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Title: An unfished area enhances a spiny lobster (*Panulirus argus*) fishery: Implications for management and conservation within a Biosphere Reserve in the Mexican Caribbean

Running head: unfished area and spiny lobster conservation

ABSTRACT

The Caribbean spiny lobster (*Panulirus argus,* Latreille, 1804) is the main source of income for the communities in the Sian Ka´an Biosphere Reserve Mexico. The fishery has recently been certified as "sustainable" by the Marine Stewardship Council provided that further stock assessment is carried out. A total of 379 lobsters were tagged in an unfished area offshore from the Bahía del Espíritu Santo fishing grounds to assess whether lobsters remained within these areas and were thus fully protected. The lobsters recaptured in the shallow area (5.3%), were sufficient to develop a multi-state mark recapture model, which takes into account fishing and natural mortality, tag reporting rate and tag loss. This estimated that between 15 and 20% of all adult lobsters dwelling in the unfished area moved into the fishery and were subjected to exploitation. This study suggests that the offshore unfished area provides protection to the majority of the stock in this area while adding to and maintaining fishing yields within the inshore commercial fishery.

Key words

Caribbean, Fisheries, Lobsters Migration, Population Dynamics

Introduction

Marine Protected Areas- (MPA's) are often defined as no take zones where fishing is prohibited. As part of the conservation efforts to sustain exploited species such as lobsters, MPA's are designed to preserve important habitats that serve as shelter, foraging grounds or movement corridors, as well as protecting the breeding stocks and increasing the fishery yield of the target species (Acosta, 1999; Goñi, *et al* 2010). In Biosphere Reserves like Sian Ka'an (SK-BR see map rectangular insert Fig. 1), where fishing is allowed but access is restricted and operations only occur within areas of less than 20 m depth (Ley-Cooper, *et al* 2013; MRAG-Americas, 2012), management initiatives are also expected to replenish stocks by increasing biomass and abundance. However few empirical studies have demonstrated whether these management initiatives optimize population viability, and how they may affect benthic dispersal dynamics of the Caribbean spiny lobster *Panulirus argus,* Latreille, 1804 (Acosta, 1999).

Assigning no take areas where fishing is totally banned is being promoted as a conservation strategy for heavily exploited species such as *P. argus*, although there is generally only limited evidence that movements of adult individuals from unfished areas replenish the populations in areas subject to fishing ('spillover effect') (Russ, *et al* 1996; Goñi, *et al* 2010). This is also the case in the SK-BR where un-fished offshore areas deeper than 20 m are unofficially conceived as no take areas of the MPA. These areas are especially valuable for sustainability since they are predominantly populated by mature-sized lobsters (Ley-Cooper *et al.*, 2013: Lozano-Álvarez *et al.*, 1993). Understanding both recruitment and lobster movement patterns from the deep unfished area into the fishery can help evaluate the Biosphere Reserve's potential to meet management performance standards, by providing information about habitat use, home range, migrations, retention times/spillover, and location of spawning grounds (Goñi *et al*., 2006; Bertelsen, 2013). Given the complexity of the post larval settlement and recruitment patterns of *P. argus* (Briones-Fourzán, 2008), the only tangible fishery benefit that can be demonstrated in favour of the deep unfished areas is the recruitment of adults which replenish the shallow fishing grounds (< 20 m) enhancing fishing yields (Russ & Alcala 1996; Bevacqua *et al.* 2010). This is usually examined via tagging experiments (Frusher & Hoenig, 2003; Goñi *et al.*, 2010; Bertelsen 2013).

Spiny lobster *Panulirus argus* is the most valued single species fished in the Caribbean and the main economic source for families living in the Sian Ka´an Biosphere Reserve, Mexico (SK-BR). The marine segment of the SK-BR is an MPA, where restricted fishing for lobsters is permitted to three cooperatives with exclusive concession rights within both existing bays - Bahía de la Ascensión and North and Bahía Espíritu Santo-South (Fig. 1) Ley-Cooper *et al.* (2013). Fishing operations are confined to the shallow areas (<20 m) west from the barrier reef due to restrictions in fishing gear and regulations, since only free diving is allowed and the use of any sort of alternate air source or deep trap is banned (Ley-Cooper *et al.*, 2013; Sosa-Cordero *et al.*, 1999). As a result, only the portion of the whole lobster stock lying within shallow waters is exploited (area I, Fig 1) and the deep offshore area (>20 m) is effectively a no take zone which is unfished (area II, Fig 1). This limitation is a main criterion for the sustainable management of this fishery. However the MSC certification process identified the multiple sources of recruitment variation and movement of adult lobsters to and from the deep areas as one of the main sources of uncertainty in assessing the stock status (MRAG-Americas, 2012).

Panulirus argus displays movement behaviours throughout its life cycle for many purposes, including relocating to more appropriate habitat and foraging for food and reproduction (Acosta, 1999; Briones-Fourzán *et al*,. 2003; Ríos-Lara *et al.,* 2007). After settlement within shallow vegetated areas juveniles attain a transitional size (typically >15-20 mm carapace length CL) at which they begin to seek shelters (rock crevices, holes and ledges; undercut coral heads and sponges). Emigration out to deeper reef areas for reproductive purposes begins to occur in pre-adult lobsters (size ≈75 mm CL).

How the physical characteristics of the deep segment (>20 m) of the SKBR MPA interacts to support a viable population of *P. argus* in the shallows has been the focus of much discussion, but few empirical studies have investigated the mechanisms which affect adult dispersal, distribution or abundance - information important for designing protected areas (Acosta, 1999; Bertelsen, 2013). Little is known about the population dynamics of lobsters that dwell in the deep platform and the offshore areas (≥20m) of the SK-BR (Lozano-Álvarez *et al.*, 1993, Ley-Cooper *et al.*, 2013). It is possible that some adult lobsters from the deep water stock may migrate into the shallow areas as a result of dispersal movements, for reasons such as: returning after spawning (Bevacqua *et al.*, 2010; Bertelsen, 2013); seasonal behavioural changes (Lozano-Álvarez *et al.*, 1993; González-Cano, 1991; Herrnkind, 1980; García *et al.*, 1991); or in search of food and shelter (Ríos-Lara *et al.*, 2007). To date, the proportion of lobsters that might move inshore from deep areas has not been estimated and the assumption that the adult stock is fully protected in deeper waters should be re-examined for this BR.

More robust stock assessment and the establishment of biological reference points have been suggested as means to improve the management and evaluation of the lobster fisheries in SKBR, and now form a condition for the on-going sustainability certification granted by the Marine Stewardship Council (MSC) (MRAG-Americas, 2012). In this fishery, exploitation rates are high within the shallow bays (depths <20 m, area I), and it has been suggested that, in order to sustain such catch rates lobsters, recruitment to this fishery must be frequently replenished by growth of juveniles and/or by an input of lobsters moving in from unfished areas such as those found offshore in deeper waters (>20 m) (Lozano-Álvarez *et al.*, 1993; Lozano-Álvarez *et al.*, 1991a; Lozano-Álvarez *et al.*, 1991b; Ley-Cooper *et al.*, 2013; Briones-Fourzán *et al.*, 2007; González-Cano, 1991).

This paper addresses the question of how the present management regulations, which constrain fishing to depths less than 20 m, may affect benthic dispersal dynamics of the Caribbean spiny lobster, and their catch rates within the Sian Ka'an Biosphere Reserve. We used a multi-state mark recapture model to test the hypothesis that an autumn season migration takes place, with a proportion of lobsters moving from the offshore (>20 m) unfished areas of the MPA into to the shallow areas which are fished. The impact this has on fishing yields is examined and discussed.

Materials and Methods

Study area

The study was conducted in the Mexican Caribbean, in the central segment of the coast of Quintana Roo/Yucatan Peninsula within the SKBR/MPA. Here, the continental shelf is narrow, not exceeding four km from the coast and ending at depths averaging 50 to 60 m, after which depths rapidly reach >400 m (Lozano-Álvarez *et al.*, 1991 a; Lozano-Álvarez *et al.*, 1991b;). The SK-BR encompasses two large marine embayment's named Bahía del Espíritu Santo (south) and Bahía de la Ascensión (north) (Fig.1). Bahía del Espíritu Santo is a large and shallow bay ranging in depths from 1-20 m, with an area of approximately 300 km^2 (Sosa-Cordero *et al.*, 1999). Within this bay there is a limited access fishery exclusively exploited by two cooperatives, and co-managed by environmental and fishery federal government authorities (Sosa-Cordero *et al*, 2008).

For the purposes of our study, the bay was divided into two areas (Fig.1): area I, the commercially exploited shallow bay (<20 m) to the west and area II, the un-exploited offshore deeper area (>20 m) to the east. In practice, area II is a "no take" zone within this BR, since diving with the use of alternative air sources (eg. SCUBA) is prohibited, although lobsters (*P. argus*) are naturally distributed in both areas (Phillips, 2006).

Description of the fishery and local stock

The lobster fishery is based on concessions to two cooperatives which fish using a "Casita/Campo" system. Casitas are large artificial shelters that can harbour the full size range of lobsters, and are allotted to individual fisher families associated to the cooperative. The bay and fishing areas are divided into parcels called Campos, and are hence owned by the "family" who manage them in a semi-ownership arrangement (Lozano-Álvarez *et al.*, 1991a; Lozano-Álvarez *et al.*, 1991b; Briones-Fourzán *et al*, 2000; Sosa-Cordero *et al.* 2008). Permits are renewed annually and cooperatives must comply with the federal fishing regulations, which include a closed season from March 1 to June 30; a minimum tail size of 13.5 cm (~74.5 mm, CL; Lozano-Álvarez et al. 1991a; Lozano-Álvarez et al. 1991b); and prohibition of capturing egg bearing females.

Lobsters are caught mainly in the bays within the fringing reefs using small boats and by skin diving to a maximum depth of 20 m (Ley-Cooper *et al.*, 2013). For the purpose of this study we refer to the "local" stock as the proportion of the population found within the bay, including the adjacent water areas found beyond the reef and to the east of Bahía del Espíritu Santo (depths ≤100 m) (Briones-Fourzán & Lozano-Álvarez, 2001; Briones-Fourzán *et al.*, 2007).

Lobster tagging and recapture:

Tagging: A total of 379 lobsters, (56 in August and 323 in September, 243 females and 136 males), were tagged and released where they had been caught, in water depths which ranged between >20m and < 40 m, in area II (Fig.1), during the first five days of each month in 2011. All lobsters were caught using hand nets or snares while fished using SCUBA, and were tagged with T-Bar tags ("Hallprint", Australia) in their ventral abdomen region as described by (Ley-Cooper *et al.*, 2013). The size range of tagged lobsters was 70.1 to 140.5 mm CL. Fishing location, sex, and size (CL), were recorded for each lobster.

Recaptures: Recaptures were obtained from both licenced fishing boats and the cooperative depots during the fishing seasons 2011/2012 and 2012/2013. Research observers went on-board boats for 10 days during every month of the fishing season. Additionally information on tag reporting in log books was obtained at reception points.

The Multi-State Tag Recapture Model:

In order to estimate the monthly movement rates of tagged lobsters from an unfished area (area-II) to a fished area (area-I) during each month of the fishing season following the tag releases (i.e. August 2011 – January 2012), a multi-state tag-recapture model (MSTR) was developed based on a model framework described by Hilborn (1990). The model, built in "R" (R Development Core Team, 2012), encompassed only the first fishing season following release (2011/12) since this period covered the majority of tag returns. Returns in the 2012/13 season were so few they provided too little information for the MSTR model to determine movement rates with any degree of confidence.

A model was custom-built for this study because previously developed models, such as those found in packages like 'MARK' (White & Burnham, 1999), required tagging and recaptures to occur in both areas in its multi-state design. In our study, lobsters were only tagged and released in the unfished deep area >20 m (area II) and recaptured only in the shallow fished area < 20 m (area I). The MSTR model incorporated fishing and natural mortality, reporting rate, and tag loss. It differed slightly from that described by (Hilborn, 1990), in that it also included natural mortality, all mortality was treated as instantaneous, and a four- rather than a three-dimensional array was used to track lobsters.

The model consisted of four main components, which combined allowed us to determine the likelihood of recapturing a tagged lobster in the shallow fished area. These components represented the processes of tag-release, migration, mortality (fishing/natural/tag-loss) and likelihood of recoveries. The model employed a monthly time-step (August - January) and considered the numbers of tagged lobsters at liberty and recaptured in each time interval starting in the calendar month when lobsters were first released (August 2011) and terminating at the calendar month when the last recaptured lobster of that fishing season was recorded (January 2012). The model grouped lobsters into two areas: I) the fished shallow-waters (<20 m), and II) the offshore unfished deeper-waters (>20 m). The model contained a series of assumptions:

1. Tag loss would occur at a rate previously determined from aquaria studies (Ley-Cooper *et al.*, 2013). The exponential decay relationship describing the monthly proportion of tags retained was: $TL = 0.953 * e^{(-0.151*L)}$, where TL is the proportion of lobsters still tagged and L is the number of months after release. This rate of tag loss lies within the ranges obtained by other lobster studies (Dubula *et al.*, 2005; Montgomery & Brett, 1996; Forcucci *et al.*, 1994; Sharp *et al.*, 2000; Ehrhardt, 2008)
2. Commercial fishing effort was homogenous across the entire fishery.
3. Each lobster within the model had the same probability of being captured.
4. During the study tagged lobsters will not migrate twice, i.e. will not enter the fishery and then leave.
5. Natural mortality was previously determined within the bay in a study carried out during the previous fishing season (Ley-Cooper *et al.*, 2013), and is assumed to be constant over time and model area.

Analysis of tag data

Data from tagged lobsters were recorded within the MSTR model, using a four-dimensional array that recorded their expected abundance against: a) their initial release location, b) the month they were released, c) their recapture location and d) the month of recapture. At the start of each time-step, tagged lobsters were recruited into the model using the equation:

$$N_{r,m,a,t} = T_{r,m} + N_{r,m,a,t-1}$$

where $N_{r,m,a,t}$ represents the number of tagged lobsters from the release area (*r*) (area II), released in month *m* and currently residing in area *a* (area I), during the model time-step *t*, and $T_{r,m}$ represents the number of tagged lobsters initially released: *m* and *t* range from May to January (n=11), whilst *r* and *a* represent lobsters moving from deep to shallow (n=2).

Migration

Following the recruitment of tagged lobsters, the MSTR model estimated a time-step specific proportion of tagged lobsters (P_t,) that were uni-directionally migrating from the unfished area to the fished area using the equations:

$$N_{r,m,1,t} = N_{r,m,2,t} * P_t,$$

$$N_{r,m,2,t} = N_{r,m,2,t} * (1 - P_t).$$

Estimates of mortality, recoveries and tag loss

Estimates of *F* and *M* were based on previous estimates determined for this same fishery in the previous fishing season 2010/11 and were assumed to remain constant across the fishing season (Ley-Cooper *et al.*, 2013). These values were not determined by the MSTR model since no tagging occurred within the fished area (I). Since the average monthly estimate for *F* had been determined for the previous fishing season at ~ 0.3 (Ley-Cooper *et al.* 2013), a range of values that encompassed this (e.g. 0.1, 0.15, 0.2, 0.25, 0.4, and 0.5) were utilised to determine how sensitive the model was to the estimate of *F*. The instantaneous rate of natural mortality (*M*) of 0.02 $^{-month}$ used in this study was also taken from the Ley-Cooper *et al.*, (2013).

The rate of tag loss used in the model (about 14% month^{-1}) was based on the rate previously reported for *P. argus* in the same fishery (Ley-Cooper *et al.*, 2013), and it represented the expected reduction in the number of tagged lobsters at liberty, due to tag shedding and tag induced mortality. After allowing for the migration of lobsters between areas, 50% of the estimated monthly tag loss was applied to the simulated population of lobsters, both before and after fishing and natural mortality had both been applied. Tag loss was applied to the simulated population of lobsters in the model by using the equation:

$$N_{r,m,a,t} = N_{r,m,a,t}(1 - e^{-2.65}).$$

Interviews with fishers indicated that the tag reporting rate for this study was ~ 30% less than that of the previous seasons estimate of 100% return rate (Ley-Cooper *et al.*, 2013). This was considered to be due to less direct interaction with the fishers and that tag reporting was becoming less novel. As such a range of tag reporting rates encompassing this estimate (60 – 80%) were trialed in the model to assess its sensitivity to this parameter.

Instantaneous rates of fishing (*F*) and natural mortality (*M*) were applied to the population once tagged lobsters had been released, migrated and reduced in magnitude through tag loss. Simulated catches were also affected by a tag reporting rate (λ) which was applied before the lobsters were considered to have been reported to the survey team. The estimated number of recaptured lobsters reported to the survey team and the numbers left in the water were determined using a Baranov catch equation:

$$\hat{R}_{r,m,a,t} = N_{r,m,a,t} * \frac{F_{a,t}}{F_{a,t}+M} * \left(1 - e^{\left(-(F_{a,t}+M)\right)}\right) * \lambda_{a,t},$$

$$N_{r,m,a,t} = N_{r,m,a,t} * e^{\left(-(F_{a,t}+M)\right)},$$

where $\hat{R}_{r,m,1,t}$ is the estimated reported catch of tagged lobsters and $M = 0.24/12^{\text{-month}}$. Note fishing mortality in the unfished area is assumed to be zero ($F_{1,t} = 0$).

Likelihood of tag recoveries

A non-linear function minimisation procedure was used to estimate the values of the six migration parameters that maximised the likelihood of the observed tag recoveries. The parameters estimated represented the month-specific proportion of lobsters migrating from the unfished to the fished area, in each month from August to January ($P_{t=1-6}$). Initial parameter estimates used were 0.05 for each of the six months, i.e. 5%, of tagged lobsters migrated in every month. The negative log-likelihood (LL) of the observed recoveries of tagged lobsters (R) given by the monthly proportions of lobsters migrating (P_t) and our MSTR model was assumed to have a Poisson distribution (Hilborn, 1990) and was represented by the equation:

$$LL = -\sum\left(-\hat{R}_{r,m,2,t} + R_{r,m,2,t}\left(ln\left(\hat{R}_{r,m,2,t}\right)\right) - ln\left(R_{r,m,2,t}!\right)\right).$$

The log-likelihood was maximised using the "optim" routine in "R", with the square-root of the diagonal of the inversed hessian matrix, being produced to approximate the standard errors of the parameter estimates.

Results

Size class differences between unfished areas (>20 m) and fished areas (<20 m)

In Bahía del Espíritu Santo there was a significant difference (P<0.001) in size composition between the lobsters found in the deeper unfished area (>20 m, area-II) and those in the shallower commercially fished bay (area-I). In the deeper area the mean CL of lobsters was 94.2 mm CL, with 99% of lobsters being larger than the minimum legal size (74.5 mm CL). In contrast, lobsters in the fished area (area I) had a mean CL of 73.0 mm, and 75% were smaller than the minimum legal size CL (Fig. 2).

Movements

Out of 379 lobsters released, 20 were recaptured (5.3%) within the fishery (area I) during the 2011/12 fishing season. A further four lobsters were recaptured within the fishery during the subsequent

2012/13 fishing season (total 6.3%). Recaptured lobsters comprised 50% females (average size: 85.9 mm CL, size range: 79.1-109.9 mm CL) and 50% males (average size: 101.4 mm CL, size range: 82.2-114.5 mm CL) and were caught over seven separate months starting from October 2011 (n=10), November 2011 (n=8), December (n=1) 2011, January 2012 (n=1) toward the end of the first season; and then July 2012 (n=2), November 2012 (n=1) and January 2013 (n=1) toward the end of the second season. Recaptured lobsters had mostly travelled in a southwest direction over distances ranging from 3.5 to 29.2 km when measured in a straight-line, with a mean distance of 7,602 m (Fig. 3). The lobsters recaptured in October 2011 were located near the fringing reef, whereas those recaptured in November and December 2011 had moved far greater distances and were found closer to the centre of the bay (Fig. 3). All of the lobsters recaptured in the second season following tagging (2012/2013) were captured near the fringing reef on the outside edge of the bay (Fig. 3).

Catch trends, effort and catch rates for the inshore fished area

In Bahía Espíritu Santo, catch trends follow a similar pattern throughout the years, starting at the highest levels at the beginning of the fishing season in July, and progressively declining as the season advances towards the end in February. Catch per unit of effort (CPUE) is also highest in July, after which it remains relatively constant from August to November, except for a second peak during the autumn-period. This latter peak in CPUE generally occurs in October or November and may be associated with the onset of the 'Nortes' (cold fronts arriving from the north).

Outputs of the model

Captures of lobsters from the two release pulses (i.e. August and September 2011) displayed similar patterns during the 2011/2012 fishing season, with no recoveries being reported prior to a peak in recaptures in October/November before progressively reducing through until January 2012 toward the end of the first fishing season. The MSTR model was able to recreate a very similar distribution of the tag recapture pattern observed in the fishery during the 2011/2012 season, also estimating tag recaptures peaked in October 2011 and declined slowly through until January 2012 (Figs. 4 & 5).

Under all sensitivity scenarios, a consistent pattern of migration from the unfished area (area-II) into the fished area (area-I) was estimated to have occurred as a single pulse during the month of October (Fig. 4 A). The proportion of lobsters estimated to have migrated had a median value of 20% and was relatively consistent across the majority of the scenarios tested for the different variables, i.e. ranging from 10 to 40%. The largest percentage of lobsters estimated to be migrating (~40%) occurred under the scenario of a low tag reporting rate (60%) and low exploitation rate (10%) (Fig. 4 B).

Discussion

Results from this study suggest that legal sized lobsters (sub-adults 74.5-80.0 mm CL and adults >80.0 mm CL) move from the offshore unfished area and enhance the commercially fished area in the shallows within the SK-BR. The movement rates of the tagged lobsters were examined using a purpose built multi-state tag-recapture model, which was able to replicate the observed tag recoveries obtained from the commercial fishery. Based on an assumed monthly rate of fishing mortality 30% (which was reported the previous season e.g.; Ley-Cooper *et al.,* 2013), and a rate of tag-reporting of 70%, about 20% of the lobsters originally dwelling offshore migrated into the bay. Sensitivity analysis indicated that if the assumptions for fishing mortality and tag reporting were varied within sensible ranges the proportion estimated to be migrating did not vary radically, generally remaining within the range of 15 – 20%.

The model estimated that the movements all occurred within the same month, (October 2011), a period within that year that coincided with the start of a cold front system, as well as an annual increase in the catch per unit of effort in the commercial fishery of both the north and southern bay of the Biosphere Reserve (Ley-Cooper *et al.*, unpublished data). The movement of spiny lobsters has been well documented for many spiny lobster species and has been generally categorised into three types, homing, nomadic or migratory movements (Herrnkind, 1980; Phillips, 2006). Migratory movements are unidirectional, occur in mass quantity, during a confined period of time, and have been attributed to several factors such as ontogenetic behaviour; seasonal movements towards feeding grounds (Briones-Fourzán *et al.*, 2003; Ríos-Lara *et al.*, 2007; Acosta, 1999); spawning migrations (Bertelsen, 2013); or as a response to environmental stimuli such as moon cycles, changes in water temperatures, and changes in wind strengths and direction (García *et al.*, 1991). In Florida, Bahamas and Cuba, movements of *P. argus* were reported to be initiated by cold fronts in autumn, as increasing wind speed and direction increased water turbidity and decreased water temperature, which in turn triggered lobster mass migration behaviours (García *et al.*, 1991, Herrnkind, 1985, Herrnkind, 1980). Data from 1984 to 2012 from the northern bay of SK- Bahía de la Ascensión has shown that an increased Meridional wind speed and change of direction results in a direct relationship with increased catch rates during the autumn period (Ley-Cooper *et al.,* unpublished data). Using CPUE as an indication of abundance, a plausible hypothesise is that cold fronts generate additional nomadic movements of lobsters due to changes in temperature, and increased turbidity which allows for greater foraging distances, which may result in movements from the deep (area II) to the shallow bay (area I). The model estimated that most movements occurred as a single pulse, which suggests that a migration-like behaviour could have been the causative factor.

Regardless of the motive, the lobster movements (mainly large adults see Fig.2) from an unfished offshore area into the shallower commercially fished bay is contrary to the general pattern of migration observed in spiny lobsters, since the paradigm is usually small immature lobsters moving offshore as part of their normal ontogenetic behaviour (Phillips, 2006; Melville-Smith & de Lestang, 2006; Briones-Fourzán *et al.*, 2003). Movements of juveniles and adults within the bay and towards offshore areas have also been documented in previous tagging studies in this area (Ley-Cooper *et al*., 2013), yet the migration of these large lobsters from the deep offshore towards the shallow bay had not previously been documented.

In a previous study conducted in Bahía de la Ascensión (BA) (see Fig 1), (Lozano-Álvarez, *et al* 1993) suggested that adult lobsters probably returned to that shallow bay after breeding in offshore areas of the deeper shelf. González-Cano (1991) analysed recruitment using size structure and catch data, suggesting that seasonal migrations from deep to shallow areas could occur annually as lobsters are re-distributed in Isla Mujeres (further north) (Fig 1). The latter study supports our findings in this assessment, but the use of a multi-state tag-recapture model as the one presented here had additional benefits, as it was able to provide an estimate of the proportion of the population moving into the bay, a measure that is particularly useful for conducting spatial stock assessments (McGarvey *et al.*, 2010; Goñi *et al.*, 2010; Ziegler *et al.*, 2003).

Lobsters which had previously been tagged in Bahía de la Ascensión (BA) have also been recaptured in Bahia Del Espíritu Santo. These movements took two years, with lobsters covering a distance of about 43.5 km (Ley-Cooper *et al.* 2013). Whether the lobsters tagged for this study originated in BA when they started to migrate remains unknown, yet the estimated 15-20% proportion indicates that recruitment into these fisheries from deep waters occurs, and that there is some level of offshore adult connectivity after 20 m depths between both bays of the SKBR.

This migration also provides new evidence for the potential maintenance or enhancement of fishing yields into areas which are adjacent to unfished reserves. In the two bays of the SK- BR maximum catch rates are observed as peaks at the beginning of the fishing season in July, and in the mid-season during autumn, between October and December (Sosa-Cordero *et al.*, 2008; Ley-Cooper *et al.*, 2013). Fishing exploitation rates are high within the shallow-bay area, and results of this study suggest that in order to sustain such high catch rates in autumn, lobsters recruited to these fisheries must be partially replenished by both juvenile growth (moulting from undersize to legal sized lobsters) (Lozano-Álvarez *et al.*, 1993; Lozano-Álvarez *et al.*, 1991b; Ley-Cooper *et al.*, 2013; Briones-Fourzán *et al.*, 2007; González-Cano, 1991), and by the input of lobsters moving in from unfished areas found offshore in deeper waters (>20 m). The contribution to catch rates within Bahía del Espíritu Santo that were derived from growth, movements, natural and fishing mortality had been previously explored and reported (Ley-Cooper *et al.*, 2013; Sosa-Cordero *et al.*, 1999), yet the proportion of migrating lobsters from the deeper unfished areas had not been estimated, or described as a source of recruitment.

The significant difference in the size composition of lobsters between the deep unfished and shallow fished areas may be attributed either to ontogenic movements such as juvenile progressive growth and migration offshore (Lozano-Álvarez *et al.*, 1993) and/or the high rates of fishing mortality of legal sized lobsters which only occurs within the commercially fished bay, since causes of natural mortality are generally independent of depth and most likely similar in both areas (Ley-Cooper *et al.*, 2013).

A number of factors could have biased our estimates of migration in this study, including the relatively small sample size of recaptured lobsters. It would be advantageous, should the study be repeated, if a significantly greater number of lobsters were to be tagged. Tag loss is also an area where a bias may be incorporated. The rate of tag loss used in this study was based on that determined from aquaria trials and therefore may not directly mimic that which may have occurred in the reserve during our study. Different water quality, lobster densities and habitat availability all could have caused the tag loss rate to have differed. A decreased rate of tag loss would have biased our results and increased the estimate of the proportion of lobsters migrating. Future work in this area could include the double tagging a number of the individuals released to examine *in situ* tag loss.

Although tags continued to be returned during the following season (2012/2013), their numbers were too low to be added into the model. The two tags returned at the start of the second season may have been from lobsters that migrated into the bay either during the closed season (February–June) or during the previous October (2011) and survived fishing mortality during the remainder of that season. It is interesting that no other tagged lobsters were recaptured within the bay until November 2012, five months into this second season, at a point when over 70% of the season's annual catches had been landed. It is possible that the lobsters recaptured in November 2012 and January 2013 did not enter the bay during

October 2011, but rather during a second autumn migration occurring in the October/November 2012. The lack of robust information provided by these 2012/2013 tag returns highlights the value of continuous studies of this nature. A series of yearly multi-release tagging campaigns in both the fished and unfished areas is recommended for the future, which could provide annual estimates of the overall biomass contributed to the fishery by the lobsters migrating into the bay.

According to the model produced in this study the larger proportion of the deep segment of the population remains unfished, and we suggest that in the SKBR the deep areas (>20 m) should remain as such. In order to guarantee a sustainable management of this fishery and the conservation of the *P. argus* lobster population, it would be advantageous to understand the variations on the yearly proportions of large lobsters moving from the unfished areas into the shallow areas subject to fishing, and the effects that this may have on the biomass of the total stock. It is recommended that these issues be further addressed in future studies.

References

Acosta, C.A. (1999) Benthic Dispersal of Caribbean Spiny Lobsters among Insular Habitats: Implications for the Conservation of Exploited Marine Species. *Conservation Biology,* **13,** 603-612.

Bertelsen, R.D. (2013) Characterizing daily movements, nomadic movements, and reproductive migrations of Panulirus argus around the Western Sambo Ecological Reserve (Florida, USA) using acoustic telemetry. *Fisheries Research* **144,** 91-102.

Bevacqua, D., Melià, P., Follesa, M.C., De Leo, G.A., Gatto, M. & Cau, A. (2010) Body growth and mortality of the spiny lobster *Palinurus elephas* within and outside a small marine protected area. *Fisheries Research,* **106,** 543-549.

Briones-Fourzán, P., Lozano Alvarez, E. & Eggleston, D.B. (2000) The use of artifical shelters (casitas) in research and hervesting of Caribbean spiny lobsters in Mexico In: B. Phillips & K. J. (eds.) *Spiny Lobster: Fisheries and Culture. 2nd Ed. Fishing New book-Blackwell.* Oxford, U.K.

Briones-Fourzán, P. & Lozano-Álvarez, E. (2001) Effects of artificial shelters (Casitas) on the abundance and biomass of juvenile spiny lobsters Panulirus argus in a habitat-limited tropical reef lagoon. *Marine Ecology Progress Series,* **221,** 221–232.

Briones-Fourzán, P., Fernández de Lara, V.C., Lozano-Álvarez, E. & Estrada-Olivo, J. (2003) Feeding Ecology of the three juvenile phases of the spiny lobster *Panulirus argus* in a tropical reef lagoon. *Marine Biology,* **142,** 855-65.

Briones-Fourzán, P., Lozano-Álvarez, E., Negrete-Soto, F. & Barradas-Ortíz, C. (2007) Enhancement of juvenile Caribbean spiny lobsters: an evaluation of changes in multiple response variables with the addition of large artificial shelters *Oecologia* **151,** 401–416.

Briones-Fourzán, P., Candela, C. & Lozano-Álvarez, E. (2008) Postlarval settlement of the spiny lobster Panulirus argus along the Caribbean coast of México: Patterns, influence of physical factors, and possible sources of origin. . *Limnol. Oceanogr., 2008,* , **53(3),** 970-985

Dubula, O., Groeneveld, J.C., Santos, J., van Zyl, D.L., Brouwer, S.L., van den Heever, N. & McCue, S.A. (2005) Effects of tag-related injuries and timing of tagging on growth of rock lobster, Jasus lalandii. *Fisheries Research,* **74,** 1-10.

Ehrhardt, N.M. (2008) Estimating growth of the Florida spiny lobster, Panulirus argus, from molt frequency and size increment data derived from tag and recapture experiments. *Fisheries Research,* **93,** 332-337.

Forcucci, D., Butler, J.M. & Hunt, J.H. (1994) Population Dynamics of Juvenile Caribean Spiny Lobster, *Panulirus argus*, in Florida Bay Florida. *Bulletin of marine Science,* **54 (3),** 805-818.

Frusher, S.D. & Hoenig , J.M. (2003) Recent developments in estimating fishing and natural mortality and tag reporting rate of lobsters using multi-year tagging models. *Fisheries Research* **65** 379–390.

García, C., Hernández, B., Baisre, J.A. & Cruz, R. (1991) Factores Climaticos en las pesquerías cubanas de langosta (*Panulirus argus*):su relacion con las migraciones masivas. *Revista Investigaciones Marinas,* **12,** 131-139.

Goñi, R., Quetglas, A. & Reñones, O. (2006) Spillover of spiny lobsters Palinurus elephas from a marine reserve to an adjoining fishery. *Marine Ecology Progress Series*, **308,** 207-219.

Goñi, R., Hilborn, R., Díaz, D., Mallol, S. & Adlerstein-González, S. (2010) Net contribution of spillover from a marine reserve to fishery catches. *Marine Ecology Progress Series,* **400,** 233-243.

González-Cano, J.M. (1991) Migration and Refuge in the Assessment and Management of Spiny Lobster *Panulirus argus* in the Mexican Caribbean. PhD Thesis, London: Imperial College in the Faculty of Science of the University of London. 114 pp

Herrnkind, W. (1980) Spiny Lobsters: patterns of movements; In J.S. Cobb and B.F. Phillips (eds.). *The Biology and Management of Lobsters. Physiology and Behavior, Academic Press NY,* **1,** 349-407.

Herrnkind, W. (1985) Evolution and Mechanisms of mass single file migrations in spiny lobster: Synopsis. *Contributions in Marine Science Florida State University Marine Laboratory,* **27,** 197-211.

Hilborn, R. (1990) Determination of Fish Movement Patterns from Tag Recoveries using Maximum Likelihood Estimators. *Canadian Journal of Fisheries and Aquatic Sciences,* **47,** 635-645.

Ley-Cooper, K., de Lestang, S., Lozano-Álvarez, E. & Phillips, B. (2013) Estimates of exploitation rates of the spiny lobster fishery for Panulirus argus from tagging within the Bahía Espíritu Santo "Sian Ka'an" Biosphere Reserve, Mexican Caribbean *Marine Biological Research*, **9,** 88-96.

Lozano-Álvarez, E., Briones-Fourzán, P. & Gonzalez-Cano, J. (1991a) Pesca exploratoria de langostas con nasas en la plataforma continental del área de Puerto Morelos, Q.R., Méx. *Anales del Instituto Ciencias del Mar y Limnología***,** 49-58.

Lozano-Álvarez, E., Briones-Fourzán, P. & Phillips, B. (1991b) Fishery Characteristics, Growth and Movements of the Spiny Lobster Panulirus argus in Bahia de la Ascención, México *Fishery Bulletin*, **89,** 79:89.

Lozano-Álvarez, E., Briones-Fourzán, P. & Negrete-Soto, F. (1993) Ocurrence and Seasonal Variations of Spiny Lobsters, *Panulirus argus*, (Latreille) on the shelf outside Bahía de la Ascensión, México. *Fishery Bulletin*, **US 91,** 808-815.

McGarvey, R., Linnane, A.J., Feenstra, J.E., Punt, A.E. & Matthews, J.M. (2010) Integrating recapture-conditioned movement estimation into spatial stock assessment: A South Australian lobster fishery application. *Fisheries Research*, **Volume 105,** 80-90.

Melville-Smith, R. & de Lestang, S. (2006) Spatial and temporal variation in the size at maturity of the western rock lobster *Panulirus cygnus* (George 1962). *Marine Biology*, **150,** 183-195.

Montgomery , S.S. & Brett, P.A. (1996) Tagging eastern rock lobsters Jesus verreauxi: effectiveness of several types of tag *Fisheries Research*, **27,** 141-152.

MRAG-Americas, (2012). MSC, Final Report and Determination for Sian Ka'an and Banco Chinchorro Biosphere Reserves Spiny Lobster fishery. http://www.msc.org/track-a-fishery/changes-to-our-fisheries-pages/certified/western-central atlantic/sian_kaan_banco_chinchorro_biosphere_reserves_spiny_lobster/assessment-downloads-1/20120703_FR.pdf

Phillips, B.F. (2006) Chapter 1 Growth and Development: Understanding Modelling Growth and Variability in Lobsters. In: *Lobsters Biology, Management, Aquaculture and Fisheries* Oxford , UK: Blackwell Publishing, pp.11-15.

R Development Core Team (2012) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL http://www.R-project.org/. Viewed on November 2012. Computer Program.

Ríos-Lara, V., Salas, S., Bello-Pineda, J. & Peniche, I. (2007) Distribution patterns of spiny lobster (*Panulirus argus*) at Alacranes reef, Yucatan: Spatial analysis and inference of preferential habitat. *Fisheries Research* **87,** 35-45.

Russ, G.R. & Alcala, A.C. (1996) Do marine reserves export adult fish biomass? Evidence from Apo Island, Central Philippines. *Marine Ecology Progress Series,* **132,** 1-9.

Russ, G.R., Alcala, A.C., P., M.A., Calumpong, H.P. & White, A.T. (2004) MARINE RESERVE BENEFITS LOCAL FISHERIES. *Ecological Applications,* **14(2),** 597– 606

Sharp, W.C., Lellis, W.A., Butler, M.J., Herrnkind, W.F., Hunt, J.H., Pardee, W.M. & R., M.T. (2000) The use of coded microwire tags in mark-recapture studies of juvenile Caribbean spiny lobster, Panulirus argus. *Journal of Crustacean Biology,* **20** 510–521.

Sosa-Cordero, E., Ramírez-González, A. & Dominguez-Viveros, M. (1999) La Explotación de Langosta *Panulirus argus* en Bahía Espíritu Santo, Quintana Roo, México: Un Estudio Descriptivo. *Proceedings of the 45th Gulf and Caribbean Fisheries Institute Charleston,* **45,** 820-839.

Sosa-Cordero, E., Liceaga-Correa, M.L.A. & Seijo, J.C. (2008) The Punta Allen lobster fishery: Current status and recent trends. *Case studies on fisheries self-governance.FAO Fish Tech Pap No 504, 149-162* No. 149-162 pp.

White, G.C. & Burnham, K.P. (1999) *Brithish Trust for Ornitology, Bird study* **46 (suppl.),** 120-139.

Ziegler, P.E., Frusher, S.D. & Johnson, C.R. (2003) Space–time variation in catchability of southern rock lobster Jasus edwardsii in Tasmania explained by environmental, physiological and density-dependent processes. *Fisheries Research* **61** 107–123.

Figure legends

Figure 1. Map showing Mexico and the study area called Bahía del Espíritu Santo, which is the southern bay of the Sian Ka'an Biosphere Reserve (the reserve area is identified by the rectangle on the map

insert). Bahía de la Ascensión is neighbouring to north, and the Caribbean sea to the east of the Yucatan Peninsula. Areas are marked as “I” the fished shallow bay (<20 m deep), and “II” the unfished offshore area (>20 m deep) respectively.

Figure 2 Graph showing the relative size frequency composition of *Panulirus argus* lobsters sampled within Bahía del Espíritu Santo, in the Biosphere Reserve Sian Ka’an- Mexico. Relative frequencies of carapace length (CL) in the fished shallow waters (<20 m) are depicted in light grey (top), and unfished offshore areas (depths > 20 m) in darker grey (bottom). The dotted line crosses the X axis showing the boundry between illegal and legal sized lobsters carapace length CL (74.5 mm CL).

Figure 3 Shows a series of maps focusing on Bahía del Espíritu Santo (Southern bay) and Bahía de la Ascensión (Northern bay), in the Biosphere Reserve Sian Ka’an Mexico. It shows where lobsters were released (dots) and recaptured (arrows point) for each month in which the tagging program took place. Arrows show the distance and direction of lobsters travelling from the unfished areas (>20 m) where they were tagged, into Bahía del Espíritu Santo.

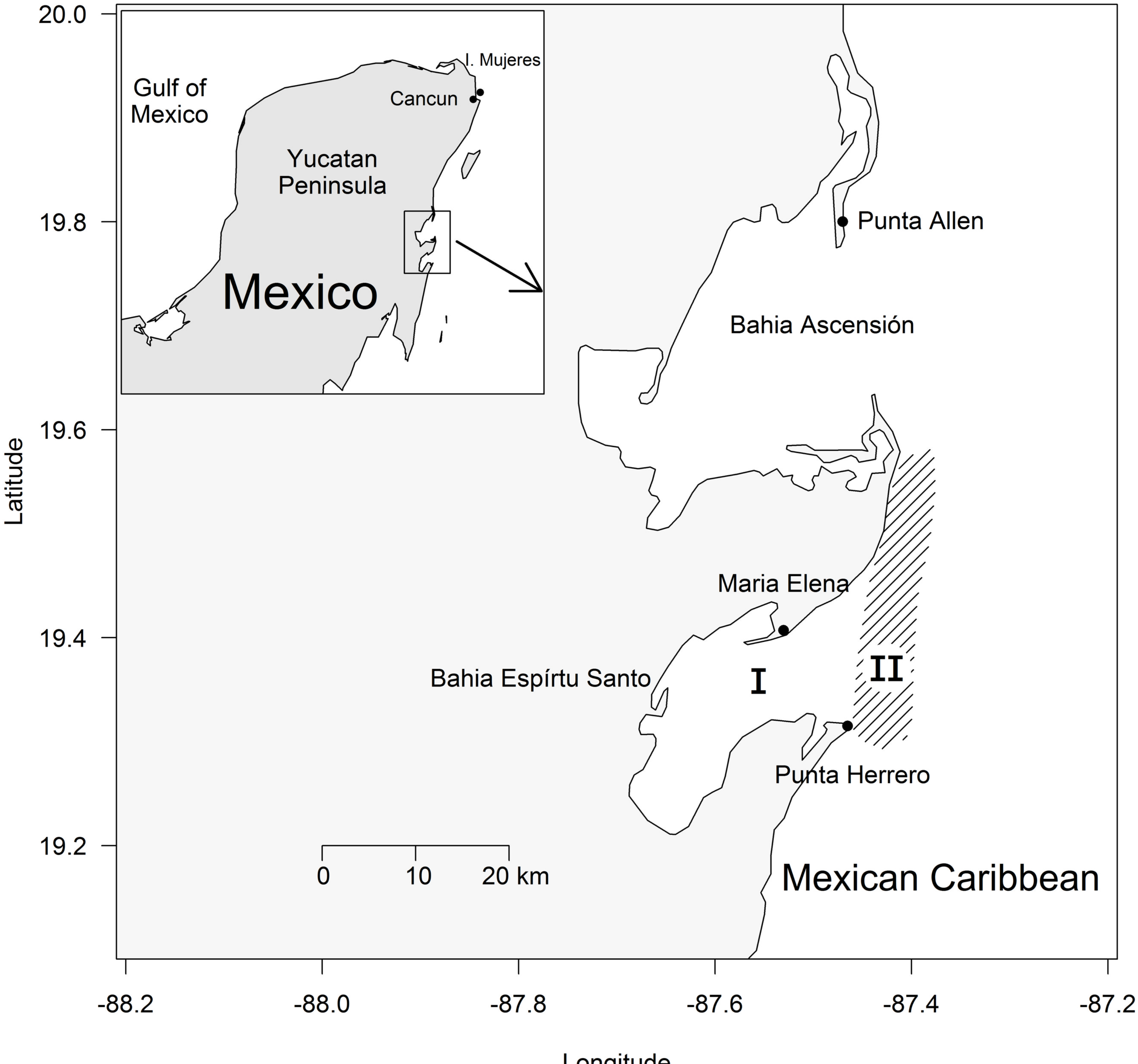
Figure 4 Results from the multi-state tag-recapture model modified from (Hilborn, 1990) and sensitivity analysis for the most likely exploitation rates and tag reporting scenarios.

(A) Left panel: Illustrates the most likely percentage of lobsters which migrate from the unfished-II areas towards the fished shallow bay -I, with a mean value of 20%, and range between 40 - 10%. Scenarios are based on data which replicate the observed tag recoveries under the most likely exploitation rates from the sensitivity analysis. The model simulations show that October is the month in which a most lobsters moved as in one pulse, with a very small probability of occurring in the other months (outliers are less than 2%).

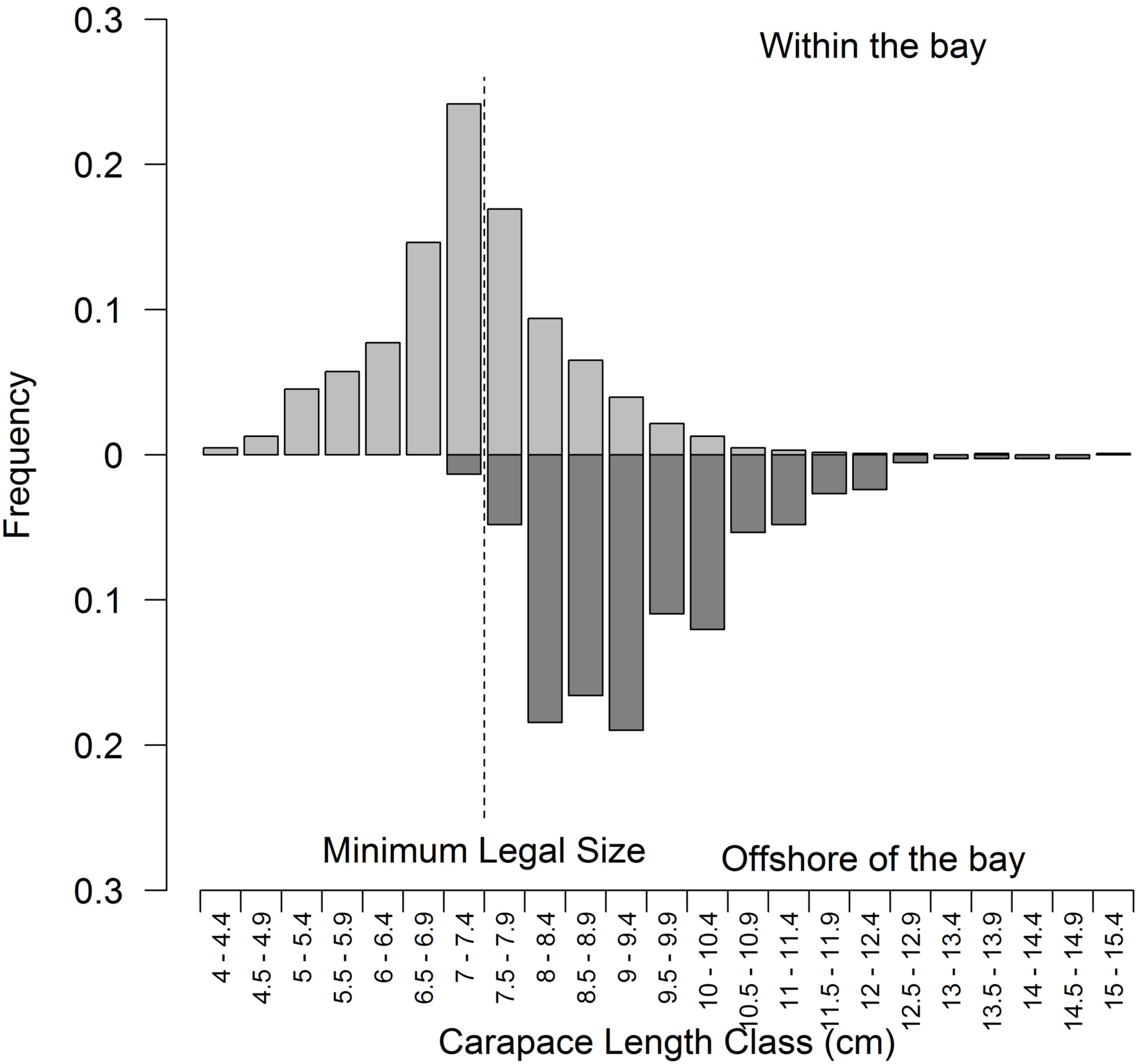
(B) Right panel: Illustrates the percentage of lobsters which have migrated from the deep unfished areas-II, towards the fished shallow bay -I, as a result of the scenario outputs derived from multi-state tag-recapture model based on tag recapture data. The span of range values used in the sensitivity analysis was

based on the most likely estimates for exploitation rates (0-40%) and tag reporting rates (60% and 80%) resulting in the simulation scenarios on the black and grey lines.

Figure 5: Shows the results derived from multi-state tag-recapture model which recreates the distribution of the tag recapture patterns observed in the fishery. Data was obtained from lobsters tagged in unfished areas-II offshore and recovered in the fished shallow bay-I in the study site of Bahía Del Espíritu Santo Sian Ka'an. The panels show the fitting of the observed against the predicted tag recapture patterns. The left panel corresponds to the batch of lobsters released during August and the right panel to the batch released in September within the unfished area-II offshore.



Gulf of Mexico
I. Mujeres
Cancun
Yucatan Peninsula
Mexico
Punta Allen
Bahia Ascensión
Maria Elena
Bahia Espírtu Santo
I
II
Punta Herrero
0
10
20 km
Mexican Caribbean
20.0
19.8
19.6
19.4
19.2
Latitude
-88.2
-88.0
-87.8
-87.6
-87.4
-87.2
Longitude



0.3
0.2
0.1
0
0.1
0.2
0.3
Frequency
Within the bay
Minimum Legal Size
Offshore of the bay
4 - 4.4
4.5 - 4.9
5 - 5.4
5.5 - 5.9
6 - 6.4
6.5 - 6.9
7 - 7.4
7.5 - 7.9
8 - 8.4
8.5 - 8.9
9 - 9.4
9.5 - 9.9
10 - 10.4
10.5 - 10.9
11 - 11.4
11.5 - 11.9
12 - 12.4
12.5 - 12.9
13 - 13.4
13.5 - 13.9
14 - 14.4
14.5 - 14.9
15 - 15.4
Carapace Length Class (cm)