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Research Article

Reproductive and recruitment seasons for *Penaeus aztecus* in the Tamaulipas-Veracruz area, Gulf of Mexico

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ABSTRACT. An integral fishery analysis was made for the population of *Penaeus aztecus* in the Tamaulipas-Veracruz area from 1974 to 1995. Fourteen age classes between 3 and 16 months old were found, and their respective total abundances were virtually reconstructed (this included shrimp that was caught and shrimp that were not caught in the study area). Age classes were statistically separated into two statistical population indices: the abundance of spawners (or SI index) and the abundance of recruits (or RI index).Time series were generated for these indices to establish when reproductive and recruitment seasons began, ended, and reached maximum abundance. SI index was structured with reproductive ages from 6 to 13 months old, and RI index with young recruits of 4 months old. Reproductive season (or lagoon recruitment) spanned from middle December to early May, with the highest spawners abundance in February. Recruitment season (or marine recruitment) spanned from early April to middle September, with the highest abundance of young recruits during June/July. The seasonal changes in the abundance of spawners were described with lagoon recruitment (in the marine environment). The seasonal changes in the abundance of recruits were described with marine recruitment (between lagoons systems and the marine environment). A higher exploitation level of spawners than for young recruits was recorded. Recently closure seasons are implemented between May and August/September/October. These completely protect marine recruitment, and the lagoon recruitment remains unprotected.

Keywords: *Penaeus aztecus*; brown shrimp; reproduction; recruitment; shrimp abundance; Gulf of Mexico

INTRODUCTION

The shrimp is an important economic resource in Mexico, and throughout the Gulf of Mexico the main shrimp fishery areas are in: 1) Tamaulipas-Veracruz (T-V) where the Madre and Tamiahua Lagoons are located (Fig. 1), 2) Sonda de Campeche and 3) Contoy, Quintana Roo. In the first of these areas, the brown shrimp *Penaeus aztecus* Ives, 1891 is the most abundant species. In the second area, the white *Penaeus setiferus* Linnaeus, 1767 and the pink shrimp *Penaeus duorarum* Burkenroad, 1939 are the most abundant species. In the third area, the red shrimp *Penaeus brasiliensis* Latreille, 1817 is the most abundant species (Gracia, 2004).

In the Gulf of Mexico, the shrimp fishery operations began in 1950 without neither catch regulation nor a closure season system (Cervantes-Hernández & Gracia, 2011). Due to the growing over-exploitation, in 1993, an official closure season was implemented throughout the Gulf of Mexico, and within its lagoon systems (currently, this is often implemented from May to August with modifications until September/October) (SAGARPA-INP, 2012). In T-V area maximum, *P. aztecus* catch was recorded at 10,000 t (Arreguín-Sánchez & Chávez, 1985), and recently it was recorded at 13,210 t (SAGARPA-CONAPESCA, 2017).

The Mexican Fishery Department has records of commercial shrimp catch classified by size categories from 1972 and 1995, but this information was scarcely used to monitor the *P. aztecus* fishery based on studies of mortality (Klima, 1989; Arreguín-Sánchez *et al.*, 1997; Gracia, 1997), length growth parameters estimation, and analysis of closure seasons (Gracia, 1997). After 1995, shrimp commercial catch classified by size

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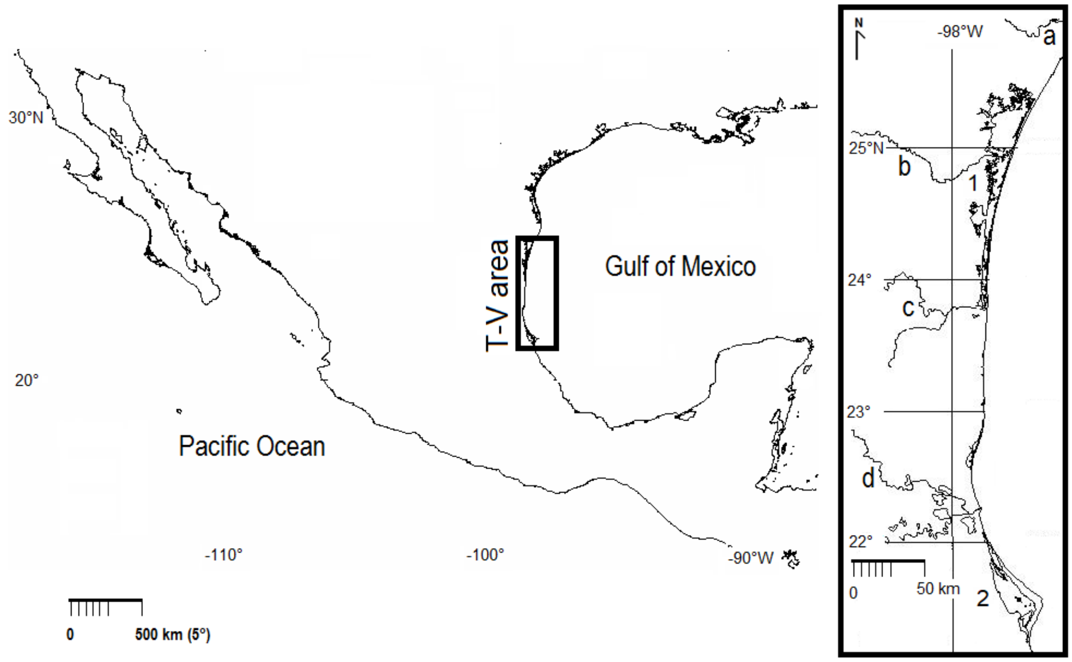

Figure 1. Geographical location of the Tamaulipas-Veracruz area (T-V) in the Gulf of Mexico. The main rivers are: a) Bravo River, b) San Fernando River, c) Soto La Marina River, d) Tamesí River. 1) Mother Lagoon, 2) Tamiahua Lagoon.

categories ceased to be documented in the Gulf of Mexico (Cervantes-Hernández, 2015).

Records of commercial shrimp catch classified by size category are available for the population of *Penaeus californiensis* Holmes, 1900 in the Gulf of Tehuantepec, Mexico, from 1989 to 1998. These records were used by Cervantes-Hernández (2008) to delimit reproductive and recruitment seasons and this analysis was, in turn, used to perform the first exploitation assessment in this fishery. The author indicated that records of commercial shrimp catch classified by size categories were an excellent tool to monitor shrimp fisheries in this gulf. After 1998, shrimp commercial catch classified by size categories ceased to be documented in the Gulf of Tehuantepec.

As was established, for *P. aztecus* fishery records of commercial shrimp catch classified by size categories have not been thoroughly analyzed to complement studies such as those conducted by Cervantes-Hernández (2008). Therefore, this study aimed to delimit the reproductive and recruitment seasons of *P. aztecus* and perform the first exploitation assessment of this fishery. This analysis can serve to inform on current catch behavior and management of the *P. aztecus* fishery in T-V area.

Information about the fishery recruitment of *P. aztecus* was used as a primary resource to perform this study. This recruitment type included all shrimp caught by the fishing effort from 1974 to 1995, and that was recorded as commercial shrimp catch classified by size categories (10-14, 15-20, 21-25, 26-30, 31-35, 36-40, 41-50, 51-60 and 60 tails per pound).These records were ordered in age classes (Gracia, 1991), and their abundances were approximated with a virtual reconstruct method (Pope, 1972; Hilborn & Walters, 1992) (these abundance estimates include shrimp that were not caught in T-V area). Afterward, the age classes were statistically separated into two population indices: the abundance of spawners (or SI index) and the abundance of recruits (or RI index). This separation was taken into account to examine the following recruitment types for the population of *P. aztecus*. 1) Lagoon recruitment constitutes the movement of shrimp’s post-larvae from the marine environment in T-V area towards inside of the Madre and Tamiahua Lagoons. During this recruitment type, the abundance of spawners increases (Cervantes-Hernández *et al.*, 2017). A time-series analysis was performed with SI index to explain seasonal lagoon recruitment changes (or reproductive seasons) (Cervantes-Hernández, 2008). 2) Marine recruitment constitutes the movement of young shrimp from the aforementioned lagoon system towards the marine environment in T-V area. During this recruitment type, the abundance of young shrimp recruits increases (Cervantes-Hernández *et al.*, 2017). A time series was performed with the RI index to explain seasonal marine recruitment changes (or recruitment seasons) (Cervantes-Hernández, 2008). Based on the obtained results were established when both recruitment seasons began, ended, and reached maximum abundance in T-V area.

Complementary analysis of natural mortality, fishing mortality by age classes, and the first exploitation assessment were provided for *P. aztecus* fishery.

MATERIALS AND METHODS

Shrimp commercial catch classified by size categories of *Penaeus aztecus* from 1974 to 1995 was used. This information was recorded by the Mexican Fishery Department (Regional Centers for Fisheries Research from Tamaulipas and Veracruz, Mexico). On the other hand, complete fishery analysis process was made in the Crustacean Fisheries Ecology Laboratory, ICMYL, UNAM, Mexico.

Age classes

In a study conducted in T-V area, Gracia (1997) examined the commercial landings to generate a total length (Lt in mm) data set for *P. aztecus* between 1983 and 1992. The author used this Lt data to construct a size-frequency histogram (Zar, 1999), classifying Lt values into 16 length-ranges. In the present study and for each reported length-range, the mean value for age was calculated (Et in months). These age averages were referred to as the age classes. Thus,

$$Et = (E_{es} / n) \tag{1}$$

where E_{es} is the specific age corresponding to each Lt record included at each length-range, and E_{es} was estimated using Equation 3 indicated below (Gómez-Márquez, 1994), where n is the total number of Lt records at each length-range.

Gracia (1997) compiled and reported the length growth parameters for *P. aztecus* (Eq. 2), but this author did not mention the respective literature consulted [the asymptotic length L_∞ = 204 mm, hypothetical age at zero t_0 = 0.2914 mm, and the metabolic monthly growth rate of the shrimp body k = 0.215].

$$Lt = L_\infty \times [1- \exp(-k \times (E_{es} - t_0) \tag{2}$$

The Lt data and length growth parameters are known in Equation 2, except for the E_{es} parameter, which was calculated from Equation 3. Thus,

$$E_{es} = [(1 / k) \times \ln(L_\infty / (L_\infty - Lt)] + t_0 \tag{3}$$

Estimated age classes were arranged in ascending order from the youngest to the oldest, and with this information, a matrix called N matrix was partially constructed, consisting of *i* rows (the months) and *j* columns (the age classes). Following the method of Gracia (1991), the total shrimp caught number at each month/age class combination (*i*,*j*) was estimated.

Thus, the related process was:

1. From commercial shrimp catch classified by size categories of *P. aztecus*, it was assumed that weight (wi) of the shrimp tails at each size category is distributed in a regular manner *N*(0, 1). Based on these criteria, averages and standard deviations were calculated at each size category to estimate the probabilities of weight for each shrimp tail P(wi).
2. For each size category the division of the total weight by its corresponding sum of probabilities P(wi) generates a conversion factor (FCi). Then, to determine the total shrimp caught number (TSCN) for each shrimp tail, the following equation was used:

$$TSCN = [P(ti) \times FCi] / ti \tag{4}$$

3. Obtained TSCN results were arranged by monthly and associated with generated age classes. Finally, catch-at-age data were generated, and the N matrix was completed.

This method was adapted for a combination of *P. aztecus* sexes, as data for separate sexes was not available between 1974 and 1995.

Natural mortality and virtual population analysis (VPA)

The method of Cervantes-Hernández *et al.* (2016) was used to estimate the monthly natural mortality rate. From the N matrix, the total sum of *j* columns was calculated for each *i* row, and with this information, a new matrix called Y_N was constructed. The Y_N matrix was arranged in descending order to apply the negative exponential model:

$$N_{esp} = N_0 \times \exp^{(-M \times t)} \tag{5}$$

were N_{esp} is the expected sum of caught shrimp, N_0 is the initial population size, *t* is the time in months, and M is the natural mortality rate.

The negative exponential model was resolved using the Bayesian method of likelihood with log-normal distribution (Haddon, 2011), allowing for the estimation of a single natural mortality rate value. For the present study, a single estimate of this rate was not considered as reliable (Ricker, 1975), because the natural mortality rate was not constant in the population of *P. aztecus* between 1974 and 1995. Therefore, the Y_N matrix was re-sampled 1,000 times with replacement using the bootstrap technique, and after for each simulated re-sampling, the negative exponential model was applied using the Monte Carlo technique (Haddon, 2011). Thus 1,000 values were estimated for the natural mortality rate, and with these, a histogram of frequencies was generated (Zar, 1999). Estimated values for the natural mortality rate were analyzed in relation to the number of times that these estimates were repeated, and based on their respective frequencies; a confidence interval for the monthly natural mortality rate was established. This interval included the minimum and maximum natural mortality rates, with the most frequent repeats between 1974 and 1995.

The negative exponential model was not applied to a single shrimp cohort from the N matrix because an estimated natural mortality rate for a single cohort is not representative of the shrimp population (Ramos-Cruz *et al.*, 2006). Therefore, the Y_N matrix was constructed, incorporating all monthly *P. aztecus* cohorts to generate a representative study. For exploited populations, Paloheimo (1961) and Berry (1967) suggested that all available cohorts should be considered to estimate the natural mortality rate correctly.

In the present study, since the N_0 parameter is a general shrimp-catch value and this analysis is related to shrimp-catch numbers by age classes, this parameter was not used because it was not required in the subsequent analysis.

In fisheries research, the VPA is used to iteratively construct total population abundance in past years via past or current catch records (fishery recruitment data) (Hilborn & Walters, 1992); the following data are required to develop the VPA: 1) the monthly natural mortality rate value, and 2) a matrix type such as the N matrix. For this reason, the N matrix was constructed, and a confidence interval for the monthly natural mortality rate was established. Two matrices were generated from VPA, the first matrix was called "shrimp abundance reconstruction by age classes" or N_{VPA} matrix, and the second matrix was called "fishing mortality estimation by age classes" or Fe_{VPA} matrix. Both matrices have the same *i* rows (for months) and *j* columns (for age classes) such as N matrix.

Direct interactions between *P. aztecus* and other populations in T-V area were not considered in the VPA. However, effects on natural mortality caused by density-dependence and density-independence (Beverton & Holt, 1957) were indirectly included in the N_{VPA} matrix via the age-cohort analysis of Pope (1972). Thus, during shrimp abundance reconstruction by age classes, each cohort's monthly had a shrimp removal equal to the maximum natural mortality rate. So, shrimp that died of natural causes were not included in the N_{VPA} matrix.

Mortality analysis and the VPA were programmed and executed in PopTools v.2.7.5.

Population indices

Two population indices were constructed for the population of *P. aztecus*, and these were made in accordance with Cervantes-Hernández (2008) as follow:

1. Based on matrix operations described by Pielou (1984), a correlation matrix for the age classes including in the N_{VPA} matrix, was estimated.
2. A principal component analysis (PCA) was applied to the mentioned correlation matrix to perform a statistical separation of the age classes into two principal components or population indices. These were called as following: 1) SI index and 2) RI index.
3. The significant factor loading values greater than or equal to 0.70 were used to identify and validate into SI and RI indices, the age classes that can be correctly considered as spawners and young recruits.
4. Following Hair *et al.* (1999), negative factor loading values were interpreted applying their respective absolute values.
5. Once population indices were structured, two multiple linear functions were constructed to made SI and RI time series:

$$SI = RI = \lambda_i \times E_{xi} \quad (6)$$

where λ_i are the linear coefficients or estimated eigenvectors for each *i* age class with significant factor loading found into the SI index or RI index. E_{xi} is the virtual abundance in the month *x* for *i* age class included in the N_{VPA} matrix.

Reproductive seasons (lagoon recruitment) and recruitment seasons (marine recruitment)

Estimated time series were analyzed with the CENSUS method to estimate their "harmonic patternsof variations (HPV)" (these are referred to as seasonal factors in Statistica v.7.0) (Cervantes-Hernández *et al.*, 2016). With HPV mathematical transformation, monthly cyclical anomalies for SI and RI time series were generated. The monthly cyclical anomalies can be positive or negative, with the zero value as the midpoint of change. Positive cyclical anomalies represented the increases in the abundance of spawners and recruits, and negative cyclical anomalies represented decreases. Specifically, the positive cyclical anomalies were used to describe how the abundance of spawners and recruits changed throughout a whole year, and this information was, in turn, used to establish when lagoon and marine recruitment seasons began, ended, and reached maximum abundance in T-V area. In this study, the estimated cyclical anomalies time series were called HPV-SI for the SI index and HPV-RI for the RI index. ACP and the CENSUS method were applied via Statistica v.7.0.

Fishing mortality and exploitation assessment

Using Fe-$_{VPA}$ matrix data, a mean value of fishing mortality rate were estimated for each age class (Ramos-Cruz *et al.*, 2006; Cervantes-Hernández, 2008), and with this information, the exploitation pattern by age classes was explained. Based on those mentioned above, the age classes that were overfished and under-fished were identified. Afterward, all estimated fishing mortality rates were averaged to approximate the total fishing mortality rate value (F), with the model:

$$Z = F + M \tag{7}$$

(Beverton & Holt, 1957; Ricker, 1975), the total mortality (Z) was approximated (M is the maximum natural mortality rate value included in the confidence interval).

The spawners-recruits relationship model of Ricker (1975) was used to make an exploitation assessment of *P. aztecus* fishery. With the model aforementioned, a critical exploitation zone was established to separate possible periods of exploitation. For these periods, it was corroborated if spawners were highly exploited compared to young recruits or whether the opposite happened.

The complete fishery analysis process is shown in Table 1.

RESULTS

Ageclasses, natural mortality and VPA

The age structure for the population of *Penaeus aztecus* was composed of 16 age classes, between 3 and 16 months old. Respective shrimp tail weight ranges were 4-6 g (3 months old), 7-10 g (4 months old), 11-14 g (5 months old), 15-19 g (6 months old), 20-24 g (7 months old), 25-28 g (8 months old), 29-33 g (9 months old), 34-37 g (10 months old), 38-41 g (11 months old), 42-44 g (12 months old), 45-47 g (13 months old), 48-50 g (14 months old), 51-52 g (15 months old) and >53 g (16 months old).

The N matrix was composed of 264 months and 16 age classes. A reliable interval for the monthly natural mortality rate from 0.15 to 0.20 was established with a repeat frequency of 70% and 0.05 standard deviation. The monthly natural mortality rate of 0.20 was used to perform the VPA with the N matrix.

Population indices

Two principal components were generated by the PCA, Cp1 = SI index (eigenvalue = 7.36) and Cp2 = RI index (eigenvalue = 2.46). The estimated statistical variance to order 16 age classes into two principal components was 80% (61% + 20%). The SI index presented significant factor loading in the age classes of 6, 7, 8, 9, 10, 11, 12 and 13 months old, while in the RI index, a significant factor loading in the age class of 4 months old was recorded (Table 2, Eq. 8).

Obtained SI and RI time series are shown in Figure 2, and these were structured using the following multiple linear functions:

$$SI=0.30\times E_6+0.16\times E_7-0.25\times E_8-0.41\times E_9+0.68\times E_{10}-0.17\times E_{11}-0.05\times E_{12}-0.03\times E_{13} \tag{8}$$

$$RI = 0.41\times E_4$$

were, E_i are specific age classes.

Reproductive seasons (lagoon recruitment) and recruitment seasons (marine recruitment)

The original time series for the SI index is shown in Figure 2. The spawners of *P. aztecus* were present throughout the whole year. Based on the HPV-SI (Fig. 3), it was concluded that approximately a complete lagoon recruitment season spanned from middle December to early May, with the highest signal in the abundance of spawners during February.

The original time series for the RI index is shown in Figure 2. The recruits of *P. aztecus* were present throughout the whole year. Based on the HPV-RI (Fig. 3), it was concluded that approximately a complete marine recruitment season spanned from early April to middle September, with the highest signal in the abundance of recruits during June/July.

Fishing mortality and exploitation assessment

The fishing mortality rate by age classes had a sustained increase between 4 (0.23 monthly) and > 14 months old (>0.99 monthly) (Fig. 4). The lowest rate was observed in the age class of 3 months old (0.03 monthly), and this was followed by the relatively low rates found in the age classes from 4 to 5 months old (the average monthly rate was estimated at 0.30). Medium rates were recorded in the age classes from 6 to 13 months old (the average monthly rate was estimated at 0.60). The highest rates were recorded in the age classes from 14 to 16 months old (>0.99 monthly).

The total monthly F rate value was estimated at 0.5 monthly, and considering the monthly value of the natural mortality rate at 0.20, the total monthly Z rate value was estimated at 0.74 monthly.

From 1974 to early 1991 (the first exploitation period), critical abundance levels for spawners (~16×10^7 shrimp at average) and recruits (~73×10^7 shrimp at average) were recorded inside the critical exploitation zone (Fig. 5). On the other hand, a recovery in abundance for spawners (~28×10^7 shrimp at average) and recruits (~115×10^7 shrimp at average)

Table 1. Complete fishery analysis process description. N matrix: caught shrimp by age classes, Y_N matrix: representative population cohort of *Penaeus aztecus*, VPA: virtual population analysis, N_{VPA} matrix: shrimp abundance reconstruction by age classes, Fe-$_{VPA}$ matrix: fishing mortality estimation by age classes, PCA: principal components analysis, SI index: the abundance of spawners, RI index: the abundance of recruits, HPV-SI: harmonic patterns of variations for SI index, HPV-RI: harmonic patterns of variations for RI index, F: total fishing mortality rate, Z: the total mortality rate.

Process 1	input: monthly shrimp commercial catch classified by size categories
	output: age classes estimation
	output: N matrix
	output: Y_N matrix
Process 2	input: Y_N matrix
	output: natural mortality rate (M) interval estimation
Process 3	inputs: N matrix, maximum M value, and VPA application
	output: N_{VPA} matrix
	output: Fe-$_{VPA}$ matrix
Process 4	inputs: N_{VPA} matrix, and PCA application
	output: SI and RI indices
	output: SI and RI time series
Process 5	input: SI, RI time series, and CENSUS method application
	output: HPV-SI and HPV-RI time series
	output: lagoon season and marine season delimitation
Process 6	input: Fe-$_{VPA}$matrix
	output: fishing mortality rates by age classes
	output: F and Z rates estimation
	output: spawners-recruits relationship model estimation
	output: exploitation assessment

Table 2. Estimated factor loadings by age classes (Ei) into SI (the abundance of spawners), and RI (the abundance of recruits) indices. Eigenvalues (ev), statistical variance of ordination (sv = eigenvalue/12 age classes). The marked values are factor loading values greater than or equal to 0.70 ($P < 0.05$). The absolute value was applied to interpret negative factor loading values.

	E_3	E_4	E_5	E_6	E_7	E_8	E_9	E_{10}	E_{11}	E_{12}	E_{13}	E_{14}	E_{15}	E_{16}	ev	sv
SI	0.34	0.53	0.66	*0.79	*0.88	*0.93	*0.93	*0.91	*0.86	*0.81	*0.74	0.58	0.43	0.34	7.36	61%
RI	-0.69	-*0.81	-0.69	-0.47	-0.17	0.09	0.27	0.32	0.35	0.33	0.27	0.17	0.10	0.28	2.46	20%

was recorded outside the critical exploitation zone from 1992 to 1993 (the second exploitation period) (Fig. 5). In both exploitation periods, a higher exploitation level of spawners than for young recruits was observed. However, those mentioned above were more evident in the first exploitation period.

DISCUSSION

Age classes

In T-V area, the estimated age structure for the population of *Penaeus aztecus* was the same as for other Mexican shrimp populations where the age classes were estimated using commercial shrimp catch classified by size categories. In the gulfs of Mexico and Tehuantepec, the age structure was documented between 3 and 16 months old for the populations of *P. duorarum* (Cervantes-Hernández & Gracia, 2011), *P. californiensis* (Cervantes-Hernández, 2008), and *P. vannamei* (Cervantes-Hernández *et al.*, 2008a).

The apparent similarity between the age structures in Mexican shrimp populations is due to the fact that their reported length growth parameters are partially consistent. For *P.azte*cus [L_∞ = 204 mm, t_0 = -0.2914 mm, k= 0.215 monthly] (Gracia, 1997). For *P. californiensis* [L_∞ = 242 mm, t_0 = -0.344 mm, k = 0.186 monthly] and for *P. vannamei* [L_∞ = 200 mm, t_0 = -0.293 mm, k = 0.266 monthly] (Chávez, 1979). For *P. duorarum* [L_∞ = 203 mm, t_0 = -0.466 mm, k = 0.216 monthly] (Gracia, 1995).

Similar results for the age structure were documented for *P. californiensis* in Sonora, Mexico (López-Martínez *et al*., 2003), and for *Penaeus notialis* Pérez-Farfante, 1967 in the Araya Peninsula, Venezuela (Marval-Rodríguez *et al.*, 2015).

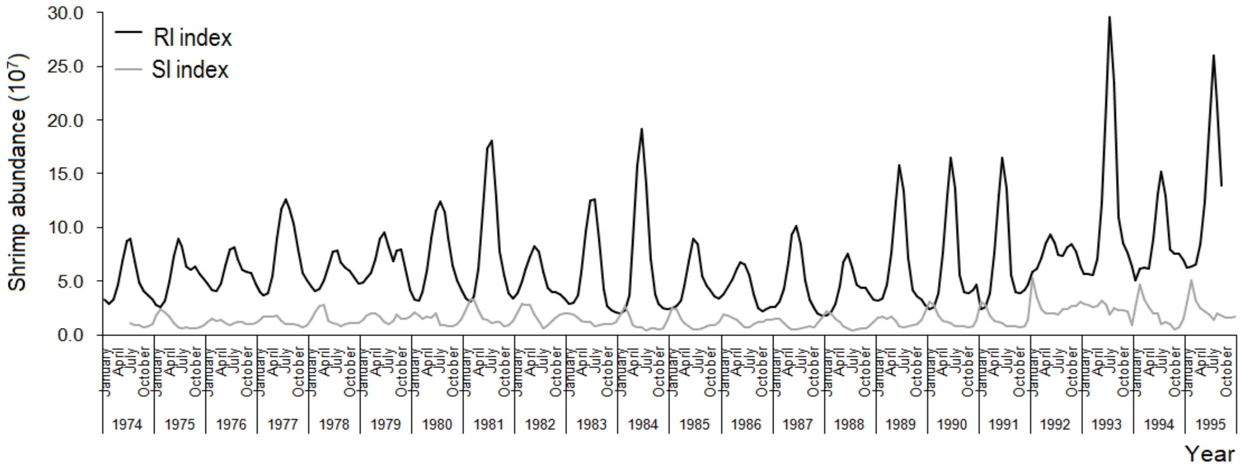

Figure 2. Abundance time series for spawners (SI index) and recruits (RI index).

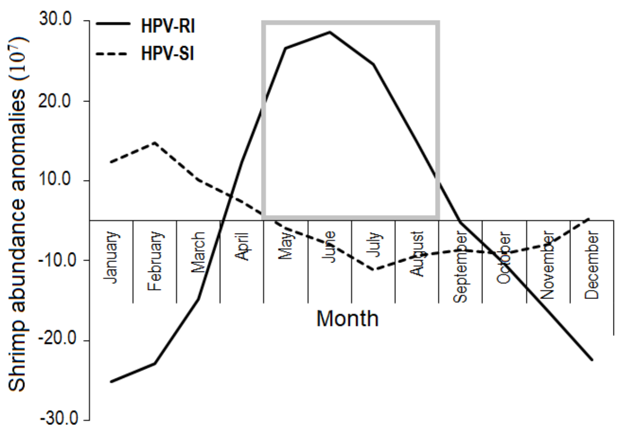

Figure 3. Monthly shrimp abundance anomalies shown a seasonal cycle for HPV-SI (harmonic patterns of variations for SI index), and HPV-RI (harmonic patterns of variations for RI index). A marine closure season is shown with a gray rectangle (explanation in the text).

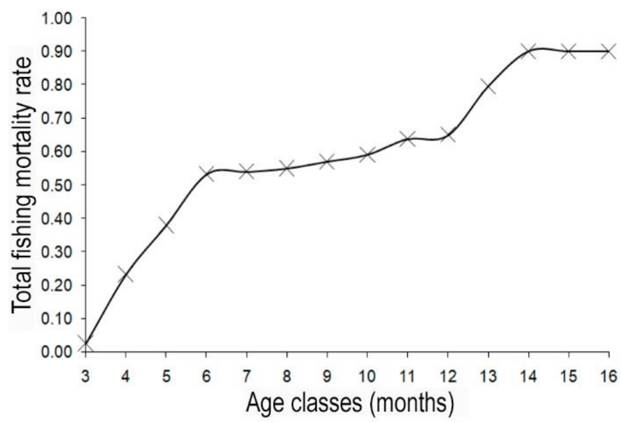

Figure 4. Estimated exploitation pattern by age classes in the population of *Penaeus aztecus*.

Length growth parameters reported by Gracia (1997) documented the 1983-1992 period, a period completely overlapping, therefore, with the present study.

Natural mortality and VPA

In T-V area studies on the natural mortality of *P. aztecus* are scarcely documented (Klima, 1989; Arreguín-Sánchez *et al.*, 1997; Gracia, 1997). The mentioned studies were taken into account to make a literature reference interval for the natural monthly mortality rate of between 0.19 and 0.31 monthly. In the present study, the natural monthly mortality rate ranged from 0.15 to 0.20. Since the estimated maximum value for the natural monthly mortality rate resulted within the literature reference interval, this value was used to perform the VPA.

In the present study, the estimated natural monthly mortality rate at 0.20 was consistent with estimated natural monthly mortality rates in other Mexican shrimp populations. In the Gulf of Mexico, monthly M rates were documented for the populations of *P. setiferus* (at 0.25) (Gracia, 1989) and *P. duorarum* (at 0.22) (Cervantes-Hernández, 1999; Cervantes-Hernández & Gracia, 2011). In the Gulf of Tehuantepec, monthly M rates were reported for the populations of *P. californiensis* (at 0.22), and *P. vannamei* (at 0.20) (Ramos-Cruz *et al.*, 2006). Similar results were documented for the populations of *P. californiensis*, *P. vannamei*, and *Penaeus stylirostris* in the Gulf of California, Mexico (Aranceta-Garza *et al.*, 2016).

Obtained results and the studies, as mentioned earlier, suggest that the most reliable interval for M rate in Mexican shrimp populations would be between 0.20 and 0.25 monthly. Following Gracia (1997), these M rate values appear to be reasonable and compatible with

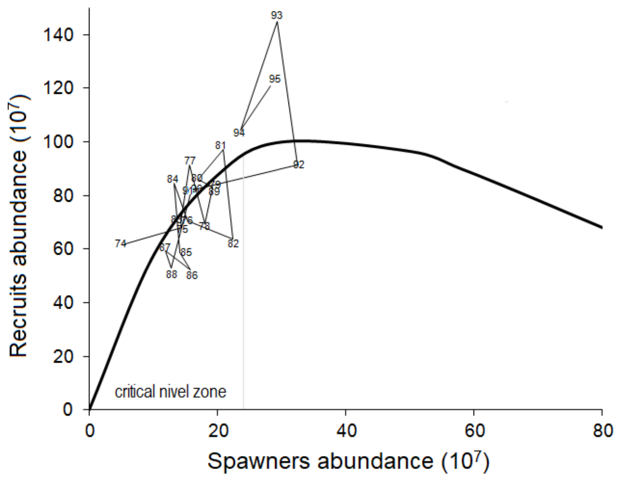

Figure 5. Annual spawners-recruits relationship model and exploitation assessment for the population of *Penaeus aztecus* from 1974 to 1995.

the annual life history of penaeid shrimp. For this reason, the minimum 0.15 value was not considered in order to perform VPA. These considerations governed the decision to use the 0.20 value in VPA.

Population indices

In SI index, the age classes of 6, 7, 8, 9, 10, 11, 12 and 13 months old were identified as spawners (Table 2). These ages were similar to spawner ages reported for the population of *P. duorarum* in the Sonda de Campeche area (Cervantes-Hernández & Gracia, 2011), as well as for the populations of *P. californiensis* and *P. vannamei* in the Gulf of Tehuantepec (Cervantes-Hernández, 2008; Cervantes-Hernández *et al.*, 2008a).

Spawner age classes included in SI index were validated with recognition of the fact that in the Penaeidae family sexual maturity is prevalently reached between 6 and 7 months old, while the rest of the population is sexually mature when they are more than 8 months old (Gracia *et al.*, 1997; Cervantes-Hernández, 2008).

In the RI index, the age class of 4 months old represented to young shrimp recruits (Table 2). This age was equal to the marine recruitment age reported for the population of *P. duorarum* in the Sonda de Campeche area (Cervantes-Hernández & Gracia, 2011), as well as for the populations of *P. californiensis* and *P. vannamei* in the Gulf of Tehuantepec (Cervantes-Hernández, 2008; Cervantes-Hernández *et al.*, 2008a). These reports suggest that marine recruitment age in Mexican shrimp populations is common for 4 months old.

Reproductive season (lagoon recruitment)

For the population of *P. aztecus* in T-V area, a complete lagoon recruitment season spanned from middle December to early May, with the highest signal in the abundance of spawners during February (Fig. 3). These results were consistent with other Mexican shrimp populations where the commercial shrimp catch classified by size categories was recorded. In the Sonda de Campeche area, the populations of *P. duorarum* and *P. setiferus* were documented with a high abundance of spawners from October to February (Gracia & Soto, 1990; Cervantes-Hernández & Gracia, 2011). In the case of the population of *P. californiensis* in the Gulf of Tehuantepec, a complete lagoon recruitment season spanned from July to February, with the highest signal in the abundance of spawners during October/November (Cervantes-Hernández *et al.*, 2008b).These reports suggest that Mexican shrimp populations have higher reproductive activity during late autumn and winter.

Supplementary, in Quintana Roo, Mexico, higher reproductive activity during October/November was reported for *P. brasiliensis* (Sandoval-Quintero & Gracia, 1998). Also, higher reproductive activity in winter seasons (mainly from September to October) was reported for the populations of *P. notialis* in the Araya Peninsula, Venezuela (Marval-Rodríguez *et al.*, 2015), and *P. duorarum* in the Gulf of Ana Maria, Cuba (Giménez-Hurtado *et al.*, 2012).

Cervantes-Hernández *et al.* (2008b) explained why Mexican shrimp populations have high reproductive activity during late autumn and winter. In the Gulf of Tehuantepec, *P. californiensis* reproduces in winter when oceanographic conditions are with higher Chlorophyll-*a* levels (Chl-*a*, ~1.10 mg m^{-3}) and colder sea surface temperature (SST, ~26-27°C). The presence of Chl-*a* is relevant because it is with this that the trophic chain is activated, and shrimp's larval stages can feed directly on phytoplankton and zooplankton biomass. Therefore, higher Chl-*a* levels promote the survival of shrimp's post-larvae, increasing lagoon recruitment.

In the Gulf of Mexico, Chl-*a* levels were recorded >1.0 mg m^{-3} from November to January, and <1.0 mg m^{-3} between April and October (1998-2008 period) (Salmerón-García *et al.*, 2011). During winter in T-V area, Chl-*a* concentrations ranged from 0.5 to 1.0 mg m^{-3}, and the SST from 21 to 24°C was recorded (Cervantes-Hernández, 2015). In a complementary study conducted in the gulfs of Mexico and Tehuantepec, Romero-Centeno & Zavala-Hidalgo (2003) indicated that a high Chl-*a* level is related to immense offshore transport caused by stronger winds in winter from December to January, while the effect of the wind is at its minimum in summer between May and June.

To determine the reproductive season of *P. setiferus* and *P. duorarum*, Flores-Coto *et al.* (2018) and Gómez-

Ponce *et al.* (2018) estimated the density of the post-larvae that entered Terminos Lagoon. The maximum post-larvae density occurred from June to September during the rainy season, and the minimum post-larvae density was reported during winter.

When closure seasons did not exist in the Gulf of Mexico, Gracia (1989) estimated the density of the post-larvae that entered Terminos Lagoon and concluded that Mexican shrimp populations have on two reproductive seasons. The first reproductive season is as was reported for the population of *P. aztecus* in the present study (Figs. 2-3). The second reproductive season is as was documented for the populations of *P. setiferus* and *P. duorarum* by Flores-Coto *et al.* (2018) and Gómez-Ponce *et al.* (2018).

On the other hand, Gracia (1991) reported that due to changes in oceanographic conditions, the post-larvae density is highest during the first reproductive season. These details have implications for shrimp populations in the Gulf of Mexico because recent closure seasons have been implanted between May and August/ September/October (SAGARPA-INP, 2012). Thus, it is clear that closure seasons are implanted throughout the second reproductive season, and the first reproductive season is completely unprotected (Fig. 3).

In response to that mentioned by Flores-Coto *et al.*(2018) and Gómez-Ponce *et al.* (2018), about minimum postlarvae density recorded in winter, it was concluded that their method of estimation did not work during the first reproductive season because fishing effort quickly reduces the abundance of spawners in the marine environment, thus as an immediate response, post-larvae abundance abruptly declines. Its entrance into lagoon systems becomes almost undetectable. When closure seasons are implemented, the opposite case occurs; fishing effort does not affect the abundance of spawners in the marine environment, thus as an immediate response, post-larvae abundance does not decline, and its entrance into lagoon systems can detect with the mentioned method.

In the present study, the post-larvae density of *P. aztecus* was not measured, but in accordance with Gracia (1991), it was indirectly observed that during the first reproductive season, the abundance of spawners was highest than during rainy season (Figs. 2-3). Gracia *et al.* (1997) indicated that generally, in shrimp populations, the massive post-larval density coincides with an increase in the abundance of spawners in the marine environment (lagoon recruitment).

In the Gulf of Tehuantepec, the maximum percentage of brown shrimp mature females in phase IV was reported from October to January (in the first reproductive season), and the minimum percentage was documented from July to September (in the second reproductive season) (Cervantes-Hernández, 2008). Similar results were documented in the Campeche Bank area by SAGARPA-INP (2012). These results support the conclusion of Cervantes-Hernández *et al.* (2008b) that in the first reproductive period, higher concentrations of Chl-*a* promoted the survival of shrimp's post-larvae, increasing the lagoon recruitment between late autumn and winter.

From obtained results, it was concluded that in the Gulf of Mexico, the populations of *P. aztecus* (Figs. 2-3), *P. setiferus* and *P. duorarum* have two reproductive seasons throughout the whole year. Nevertheless, this must be recognized that the fishery analysis process undertaken in the present study (Table 1) could not detect the second reproductive season because the information analyzed referred to shrimp caught in the marine environment (fishery recruitment). On the other hand, the post-larvae density method cannot detect the first reproductive season because information about shrimp caught in the marine environment is not, in this case, included. Thus, both methods are complementary. For this reason, it is recommended that these studies are performed perpetually in the Gulf of Mexico.

Recruitment season (marine recruitment)

For the population of *P. aztecus* in T-V area, a complete marine recruitment season spanned from early April to middle September, with the highest signal in the abundance of recruits during June (Fig. 3). These results were consistent with other Mexican shrimp fisheries where the commercial shrimp catch classified by size categories was recorded.

In the Sonda de Campeche area, the *P. setiferus* and *P. duorarum* populations were documented with a high abundance of recruits during June/July, and May/June (Gracia & Soto, 1990; Cervantes-Hernández, 1999). In the cases of the *P. californiensis* and *P. vannamei* populations in the Gulf of Tehuantepec, a complete marine recruitment season spanned from April to October (with the highest signal in the abundance of a recruit during July/August), and from April to August (with the highest signal in the abundance of a young recruit during June/July) (Cervantes-Hernández *et al.*, 2008a; Cervantes-Hernández *et al.*, 2017). Also, a higher abundance of recruits from July to August was reported for the *P. notialis* population in the Gulf of Ana Maria, Cuba (Giménez-Hurtado *et al.*, 2012). These reports suggest that Mexican shrimp populations have higher marine recruitment activity during the rainy season.

Fishing mortality and exploitation management

Like in the population of *P. aztecus* at 3 months old (F = 0.03 monthly) (Fig. 4), the lowest fishing mortality rates are documented for this same age class in the populations of *P. californiensis*, *P. vannamei* (Ramos-Cruz *et al.*, 2006), and *P. duorarum* (Cervantes-Hernández, 1999; Cervantes-Hernández & Gracia, 2011). They suggest that in Mexican shrimp populations, this age class is not intensively exploited (Cervantes-Hernández *et al.*, 2017) because usually, this age class is more abundant within lagoon systems. The age classes from 4 to 5 months old were recorded with relative low fishing mortality rates (the average monthly rate was estimated at 0.30) (Fig. 4). For this reason, they were partially included in the records of commercial shrimp catch classified by size categories. For these latter age classes, similar exploitation levels are documented in the aforementioned Mexican shrimp populations.

The highest rates were recorded in the age classes from 14 to 16 months old (>F = 0.99 monthly) (Fig. 4). Similar exploitation levels are documented for these same age classes in populations of *P. californiensis*, *P. vannamei* (Ramos-Cruz *et al.*, 2006), and *P. duorarum* (Cervantes-Hernández, 1999; Cervantes-Hernández & Gracia, 2011). Suggesting that in Mexican shrimp fisheries, these age classes are more intensively exploited (Cervantes-Hernández *et al.*, 2017), and thus in T-V area they were scarcely included in the records of commercial shrimp catch classified by size categories. For this reason, in the SI index, statistically, these age classes did not show significant factor loading values greater than or equal to 0.70.

Medium rates were recorded in the age classes from 6 to 13 months old (the average monthly rate was estimated at 0.60) (Fig. 4). Although these exploitation levels were considered high, it was concluded that these age classes had maintained the continuity of this shrimp fishery from 1974 to 1991. As was estimated, these age classes were dominant in commercial shrimp catch classified by size categories.

In both exploitation periods, a higher exploitation level of spawners than for young recruits was observed. However, those above were more evident in the first exploitation period. Thus, it was concluded that in T-V area the population of *P. aztecus* was higher over-fished between 1974 and 1991. The apparent recovery in spawners and recruits abundance during the second period was associated with the experimental closure works conducted in the Gulf of Mexico before the official closure season was implemented.

Recently, the fishery of *P. aztecus* was recorded with a total production of 13,210 t (SAGARPA-CONAPESCA, 2017), and during this study, the total production was reported at 10,000 t (Arreguín-Sánchez & Chávez, 1985). In conclusion, closure season implementation has maintained almost equal catch levels since 1993, probably because the first reproductive season is completely unprotected (Fig. 3).

Closure seasons are not beneficial for *P. duorarum* and *P. setiferus* populations because they are documented as over-fished in the Sonda de Campeche. This difference in comparison to the populations of *P. aztecus* is due to an increase in the oil industry activities in the Gulf of Mexico south region, as marine and lagoon recruitment are being negatively affected by these actions (Cervantes-Hernández & Gracia, 2011). Finally, it is important to consider that as the population of *P. aztecus*, the first reproductive season is wholly unprotected in *P. duorarum* and *P. setiferus*.

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