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

Ley-Cooper Kim.[1*], de Lestang, Simon.[2], Phillips, Bruce. F.[1] & Lozano-Álvarez, Enrique[3]

[1] Department of Environment and Agriculture, Curtin University, Western Australia.

[2] Department of Fisheries, Western Australia.

[3] Reef Systems Unit at Puerto Morelos, Institute of Marine Sciences and Limnology, National Autonomous University of Mexico.

*Corresponding author:

MSc. Kim Ley-Cooper

Aquatic Science Research Unit, Curtin University of Technology, Brodie Hall Building, 1 Turner Avenue, Technology Park, Bentley, Western Australia 6102,

Phone: +52 15554381590. Fax +525555542015

e-mail: kim.ley@postgrad.curtin.edu.au

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ABSTRACT The Caribbean spiny lobster *(Panulirus argus)* fishery is currently being assessed for a certification process. It is the main economic activity within the Biosphere Reserve of Sian Ka´an-Mexico (SK), which is a marine protected area where restricted access fishing is allowed. In this study, commercial catch rates were examined, and lobsters over a wide size range were tagged throughout the 2010/2011 fishing season, to assess fishing mortality rates and movement patterns in Bahía Espíritu Santo-SK. Lobster tag recovery data were aggregated into two-week periods and analysed using a modified Brownie model that was parameterized to account for lobster tag-reporting, and the lobster tag-retention rates. This allowed the estimation of instantaneous rates of lobster natural and fishing mortality, considering catchability and fishing effort. Independent aquaria trials were conducted to better estimate lobster tag retention, tagging induced mortality and interviews with fishers were conducted to better estimate lobster tag reporting. Based mainly on legal-sized juveniles with fast growth rates found in casitas, the stock subject to fishing is limited to a maximum depth of 20 m, because of the prohibition of SCUBA diving and the use of other fishing gear. The Brownie model indicated that exploitation rates within this bay area were high, >0.94. Changes in catch per unit of effort and catchability throughout the season explain how the "casita/campo" system allows for a seasonal replenishment of juveniles and adults, which has kept the landings relatively stable for the past decade.

Keywords: lobster fishery; *Panulirus argus*; tagging, marine protected areas, exploitation rates

Introduction

The Caribbean spiny lobster *Panulirus argus* (Latreille, 1804) is widely distributed from the southern USA to Brazil and throughout the Caribbean (Butler et al. 2011). This species is the most valuable resource fished within the Mexican Caribbean, but there is still a lack of knowledge regarding the basic mechanisms and processes that determine the dynamics of the local populations which are part of the Caribbean's meta-population. Historically, spiny lobster fisheries have supported important commercial fisheries along the Caribbean, but increased fishing pressure has reduced lobster abundance, and currently most fisheries are being depleted (Ehrhardt et al. 2010).

This study was based in Bahía Espiritu Santo, which is located on the central coast of the State of Quintana Roo, in the Mexican Caribbean (Fig. 1). It is a shallow bay with an area of approximately 300 km^2 (Sosa-Cordero et al. 1999) with very similar habitat characteristics and oceanographic conditions to Bahía de la Ascensión (Lozano-Álvarez and Negrete-Soto 1991, Sosa-Cordero et al. 1998) which is to the north. Bahía de la Ascensión has been more thoroughly studied (see review by Briones-Fourzán et al. 2000, Sosa-Cordero et al. 2008). Both bays are within the Sian Ka´an Biosphere Reserve (SK), which is a protected area where the fishery is currently co-managed by federal government authorities such as the National Commission for Protected Areas (CONANP) and the National Commission for Fisheries and Aquaculture (CONAPESCA).

In Bahía Espíritu Santo, as in its neighbouring Bahía de la Ascensión (north), the community-based fishers are organized into cooperatives, and the lobster fishery is based on a ‘casita/campo” system. Casitas are large artificial shelters that can hold the full size range of lobsters. Casitas are made of cement, with a structural frame of approximately 1.8 x 1.2 m, raised about 10–15 cm above the bottom by two slabs along the longer sides. One or two shorter sides are fully open, allowing lobsters to freely enter and exit the shelter. Ownership of casitas within these bays is subject to an organizational scheme, which consists of partitioning the fishing areas into parcels (“campos”) allotted to individual fishers, which vary in size from areas of 3 km^2 to 20 km^2. A fisher does not own the campo (as ownership of any sea areas is forbidden by law), but he is free to deploy casitas within it, and hence he owns the casitas and manages his campo in a semi-ownership arrangement (Lozano-Álvarez *et al*. 1991, Briones-Fourzán et al 2000, Defeo and Castilla 2005, Sosa-Cordero *et al.* 2008). The fishers fish their campos using small boats (7 m long, 60 HP motor) and some GPS devices, and extract lobsters from casitas by skin diving, exclusively using hand nets or snares (Lozano-Álvarez et al. 1989, INE-SEMARNAT 1996, Lozano-Álvarez et al. 1993, Sosa-Cordero et al. 1998). Skin diving limits fishing to depths shallower than 15-20 m, (Lozano-Alvarez et al. 1991a, b; Sosa-Cordero 2003, Ley-Cooper 2006). Both the cooperatives licence and fishers individual permits are renewed annually, and cooperatives must comply with the federal fishing regulations: a closed season from March to June, a minimum capture size of 135 mm tail length (~74.5 mm carapace length, CL) (Lozano-Alvarez et al. 1991b) and a prohibition on the capture of ovigerous females, as well as specific park management rules, such as no-take zones. Internal regulations of the cooperatives forbid the use of SCUBA or hookah-diving, the use of lobster traps, and fishing in someone else's campo. Historically the semi-ownership of the campos has allowed self-surveillance and provided an efficient management arrangement for these fisheries.

Exclusive concession rights have been historically granted to three main fishing Cooperatives that have managed to maintain the total landings relatively stable in the last two decades (Sosa-Cordero et al. 2008). The age structure of caught lobsters showed a reduced adult mortality, since the catch consists mainly of sub-adult lobsters that inhabit the shallow fishing areas within the bays (Briones-Fourzán et al. 2000), whereas most of the adult lobsters inhabit deeper areas beyond the bays which are not fished (Lozano-Álvarez et al. 1993).

Despite the economic importance of the lobster fishery for the local communities, limited information exists on the lobster population dynamics and exploitation rates of lobsters in Bahía Espíritu Santo (Sosa-Cordero et al. 1999). In the present study, we implemented a mark-recapture programme to assess fishing and natural mortality of adults and sub-adult *P. argus* lobsters inhabiting this bay.

Materials and Methods

Pilot study: Examining Lobster Tag loss

Panulirus argus lobsters (> 74 mm CL) were collected at the study site of Bahía del Espiritu Santo, with hand nets. Lobsters were kept in sea cages for a few days and then transported to the Reef Systems Unit of the National Autonomous University of Mexico at Puerto Morelos. There, lobsters were distributed among three circular fibreglass tanks (3 m in diameter and 0.9 m in height), covered with a dark mesh netting for shading, and supplied with a continuous flow-through seawater system that maintained water temperature and salinity. Each tank contained one or two relatively small casitas to provide shelter for the lobsters.

Other than being fed frozen molluscs and shrimp every three days, the lobsters remained undisturbed for a 10-d acclimatization period. After this period, lobsters were measured (CL, from between the rostral horns to the posterior edge of the cephalotorax) using vernier callipers (± 0.1 mm) and sexed based on dimorphic characters. Lobsters were tagged with plastic T-bar anchor tags of 50 mm in length (Hallprint, Australia) inserted into the tail extensor muscle between the posterior edge of the carapace and the first abdominal segment using a tag applicator. The applicator needle was sterilized in 100% ethanol before each subsequent tagging.Twenty-six and 32 lobsters were tagged in two separate tagging trials. The first trial lasted for 135 d, and the second trial lasted for 195 d. Throughout these periods, the tanks were examined daily for dead lobsters and loose tags. Every 2–3 weeks the lobsters were re-measured and examined daily for the presence and condition of their tags. Although these operations may have disturbed lobsters and/or caused tag shedding, tags that were lost were usually recovered on dates not related with those in which these operations were performed.

The lobster tag-recapture model (see below) runs on a monthly timescale and requires a single average lobster tag-loss proportion in each time-step. Therefore, to obtain a monthly average tag loss, the proportion of tagged lobsters in the aquaria each day was averaged by 30-d periods (Fig. 2). The average monthly proportion of tagged lobsters was then described by a exponential decay equation for input into the tag-recapture model (Fig.2).

We did not differentiate between tag-shedding, natural mortality resulting in the tags to be lost, and tagged induced mortality because for the purpose of the model, the important factor was the proportion of lobsters that remained tagged after a specified time.

Brownie Model

Lobster Tagging Protocol

Lobsters were captured from "casitas" across the bay and lagoon areas of Bahía Espíritu Santo (1–7 m in depth) by using hand nets and carried back to the boat for tagging. Lobsters were tagged in the same manner as the tag-loss trials. The tag number, tagging date, location, sex and carapace length were recorded for each tagged lobster and then the lobster was immediately returned to the same casita. Tagging was conducted in June (during the closed season) and in July, September and October 2010 (during the fishing season). Only lobsters ≥ 44.0 mm CL were tagged to reduce incidental mortality (Lozano-Alvarez *et al.* 1991b), with the majority of tagged lobsters being >60 mm CL.

Estimating the reporting rate

The tagging program was advertised widely and included a reward system to encourage lobster tag returns. Throughout the July 2010 to February 2011 fishing season, two technicians were in frequent contact with fishers and administrators of the two cooperatives that fish at Bahía Espíritu Santo. Fishers were interviewed weekly to discuss the progress of the study and to prompt them to continue to report tagged lobsters. During these interviews, the fishers were asked whether they had caught but not reported tagged lobsters and, if so, to provide at least information on the tag numbers. Because of the high level of interaction between researchers and fishers the tag-reporting rate was considered to be 100%.

Mortality estimates

Instantaneous rates of fishing and other mortality for *P. argus* in Bahía Espíritu Santo were estimated using a Brownie model (Brownie et al. 1985) that was modified to allow for the incomplete mixing of tagged lobsters during the first period of recapture and to incorporate fishing effort data (Hoenig et al. 1998) (Table 1). These modified attributes of the Brownie model were important as they accounted for the behaviour of *P. argus* after tagging. Since previous tagging work in Bahia de Ascención (Lozano-Álvarez et al. 1991b) was unable to determine whether natural mortality or emigration were the cause of tag-loss, our model assumes that mortality other than that due to fishing is a combination of natural mortality and emigration.

Because tagged lobsters were returned to the same casita from which they were captured, initially all tagged lobsters were heterogeneously distributed throughout the bay. However previous studies showed that lobsters actively move between casitas (Briones-Fourzán et al. 2000, Briones-Fourzán and Lozano-Álvarez 2001), and that one month after tagging the distribution of tagged lobsters throughout the bay could be considered more homogeneous (Lozano-Álvarez et al. 2003). The re-parameterisation of the model accounts for this initial non-mixing of tagged and untagged lobsters by applying a specific non-mixed estimate of catchability ($\hat{q}_j$) for all lobsters recaptured with a liberty time of less than two months.

In the modified model, other forms of mortality (eg. natural mortality, emigration) were assumed to remain constant over the entire fishing season, whereas catchability (q) was allowed to vary between months. Estimates of the instantaneous rate of fishing mortality (F) were determined as $F = qE$. Catch and effort data were collected from the fishing cooperatives landing logbooks and verified against data from tax declaration forms. All catches were converted to whole weights (kg) using a conversion factor based on the relationship between tail weight and whole weight previously reported by Lozano et al. (1991b). The unit of effort used was fishing trip adjusted to a monthly proportion of the entire seasons fishing effort.

The lobster tag-recovery data were analysed using a Brownie model (Brownie et al. 1985) as modified by (Hoenig et al. 1998) and described in this paper. The model was constructed in R (R Development Core Team 2010) with its Log-Likelihood maximised using a Nelder-Mead method in the optimum routine (Nash 1990, Nelder and Mead 1965)

Results

Examining lobster tag loss and tag reporting rates

In both trials, the rate of average monthly lobster tag loss for each trial was initially rapid before progressively lessening through time until the end of the experiments, 4.5 and 6.5 months later respectively (Fig. 2). The relationship between the number of months after release (time at liberty) and the proportion of lobsters retaining tags was better described by an exponential decay (Akaike's An Information Criterion (AIC) = –23.2, $r^2 = 0.86$) rather than by a linear relationship (AIC = -18.9, $r^2 = 0.8$) (Sakamoto et al. 1986). The exponential decay relationship describing the monthly proportion of tags remaining on lobsters 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.

Brownie model

Tag recaptures

During the first two months of the fishing season, the fishers actively contacted research staff and submitted all requested information. However many became less interested from about the third month of the season, and had to be prompted to provide the data. The cooperatives retained all information and passed it onto researchers every month. Fishers had three opportunities to search for tags before handing lobsters to third parties: a) when catching them by free diving, b) when taking them from personal cages to where they are weighed, and c) when weighed at the cooperatives headquarters for sale.

In total, 786 lobsters were tagged throughout the Bay of Bahía Espíritu Santo, of which 268 (34%) were recaptured, with most recaptures occurring at the beginning of the fishing season from July through September (Table 2). Many lobsters that were recaptured in July and August had been released near the point of recapture (see Fig. 1), whereas many lobsters that were recaptured from October to December were found near the coral reef areas located east of the bay. These lobsters travelled distances ranging from 1.3 to 18.2 km within the bay. However, five lobsters that were originally tagged in Bahía de la Ascensión on April 2010 as part of a separate study (Lozano-Álvarez et al. unpublished data) were recaptured in Bahía Espíritu Santo. These lobsters travelled an average of 43.5 km in a southward direction.

Fishery Catch and Effort statistics

In Bahía Espíritu Santo, the monthly catch (whole weight) and effort (fishing trips) showed slightly different trends over the course of the fishing season (Fig.3). Effort decreased progressively from its maximum value in the first month of the fishing season (July 2010) to its minimum level by December 2010 and then remained relatively constant through to the end of the fishing season (February 2011) (Fig.3). Catch declined after the first month, and then increased over the next three months before decreasing again to stabilize at a low level (Fig.3). The catch per unit of effort (CPUE) began in July near maximum levels at 50 kg/trip before decreasing to the lowest level of 28 kg/trip the following month (August) (Fig. 3). Catch rates subsequently improved over the next three months to a maximum catch rate of 52 kg/trip in November before declining slightly to between 35 and 46 kg/trip from December to February 2011 (Fig. 3).

Lobster Tag recaptures and estimates of Exploitation rate

A 34% recapture rate allowed for a good estimation of the fishing parameters and criteria for outputs of the model. Tagged lobsters that were released in the four discrete pulses (June, July, September and October) were recaptured in large proportions, i.e. 33, 39, 100 and 29 %, respectively. The Brownie model estimated the monthly levels of exploitation required to reproduce similar proportions of tag-recaptures and the numbers of tags never seen again (NSA) (i.e. never recaptured) (Table 2, Fig. 4). The numbers of NSA tags were relatively high for the first, second and fourth tag release pulses since large numbers of lobsters were released in these pulses and only a fraction of lobsters were recaptured (Table 2, Fig. 4).

A residual plot of the model fit to the observed data indicated that the model was able to closely reproduce the pattern of tagged lobster recaptures with the error in the model estimates being evenly distributed (unbiased) between the four tagging/release periods and nine recapture periods (Fig. 5).

Model estimates of relative catchability differed dramatically between those representing unmixed ($\hat{q}$) and mixed catchability for the same time periods (eg. 0.99 and 6.47 (unmixed) versus 1.89 and 2.47 (mixed) in July through September, respectively). Estimates of relative catchability (q) remained fairly constant between July 2010 and November 2010, with a tight fit of values and their standard errors (see inset in Fig. 6). Mean catchability (q) increased in the last three months of the fishing season although the confidence intervals for December and January continued to overlap those of earlier months. Estimates of monthly exploitation rates showed a slightly different pattern than those of catchability. Exploitation rates ranged between 0.22 and 0.35 with highly overlapping confidence limits in all months (Fig.6). The total exploitation rate (the cumulative sum of monthly exploitation) and average rate of other mortalities estimated by the model were 0.94 and 0.24.

Discussion

The difficulty in holding lobsters in captivity for a long period limited the number of lobsters that we used for estimating tag loss. In addition, the potential effects of the behaviour, moulting, and the size and sex of lobsters on tag shedding have not been explored. Although further studies taking into account these factors may provide more information on the lobsters shedding of tags and lobster tag-induced mortality (Ehrhardt 2008), the data on "tag loss" that we obtained during the tank trials lies within the range obtained in previous studies on other lobster species (Montgomery and Brett 1996, Dubula et al. 2005). Considering that the trend in tag-loss in both trials followed the same pattern after time-step 4 (as shown in Fig. 2), the equation for tag loss would be valid for the time-steps remaining after the experiment was suspended; therefore, the longer period for field recaptures would be unaffected in the model.

The monthly tag loss obtained from the tank trials indicated that over time there is an exponential-like loss of individuals from a tagged *P. argus* population. Other lobster species, patterns showing an abrupt initial "tag loss" in the first few weeks post-tagging have been attributed to tag-induced mortality (Dubula et al. 2005) and tag shedding (Montgomery and Brett 1996). In our tank experiment, we observed that tag loss in lobsters was also associated with molting activity and occasionally with cannibalism of lobsters about to molt or recently molted. The latter behavior can reflect stress associated with conditions of captivity (Moriyasu et al. 1995, Lozano Álvarez 1996). However, tag loss because of these factors could be lower in natural habitats, where lobsters about to molt may isolate themselves.

Non-linear mortality patterns among tagged lobsters that were initially greater and then comparable to the control (untagged lobsters) were reported by Montgomery and Brett (1996).

They concluded that tagging causes only a short-term increase in mortality but is not significant in the long term when compared to the effects of natural mortality. This precedent supports our case in which an exponential decrease in tag loss (as is shown in Fig. 2) is representative.

Having a continued presence of observers on the field, along with a reward-based, tagged lobster reporting scheme, should be comparable to high-reward tagging studies that have shown it is possible to determine an exploitation rate from the tagged lobster recovery rate (Hoenig et al. 1998). The increase in likelihood of fishers not reporting tags as the months advanced was not a concern in this study for the above reasons. The model under this scheme is hereby considered an effective mortality estimation tool.

We assumed that it would take approximately two months for newly tagged lobsters to disperse and fully mix with the rest of the population. Consequently, our non-mixing model was developed to account for these differences, because tagged lobsters were immediately placed under the same casita in which they were found, and considering that they exhibit a certain degree of shelter fidelity because of their foraging and gregarious behaviour (Briones-Fourzán et al. 2007).

The model estimated that all other sources of mortality had a rate of 0.24 ± 0.02 (mean ± SE). This estimate represents all removals of lobsters by factors other than fishing, tag loss or tag induced mortality, such as natural mortality and emigration. Since none of the tagged lobsters were recaptured outside of the bay, and very few were recaptured in the outer reef area, it is likely our estimate is a measure of predominately natural mortality. This estimate is well within the range of other estimates form in *P. argus* in the Mexican Caribbean (Lozano-Álvarez et al. 1991b, Lozano-Álvarez 1994, Arceo et al. 1997, Arce et al. 2001, Sosa-Cordero 2003, Sosa-Cordero et al. 2008) This natural mortality rate, in conjunction with a total annual exploitation rate of 0.94, imply a large amount of recruitment (growth and/or immigration) must occur within this bay to maintain catch rates throughout the fishing season.Thus suggesting that throughout the 2010-2011 fishing season, all legal-sized lobsters found within the bay and at depths <20 m (depth limit for free-diving) were fished. It remains to be determined whether lobsters found deeper than 20 m have an effect on the dynamics related to the yearly casita replenishment processes.

In Bahía de la Ascensión, the highest annual CPUE (kg tail weight per boat per day) in the fishery also occurs in July, at the onset of the fishing season, and declines sharply during the rest of the fishing season. This trend has been mainly attributed to the combined effects of natural and fishing mortality (Lozano-Alvarez et al. 1991b). According to Sosa-Cordero et al. (2008) fishing effort tracks the catch trajectory, an indication that fishers reduce their activities (and hence their costs) when the local lobster resource is scarce. That is, the annual CPUE reflects fishing efficiency rather than resource abundance. This notion may also explain why, in Bahía Espíritu Santo, despite a relatively constant monthly catch from August to November, CPUE values showed an increasing trend during this period (see Fig. 3). In particular, the high levels of CPUE during October and November may be associated with the onset of the "Nortes" (cold fronts arriving from the north), which may increase movements of lobsters into the bay (Lozano-Álvarez et al. 1993) and the potential for casita replenishment. This is also suggested by the recapturing in Bahía Espíritu Santo of five lobsters that were tagged outside of the bay (Lozano-Álvarez et al. unpublished data).

At Bahia Espíritu Santo, the regulations on fishing gear result in a limited access to the deep lobster stock (> 20 m), where reef areas and a high proportion of reproductive adults are found (Lozano-Álvarez et al. 1993, Ley-Cooper 2006). Results from the non-mixing tagging Brownie models analysis presented here, imply that to sustain a 0.94 annual exploitation rate of the population subject to fishing, there must be a constant source for lobster replenishment into the casitas found within this bay.

A fishery with a management scheme based on casita/campo system may well be functioning as an artificial refuge area that increases abundance and population density from several sources, such as larval recruitment, enhanced juvenile survival and growth (Briones-Fourzán et al. 2000, Briones-Fourzán et al. 2007) and adult attraction of lobsters migrating inshore and south during the early winter and closed season (Herrnkind 1980).

A trend observed is that as the fishing season advances from July to February, the CPUE does not decrease substantially, yet total landings do so, while fishing mortality (F) remains relatively stable. These results suggest a continuous input of lobster biomass into the casitas that is clearly higher during the closed season, potentially explaining the peak in catch at the beginning of the fishing season (Lozano-Álvarez et al. 1991b, Lozano-Álvarez et al. 1993). However, as the season advances, lobster availability decreases as indicated by the increase of catchability of tagged lobsters (see Fig. 6). Periodic and yearly casita replenishment shows the need for assessing the proportion of the lobster stocks dwelling outside the bay (Lozano-Álvarez et al. 1989, Lozano-Álvarez et al. 1993, Sosa-Cordero et al. 1998, Ley-Cooper 2006).

An option for dealing with non-mixing models is to increase the number of recaptures and tagged lobster reporting rates or to use a model that assumes the period of non- mixing lasts for less than a year. We have provided a type of model intermediate between the Brownie-like models and exact time of recapture models (see Hearn 1986, Hearn et al. 1987) considered to apportion the total recaptures from a cohort to sub-annual two month periods. We have determined an expression for the expected value for each cell of the recovery matrix and raised the expected value to the observed number in the cell, as suggested by Hoenig et al. (1998). In addition to increasing the precision of the estimates, this type of model enables one to estimate the fishing mortality in the first time step of the study and consider a solid statistical theory captured in the Hoenig et al. (1998) models. More definitive information on emigration and the tagged lobsters reporting rate would be very valuable.

Acknowledgements

This project was partially funded by Colectividad Razonatura A.C., MAR Fund, FANP-FMCN and a scholarship (No. 202251), provided by CONACYT to KLC. We thank Oscar Guzmán and Mara Ley for technical support in field work, and Fernando Negrete-Soto and Cecilia Barradas-Ortiz for their help in the tank experiments. Permits to study and collect lobsters were provided by CONANP and CONAPESCA. We greatly appreciate the field help from fishers from the cooperatives "Cozumel" and "José Ma. Azcorra", represented by Eduardo Pérez and Ruben Hoil respectively.

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Figure legends

Fig.1. Map of Bahía Espíritu Santo South of "Sian Ka´an" Biosphere Reserve Mexican Caribbean. The locations and numbers of lobsters tagged are represented by the numbers in the white circles. The small map insert shows the location of the bay within the state of Quintana Roo

Fig.2. Proportion of lobster retaining tags over time derived from experimental aquaria tanks using T-bar Hall print tags in two independent trials.

Fig.3. Catch per unit of effort (CPUE -Kg/trip) (top figure), Catch (t) [black circles] (bottom figure) and Effort (trips) [grey squares] (bottom figure), in each month of the fishing season from July 2010 to February 2011.

Fig.4. Observed (grey) and estimated (red) tag recoveries in each month of the fishing season from July to February with all non recovered tags represented on the right hand side of the plot (Never Seen Again: NSA).

Fig.5. Residuals from the Brownie model (observed - estimated).

Fig.6. Exploitation rate ± 1 standard error and relative catchability ±1 standard error (small insert) in each month of the fishing season from July 2010 to February 2011.

Tables

Table 1 Expected number of tag recoveries when additional lobsters are tagged and added to the population at the start of each fishing month. Symbols are as follows: N_j number of tagged lobsters released in month j; Φ probability of retaining a tag; λ tag reporting rate; q_j catchability of the lobsters in month j; $\hat{q}_j$ incomplete mixed catchability of the lobsters in month j; E_j proportion of seasons total effort in month j; M instantaneous rate of natural mortality.

	Expected recoveries in each month		
Month	1	2	3
1	$\frac{N_1\phi\lambda\hat{q}_1E_1}{\hat{q}_1E_1+M}\left(1-e^{-\hat{q}_1E_1-M}\right)$	$\frac{N_1\phi\lambda q_2E_2}{q_2E_2+M}\left(1-e^{-q_2E_2-M}\right)e^{-\hat{q}_1E_1-M}$	$\frac{N_1\phi\lambda q_3E_3}{q_3E_3+M}\left(1-e^{-q_3E_3-M}\right)e^{-\hat{q}_1E_1-q_2E_2-2M}$
2		$\frac{N_2\phi\lambda\hat{q}_2E_2}{\hat{q}_2E_2+M}\left(1-e^{-\hat{q}_2E_2-M}\right)$	$\frac{N_2\phi\lambda q_3E_3}{q_3E_3+M}\left(1-e^{-q_3E_3-M}\right)e^{-\hat{q}_2E_2-M}$
3			$\frac{N_3\phi\lambda\hat{q}_3E_3}{\hat{q}_3E_3+M}\left(1-e^{-\hat{q}_3E_3-M}\right)$

Table 2 Data represented in the input form for the Brownie model with rows and columns representing tag release and recapture respectively. NSA represents the tags Never Seen Again.

Tag Recaptures by Month											
Month	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Released	NSA
Jun	0	105	35	29	9	2	5	0	0	568	383
Jul		27	15	14	5	3	1	1	2	174	106
Aug			0	0	0	0	0	0	0	0	0
Sep				2	1	0	0	0	0	3	0
Oct					0	8	2	2	0	41	29