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Research Article

Multimodel approach for growth analysis of purple snail *Plicopurpura columellaris* (Lamarck, 1816) in the rocky intertidal of Guerrero, Mexico

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ABSTRACT. The growth of *Plicopurpura columellaris* has been described using the von Bertalanffy growth model, assuming asymptotic growth. In the present study, a growth analysis was conducted using the five cases of Schnute's model to determine the type of growth *P. colummellaris* exhibits. Length frequency data for males and females, collected between September 2000 and December 2001 at six sites in the rocky intertidal of Guerrero, Mexico, were analyzed. Five cases of the Schnute model were estimated for males and females, and according to the bias-corrected Akaike information criterion (AIC$_c$), case 2 with two parameters best describes growth in males (L_∞= 42.5 mm and κ = 0.60) and females (L_∞ = 56.9 mm and κ = 0.89); on the other hand, case 5 with two parameters also provided valuable information on growth in males (L_∞ = 56 mm and κ = 0.20) and females (L_∞ = 63.4 mm and κ = 0.44). Because cases 2 and 5 did not reach an Akaike weight (ωi) ≥ 90%, an average model was estimated and modeled together with the two best cases. Using the parameters of case 2, the Kimura test showed highly significant differences in growth between males and females. In conclusion, the growth of males and females of *P. columellaris* is slow, asymptotic, sigmoidal, or inverse-exponential (von Bertalanffy type), characteristic of long-lived species.

Keywords: condition factor; size structure; modal groups; Schnute's model; Mexican Pacific

INTRODUCTION

The purple snail, *Plicopurpura columellaris* (Lamarck, 1816), is a species characteristic of the rocky intertidal areas of the Mexican Pacific (García-Ibáñez et al. 2004). It is distributed from the south of the Baja California Sur Peninsula, Mexico (Keen 1971), to northern Peru (Paredes et al. 1999), including the Cocos, Malpelo, and Galapagos Islands (Keen 1971). The species has been exploited since pre-Hispanic times for its dye, used to color clothing. Due to mismanagement, the population declined and is now considered a species subject to special protection based on the official Mexican standard NOM-059-ecol-1994 (Flores-Garza et al. 2007).

The growth pattern of individuals provides important information on the age structure of the stock, mortality, and productivity. This information is important for the assessment and management of fishery resources (Montgomery et al. 2010). Sparre & Venema (1997) quantify growth in terms of body size as a function of age, while Schnute (1981) and Haddon

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(2011) quantify growth in terms of length and weight as a function of time or age.

Several mathematical functions have been developed for growth estimation (Quinn & Deriso 1999), the most widely used being the von Bertalanffy growth model (VBGM) (Montgomery et al. 2010). In many studies, the VBGM has been shown to have biological validity, as it has predicted asymptotic mean lengths similar to the observed maximum lengths. However, this need not always be the case (Knight 1968). On the other hand, it has been questioned whether the VBGM is always appropriate for describing growth, due to its discontinuity and the importance of incorporating growth variability (Knigth 1968, Schnute 1981, Montgomery et al. 2010). To address these weaknesses, several alternative growth model functions have been used, including Richards (1959), Gompertz (Haddon 2011), and Schnute (1981), thereby enabling multimodel inference. The Schnute model is very general and incorporates the VBGM, Gompertz, Richards, and logistic curves as special cases (Quinn & Deriso 1999). Alternatively, a two-stage VBGM has been adjusted separately to the different life stages of certain populations (Hearn & Polacheck 2003). The Schnute model is a differential equation that yields eight curves as functions of the parameters. Instead of modeling the instantaneous rate of change, it focuses on the relative rate of change (Ortega-Lizárraga et al. 2016).

Growth studies of *P. columellaris* in the Mexican Pacific have demonstrated its slow growth rate (Fonseca-Madrigal 1998, Michel-Morfín et al. 2000, Ramírez-Rodríguez & Naegel 2003). However, traditional methods have been used in these studies, assuming asymptotic VBGM-type growth. Therefore, in this research, five cases of Schnute's model were tested, using a multimodel inference to determine the growth type of males and females of *P. columellaris* in the rocky intertidal of Guerrero, Mexico. We hypothesize that the growth of *P. columellaris* will be explained by asymptotic models. On the other hand, males will show differential growth compared to females, growing faster as a possible response to reproductive strategies.

MATERIALS AND METHODS

Study area

The Guerrero State is in the southeast of the Mexican Pacific, between coordinates 16º18'N-18º48'N, and 98º03'W-102º12'W, with a coastline of 470 km. Sampling of the purple snail, *P. columellaris*, was carried out in six rocky intertidal sites: 1) Punta Maldonado (16°19.43'N-98°34.08'W), 2) Las Peñitas (16°33.24'N-98°46.37'W), 3) Playa Ventura (16°32.14'N-98°54.74'W), 4) Acapulco (16°51.53'N-99°53.66'W), 5) Tlacoyunque (17°15.24'N-101°0.77'W), and 6) Barra de Potosí (17°32.29'N-101°27.32'W) (Fig. 1).

Data collection

Six samplings were conducted every three months from September 2000 to December 2001. The organisms were collected using the transect method; the work area was delimited by a 30 m-long line parallel to the coast, 2 m wide, following the methodology of García-Ibáñez et al. (2004). The collected organisms were separated by sex; later, the shell length (SL) of each organism was measured with a digital vernier caliper (± 0.01 mm). The total weight (TW) was recorded using a digital balance accurate to 0.01 g. At the end of the biometrics, the specimens were returned to the rocky intertidal, placed in shaded crevices, and protected from the waves.

Data analysis

Size ranges by sex were estimated using violin plots for each site and each sampling campaign. The Kolmogorov-Smirnov two-independent-sample goodness-of-fit test (Gotelli & Ellison 2004) was used to test for differences in the SL distributions of males and females. The analysis was performed using IBM SPSS Statistics 25.

The relationship between SL and TW was estimated by pooled data and by sex (males and females), adjusting the potential model ($\mathrm{TW} = a \times \mathrm{SL}^{b}$), where TW is total weight (g); SL is shell length (mm), a is the intercept, and b is the allometric coefficient. Before analysis, the paired SL/TW data were transformed to the natural logarithm (Ln) to identify out-of-range data and exclude them from the analysis. The coefficient of determination (R^2) was used to measure goodness-of-fit for each regression. The 95% confidence interval of b was estimated, and a *t*-Student test (Zar 2014) was performed to determine if isometric growth exists (H_0: $b = 3$, $\alpha = 0.05$). Significant differences between sexes in the relationships of the SL/TW were evaluated with one-way analysis of covariance (ANCOVA) once assumptions of homoscedasticity of the slopes (parallelism) were found with the data transformed to the logarithm (Zar 2014). IBM SPSS Statistics 25 was used for this analysis.

The condition factor (K) (Ricker 1975) was estimated to assess the health of males and females of *P. columellaris* using the equations: $\mathrm{K_I} = (\mathrm{TW}/\mathrm{SL}^3) \times 100$ for isometric growth or $\mathrm{K_A} = \left(\mathrm{TW}/\mathrm{SL}^{\mathrm{b}}\right) \times 100$

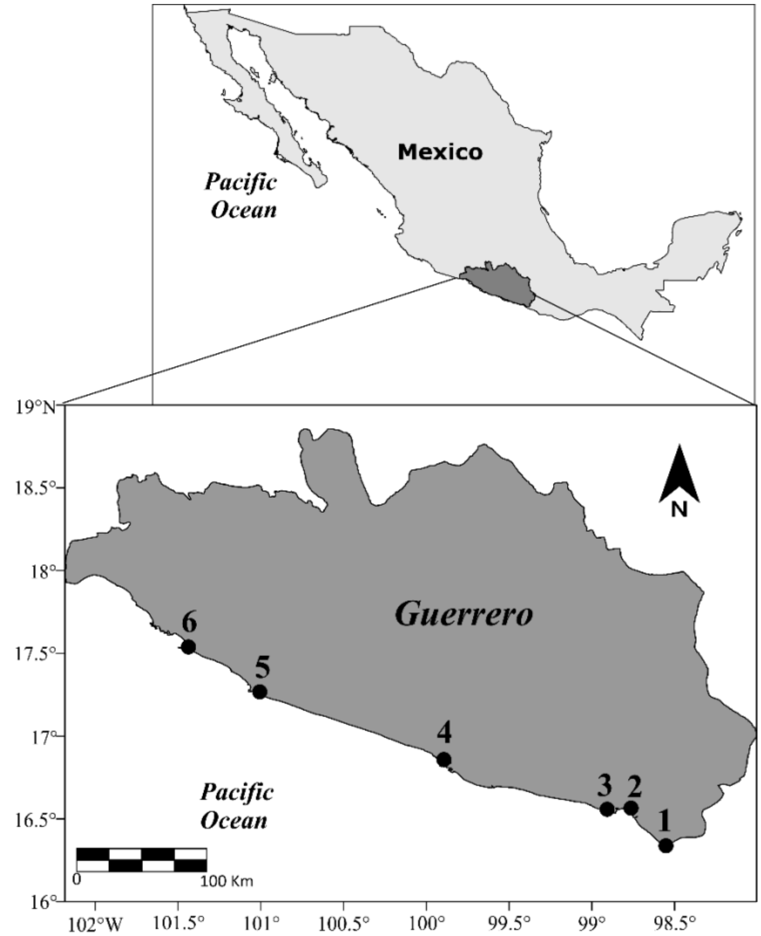

Figure 1. Collection and sampling sites of *Plicopurpura columellaris* in the state of Guerrero, Mexico. 1) Punta Maldonado, 2) Las Peñitas, 3) Playa Ventura, 4) Acapulco, 5) Tlacoyunque, and 6) Barra de Potosí.

for allometric growth, where TW is the total weight, SL is the shell length, and the exponent b is the coefficient of regression between SL/TW for allometric growth. The mean and 95% confidence intervals of K were estimated at 1.5 mm SL intervals. Tukey's test was performed to determine significant differences in K among size intervals. To explore changes in K with age (Rodríguez-Domínguez et al. 2018), a frequency analysis was performed, in which age groups were identified by fitting the data to a multinomial model, as described below.

The size structure for males and females was determined for each sampling period. Data were grouped into 1.5 mm intervals, and multinomial analysis was performed to identify the modal groups. This analysis is based on the observed distribution using frequency histograms in such a way that the estimate of each modal group (F_{ia}) was calculated using a normal probability density function, according to the following:

$$F_{ia} = \sum_{a=1}^{n}\left[\frac{1}{\sigma_a\sqrt{2\pi}}e^{\frac{(x_i-\mu_a)^2}{2\sigma_a^2}}\right] \times P_a$$

where F_{ia} is the expected frequency of the length interval i for the whole sample, xi is the midpoint of the length interval i, μa is the mean of the group a, and P_a is the weight factor of the cohort a. The analysis was fitted using the maximum likelihood method according to the following:

$$-LL_{\{X|\mu a,\sigma a,Pa\}} = \left[\sum_{i=1}^{n} f_i Ln\left(\frac{F_i}{\sum F_i}\right)\right] - \left[\sum f_i - \sum F_1\right]^2$$

where $-LL_{\{X|\mu a,\sigma a,Pa\}}$ is the log-likelihood of the data given the parameters μa, σa, and Pa; f_i is the observed total frequency of size class i, and F_i is the estimated total frequency of size class i according to the multinomial distribution (Montgomery et al. 2010, Haddon 2011). Finally, the modal groups were separated according to the separation index (SI) using the following equation (Sparre & Venema 1997):

$$\mathrm{SI} = 2 \times \frac{(\mu_n - \mu_i)}{(\sigma_n + \sigma_i)}$$

where μ_n and μ_i are the mean SL of modal groups *n* and *i*, respectively; σ_n and σ_i are the standard deviations of modal groups *n* and *i*. Therefore, if SI >2, then it is feasible to separate the normal components from the observed frequencies (Sparre & Venema 1997).

The mean lengths for each identified modal group were plotted on a time scale. The probable number of cohorts supporting growth was obtained by modal progression through time in an ordered sequence (Montgomery et al. 2010). The criteria for selecting the best progressions modals were as follows: 1) first, the clearest sections of the progression were visually identified and whether they were in range of the proportional rate of increase; 2) if there were doubts about the progression of means, all alternative hypotheses were considered, and the one that was closest to the growth rate identified in the previously identified segments of progression was chosen.

The size and time increase data were obtained from all modal progressions; these were fitted to the five cases of the Schnute (1981) model; one of these (case 5) is a special case equivalent to VBGM (Baker et al. 1991). The five cases used were the following:

Case 1 (assuming $\kappa \neq 0$ and $\gamma \neq 0$)

$$\mathrm{SL_{2j}} = \left[\mathrm{SL}_1^{\gamma} \times e^{-\kappa\Delta t} + \varepsilon^{\gamma}(1 - e^{-\kappa\Delta t})\right]^{1/\gamma}$$

Case 2 (assuming $\kappa \neq 0$ and $\gamma = 0$)

$$\mathrm{SL_{2j}} = exp[ln(\mathrm{SL_1}) \times e^{-\kappa\Delta t} + ln(\varepsilon)(1 - e^{-\kappa\Delta t})]$$

Case 3 (assuming $\kappa = 0$ and $\gamma \neq 0$)

$$\mathrm{SL_{2j}} = (\mathrm{SL}_1^{\gamma} + \varepsilon^{\gamma}\Delta t)^{\frac{1}{\gamma}}$$

Case 4 (assuming $\kappa = 0$ and $\gamma = 0$)

$$\mathrm{SL_{2j}} = \mathrm{SL_1} \times \varepsilon^{\Delta t}$$

Case 5 (assuming $\kappa \neq 0$ and $\gamma = 1$)

$$\mathrm{SL_2} = [\mathrm{SL_1} \times e^{-\kappa\Delta t} + \varepsilon(1 - exp^{-\kappa\Delta t})]$$

In the five cases $\mathrm{SL_1}$ and $\mathrm{SL_2}$ are mean shell lengths for the same cohort at collection times t_1 and t_2; κ is the growth parameter; γ is related to the inflection point within the growth curve; Δt is the elapsed time between t_1 and t_2, and ε in the cases 1, 2, and 5 is an asymptotic maximum length (L_∞) (Montgomery et al. 2010). The cases were fitted with maximum log-likelihood LL (Haddon 2011), considering additive error with the following equation:

$$LL\ (\Phi|data) = \left(-\frac{n}{2}\right) \times [Ln\ (2\pi) + 2 * Ln(\sigma) + 1]$$

where Φ represents the model parameters, n the number of observations, and σ the standard deviation calculated by additive error. The formula for the standard deviation is as follows:

$$\sigma = \sqrt{\frac{\sum(\mathrm{SL_{obs}} - \mathrm{SL_{cal}})^2}{n}}$$

where $\mathrm{SL_{obs}}$ is the observed shell length, $\mathrm{SL_{cal}}$ is the calculated shell length, and n is the number of observed SL data.

For comparisons of the Schnute model cases and selection of the best model describing SL as a function of time, Akaike corrected form ($\mathrm{AIC_c}$) scores were used. The lowest $\mathrm{AIC_c}$ score is the one that will define the best model (Burnham & Anderson 2002) and is expressed by:

$$\mathrm{AIC_c} = 2(k - LL) + (2k(k+1)/(n - k - 1))$$

where k is the number of parameters of each model, n is the number of observations, and LL is the maximum log-likelihood function. The difference in the $\mathrm{AIC_c}$ (Δi) of a given model with respect to the $\mathrm{AIC_{min}}$ of the best model was estimated as follows:

$$\Delta i = \mathrm{AIC_c} - \mathrm{AIC_{min}}$$

This analysis yields three possible answers for selecting the best model growth. In the first case, if $\Delta i > 10$, the candidate growth model should be discarded since it does not describe the observed growth and is not supported by the data. In the second case, if $4 < \Delta i < 7$, the model partially supports and weakly explains the growth data. Finally, in the third case, if $\Delta i < 2$, the candidate growth model adequately describes the observed growth data (Burnham & Anderson 2002). Normalized weights for each growth model (Akaike 1983, Burnham & Anderson 2002) were estimated using the Akaike weight (ωi), expressed as a proportional index defined as:

$$\omega i = \frac{e^{(-0.5\Delta_i)}}{\sum_{k=1}^{5} e^{(-0.5\Delta_i)}}$$

Confidence intervals for the growth parameters were estimated based on the likelihood profiles and chi-square distribution (X^2) (Venzon & Moolgavkar 1988). The confidence interval was defined as all values θ satisfying the following inequality:

$$2(L(Y|\theta) - (L(Y|\theta_{best})) < X^2_{1,1-\alpha}$$

where $L(Y|\theta_{best})$ is the negative log-likelihood of the most likely value of θ and $X^2_{1,1-\alpha}$ is the value of X^2 with one degree of freedom at the $1 - \alpha$ confidence level.

Thus, the confidence interval at 95% of the value θ covers all values that are twice the difference between the log-likelihood of a θ given, and the log-likelihood of the best estimate θ given, that is, less than 3.84 (Haddon 2011).

If there is no best candidate model with an Akaike weight (ωi) greater than 90%, an average model must be calculated as required when using the multimodel approach (Burnham & Anderson 2002). Once the best cases were selected, growth curves could be generated. The growth curves were generated from an initial length of 10.98 mm in males and 9 mm in females. The initial length was the estimated minimum mean length for the modal groups, determined using multinomial analysis. We used the Kimura test (Kimura 1980) to analyze significant differences in the growth curves between males and females. The following formula was used:

$$x_k^2 = -N \times LN\left[\frac{\sum RSS_i}{RSS_p}\right]$$

where k is the degrees of freedom (number of model parameters), N is the total number of observations for both curves combined, RSS_i is the total sum of squared residuals derived from fitting each curve separately, and RSS_p is the total sum of squared residuals derived from fitting the pooled curves.

RESULTS

A total of 5,246 *P. columellaris* organisms were analyzed; 2,743 were males (52.3%), and 2,503 were females (47.7%). Males had a mean SL of 20.4 ± 4.8 mm; the Kolmogorov-Smirnov test showed that comparisons between sites were different ($P < 0.05$); violin plots showed that the SL of sites 3 and 6 were bimodal (Fig. 2a). Females had a mean SL of 20.2 ± 7.3 mm, and sites 1 and 3 showed no significant difference ($P = 0.932$); violin plots showed that SL data were bimodal at site 3 (Fig. 2b). Comparisons of the distribution of SL in males across the study area by season showed no significant differences between September 00-March 01, September 00-June 01, December 00-March 01, December 00-September 01, March 01-June 01, and March 01-September 01 ($P > 0.05$), and the violin plot showed that the distribution of SL data was unimodal for the sampling seasons (Fig. 2c). In females, only the December 00-March 01 comparison did not differ significantly in SL distribution ($P > 0.05$), and violin plots showed that SL data were bimodal in September 2001 (Sep 01) (Fig. 2d).

Relationship analysis between SL/TW for the population showed $b = 2.7$, $a = 0.000423$, and $R^2 = 0.99$, and the Student-*t* test showed negative allometric growth ($P = 0.0003$) (Table 1). In males, the values were $b = 2.8$, $a = 0.000331$, and the coefficient of determination R^2 was 0.98; the *t*-test showed negative allometric growth ($P = 0.002$) (Table 1). In females, the correlation parameters were $b = 2.7$, $a = 0.000390$, and $R^2 = 0.99$; the *t*-test showed negative allometric growth ($P = 0.0005$) (Table 1). ANCOVA analysis showed significant differences in the SL/TW ratio between females and males ($P < 0.001$) (Table 1).

The condition factor (K_A), estimated by allometric growth for males and females of *P. columellaris*, increased with greater length and age. Tukey's test, used to compare K_A between size intervals, is shown in Figure 3. In males, an increase in K_A was observed across the range of 9 to 22.5 mm of SL (modal groups 1, 2, and 3), with significant differences among their values. On the other hand, K_A decreased in the 24-31.5 mm SL range (modal groups 3 and 4), showing significantly lower values than the second modal group. The highest K_A values occurred in the 34.5-37.5 mm SL range (modal group 5), differing significantly from the second modal group (Fig. 3a). In females, K_A values increased significantly across modal groups, with a decrease apparent in modal groups 3 and 4 (ranges 25.5-31.5 mm SL). The values showed a positive trend with significant differences with increasing size (Fig. 3b).

Size structure and modal groups

The size structure ranged from 7.3 to 43.5 mm SL in males and from 6.5 to 65.6 mm SL in females; males were smaller than females. The multinomial analysis applied to the size structure of males showed two to three modal groups per sample; only in September 01, five groups were observed; on the other hand, during June 01 and September 01, the entry of one modal group of small-sized organisms could be identified (Fig. 4a). Females showed multimodal behavior with three, four, and five modal groups per sample; the presence of small size modal groups was observed in September 00, December 00, and September 01 (Fig. 4b). In the modal progression through time, four cohorts were identified in males (Fig. 4a) and six cohorts in females (Fig. 4b). When plotting the mean lengths of each modal group in males, we observed a slower growth that approached a straight line. In contrast, females showed a steeper slope at smaller lengths, with a decrease after 40 mm SL.

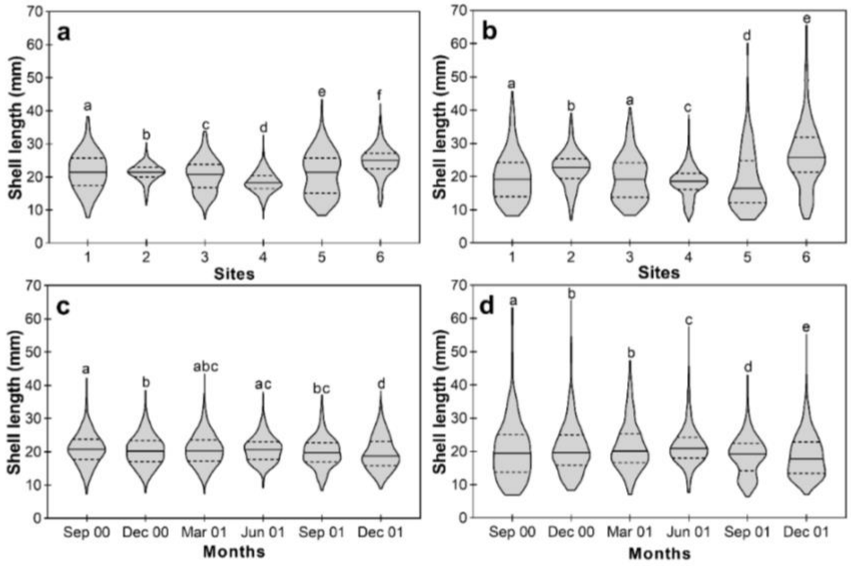

Figure 2. Length ranges of *Plicoporpura columellaris* between sites, a) males, b) females, and between months, c) males, and d) females. Different letters above each graph indicate significant differences ($P < 0.05$).

Table 1. Summary of length-weight regression values for males, females, and both sexes of *Plicopurpura columellaris*. *F* and *P* values from the one-way analysis of covariance (ANCOVA).

Sex	*a*	*b*	*b* (IC 95%)	R^2	*t*-test (*b*) *P*	*F* (ANCOVA)	*P* (ANCOVA)
Males	0.000331	2.80	2.78-2.83	0.98	$P < 0.002$		
Females	0.000390	2.74	2.72-2.75	0.99	$P < 0.0005$		
Both	0.000423	2.72	2.71-2.73	0.99	$P < 0.0003$	73.7	$P < 0.001$

Growth

Although the modal progression suggested linear growth in males, the model fit showed that case 2 was optimal for both sexes, indicating asymptotic sigmoidal growth. In males, case 2 showed values of $\varepsilon(L_\infty)$ = 42.5 mm and κ = 0.6 with a plausibility ωi = 40%; on the other hand, cases 5 and 3 also provide valuable information on growth ωi = 27% and ωi = 20% (Table 2). However, case 3 shows indeterminate linear growth, while cases 2 and 5 show determinate asymptotic growth. For females, case 2 showed values of $\varepsilon(L_\infty)$ = 56.9 mm and κ = 0.89 with a plausibility of ωi = 56.5%. Case 5 contributes valuable information ωi = 28.8%; on the other hand, case 1, despite being the third best (ωi = 11.6%), only partially and weakly supported the data (Δ_i= 3.2). Figure 5 shows the estimated male and female growth curves for the best cases and the average model. Growth was faster in both sexes during the first four years, with females growing faster than males. The two best cases and the average model indicate that $\varepsilon(L_\infty)$ is reached at 12 years, suggesting *P. columellaris* is a slow-growing and long-lived organism. Considering the best model (case 2), Kimura's test showed significant differences between male and female growth curves (RSS = 147.69, X_2^2= 18.26, P = 0.0001).

DISCUSSION

P. columellaris is currently considered a synonym of *P. pansa* (Claremont et al. 2013), so this will be considered as *P. columellaris* when making comparisons with other studies. The mean and maximum lengths of males and females of *P. columellaris* in Guerrero were smaller than those reported in other areas (Acevedo et al. 1990, Fonseca-Madrigal 1998, Michel-Morfín et al. 2000). In the northernmost study, Ramírez-Rodríguez & Naegel (2003) reported males' ranges similar to those observed in our study, but larger females (74 mm), attributing length differences between localities to the extreme variability that exists in the intertidal zones of each locality, including aerial exposure, temperature, and desiccation time. Michel-Morfín et al. (2002) reported that *P. columellaris* lengths increased southward across four Mexican Pacific states, in relation to the species'

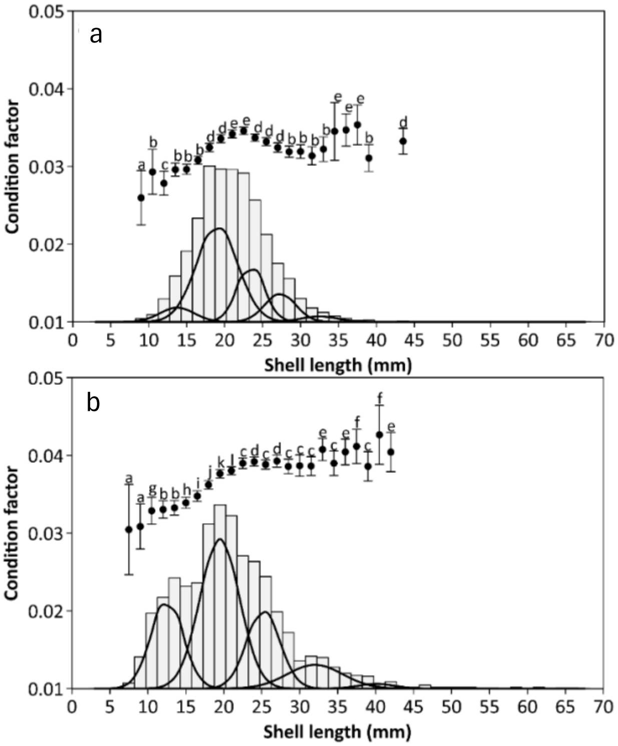

Figure 3. Condition factor (K_A) for length and age group of a) males and b) females. Dark bell-shaped line indicates modal groups. Black dots and vertical lines indicate the K_A and 95% confidence intervals. Similar letters above the K_A indicate no significant differences by Tukey's test.

tropical biogeographic affinity. Therefore, the lengths will be greatest in the center of its distribution area. However, they suggest that age and growth studies should be carried out by region to determine this aspect. Because our study was conducted between locations that had been studied (to the north and south), and we observed shorter lengths, we believe the differences are due to environmental conditions at each study site. In the present study, we lack data on environmental variables to assess their effects on the length and growth of *P. columellaris*; therefore, explanations for the differences in length are hypothetical. However, in a study of the violet oyster (*Chama coralloides*) conducted in Oaxaca, Guerrero, and Michoacán, length variations were observed among sampling sites. These differences showed that larger organisms grew at warmer temperatures, and it was concluded that this was not a response to latitudinal variability but rather to the site's environmental characteristics (Flores-Garza et al. 2022).

The SL/TW relationships in fisheries biology describe changes in individual length, growth patterns, maturity, reproduction, and nutrition, and are therefore important for determining the condition of individuals and populations (Hilborns & Waiters 1992, Albuquerque et al. 2009, Cifuentes et al. 2012, Simon et al. 2014). Negative allometric growth in males and females of *P. columellaris* in the state of Guerrero describes a growth pattern in which the organism grows more slowly than expected. Still, its weight does not increase in the same proportion. This behavior differs from that described by Michel-Morfín et al. (2000) in Bahía de Navidad (Jalisco), who reported isometric growth in both sexes, meaning that length and weight increase in the same proportion. However, they found that the slope differed between sexes, as observed in our study. Researchers have proposed various explanations for the negative allometric growth. For example, in the gastropod *Turbo sparverious*, this growth pattern was attributed to a greater abundance of juveniles, which prioritize length growth over weight gain (Saleky et al. 2016). In our case, we ruled out this effect because there is a good proportion of juvenile and adult organisms.

On the other hand, the isometric growth estimated by Michel-Morfín et al. (2000) for *P. columellaris* in Jalisco and the allometric growth in Guerrero (this study) lead us to hypothesize that other external factors, such as environmental conditions (temperature, waves, food availability, etc.), influenced this difference. Innal et al. (2015) note that differences in growth patterns within the same species are due to several factors, including sample size, sex differences, and environmental conditions that favor growth. For example, Jisr et al. (2018) found in three fish species that parameter *b* tends to be higher during warm periods, as high temperatures increase metabolic rate by accelerating digestion, leading to faster growth, leading us to conclude that the differences in proportional growth between length and weight (isometric) of *P. columellaris* in Jalisco (Michel-Morfín et al. 2000) and slower weight growth relative to length (negative allometric) in Guerrero could be explained by differences in local environmental conditions. Sparre et al. (1989) demonstrated that length-weight relationships vary geographically due to the specific conditions of each locality. Although we do not have records of environmental variables such as temperature in the present study, in our research with the bivalve *C. coralloides* in the intertidal zone of the south-central part of the Mexican Transitional Pacific (MTP), we observed shorter lengths than those reported for the subtidal zone, because when organisms are exposed to high temperatures that exceed their tolerance threshold, some biological processes may be halted (Flores-Garza et al. 2022). Therefore, it is important to conduct studies on the effects of environmental variables on species' relative growth.

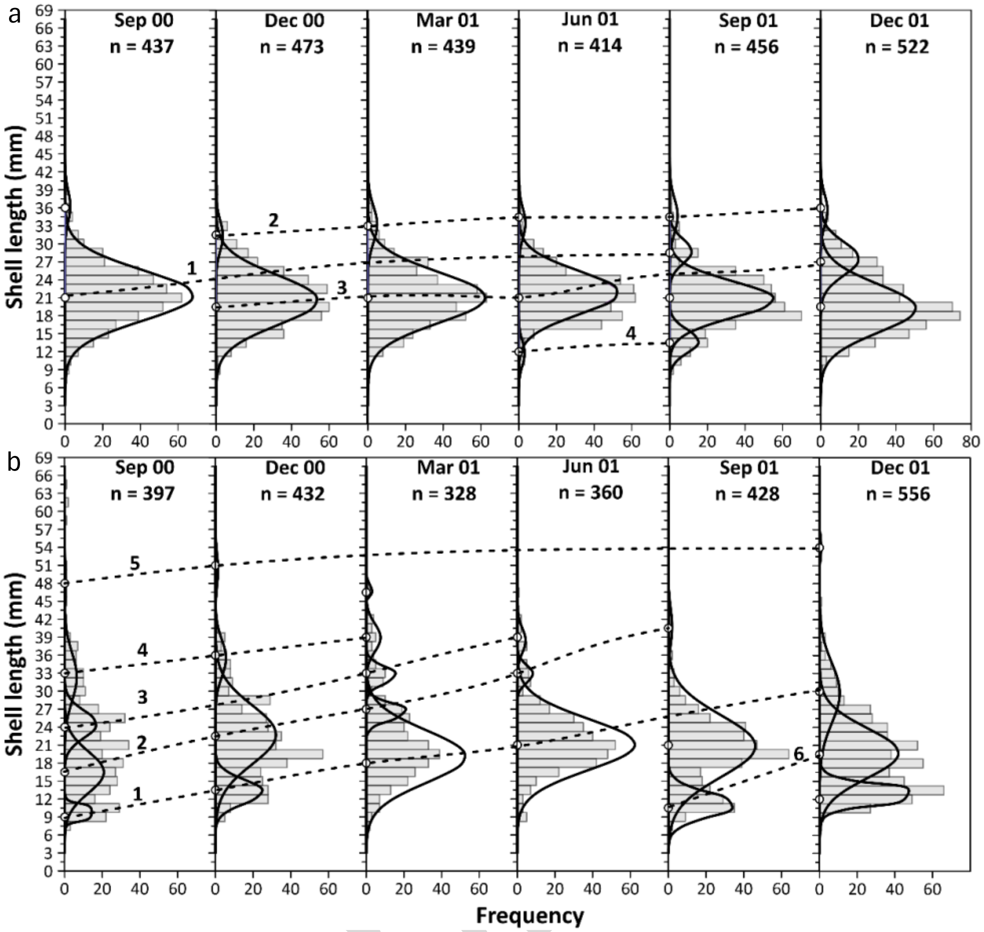

Figure 4. Length-frequency data separated into modal groups (dark bell-shaped lines) and modal progression (dotted line) for a) males and b) females of *Plicopurpura columellaris*. White dots indicate the mean for each modal group, and the numbers indicate the number of cohorts.

The K_A provides information about growth strategies, nutritional and reproductive status, and the effects of environmental conditions on populations in aquatic ecosystems (Cifuentes et al. 2012), thereby indicating species health status. The tendency to increase in K_A with greater length and age in *P. columellaris* may be attributed to maturation processes in both females and males. This pattern also reflects their development process, since this index shows a greater sensitivity to weight changes, which explains why in organisms with greater length, weights tend to stabilize and the rate of loss decreases (Gerking 1971), likely resulting in higher K_A values in organisms of greater length and age. Additionally, we suggest that larger and older organisms are better adapted to tolerate changes in environmental factors in the rocky intertidal zone, an area characterized by constant stress that could particularly affect juvenile organisms. Therefore, larger organisms perform their physiological functions better and maintain their body weight.

Size distribution analysis of *P. columellaris*, with a 1.5 mm interval width, was key to identifying groups from the same recruitment event, enabling efficient separation of young and old cohorts. This interval width is smaller than those used in previous research, which employed widths of 3 mm (Ramírez-Rodríguez & Nagel 2003), 4 mm (Michel-Morfín et al. 2000), and 10 mm (Cervantes-Hernández et al. 2010). Montgomery et al. (2010) mention that size distribution analysis has two main limitations. First, older cohorts tend to overlap as the growth rate decreases and individual growth becomes more variable. Second, prolonged recruitment makes it difficult to distinguish the new recruitment cohort from the existing one in stock. Despite using a fine-interval width analysis for *P. columellaris* in this study, separating male cohorts proved challenging

Table 2. Growth parameters estimated for each model assuming additive error with their respective Akaike information criterion (AIC_c) and Akaike weight values (ωi). Best cases are indicated in bold. Superscript indicates ^{1}first best case, ^{2}second best case, and ^{3}third best case. ^{4}fixed values do not need to be computed. CI: confidence interval.

Models	AIC_C	Δi	ωi (%)	ε (CI)	κ (CI)	γ (CI)
Males						
Case 1	36.8	4.5	4	37.6 (33.5, 42.9)	1.1 (0.84, 1.41)	-1.9 (-0.8, -3.4)
Case 2^1	**32.4**	**0.0**	**40**	**42.5 (37, 48.5)**	**0.6 (0.42, 0.71)**	**0^4**
Case 3^3	**33.7**	**1.4**	**20**	**13.6 (11,16.1)**	**0^4**	**1.5 (1.28, 1.72)**
Case 4	35.2	2.9	9	1.3 (1.21, 1.44)	0^4	0^4
Case 5^2	**33.1**	**0.8**	**27**	**56 (47.4, 64.5)**	**0.2 (0.18, 0.29)**	**1^4**
Females						
Case 1^3	**71.3**	**3.2**	**11.6**	**57.2 (51.7, 63.1)**	**0.8 (0.68, 1.02)**	**0.09 (0.02- 0.14)**
Case 2^1	**68.1**	**0.0**	**56.5**	**56.9 (51.5, 62.7)**	**0.89 (0.71, 1.07)**	**0^4**
Case 3	74	5.8	3.1	25.9 (21.9, 29.6)	0^4	1.89 (1.6, 2.4)
Case 4	91.6	23.5	0.0	1.2 (1.1, 1.3)	0^4	0^4
Case 5^2	**69.5**	**1.3**	**28.8**	**63.4 (56.2, 70.6)**	**0.44 (0.34, 0.54)**	**1^4**

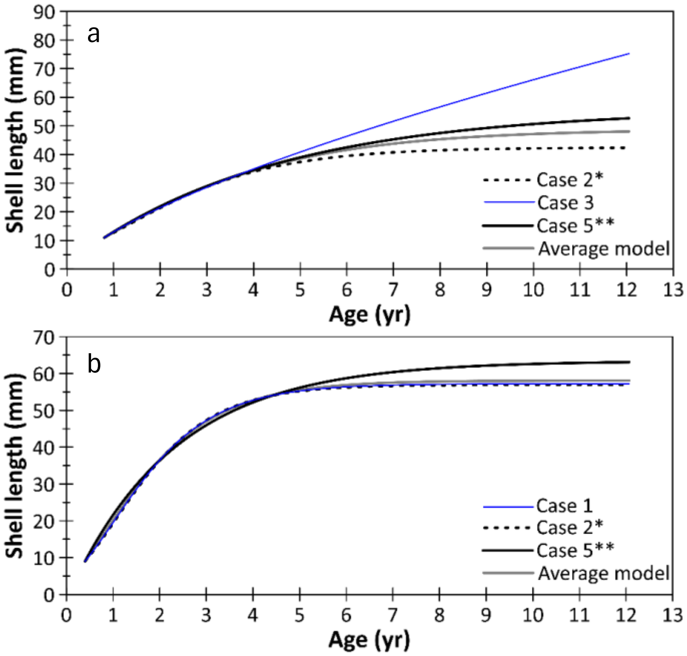

Figure 5. Growth curves for a) males and b) females of *Plicopurpura columellaris*. Estimates were made using three best-case scenarios, and the average model was estimated. *First best case and **second best case.

because their SL range was narrower than that of females. Using a wider range of intervals would likely have resulted in the loss of some modal groups.

Growth modeling of *P. columellaris* in this research followed Montgomery et al. (2010), in which growth functions were fitted to individual cohorts to account for individual variability in growth (Quinn & Deriso 1999, Punt et al. 2009). Furthermore, model selection was based on probability theory, providing a robust analysis framework aligned with modern statistical approaches (Burnham & Anderson 2002). Using Schnute's five cases is considered a multimodel inference approach that provides two key advantages (Burnham & Anderson 2002). First, the analyses extended beyond single-model evaluation with arbitrary probability thresholds, allowing direct comparisons between competing cases and assessing their relative support of the observed data. Second, cases could be ranked and weighted to provide quantitative measures of relative support. Therefore, the approach in this study provided us with an analysis of uncertainty in the growth pattern of *P. columellaris.*

The growth of the males in this study was adequately described by cases 2, 3, and 5, which is contradictory because cases 2 and 5 show asymptotic growth, whereas case 3 shows linear growth. Although we considered discarding this model because of this contradiction, we found this behavior interesting, as it would suggest that males continue to grow after maturity. This type of growth, known as indeterminate growth, has been reported for invertebrates, including clams and other mollusks (Karkarch 2006). Statistics used to determine the best growth model suggest that alternative growth trajectories may occur in both sexes, with males showing them more often. It was also observed for the gastropods *Trochita trochiformis* (Cerros-Cornelio et al. 2023) and *Titanostrombus galeatus* (López-Rojas et al. 2023), where case 3 was the third-best model in females of *T. trochiformis* and for both sexes in *T. galeatus*. Although this behavior has not been explained in these studies, Félix-Salazar et al. (2020) observed something similar in yellowlegs shrimp (*Penaeus californiensis*), arguing that in immature organisms, energy is directed towards somatic growth, resulting in constant linear growth (case 3), while in adults, part of the energy is focused on gonadal maturation and somatic growth is reduced, representing the part of the growth slowdown that tends towards an asymptotic size. We observed differential growth between males and females (according to Kimura's test), with females growing faster, a mechanism that synchronizes reproduction with males at maturity because females reach a larger size. Although both sexes showed rapid growth in the first four years, case 2 showed slower growth in the first two years (Fig. 5). This sigmoid growth pattern is characteristic of species during early life stages (Griffiths et al. 2010).

In males, the estimated $\varepsilon(L_\infty)$ value, with case 2 (42.5 mm), was very similar to the maximum observed length (43.5 mm), whereas case 5 (56 mm) was overestimated. For females, the maximum observed length was 65.6 mm; case 2 underestimated $\varepsilon(L_\infty)$ (56.9 mm), and case 5 showed a slightly lower $\varepsilon(L_\infty)$ (63.4 mm). Estimates of $\varepsilon(L_\infty)$ would be expected to be similar to the maximum observed lengths. Although Knight (1968) does not consider this to be of biological significance, when samples span the entire life cycle of a species, the resulting growth curve should fit well with the larger-sized organisms sampled (Montgomery et al. 2010). In *P. columellaris,* the under- and overestimation of $\varepsilon(L_\infty)$ can be explained by the under-representation of larger organisms. When there is under-representation of both small and large sizes, $\varepsilon(L_\infty)$ may be under- or overestimated due to a regression range problem (López-Martínez et al. 2014), which has been documented for penaeid shrimp (Lopéz-Martínez et al. 2005) and fish (Rábago-Quiroz et al. 2008).

The $\varepsilon(L_\infty)$ values obtained in this study for both sexes are lower than those reported for the northern region (Fonseca-Madrigal 1998, Michel-Morfín et al. 2000, Ramírez-Rodríguez & Nagel 2003). In the southern region, Cervantes-Hernández et al. (2010) and Calderón-Robles (2013) reported lower L_∞ values for females than those obtained in this study; however, Hernández & Acevedo (1987) reported a higher L_∞ value (Table 3). In males, the L_∞ values from this study were slightly higher than those reported in the southern region (Table 3). The lower L_∞ observed in females by Cervantes-Hernández et al. (2010) and Calderón-Robles (2013) could be due to a fishing effect; they argue that in their study area, *P. columellaris* is exposed to overfishing, which considerably influenced the estimate. In previous research, growth parameters were estimated by different methods and fitted to the VBGM, assuming asymptotic growth, so there are no precedents to compare with the models used in this research. L_∞ values from previous research show considerable variation. Some studies reported overestimates (Hernández & Acevedo 1987, Fonseca-Madrigal 1998, Michel-Morfín et al. 2000, Ramírez-Rodríguez & Nagel 2003), while others reported underestimates (Calderón-Robles 2013). Therefore, this lack of fit to the data suggests poor sampling of large snails or the absence of individuals of maximum length due to natural and fishing mortality (Montgomery et al. 2010).

We previously discussed the uncertainty involved in determining modal groups. Our results show constant recruitment, driven by a high number of cohorts during the study period. Therefore, the estimated growth for *P. columellaris* should be considered as an approximation at the population level rather than precise individual growth trajectories. Although continuous recruitment ensures an open population, the constant arrival of recruits delays the increase in average length, causing an underestimation of the growth rate (Wang & Somers 1996), mainly by decreasing the growth rate, which estimates individual growth unreliable (Montgomery et al. 2010) and leading to biases in growth parameters (Wang & Somers 1996).

In conclusion, males and females of *P. columellaris* showed differences in length between sampling sites and months. They were also smaller than those reported

Table 3. South-to-north behavior of L_∞ and the method used to estimate it at different locations in the Mexican Pacific. The investigations are in descending order from south to north. *Case 2 and **Case 5 of Schnute's models (Case 5 is a special model of von Bertalanffy's growth model). The investigations are ordered from top to bottom in a south-to-north direction. BCS: Baja California Sur. M: male, F: female.

Locality	Sex	L_∞(mm)	Method	Author
Punta Conejo, Oaxaca	M	72	Petersen, Battacharya	Hernández & Acevedo (1987)
Punta Conejo, Oaxaca	F	101	Petersen, Battacharya	Hernández & Acevedo (1987)
Huatulco, Oaxaca	M	48.6	Modal progression	Calderon-Robles (2013)
Huatulco, Oaxaca	F	47.9	Modal progression	
Huatulco, Oaxaca	M	53.3	Modal progression	Cervantes-Hernández et al. (2010)
Huatulco, Oaxaca	F	54.6	Modal progression	
Guerrero	M	42.5	Schnute models*	This study
Guerrero	F	56.9	Schnute models *	
Guerrero	M	56.0	Schnute models **	
Guerrero	F	63.4	Schnute models **	
B. Navidad, Jalisco	M	102	ELEFAN I	Michel-Morfín et al. (2000)
B. Navidad, Jalisco	F	110	ELEFAN I	
Bahía de Banderas, Jalisco	M	63	Cassie	Fonseca-Madrigal (1998)
Bahía de Banderas, Jalisco	F	104	Cassie	
Playa Punta Perico, BCS	B	85	ELEFAN I	Ramírez-Rodríguez & Naegel (2003)
Playa Cerritos, BCS	B	90	ELEFAN I	Ramírez-Rodríguez & Naegel (2003)

in other study areas. Relative growth was allometrically negative, with significant differences between sexes, and was not influenced by the presence of juvenile organisms. The condition factor K_A showed higher values in larger and older organisms for both sexes. The estimation of growth from length-frequency data using the Schnute model cases is the first for this species and proved adequate for describing its growth. According to the two best cases, *P. columellaris* exhibits determinate asymptotic growth, which can be either sigmoid or inverse-exponential (VBGM type), a characteristic of long-lived, slow-growing species.

Credit author contribution

C. Torreblanca-Ramirez: conceptualization, validation, methodology, formal analysis, writing-original draft; R. Flores-Garza: conceptualization, validation, formal analysis, funding acquisition, and project administration; J.G. Padilla-Serrato: conceptualization, data curation, validation, methodology, formal analysis, writing-original draft, supervision, investigation, review, and editing; S. García-Ibañéz & P. Flores-Rodríguez: funding acquisition, project administration, methodology, and review; C. Valencia-Cayetano: methodology, formal analysis, review and editing; J.G. Kuk-Dzul: formal analysis, review and editing. All authors have read and accepted the published version of the manuscript.

Conflict of interest

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

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