

Population dynamics of the native apple snail *Pomacea flagellata* (Ampullariidae) in a coastal lagoon of the Mexican Caribbean

Frank A. Ocaña*, Alberto de Jesús-Navarrete, José Juan Oliva-Rivera, Rosa María de Jesús-Carrillo and Abel Abraham Vargas-Espósitos

Departamento de Sistemática y Ecología Acuática. El Colegio de la Frontera Sur (ECOSUR), Unidad Chetumal. Av. Centenario km 5.5, Chetumal, Quintana Roo, México

* Corresponding author: frankocisat@gmail.com

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ABSTRACT

Population dynamics of the native apple snail *Pomacea flagellata* (Ampullariidae) in a coastal lagoon of the Mexican Caribbean

Apple snails *Pomacea spp* inhabit tropical and subtropical freshwater environments and are of ecological and economic importance. To evaluate the population dynamics of *P. flagellata*, monthly samples were collected from Guerrero Lagoon (Yucatán Peninsula) from June 2012 to May 2013. The measured environmental variables did not differ significantly among the sampling stations. However, salinity was lower during the rainy season, and the temperature was lower during the north season (i.e., the season dominated by cold fronts). The snails were more abundant during the rainy season, and they were restricted to the portion of the lagoon that receives freshwater discharges. The snails ranged from 4 to 55 mm in size, with a maximum estimated length of $L_{\infty} = 57.75$ mm and a growth rate of $K = 0.68 \text{ y}^{-1}$ (the abbreviation “y” means “year”) with a seasonal oscillation; the lowest growth rate occurred in early December. Longevity was estimated at 3.3 y and the mortality rate at 1.89 y^{-1} . Mean biomass was 124.65 g/ha, with a somatic production of $178.32 \text{ g ha}^{-1} \text{ y}^{-1}$ and a turnover rate of 1.43 y^{-1} . We conclude that the abundance of *P. flagellata* was very low and could be influenced by salinity. Moreover, the population parameters estimated for *P. flagellata* are the lowest reported in the literature for a freshwater snail. This is the first study of a population of *Pomacea* in a brackish environment.

Key words: Apple snail, mollusc, growth, freshwater, brackish, Yucatán Peninsula.

RESUMEN

Dinámica poblacional del caracol manzana nativo *Pomacea flagellata* (Ampullariidae) en una laguna costera del Caribe mexicano

El caracol manzana habita en cuerpos de agua dulce en regiones tropicales y subtropicales y tienen importancia ecológica y socioeconómica. Con el objetivo de evaluar la dinámica poblacional de *Pomacea flagellata* se realizaron muestreos mensuales en la laguna Guerrero (Península de Yucatán) desde junio de 2012 hasta mayo de 2013. Las variables ambientales no mostraron diferencias significativas entre las distintas estaciones de muestreo de la laguna. No obstante, la salinidad fue menor durante el periodo de lluvias y la temperatura fue menor en la época de Nortes o Frentes fríos. Las mayores abundancias de caracoles se registraron en la época de lluvias y los individuos sólo aparecieron en la parte de la laguna que recibe descargas de agua dulce. La talla de los caracoles osciló entre 4 y 55 mm, con una longitud máxima estimada de $L_{\infty} = 57.75$ mm y una tasa de crecimiento de $K = 0.68/\text{año}$, la cual mostró una variación estacional, registrándose el menor crecimiento a principios de diciembre. La longevidad de la población fue estimada en 3.3 años y la tasa de mortalidad en $1.89/\text{año}$. La biomasa media fue de 124.65 g/ha, con una producción somática de $178.32 \text{ g ha}^{-1} \text{ año}^{-1}$ y una tasa de renovación de $1.43/\text{año}$. Concluimos que la abundancia de *P. flagellata* es muy baja y pudiera estar influenciada por la salinidad. Por otra parte, los parámetros poblacionales estimados para *P. flagellata* son los más bajos de todos los reportados en la literatura para cualquier especie de caracol de agua dulce. Este es el primer estudio de una población de *Pomacea spp.* en un ambiente salobre.

Palabras clave: Caracol manzana, molusco, crecimiento, agua dulce, salobre, Península de Yucatán.

INTRODUCTION

Snails of the family Ampullariidae are an important component of the freshwater macrofauna (Cowie & Thiengo, 2003). *Pomacea* Perry is the largest genus within this family, with an estimated 75-150 species (Perera & Walls, 1996) distributed from the southeastern United States to South America (Cowie & Thiengo, 2003). Snails of this genus are commonly called apple snails and are found in slow-moving water bodies, marshes, dikes, channels, reservoirs, rivers and floodplains. Certain species (e.g., *P. insularum* D'Orbigny) are able to tolerate low levels of salinity up to 10.2 practical salinity units (psu) (Byers *et al.*, 2013), but they do not generally live in brackish water (Cowie, 2002).

Apple snails are ecologically and economically important. For this reason, they have been the focus of studies by many researchers (Estebenet & Martín, 2002). These organisms generally feed on a wide variety of aquatic plants (Howells, 2002; Burlakova *et al.*, 2009; Morrison & Hay, 2011) and are able to drastically reduce the biomass of macrophyte communities in a short period of time (Lach *et al.*, 2000; Carlsson *et al.*, 2004). They are a very important food resource for certain fish, reptiles and birds (Cowie, 2002), and because of their colours, shape and meat, certain species are important for the aquarium trade and for fisheries (Naranjo-

García & García-Cubas, 1986; Ramnarine, 2003; Alves *et al.*, 2006; Iriarte-Rodríguez & Mendoza-Carranza, 2007; Wu *et al.*, 2011; Vázquez-Silva *et al.*, 2012; Seuffert & Martín, 2013). In several cases, their introduction, intentional or otherwise, has severely affected the functioning and services associated with natural and artificial wetlands worldwide (Yusa & Wada, 1999; Cowie, 2002; Carlsson *et al.*, 2004; Rawlings *et al.*, 2007; Fang *et al.*, 2010; Horgan *et al.*, 2014).

Two species of *Pomacea* inhabit Mexican waters: *P. patula catemacensis* Baker, restricted to Catemaco Lake in Veracruz, and *P. flagellata* Say, with a wider distribution ranging from Veracruz to the Yucatán Peninsula and Chiapas State; *P. flagellata* is also found from Mesoamerica to Colombia (Naranjo-García, 2003). A few studies on the biology and ecology of *P. flagellata* have been conducted (Naranjo-García & García-Cubas, 1986; Rangel-Ruíz, 1988; Naranjo-García, 2003), but no previous studies have focused on the population dynamics of this species. In general, knowledge of the dynamics of natural populations of *Pomacea* is scarce (Estebenet & Martín, 2002; Kwong *et al.*, 2010).

In southern Quintana Roo State, Mexico, *P. flagellata* is known as “chivita” and represents an important fishery resource for the local communities. Nevertheless, it has been exploited without any study of the impact of exploitation on the nat-

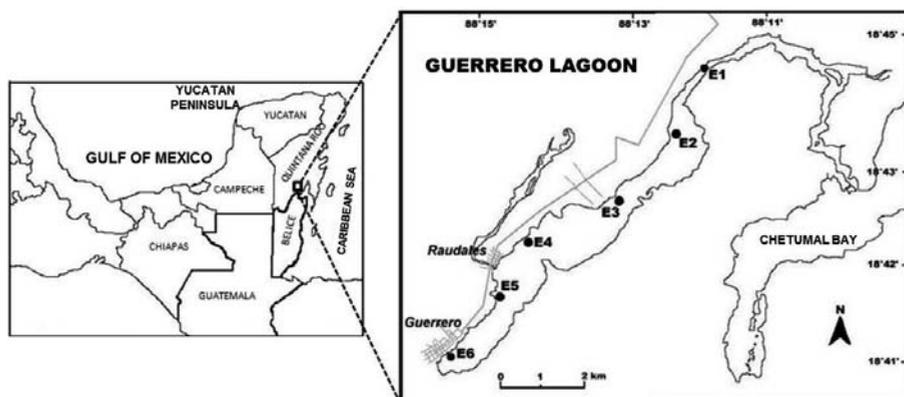


Figure 1. Map of Guerrero Lagoon. E1-E6: sampling stations. *Mapa de localización de la laguna Guerrero. E1-E6: estaciones de muestreo.*

urally occurring populations. Accordingly, local authorities are concerned about possible declines in the abundance of this species. For this reason, the present investigation was conducted in Guerrero Lagoon with the aim of estimating the abundance and distribution of *P. flagellata*, determining the factors affecting its abundance and distribution and estimating the growth, mortality and secondary production of its population.

MATERIALS AND METHODS

Study site

Guerrero Lagoon (18°42'N, 88°14'W) is part of the Bacalar-Chetumal Bay aquatic system, located on the southern Caribbean coast of Mexico (Fig. 1). The lagoon is connected with the bay by a channel. It is 8.5 km long and 1.4 km wide, with a mean depth of 3 m. The southern part of the lagoon is very shallow (less than 1 m deep) and is approximately 5 m deep at its centre. The bottom is primarily sandy, with patches of rocks covered by flocculated materials and periphyton. The aquatic vegetation consists of patches of turtle grass (*Thalassia testudinum*) in the north (Espinoza-Avalos *et al.*, 2009) and unidentified filamentous algae in the south. Freshwater is supplied to the lagoon by a natural channel (Raudales Channel) from Bacalar Lagoon and by many springs that are part of a karst system. The climate of this region is characterised by three seasons: the rainy season (June-October), the north season or season of cold fronts (November-February) and the dry season (March-May) (Carrillo *et al.*, 2009).

Sampling

Monthly field surveys were conducted from June 2012 to May 2013, although field collections could not be performed in November because of bad weather. Six sampling stations (denoted E1-E6) were placed from the channel to the inner part of the lagoon (Fig. 1); at each sampling station, six 50 × 2 m (100 m²) random transects were located along the shore, with three of these

six transects on the eastern shore and three on the western shore. Individuals of *P. flagellata* found on each transect were collected and stored in plastic bags filled with water and then brought to a boat where they were counted, weighed (*W*, g) on a semianalytical scale, and measured to determine the shell length (*L*, mm). The shell length was measured from the apex to the farthest point of the aperture with a vernier caliper; the individuals were then released into the lagoon. Stock density (ind/ha; mean ± standard error) was estimated on a monthly basis by extrapolating the number of snails collected on each of the 36 transects.

During every sampling period, salinity (psu), temperature (°C), dissolved oxygen (mg/l) and pH were recorded at each station using a Horiba 50 multiparameter water testing device. Sediment samples were taken using a PVC core sampler 5 mm in diameter and then analysed in the laboratory for mean grain size (Md₅₀, mm) and organic matter content (%) according to methods specified by Buchanan (1984).

Growth, life span and mortality

A series of 11 length-frequency distributions were used for growth estimation. A modified version of the von Bertalanffy growth function (VBGF) that incorporates seasonal oscillations in growth was fitted using the ELEFAN I routine of the FiSAT II program package (Gayaniño *et al.*, 2005):

$$L_t = L_\infty \left[1 - e^{(-K*(t-t_o) - (CK/2\pi)*\text{sen}(2\pi*(t-SP)))} \right]$$

where L_t is length (mm) at time t , L_∞ is the asymptotic maximum shell length, K is the growth coefficient, C defines the degree of seasonal oscillation when growth is slower (the winter season point, WP , calculated as a fraction of a year), SP is the summer season point ($SP = WP - 0.5$) and t_o is the theoretical age at zero length.

Preliminary estimates of L_∞ and K were used to identify the VBGF that best fit the monthly size-frequency data based on the K-scan and response surface analysis subroutines of ELEFAN I. The best combinations of L_∞ and K were selected

according to the highest value of the goodness-of-fit index (Rn) (Pauly & David, 1981). The Rn value was used as a criterion of fit.

The theoretical life span t_{\max} was estimated by the inverse $VBGF$ (Taylor, 1958):

$$t_{\max} = [\ln L_{95\%} - \ln (L_{\infty} - L_{95\%})]/K$$

where $L_{95\%}$ represents 95% of the maximum L recorded during field sampling.

The mortality rate (Z) of the population was estimated using the exponential extinction model, which was based on the length-converted catch curve of the cumulative sampling data (Pauly, 1984):

$$N_t = N_{t-1} (e - Z * \Delta t)$$

where N_t is the number of individuals at time t and Z is the curvature parameter in the equation.

Biomass and production

Length-weight relationships were determined with a nonlinear regression using the exponential equation

$$W = a * L^b$$

where a and b are constants.

Total annual production P ($\text{g ha}^{-1} \text{y}^{-1}$) was computed with the mass specific growth rate me-

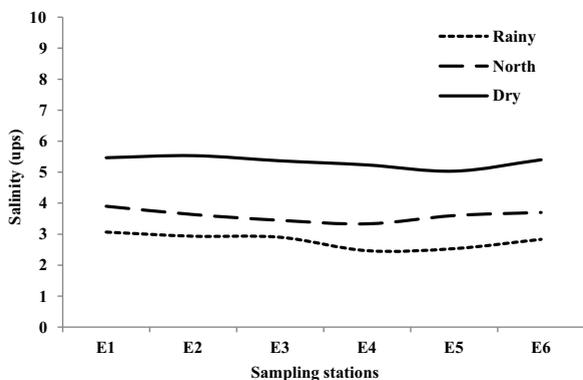


Figure 2. Mean Guerrero Lagoon salinity values by climatic season. *Salinidad media registrada a lo largo de la laguna Guerrero durante las tres épocas climatológicas.*

thod (Crisp, 1984) using abundance data and size-class frequencies of all samples pooled together, $VBGF$ parameters and length-weight relationships:

$$P = \sum N_i M_i G_i$$

where N_i is mean abundance (ind/ha), M_i is the mean individual weight of length class i and G_i is the mass-specific growth rate:

$$G_i = bK \left(\frac{L_{\infty}}{L_i} - 1 \right)$$

where b is the exponent of the length-weight relationship and L_i is the mean length of snails of size class i .

In addition, the mean annual biomass (g/ha) was estimated with the equation

$$B = \sum N_i M_i$$

and the annual renewal rate (P/B) of the population was calculated from total annual production and mean annual biomass.

Data analysis

Differences in density of *P. flagellata* among sampling stations and seasons were analysed with a two-way ANOVA. To balance the data within the treatment seasons, three months were chosen for every season (rainy: July, September and October; north: December, January and February; dry: March, April and May); the same analysis was conducted with the water parameters. To meet the assumptions of ANOVA, density was transformed to $\sqrt{(x+1)}$, and water parameters were log-transformed and then checked for normality (Kolmogorov-Smirnov test) and for homoscedasticity (Cochran test). If significant differences were found, a Tukey *post hoc* test was performed. Grain size and organic matter content were compared among sampling stations using a Kruskal-Wallis (H) test because the ANOVA assumptions were not met. A multiple linear regression analysis was used to test for a

relationship between the abundance of *P. flagellata* and each environmental variable. In all cases, significant differences were evaluated in terms of a significance level of $\alpha = 0.05$ (Zar, 1999).

RESULTS

The values of the water parameters did not differ among the sampling stations (ANOVA, $p > 0.05$). Dissolved oxygen and pH ranged from 6.6 to 7.0 mg/l and from 7.1 to 7.5 l⁻¹, respectively, and showed no variation among seasons. Salinity did not follow a gradient along the lagoon but differed significantly among the three seasons, with the lowest levels recorded during the rainy season and the highest during the dry season (Tukey, $p < 0.05$; Fig. 2). The temperature was significantly lower during the north (26.8 °C) than during the rainy (29.5 °C) and dry (28.7 °C) seasons (Tukey, $p < 0.05$). The sediments were categorised as coarse to very coarse sands, with mean diameters ranging from 0.59 to 1.83 mm, and they did not differ in size among the sampling sites ($H = 8.61$; $p = 0.125$). The organic matter content in the sediments

ranged from 4.28 to 9.65% and did not differ among the sampling sites ($H = 8.24$; $p = 0.143$).

During the study period, no snails were found at stations E1, E2 and E3. At stations E4, E5 and E6, snail abundance averaged 130.8 ± 58.0 ind/ha. Significant differences occurred among stations E4, E5 and E6 (Tukey, $p < 0.05$). The highest abundance occurred at station 5 (225.7 ± 47.6 ind/ha), whereas the lowest occurred at station 4 (59.1 ± 18.1 ind/ha). In terms of temporal variation, the highest abundance occurred during the rainy season (168.5 ± 41.4 ind/ha), then decreased during the north season (138.9 ± 41.1 ind/ha) and reached its minimum during the dry season (90.7 ± 24.0 ind/ha); however, no significant differences were detected among seasons (ANOVA: $F = 1.05$; $p = 0.352$). Abundance showed no significant relationship with any of the environmental variables ($R^2 = 0.05$; $p = 0.64$).

Length-frequency histograms (Fig. 3) show that *P. flagellata* population from Guerrero Lagoon is mainly composed of adult snails. During the study period, at least two cohorts were detected, and a new cohort was recruited in May 2013. A total of 271 snails were collected

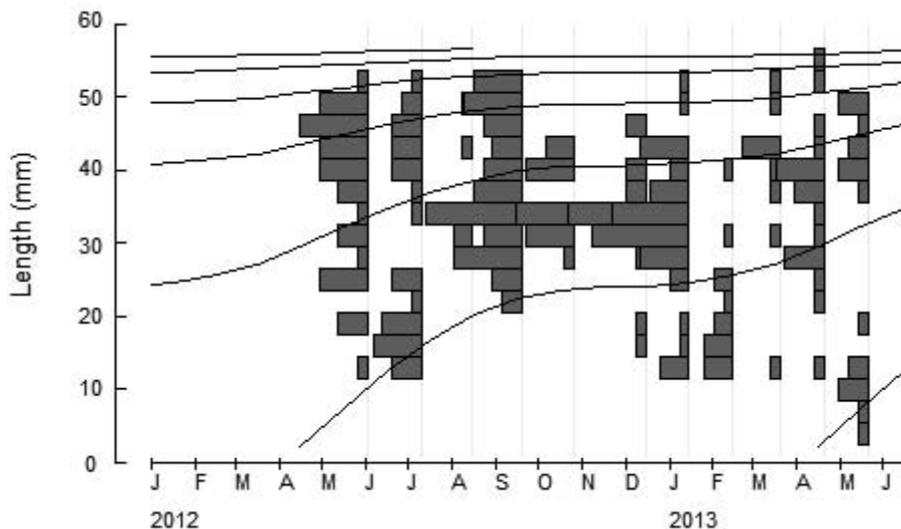


Figure 1. Monthly length-frequency histograms of *Pomacea flagellata* from Guerrero Lagoon from June 2012 to May 2013. Black lines represent growth curves estimated with the FISAT II program. *Histogramas mensuales de frecuencias de tallas de Pomacea flagellata en la laguna Guerrero desde junio de 2012 hasta mayo de 2013. Las líneas negras representan las curvas de crecimiento estimadas con el programa FISAT II.*

during the field surveys, with shell lengths ranging from 4 to 55 mm. The ELEFAN I routine estimated the following populations parameter values: $L_{\infty} = 57.75$ mm, $K = 0.68$ y^{-1} , $C = 0.90$ and $WP = 0.92$, with a criterion of fit $Rn = 0.28$. These estimates were used to develop the population growth model (Fig. 3).

The life span (t_{max}) was estimated as 3.3 y. The mortality rate was estimated as 1.89 y^{-1} using the length-converted catch curve, which showed a high degree of correlation ($R^2 = 0.967$). The length-weight relationship was estimated by the equation $W = 0.0031 * L^{2.33}$ ($R^2 = 0.857$). This equation yielded a mean annual estimated biomass of $B = 124.65$ g/ha, a total annual estimated production of $P = 178.32$ $gha^{-1} y^{-1}$ and a P/B ratio of 1.43 y^{-1} .

DISCUSSION

The abundance of *P. flagellata* recorded in Guerrero Lagoon is very low compared with most reports of natural populations of *Pomacea*. If the abundance of this species is expressed in ind/m² (1 ha = 10 000 m²) to allow comparisons with other studies, the highest density in Guerrero Lagoon was only 0.03 ind/m². Similarly, Karunaratne *et al.* (2006) reported very low densities (0.05-1 ind/m²) of *P. paludosa* Say from Florida wetlands. In contrast, *P. dolioides* Reeve reached a density up to 100 ind/m² in Venezuela (Donnay & Beissinger, 1993), and the density of *P. haustum* Reeve ranged from 20 to 215 ind/m² (Freitas *et al.*, 1987). The densities of the invasive *P. canaliculata* Lamarck ranged from 25.6 to 42.7 ind/m² in Hong Kong (Kwong *et al.*, 2010) and reached values of more than 130 ind/m² in Hawaii (Cowie, 2002).

A plausible explanation for the low estimated abundance of *P. flagellata* in Guerrero Lagoon is that the values reported are underestimates due to errors in the sampling method. During the study period, hatchlings could be found only in June 2013, although egg clutches were observed in July, August, September and December 2012 and in January 2013. Hatchlings of *P. flagellata* are unpigmented. For this reason, they are extremely

difficult to recognise, especially when they are attached to different types of substrates. Most likely for this reason, it is extremely difficult to collect snails smaller than 5 mm. Nevertheless, these new hatchlings should have contributed to a significant increase in abundance during the following months, but no such increase occurred.

According to local people, snails were relatively more abundant several years ago but were gradually collected for food. Fishing could be a major factor that explains the low density of *P. flagellata* in Guerrero Lagoon, but no previous data on the abundance of the species are available to confirm this suggestion. Salinity levels might also explain the low density of this species, as they have been reported to limit the distribution and abundance of other apple snails (i.e., *P. bridgesii* Reeve and *P. insularum*), with tolerance levels of 6.8 psu (Jordan & Deaton, 1999; Cowie, 2002; Byers *et al.*, 2013).

The spatial distribution of *P. flagellata* could not be explained by any of the environmental variables studied. Other factors could be determining the restricted distribution of *P. flagellata* in Guerrero Lagoon. *P. flagellata* lives in many surrounding freshwater habitats and is very common in Bacalar Lagoon, upstream from Guerrero Lagoon. Its abundance is higher in Bacalar Lagoon (unpublished data). Most likely, the population at Guerrero Lagoon is a "sink" population. Several lines of evidence support this suggestion: 1) the abundance of the snail was highest at station E5, located near Raudales Channel, and was relatively less at stations E6 and E4; 2) because the snail appears to be living close to its salinity tolerance, small changes in salinity in the direction of these tolerance limits could allow only a few individuals to survive; and 3) because the aquatic vegetation is poor and is mainly composed of unidentified filamentous algae, which are particularly abundant in the southern portion of the lagoon, the food resources are not adequate to maintain large apple snail populations. Another factor explaining the low abundance could be the previous fishery for this species in the lagoon, which might have decreased the population to a level from which no recovery has yet occurred.

No temporal differences in abundance were found, but the number of snails decreased from the rainy to the dry season. This decrease is consistent with the changes in temperature and salinity, which differed among the seasons. Temporal population fluctuations in other species of *Pomacea* have been explained by various factors, such as temperatures and rainfall (Cowie, 2002). The existing population of *P. flagellata* in a brackish environment, i.e., the population in Guerrero Lagoon, makes it possible to classify this species as a euryhaline limnobiont of second degree (Remane & Schlieper, 1971), as proposed for *P. bridgesi* Reeve (Jordan & Deaton, 1999).

Growth is one of the most salient components of the life history of *Pomacea*, but most previous studies have been performed under laboratory conditions (Estebenet & Martín, 2002; Alves *et al.*, 2006; Iriarte-Rodríguez & Mendoza-Carranza, 2007; Garr *et al.*, 2011; Wu *et al.*, 2011; Vázquez-Silva *et al.*, 2012; Seuffert & Martín, 2013). In natural populations, Burky (1974) evaluated the growth of *P. urceus* Müller in Venezuelan wetlands; hatchlings of this species aestivated for approximately four months, and they grew extremely rapidly when the rains began, increasing 75 mm in six months to reach adult size (Burky, 1974). In the laboratory, (unpublished data), we have determined a mean adult size of 35 mm for *P. flagellata*. Furthermore, according to the growth model for the species at Guerrero Lagoon, the snails attained adult size approximately 12 months after eclosion. Under laboratory conditions, *P. canaliculata* and *P. scalaris* achieve adult size in six months (Wu *et al.*, 2011). Vázquez-Silva *et al.* (2012) have evaluated the growth of *Pomacea patula catemacensis* under culture conditions using three different diets and estimated a value of K from the *VBGF* that was very much lower (0.11-0.14) than the value of 0.68 estimated in the present study.

The population of *P. flagellata* from Guerrero Lagoon has relatively slow growth. Temperature is a major factor affecting the growth of *Pomacea* spp. (Burky, 1974; Estebenet & Cazzaniga, 1992; Cowie, 2002; Meyer-Willerer & Santos-Soto, 2006; Seuffert & Martín, 2013). Al-

though this population is located in a tropical area where temperature is, most likely, not a determining influence on the life history traits of *P. flagellata*, the slowest growth coincides with the north season, indicating that low temperatures could be influencing the growth of *P. flagellata* in Guerrero Lagoon.

The life span estimated for this population is in agreement with that estimated for other species of the same genus, e.g., *P. urceus* (3.5 y) (Burky, 1974) and *P. canaliculata* (4 y) (Estebenet & Cazzaniga, 1992). In the current study, mortality was due to natural causes because fishing for snails ceased some time ago. During field surveys, the principal bird predators of *P. flagellata* (the limpkin *Aramus guarauna* and the snail kite *Rothramus sociabilis*) were not recorded, and this finding suggests very low predation pressure. According to the method proposed by Jensen (1996), the theoretical natural mortality (M) is related to the growth coefficient (K) of the *VBGF* as follows: $M = 1.5K$. Based on this method, the expected natural mortality for *P. flagellata* in Guerrero Lagoon was 1.02, lower than the estimated mortality rate (1.89). This result reinforces the idea that the habitat characteristics are the factor governing population abundance.

The first report on the secondary production and biomass of apple snails was obtained for a population of *P. urceus* by Burky (1974), but these previous results are not sufficiently clear (productivity rates expressed as (g Carbon week m^{-2} 100 ind $^{-1}$) to allow comparisons. Kwong *et al.* (2010) estimated the secondary production of the invasive *P. canaliculata* in four wetlands from Hong Kong based on class-size frequencies and abundance. Those authors reported that *P. canaliculata* has a somatic production of 165.9-312.7 g m^{-2} y^{-1} of ash-free dry mass (AFDM) and a P/B ratio of 7.7-9.4, higher than the $P/B = 1.43$ estimated in the present study. Although the present study used total mass for biomass and production estimates, the values obtained were substantially lower than those obtained by Kwong *et al.* (2010). Extrapolating our results to allow comparisons, we estimated the secondary production of *P. flagellata* at Guerrero Lagoon to be 0.018 g m^{-2} y^{-1} , a lower value for somatic pro-

duction than any values known for other freshwater snail species (cited by Kwong *et al.*, 2010).

The apple snail *P. flagellata* from Guerrero Lagoon showed very low abundance, relatively slow growth and extremely large sizes. These factors resulted in the low secondary production of this population. This is the first report addressing the population dynamics of *P. flagellata* and the first on a species of *Pomacea* inhabiting a brackish environment. Although the factors regulating the abundance and distribution of this species remain unclear, we hypothesise that this is a “sink” population living in a marginal habitat; because *P. flagellata* is a freshwater snail living in a brackish environment close to its limit of tolerance, small changes in salinity could be responsible for its low abundance and the restriction of the distribution of this species to the southern zone of the lagoon. In addition, as Guerrero Lagoon is very shallow, with extremely clear water, the snail is very vulnerable to collectors. Considering all these factors, we suggest that fishing for *P. flagellata* in Guerrero Lagoon be prohibited.

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