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Abundance and catchability estimates of the Atlantic blue crab *Callinectes sapidus* based on mark-recapture data from the northern Yucatan Peninsula

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*A short-term Jolly–Seber mark-recapture model experiment is described. This experiment was aimed at estimating the rate of catch per unit effort (CPUE) and the catchability coefficient (q) of the Atlantic blue crab (*Callinectes sapidus*) in the fishing port of Sisal, Yucatan, Mexico. To estimate the local population size, 52 traps were deployed along four transects located in a coastal capture area of 3600 m^{-2}. The CPUE and q were compared between the daily mark-recapture Jolly–Seber experiment and the bi-monthly (carried out every 2 months) samplings. The average abundance was estimated at 3475 individuals. All three suggested scenarios, applied to estimate densities, gave similar estimates, i.e. 0.0386, 0.0350, 0.0365 crabs m^{-2} for the first (Previously Cited Attraction Radius), second (CPUE per transect) and third (Catchability-Density Relationship), respectively. Based on the latter scenario, densities ranged from 27,900 (annual average) to 36,500 (Spring) crabs km^{-2}. The average CPUE of the daily mark-recapture experiment was estimated at 1.96 crabs $trap^{-1}$, whereas the average bi-monthly CPUE was estimated at 1.13 crabs $trap^{-1}$. The q (per trap) was estimated at 0.0186 for the daily mark-recapture experiment and at 0.0247 for the bi-monthly sampling. Both catchability and CPUE increased in individuals whose size ranged between 110 and 170 mm CW. However, no significant difference (ANCOVAs) was found between the daily and bi-monthly samplings neither in CPUE nor in catchability. The use of both mark-recapture data and the Jolly–Seber model proved to be a fast and reliable method for estimating the abundance and catchability of Atlantic blue crab.*

Keywords: *Callinectes sapidus*, Atlantic blue crab, density, Jolly–Seber model, catchability, CPUE

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INTRODUCTION

Crustacean fisheries (for shrimps, lobsters and crabs) have become very important due to the high demand in world markets (FAO, 2008). There are a variety of shellfish that can be exploited commercially, with the potential to develop regional artisanal fisheries (Boschi, 1997; Villasmil & Mendoza, 2001), e.g. the Atlantic blue crab *Callinectes sapidus*, which is a common decapod crustacean in estuarine and nearshore waters of the Gulf of Mexico. In many countries, Mexico included, this species has been widely accepted and highly demanded by both domestic and international markets, generating jobs and additional income for fishermen in coastal areas, since this species is used as food or bait in other regional fisheries (Rocha-Ramírez *et al.*, 1992; Celis-Sánchez *et al.*, 2014).

In Yucatan (Mexico) the catch of *C. sapidus* is carried out throughout the year (Defeo *et al.*, 2005; Rosas-Correa & de Jesús-Navarrete, 2008; Celis-Sánchez *et al.*, 2014). Due to a constant increase in fishing effort in recent years there has been a progressive decline in their catch from a maximum of 127.31 tons in 2003 to 37.87 tons in 2011 (Mexicano-Cíntora *et al.*, 2007; CONAPESCA, 2014). To date, this fishery has no regulatory measures (closed seasons, quota or minimum catch size) and low operating costs, which make this resource capable of being exploited with no control at all.

For proper fisheries management, Perry *et al.* (1999) identified three broad management strategies (limiting size per sex, regulating the total allowable catch, and controlling the rate of exploitation) and the need for scientific information to determine the size of the stock and vulnerability of the resource. In this sense, population studies on shellfish can be of great help when managing fisheries, especially when mark-recapture models are applied (Smith & Addison, 2003). Mark-recapture studies can be used to estimate abundance and other population parameters such as mortality, dispersal and growth (Hightower & Gilbert, 1984; Pollock *et al.*, 1990; Krebs, 1999; Bell *et al.*, 2003). They can be applied in both closed and open populations, with the basic requirement that all individuals, both marked and unmarked, have the same chance of being caught and that they can be recognized

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when they are recaptured (Pollock *et al.*, 1990; Bell *et al.*, 2003).

For organisms such as crustaceans, the use of marks on the exoskeleton has been successful when used in adult individuals and considering short periods of recapture, since as adults their moulting frequency is relatively lower than in juvenile specimens (Muñoz *et al.*, 2006). One of the most widely used fishing gears to capture decapod crustaceans is baited traps, the effectiveness of which depends mainly on the type of bait used, the design of the trap, time of immersion, and distance between traps (McElman & Elner, 1982; Lovewell *et al.*, 1988; Miller, 1990; Arena *et al.*, 1994). In order to determine the radius of attraction of the traps (R_{at}) and the density of crustaceans, several authors have focused on estimating the response of catch per unit effort (CPUE), placing traps along a ground line at different distances along with visual censuses to validate the estimated density (Eggers *et al.*, 1982; Tremblay *et al.*, 1998; Aedo & Arancibia, 2003; Ahumada & Arana, 2009). However, there is no information on the methods used to estimate the density of crustaceans when several adjacent ground lines are used.

There are other fishing indicators, that could shed light on population size estimates of organisms, based on the rate of CPUE and the catchability coefficient (q) which is considered proportional to population size since it is obtained from the ratio between CPUE and density of stock (Miller, 1975; Arreguín-Sánchez, 1996; Morales-Bojórquez & Nevárez-Martínez, 2002; Smith & Addison, 2003). Therefore, the aim of this study was to determine the abundance and catchability rate of Atlantic blue crab (*C. sapidus*) using mark-recapture data as a fast, reliable and efficient manner to estimate the density of organisms and population size.

MATERIALS AND METHODS

Study area

This study was conducted in Sisal, a fishing port in the Gulf of Mexico on the north-western coast of the Yucatan Peninsula (Mexico) (Figure 1). It is located between latitude 90°01′50″ and longitude 21°09′55″ and where the climate is warm and humid with regular rainfall, predominantly during the summer (Mexicano-Cíntora *et al.*, 2007). The average annual temperature is 25.6°C, with the highest temperatures usually recorded in May and the lowest recorded in January. Sisal is influenced by easterly trade winds with speeds between 10 and 15 knots. The winter season is characterized by the entrance of northern cold fronts (known locally as 'northerlies'), which bring rainfall and low temperatures.

Sampling methods

A blue crab mark-recapture experiment was conducted from 17–24 April 2013 in Sisal, Yucatan, Mexico, which included 6 days of sampling; however, the marking of *C. sapidus* individuals was only performed during the first 4 days. In order to obtain the crab samples a total of 52 traps, 50 × 30 × 30 cm with a mesh size of 2 cm and an entry diameter of 12 cm, were used. Both fishing gear and effort were applied according to the techniques used by local fishermen. Additionally, bi-monthly (carried out every 2 months) sampling was conducted to compare catchability and abundance in an annual cycle (February–December 2013). This region is influenced by three seasons: dry season (March–May); rainy season (June–October) and northerlies season (November–February) that determine the environmental and ecological dynamics of the system (Vega-Cendejas, 2004).

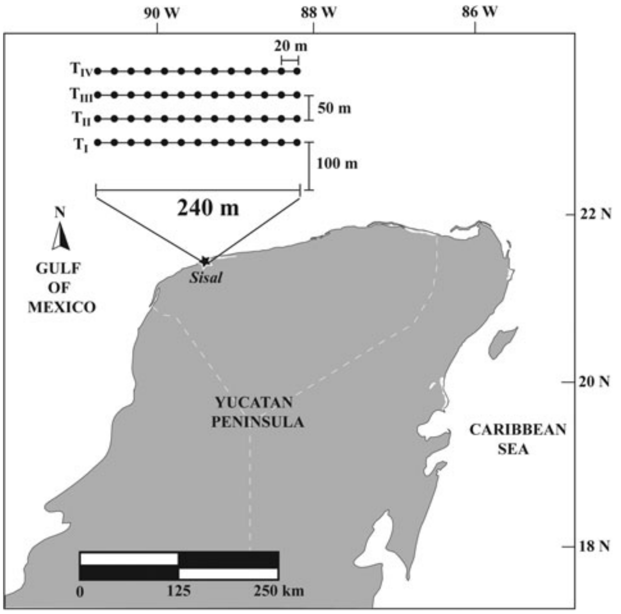

Fig. 1. Location of four transects in the port of Sisal (Yucatan, Mexico) where the sampling procedures were applied to collect the Atlantic blue crab (*C. sapidus*). The depths of the transects were: $T_I = 1.48$, $T_{II} = 1.96$, $T_{III} = 3.0$, $T_{IV} = 3.5$ m.

The 52 traps were divided into four transects which were deployed parallel to the coastline. Each transect included 13 traps separated from one another by 20 m in a straight line of 240 m (Figure 1), giving a 150 × 240 m (3600 m^{-2}) experimental capture area. The first transect was located ~100 m from the coast, and the following transects were placed at 50 m from the previous one, and so on. The depth where transects were placed was measured with a sounding line marked at intervals of 10 cm. The 52 traps were placed at dawn with fish scraps (300 g per trap of white grunt *Haemulon plumieri*) as bait, then they were checked at sunset so that the standardized fishing effort was estimated in 17 h $trap^{-1}$ day^{-1}.

Once crabs were caught, each one of them was identified according to the identification guide of Perry & Larsen (2004). Subsequently, the carapace width (CW) was measured as the distance between the bones on the left and right side, with an accuracy of 0.01 mm. Two numerical marks (with two random numbers) were assigned per individual to prevent the loss of marked organisms or any of the marks. To do this a rubber band was used to mark the carapace and a plastic strip was used to mark one of the chelae. These numerically coded marks made it possible to identify the individual and the day on which it was marked. Once marked, each specimen was released in the middle of the transect where it had been found.

Jolly–Seber model of mark-recapture

The mark-recapture studies are based on the assumption of proportionality of the population '*N*' and the organisms caught, marked and released with regards to the previous sample which includes individuals both marked and unmarked, as a proportion of the total population size (Krebs, 1999; Tenningen *et al.*, 2011). The Jolly–Seber model requires multiple captures and recaptures data to estimate abundance, excluding the first and the last sample (Pollock *et al.*, 1990).

Since this model estimates the abundance per day, an average was applied to obtain a population estimate for the entire sampling period. It is worth mentioning that the J-S model makes the following assumptions: (1) tags are permanent and their codes are identified correctly upon recapture, (2) every crab within the population, regardless of tag presence, age, etc., has the same probability of capture, (3) every crab has the probability of survival, and (4) emigration is permanent (Krebs, 1999).

Several statistics and parameters from the Jolly–Seber model were estimated in accordance with Jolly (1965) and Krebs (1999), such as the proportion of marked organisms ($\hat{a}_t$), the size of the marked population ($\hat{M}_t$), the abundance at the time the sample was collected t ($\hat{N}_t$), the probability of survival from sample time t to sample $t+1$ ($\hat{\Phi}_t$) and the addition rate of the population ($\hat{B}_t$), which were estimated using the following equations (see Table 1 for notation used):

$$\hat{a}_t = \frac{m_t + 1}{n_t + 1} \tag{1}$$

$$\hat{M}_t = \frac{(re_t + 1)z_t}{ra_t + 1} + m_t \tag{2}$$

$$\hat{N}_t = \frac{\hat{M}_t}{\hat{a}_t} \tag{3}$$

$$\hat{\Phi}_t = \frac{\hat{M}_{t+1}}{\hat{M}_t + (re_t - m_t)} \tag{4}$$

$$\hat{B}_t = \hat{N}_t - \hat{\Phi}_t[\hat{N}_t - (n_t - re_t)] \tag{5}$$

To estimate the population size variance, $\hat{N}_t$ was transformed, according to Krebs (1999):

$$T_1(\hat{N}) = \log_e(\hat{N}_t) + \log_e\left[\frac{1 - (p_t/2) + \sqrt{1 - p_t}}{2}\right] \tag{6}$$

where $\hat{p}$ is the catch probability estimated as:

$$\hat{p} = \frac{n_t}{\hat{N}} \tag{7}$$

The variance of this transformation is given by:

$$\begin{aligned} \mathrm{Var}[T_1(\hat{N}_t)] = {} & \left(\frac{\hat{M}_t - m_t + re_t + 1}{\hat{M} + 1}\right) \\ & \times \left(\frac{1}{ra_t + 1} - \frac{1}{re_t + 1}\right) + \frac{1}{m_t + 1} \\ & + \frac{1}{n_t + 1} \end{aligned} \tag{8}$$

The upper (T_{1L}) and lower 95% confidence limits for T_1 are given by:

$$T_{1L} = T_1(\hat{N}_t) - 1.6\sqrt{\hat{V}ar[T_1(\hat{N}_t)]} \tag{9}$$

$$T_{1U} = T_1(\hat{N}_t) - 2.4\sqrt{\hat{V}ar[T_1(\hat{N}_t)]} \tag{10}$$

Analysis of the catches

Crab catch data were analysed to determine the changes in catch per unit effort (CPUE) in terms of crabs per trap. Thus, CPUE (crab trap^{-1}) was estimated separately for the annual (bi-monthly basis) sampling and for the mark-recapture (daily) sampling. Organisms were classified into class intervals of 10 mm carapace width (CW) for size frequency histograms.

Table 1. Notation for the Jolly–Seber model using the terminology of Jolly (1965) described in detail in Krebs (1999) and used in this study.

Parameters	Description
$\hat{M}_t$	Number of marked animals in the population at the time sample t is taken
$\hat{N}_t$	Total number of animals in the population at the time the sample t is taken
$\hat{\Phi}_t$	Probability of survival from sample time t to sample time $t+1$ (an estimate of the loss rate and the addition rate of the population)
$\hat{B}_t$	Number of new animals joining the population between time t and $t+1$ and still alive at time $t+1$
Statistics	
$\hat{a}_t$	Proportion of the marked organisms
m_t	Number of marked animals caught in sample t
u_t	Number of unmarked animals caught in sample t
n_t	Total number of animals caught in sample $t = m_t + u_t$
re_t	Total number of animals released after sample $t = n_t$ – accidental deaths or removals
ra_t	Number of the re_t individuals released at the sample t and caught again in some later sample
z_t	Number of animals marked before the time t, not caught at sample t, but caught in some sample after sample t
$\hat{p}$	Capture probability for all animals in the sample t

Catchability coefficient

Catchability was estimated according to the method proposed by Arreguín-Sánchez & Pitcher (1999). This method is based on data length frequency distribution, which represents the structure of the population, and the Leslie transition matrix (Shepherd, 1987; Caswell, 1988) of the form:

$$N(\lambda, t+1) = A(\lambda, k)N(\lambda, t) \tag{11}$$

where k and λ are the successive length intervals; $N(\lambda, t)$ is the size of the population at time t; A is the transition matrix dependent on growth and mortality, which can be expressed as the product of two terms (Shepherd, 1987) as:

$$A(\lambda, k) = G(\lambda, k)S(k) \tag{12}$$

where G is the effect of growth in the absence of mortality; S is the survival to capture. The matrix $G(\lambda, k)$ was estimated by assigning probabilities of growth to each size class (Shepherd, 1987). The survival matrix $S(k)$ can be expressed in terms of mortality as:

$$S(k) = e^{-Z(k)t} = e^{-[M+q(k,t)s(k)E(t)]} \tag{13}$$

where $S(k)$ are the diagonal elements of the matrix of survival; $Z(k)t$ is the instantaneous rate of total mortality for the group of length k at time t; M is the instantaneous rate of natural mortality; $s(k)$ is the probability of selection by the fishing gear for length group k; $E(t)$ is the fishing effort at time t; $q(k, t)$ is the catchability (q) for the group of length k at time t; and the fishing mortality (F) is given by

$$F(k, t) = q(k, t)s(k)E(t) \tag{14}$$

It is worth mentioning that since $N(\ell, t+1)$, $N(k, t)$, $G(\lambda, k)$, M, $s(k)$ and $E(t)$ are all known, the estimate of $q(k, t)$ was performed iteratively, solving for $q(k, t)$ in equation (13). The adjustment process was performed by the least squares algorithm.

For the estimation of the G growth matrix, it was assumed that the individual growth of *C. sapidus* can be represented by the von Bertalanffy equation with the following values: $L_\infty = 231.5$ mm, $K = 0.51$ years^{-1} and a natural mortality coefficient $M = 0.66$ (Rosas-Correa & de Jesús-Navarrete, 2008). The selection factor for each length class $s(k)$ was set as $s(\lambda) = 1$.

The iterative procedure described by equation (13) was applied to each pair of consecutive CW-CPUE data to obtain the initial values for catchability by size class (CW) and per day. The Catchability program (Martínez-Aguilar *et al.*, 1999) was used to carry out all estimations.

Density

In order to estimate the density of crabs within the study area two approaches (the radius of attraction and the catchability) were used separately in accordance with three different scenarios. In the first scenario (called *Previously Cited Attraction Radius*), based on the previously reported radius of attraction of the traps (R_{at}) for other crustacean species (Aedo & Arancibia, 2003; Ahumada & Arana, 2009), an average R_{at} of 54.25 m was added to each side of the experimental capture area (150×240 m $= 3600$ m^{-2}) and the average abundance was divided by the new area to estimate the density crabs m^{-2}.

Subsequently, under the same approach (abundance-area ratio) the second scenario (called *CPUE per transect*) was conducted based on the empirical assumption that the external transects (T_{I} and T_{IV}) may have a lower CPUE than the internal ones (T_{II} and T_{III}) (Figure 1) due to the effect of bait attractiveness. Thus, CPUE per transect (from the mark-recapture experiment) as well as the distance from the coastline were used to fit their relationship to a convex quadratic function. Once this function was adjusted a projection of distance from the coast was carried out, until CPUE was ≤10% of the maximum CPUE. Just as in the first scenario, the average distance of attraction was added to all four sides of the experimental capture area and the number of crabs m^{-2} was then calculated.

Since the relationship between CPUE and stock abundance often seems to be non-linear (Arreguín-Sánchez, 1996), the third scenario (called *Catchability-Density Relationship*) was focused on the argument that the value of q is obtained from the ratio between CPUE and stock density (Miller, 1975; Arreguín-Sánchez, 1996) where density (D) was calculated according to:

$$D = q \bullet \text{CPUE} \tag{15}$$

Statistical analysis

An analysis of covariance (ANCOVA), using size (CW) as a covariate, was used to find out whether, on average, the CPUE and the catchability coefficient were statistically different among sampling procedures (daily *vs* bi-monthly). If the ANCOVA indicated significant differences, Fisher's least significant difference (LSD) procedure was then applied for *post hoc* comparisons of significant effects (Sokal & Rohlf, 1995). It should be noted that a P-value of $\alpha = 0.05$ or less was considered to be statistically significant, and prior to the ANCOVAs, for all the aforementioned variables, the Shapiro–Wilk test was used to test the assumptions of normality and Levene's test was used to test the homogeneity of variances (Zar, 1996).

RESULTS

The size of the collected specimens ranged from 71 to 186 mm CW, with an average length of 144.65 (±14.5) mm CW in both the daily mark-recapture experiment and the bi-monthly sampling (Figure 2).

In the bi-monthly sampling, 351 specimens were collected: February (56), April (56), June (141), August (42), October (16) and December (40). Thus, the abundance of specimens varied over the annual cycle (February–December).

In the daily mark-recapture sampling, after 6 consecutive fishing days a total of 614 crabs were recorded, of which 336 were marked, and 20 of them were recaptured (Table 2), showing a fluctuation in the catch with a maximum of 138 individuals and minimum of 25 individuals. It is worth mentioning that no accidental deaths occurred during the sampling, therefore, the same number of captured crabs were

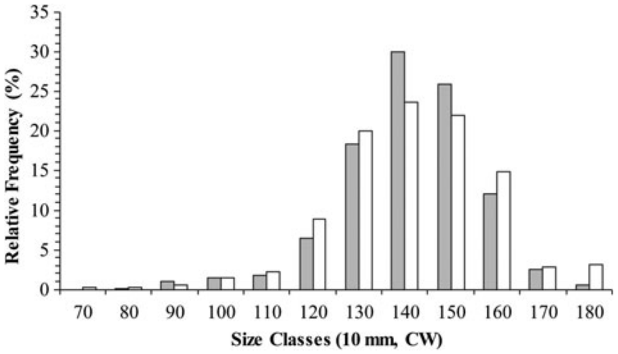

Fig. 2. Relative frequency of the Atlantic blue crab (*C. sapidus*) by size class (10 mm CW) for the daily mark-recapture experiment (grey bars) and the bi-monthly sampling (white bars) in Sisal (Yucatan, Mexico).

Table 2. Data obtained from the mark-recapture of the Atlantic blue crab (*C. sapidus*) in 6 days of sampling in Sisal, Yucatan, Mexico.

	Date (April)					
Days of sampling	**18**	**19**	**21**	**22**	**23**	**24**
1	0	10	0	2	2	0
2		0	0	1	0	0
3				0	3	1
4					0	1
5						0
6						0
Total recaptures (m_t)	0	10	0	3	5	2
Total organisms unmarked (u_t)	138	82	25	78	132	139
Total catch ($n_t = m_t + u_t$)	138	92	25	81	137	141
Total organisms released (re_t)	138	92	25	81	137	141

released per day. In addition, 5 days after the final day of marking, local fishermen caught two marked crabs 5 km from the study area over a period of 24 h, and later other marked crabs were reported 40 km from the study area, indicating that the marks remained on the crabs for more than 6 days.

Behaviour of the catches

Since transects were placed parallel to the coastline at 50 m from each other, this meant that the traps were at different depths: $T_{I} = 1.48$ ($\pm$0.13), $T_{II} = 1.96$ ($\pm$0.36), $T_{III} = 3.0$ ($\pm$0.33) and $T_{IV} = 3.51$ ($\pm$0.25) m depth. On the first and second day of capture shallower transects (I and II) accounted for 60% and 57% of the total catch, respectively. Meanwhile on the fourth, fifth, and sixth day of capture these shallower transects (I, II and III) accounted for 70%, 82% and 66% of catches, respectively (Table 3).

On a daily basis from the mark-recapture sampling, the average CPUE was estimated at 1.96 ($\pm$1.31) crabs trap^{-1} (Table 3). The highest CPUE appeared on the sixth day (CPUE = 2.71 crabs trap^{-1}) and the lowest on the third (CPUE = 0.48 crabs trap^{-1}) (Figure 3A). On a bi-monthly basis, average CPUE was estimated at 1.13 ($\pm$0.83) crabs trap^{-1}. The highest CPUEs were observed in April (total = 2.71 and mean = 0.27 crabs trap^{-1}) while the lowest values were observed in August (total = 0.31 and mean = 0.06 crabs trap^{-1}) (Figure 3B). Notably, CPUE values were quite similar in both the daily and bi-monthly sampling procedures (Figure 3). In fact, the CPUE estimates for these sampling procedures were not significantly different from each other (ANCOVA, $F_{1,21} = 1.08$, $P = 0.312$).

Catchability coefficient

Based on the mark-recapture experiment, the overall catchability (q) per trap used in this study was estimated at 0.0186 ($\pm$0.02) (Figure 4A), while the catchability for the bi-monthly samplings was estimated at 0.0247 ($\pm$0.02) (Figure 4B). Notably, mean catchability values were similar in both sampling procedures. In fact, the catchability estimates between these sampling procedures were not significantly different from each other (ANCOVA, $F_{1,21} = 0.32$, $P = 0.578$).

The size effect (CW) on the catchability (q) of *C. sapidus* (Figure 4A) was estimated by the fitted regression model (3rd order polynomial) and showed a remarkable relationship ($R^2 = 0.8329$). Moreover, catchability was considerably increased in those individuals whose size ranged between 110 and 170 mm CW with a remarkable mode in the size class of 140–150 mm, since the highest q value was attained at 150 mm CW. Finally, it is worth mentioning that in terms of the seasonality within the study area, the highest catchability values were observed during the dry season (Figure 4B).

Estimated abundances from the mark-recapture model

During this mark-recapture experiment, daily estimated abundances ($\hat{N}_t$) ranged from 676 to 6463 crabs, with an overall average of 3475 individuals (Table 4) within the 36,000 m^{-2} experimental capture area. However, under the first scenario the area of influence of the traps was increased

Table 3. Catch in number of individuals (N) and CPUE per trap (13 traps per transect) during mark-recapture experiment.

	Sampling time (days)												
Transects	**1**		**2**		**3**		**4**		**5**		**6**		**Average**
	N	**CPUE**	**N**	**CPUE**	**N**	**CPUE**	**N**	**CPUE**	**N**	**CPUE**	**N**	**CPUE**	**CPUE**
T_{I}	36	2.77	30	2.31	7	0.54	9	0.69	15	1.15	13	1.00	1.41
T_{II}	47	3.62	21	1.62	6	0.46	15	1.15	40	3.08	34	2.62	2.09
T_{III}	30	2.31	26	2.00	7	0.54	38	2.92	50	3.85	40	3.08	2.45
T_{IV}	25	1.92	15	1.15	5	0.38	19	1.46	32	2.46	54	4.15	1.92
Total	**138**	2.66	**92**	1.77	**25**	0.48	**81**	1.56	**137**	2.64	**141**	2.71	**1.96**

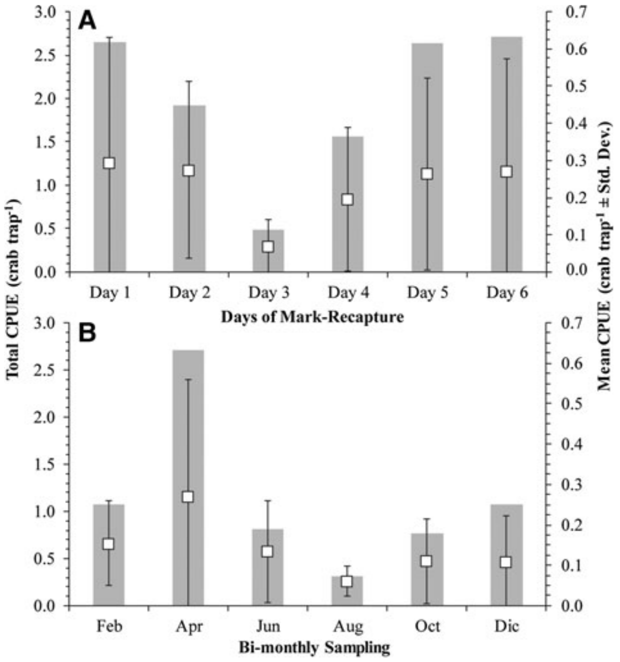

Fig. 3. Total CPUE (grey bars) and Mean CPUE (□ ± SD) of the Atlantic blue crab (*C. sapidus*) for (A) the daily mark-recapture experiment and (B) the bi-monthly sampling in Sisal (Yucatan, Mexico).

to 90,087 m^{-2} (54.25 m per side was added), which resulted in a density estimate of 0.0386 crabs m^{-2} (Table 5).

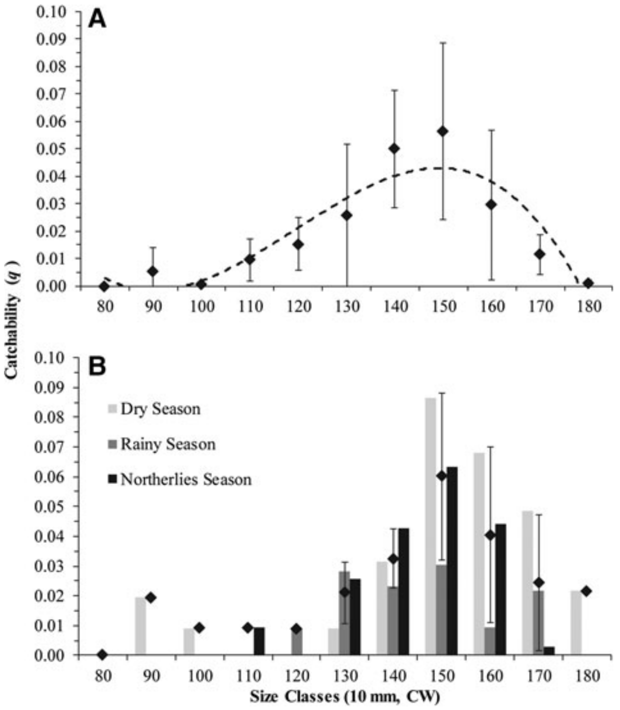

Fig. 4. Mean catchability (◆ ± SD) estimates of the 52 traps used for the Atlantic blue crab (*C. sapidus*) by size class (10 mm CW) for (A) the daily mark-recapture experiment and (B) the bi-monthly sampling (dry: February–April, rainy: June–August and northerlies: October–December). The mark-recapture data (dashed line) was accurately ($R^2 = 0.8329$) fitted to a 3rd order polynomial regression model ($q = -0.0004x3 + 0.0064x2 - 0.0204x + 0.0173$).

Table 4. Population estimates derived from data obtained from the Jolly–Seber mark-recapture model for population estimation of *C. sapidus*.

Sample (day)	$\hat{a}_t$	$\hat{M}_t$	$\hat{N}_t$	Confidence limits for $\hat{N}_t$		$\hat{\Phi}_t$	$\hat{B}_t$
				Lower	Upper		
1	0.0	0	–	–	–	1.420	–
2	11.8	196	1657	1503	1899	0.094	521.0
3	3.8	26	676	642	706	4.882	1804.0
4	4.9	249	5104	4891	5290	0.859	2076.6
5	4.3	281	6463	5896	6928	–	–
6	2.1	2	–	–	–	–	–
Average abundance			3475	3233	3705	1.814	1467

– means that no estimate can be made of this parameter from the data available.

Under the second scenario a quadratic function (Figure 5) was fitted to the results of CPUE per transect (Table 3) and the distance between the transects in relation to the coastline (d), which resulted in the following equation: $CPUE = -0.000123d^2 + 0.0466d - 2.0097$ ($R^2 = 0.9715$). In this case the area of influence of the traps was estimated at 99,218 m^{-2}. This latter was used to estimate density at 0.0350 crabs m^{-2} (Table 5).

Meanwhile, the values of CPUE (Table 3) and q for the bi-monthly sampling allowed us to estimate the average annual density for the third scenario as: density = CPUE (1.96) • q (0.0186) = 0.0365 crabs m^{-2} (Table 5). Based on density estimates from the latter scenario, the population size of crabs in Sisal was estimated at 36,500 crabs km^{-2} during the season with the highest abundances (Spring), whereas the annual average was estimated to be 27,900 crabs km^{-2}.

DISCUSSION

For most marine animals, it is almost impossible to count the total number of individuals in a population, especially in fast-moving species with cryptic or inaccessible habits. In fisheries, population studies tend to focus on catch data, visual census, mark-recapture and other mathematical models (Perry *et al.*, 1999; Smith & Addison, 2003). However, the advantage of mark-recapture methods is that they can be used to simultaneously estimate abundance and other population parameters such as mortality, dispersion, density and growth (Krebs, 1999) and have been successfully applied in the stock assessment of crustaceans with different models.

Fitz & Wiegert (1992) conducted a study using the Jolly–Seber mark-recapture model to estimate the population of *C. sapidus* in Georgia (USA) reporting between 150,000 and 200,000 specimens in 112 hectares, that is to say from 133,930 to 178,572 crabs km^{-2}. In our study, *C. sapidus* densities ranged from 36,500 (spring) to 27,900 (annual average) crabs km^{-2}. Although Fitz & Wiegert (1992) and our study both estimated *C. sapidus* densities using the Jolly–Seber model, we found lower densities (on average 0.0365 crabs m^{-2}) than those observed in the estuary of Georgia (0.2 crabs m^{-2}). Despite the fact that this latter study was carried out in a different study area, discrepancies in density estimates with our study might be related to the sampling procedures applied by these authors since they used trawl tows, whereas we used baited traps to collect *C. sapidus* specimens.

Table 5. Density (crabs m^{-2}) estimates of *C. sapidus* under three different scenarios.

Scenario	Previously cited attraction radius	CPUE per transect	Catchability-density relationship
Abundance	3475	3475	—
Area of influence of the traps (m^{-2})	90,087	99,218	—
Density (crabs m^{-2})	0.0386	0.0350	0.0365[a]

[a] Density = CPUE (1.96) • *q* (0.0186).

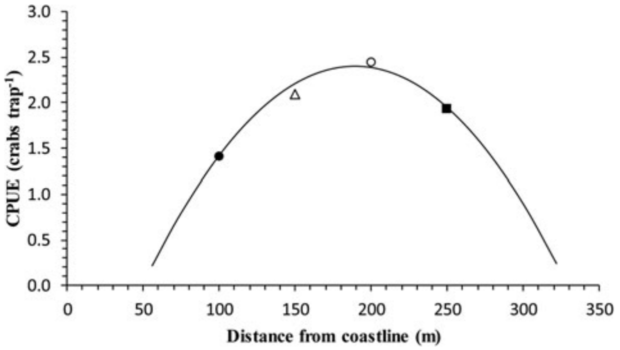

Fig. 5. Relationship plot between CPUE per transect and the distance between the transects in relation to the coastline (d) used to estimate density of crabs under the second scenario. A quadratic function, $CPUE = -0.000123d2 + 0.0466d - 2.0097$ ($R^2 = 0.9715$), was fitted to data and the estimated CPUE is shown as a continuous straight line. Observed CPUE (mark-recapture experiment) from each transect are shown as: T_I(•), T_{II}(△), T_{III}(○) and T_{IV}(■).

Moreover, Velazquez de la Cruz *et al.* (2012) mentioned that abundances of *C. sapidus* may vary due to the capture zone where the traps are placed whether it be a lagoon, an estuary, or the coast, where uneven densities are observed. The latter might be related to migration behaviour of this species (Celis-Sánchez *et al.*, 2014).

When traps are used, the type and amount of bait used are very relevant, as well as the interaction of organisms caught with the environment, the design of the trap, and the distance between the traps (Aedo & Arancibia, 2003). In this sense the effective radius of attraction (R_{at}) for the baited traps can be useful for defining the study area and density of organisms (Gedamke *et al.*, 2004; Ahumada & Arana, 2009). Several authors have focused on estimating the response of CPUE placing traps along a ground line at different distances, along with visual censuses to validate the estimated density (Eggers *et al.*, 1982; Tremblay *et al.*, 1998; Aedo & Arancibia, 2003; Ahumada & Arana, 2009). However, there is no information on the methods used to estimate the density of crustaceans when several adjacent ground lines are used, as carried out in our study. Unfortunately, we were unable to validate the estimated densities with visual censuses, however we focused our density estimates on three different scenarios: (1) *Previously Cited Attraction Radius*, (2) *CPUE per transect* and (3) *Catchability-Density Relationship*, which gave similar results (Table 5).

In addition to this latter issue, the attraction of the baited traps could influence the estimates of abundance and catchability. Nevertheless, although we recognize that baited trapping may significantly increase capture rates and thus bias the estimates of organism density, this capture method has been proved to be more efficient and cheaper than the unbaited methods (such as visual censuses), and it also has the potential to accurately survey unmonitored populations where their density is too low to determine accurately via other means (Eggers *et al.*, 1982; Priede & Merrett, 1996; du Preez *et al.*, 2014).

This study showed that crabs kept their marks for several days after the experiment, since recaptures of marked individuals were observed in the port of Chelem (~40 km from our study area) 5 days after the last day of marking. It is known that congeners of *Callinectes* sp. are highly mobile, enabling them to locate food and occupy diverse habitats and depths (Fitz & Wiegert, 1992; Ortiz-León *et al.*, 2007). In this sense, the blue crab population that we studied fluctuated in abundance daily since a decline in its abundance was observed on the 2nd, 3rd and 4th day of sampling, probably as a result of the emigration and immigration of *C. sapidus* within the study area. Moreover, it is worth mentioning a weather event, commonly known as 'Northerlies', which is characterized by the presence of strong north winds with low rainfall and low air temperatures (Herrera-Silveira, 1994), was observed within the study area during these days of sampling. This might have triggered a migration of *C. sapidus* to deeper areas, since a reduction in catches was observed in the near-shore transects (T_I and T_{II}) and an increase in those transects most distant from the coast (T_{III} and T_{IV}).

In relation to catch per unit effort (CPUE), the greatest abundance estimate was recorded in April and its lowest value in August (Celis-Sánchez *et al.*, 2014). Catchability (*q*) has been defined as a measure of the interaction between abundance and fishing effort. Catchability is in practice not constant between time periods, and the relationship between CPUE and stock abundance often seems to be non-linear (Arreguín-Sánchez, 1996). Its variability has been recognized to be the cause of variation in the environmental factors within the study area and the relative distribution of the population (Morales-Bojórquez & Nevárez-Martínez, 2002; Chávez & Pérez, 2009). In this sense, the catches in this study were composed primarily of females, which could be related to the sampling location (probably a habitat where females choose to release eggs), as it is known that after copulating, female *C. sapidus* migrate into areas where they remain throughout their life cycle (Uscudun, 2014). This affects the bias towards a large proportion of females during samplings. This kind of bias towards females contradicts the values obtained by Rosas-Correa & de Jesús-Navarrete (2008) for this species in the Bay of Chetumal, (Quintana Roo, Mexico), where males had higher dominance over females. It is important to note that in Sisal there may be a division of habitat by sex, which agrees with what was reported in the Bay of Chetumal (Ortiz-León *et al.*, 2007). Thus, in order to make a proper diagnosis of the fishery of our study species, in future studies various areas (including coastal lagoons) should be established in order to cover areas of breeding, reproduction and growth.

Catchability research has developed to provide a measure of fishing gear efficiency, or to find the relationship between population size and fishing effort. Whatever the adopted approach, the interpretation may be elusive unless there is a clear understanding of other associated concepts, such as selection, selectivity, accessibility, availability and vulnerability (Arreguín-Sánchez, 1996). For example, selectivity is the measure of catchability of one component of the population (e.g. size class) relative to another component of the population for those animals that encounter a given type of fishing gear (Frusher & Hoening, 2001). It is also very important to consider that homogeneous capture probability among specimens of varying sizes is assumed in population size and density estimates based on Jolly–Seber models from mark-recapture studies, however natural populations will never be completely homogeneous in all respects, especially in open populations from marine environments. In our study the sampling efficiency (catchability) of the baited traps that we used is somehow biased towards specific sizes (between 110 and 170 mm CW), however the size selectivity of traps used actually ranged from 71 up to 188 mm CW, indicating that the population of crabs in our study area consisted mainly of adults (>70 mm CW specimens) (Lipcius & Stockhausen, 2002). Therefore, in the catchability estimates, the selection factor for each length class $s(k)$ was set to $s\ (\lambda) = 1$. However, in future studies this inconvenience should be considered since an effective sampling device is necessary for capturing all sizes of crabs including juveniles ($35 \leq$ mm CW ≥ 70). There is evidence that very small juveniles of *C. sapidus* are usually found at high densities in the shallowest habitats (<1 m depth) of estuarine waters of most geographic regions (Fitz & Wiegert, 1992). Thus further studies should focus sampling in shallow areas in order to capture a wider range of sizes.

The present study investigated the efficiency of the mark-recapture, compared with annual samplings, data to determine the abundance and catchability and thus estimate the density of organisms and population size of the Atlantic blue crab (*C. sapidus*). Although the Jolly–Seber mark-recapture model has been widely used in other marine species to estimate density of populations, as shown in our study of *C. sapidus*, the use of a daily mark-recapture experiment has proved to be faster than, and as reliable as, annual samplings to estimate the abundance and catchability since both approaches gave similar estimates. However, in further studies long-term tagging samplings are encouraged in order to reduce any biase effect and to give more precise estimates of abundance of this important fishing resource of the northern Yucatan Peninsula.

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