Research Article

Stock assessment of the red spiny lobster (*Panulirus argus*) caught in the tropical southwestern Atlantic

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ABSTRACT. The stocks of the red spiny lobster (*Panulirus argus*) (Latreille, 1804) in the Caribbean and in the Brazilian coast are of considerable economic importance. There are important genetic differences between the Brazilian and Caribbean populations, which support separated stock assessment. The present study provides an assessment of the Brazilian stock of *P. argus* using a biomass dynamic model based on a Bayesian approach. Assuming that the catch per unit effort is a valid index of relative abundance, the results of the analysis indicate that stocks have been heavily overexploited since the 1980s. The present-day scenario is pessimistic, and there is evidence that the stock may be close to collapse.

Keywords: *Panulirus argus*, red spiny lobster stock, assessment, biomass, production model, Bayesian analysis.

Evaluación del stock de la langosta roja (*Panulirus argus*) en la zona tropical del Atlántico sudoccidental

RESUMEN. Los stocks de la langosta roja (*Panulirus argus*) (Latreille, 1804) en el Caribe y en la costa de Brasil son de considerable importancia económica. Hay importantes diferencias genéticas entre las poblaciones del Brasil y del Caribe, que sustentan la evaluación de stocks separados. El presente estudio proporciona una evaluación de la población brasileña de *P. argus* utilizando un modelo dinámico de biomasa sobre la base de un enfoque bayesiano. Suponiendo que la captura por unidad de esfuerzo es un índice válido de abundancia relativa, los resultados del análisis indican que las poblaciones han sido fuertemente sobreexplotadas desde 1980. El escenario actual es pesimista, y hay evidencia de que la población puede estar al borde del colapso.

Palabras clave: *Panulirus argus*, langosta roja, evaluación de stock, biomasa, modelo de producción, análisis bayesiano.

INTRODUCTION

The harvesting of spiny lobsters is a traditional fishery activity in the Caribbean and adjacent areas of the western Atlantic Ocean. In recent years, the largest catches have been landed in Brazil, Cuba, and the Bahamas. While the fisheries of Cuba and the Bahamas are concentrated in the Caribbean, in Brazil, the activity occurs over a vast area of the western Atlantic, between 5°N and 20°S (Fig. 1), where lobsters are harvested by recreational, artisanal, and industrial fisheries. An estimate of 7,000 ton of spiny lobster has been landed in Brazil yearly over the past few decades (MPA, 2012).

Spiny lobster tails are Brazil's principal fishery export product, corresponding to an annual income of approximately 85 million dollars during the 2000's. In addition to the importance of this product for the country's balance of payments, Brazil's lobster fisheries are important employers, providing a large number of jobs, both directly and indirectly.

Three species of spiny lobsters are harvested within the study area the red spiny (*Panulirus argus*) (Latreille, 1804), smoothtail (*Panulirus laevicauda*) (Latreille, 1817), and brown spiny lobsters (*Panulirus echinatus*) (Smith, 1869). The present study focuses on *P. argus*, which corresponds to the bulk of the catch,
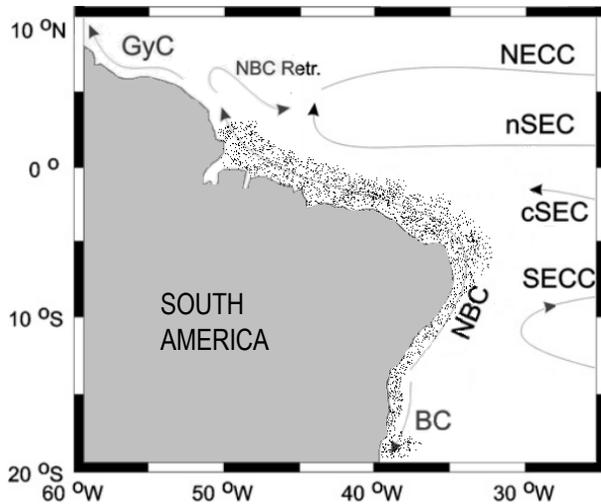

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Figure 1. Oceanic currents in the western Atlantic tropical region off South American coast. The Brazilian fishing grounds for the red spiny lobster (*Panulirus argus*) are indicated by the dotted area, adapted from Fonteles-Filho (1997). The configuration of the oceanic currents is adapted from Stramma & Schott (1999), Lumpkin & Garzoli (2005), and Rudorff *et al.* (2009). Guyana Current (GyC), North Equatorial Countercurrent (NECC), South Equatorial Current (SEC), South Equatorial Countercurrent (SECC), North Brazil Current (NBC), and Brazil Current (BC).

that is, an estimate of 5,000 ton per annum over the past few years (MPA, 2012).

The life cycle of *P. argus* is complex. The eggs carried by the females are released into open oceanic waters, where there is a long planktonic larval period (6 to 12 months) with a number of different phyllosomal phases (Lewis, 1951; Baisre, 1964). Subsequently, the animals reach the puerulus phase and migrate from oceanic waters to coastal habitats (Acosta & Butler, 1999), where they occupy shallow nursery areas for a further six to eight months (Farmer *et al.*, 1987; Kittaka, 1994; Cruz & Bertelsen, 2009). After this, as they begin to develop into juveniles and pre-adults, the lobsters migrate into deeper waters increasingly distant from the coast, where they mature and then mate, completing the life cycle (Cruz *et al.*, 2001).

The economic importance of the spiny lobster fisheries, and the growing evidence of the negative effects of the exploitation of stocks, led the Brazilian government to introduce measures for the management of the industry in the 1960's. Since this time, a number of different regulatory measures have been enforced, such as the establishment of a minimum legal body size for the commercial exploitation of lobsters, and limitations on equipment and harvesting seasons. However, the regulations have suffered many

alterations, in particular with regard to the restrictions on equipment and techniques. Currently, while lobster pots are permitted, fishing with driftnets and diving - free- or SCUBA-diving - are prohibited (IBAMA, 2008).

Up until the end of the 1990s, a number of analyses were conducted based on surplus production models (*e.g.*, Santos *et al.*, 1973; SUDEPE, 1978, 1985; Fonteles-Filho *et al.*, 1988; Paiva, 1997), with the aim of providing estimates appropriate for the development of effective management practices. More recently, Barroso (2012) and Cruz *et al.* (2013) produced new analyses based on the same type of models. In the vast majority of cases, the estimates produced by the models indicated that the maximum sustainable yields are equivalent to or greater than those recorded over the past decade. It is important to note, however, that all these studies were based on biomass dynamic models that assume equilibrium, which is not the recommended approach (Hilborn & Walters, 1992).

A number of estimates based on alternative models for Caribbean lobsters were produced by the Western Central Atlantic Fishery Commission (WECAFC) in the 2000s, most recently at the 2006 meeting. The resulting report (FAO, 2007) included the results obtained by Ehrhardt & Aragão (2007) for red lobster caught in Brazil, who used the ADAPT program (Gavaris, 1988), which permits the calculation of "analyses of virtual populations" based on the inclusion of auxiliary data. The results indicated intolerably high mortality at this time. Freire *et al.* (2007) subsequently published results obtained using an ecosystem model for two pooled spiny lobsters, which predicted that the stocks would be extirpated from the system within a few years, but it did not occur.

In all the preceding assessments, uncertainties were either ignored or, when recognized, were simply not included in the analyses. All the available estimates are deterministic and case-specific. It is important to note, once again, that all the estimates of management reference points ("maximum sustainable yield") were based on unrealistic assumptions of equilibrium. In the present study, these limitations are overcome. The analysis was based on a Bayesian biomass dynamic model with no assumption of equilibrium. The results are presented and discussed with the primary objective of outlining potential measures applicable to the effective fishery management of the red spiny lobster on the Brazilian coast.

MATERIALS AND METHODS

Data collection

The data analyzed in the present study were extracted from Silva & Fonteles-Filho (2011). This study

compiled the data on catches in Brazil for the period between 1955 and 2009. In addition to traditional lobster pots, the crustaceans are also harvested using illegal techniques such as driftnets and skin diving. Official CPUE values are calculated only for legal lobster pots, although the contribution of illegal techniques to total catch can be estimated based on exported tonnage (Lins-Oliveira *et al.*, 1993). Continuous data for effort (pot-days) and CPUE are available only for the period between 1965 and 1997, although isolated data are available for 2002 and 2004 (Silva & Fonteles-Filho, 2011). Estimates of effort are derived from the ratio between total catches and estimated CPUE. The data publish by Silva and Fonteles-Filho (2011) was obtained from the reports of the Brazilian government official institutions: the Brazilian Fishery and Agriculture Ministry (MPA) and the Federal Environment Institute (IBAMA).

Size composition data from 1970 to 1993 were kindly provided by Dr. Aragão (Instituto Brasileiro do Meio Ambiente e dos Recursos Naturais Renováveis – Ministério do Meio Ambiente – Brazilian Government). However, some of the size data samples seem biased because central trends of length distributions (*e.g.*, mean, median) increase at the end of the time series. This result contradicts other fishery indicators (*e.g.*, CPUE and effort) which suggest that fishing mortality also increased at the end of the time series. The available size samples need to be carefully revised before using it in stock assessment analyses; hence only catch and CPUE data were considered in this paper.

Bayesian stock assessment model

The observed data are represented by vectors with values for yields and abundance indices denoted by Y_t and I_t, respectively, where $t=1,…,N$ is the index for the year. Biomass dynamic models are the principal alternative available for stock assessment where only data on catches and abundance indices are available (Hilborn & Walters, 1992). The general equation for these models is:

$$B_t = B_{t-1} + g(B_{t-1}) - Y_{t-1} \qquad (1)$$

where B_t is the biomass at the beginning of year t; Y_t is the yield obtained during this year, and $g(B_{t-1})$ is the "surplus production" function.

The formulae of Schaefer (1954)

$$g(B_{t-1}) = rB_{t-1}\left(\frac{1 - B_{t-1}}{k}\right),$$

and Fox (1970)

$$g(B_{t-1}) = rB_{t-1}\left[\log\left(\frac{k}{B_{t-1}}\right)\right]$$

are usually used here, where k is the carrying capacity and r is the intrinsic growth rate of the population.

It is often assumed that a linear relationship exists between abundance index (I_t) and biomass, in which case the link between the unobserved state (B_t) and the observed abundance indices in the tth year can be represented by the equation:

$$I_t = qB_t \qquad (2)$$

where q is the catchability coefficient. Management reference points may be calculated based on the estimations of the parameters r, k and q. For example, whenever using Schaefer model, the "maximum sustainable yield", $Y_{MSY} = rk/4$, is attained with biomass $B_{MSY} = k/2$ and effort $E_{MSY} = r/(2q)$.

These calculations can be considered including uncertainties. Usually the observed series of data (I_t) is linked to the unobserved states (B_t) through a stochastic model. This version of the model is reparametrized by the calculation of the proportion of the annual biomass in relation to the carrying capacity ($P_t = B_t/k$)), which results in an improvement in the performance of the Gibbs sampler used in the Bayesian approach to generate the sample of the posterior distribution (Meyer & Millar, 1999). The equations may thus be written in the stochastic form, as:

$$P_t \mid P_{t-1}, k, r, \sigma^2 = \left[P_{t-1} + g(P_{t-1}) - Y_{t-1}/k\right]$$
$$t = 2,…,N \qquad (3)$$

and

$$I_t \mid P_t, q, \tau^2 = qkP_t e^{v_t} \qquad t = 1,…,N \qquad (4)$$

Where v_t is an independent and identically distributed (*iid*) normal random variable with mean 0 and variance τ^2. In the present case $N = 55$, given that the data series begins in 1955 and ends in 2009. In order to solve the above equations an initial biomass ($P_1 = B_1/k$) is required. The first biomass was assumed to be equal to the carrying capacity (k). This assumption is reasonable because catches were probably very low before the start of the commercial fishery. Furthermore, bias in the estimate of effort at *MSY* is not of concern under the assumption $B_1 = k$ whenever the observational error is used to fit the model (Punt, 1990).

If independent priors are assumed for the parameters of the biomass dynamic model (k, r, q) and for τ^2, the joint prior distribution is $p(k, r, q, \tau^2) = p(k)p(r)p(q)p(\tau^2)$. Informative or non-informative priors can be used here, depending on

the availability of information and knowledge on the species and the stock being analyzed, or even on similar species or stocks (McAllister *et al*., 1994; Punt & Hilborn, 1997; McAllister & Kirkwood, 1998). As no relevant data were found on these parameters in the literature, the priors used for analysis are non-informative or convey little information. Jeffrey's non-informative reference prior for q is independent of r and k, and is equivalent to a uniform prior on a logarithmic scale (Millar, 2002). Therefore, the uniform prior $U(-20, -5)$ on the logarithmic scale was used in the present study for q. For r and k, wide uniform priors that convey little information on the parameters were used. The uniform prior for k, with lower and upper limits defined in tonnes was $U(8500,300000)$. The lower limit is just a little over the maximum annual yield recorded for the species in the study area. The prior for r was $U(0,2)$, and τ^2 was $IG(2,1)$ Numerical Monte Carlo procedures can be used to obtain a sample of the joint posterior distribution. In the present study, a Markov Chain Monte Carlo (MCMC) algorithm was used, and the Gibbs sampler was implemented in the JAGS program (Plummer, 2005) available in the R program (R Core Team, 2012) with the *runjags* package (Denwood, 2009). Three chains were initiated with different initial values for the parameters. The first 2,000,000 values of each chain were eliminated as burning, and values were retrieved at every 1,000 steps (slice sampling) of the subsequent 3,000,000 steps of the chain, providing a set of 3,000 values of the posterior distribution for each chain. Deviance Information Criterion (DIC) (Spiegelhalter *et al.*, 2002) was calculated to compare models.

Diagnostics

Graphs and diagnostic tests were used to determine whether a stationary distribution had been reached. These analyses were run in the CODA library (Plummer *et al*., 2006). Gelman & Rubin's (1992) statistic was used for diagnosis. When the 97.5% quantile of the Potential Scale Reduction Factor (PSRF) was equal to or lower than 1.05 convergence was assumed. Autocorrelations were also used to evaluate the mixing degree of the samples of the posterior distribution.

Residuals and posterior predictive tests were evaluated to check the fits of the models. Posterior predictive test approach is described in Gelman *et al*. (1995). Lack of fit of data is measured by the tail-area probability, or Bayes *P*-value calculated by $\Pr[T(y^{rep},\theta) \geq T(y,\theta)\,|\,y]$, in which y^{rep} is a replicated data set calculated based on the posteriors of parameters θ, y is the data, and $T(y, \theta)$ is a test scalar quantity. In this work the test quantity is the slope of a

linear regression between year and CPUE series. The motivation was to assess if rough time trend of the predicted CPUE series is not much different of the time trend of CPUE calculated based on the data. Regressions were calculated for the period starting in a given x year until 2004, which is the very end of the CPUE time series. Values of x were between the first year to show up in the time series and 1997, which is the end of the continuous CPUE time series.

Sensitivity analysis

In the initial exploratory analyses, it was apparent that the models do not fit well to the CPUE data backward the beginning of 1970's. Hence, a sensitivity analysis was adopted, in which the models were fitted to full time series, and also to data from a given y year onwards. Different values of y close to the beginning of 1970's were used, but only two solutions ($y = 1969$ and $y = 1971$) are shown to not clutter. Hereafter full time series, data from 1969 (inclusive) onwards, and data from 1971 (inclusive) onwards are denominated as databases A, B, and C respectively.

RESULTS

Catch, effort and CPUE

Catches increased rapidly in the beginning of the commercial fishery reaching approximately 5,600 ton per annum in the 1970's (Fig. 2). Between 1970 and the mid-1980's, yields began to oscillate, but without any clear tendency of growth or decline. At the end of the 1980's, catches increased and remained at around 6,800 ton per annum until the mid-1990s, when there was an abrupt decline to values of less than 4,000 ton. Catches increased again between 1999 and 2004, followed by a decline. Between 2005 and 2009, annual catches were approximately 5,000 ton.

Continuous data on fishery effort are available only from the mid-1960's until 1997 (Fig. 2). Subsequently, data are only available for 2002 and 2004. Effort, based on the number of lobster pots used, increased in a virtually linear manner over the course of the period for which continuous data were available.

The relationship between fishing effort and CPUE is shown in Figure 3. While effort increased steadily over the years, CPUE decreased. Whereas CPUE was 800 ton per million pots-days (mpd) in the mid-1960s, it had decreased to 400 ton mpd^{-1} in the early 1970s, and continued at below 200 ton mpd^{-1} between the 1980's and the 2000's.

Model convergence and fits

Values of the 97.5% quantiles of the PSRF estimates were equal to or below 1.05 for both Fox and Schaefer
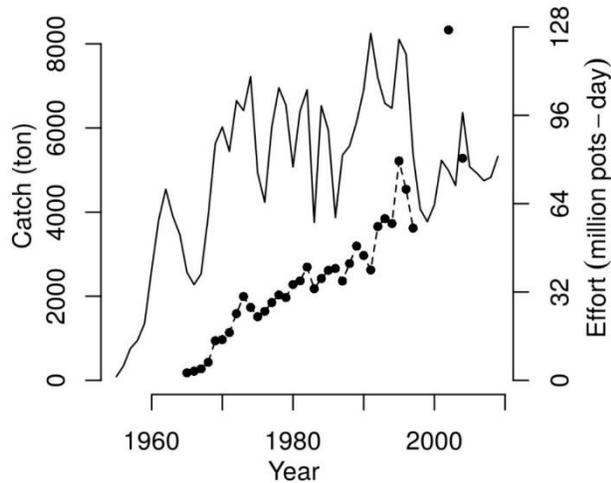
Figure 2. Fishing effort and catches of the red spiny lobster (*Panulirus argus*) off the eastern coast of South America between 5°N and 20°S. Source: Silva & Fonteles-Filho (2011).

Figure 3. Relationship between fishing effort and catch per unit effort (CPUE) for the red spiny lobster (*Panulirus argus*) harvested off the eastern coast of South America between 5°N and 20°S.

models; hence we assumed the models converged. Autocorrelation calculations for samples with lags larger than 12 were low for all the parameters (r, k, q and τ^2), which indicates good mixing in the chain and that the information carried by the subsequent values are not very redundant.

The models fittings and the credibility intervals as calculated based on the posterior distributions are shown in Figure 4. The fit based on the complete time series (A) is represented by the continuous line, with the area of the 99% credibility interval shown in light gray. The fits for the partial time series B (1969 onwards) and C (1971 onwards) are represented by dashed and dotted lines, respectively, with credibility intervals in darker gray. The credibility intervals overlap considerably, such that only the lower limits of the models fitted to the B and C time series are visible in Figure 4. Projections for years after 2004 are shown just for illustrative purposes. They are unconstrained because catch data are available until 2009, but CPUE data are not.

The expected CPUE values based on the posterior distributions calculated for B and C databases are very similar. The fits are all pessimistic as indicated by the monotonous negative slope of the curves, in particular in the case of the complete time series (A). However it is important to highlight that catch data are available for the end of the time series, but CPUE data are not. Hence predictions from 2005 to 2009 might be carefully considered because they are unconstrained. In general, the credibility intervals start including null values from the mid-2000s onwards, reinforcing the negative aspects of the scenario.
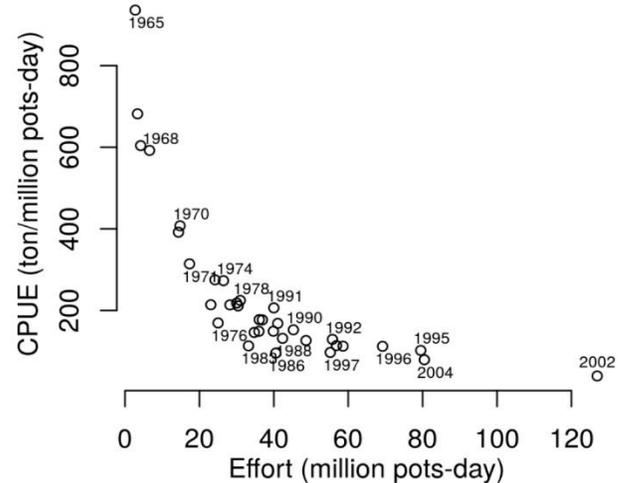
The distribution of the standardized residuals calculated from the 9,000 values (3 chains of 3,000 slice values) of the posterior distributions shown in Figure 5 reinforce the deficiencies of the models fittings to the CPUE of early years of the time series. The modal groups of the residuals greater than 2 correspond to the extremely high CPUE values observed in the years prior to 1971. Calculations of DIC of Fox model (dataset A: -568.831; dataset B: -538.681; dataset C: -510.996) were smaller than DIC of Schaefer model (dataset A: -563.451; dataset B: -536.390; dataset C: -510.093), which suggest there are support for Fox model.

Bayes *P*-values calculated based upon a test quantity $T(y,\Theta)$ concerning time trends of CPUE are shown in Figure 6. Major failures of the models correspond to *P*-values typically corresponding to extreme tail-area (*e.g.*, lower than 0.01 or higher than 0.99) (Gelman *et al*., 1995). Results for Fox models appear slightly better than those for the Schaefer models. However, all the models showed lesser failures which suggest they are useful though improvements are desired. The models poorly fits the CPUE in the very beginning of the time series, but the calculated *P*-values indicate that discrepancies between the coarse time series trends of predicted and of observed CPUEs are not large. In spite the models are not ideal, they were considered satisfactory in the light of the available data.

Posterior distributions

All the posterior distributions of r have positive asymmetry (Fig. 7a). Most of the samples of the posterior distribution of r are between 0.10 and 0.35
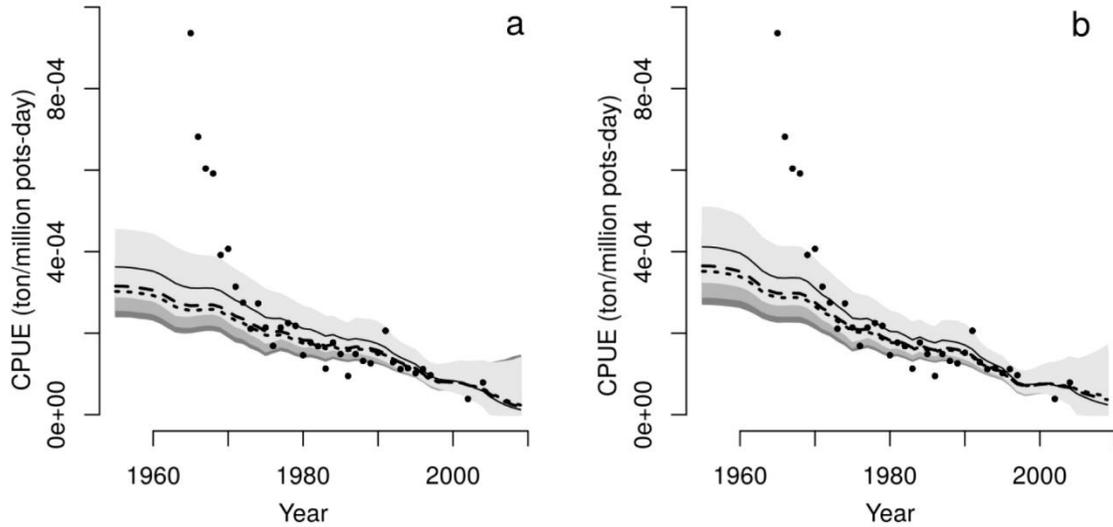
Figure 4. a) Schaefer and b) Fox model fittings. The continuous lines represent the means of the posteriors sample calculated for the complete data set, while the dashed and dotted lines correspond to the means calculated for the partial data sets, excluding records collected prior to 1969 and 1971, respectively. The area shaded in light gray represents the 99% credibility interval for the calculations based on the complete data set. This interval overlaps with those for the other data sets, shown in darker gray.
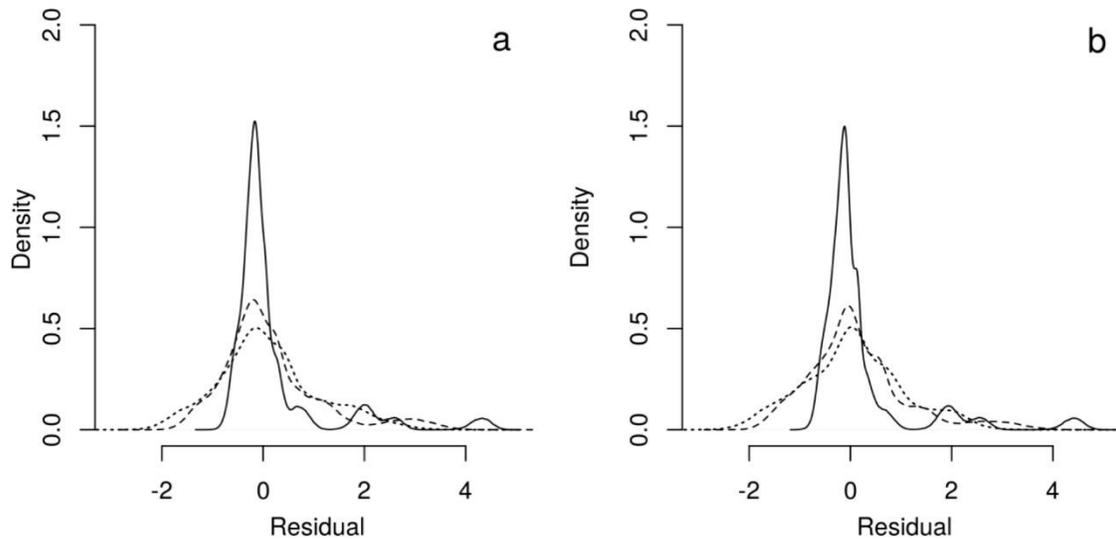

Figure 5. Standardized residuals of the a) Schaefer and the b) Fox production models. The continuous, dashed, and dotted lines correspond, respectively, to the complete, post-1968, and post-1970 data sets.

for both analytical models, although the Schaefer model generally produced higher values than the Fox model. The central tendency (*e.g.*, median) of the posterior distribution of r tends to increase as the CPUE's from the beginning of the time series are omitted. In other words, the medians for the C database are higher than those for B, which in turn are higher than those for A.

All the posterior distributions of k are wide and present positive asymmetry (Fig. 7b). The median values are between 79,900 and 94,300 ton. The only exception is the much higher value obtained using the data from the a database analyzed by the Schaefer model. In general, the medians calculated using the Schaefer model decrease as the data from the early years of the time series are omitted. Even so, once again,
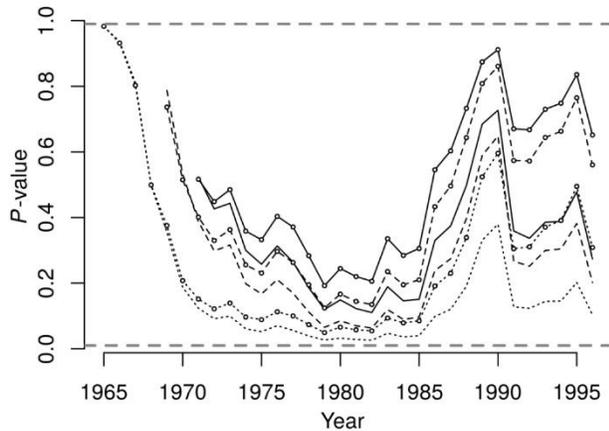
Figure 6. Bayes *P*-values calculated based on the test quantity that is a measure of discrepancy between the rough linear time trends of predicted and observed CPUEs. Regressions were calculated for different periods. The periods considered start in the years showed in the x-axis and end in 2004, which is the last year to show up in the CPUE time series. Dotted lines stand for full time series, while dashed and solid lines stand for the time series from 1969, and from 1971 onwards, respectively. Fox model results are indicated by lines with empty circles, while the other lines stand for Schaefer model results.

the estimates obtained using the Schaefer model are invariably higher than those produced by the Fox model.

All the posterior distributions presented for *q* are also characterized by positive asymmetry (Fig. 7c). Most of the posterior samples present values of between 2.5×10^{-9} and 7×10^{-9}. In this case, the medians are mostly higher for the Fox model and decrease when the data from the first years of the time series are omitted. The posterior distributions of τ^2 also show positive asymmetry (Fig. 7d). The medians also tend to decrease when the highest CPUE values of the early years of the time series are omitted, which would be expected, given the fact that τ^2 is the variance of the observational error.

Maximum sustainable yields and phase plots

The posterior distributions of the Y_{MSY} values are negative skewed and are centered on a value of 5,000 ton (Fig. 8). Once the initial data of the time series are discarded, the posterior distributions calculated for the Fox and Schaefer models are highly similar to one another. The one exception is the distribution calculated by the Schaefer model based on the complete data set, which presents the greatest dispersal and marked negative asymmetry.

For comparative purposes, the estimates of Y_{MSY} provided by previous studies based on assumptions of equilibrium, are indicated by letters in Figure 8. The estimates provided by the analyses presented here are clearly much lower than most of those found in these previous studies. The difference is especially pronounced when comparing the posterior sample of the present study with the value obtained by Cruz *et al.* (2013) for the data collected between 1974 and 1991 (Fig. 7d). The only estimate that is similar to the results of the present study is that provided by Cruz *et al.* (2013) calculated using data from 2000 to 2009 (E, in Fig. 8).

The expected mean values and 95% credibility intervals estimated from the ratio between observed annual yield (*Y*) and estimates of Y_{MSY} obtained using the Fox model are shown in Figure 9. As the results of the Schaefer model are closely similar, they are not shown here. There is marked positive asymmetry in the credibility intervals, as indicated by the position of the mean values close to the lower limit of the area shaded in gray. The results indicate that there was a very high probability of the catches being greater than the Y_{MSY} by the end of the 1960's. Between this point and the end of the time series, there is some oscillation, but there is a general tendency for catches to be much higher than the Y_{MSY}. Based on the Y/Y_{MSY} ratio, then, it is reasonable to conclude that overfishing began more than 40 years ago, and has continued to the present day.

Phase plots, such as that shown in Figure 10 (based on the results of the Fox model) are useful for the evaluation of the development of the lobster fishery industry up until the present day. If *MSY* is the reference benchmark the values of $F/F_{MSY} > 1$ and $B/B_{MSY} < 1$ indicate the points in time at which the stocks were overexploited. When $F/F_{MSY} \leq 1$ and $B/B_{MSY} \geq 1$, the scenario was more optimistic, in biological terms, with exploitation-based mortality being lower than *MSY*, and biomass higher than that of the *MSY*. The other two scenarios – $F/F_{MSY} > 1$ and $B/B_{MSY} \geq 1$ and $F/F_{MSY} \leq 1$ and $B/B_{MSY} < 1$ – represent intermediate situations. Based on the ratios F/F_{MSY} and B/B_{MSY}, it is possible to confirm that the commercial lobster fisheries that began in 1955 initially underexploited the stock, evolved over the subsequent years to an intermediate stage of impact. In 1982, the first signs of overexploitation appeared, based on the criterion of $F/F_{MSY} > 1$. From this point onwards, there has been some oscillation, but the predominant scenario is one of high levels of exploitation. After mid 1980's the fishery moved rapidly towards an extremely pessimistic situation by 1992. Overexploitation levels increased until mid 1990's. In spite there was a reduction in the exploitation pressure in the subsequent years, in the end 1990's the biomass is well below *MSY*,
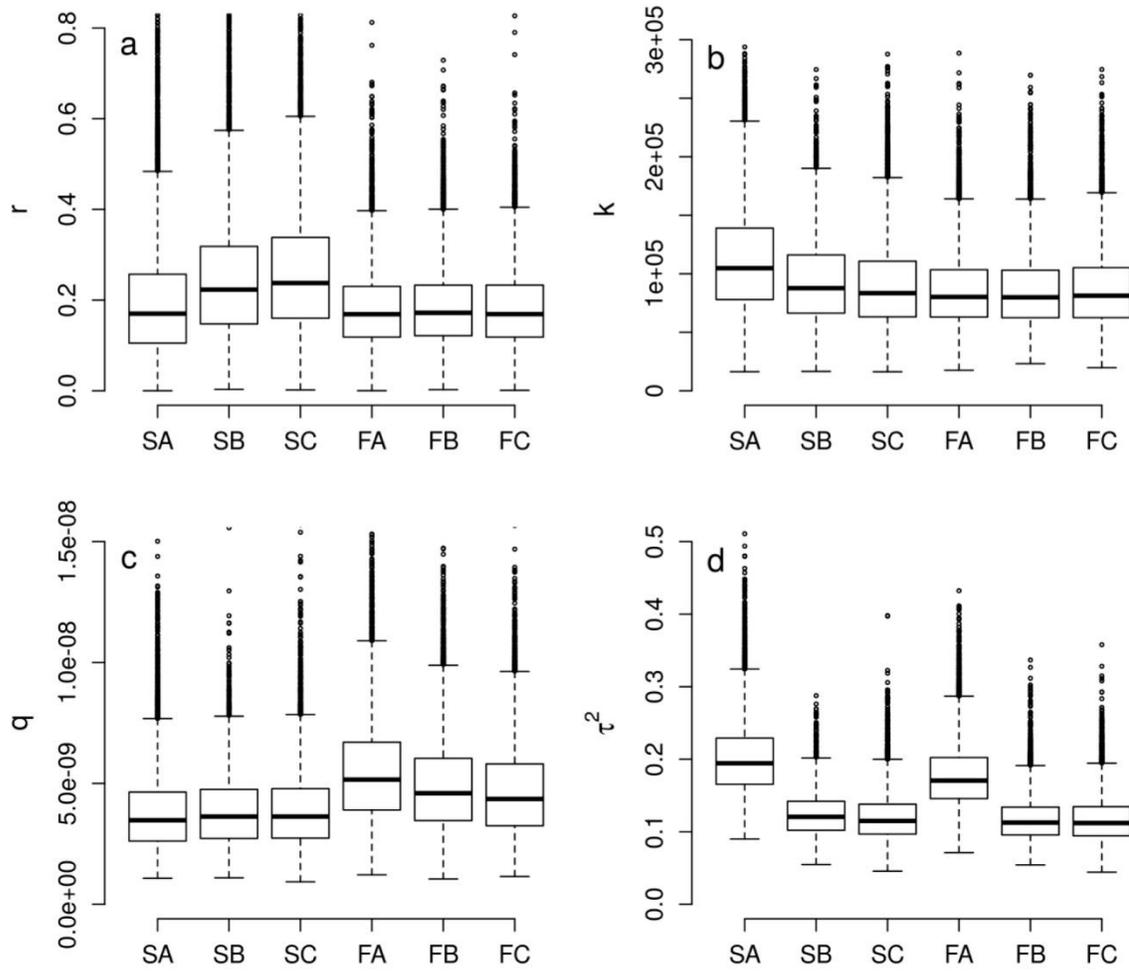
Figure 7. Marginal posterior distributions for the parameters a) *r*, b) *k*, c) *q* and d) τ^2. The fits for the Schaefer model are indicated by the letter "S", and those for the Fox model by the letter "F". The data sets analyzed were a) complete time series, b) post-1968 time series, and c) post-1970 time series.
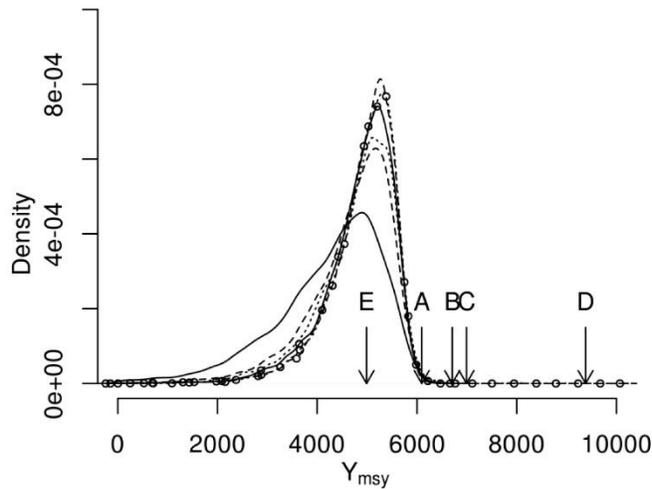

Figure 8. Densities of the posterior distributions of Y_{MSY} calculated with the Schaefer and Fox production models. The latter are indicated by overlapping lines and circles. The data sets analyzed were complete time series (continuous line), post-1968 time series (dashed line), and post-1970 time series (dotted line). Arrows stand for punctual estimations of Y_{MSY} calculated by Fonteles-Filho (1992) (A), Paiva (1997) (B), Fonteles-Filho (2007) (C), Cruz *et al.* (2013) based on data collected between 1974 and 1991(D), and Cruz *et al*. (2013) based on the data from 2000 to 2009 (E).
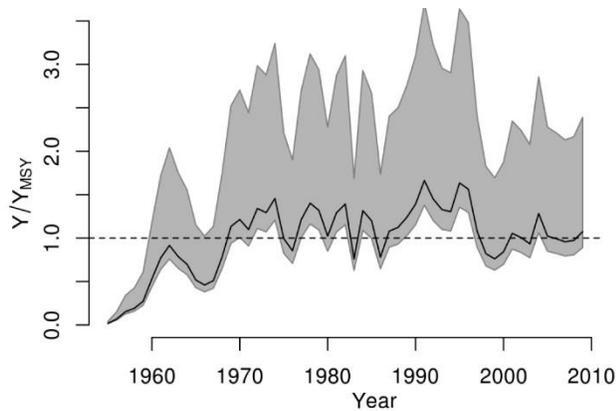
Figure 9. Posterior distributions of ratio between observed (Y) and maximum sustainable yields (Y_{MSY}). Solid line stands for median while area shaded gray stands for the 99% credibility interval.

and fishing mortality is still higher than *MSY* benchmark. At the beginning of the twenty-first century, there was an accentuated increase in the overexploitation of the stock.

DISCUSSION

One of the major issues in the analysis of the potential of fishery resources is the evaluation of the different hypotheses raised regarding to stock structure. In the specific case of the Brazilian stocks of *P. argus*, a number of possible scenarios were identified: (a) single stock, (b) combined set of stocks or (c) group inhabiting sink or source of larvae regions (metapopulation). None of the three options can be discarded. Given this, it is essential to consider all three alternatives in the context of the known life cycle of the species and the oceanographic dynamics of the environment within which the lobster fisheries operate.

The extensive planktonic larval period, of six to twelve months (Baisre, 1964; Farmer *et al*., 1987; Kittaka, 1994) implies that the ocean currents may transport the larvae over distances of hundreds of kilometers which, together with the available genetic evidence (Silberman *et al*., 1994), suggests the presence of a single stock in the Caribbean and adjacent areas. In the equatorial region, however, the Northern Brazilian Current (NBC) and Guyanas Current (GC) flow towards the Caribbean. Indeed the simulation of Rudorff *et al*. (2009) indicates that the dispersal of larvae from the northern coast of South America occurs in the direction of the Caribbean. Briones-Fourzan *et al*. (2008) also provide evidence that the planktonic larvae in the tropical Atlantic disperse parallel to the northern coast of South America towards the Caribbean. Cruz *et al*. (2013) nevertheless suggest that the retroflection of
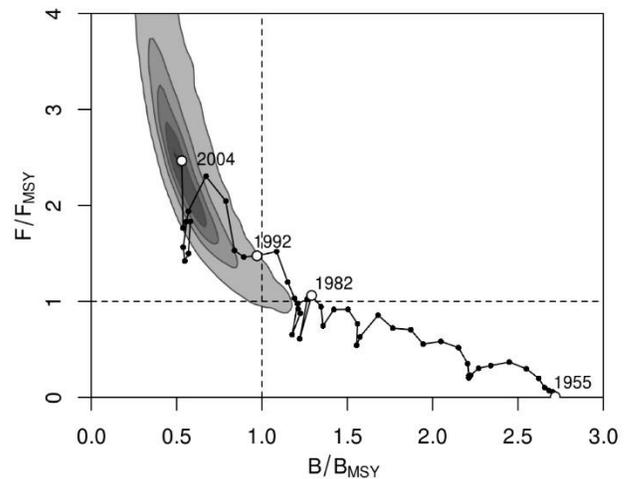

Figure 10. Phase plot for the exploitation of the red spiny lobster (*Panulirus argus*) in eastern South America between 5°N and 20°S. Contour lines are at 0.025, 0.25, 0.50, 0.75 and 0.975 of the largest density.

the NBC may in fact return these larvae to the South American areas from which they originated, and that the Brazilian populations are characterized by a considerable degree of self-recruitment, and may thus be independent of the Caribbean populations. In fact, based on the differences identified in DNA sequences, Sarver *et al*. (1998) suggested that two subspecies should be recognized, *P. argus argus* in the Caribbean, and *P. argus westonii* in Brazil. More recently, Diniz *et al*. (2005) also found considerable differences in the mitochondrial DNA of lobsters caught in the Caribbean and Brazil. In addition, while lobsters with genetic characteristics typical of the Brazilian population may be found in the Caribbean (Sarver *et al*., 2000), the occurrence of individuals of Caribbean origin in Brazil has not been reported. The sum of those evidences reinforces the hypothesis that the Brazilian stock is distinct from that exploited by Caribbean fisheries, or at least that the local Brazilian population is a source part of a metapopulation, which exports phyllosoma to the Caribbean, but has high levels of self-recruitment. Overall, then, it seems reasonable to conclude that the stocks exploited in Brazil can be analyzed separated from those harvested in the Caribbean.

The question of whether one or more stocks of *P. argus* exist in Brazilian waters arises due to oceanic currents dynamics off the eastern coast of South America between 5°N and 20°S. Studies of the circulation of ocean currents in the tropical Atlantic (*e.g.*, Stramma & Schott, 1999; Lumpkin & Garzoli, 2005) indicate the presence of a divergence between the Brazilian Current (BC), which flows southwards, and the NBC, which flows to the north, between 10° and 15°S near the coast of northeastern Brazil. This

suggests a reduced interchange of larvae between the stocks located to the north of 10°S and south of 15°S. In fact, Diniz *et al.* (2005) found some evidence that the lobsters harvested near the equator and at approximately 20°S may represent distinct lineages. However, the sample size was small, and these findings should be treated with caution. Hopefully, future genetic studies may provide more insights into the transportation of larvae or the migration pattern of juveniles and adults, which might contribute to the interpretation of the structure of the Brazilian stocks of *P. argus*. Nowadays, few data are available, and it is not possible to define the structure of the Brazilian stocks reliably. If the interchange among populations is considerable, the evaluation of stocks can be based on simple models of a single large group, but reduced levels of interchange would indicate the need to incorporate a more complex model of stock structure.

A more detailed investigation of catches and catch rates stratified by geographic area would provide valuable data for the understanding of the complexity of the spatial structure of the Brazilian stocks of *P. argus*. The data are limited, however. The studies of Coelho *et al.* (1974), SUDEPE (1978, 1985), Fonteles-Filho *et al.* (1988), Fonteles-Filho (1992), and Paiva (1997) provide some results of equilibrium models fitted to data by region available prior to the 1990's. Nevertheless, they did not publish time series used. This means that by now it is impossible to apply metapopulation models or analyses of spatially-structured populations (*e.g.*, Polovina, 1989) due to data limitation. The only option is to use the aggregated data sets provided by Paiva (1997) and Silva and Fonteles-Filho (2011).

Given the relative isolation of the coast of northern and northeastern Brazil (5°N-20°S) from other nations, the harvesting of *P. argus* in these waters is conducted exclusively by Brazilian fleets. This implies that the official data reported by Paiva (1997) and Silva & Fonteles-Filho (2011) should correspond closely to the actual catches. However, these figures are usually derived from export data, which do not include the lobsters marketed internally within Brazil or the animals caught illegally, with a tail length of fewer than 13 cm (Lins-Oliveira *et al.*, 1993). While the official figures represent an underestimate of the actual catch, there is no reliable information to minimize the bias. It is thus important to recognize the fact that the reference points obtained in the present study (*e.g.*, Y_{MSY}) should only be considered in the light of officially declared catches.

The biomass dynamic models with observational error are not flexible enough to characterize the abrupt decline in the CPUE during the 1960s. There are a number of alternative explanations for the failure to fit the model to the complete data set. These include a) the CPUE values from the early records are not valid as indices of the relative abundance of the population as a whole, b) the assumption of a linear relationship between the CPUE and abundance is invalid, c) the models are unrealistic due to the fact that they do not take changes in the size, age or sex structure of the population into account. Any one of these alternatives may apply in the present case, and are discussed in more detail below.

A number of factors are known to affect the reliability of the CPUE as an index of relative abundance (Cooke & Beddington, 1984; Hilborn & Walters, 1992; Harley *et al.*, 2001). The interpretation of CPUEs as an index of abundance may be erroneous when there is no understanding of the spatial development of fishery activities (Paloheimo & Dickie, 1964). In the specific case of *P. argus*, there are a range of confounding variables for the analysis of spatial-temporal dynamics. Commercial fisheries were first established off the coast of the Brazilian State of Ceará, which lies between 2.8°S and 5°S, and then expanded gradually until the 1980's, when they covered the whole of the region between 5°N and 20°S (Cavalcante, 1982; Fonteles-Filho, 1979, 1997). Fonteles-Filho (1997) concluded that the expansion of the area exploited in the 1970's and 1980's were motivated by the depletion of stocks. Historical differences in the local depletion of stocks imply that densities will have varied differentially over time in distinct sectors of the species' geographic range. Given these considerations, it seems likely that the abrupt decline in the CPUE observed during the 1960s reflected the local depletion of stocks in Ceará, rather than a general decline in the Brazilian population of the species.

The poor fit observed in the early portion of the time series may have been derived not only from specific aspects of the data set, but also an inadequate model structure. In the present study, as in most assessments of fishery stocks based on biomass dynamic models, it was assumed that the CPUE is linearly related to abundance. However, a range of factors are known to violate this assumption (Hilborn & Walters, 1992; Harley *et al.*, 2001), including local depletion, as mentioned above. Violations of the assumption of a linear relationship between the variables may be the explanation for the lack of fit of the models to early catch rate data. One possible alternative would be to change equation 4 for a non-linear approach, although this would cause an increase in the dimensions of the model due to the introduction of new parameters. However, when available, fishery independent estima-

tions of relative abundance may be analyzed together with the CPUE in order to estimate additional parameters necessary to describe the non-linear relationship between CPUE and abundance (*e.g.,* Dunn *et al.*, 2000; Harley *et al.*, 2001). While they are expensive, scientific cruises should be encouraged in order to obtain those fishery independent estimations in order to support a more systematic analysis of the relationship between CPUE and abundance, in additional to other important questions, such as the structure of the *P. argus* stocks mentioned earlier.

The poor fit of the models to the early data may also be a consequence of the unrealistic simplicity of the biomass dynamic models that do not consider size, age or sex structure of the catches, recruitment failures and successes. These details may be especially important where the target populations and fishery activities are complex, as in the Brazilian case, where there is major spatial and temporal stratification in lobster size and age. Juveniles of lobster occupy shallow coastal waters and migrate to deep waters as they mature (Cruz *et al.*, 2001), while different harvesting techniques are used to varying degrees in the different zones of the continental shelf (Silva & Fonteles-Filho, 2011). These factors combine to produce a complex structuring of the characteristics of catches (size, age, and sex ratio), which vary over time. One alternative to cope with those factors and to improve the fittings is to use state-space models (observational plus process errors) which are more flexible than observational error only models.

Closure periods were not the same all over the years. Based on the information published by Silva & Fonteles-Filho (2011) one can realize that the periods of closed seasons ranged 1.75 months on average from 1975 to 1986, four months from 1987 to 2006, and six months after 2007. In this paper annual scale models were used. The calculations suggest that increasing the range of the closure season did not resulted in recovering CPUEs on annual scale, at least until 2004. However, it is important to stress that input data on monthly scale (*e.g.*, CPUE and catch) are requested in order to fully assess the closure season effects. Such data are not available at the moment.

Catches have traditionally been estimated based on the export data (Lins-Oliveira *et al.*, 1993), which provide no information on the location of the fishing operation and on the fishing gear used. Information on catch rates is also limited. The only estimate is for pots in Brazil as a whole, and there are no data for other harvesting techniques, such as diving and drift-netting. Given this, the poor fit recorded for the early data may be a consequence of the simplicity of the model in comparison with the overall complexity of the phenomenon. There is thus a clear need for the

collection of more detailed information (*e.g.*, catches and catch rates by area and harvesting technique) that can contribute to the production of more reliable estimates of lobster stocks in the future. However, it is important to note that, while the estimates obtained in the present study are not ideal, they are the most reliable figures obtainable at the present time.

Given the potential unreliability of the early CPUE data or the reduced quality of the data from this period, a sensitivity analysis was included. The model fits were not biased when these doubtful data were excluded, apart from which, the results for the partial data sets were highly similar to those of the complete time series. In this sense, the reliability of the conclusions on the current status of *P. argus* stocks or exploitation levels is unaffected by the quality or validity of the early data.

The results of the present study contradict considerably most previous estimates based on assumptions of equilibrium (*e.g.,* Fonteles-Filho, 1992, 2007; Paiva, 1997; Cruz *et al.*, 2013). This approach usually results in an overestimate of surplus production, in particular when the data are collected during a period of decline of the abundance of the stock (Hilborn & Walters, 1992). In fact, catch rates indicate a marked decline of the *P. argus* stock, and most estimates obtained using equilibrium models proved to be overestimated in comparison with those obtained in the present study. Assuming that the estimates obtained in the present study are less biased and more useful to assess the stock and the impact of harvesting, they indicate clearly that the Brazilian population of *P. argus* has been heavily overexploited since the beginning of the 1980's.

Despite the uncertainties, what is clear is that the Brazilian lobster fishery has been passing through a critical period since the end of the 2000s. While the purpose of the present study does not include the discussion of fishery management policies, some comments are warranted. Despite all the measures employed by the Brazilian government to regulate the harvesting of *P. argus*, there is clear evidence that the stocks are being overexploited. This indicates either that these measures are ineffective or are not being adequately implemented. Some of the problems are well known – for example, Silva & Fonteles-Filho (2011) estimated that more than 85% of the total Brazilian catch was produced by illegal harvesting. The preoccupying situation indicated by the results of the present study appear to be a direct result of this and similar problems concerning the failure of the management of *P. argus* stocks in the tropical waters of the western South Atlantic.

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