

Research Article

## Morphometry and allometry of *Hexaplex nigritus* (Gastropoda: Muricidae) from a coastal lagoon of the Gulf of California

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**ABSTRACT.** Although muricid snails are an important ecological and fisheries resource in northwest Mexico, information on their allometry and morphometry is scarce. For one year (February 2022-January 2023), 30 specimens of the “Chinese black” snail, *Hexaplex nigritus* (shell height =  $101.4 \pm 13.7$  mm, total snail weight =  $192.3 \pm 89.1$  g) were monthly collected from a coastal lagoon of the southeastern Gulf of California. The biometrics of shells (height SH, length SL, width SW, and shell opening width WSO) and operculum (height OH, length OL, and width OW) and weight variables (total snail weight TWS, total shell weight TSW, total tissue weight TTW, total gonad weight TGW, and total operculum weight TOW) of sampled snails were morphometrically analyzed. All biometric indicators of the snail shell and operculum showed significant differences ( $P < 0.05$ ) monthly and presented linear and positive equations in all associations. The SH/SL relationship represents the most appropriate tool to describe the relative growth of this gastropod (coefficient of determination,  $R^2 = 0.80$ ), considering an empty shell; meanwhile, TWS/SL better describes the shell/weight interaction ( $R^2 = 0.80$ ) for live snails. The water temperature showed a positive correlation with the biometric indicators. The measurements obtained from the shell dimensions of this gastropod indicate that the sampled population consisted of adult snails. These data are fundamental for the management and conservation of this muricid species in the study area, providing valuable information for planning sustainable management strategies.

**Keywords:** morphometric relationships; marine snail; shell-operculum biometrics; shell dimensions-body weight associations; Gulf of California

## INTRODUCTION

The marine gastropod *Hexaplex nigritus* (Mollusca: Muricidae) is a species endemic to the coastal lagoons of the Gulf of California (GC), commonly known as the "black Chinese snail". Its distribution ranges from the GC in Mexico to Peru (Coan & Valentich-Scott 2012). It is distinguished by its opaque white external coloration, tinged with brown to black on the spiral ribs and spines, while the aperture is porcelain white. The height of its shell can reach up to 143.5 mm (Cudney-Bueno et al. 2008). This snail is an economically important fishery resource in the GC, but its catch is not individually recorded as a species; instead, it is combined with other muricids, forming the entire "Chinese snail" fishery resource. Furthermore, the economic exploitation of this species is not controlled, either permanently or temporarily, and its management strategy is classified as "maximum sustainable use" in the northeast of GC and "undetermined" in the rest of GC (DOF 2023), including the study area of this research. Only its minimum catch size of 90 mm (shell height, SH) is established (DOF 2023).

The challenges in managing this sea snail fishery are magnified by the fact that other muricid species (*Hexaplex princeps*, *H. ambiguus*, *H. radix*, *Phyllonotus erythrostomus*, *P. brassica*, and *P. regius*) are considered a single fishery resource along with *H. nigritus*. Consequently, the catch volume by species is uncertain, and there is insufficient information to classify the true production status of the black Chinese snail. On the other hand, the integral functioning of the aquatic ecosystems where *H. nigritus* lives faces constant modifications caused by natural and anthropogenic activities -the latter since the industrial revolution (Ekins & Zenghelis 2021)- which are exacerbated by the fact that water bodies concentrate a large part of industrialized waste, causing alterations in the dynamics of environmental variables (Häder et al. 2020, Thanigaivel et al. 2024) and, even, being able to modify the phenotype of the snails and other mollusks that inhabit them (Clark et al. 2020, Lee et al. 2025).

The specific genetic information, inherent and involved in the elaboration of the shell of snails and all mollusks in general -through the arrangement, composition, and proportion between bioavailable minerals- dictates the construction of their exoskeleton (Gemmell et al. 2018); however, organisms must develop a certain phenotypic plasticity that, mostly, obeys multiple variables of a biological/ecological nature (density, interrelation with other species, parasites, quantity and quality of food, etc.) (Whelan

2021), non-biological (environmental variables, waves and currents, fixation substrates, desiccation, elements derived from anthropogenic activities, etc.) (Abdelhady et al. 2018) or the combination of both. Factors such as water temperature, salinity, and pH, among others, have been associated with changes in the morphological geometry of various marine mollusk species. Although they are mostly sessile or slow-moving, they also serve as excellent biological indicators of ecosystem health (Bourdeau et al. 2015). Thus, heterogeneity in shell shape is common within populations of mollusks, whether wild or farmed, even within the same species (Kandratavicius & Brazeiro 2014).

The three-dimensional geometry of marine snail shells offers the possibility of associating multiple morphological variables -such as height, length, width, opercular opening, operculum, and total weight, among others- that contribute to the knowledge of their proportionality, growth, and reproduction, studying both living organisms (Moran & Emlet 2001, Elessawy et al. 2022) and their empty shells (de Oliveira & de Oliveira 2019), and even using the operculum alone (Miranda et al. 2008, Mueller & Stoner 2013). The morphological study of marine gastropods involves obtaining and contrasting functional parameters of the shell (height, length, and total width; and height and width of the shell opening) by evaluating their linear dimensions and their correspondence (Modestin 2017, Telesca et al. 2018). On the other hand, morphometric relationships and relative growth represent useful tools with multiple applications, since they: allow a detailed description of each metric dimension that contributes to the construction of shell shape and the associations between them all (Matos et al. 2020), interpret the development and relative growth of organisms by calculating proportionality equations (Yusof et al. 2020), establish calculations to obtain the condition index (Samsi et al. 2020), and morphologically compare -by or between species- populations in the same or different habitats (Afiademanyo et al. 2021). The above is achieved through the creation of mathematical tools applicable in fisheries biology, fisheries management, and population dynamics, among other uses. As the only reports in the region, Cudney-Bueno & Rowell (2008) documented the growth, longevity, and morphological variations of *H. nigritus* in the northern GC, while Arias-López et al. (2023) analyzed the size composition of *H. nigritus* in the southeastern GC using the morphometric proportionality of size vs. weight of the snail. No information is available on the morphometric relationships and relative growth of *H. nigritus* in the GC. In

in this context, the morphometric relationships and allometric growth of this muricid species in a lagoon of the GC were exhaustively evaluated, considering the biometrics (height, length, width, and aperture) of the shell and operculum, and the weight of its components (total tissues, gonad, shell, and total weight). The results aim to provide information that contributes to understanding its growth and morphometry to propose tools applicable to its protection and conservation.

## MATERIALS AND METHODS

### Study location

A total of 360 organisms (30 snails month<sup>-1</sup>) were analyzed over the course of one year (February 2022–January 2023). The muricid was sampled in the Navachiste Lagoon (Guasave Municipality, Sinaloa, Mexico) (Fig. 1). The snails were captured manually and directly during low tide. The snails were transported alive to the laboratory in plastic containers with seawater. Also, monthly, physicochemical (temperature, dissolved oxygen DO, pH, salinity, depth, and transparency) and biological (total suspended solids TSS, particulate organic matter POM, and chlorophyll-a Chl-a) (Jeffrey & Humphrey 1975, APHA 1995) variables were obtained from the water at the sampling site.

### Biometrics and statistics

In the laboratory, snails were washed and brushed to remove sediment and epiphytic organisms. They were then measured with a digital Vernier ruler (0.01 mm) to obtain four linear shell variables (shell height SH, length SL, width SW, and shell opening width WSO) and three linear operculum variables (operculum height OH, length OL, and width OW) (Fig. 2). In addition, each organism was weighed using a precision balance (0.01 g) to estimate five weight variables (total snail weight TWS, total shell weight TSW, total tissue weight TTW, total gonad weight TGW, and total operculum weight TOW). Male snails were identified by the presence of a penis and the absence of a capsular gland, while females were distinguished by the presence of the ovigerous canal (Lee 2008). Descriptive statistics (mean, standard deviation, coefficient of variation CV, maximum, and minimum values) were used for shell and operculum dimensions, as well as body, tissue, and operculum weights of the snail. Data normality and homoscedasticity were studied using the Shapiro-Wilk and Bartlett tests, respectively. Since the data did not fit a normal distribution, a Kruskal-Wallis test (Statgraphics Centurion XV) and a Dunn test were

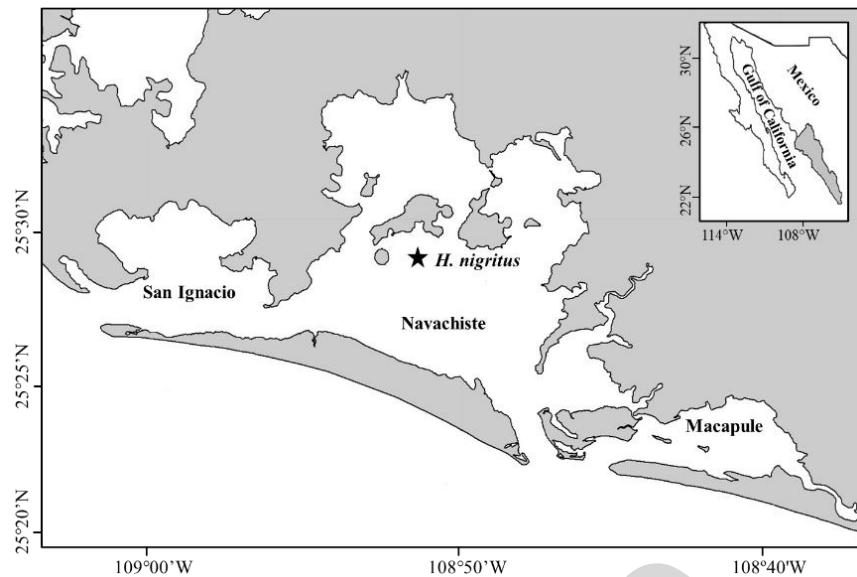
applied to detect and indicate monthly differences ( $\alpha = 0.05$ ) (Sokal & Rohlf 1995).

### Morphometry and statistics

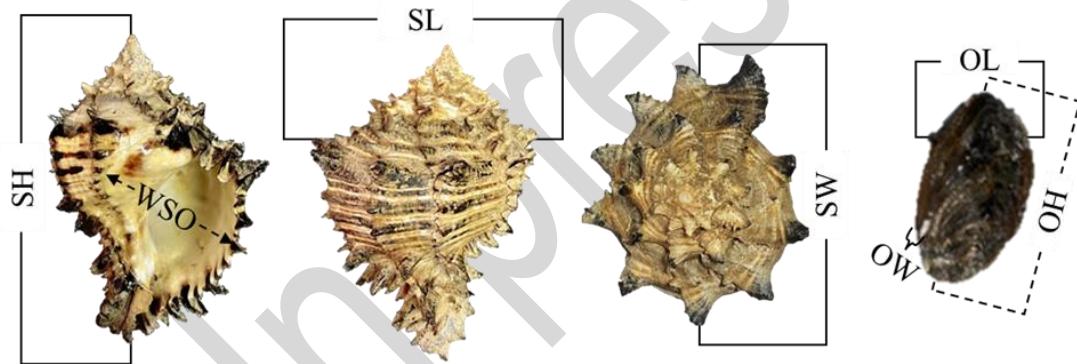
Morphometric relationships of *H. nigritus* were established by regression analysis using the least squares method. Linear regression was fitted for variables with the same unit by using  $Y = bX + a$ , where Y and X are shell, tissue, or operculum dimensions or weights;  $a$  = intercept; and  $b$  = slope. A potential regression model,  $Y = aX^b$ , was used to compare variables across different units. The degree of association between variables was assessed using Spearman's correlation coefficient ( $r$ ). When comparing variables with the same unit (linear vs. linear or ponderal vs. ponderal), isometric growth is indicated when  $b = 1$ ; for variables with different units (linear vs. ponderal), isometry is indicated as  $b = 3$ . The  $b$  value obtained in the regression equations is significantly different from the isometric value ( $b = 1$  or  $3$ ) when indicated by the  $t$ -test ( $H_0: b = 1$  or  $3$ , confidence level = 95%), according to Vasconcelos et al. (2018):  $t = (b - 1) / Sb$ , where  $t$ :  $t$ -test value,  $b$ : slope of the equation, and  $Sb$ : standard error of the regression equation. In all statistical analyses, the significance level was set at  $P < 0.05$ . Finally, a multiple correlation analysis (Spearman) was performed with the environmental variables and the morpho-biometric and allometric indicators ( $P > 0.05$ ), transforming the data to LOG, and a principal components analysis (PCA) was performed to determine the group effect between the variables.

## RESULTS

The physicochemical characteristics of the water are shown (Figs 3a,c). Water temperature exhibited a clear seasonal pattern, reaching  $>30^\circ\text{C}$  during summer and ranging overall from 21.00 to 32.30°C (mean  $26.17 \pm 4.34^\circ\text{C}$ ). Salinity fluctuated between 38 in May and 33 in September, with an annual mean of  $35.93 \pm 1.34$ . pH showed slight seasonal variability, with a maximum of 8.48 in November 2022 and a minimum of 7.85 in June 2022 (mean  $8.06 \pm 0.19$ ). Dissolved oxygen varied from 4.23 to 9.44 mg L<sup>-1</sup> (mean  $5.97 \pm 1.74$  mg L<sup>-1</sup>). Depth also fluctuated throughout the year, reaching its maximum between June and July (2.30 m) and its minimum in April (0.82 m), with an annual mean of  $1.50 \pm 0.58$  m. Water transparency ranged from 0.29 to 1.00 m. Biological variables are shown in Figure 3d. Total suspended solids ranged from 10.94 to 152.73 mg L<sup>-1</sup> (mean  $56.69 \pm 44.99$  mg L<sup>-1</sup>). Particulate organic



**Figure 1.** Sampling site of the black Chinese snail *H. nigritus* (star), in the San Ignacio-Navachiste-Macapule lagoon system (southeastern Gulf of California, Mexico).



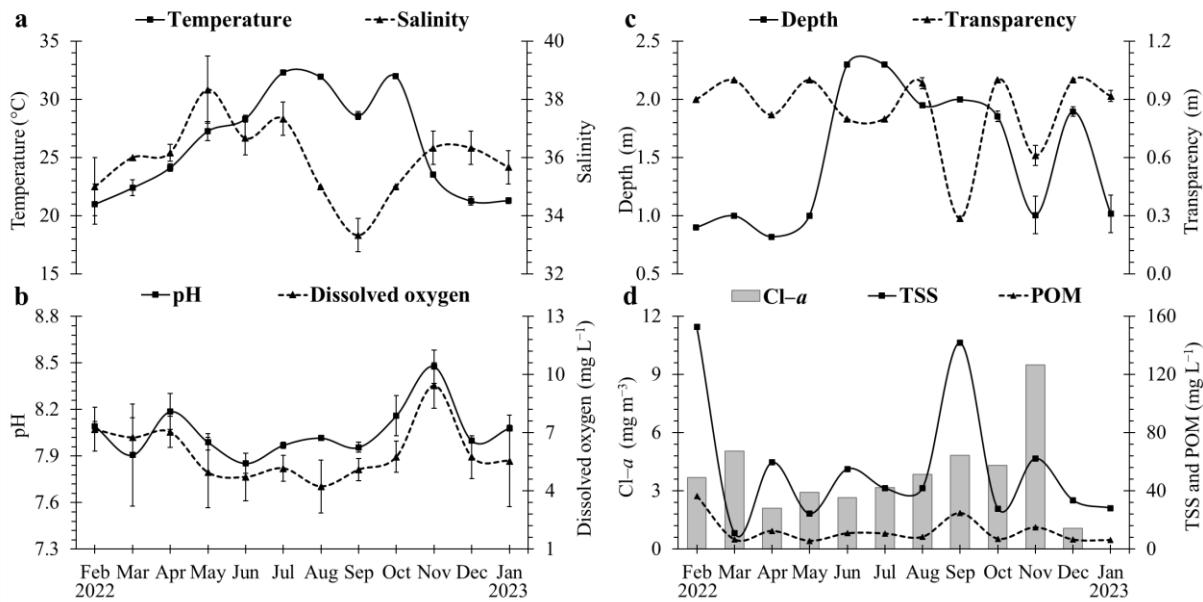
**Figure 2.** Morphometric indicators recorded from the shells and operculum of snails (SH: shell height, WSO: shell opening width, SL: shell length, SW: shell width, OH: operculum height, OL: operculum length, OW: operculum width).

matter peaked in February ( $36.27 \text{ mg L}^{-1}$ ) and reached its minimum in May ( $5.67 \text{ mg L}^{-1}$ ), with an annual average of  $12.53 \pm 9.19 \text{ mg L}^{-1}$ . Chl-*a* concentrations ranged from  $1.06 \text{ mg m}^{-3}$  in December to  $9.48 \text{ mg m}^{-3}$  in November (mean  $3.91 \pm 2.19 \text{ mg m}^{-3}$ ).

All biometric indicators of the snail shell and operculum (Table 1) showed significant monthly differences ( $P < 0.05$ ). The largest specimens of the black Chinese snail ( $\text{SH} = 116.8 \pm 11.2 \text{ mm}$ ,  $\text{OH} = 48.0 \pm 3.4 \text{ mm}$ ,  $\text{TWS} = 308.6 \pm 90.3 \text{ g}$ ) were recorded in August, while the smallest ( $\text{SH} = 91.6 \pm 12 \text{ mm}$ ) was recorded in April. The TGW of *H. nigritus* was highest in August ( $31.2 \pm 8.3 \text{ g}$ ) and decreased to its lowest average in October ( $6.0 \pm 2.4 \text{ g}$ ). TSW accounted for

57% of the TWS. The CV for shell (SH, SL, SW, and WSO) and operculum (OH and OL) dimensions was below 20%.

The morphometric relationships between shell dimensions (SH/SL, SL/WSO, SL/SW, SW/SH, WSO/SH, and WSO/SW), weight values (TSW/TWS, TTW/TSW, TTW/TWS, TGW/TSW, TGW/TWS, and TGW/TTW), and operculum biometrics (OH/OL, OW/OH, OW/OL, TOW/OH, TOW/OL, and TOW/OW) are illustrated in Table 2. The snail *H. nigritus* presented linear and positive equations in all associations. The SH/SL and SL/WSO relationships indicated a relative growth of the positive allometric type ( $b > 1$ ); SL/SW showed isometry ( $b = 0.988$ ), and



**Figure 3.** Monthly variation of the physicochemical and biological variables of the water, during the collection of the snail *Hexaplex nigritus*: a) temperature and salinity, b) pH and dissolved oxygen, c) depth and transparency, d) total suspended solids (TSS), particulate organic matter (POM), and chlorophyll-*a* (Cl-*a*).

the rest of the associations obtained slope values less than 1 (negative allometry). Except for OH/OL ( $b = 1.3982$ , positive allometry), the relationships of shell weight and biometric values of *H. nigritus* indicated relative growth of the negative allometric type ( $b < 1$  for OW/OH and OW/OL, and  $b < 3$  for the associations between TOW/OH, OL, and OW). The correlation value ranged from 0.7835 (WSO/SH) to 0.8997 (SH/SL) for shell dimensions, from 0.584 (TGW/TSW) to 0.9766 (TSW/TWS) for weight values, and from 0.4127 (OW/OL) to 0.9490 (OH/OL) for biometrics of the operculum.

The morphometric relationships between OL, OH, and OW and the shell dimensions (SL, SH, SW, and WSO) were linear and positive. The strongest correlations were observed for OL with SL ( $r = 0.7750$ ), SH ( $r = 0.7407$ ), SW ( $r = 0.7574$ ), and WSO ( $r = 0.6396$ ) (Table 3). The relationships between total wet soft tissue weight (TWS) and the shell dimensions of the *H. nigritus* (SL, SH, and SW) were also positive (Fig. 4). Except for the TWS-SH relationship, which exhibited isometric relative growth ( $b = 3.0211$ ), the remaining relationships (TWS-SL and TWS-SW) showed negative allometric growth ( $b < 3$ ). Among the morphometric comparisons evaluated, *H. nigritus* yielded the highest coefficients of determination ( $R^2$ ). The TWS-SL relationship had the greatest explanatory power ( $R^2 = 0.80$ ), while the TWS-SH and TWS-SW

relationships displayed similar  $R^2$  values (0.69), indicating moderately strong associations.

The physicochemical variables of the water (DO, pH, and temperature) showed a correlation with the biometric indicators and relative growth of *H. nigritus*, with correlation coefficients ranging from  $r = -0.57$  (pH vs. TGW) to  $r = 0.67$  (temperature vs. TGW) (Table 4).

Of the variances of all variables analyzed (28) for *H. nigritus*, the eigenvalues of five components satisfactorily explain 96% of its correlations. The points obtained in the PCA for the black Chinese snail show two groupings of the biometric variables with the depth and temperature of the water in direct association, and indirectly, the relative growth with the pH and DO (Fig. 5), showing an interval in the dispersion values from -9.75 to 4.08.

## DISCUSSION

Variation in the proportional relationships among shell dimensions in marine mollusks is influenced by both external factors -primarily environmental conditions- and internal factors such as age, sex, and genetic background. In this study, the physicochemical and biological variables recorded at the sampling site exhibited temporal fluctuations consistent with those expected for a semi-tropical system. Navachiste Lagoon

**Table 1.** Monthly biometric indices of *Hexaplex nigritus* in the Navachiste Lagoon, Guasave, Sinaloa (means  $\pm$  standard deviation, SD). SH: shell height, SL: shell length, SW: shell width, WSO: shell opening width, OH: operculum height, OL: operculum length, OW: operculum width, TOW: total operculum weight, TWS: total snail weight, TSW: total shell weight, TTW: total tissue weight, TGW: total gonad weight, Max: maximum, and Min: minimum. Columns with different superscript letters denote significant differences ( $P < 0.05$ ) among sampling months.

Months	SH	SL	SW	WSO	OH	OL	OW	TOW	TWS	TSW	TTW	TGW
February 2022												
Mean $\pm$ SD	105.5 $\pm$ 12.2 <sup>d</sup>	72.6 $\pm$ 8.3 <sup>cde</sup>	58.6 $\pm$ 7.2 <sup>c</sup>	34.3 $\pm$ 4.9 <sup>bc</sup>	42.6 $\pm$ 5.3 <sup>e</sup>	28.3 $\pm$ 3.7 <sup>e</sup>	2.6 $\pm$ 1.1 <sup>a</sup>	2.8 $\pm$ 0.9 <sup>bc</sup>	200.4 $\pm$ 67.6 <sup>cd</sup>	127.9 $\pm$ 41.7 <sup>cd</sup>	55.6 $\pm$ 21.0 <sup>de</sup>	12.2 $\pm$ 6.4 <sup>b</sup>
CV	11.6	11.4	12.3	14.4	12.4	12.9	43.3	32.3	33.7	32.6	37.8	52.2
Max-Min	126.6-73.0	84.5-55.5	68.8-43.0	41.9-23.0	51.6-31.3	33.3-20.3	5.0-0.7	4.9-1.0	311.9-72.8	205.8-45.0	95.8-20.0	27.7-3.2
March 2022												
Mean $\pm$ SD	96.6 $\pm$ 13.2 <sup>ab</sup>	68.1 $\pm$ 8.1 <sup>abc</sup>	57.7 $\pm$ 7.7 <sup>cd</sup>	36.2 $\pm$ 4.5 <sup>bc</sup>	39.5 $\pm$ 5.5 <sup>def</sup>	26.0 $\pm$ 3.6 <sup>cd</sup>	3.9 $\pm$ 1.1 <sup>de</sup>	1.6 $\pm$ 0.6 <sup>a</sup>	158.9 $\pm$ 57.6 <sup>ab</sup>	100.1 $\pm$ 34.9 <sup>ab</sup>	46.2 $\pm$ 17.4 <sup>abcd</sup>	11.9 $\pm$ 8.5 <sup>b</sup>
CV	13.7	11.9	13.3	12.3	13.9	14.0	27.4	38.7	36.3	34.9	37.8	71.7
Max-Min	126.6-72.6	82.0-53.7	71.1-41.1	45.3-26.9	49.7-28.2	31.5-19.1	6.2-1.9	3.3-0.6	277.5-69.6	184.8-45.6	76.8-17.3	48.5-2.4
April 2022												
Mean $\pm$ SD	91.6 $\pm$ 12.0 <sup>a</sup>	64.8 $\pm$ 9.7 <sup>ab</sup>	51.7 $\pm$ 7.6 <sup>a</sup>	32.1 $\pm$ 4.7 <sup>ab</sup>	34.3 $\pm$ 5.5 <sup>ab</sup>	23.7 $\pm$ 3.9 <sup>ab</sup>	3.2 $\pm$ 0.8 <sup>b</sup>	1.3 $\pm$ 0.6 <sup>a</sup>	148.3 $\pm$ 81.0 <sup>ab</sup>	91.0 $\pm$ 53.0 <sup>a</sup>	40.6 $\pm$ 25.3 <sup>ab</sup>	6.8 $\pm$ 6.0 <sup>a</sup>
CV	13.1	15.0	14.8	14.5	16.2	16.4	25.5	47.7	54.6	58.3	62.2	88.7
Max-Min	137.2-71.2	99.0-48.6	78.1-38.0	46.3-21.9	54.4-27.0	37.3-16.7	5.8-1.8	3.6-0.5	507.5-70.7	307.4-22.3	145.7-13.0	35.5-2.6
May 2022												
Mean $\pm$ SD	102.8 $\pm$ 14.3 <sup>cd</sup>	73.6 $\pm$ 12.8 <sup>de</sup>	57.8 $\pm$ 10.8 <sup>bc</sup>	35.8 $\pm$ 6.4 <sup>cd</sup>	40.2 $\pm$ 6.2 <sup>ef</sup>	26.4 $\pm$ 4.5 <sup>d</sup>	4.5 $\pm$ 0.9 <sup>fg</sup>	2.9 $\pm$ 1.4 <sup>d</sup>	213.4 $\pm$ 112.7 <sup>cd</sup>	129.5 $\pm$ 69.1 <sup>cd</sup>	62.9 $\pm$ 34.9 <sup>e</sup>	15.8 $\pm$ 9.9 <sup>c</sup>
CV	13.9	17.4	18.6	17.9	15.3	17.1	20.9	48.6	52.8	53.3	55.4	62.5
Max-Min	125.7-80.8	97.2-54.1	75.6-41.3	48.6-23.8	53.3-29.2	34.5-19.7	6.3-3.0	6.6-1.1	496.5-75.3	303.1-48.9	158.1-15.5	46.1-2.8
June 2022												
Mean $\pm$ SD	114.4 $\pm$ 10.9 <sup>e</sup>	80.8 $\pm$ 6.0 <sup>ef</sup>	68.5 $\pm$ 6.3 <sup>d</sup>	35.8 $\pm$ 3.2 <sup>cd</sup>	46.4 $\pm$ 4.4 <sup>h</sup>	30.3 $\pm$ 3.0 <sup>f</sup>	4.5 $\pm$ 1.1 <sup>fg</sup>	3.0 $\pm$ 0.9 <sup>cd</sup>	272.6 $\pm$ 62.4 <sup>e</sup>	162.3 $\pm$ 35.4 <sup>ef</sup>	84.2 $\pm$ 23.4 <sup>f</sup>	22.2 $\pm$ 8.6 <sup>d</sup>
CV	9.5	7.4	9.2	9.0	9.5	9.8	25.6	28.7	22.9	21.8	27.8	38.9
Max-Min	132.0-81.7	91.7-65.3	77.0-52.9	40.6-27.2	53.3-30.8	35.6-19.8	6.6-1.8	4.6-1.4	353.1-124.2	214.0-90.8	127.1-22.7	37.3-3.9
July 2022												
Mean $\pm$ SD	96.4 $\pm$ 6.7 <sup>ab</sup>	67.2 $\pm$ 4.9 <sup>abc</sup>	54.1 $\pm$ 4.6 <sup>ab</sup>	33.7 $\pm$ 2.3 <sup>bc</sup>	38.2 $\pm$ 3.3 <sup>de</sup>	24.6 $\pm$ 1.6 <sup>bc</sup>	3.9 $\pm$ 0.9 <sup>de</sup>	1.7 $\pm$ 0.4 <sup>a</sup>	148.2 $\pm$ 31.2 <sup>ab</sup>	89.7 $\pm$ 18.8 <sup>a</sup>	48.2 $\pm$ 14.6 <sup>bcd</sup>	14.8 $\pm$ 9.8 <sup>bc</sup>
CV	6.9	7.3	8.5	7.0	8.8	6.4	22.4	21.4	21.0	21.0	30.2	66.4
Max-Min	113.8-82.9	78.6-57.3	62.8-43.1	39.9-29.7	43.6-30.0	27.2-21.6	5.8-1.9	2.4-0.9	209.2-83.8	134.9-52.6	74.0-24.5	55.5-3.2
August 2022												
Mean $\pm$ SD	116.8 $\pm$ 11.2 <sup>e</sup>	84.6 $\pm$ 7.5 <sup>f</sup>	72.0 $\pm$ 8.1 <sup>d</sup>	47.1 $\pm$ 5.3 <sup>f</sup>	48.0 $\pm$ 3.4 <sup>h</sup>	31.7 $\pm$ 2.8 <sup>f</sup>	4.2 $\pm$ 0.7 <sup>ef</sup>	2.5 $\pm$ 0.6 <sup>bc</sup>	308.6 $\pm$ 90.3 <sup>e</sup>	176.9 $\pm$ 60.3 <sup>f</sup>	97.7 $\pm$ 25.5 <sup>g</sup>	31.2 $\pm$ 8.3 <sup>e</sup>
CV	9.6	8.9	11.3	11.3	7.1	8.9	16.0	24.9	29.3	34.1	26.1	26.8
Max-Min	136.5-99.5	98.0-71.0	89.7-57.7	55.5-39.1	56.0-40.9	37.3-26.5	5.7-2.8	3.7-1.4	481.5-165.2	299.5-95.6	150.5-51.5	45.1-16.0
September 2022												
Mean $\pm$ SD	105.4 $\pm$ 7.2 <sup>d</sup>	75.9 $\pm$ 4.3 <sup>e</sup>	57.9 $\pm$ 5.9 <sup>bc</sup>	40.2 $\pm$ 4.1 <sup>e</sup>	40.7 $\pm$ 3.1 <sup>fg</sup>	27.2 $\pm$ 2.4 <sup>de</sup>	4.9 $\pm$ 1.0 <sup>g</sup>	2.4 $\pm$ 0.7 <sup>b</sup>	227.3 $\pm$ 46.8 <sup>d</sup>	150.5 $\pm$ 31.7 <sup>de</sup>	56.4 $\pm$ 13.5 <sup>cde</sup>	7.8 $\pm$ 2.8 <sup>a</sup>
CV	6.9	5.7	10.2	10.1	7.7	9.0	20.1	27.7	20.6	21.0	24.0	35.3
Max-Min	121.6-94.6	82.2-63.8	76.2-49.3	47.3-32.8	46.7-33.7	32.1-22.2	6.8-2.6	3.9-1.2	306.9-130.1	212.1-82.6	80.6-27.7	13.1-3.3
October 2022												
Mean $\pm$ SD	92.4 $\pm$ 7.8 <sup>a</sup>	64.4 $\pm$ 9.2 <sup>a</sup>	54.0 $\pm$ 7.3 <sup>ab</sup>	34.0 $\pm$ 5.4 <sup>bc</sup>	36.5 $\pm$ 3.3 <sup>bc</sup>	23.8 $\pm$ 2.8 <sup>ab</sup>	3.4 $\pm$ 0.7 <sup>bc</sup>	1.2 $\pm$ 0.7 <sup>a</sup>	141.8 $\pm$ 64.5 <sup>a</sup>	91.0 $\pm$ 38.9 <sup>a</sup>	36.2 $\pm$ 22.1 <sup>a</sup>	6.0 $\pm$ 2.4 <sup>a</sup>
CV	8.4	14.2	13.5	15.8	9.0	11.6	21.0	61.9	45.5	42.8	61.2	40.2
Max-Min	120.9-83.2	106.0-54.2	83.7-43.1	50.2-27.8	49.9-32.2	36.1-21.2	5.6-2.1	4.8-0.7	461.7-97.2	279.4-58.7	149.1-21.6	11.9-2.8
November 2022												
Mean $\pm$ SD	96.3 $\pm$ 9.7 <sup>ab</sup>	63.2 $\pm$ 8.4 <sup>a</sup>	53.3 $\pm$ 7.6 <sup>a</sup>	30.7 $\pm$ 5.8 <sup>a</sup>	34.0 $\pm$ 3.8 <sup>a</sup>	22.9 $\pm$ 2.7 <sup>a</sup>	3.3 $\pm$ 0.8 <sup>bc</sup>	1.1 $\pm$ 0.6 <sup>a</sup>	150.6 $\pm$ 61.7 <sup>ab</sup>	99.5 $\pm$ 44.6 <sup>ab</sup>	34.9 $\pm$ 13.8 <sup>a</sup>	6.1 $\pm$ 3.2 <sup>a</sup>
CV	10.1	13.2	14.3	18.9	11.3	12.0	23.7	48.2	40.9	44.8	39.6	52.8
Max-Min	122.1-80.1	82.8-51.2	73.0-40.9	42.9-19.8	41.0-28.5	28.5-18.2	5.1-2.2	2.4-0.1	359.0-76.5	258.1-47.1	67.7-17.3	12.6-2.1
December 2022												
Mean $\pm$ SD	99.7 $\pm$ 13.8 <sup>bcd</sup>	69.4 $\pm$ 10.2 <sup>bcd</sup>	55.2 $\pm$ 9.3 <sup>abc</sup>	37.2 $\pm$ 6.4 <sup>d</sup>	37.1 $\pm$ 5.3 <sup>cd</sup>	24.5 $\pm$ 3.7 <sup>abc</sup>	3.7 $\pm$ 1.0 <sup>cd</sup>	1.6 $\pm$ 0.9 <sup>a</sup>	182.4 $\pm$ 85.0 <sup>bc</sup>	117.7 $\pm$ 57.2 <sup>bc</sup>	43.7 $\pm$ 22.7 <sup>abc</sup>	7.8 $\pm$ 4.9 <sup>a</sup>
CV	13.8	14.7	16.8	17.3	14.3	15.1	26.8	55.4	46.6	48.5	51.9	62.9
Max-Min	126.2-76.1	93.0-50.3	78.8-38.2	53.0-26.9	50.7-27.4	34.3-18.3	6.1-2.2	4.2-0.5	423.9-63.1	260.3-40.5	128.2-16.5	19.6-1.1
January 2023												
Mean $\pm$ SD	98.8 $\pm$ 15.5 <sup>bc</sup>	65.5 $\pm$ 11.5 <sup>ab</sup>	55.3 $\pm$ 10.2 <sup>abc</sup>	36.3 $\pm$ 6.3 <sup>cd</sup>	36.4 $\pm$ 5.9 <sup>abc</sup>	23.4 $\pm$ 4.2 <sup>ab</sup>	3.7 $\pm$ 1.0 <sup>cd</sup>	1.5 $\pm$ 0.9 <sup>a</sup>	156.3 $\pm$ 83.5 <sup>ab</sup>	95.1 $\pm$ 50.5 <sup>ab</sup>	40.1 $\pm$ 27.9 <sup>ab</sup>	6.2 $\pm$ 4.8 <sup>a</sup>
CV	15.7	17.5	18.5	17.3	16.1	17.8	26.6	57.4	53.4	53.2	69.6	77.2
Max-Min	130.4-75.5	90.7-51.4	76.6-42.3	48.1-27.5	47.5-26.9	31.6-15.3	7.3-2.6	4.2-0.6	385.0-64.3	217.7-39.6	139.2-14.1	16.6-1.4
Total												
Mean $\pm$ SD	101.4 $\pm$ 13.7	70.0 $\pm$ 11.3	58.0 $\pm$ 9.8	36.1 $\pm$ 6.5	39.5 $\pm$ 6.3	26.1 $\pm$ 4.3	3.8 $\pm$ 1.1	2.0 $\pm$ 1.0	192.3 $\pm$ 89.1	119.2 $\pm$ 54.4	53.9 $\pm$ 29.1	12.4 $\pm$ 10.0
CV	13.5	16.1	16.8	17.9	15.9	16.4	29.1	52.5	46.3	45.7	54.0	80.7
Max-Min	137.2-71.2	106.0-48.6	89.7-38.0	55.5-19.8	56.0-26.9	37.3-15.3	7.3-0.7	6.6-0.1	507.5-63.1	307.4-22.3	158.1-13.0	55.5-1.1

**Table 2.** Morphometric relationships of shell dimensions, weight, and biometric values of the operculum of *Hexaplex nigritus*. SH: shell height, SL: shell length, WSO: width of the shell opening, SW: shell width, TSW: total shell weight, TWS: total weight of snail, TTW: total tissue weight, TGW: total gonad weight, OH: operculum height, OW: operculum width, OL: operculum length, TOW: total operculum weight, *a*: intercept, *b*: slope, *r*: Spearman's correlation ( $P \leq 0.05$ ).

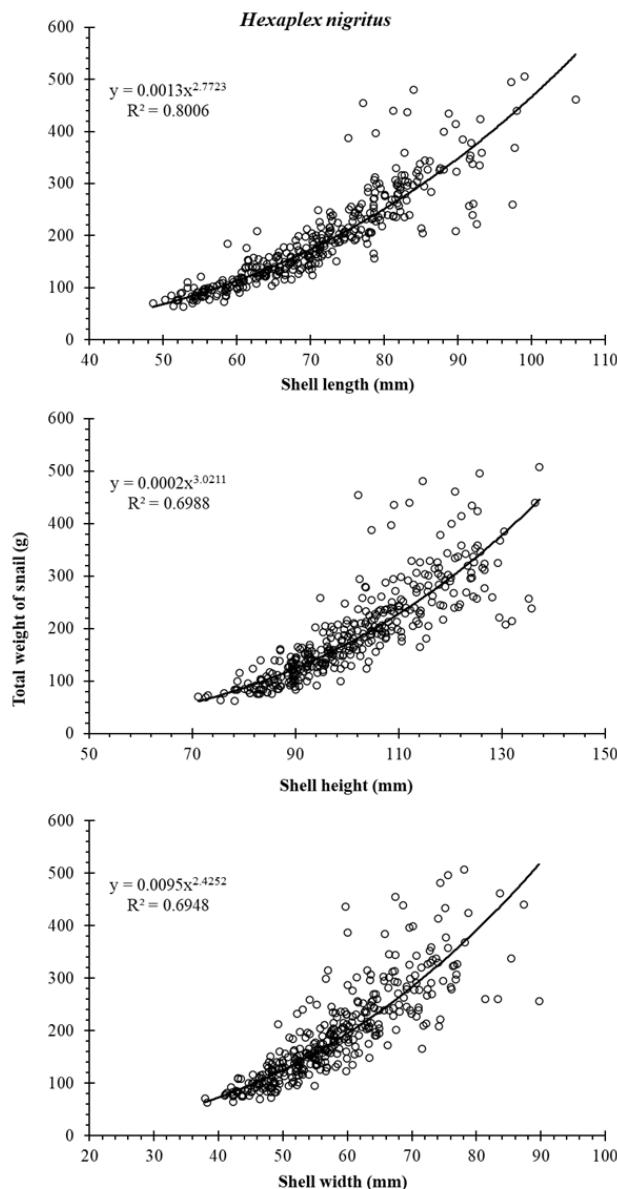
Relationships	<i>a</i>	<i>b</i>	<i>r</i>	<i>t</i> -test	Type of growth
Shell dimensions					
SH/SL	20.678	1.1389	0.8997	4.76	+Allometric
SL/WSO	20.222	1.4026	0.8358	8.22	+Allometric
SL/SW	13.536	0.988	0.8911	-0.45	-Allometric
SW/SH	-4.2547	0.6142	0.8619	-20.20	-Allometric
WSO/SH	-1.2998	0.3689	0.7835	-40.98	-Allometric
WSO/SW	5.7971	0.5223	0.7905	-22.32	-Allometric
Weight values					
TSW/TWS	4.4487	0.5966	0.9766	-58.46	-Allometric
TTW/TSW	-1.089	0.4613	0.8619	-37.67	-Allometric
TTW/TWS	-4.8432	0.3054	0.9342	-113.86	-Allometric
TGW/TSW	-0.4245	0.1082	0.5840	-113.01	-Allometric
TGW/TWS	-1.9217	0.0748	0.6619	-210.38	-Allometric
TGW/TTW	-1.9544	0.2675	0.7753	-64.31	-Allometric
Operculum biometrics					
OH/OL	3.0131	1.3982	0.9490	16.24	+Allometric
OW/OH	0.8637	0.0746	0.4228	-110.01	-Allometric
OW/OL	1.0108	0.1072	0.4127	-71.42	-Allometric
TOW/OH	-1.525	0.0771	0.6432	-192.27	-Allometric
TOW/OL	-1.6182	0.1179	0.7211	-149.5	-Allometric
TOW/OW	0.1084	0.2677	0.5513	-34.21	-Allometric

**Table 3.** Morphometric relationships between shell dimensions and operculum biometrics of *Hexaplex nigritus*. OL: operculum length, SL: shell length, OH: operculum height, OW: operculum width, SH: shell height, SW: shell width, WSO: width of the shell opening, *a*: intercept, *b*: slope, *r*: Spearman's correlation ( $P \leq 0.05$ ).

Relationships	<i>a</i>	<i>b</i>	<i>r</i>	<i>t</i> -test	Type of growth
OL/SL	4.4320	0.3055	0.7750	-53.01	-Allometric
OH/SL	8.3641	0.4391	0.7561	-27.90	-Allometric
OW/SL	1.1071	0.0381	0.3721	-192.38	-Allometric
OL/SH	2.6972	0.2306	0.7407	-76.40	-Allometric
OH/SH	5.9417	0.3308	0.7211	-39.83	-Allometric
OW/SH	0.9646	0.0280	0.3466	-243	-Allometric
OL/SW	6.8808	0.3309	0.7574	-44.31	-Allometric
OH/SW	11.7393	0.4782	0.7427	-22.88	-Allometric
OW/SW	1.8027	0.0345	0.3044	-169.38	-Allometric
OL/WSO	10.8091	0.4230	0.6396	-21.44	-Allometric
OH/WSO	17.6536	0.6046	0.6204	-9.78	-Allometric
OW/WSO	1.6656	0.0594	0.3453	-110.65	-Allometric

lies within a transitional zone between very warm semi-dry (BS(h<sup>+</sup>)) and very dry warm (BW(h<sup>+</sup>)) climates (Peel et al. 2007). Among all variables analyzed, only water temperature displayed a clearly defined seasonal pattern. The remaining variables fluctuated in a manner comparable to observations reported by Rodríguez-Quiroz et al. (2016), Villanueva-Fonseca et al. (2017),

Góngora-Gómez et al. (2018), and Sepúlveda et al. (2023) for the same lagoon. Among the correlations evaluated between environmental variables and shell or operculum biometrics, dissolved oxygen, pH, and water temperature showed predominantly moderate and negative associations with most traits. Exceptions included SL, TTW, TGW, and OW, which exhibited



**Figure 4.** Morphometric relationship between total weight and shell dimensions (length, height, and width) of the *Hexaplex nigritus* snail from the Navachiste Lagoon, Guasave, Sinaloa.

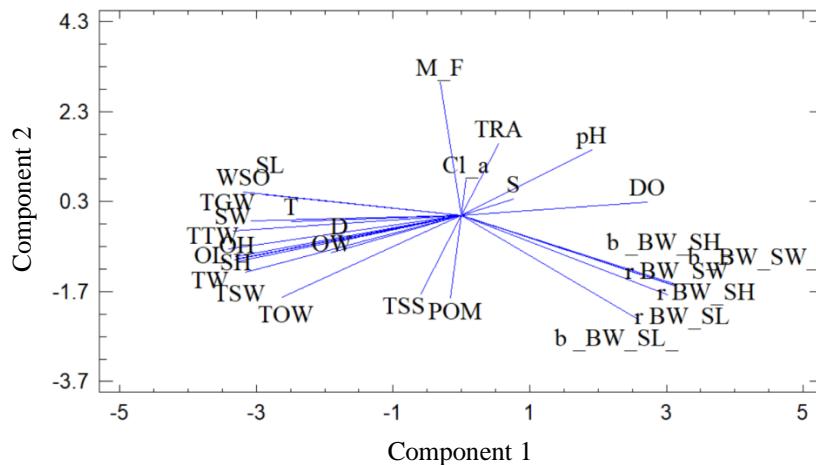
moderate positive correlations with temperature. Although assessing the isolated effects of environmental factors on marine benthic organisms remains challenging (Pardo & Johnson 2005), the annual temperature range in Navachiste Lagoon (21.5-32°C) appeared to exert a stronger influence on several biometric indicators of *H. nigritus*. Given that temperature is a key regulator of growth and physiological performance in aquatic organisms (Cloyd et al. 2019, Ou et al. 2022), its association with the biometric traits of the black Chinese snail is consistent with expectations.

**Table 4.** Spearman correlations ( $r$ ) between the physicochemical and biological variables of the water, the relative growth and weight data of the *H. nigritus* snail from the Navachiste Lagoon, in the southeast of the Gulf of California. DO: dissolved oxygen, SH: shell height, SL: shell length, WSO: width of the shell opening, SW: shell width, TSW: total shell weight, TWS: total weight of snail, TTW: total tissue weight, TGW: total gonad weight, OH: operculum height, OW: operculum width, OL: operculum length, TOW: total operculum weight.  $b$  TWS/SW: relative growth,  $r$  TWS/SL: morphometric association. Only significant correlations ( $P < 0.05$ ) are included.

Correlations	$r$	$P$
DO vs. SH	-0.60	0.03
DO vs. OH	-0.66	0.01
DO vs. SW	-0.62	0.02
DO vs. WSO	-0.73	0.00
DO vs. OW	-0.69	0.01
DO vs. SL	-0.59	0.04
DO vs. OL	-0.59	0.04
DO vs. TTW	-0.71	0.00
DO vs. TGW	-0.61	0.03
DO vs. TOW	-0.58	0.04
DO vs. TWS	-0.63	0.02
pH vs. OH	-0.64	0.02
pH vs. OW	-0.59	0.04
pH vs. OL	-0.58	0.04
pH vs. TTW	-0.60	0.03
pH vs. TGW	-0.57	0.04
pH vs. TOW	-0.63	0.02
Temperature vs. OW	0.65	0.01
Temperature vs. $b$ TWS/SW	-0.59	0.04
Temperature vs. SL	0.60	0.03
Temperature vs. TTW	0.65	0.02
Temperature vs. TGW	0.67	0.01
Temperature vs. $r$ TWS/SL	-0.60	0.03

On the other hand, the annual averages of pH and DO do not imply apparent metabolic demands that require changes in the energetic pattern of the snails and significantly alter their development (Chan et al. 2008, Chatzinikolaou et al. 2021), since they did not show significant fluctuations and are within the range of occurrence dictated by the values reported in other years within the same lagoon (Rodríguez-Quiroz et al. 2016, Villanueva-Fonseca et al. 2017, Góngora-Gómez et al. 2018, Sepúlveda et al. 2023).

The maximum SH of *H. nigritus* recorded in this study was lower than the values reported by Brusca (1980), Escamilla-Montes et al. (2018), and Arias-López et al. (2023) (150, 120, and 125.1 mm, respec-



**Figure 5.** Principal component analysis of the physicochemical and biological variables of the water and biometric indicators of the black Chinese snail *Hexaplex nigritus*, from Navachiste Lagoon, Sinaloa, Mexico. T: temperature, S: salinity, DO: dissolved oxygen, pH, TRA: transparency, D: depth, TSS: total suspended solids, POM: particulate organic matter, Cl<sub>a</sub>: chlorophyll a, SH: shell height, SL: shell length, SW: shell width, WSO: width of the shell opening, OH: operculum height, OL: operculum length, OW: operculum width, TOW: total operculum weight, TWS: total weight of snail, TSW: total shell weight, TTW: total tissue weight, TGW: total gonad weight, M\_F: sex ratio, b\_BW/SL: allometry body weight/shell length, b\_BW/SH: allometry body weight/shell height, b\_BW/SW: allometry body weight/shell width, r\_BW\_SL: relation body weight/shell length, r\_BW\_SH: relation body weight/shell height, and r\_BW\_SW: relation body weight/shell width.

tively), but higher than the 100 mm documented by Ortiz-Arellano & Flores-Campaña (2008). All of these studies were conducted within the GC, and the two most recent investigations focused specifically on the Navachiste Lagoon population of the black Chinese snail. The monthly distribution of the largest individuals indicates that the morphometric analysis was performed on adult, reproductively mature snails, which is consistent with observations by Cudney-Bueno et al. (2008) and Góngora-Gómez et al. (2010, 2011, 2020), who collected similarly sized specimens (123.3, 102.91, 109.10, and 82.99 mm SH, respectively) from the GC, including the Navachiste population, for use as broodstock in laboratory reproduction studies. Additionally, the monthly coefficients of variation for TWS and TGW exceeded 20%, suggesting pronounced variability likely associated with gonadal maturation and reproductive activity (Çelik et al. 2018). This interpretation could be further substantiated through histological examination of the gonads.

Operculum size increased with specimen size; however, despite the linear, positive trends, the relationships between operculum biometrics and shell dimensions showed only weak to moderate correlations. According to Paul (1991), the operculum

contributes to gastropod protective mechanisms. Yet, its shape and proportions may change throughout ontogeny due to growth-related adjustments, modifications in body coiling within the shell, and environmental influences (Chiu et al. 2002).

Several factors may account for the allometric patterns observed in *H. nigritus*, including age and sex. Starunova et al. (2021) reported that age is a key determinant of relative growth in marine snails: younger individuals generally exhibit near-isometric growth owing to proportional increases across exoskeletal dimensions, whereas older, sexually mature individuals tend to display more pronounced allometric patterns. Likewise, Hollander et al. (2006) documented sex-specific growth trajectories in the intertidal gastropod *Littorina saxatilis*, with males tending toward isometry. As noted above, all specimens collected in the present study were adults, which likely contributed to the observed differences in relative growth patterns in the morphometric comparisons, reflecting their age and sexual maturity.

The strongest correlation coefficient among shell dimensions indicated a robust dependence among the variables, suggesting that this relationship provides the most adequate descriptor of *H. nigritus* growth in Navachiste Lagoon. In particular, the association

between SH and SL was best represented by the equation  $SH = 1.1389 SL + 20.678$ . Although Arias-López et al. (2023) reported a similar correlation coefficient ( $r = 0.8785$ ) for the same species and lagoon, their relative growth exponent differed ( $b = 0.5739$ ), indicating negative allometry. These discrepancies likely reflect differences in the size structure of the sampled populations (Arias-López et al. 2023), as well as the potential influence of sex (Hollander et al. 2006) and age (Cudney-Bueno & Rowell 2008).

Regression equations involving TWS with shell dimensions indicate negative allometric growth ( $b < 3$ ) for TWS/SL and TWS/SW, but isometric growth with TWS/SH, meaning that the increase in TWS is proportional to the cube of SH. In contrast, the value of  $r$  (0.8359) indicates a strong relationship. In this case, the equation  $TWS = 0.0002SH^{3.0211}$  best describes the growth of *H. nigritus* in Navachiste Lagoon. The type of allometry found in the present work between SH and TWS of the snail (isometric) coincides with the conclusions reported by Cudney-Bueno & Rowell (2008) and Arias-López et al. (2023) with the same species in the Navachiste Lagoon, which suggests that its growth could be linked to a consistent reproductive strategy (Sotelo-Gonzalez et al. 2020), the genetics of the species (Galindo et al. 2019) and the environmental stability in the area (Rodríguez-Quiroz et al. 2016, Villanueva-Fonseca et al. 2017, Góngora-Gómez et al. 2018, Sepúlveda et al. 2023).

The operculum of gastropods is an organic-mineral structure whose shape conforms to the outline of the shell aperture; its coloration and composition vary among species, and it serves as a primary defense mechanism against predators (Vasconcelos et al. 2012, Mueller & Stoner 2013). Although all morphometric relationships between operculum biometrics and shell dimensions were linear and positive, relative growth exhibited negative allometry ( $b < 1$ ), and Spearman's correlation coefficients indicated weak proportionality among the variables. The relevance of operculum measurements for estimating the morphometric and growth characteristics of *H. nigritus* in Navachiste Lagoon stems from the common practice of fishermen retaining only the soft tissue attached to the operculum when landing the catch; the shell is typically discarded at sea on the return trip. Similar practices have been reported for the queen conch *Strombus gigas* in the Bahamas (Theile 2005, Mueller & Stoner 2013). Consequently, the absence of shells limits the application of calcareous structures for estimating age, size, shape, and growth over time, thereby enhancing the morphometric value of operculum measurements

(Uneputty 2007, Miranda et al. 2008). Within this context, the OL/SL relationship appears to be the most suitable operculum-shell association for estimating the morphometric characteristics of the black Chinese snail.

The distribution of points along the principal component axes revealed a cohesive set of physicochemical and biological variables interacting directly with morphometric indicators, with depth and temperature showing the strongest associations with shell dimensions, biomass variables, and operculum biometrics. The influence of temperature on the physiological processes underpinning gastropod growth is well documented (Wong & Lim 2017, Cloyd et al. 2019, Chatzinikolaou et al. 2021), and its effects are amplified in intertidal or shallow-water populations such as *H. nigritus* in Navachiste Lagoon. Hu et al. (2021) reported that growth in the muricid *Rapana venosa* increases under high temperatures characteristic of its coastal habitat, provided conditions remain within its metabolic tolerance limits. The combined temperature-depth pattern associated with shell dimension variability in the present study aligns with these observations.

Results are presented that constitute essential information about the morphometry and allometry of *H. nigritus* in Navachiste Lagoon, Sinaloa, Mexico. It is concluded that: 1) the physicochemical and biological variables of the locality influence the morphometric relationships and relative growth of the black Chinese snail, mainly the water temperature; 2) the measurements obtained from the shell dimensions of this gastropod indicate that the sampled population consisted of adult snails; 3) specifically, the coefficient of variation for the weight values (total weight, shell weight, tissue weight and gonad weight) would indicate the possibility of reproductive events during the sampling year; 4) all morphometric equations were linear and positive; 5) except for SH/SL, SL/WSO and OH/OL, the other morphometric relationships between shell dimensions, weight values, operculum biometrics and the association between shell dimensions/operculum biometrics, showed a relative growth of the negative allometric type ( $b < 1$ ); 6) the SH/SL relationship represents the most appropriate tool to describe the relative growth of this gastropod. These data are fundamental for the management and conservation of these muricid species in the study area, providing valuable information for planning sustainable management strategies.

## Credit author contribution

C.O. Montoya-Ponce: data collection and processing, supervision, writing and review; A.M. Góngora-Gómez: conceptualization, funding acquisition, project administration, methodology, review and supervision; Y.L. Guerrero-Beltrán: data collection and processing, writing and review; C.H. Sepúlveda: writing, data curation, formal analysis, review and editing; L.C. Villanueva-Fonseca: methodology, review and supervision; B.P. Villanueva-Fonseca: methodology, review and supervision; M.I. Sotelo-Gonzalez: methodology, review and supervision; J.A. Hernández-Sepúlveda: methodology, review and supervision; T.E. Isola: validation, review and writing; V.M. Peinado-Guevara: validation, review and writing; M. García-Ulloa: conceptualization, validation, methodology, supervision, data curation, formal analysis, funding acquisition, writing, review and editing. All authors have read and accepted the published version of the manuscript.

## Conflict of interest

The authors declare no potential conflict of interest in this manuscript.

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