODUCTION

Anomalocardia flexuosa (Linnaeus, 1767) (Bivalvia: Veneridae) has a broad geographic distribution, ranging from the Antilles to Uruguay. It inhabits calm, sheltered waters such as bays and coves (Narchi, 1974; Rios, 2009). This bivalve is widely found along the Brazilian coast and serves as an important source of subsistence and income for many coastal communities, highlighting its socio-economic significance (Barletta & Costa, 2009; Boehs et al., 2010).

As an euryhaline and eurythermic species, *A. flexuosa* is resilient to variations in salinity, temperature, and dissolved oxygen levels (Schaeffer-Novelli, 1980). However, hypersaline conditions can limit the growth and survival of marine clams (Brown & Hartwick, 1988). While several studies have focused on the biology and ecology of *A. flexuosa* (Barreira & Araújo, 2005; Boehs et al., 2008; Corte et al., 2015; Grotta & Lunetta, 1980; Luz & Boehs, 2011; Pezzuto & Echternacht, 1999), research on growth-related aspects, particularly allometric studies that describe morphological growth patterns, remains scarce.

Growth in bivalves is a continuous process, but different parts of the organism may grow at varying rates, influenced by environmental conditions and physiological characteristics, which defines relative growth (Fonteles-Filho, 2011). The concept of allometry, established in ecological studies of marine animal growth since the 19th century, provides insights into the shape and growth patterns of organisms (Broad, 1998). Additionally, analyzing shell morphometrics can reveal information about the relationship between the organism and its environment, especially regarding substrate interactions (Estrada, 2004).

Energy allocated for growth in bivalves may vary, with juveniles focusing primarily on body development, while adults may direct energy toward reproductive structures. This differential allocation results in distinct growth patterns throughout the life cycle, which can be studied through size-weight relationships and biometric ratios, defining isometry and allometry (Fonteles-Filho, 2011).

Understanding population dynamics, especially growth and reproduction, is crucial for assessing the impact of environmental and anthropogenic factors, such as shellfish harvesting, on the population structure of exploited species. This knowledge is vital for developing effective fishery management plans (Araújo, 2001). Determining the size at sexual maturity is particularly important for commercially exploited populations. Although previous research has explored various aspects of *A. flexuosa* biology (Barreira & Araújo, 2005; Boehs et al., 2010; Grotta & Lunetta, 1980; Lavander et al., 2011), few studies have focused on shell growth patterns to accurately determine the size at sexual maturity. This gap makes it challenging to compare size estimates across different environmental conditions and limits our understanding on how these variables affect growth and reproduction.

Furthermore, *A. flexuosa* is a dioecious species without external shell differences or gonadal coloration that would allow for easy sex identification without histological analysis (Grotta & Lunetta, 1980). Many studies have not established a clear maturation size (Boehs et al., 2010; Grotta & Lunetta, 1980; Lavander et al., 2011), complicating comparisons across different environments and limiting insights into environmental impacts on gonadal development. Most assessments of sexual maturity rely on histological techniques, which are costly and labor-intensive.

For bivalves, the shape stabilization index (SSI) of the shell is determined, as proposed by Gil et al. (2007), which analyzes different ratios between the measurements of height, width and length of the shell, indicating a period of growth stabilization, which would be the inflection point, in which sexual maturity would probably occur. Some studies have already been developed using this methodology, such as López-Rocha et al. (2018), in which for species of the genus *Megapitaria* this method was applied well. However, for *Donisia ponderosa* it was not possible to identify the inflection point through the SSI. In the same way, we were unable to perform it for *A. flexuosa*.

In this context, the present study aimed to determine the morphometric relationships between shell measurements of *A. flexuosa* to identify differences in growth patterns between juveniles and adults and to establish the size at sexual maturity using a morphometric methodology.

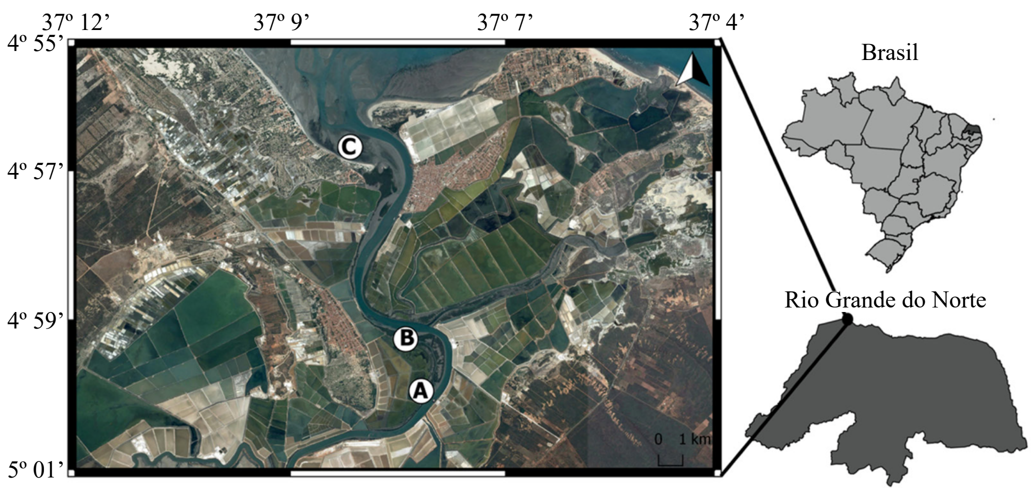
MATERIAL AND METHODS

Study area and sampling work

The study area was the Apodi/Mossoró Estuary (4°56’51”S and 37°08’55”W), on the semi-arid coast of northeastern Brazil, in the state of Rio Grande do Norte, in the Costa Branca region. This is the second largest estuary in the region and is known to have records of high abundance of bivalve *A. flexuosa,* which provides livelihood for many families (Silva et al., 2014).

The water bodies have peculiar abiotic characteristics, such as high natural evapotranspiration rates, exceeding rainfall, and low runoff, allowing the formation of hypersaline plains, as in the Apodi-Mossoró Basin (Medeiros, 2016). Thus, the Apodi-Mossoró rainfall is classified as a negative or inverse estuary (Medeiros, 2016), in which an increasing salinity gradient occurs from the outfall to the upper areas, promoting hypersalination of water and sediment, which represents its main abiotic characteristic.

For the purpose of expanding sampling in the estuary, 27 monthly samplings (nine sample per area) were conducted from November 2015 to October 2016 in three different sites: A (a sand-mud bank); B (a muddy bank); and C (covered by sparse beds of the seagrass *Halodule wrightii* Asch.), where *A. flexuosa* is distributed at the mouth and in the upper areas of the estuarine region (Fig. 1).



Source: Adapted from Google Earth (2017) and Wikipedia (2017).

Figure 1. Location of the Apodi-Mossoró Estuary, semi-arid coast of Brazil. (a, b and c) *Anomalocardia flexuosa* sampling sites.

During the low spring tides, individuals were captured with a fixed-quadrat sampler (50 × 50 m) and a shovel, taking a sediment layer of approximately 10 cm. In the laboratory, every individual was measured for shell length (maximum distance on the anteroposterior axis), shell height (maximum distance on the ventral-dorsal axis), and shell width (maximum distance on the left-right axis, with closed valves) (Gosling, 2003; Stanley, 1970), using a digital caliper (0.05 mm) (Fig. 2). Sediment samples were also taken for particle size analysis, and the salinity of the percolating water was measured. Rainfall data was obtained online from the Agricultural Research Company of Rio Grande do Norte (EMPARN).

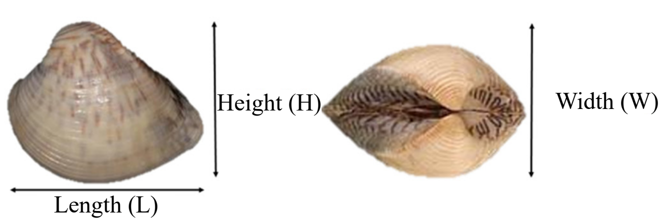


Figure 2. Shell dimensions and morphometric variables measured in *Anomalocardia flexuosa* specimens obtained in the Apodi-Mossoró Estuary, semiarid coast of Brazil.

Morphometric analysis

Morphometric relationships length-height and length-width were established by the Eq. 1:

$$Y = a + bX \qquad (1)$$

Where: X: length; Y: width/height; a: y-axis intercept; b: slope coefficient of straight or constant allometric growth, as proposed by Singh (2016).

Data were logarithmized to normalize and reduce variance heterogeneity, and equation parameters were estimated by linear regressions. The *t*-test ($\alpha = 0.05$) was used to verify the allometry, analyzing the ‘b’ value, using as null hypothesis (b) = 1, which indicates the differences between the growth rates of the two body dimensions, thus setting allometry positive (b > 1), negative (b < 1) or isometry (b = 1).

K means clustering technique was adopted to separate the data set [length (L), height (H), and width (W)] of juvenile and adult categories. This methodology is widely applied in marine invertebrate studies (Castiglioni & Coelho, 2011; Hirose et al., 2017). Morphometric relationships between length and height were evaluated for juveniles and adults; subsequently, the respective estimated linear and angular coefficients were compared by analysis of covariance (ANCOVA).

Determination of morphological sexual maturity

Morphological size at sexual maturity was determined by fitting a logistic model between immature and mature individuals (juveniles and adults separated by *K means*), relating the probability of maturation (probability of occurrence of adults) and length (Eq. 2):

$$[y = a/(1 + be\text{-}cx)] \quad (2)$$

The length class in which 50% of individuals have reached sexual maturity (L50) is defined as the average length of sexual maturity or maturation size (Fonteles-Filho, 2011; Hirose et al., 2017; Severino-Rodrigues et al., 2016). The definition of the L50 allows the determination of the transitional moment from juvenile to adult phase, based on the definition of an average length at which the stock separation occurs (Fonteles-Filho, 2011), considering a representative portion of the population, and it can be established from studies of allometry.

All analyses were performed using spreadsheets and the R 4.4.0 program (R Core Team, 2024).

RESULTS

The total of 52,872 individuals was captured and measured, with mean values of length, height, and width of 15.30 (± 6.99), 12.87 (± 6.11), and 8.90 mm (± 4.38), respectively (Table 1). The highest densities were recorded for area A and the lowest for area C (Table 2).

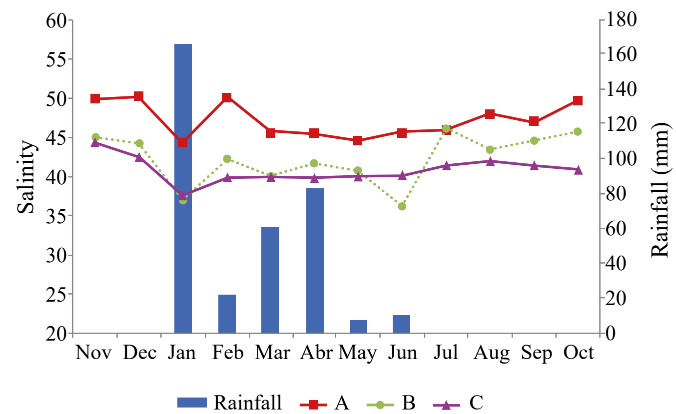
Salinity showed an inverse decreasing pattern in the estuary, where the highest values were found in A (Table 2, Fig. 3). The three areas analyzed throughout the entire study period always recorded high values (above sea salinity), even with rainfall, thus remaining hypersaline all year round (Fig. 3). The particle size characterization showed a higher percentage of silt and clay in sites A and B and a higher percentage of sand in site C (Table 2).

Table 1. Minimum, maximum, mean, and standard deviation of length, height, and width of *Anomalocardia flexuosa* shells, collected in the Apodi-Mossoró Estuary, semiarid coast of Brazil.

Morphometric variables	Values		
	Min	Max	Mean ± standard deviation
Length (mm)	0.40	28.70	15.30 ± 6.99
Height (mm)	0.30	24.80	12.87 ± 6.11
Width (mm)	0.10	20.00	8.90 ± 4.38

Table 2. Mean values of abiotic variables and *Anomalocardia flexuosa* population density (m^2) in the three studied areas in the Apodi-Mossoró estuary during the period from November 2015 to October 2016.

Variable	Area		
	A	B	C
Salinity	48	43	41
Silt + Clay (%)	66.7	79.4	45.6
Density (individuals/m^2)	805	784	370



Source: EMPARN (2017).

Figure 3. Monthly relationship between rainfall and salinity in the estuary Apodi-Mossoró from November 2015 to October 2016.

All allometric relationships obtained here for *A. flexuosa* were significant (α = 0.05), fitting linear models (Table 3, Fig. 4). Both relations between length × height and length × width showed a positive allometry (b > 1). The coefficient of determination (r^2) for length × height was higher than for length × width, justifying the choice of these variables to check the differences in morphometric relations between juveniles and adults (Table 3).

Table 3. Results of regression analysis and definition of the allometric relationships length/height, and length/width of *Anomalocardia flexuosa* shells, collected in the Apodi-Mossoró Estuary, semiarid coast of Brazil.

Variables	a	b	r^2	Test *t* (b=1) *p*-value	Allometric relationship
length × height	-0.27	1.03	0.995	0.00	Positive
length × width	-0.89	1.12	0.991	0.00	Positive

a: regression coefficient; b: regression coefficient; r^2: determination coefficient.

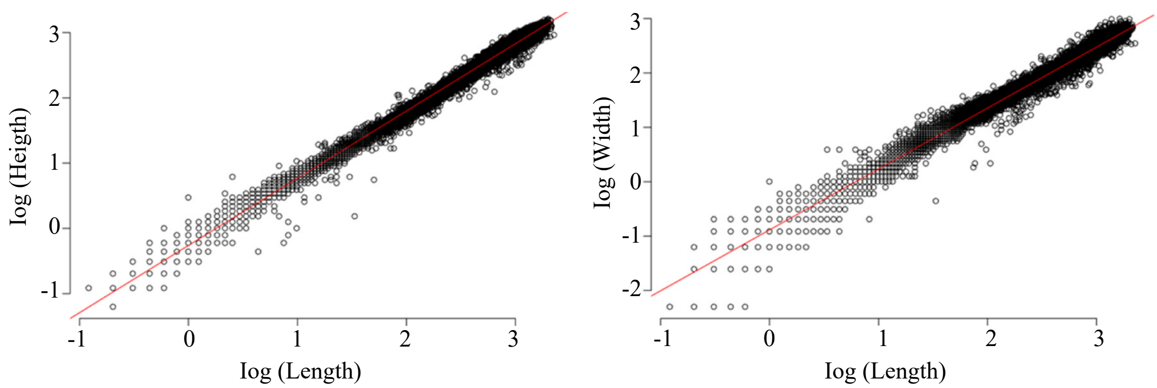


Figure 4. Logarithmized morphometric relationships for *Anomalocarida flexuosa*. (a) Length-height and (b) length-width morphometric relationships of *Anomalocardia flexuosa* shells, collected in Apodi-Mossoró estuary, semiarid coast of Brazil.

The cluster analysis (*K means*) split the data set into two categories. The test identified juveniles and adults; the length interval between 13.20 and 14.60 mm represented the transition between these categories (Fig. 5). The results provided by *K means* were used as a reference for growth analysis between the length and height of juvenile and adult shells.

The growth pattern between juveniles and adults differed significantly ($\alpha = 0.05$), in which juveniles exhibited an isometric growth (b = 1; $p > 0.05$) and adults negative allometry (b < 1; $p < 0.05$) (Table 4).

The fit of the logistic model indicated that 50% of individuals (L50) reached sexual maturity from 13.80 mm in length (Fig. 6).

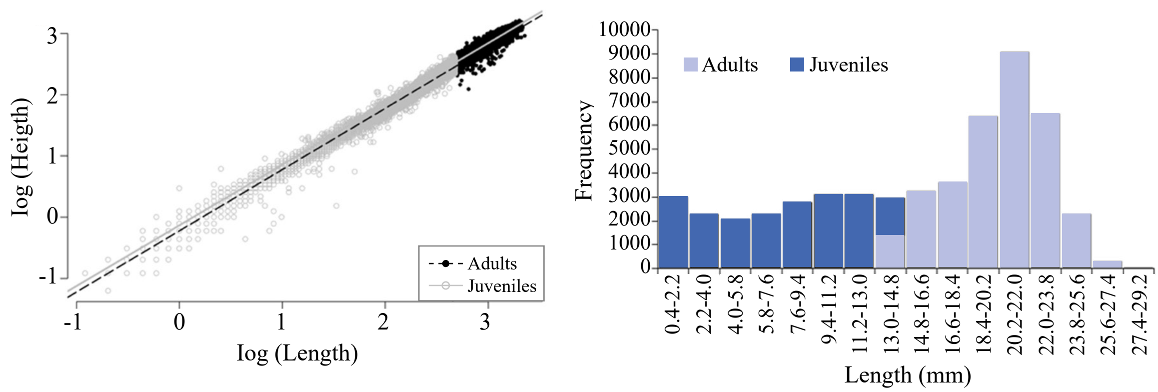


Figure 5. Definition of the transition period between juvenile and adult for *Anomalocardia flexuosa*. (a) Linear regression between length and width of *Anomalocardia flexuosa* shells; (b) length-frequency histogram for juveniles and adults, collected in the Apodi-Mossoró Estuary, semiarid coast of Brazil. The dotted line indicates the length interval between juvenile and adult categories.

Table 4. Comparison of morphometric relationships (length/height) for *Anomalocardia flexuosa* shells between juveniles and adults collected in the Apodi-Mossoró Estuary, semiarid coast of Brazil.

Variables	Category	a	b	r^2	*t*-test (b=1) *p*-value	Allometric relationship	ANCOVA *p*-value	
							a	b
length × height	Adult	-0.13	0.99	0.89	0.00	Negative	*0.00*	*0.00*
	Juvenile	-0.22	1.00	0.99	0.07	Isometric		

a: regression coefficient; b: regression coefficient; r^2: determination coefficient; ANCOVA: analysis of covariance.

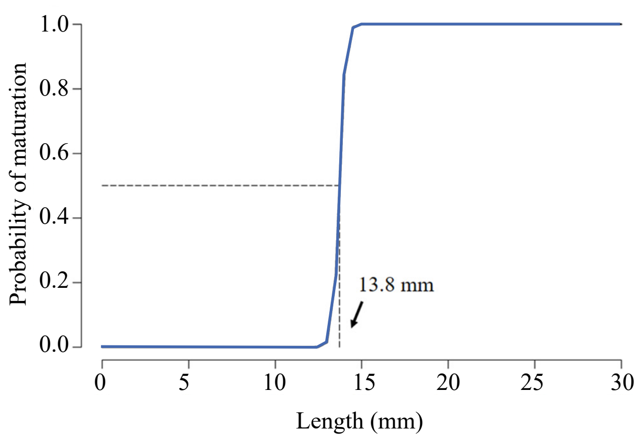


Figure 6. Maturation probability of cockle *Anomalocardia flexuosa* considering the length class. The dotted line indicates the length at which 50% of individuals reached morphological sexual maturity (L50).

DISCUSSION

Morphometric relationships between height, width, and length of *A. flexuosa* presented a positive allometry. When 'b' is higher than 1, prevailing positive allometry, the variable 'y' increases at a faster rate than 'x' (Hickman, 1979). Thus, the increase in height/width was greater than in length, leading to a taller and more inflated shell as the individual grows. This pattern also seems common in 25 different bivalve species studied on the Algarve coast, Portugal (Gaspar et al., 2002). In this area, sediment characteristics (composition and depth) and the burrowing capacity of the animals act as the main regulators of growth (Gaspar et al., 2002). *A. flexuosa* is a shallow digger and inhabits shallow sandy-muddy sediment (Narchi, 1974; Rios, 2009), which is more resistant to penetration than sandy bottoms and may reduce their burrowing capacity, interfering with their increase in length. Probably, excavation in environments with fine sediment must demand higher energy input, which may interfere with growth.

Gosling (2003) states that allometric adaptations maintain the animals' physiological condition of the area/volume rate favorable to living under a certain environmental condition. The shells of bivalves with less burrowing capacity are usually thicker to keep them stable in the sediment and close to the surface. In addition, rounded shells favor the lodging of short siphons (Newell & Hidu, 1982), such as those of *A. flexuosa*.

Different microhabitats may affect the external shell morphology, and the sediment appears to be a major factor controlling such alterations, as mentioned previously. Roopnarine and Laumer (2008) mention that *A. flexuosa* shells have different morphometric relationships for each background type. Thus, juveniles present a more rounded shell on seagrass beds than on sandy and muddy bottoms. Addino et al. (2015) also observed changes related to the growth of *Tagelus plebeius* in areas where *Spartina alterniflora* occurred, with changes in size and condition index. Reporting that there may be a limitation in growth in size, but the availability of food in these areas can help with weight incorporation. Competition for space with plant roots can interfere with the shell's development and growth and/or its burrowing capacity.

Anomalocardia flexuosa has a non-constant growth rate throughout development (Katsanevakis et al., 2007). This implies that morphometric relationships must be analyzed separately for juveniles and adults (Gil et al., 2007). Animal size and age also affect the process of animal-sediment relationships and the burrowing capacity (Stanley, 1970). Therefore, changes in the morphology of the shell with age, in order to seek the best condition to remain stable on the substrate, can influence the bivalve and its burrowing capacity. The interaction of the individual with the environment is more informative and conclusive in adults as they already achieved stability in their growth pattern. Thus, the animal age influences the growth patterns since the growth rate does not remain constant throughout animal development (Gil et al., 2007) and may interfere with regression estimations (Estrada, 2004).

In the present study, the biphasic model (young and adult) indicated that juvenile growth was isometric (b = 1), i.e., length and height grow at the same rates, and after the transitional point between phases is reached, the growth rate of length and height decrease (b < 1), obtaining a negative allometry, in which length grows faster than height. Thus, adults grow at a slower rate than juveniles, differing not only in shell size, but also in shape. Juveniles grow proportionally, obtaining a more rounded and geometrically similar shell. The triangular or trigonal shape, typical of the genus *Anomalocardia*, is less perceptible in juveniles and becomes more evident in adults. In these latter, the increase in length is more expressive, and the elongation of the shell becomes more conspicuous, leading to the posterior portion of *A. flexuosa* being more prominent. During the juvenile phase, bivalve mollusks present a major variation in shell dimensions and alterations in length, height, and width growth rates (Gil et al., 2007). Therefore, the general pattern of shells is established only in the adult stage.

In addition to the sediment type (Newell & Hidu, 1982), other environmental factors such as temperature, salinity, food availability (Brown & Hartwick, 1988), and pollution (Hédouin, 2006) may also affect allometric relationships of bivalve shells, inducing growth changes. Our study area is characterized as a hypersaline estuary, a natural condition for semi-arid environments, but the scarcity of studies that can be used for comparisons makes it difficult to interpret the influence of salinity on the growth of individuals. Aspects should be evaluated for *A. flexuosa* in the future, due to its economic importance, management, climate changes, and anthropogenic pressures.

Regarding the sexual maturity of this bivalve, Barreira and Araújo (2005) defined using histological routines a length interval for sexual differentiation between males and females between 12.9 and 17.9 mm, with a predominance of individuals with mature gonads from 12.9 mm (sexual maturity size). Thus, the morphological sexual maturity size proposed in the present study (13.8 mm) is in agreement with Barreira and Araújo (2005) in an estuary of the Ceará coast, without annual hypersalinity characteristics, but also in the Brazilian semiarid region.

Even using a methodology with space-time sampling, the differences by area and throughout the study period were not considered, since they are not decisive for defining the size of morphological maturity. The samples were used with the aim of improving the representativeness of the size classes and verifying the hypersalinity seasonality of the estuary.

This methodology for determining morphological maturity, quite applied in dynamics studies of marine invertebrate populations (Hirose et al., 2017; Severino-Rodrigues et al., 2016), seems efficient for bivalves and may assist in studies of growth and reproduction, especially of exploited species that require regulation of catch sizes, which is essential for the sustainability and management of fisheries activities. There is no regulation on capture size for this species on the Brazilian coast, where it is significantly exploited.

Comparisons between the size at morphological maturity and physiological maturity may reinforce the present findings. Histological analysis of the gonads may also support these results, and studies on population dynamics are necessary to a better understanding of the *A. flexuosa* population structure.

CONCLUSION

Based on our finding, this study yielded several significant conclusions:

- K-means cluster analysis emerged as a robust analytical tool for identifying developmental transitions between juvenile and adult stages, effectively determining morphological maturity in *A. flexuosa*;
- Through allometric analysis, we demonstrated significant differences in shell growth patterns between juvenile and adult specimens of this bivalve species;
- Our findings strongly align with existing literature on the species, validating the effectiveness of this methodological approach for studying bivalves. Furthermore, this analytical framework, which has been successfully employed in studies of other invertebrates, shows promise as a valuable tool for investigating growth and reproduction patterns across various bivalve species;
- The insights gained from this research provide crucial data for implementing effective fisheries management strategies for *A. flexuosa*, particularly given its widespread commercial exploitation along the Brazilian coastline.

These results not only advance our understanding of *A. flexuosa* developmental biology but also offer practical applications for sustainable management of this important fishery resource.

CONFLICTS OF INTEREST

Nothing to declare.

DATA AVAILABILITY STATEMENT

Data sharing is not applicable.

AUTHORS' CONTRIBUTIONS

Conceptualization: Oliveira, I., Silva, E., Barreira, C.R.; **Data curation:** Oliveira, I., Barreira, C.R.; **Formal Analysis:** Oliveira, I.; **Investigation:** Oliveira, I., Silva, E., Barreira, C.R.; **Methodology:** Oliveira, I., Barreira, C.R.; **Software:** Oliveira, I.; **Writing – original draft:** Oliveira, I., Silva, E.; **Writing – review & editing:** Oliveira, I., Silva, E., Barreira, C.R.; **Funding acquisition:** Barreira, C.R.; Project **administration:** Barreira, C.R.; **Resources:** Barreira, C.R.; **Supervision:** Barreira, C.R.; **Final approval:** Oliveira, I.

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