



Population structure and reproductive dynamics of *Octopus insularis* (Cephalopoda: Octopodidae) in a coastal reef environment along northeastern Brazil



Françoise D. Lima^{a,*}, Tatiana S. Leite^a, Manuel Haimovici^b, Marcelo F. Nóbrega^a, Jorge E. Lins Oliveira^a

^a Department of Oceanography and Limnology, Federal University of Rio Grande do Norte, Via Costeira s/n, Natal/RN CEP: 59014-100, Brazil

^b Institute of Oceanography, Federal University of Rio Grande, Rio Grande/RS CEP: 96291-900, Brazil

ARTICLE INFO

Article history:

Received 31 December 2012

Received in revised form 16 August 2013

Accepted 20 August 2013

Keywords:

Octopus
Population structure
Maturity
Management

ABSTRACT

Octopus insularis is the most important octopus commercially fished in northeastern Brazil. Its reproductive dynamics were studied in order to contribute to the biological basis for its management along Rio do Fogo, a small community in a partially protected marine area in northeastern Brazil. Overall, 1108 specimens were caught by the free diving fishery and experimental pot fishery, down to 15 m depths between November 2009 and September 2011. These specimens had their mantle length (ML) and body weight (BW) recorded. The gonads of 545 specimens were examined. The overall sex ratio did not differ from 1:1, but males were more frequent in the smaller ML classes whereas females were more frequent at over 90 mm ML. The ML (ML_{50}) and weight (W_{50}) at maturity were estimated to be 60.0 mm and 215.2 g in males, and 95.2 mm and 493.7 g in females. The peaks of maturation lasted for approximately three months and occurred at intervals of 7–10 months. Mean ML and gonadosomatic indices were strongly correlated with cycles of sea surface temperature and wind intensity. Octopods in all maturity stages were observed throughout the year; however, mature females were scarce, suggesting that they might migrate to spawn in deeper waters. Based on this study it is recommended that a minimum allowed catch size measure of around 500 g is implemented in the fishery in order to avoid catching both small mature males and maturing females, and that octopus fishing is restricted to depths of up to 15 m to avoid fishing mature spawning females. These restrictions could contribute to the sustainable exploitation of this stock that yields several hundred tons of octopuses each year.

© 2013 Elsevier B.V. All rights reserved.

1. Introduction

The study of the reproductive strategies of exploited populations is necessary to establish sustainable management regimes. This is particularly important for the short living semelparous octopus with a single reproductive event during its life on which future recruitments depend (Boyle and Rodhouse, 2005). For this reason, the seasonality of reproduction, the ontogenetic migrations and the influence of the environmental variability are the basis for establishing an adequate management strategy.

The reproductive dynamics and ecology of fished octopods species, such as *Octopus vulgaris* Cuvier, 1797 (Mangold, 1983, 1986; Quetglas et al., 1998; Tomás, 2002; Fernández-Rueda and García-Flórez, 2007), *Octopus maya* Voss and Solis Ramirez, 1966 (Avila-Poveda et al., 2009), *Octopus mimus* Gold, 1852 (Cortez et al.,

1995; Olivares Paz et al., 2001; Cardoso et al., 2004), *Octopus pallidus* Hoyle, 1885 (Leporati et al., 2008), *Octopus cyanea* Gray, 1849 (Guard and Mgaya, 2002) and *Eledone massyae* Voss, 1964 (Perez and Haimovici, 1991) have been studied. In general, sexual maturation in adult octopuses is mediated by changes in environmental conditions and various biotic or abiotic factors can influence this process, such as temperature, light and food availability (Mangold, 1983; Boyle and Rodhouse, 2005; Katsanevakis et al., 2005).

Species of *Octopus* genus are widely distributed around the globe and consist of the main targets of octopods fishery in the world (Nesis, 1987; Boyle and Rodhouse, 2005). In Brazil, two species of octopods are of commercial interest: *O. vulgaris* Cuvier, 1797 in the southern region and *O. insularis* Leite and Haimovici, 2008 (Leite et al., 2008a) in the northeastern and northern regions (Leite et al., 2009a)

Characteristic of the warm tropical waters in Brazil, *O. insularis* is a medium to large sized octopus commonly found in shallow water of rocky environments, reefs or sandstone plateaus (Leite et al., 2009a). It is the main target of octopus fisheries in

* Corresponding author. Tel.: +55 84 33424963.

E-mail address: francoisedl@yahoo.com.br (F.D. Lima).

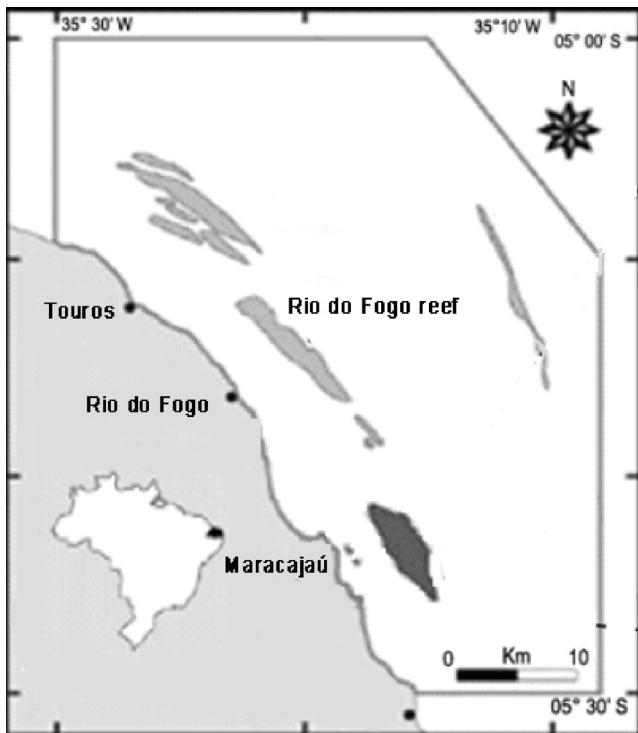


Fig. 1. Geographic localization of the marine protected area Recife dos Corais, Rio Grande do Norte, Brasil.

northeastern Brazil, where several hundred tons are fished each year, mostly in Ceará with long line pots (Braga et al., 2007) and in Rio Grande do Norte, where it is fished by free and compressor diving with the help of a hand hook (Vasconcelos, 2008).

Although artisanal fishing for octopus in northeastern Brazil has a long history, the recognition that the main target species is not *O. vulgaris* and the description of *O. insularis* are recent (Leite et al., 2008a). Thus, little is known about the biology and ecology of this species in the coastal region of Brazil, since the major scientific studies conducted to date include taxonomy (Leite and Mather, 2008c), feeding behavior (Leite et al., 2009b; Bouth et al., 2011) and fishing (Leite et al., 2009a) only on oceanic islands.

The first managed octopus fishery in northeastern Brazil was a small scale, mostly recreational fishery in Fernando de Noronha (Leite et al., 2008b). In 2005, the management of the larger scale pot fishery in Ceará began to extrapolate criteria on allowable gear, depth ranges and minimum sizes of *O. vulgaris* in industrial long line pot fisheries in southern Brazil (Braga et al., 2007), modified in 2011 to exclude a minimum allowable size in order to take into account the smaller mean sizes of the *O. insularis*.

Due to the absence of a regulation to ensure the sustainable exploitation of this species in northeastern Brazil, it is important to understand the processes regarding their life cycle. Within this context, the seasonal changes in population structure and the reproductive dynamics of *O. insularis* from Rio do Fogo were analyzed in order to provide relevant information and subsidiary management strategies.

2. Materials and methods

2.1. Study area

The main fishing grounds of *O. insularis* in Rio Grande do Norte are within the marine protected area “Costa dos Corais” (Fig. 1) which is around 180,000 hectares and where several hundred metric tons are fished annually.

This area is formed primarily of vermetid reefs, corals and coralline algae. The characteristic climate of the region is dry (September to March) and rainy (April to August) with temperatures ranging from 22 °C to 27 °C. Turbidity is mainly related to the action of the winds, and the seasons of spring and summer (October to March) are characterized by high visibility (Maida and Ferreira, 1997). The catch depths of octopus in the area ranged from 5 m to 15 m in Restinga, and up to 35 m in Risca.

2.2. Data collection

Specimens of *O. insularis* from artisanal free diving fishing with small flat bottomed wooden boats under 4 m (*jangadas*) and experimental fishing with pots in shallow waters (<15 m) were sampled monthly between November 2009 and September 2011 (except April, July, August, September and December 2010 and May 2011).

The mantle length (ML), total body weight (BW) and sex were recorded for 1108 specimens: 1001 caught by diving and 107 with long line pots. Maturity stages, ovarian weight (OW), oviducal complex weight (OCW) and oviducal gland diameter (OGD) of 288 females and testicular weight (TW) and Needham sac (NCW) of 257 males were recorded. The measurements were obtained from fresh animals with an accuracy of 0.5 mm and 0.001 g. Gonads were classified into four stages of maturation for males (I immature, II maturing, III mature, IV post-mature) and four for females (I immature, II early maturation, III final maturation, IV mature) following Lima et al. (2013). Gonadosomatic indices were calculated for males: $GSI = NCW / (BW - NCW) \times 100$ (Otero et al., 2007) and for females: $MI = OCW / (OCW + OW)$ (Guerra, 1975), for most months between January 2010 and September 2011. These indices were chosen because they showed a good correlation with the microscopic and macroscopic maturity stages of *O. insularis* (Lima et al., 2013).

For estimation of the mean ML at maturity (ML_{50}), the total number of individuals (n_i) and the total number of maturing and mature individuals in stages II to IV (y_i) were calculated in 10 mm length classes for each sex. If θ_i denotes the probability of an individual in the i -th length class being maturing or mature, y_i follows a binomial distribution: $y_i \sim Bin(n_i, \theta_i)$. Data were fitted using a logistic model, defined by a *logit* link function transforming θ_i to lie in the range [0,1] in the binomial distribution, and with m defined between $(-\infty, +\infty)$ (Kinas and Andrade, 2010). The logistic model was defined as follows:

$$m_i = g(\theta_i) = \log \left(\frac{\theta_i}{1 - \theta_i} \right)$$

$$m_i = \beta_0 + \beta_1 \times x_i$$

From this model, ML_{50} was defined as:

$$ML_{50} = \frac{-\beta_0}{\beta_1}$$

The posterior distribution $p(\beta_0, \beta_1 | D)$, where $D = \{(y_i, n_i, x_i); i = 1, \dots, k\}$, was calculated via the Monte Carlo Markov chain (MCMC) stochastic process. A normal distribution with mean 0 and large variance (1000) was used as the prior distribution which was simulated from 59,000 values, of which the first 50,000 were discarded as burn-in. Every third value of the remaining 9000 was retained, resulting in a final sample of 3000 in the posterior distribution $p(\beta_0, \beta_1 | D)$. The posterior distribution of each estimated ML_{50} provides a clear and easy way to compare the results among data sets. The MCMC was performed with OpenBUGS using the libraries R2WinBUGS (Sturtz and Gelman, 2005) and BRugs (Thomas et al., 2006).

Sexual maturation may be affected by environmental factors, as temperature (Boyle and Rodhouse, 2005) and others as wind speed that can alter visibility and affect light penetration (Schön et al., 2002). Monthly sea surface temperature (SST) data were acquired by NOAA analysis “real time global sea surface temperature” (<http://www.nsof.class.noaa.gov>) (NOAA, 2011), which also uses satellite data and observations of vessels and buoys, to verify the relationship between temperature and the octopus maturation process. The monthly values of wind speed (m/s) for the coastal region of Rio Grande do Norte along the sampling period were provided by Windguru (<http://www.windguru.cz/pt/>) (WindGuru, 2011).

Three General Linear Models (GLMs) (McCullagh and Nelder, 1989) were used to model (1) the expected ML at *O. insularis* catch (normal model and identity link function), (2) the expected GSI for females, and (3) the expected MI for males (normal model and identity link function). The level of significance was set at 5% for the identification of statistically significant factors, coefficients and interactions that explain the variability in the response variables in the three GLMs. The proposed models have the following covariate structure:

$$Y = \text{Sex} + \text{SST} + \text{Wind} + \text{Month} + \text{Sex} \times \text{Month} \quad (1)$$

$$Y = \text{Month} + \text{SST} + \text{Wind} + \text{ML} + \text{Weight} \quad (2)$$

$$Y = \beta + \text{Month} + \text{SST} + \text{ML} + \text{Weight} \quad (3)$$

where β is an intercept term.

Linear regression and covariance analysis were applied in order to evaluate the relationship between ML and the weight of males and females. The variation in sex ratio over the months and maturation stages was analyzed by chi-squared tests (χ^2). The software used to develop the analysis were Statistica 8.0, Systat 12.0, SPSS 17 and R.

3. Results

Males ranged from 56 to 190 mm ML (mean = 99.9 mm, standard deviation [SD] = 18.77, $n=510$) and from 110 g to 1600 g BW (mean = 686.20 g, SD = 302.77, $n=598$); females ranged from 50 to 190 mm ML (mean = 104.60 mm, SD = 20.07) and from 96 to 1940 g BW (mean = 746.42 g, SD = 339.08) (Fig. 2).

The relationship BW and ML was $BW = -0.02519 \text{ ML}^{2.2007}$ ($R^2 = 0.712$). Covariance analysis of log transformed ML and BW showed no significant differences between sexes ($p = 0.109$). The 95% confidence interval of the regression coefficient was 2.116 to 2.285, showing that growth is allometric; that is, the ML becomes more elongated with growth.

The overall sex ratio did not differ significantly from the 1:1 expected ratio, but was not homogeneous between size classes of 10 mm ($\chi^2 = 19.66$, $df = 11$, $p < 0.05$) showing that males were more frequent in the smaller ML classes whereas females were more frequent at over 90 mm ML. The sex ratio also varied significantly between months ($\chi^2 = 44.97$, $df = 16$, $p < 0.05$). A higher proportion of females peaked in February 2010 and July 2011, and of males, in March 2010 and September 2011 (Fig. 3).

Males of *O. insularis* in maturing (41.60%) and mature (49.24%) stages and maturing females (60.42%) were collected in almost all sampling periods (Fig. 4a), while mature females (4.51%) were of lower frequency, occurring only in some seasons (Fig. 4b).

The ML_{50} and the 95% credibility interval for males was 60.10 mm (46.50–68.00 mm) and for females was 95.20 (92.00–98.20 mm) (Fig. 5). The parameters of the weight–length relationships were used to convert ML_{50} to BW_{50} . The BW_{50} was 215.2 g (123.50–281.50 g) in males and 493.70 g (457.70–528.20 g)

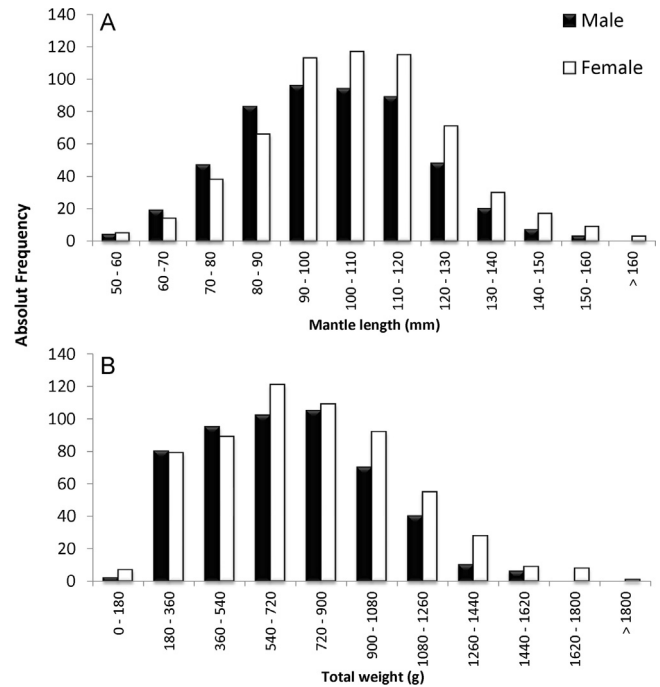


Fig. 2. Distribution of the absolute frequency of males and females of *O. insularis* in size classes (A) and weight (B).

Table 1

Parameters, standard errors (SE), confidence intervals (CI) and significance levels (p) of GLM analysis for the expected caught ML of *Octopus insularis* (normal model and identity link function).

Parameter	B	SE	95% CI		p
			Lower	Upper	
Sex (F)	-31.961	41.848	-113.983	50.059	0.000
Sex (M)	-41.521	41.857	-123.561	40.517	0.000
SST	3.545	1.273	1.048	6.041	0.005
Wind	8.466	1.148	6.215	10.717	0.000
Month	-0.788	0.208	-1.195	-0.380	0.000
Sex (F) × Month	-0.542	0.276	-1.084	0.000	0.050
Sex (M) × Month	-	-	-	-	-

in females. The ML_{50} of females was estimated with a higher precision because young immature females were larger and males were landed in small numbers by the fisherman.

The GLM showed that the ML varied significantly for sex, wind intensity, month, and the interaction between sex and month, and was marginally significant for SST (Table 1).

For both sexes, the ML expected mean values and confidence intervals estimated by the GLM in relation to months showed a maximum in November 2009 and relatively stable values through

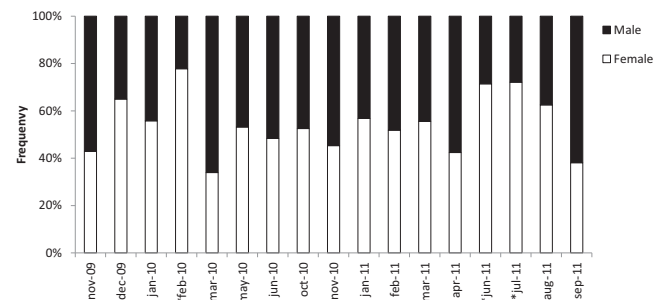


Fig. 3. Monthly proportion of males and females of *O. insularis*. Asterisks indicate significantly different sex ratios ($p < 0.05$).

Table 2

Parameters, standard errors (SE), confidence intervals (CI) and significance levels (p) of GLM analysis for the GSI of *O. insularis* (normal model and identity link function).

Parameter	B	SE	95% CI		p
			Lower	Upper	
Month	-0.030	0.008	-0.045	-0.014	0.000
SST	-0.119	0.006	-0.131	-0.108	0.000
Wind	0.078	0.027	0.025	0.130	0.004
Mantle length	0.013	0.002	0.008	0.018	0.000
Weight	0.000	0.000	-0.001	0.000	0.053

most of 2010 until November, at which point there was a further increase in the ML. This was followed by a strong decrease from January until June 2011 and then a steep recovery to a new maximum in September 2011 (Fig. 6a). There was also a negative relationship between ML and SST, while ML increased with increasing wind speeds.

The GSI of males ranged from 0.015 to 0.387 (mean=0.13, SD=0.06). Significant relationships were found between GSI, month, SST, ML and BW (Table 2). GSIs increased with ML and total weight (Fig. 6) but stabilized in the ML class of 140 mm and the BW class of 1260 g. During the two year sampling period, two cycles of GSI were closely correlated with annual environmental changes: GSI increased with both wind intensity and decreasing temperatures. The peaks of GSI occurred in the months of February and September 2011 and in November 2010, and they were significantly lower than those recorded in the months of February and May 2010 and in March 2011.

The MI of females ranged between 0.005 and 0.816 (mean = 0.29, SD=0.14). In the GLM model calculated for the MI females intercept, the covariates month, SST, ML and individual weight were statistically significant (Table 3). MI decreased with ML and BW (Fig. 6). During the two year sampling period, two cycles of MI were observed and were closely correlated with temperatures: MI

Table 3

Parameters, standard errors (SE), confidence intervals (CI) and significance levels (p) of GLM analysis for the expected MI (Maturity indices) of *Octopus insularis* (normal model and identity link function).

Parameter	B	Std. Error	95% CI		p
			Lower	Upper	
Intercept	-2.576	0.802	-4.148	-1.003	0.001
Month	0.011	0.005	0.001	0.021	0.019
SST	0.085	0.027	0.032	0.138	0.001
Mantle length	-0.008	0.001	-0.011	-0.005	0.000
Weight	-0.000	0.000	-0.000	-0.000	0.000

decreased with decreasing SST. The lowest values of MI for females, which correspond to the highest maturity in the population, took place between January and March 2010, October and November 2010, January 2011 and July to September 2011, all of which differed significantly from the month with the highest values.

4. Discussion

As the management of octopuses fisheries in Brazil begun shortly before the clear establishment of the differences between *O. vulgaris*, fished with industrial pots in southern Brazil, and *O. insularis* from the northeast, the same criteria of minimum allowable size was applied to both regions. However *O. insularis* reaches maturity at sizes and weights considerably smaller than those of *O. vulgaris* (see Table 4). For this reason the minimum size at which both species can be captured has to be established separately.

The reproductive cycle of *O. insularis* in northeastern Brazil follows the general pattern of *Octopus* in which males reach maturity at considerably smaller size than females. Precocious maturation of males of most species of the genus *Octopus* result in a decrease in the somatic growth at the expense of reproductive development, while females continue to invest in body growth during much of their life cycle (Mangold, 1983; Boyle and Rodhouse, 2005). By growing larger, females increase their fecundity and accumulate energy reserves for parental care as feeding stops after spawning (Mangold, 1986; Hanlon and Messenger, 1996; Mather et al., 2010). This difference between sexes was also observed for *O. vulgaris* (Hernández-García et al., 2002; Rodríguez-Rúa et al., 2005), *O. maya* (Avila-Poveda et al., 2009) and *Eledone moschata* (Silva et al., 2004).

A peculiarity of the reproductive biology of *O. insularis* in Rio Grande do Norte is that, despite mature specimens occurring all year round, there are peaks of maturation associated with environmental seasonality. GLM analysis showed that post juvenile body growth and gonadal development is favored in the colder and windier season and full maturity is attained in a higher proportion by the end of this season. Moreover, higher wind speeds result in more turbid marine waters, reducing light penetration that may accelerate maturation (Schön et al., 2002; Boyle and Rodhouse, 2005). According to Mangold (1983), sexual maturation in *O. vulgaris* is controlled by the gonadotropin hormone produced by the optic gland and optical experiments have shown that light has an inhibitory effect on this gland (Nishioka et al., 1970; Wells and Wells, 1975; Iwakoshi-Ukena et al., 2004).

The periods of maturation in the population coincided with the periods during which the largest average sizes of octopus in the catches occurred, lasting about three months and occurring at intervals of between seven and ten months. The intensity of maturation in *O. insularis* basically occurs with an annual periodicity and may vary depending on biotic and abiotic conditions that influence the life cycle of these animals, such as temperature, food availability, and fishing pressure (Katsanevakis and Verriopoulos, 2006).

The higher frequency of maturing individuals at lower temperatures may be related to the timing of spawning, which lasts from 20

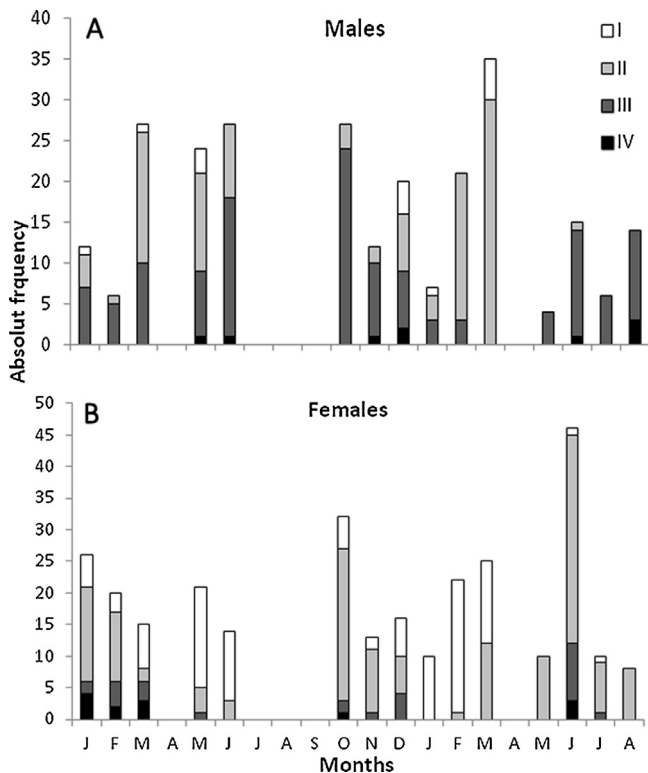


Fig. 4. Number of males (A) and females (B) *O. insularis* in different maturity stages from Rio do Fogo between January 2010 and August 2011.

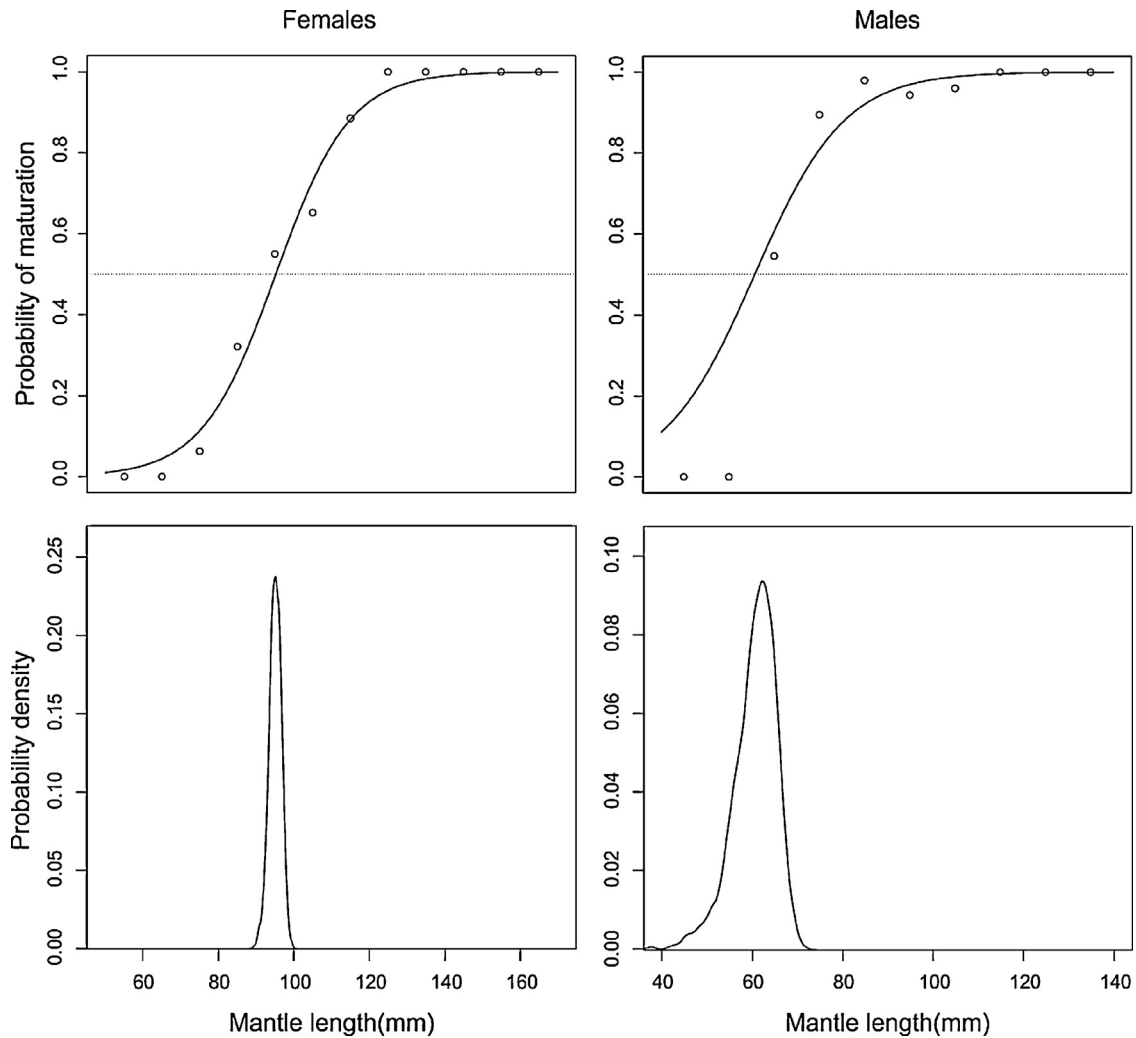


Fig. 5. Determination of the mantle length of the first sexual maturity (L_{50}) of *O. insularis* males and females.

to 50 days. Thus, the season of hatched paralarvae may be coincident with an increase in water temperature and a decrease in wind speeds. In these conditions, environments which provide greater availability of food also provide high rates of body growth (Forsythe and Hanlon, 1988; Wood and O'Dor, 2000).

In two of the three maturation peaks of *O. insularis*, the proportion of females was initially higher compared with males, and decreased at the end of the breeding season (February and March 2010, and August and September 2011). Alejo-Plata et al. (2009) analyzed the population of *Octopus hubbsorum* Berry, 1953 in Mexico, and found variation in the sex ratio over time, with an increasing proportion of females during the peaks of maturation.

However, Fernández-Rueda and García-Flórez (2007), in Asturias, found a higher ratio of male *O. vulgaris* peaks of maturation compared with females. According to Mangold (1983), changes in the sex ratio over the reproductive period may be related to migration characteristics of the species, in which males and females move to shallower regions in order to mate (Hanlon and Messenger, 1996).

Lima et al. (2013), observed the presence of sperm in the oviducal glands of immature *O. insularis* females, indicating that they may mate despite not being mature. Thus, it is likely that females do not migrate to shallow areas only to mate. Such migrations can occur due to an intense search for food in shallower waters, before spawning, where there is a greater availability of food (Leite et al.,

Table 4

Values of the mantle lengths (ML_{50}) and body weights (BW_{50}) of first gonadal maturation of *O. vulgaris* (from scientific references) and *O. insularis* (present study).

Species	Sex	Area	ML_{50} (mm)	BW_{50} (g)	References
<i>O. vulgaris</i>	♂	Southeast Brazil	104.96	–	Tomás (2002)
	♂	Canarias islands	105.00	–	Hernández-García et al. (2002)
	♀		113.00	–	
	♂	South Espanha	–	850.00	Rodríguez-Rúa et al. (2005)
	♀		–	1250.00	
<i>O. insularis</i>	♂	Mediterraneo	–	903.40	Otero et al. (2007)
	♀		–	1788.00	
	♂	Northeast Brasil	60.10	215.20	Present study
	♀		95.20	493.70	

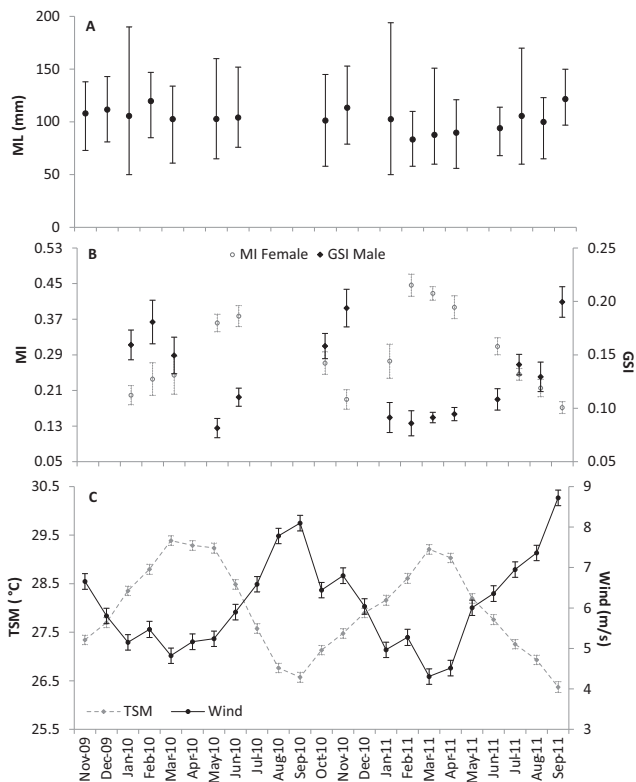


Fig. 6. (A) Mantle length (ML) variation in male and female *O. insularis* between months. The bars indicate the maximum and minimum sizes; (B) Distribution of maturity indices (MI) of females and gonadosomatic indices (GSI) of males. The bars indicate the standard error of the mean; (C) sea surface temperature (SST) and wind speed variation along the months. The bars indicate the standard error of the mean.

2009a) whereas females do not feed during the incubation period of the eggs.

In this study in, Rio Grande do Norte in depths of up to 15 m, less than 5% of the examined females were mature and only one spawned. On the other hand, in the pot fishery (Ceará State) was found mature and spawned females year round at depths between 19 and 45 m (Batista, personal communication), supporting the hypothesis of a reproductive migration to deeper waters in RN. Oosthuizen and Smale (2003), analyzing the bathymetric distribution of a population of *O. vulgaris*, detected a low number of mature individuals in the shallow areas and associated the displacement of fertilized females to deeper areas or to areas with more protected habitats in order to carry spawning (Hanlon and Messenger, 1996). Thus, mature and spawned females of *O. insularis* are not accessible for capture by fishing with snorkel diving, which is performed at a depth of up to 15 m (Vasconcelos, 2008).

The reproductive stock of octopus is less affected by fishery conducted by snorkeling. However, diving with air compressors, which is forbidden but still practiced, may be accessing this portion of the population, which emphasizes the importance of more detailed studies in areas of greater depth in order to evaluate the impact of this type of fishing in the *O. insularis* population.

Based on this study, some criteria for fishing management can be proposed: firstly, to establish a minimum size of 500 g in the landings, by avoiding the fishing of specimens under this weight. This criterion will ensure the protection of the smaller mature males and small maturing females in their copulation areas, avoiding a misbalance between sexes and a recruitment overfishing. In addition, there are primary evidences that *O. insularis* has a short life cycle and fast growth. By delaying their catch, growth overfishing is avoided and the rent of fisherman increase; and secondly, because

spawning females were not found in the catches of free diving and pots in shallow water, it is recommended that free diving and pot fishery should be restricted to rubble and biogenic beds at depths under 15 m.

These strategies can contribute to the regulation of fishing for this species in the region and the search for sustainable exploitation of this important fishery resource in northeastern Brazil.

Acknowledgements

We thank the fishermen of Rio do Fogo, who provided information about octopus fishery, and Jaciana Barbosa and Lorena Candice for their help in the sampling. We acknowledge the Brazilian Institute of the Environment (MMA/IBAMA) for logistics support, and the National Research Council (CNPq) for financial support research grant (MH), and scholarship (FD).

References

- Alejo-Plata, M.C., Gómez-Márquez, J.L., Carrillo, S.R., Herrera-Galindo, J.E., 2009. Reproducción, dieta y pesquería del pulpo octopus (*Octopus*) *huhsororum* (Mollusca: Cephalopoda) en la costa de Oaxaca, México. *Rev. Biol. Trop.* 57, 63–78.
- Avila-Poveda, O.H., Colin-Flores, R.F., Rosas, C., 2009. Gonad development during the early life of *Octopus maya* (Mollusca: Cephalopoda). *Biol. Bull.* 216, 94–102.
- Bouth, H.F., Leite, T.S., Lima, F.D., Lins-Oliveira, J.E., 2011. Atol das Rocas: an oasis for *Octopus insularis* (Cephalopoda: Octopodidae). *Zoologia* 28 (1), 45–52.
- Boyle, P., Rodhouse, P.G., 2005. *Cephalopods: ecology and fisheries*. Blackwell Science, UK.
- Braga, M.S.C., Marinho, R.A., Batista, B.B., Rocha, E.P., 2007. Histórico e descrição da pesca do polvo, *Octopus* cf. *vulgaris*, com potes, no estado do Ceará. *Arquivo de Ciências do Mar, Fortaleza* 40 (2), 5–13.
- Cardoso, F., Villegas, P., Estrella, C., 2004. Observaciones sobre la biología de *Octopus mimus* (Cephalopoda: Octopoda) en la costa peruana. *Rev. Peru. Biol.* 11 (1), 45–50.
- Cortez, T., Castro, B.G., Guerra, A., 1995. Reproduction and condition of female *Octopus mimus* (Mollusca: Cephalopoda). *Mar. Biol.* 123 (3), 505–510.
- Fernández-Rueda, P., García-Flórez, L., 2007. *Octopus vulgaris* (Mollusca: Cephalopoda) fishery management assessment in Asturias (north-west Spain). *Fish. Res.* 83 (2–3), 351–354.
- Forsythe, J.W., Hanlon, R.T., 1988. Effect of temperature on laboratory growth, reproduction and life span of *Octopus bimaculatus*. *Mar. Biol.* 98, 369–379.
- Guard, M., Mgaya, Y.D., 2002. The artisanal fishery for *Octopus cyanea* Gray in Tanzania. *AMBIO* 31 (7), 528–536.
- Guerra, A., 1975. Determinación de las diferentes fases del desarrollo sexual de *Octopus vulgaris* Lamarck, mediante un índice de madurez. *Invest. Pesq* 39 (2), 397–416.
- Hanlon, R.T., Messenger, J.B., 1996. *Cephalopod Behaviour*. Cambridge University Press, Great Britain.
- Hernández-García, V., Hernández-López, J.L., Castro-Hdez, J.J., 2002. On the reproduction of *Octopus vulgaris* off the coast of the Canary Islands. *Fish. Res.* 57, 197–203.
- Iwakoshi-Ukena, E., Ukena, K., Takuwa-Kuroda, K., Kanda, A., Tsutsui, K., Minakat, H., 2004. Expression and distribution of octopus gonadotropin-releasing hormone in the central nervous system and peripheral organs of the octopus (*Octopus vulgaris*) by in situ hybridization and immunohistochemistry. *J. Comp. Neurol.* 477 (3), 310–323.
- Katsanevakis, S., Protopapas, N., Miliou, H., Verriopoulos, G., 2005. Effect of temperature on specific dynamic action in the common octopus *Octopus vulgaris* (Cephalopoda). *Mar. Biol.* 146, 733–738.
- Katsanevakis, S., Verriopoulos, G., 2006. Seasonal population dynamics of *Octopus vulgaris* in the eastern Mediterranean. *ICES J. Mar. Sci.* 63 (1), 151–160.
- Kinas, P.G., Andrade, H.A., 2010. Introdução à Análise Bayesiana (com R). MaisQnada Porto, Alegre.
- Leite, T.S., Haimovici, M., Molina, W., Warnke, K., 2008a. Morphological and genetic description of *Octopus insularis* new species (Cephalopoda: Octopodidae), a cryptic species in the *Octopus vulgaris* complex from the tropical Southwestern Atlantic. *J. Molluscan Stud.* 74, 63–74.
- Leite, T.S., Haimovici, M., Lins, J.E., 2008b. A Pesca de Polvos no Arquipélago de Fernando de Noronha. *Brasil. B. Inst. Pesca* 34 (2), 271–280.
- Leite, T.S., Mather, J.A., 2008c. A new approach to octopuses body pattern analysis: A framework for taxonomy and behavioral studies. *Am. Malacological Bull.* 24 (1), 31–41.
- Leite, T.S., Haimovici, M., Mather, J., Lins-Oliveira, J.E., 2009a. Habitat, distribution, and abundance of the commercial octopus (*Octopus insularis*) in a tropical oceanic island, Brazil: Information for management of an artisanal fishery inside a marine protected area. *Fish. Res.* 98, 85–91.
- Leite, T.S., Haimovici, M., Mather, J., Lins-Oliveira, J.E., 2009b. *Octopus insularis* (Octopodidae), evidences of a specialized predator and a time-minimizing hunter. *Mar. Biol.* 156 (11), 2355–2367.

- Leporati, S.C., Pecl, G.T., Semmens, J.M., 2008. Reproductive status of *Octopus pallidus*, and its relationship to age and size. *Mar. Biol.* 155, 375–385.
- Lima, F.D., Leite, T.S., Haimovici, M., Lins-Oliveira, J.E., 2013. Reproductive development of the tropical octopus (*Octopus insularis*) in northeast Brazil. *Hydrobiologia* (in press).
- Maida, M., Ferreira, B.P., 1997. Coral reefs of Brazil: an overview. In: *Proceedings of the 8th International Coral Reef Symposium, Panama, Vol. 1.*, pp. 263–274.
- Mangold, K., 1983. *Octopus vulgaris*. In: Boyle, P.R. (Ed.), *Cephalopod Life Cycles. I – Species Accounts*. Academic Press, Londres, pp. 334–364.
- Mangold, K., 1986. Reproduction. In: Boyle, P.R. (Ed.), *Cephalopod Life Cycles. II – Comparative Reviews*. Academic Press, Londres, pp. 157–200.
- Mather, J.A., Anderson, R.C., Wood, J.B., 2010. *Octopus: The Ocean's Intelligent Invertebrate*. Timber press, Portland.
- Mccullagh, P., Nelder, J.A., 1989. *Generalized Linear Models*, 2nd ed. Chapman and Hall, London.
- Nesis, K.N., 1987. *Cephalopods of the world*. T. F. H. Publications, Moscow.
- Nishioka, R.S., Bern, H.A., Golding, D.W., 1970. Innervation of the Cephalopod optic gland. In: Barqmann, W., Scharrer, B. (Eds.), *Aspects of Neuroendocrinology*. Springer Verlag, Berlin, pp. 47–54.
- NOAA, National Oceanic and Atmospheric Administration, Real Time Global Sea Surface Temperature. Available in: <http://www.nsof.class.noaa.gov> (accessed on 15.06.11).
- Olivares Paz, A., Covarrubias, M.Z., Reyes, P.P., Romero, O.Z., 2001. Estudio histológico de la ovogénesis y maduración ovárica en *Octopus mimus* (Cephalopoda: Octopodidae) de la II región de Chile. *Estud. Oceanol.* 20, 13–22.
- Oosthuizen, A., Smale, M.J., 2003. Population biology of *Octopus vulgaris* on the temperate south-eastern coast of South Africa. *J. Mar. Biol. Assoc. U.K.* 83 (3), 535–541.
- Otero, J., González, A.F., Sieiro, M.P., Guerra, A., 2007. Reproductive cycle and energy allocation of *Octopus vulgaris* in Galician waters, NE Atlantic. *Fish. Res.* 85, 122–129.
- Perez, J.A.A., Haimovici, 1991. Sexual maturation and reproductive cycle of *Eledone massyae* Voss, 1964 (Cephalopoda Octopodidae) in Southern Brazil. *Bull. Mar. Sci.* 49 (1), 270–289.
- Quetglas, A., Alemany, F., Carbonell, A., Merella, P., Sánchez, P., 1998. Biology and fishery of *Octopus vulgaris* Cuvier 1797, caught by trawlers in Mallorca (Balearic Sea, Western Mediterranean). *Fish. Res.* 36, 237–249.
- Rodríguez-Rúa, A., Pozuelo, I., Prado, M.A., Gómez, M.J., Bruzón, M., 2005. The gametogenic cycle of *Octopus vulgaris* (Mollusca: Cephalopoda) as observed on the Atlantic coast of Andalusia (South of Spain). *Mar. Biol.* 147 (4), 927–933.
- Schön, P.-J., Sauer, W.H.H., Roberts, M.J., 2002. Environmental influences on spawning aggregations and jig catches of chokka squid *Loligo vulgaris reynaudii*: a “black box” approach. *Bull. Mar. Sci.* 71, 783–800.
- Silva, L., Ramos, F., Sobrino, I., 2004. Reproductive biology of *Eledone moschata* (Cephalopoda: Octopodidae) in the Gulf de Cádiz (south-west Spain, ICES Division IXa). *J. Mar. Ass. U.K.* 84, 1221–1226.
- Sturtz, U.L., Gelman, A., 2005. R2WinBUGS: a package for running WinBUGS from R. *J. Stat. Softw.* 12 (3), 1–16.
- Thomas, A., O'Hara, B., Ligges, U., Sturtz, S., 2006. Making BUGS Open. *R News* 6 (1), 12–17.
- Tomás, A.R.G., 2002. Dinâmica populacional e avaliação de estoques do polvo comum (Mollusca, Cephalopoda, Octopodidae) no sudeste de Brasil. In: *Tese de doutorado*. Instituto de Biociências da Universidade Estadual Paulista, Rio Claro SP, pp. 482.
- Vasconcelos, J.A., 2008. A pesca de polvo no Rio Grande do Norte. *Polvo News* (4), 1–5, ano I.
- Wells, M.J., Wells, J., 1975. Optic gland implants and their effects on the gonads of octopus. *J. Exp. Biol.* 62, 579–588.
- WindGuru. Previsões Meteorológicas. Disponível em: <http://www.windguru.cz/pt/> (accessed on 17.06.11).
- Wood, J.B., O'Dor, R.K., 2000. Do larger cephalopods live longer? Effects of temperature and phylogeny on interspecific comparisons of age and size at maturity. *Mar. Biol.* 136, 91–99.