PANAMJAS
Pan-American Journal of Aquatic Sciences

Population dynamics of the mangrove tree crab *Aratus pisonii* (Brachyura: Sesarmidae) in the estuarine complex of Cananéia-Iguape, São Paulo, Brazil

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Abstract. The population dynamics of *Aratus pisonii* in the coastal system of Cananéia-Iguape was evaluated by means of cohort analysis (Bhattacharya method), comparison of the reproductive output and size structure of the ovigerous females among months and seasons of the year. Most ovigerous females were sampled in the rainy season. A reproductive pause occurred during the dry season, when the sex ratio was biased toward females, indicating high feeding activity by this sex. Fecundity was compared between females captured in rainy and dry seasons to test the hypothesis of reproductive output seasonality in this subtropical population, a fact that was rejected. By analyses of the mean size of ovigerous females along of the months of their occurrence, it was detected two cohorts: larger (older) females start the breeding early in the spring and the smaller ones (primiparous) began their reproduction in the austral summer. Compared with other populations of *A. pisonii*, these crabs reached functional maturity earlier in their life cycle. Our findings reveal the response pattern of *A. pisonii* in a subtropical humid climate mangrove area with conditions of exceptionally high productivity.

Key Words: Estuarine crab, Fecundity, Mangrove, Population structure, Reproduction

Resumo: **Dinâmica populacional do caranguejo arborícola de manguezal *Aratus pisonii* (Brachyura, Sesarmidae) no complexo estuarino de Cananéia-Iguape, São Paulo, Brasil.** A dinâmica da população de *Aratus pisonii* do sistema costeiro de Cananéia-Iguape foi avaliada por análise das coortes (método de Bhattacharya), comparação do potencial reprodutivo e a estrutura de tamanho das fêmeas ovígeras entre meses e estações do ano. A maioria das fêmeas ovígeras foi amostrada na estação chuvosa. Uma pausa reprodutiva ocorreu durante a estação seca, quando a razão sexual apresentou desvio para fêmeas, indicando elevada atividade alimentar para este sexo. A fecundidade foi comparada entre fêmeas na estação seca e chuvosa para testar a hipótese de sazonalidade no potencial reprodutivo dessa população subtropical, um fato que foi rejeitado. Por análise do tamanho médio das fêmeas ovígeras ao longo de seus meses de ocorrência detectou-se duas coortes: fêmeas maiores (mais velhas) iniciam a reprodução no início da primavera e fêmeas ovígeras menores (primíparas) iniciam a reprodução no verão austral. Comparado com outras populações, o tamanho da maturidade funcional de *A. pisonii* ocorre antecipadamente em seu ciclo de vida. Nossos resultados revelam a resposta padrão de *A. pisonii* em uma área de manguezal de clima subtropical úmido, com condições de produtividade excepcionalmente elevada.

Palavras Chave: Caranguejo estuarino, Fecundidade, Manguezal, Estrutura populacional, Reprodução

Introduction

The estuarine complex of Cananéia-Iguape is one important environmental protection area (APA, Área de Proteção Ambiental), comprising an extensive plain of wetlands covered by mangroves on the southern coast of the state of São Paulo (Tessler & Mahiques 1998). Although situated in a subtropical region, the environmental conditions allow the development of exuberant and highly productive mangrove forests (Schaeffer-Novelli *et al*. 1990) that offer food, refuge and breeding sites for several species.

Brachyuran crabs are conspicuous members of mangroves systems and deserve particular attention due to its ecological roles. There are species occupying all trophic levels including deposit feeders, herbivorous, prey and predator. Because of these ecological roles, brachyurans may yield important impacts on the energy flow of ecosystems through exportation of planktonic larvae and detritus to adjacent waters (Wafar *et al*. 1997, Werry & Lee 2005, Cannicci *et al*. 2008).

The sesarmid crab *Aratus pisonii* (H. Milne Edwards, 1837) is a very common species in mangroves of the Western Atlantic (Thiercelin & Schubart 2014) where it lives in closer association with aerial roots, trunks and leaves of mangrove trees (Warner 1967, Conde & Díaz 1989a,b). In contrast to many other species, *A. pisonii* feeds on living leaves and algae (Beever *et al*. 1979, Lacerda *et al.* 1991) contributing this way for the fast fragmentation and recycling of the vegetal matter. As primary herbivores, they are an important link between mangrove primary production and the detrital food web of estuaries, and then considered key species in mangrove systems of the Western Atlantic (Erickson *et al.* 2008; Riley *et al.* 2014).

Studies on population dynamics of *A. pisonii* have been carried out in tropical regions, including Jamaica (Hartnoll 1965, Warner 1967) and the Venezuelan coast (Conde & Díaz 1989a,b, Díaz & Conde 1989). For the Brazilian coast, we have data from Rio de Janeiro (Nicolau & Oshiro 2002, 2007) and from the north coast of São Paulo state (Leme & Negreiros-Fransozo 1998, Leme 2002). In a general way, such studies have demonstrated the high phenotypic plasticity of these crabs shaped by local conditions. However, there are no studies for subtropical populations, where environmental seasonality might be an important feature influencing the population dynamics of this crab.

Considering the importance of mangrove ecosystems for ecological and fishery equilibrium in coastal environments, the goal of this study was to provide a better understanding of the population dynamics of *A. pisonii* inhabiting a subtropical area on the southern coast of São Paulo state, which has not been analyzed at a large scale. We tested the null hypothesis that reproductive traits and the size structure did not differ from populations in tropical mangroves, focusing on the size-class distribution, sex ratio, maturity size, reproductive period, and fecundity.

Materials and methods

Study area

The Coastal System Cananéia-Iguape is the principal estuarine-lagoon complex on the southeastern coast of Brazil, comprising an extensive mangrove area of ca. 72 km^2 (Herz 1991). This study was conducted in an estuarine island near Barra de Icapara (24º41'06''S; 47º28'12''W and 24º41'38.4''S, 47º27'10.8''W), municipality of Iguape (Fig. 1).

The climate of this coastal strip is classified as humid tropical without dry season (*Af*, according to Köppen), but around the studied latitude the *Am* climate (with dry winter) can occur close to *Af* climate (see Alvares *et al*. 2013). Then, the annual climatic seasonality can be influenced more by the rainfall than by the changes in temperature, with higher precipitation in spring and summer (Sant ´Anna-Neto 2005).

Procedures

Sampling was carried out monthly from February 1999 through February 2000, along transects of 4x100 m positioned perpendicularly to the mangrove edge in the direction of the salt flat ("apicum"). The trees along transect were inspected for crabs by four persons, with a capture effort of one hour. The collected crabs were kept in plastic bags together with tree leaves, in order to prevent the loss of appendages or eggs.

In the laboratory, the crabs were kept in 70% ethanol until the analyses. All specimens were grouped by demographic categories (males, females without eggs, and ovigerous females) and had their greatest carapace width (CW) measured with a precision caliper (0.05 mm). Each demographic category was arranged in 2-mm size classes of CW. Then, the size-class distribution of individuals of each category was decomposed into normal components by the Bhattacharya method, using the FiSAT Stock Assessment Tool program (FAO/ICLARM, developed by Gayanilo *et al.* 1995), with use of their respective means and standard deviations were calculated. We thus obtained different normal distributions showing the size-frequency of each age group or cohort that contributed to the total sample. The population dynamics pattern was inferred from analyses of the cohorts in the population during the year.

The sex ratio was analyzed for each month, season and dry/wet periods and further compared by χ^2 test (p= 0.05).

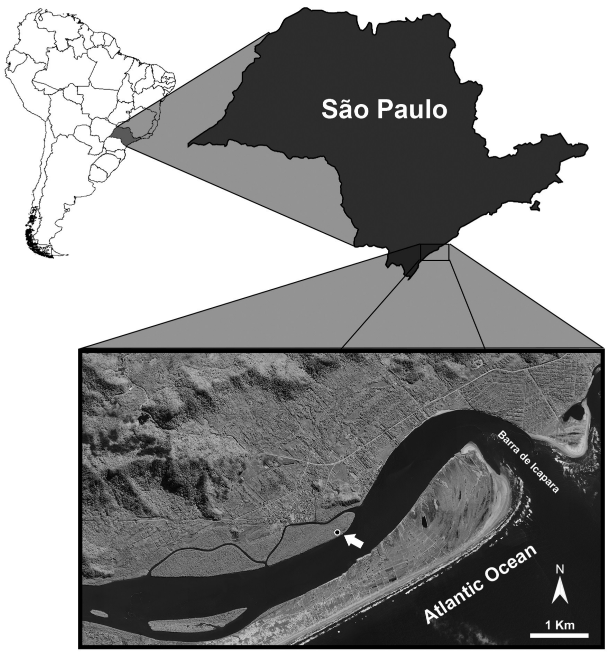

Figure 1. Mangrove island near Barra de Icapara, municipality of Iguape, in southern of São Paulo State, Brazil. Specimens of *Aratus pisonni* were captured in only one sampling point (arrow = 24º41'21"S - 47º7'24"W).

The reproductive period was determined from the proportion of ovigerous females to the total number of females caught monthly. Considering that rainfall is the most accentuated climatic variable in this subtropical region, the reproductive seasonality was tested by grouping the ovigerous females by rainy (spring-summer) and dry (autumn-winter) seasons, which were compared by the χ^2 test (p= 0.05). The same dry and rainy-season groups of ovigerous females had their fecundity (egg number) analyzed and compared as described below.

Only females with eggs in the initial stage of embryonic development (beginning blastula to gastrula) were used. The number of eggs was estimated by the gravimetric method (Pinheiro & Terceiro 2000). This consists of counting the number of eggs (EN) in three subsamples (1 mg of eggs each), which is extrapolated to the total weight of the egg mass, all previously dehydrated in an oven for 48 h at 60 °C. Data that showed a coefficient of variation higher than 15% were omitted from the analyses.

The fecundity was compared between the dry and rainy seasons after neperian logarithmic (*ln*) transformation of the data (EN and CW) and determination of the linear equation ($lny = a + b\ lnx$) for fecundity in each season. Then, the slopes and intercepts of the equations were compared by ANCOVA, taking CW as the covariable (Zar 1999).

Since most of the ovigerous females were collected in the rainy season (spring and summer), we analyzed the size of these females in each month. Monthly size data was previously submitted to normality test (Shapiro-Wilk) and that with significant normal distribution were compared by ANOVA. To identify the differences detected in the ANOVA, a Tukey multiple comparisons test was used (Zar 1999), considering a statistical significance level of 5 %.

Results

A total of 801 specimens of *A. pisonii* were collected, including 378 males, 319 females without eggs, and 104 ovigerous females. The carapace width (CW) of all individuals combined ranged from 6.5 to 25.9 mm, with a mean of 15.9 ± 3.6 mm. The 14-18 mm size classes were most frequent, and males showed a significantly larger mean size than females (p<0.05) (Fig. 2, Table I).

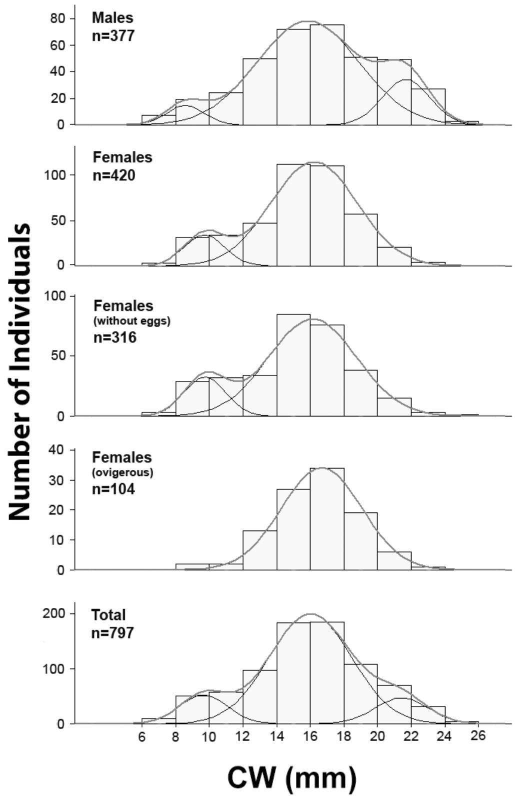

Figure 2. Distribution of individuals in size classes for each demographic category of *Aratus pisonii,* with the resolution of the normal components (Bhattacharya) showing the cohorts of the population monthly collected from February 1999 to February 2000 in the Iguape region.

Table I. Minimum, maximum, mean, and standard deviation of the carapace width (CW) for each demographic category analyzed of *Aratus pisonii*, monthly collected from February 1999 to February 2000 in the Iguape region.

Category	N	CW (mm)		
		Min.	Max.	Mean ± Standard Deviation
Males	378	6.5	25.9	16.4 ± 3.9 b*
Females (ovigerous)	104	9.8	22.6	16.5 ± 2.6 b
Females (total)	423	7.2	24.1	15.5 ± 3.2 a
Total	801	6.5	25.9	16.0 ± 3.6

* Means followed by the same letter did not differ significantly from each other (p>0.05)

The resolution of the modes by the Bhattacharya method was carried out for each demographic category, resulting in three modal classes for the males, two for females, and one for ovigerous females (Fig. 2, Table II). All modal classes were significant at 5% ($p<0.05$).

The sex-ratio analyses revealed a bias toward males in the rainy season (spring), an equilibrium of 1:1 in the autumn, and an remarked bias toward females in the dry season (winter months) ($p<0.05$) (Fig. 3).

Ovigerous females occurred from September to April, and were absent from May to August (Fig. 4). Comparison of their mean size in each month (except for December and April because only one exemplar was collected in those months) reveals two cohorts of females that began reproductive activity at different times. In the early part of the reproductive period (spring months: September, October and November) the ovigerous females were larger than those found in January trough March, the austral summer (Fig. 5). The mean size of ovigerous females caught in February in both years (1999 and 2000) did not differ significantly (Tukey test, $p>0.01$), and includes the smaller ovigerous females collected (9.8mm of CW). However, from September to November, larger ovigerous females (multiparous) occurred in the population, and their mean size was significantly different from that estimated for February ($p<0.05$).

For the fecundity analyses, 46 females with sizes ranging from 9.8 to 21.9 mm CW were used.

The number of eggs (EN) ranged from 1,824 to 21,000 eggs; the relationship to the female size is shown in Figure 6.

Seasonality in the reproductive output was determined by grouping ovigerous females in two groups according to their season of capture (dry and rainy), and then to plot a linear regression for each one, with log-transformed data (ln). The equations obtained were then compared for differences between slopes and intercepts using an ANCOVA. No significant difference was observed, indicating similarities in the number of eggs laid in the dry and rainy seasons ($p>0.05$) (Table III).

Table II. Normal components of CW for each category of *Aratus pisonii* monthly collected from February 1999 to February 2000 in the Iguape region. (n = number of individuals; SI = separation index; na = not analyzed in the first normal component).

Category (n)	Normal Components of CW (mm) (mean ± sd)	n	SI
Males (n=377)	8.57 ± 1.11	21	na
	15.86 ± 3.02	296	3.53
	21.68 ± 1.41	60	2.63
Females (total) (n=420)	9.70 ± 1.21	52	na
	16.22 ± 2.56	368	3.46
Females (without egg) (n=316)	9.74 ± 1.23	51	na
	16.13 ± 2.61	265	3.33
Females (ovigerous) (n=104)	16.37 ± 2.56	104	na
Total (n=797)	9.64 ± 1.41	93	na
	16.00 ± 2.44	612	3.30
	21.41 ± 1.57	92	2.70

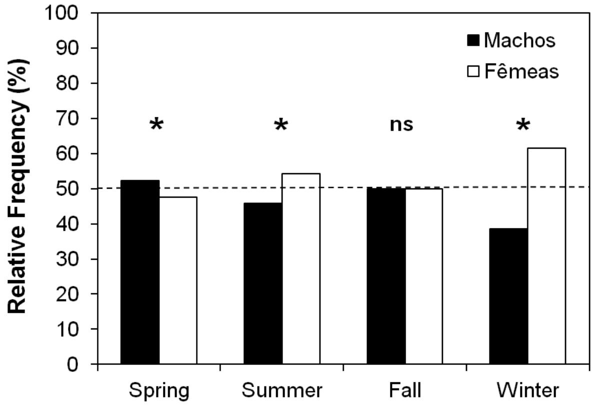

Figure 3. Seasonal relative frequency of males and females of *Aratus pisonii* collected from February 1999 to February 2000 in the Iguape region. Asterix above the bars indicate significative difference.

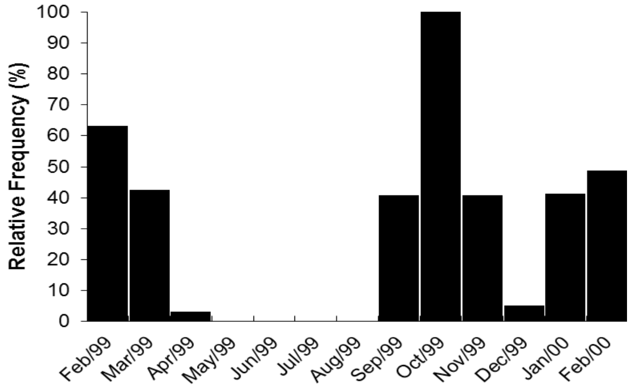

Figure 4. Monthly relative frequency of ovigerous females of *Aratus pisonii* collected from February 1999 to February 2000 in the Iguape region.

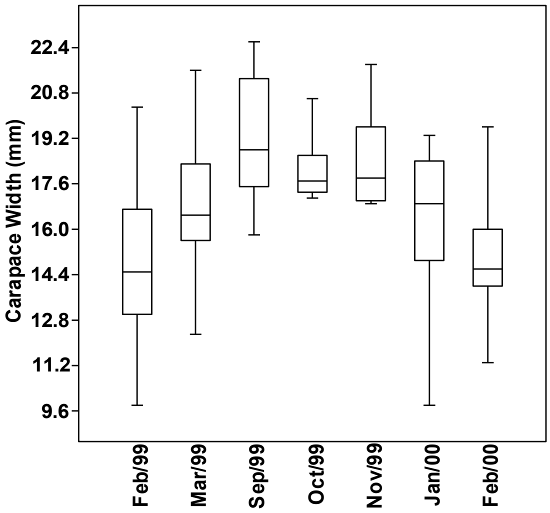

Figure 5. Monthly variation of the median size (CW) of ovigerous females of *Aratus pisonii* collected from February 1999 to February 2000 in the Iguape region. Where: box, 25-75% quartiles; horizontal line inside box, median; and wiskers, minimal and maximal values.

Discussion

To understand population dynamics, knowledge of basic life-cycle features of populations and their relationship to the environment is essential. Both reproduction and recruitment cohorts are involved in this dynamic process, and reflect evolutionary forces acting to optimize the species' survival.

In this study, we focused on cohorts to define the population dynamics of *A. pisonii*. The presence of three modal classes for males and females of *A. pisonii* reflected the differential recruitment resulting from the pause in the reproductive activity of the females during the dry months (autumn and winter) in the area.

During the one-year sampling period, the crabs caught included juvenile individuals (derived from the current recruitment), recently matured individuals (primiparous), and larger animals, probably survivors of the previous reproductive season (multiparous). We found the smaller ovigerous females during the austral summer (January and February), when the highest temperatures and rainfall occur in the region (Sant ´Anna 2005). After four or five months, these females are larger and begin a new breeding period in early spring (September). In a general way, males are larger than females due to the larger investment of females for reproductive purposes (see Warner 1967), however, an interesting fact arisen in this study is the small size of crabs in general.

The size at functional maturity, considering the size of the smallest ovigerous female (9.8 mm CW), is somewhat small. Warner (1967) reported a size of 10.8 mm in Jamaica, Conde & Díaz (1989a) found the smallest ovigerous females measuring 11.3 mm in Venezuela, and Leme (2002) reported 13.6 mm for the north coast of São Paulo state (Brazil), similar to found out by Nicolau & Oshiro (2007) for Rio de Janeiro state. Such results indicate that, apparently, the latitudinal effect on the size at maturity (Lardies & Castilla 2001, Lardies & Wehrtmann 2001) is not the main factor influencing maturation in *A. pisonii*. Overfishing is an important feature recently considered to force maturation at a smaller size in some species of commercial value (Jackson *et al.* 2001) although *A. pisonii* is not included in this category. Then, the local features that are influencing the maturity size, maybe the combination of climate and productivity.

The Cananéia-Iguape system is considered the most productive on the coast of São Paulo state.

Table III. Mean size (CW) of ovigerous females of *Aratus pisonii* collected from February 1999 to February 2000 in the Iguape region. Mean egg number (EN), and equations for fecundity for the seasons: rainy (spring + summer) and dry (autumn + winter).

Season	CW	EN	Linear function	R^2
	$\bar{x}$ ± sd	$\bar{x}$ ± sd	lny = ln a + b lnx	
Rainy (n= 37)	16.5 ± 2.8 a*	7,716 ± 4,683 a	ln EN = 1.48 + 2.60 ln CW	0.46
Dry (n = 9)	18.4 ± 2.1 a	10,166 ± 4,885 a	ln EN = 0.99 + 2.80 ln CW	0.46
Total	16.9 ± 2.8	8,195 ± 4,916	ln EN = 1.32 + 2.66 ln CW	0.48

* The means for a variable with the same letter did not differ significantly (p>0.05)

The early maturation of *A. pisonii* may be related to the local productivity, which increases the abundance of food and leads to a rapid maturation. This pattern of response to high productivity has been previously recorded in tropical areas (Conde & Díaz 1989b). However, the mean size of ovigerous females recorded in the present study (ca. 16.3 mm CW), as well as the size of females carrying no eggs (ca. 16.2 mm CW) are also smaller than those found at lower latitudes (around 18 mm CW), suggesting a high mortality rate as soon as the females became adults.

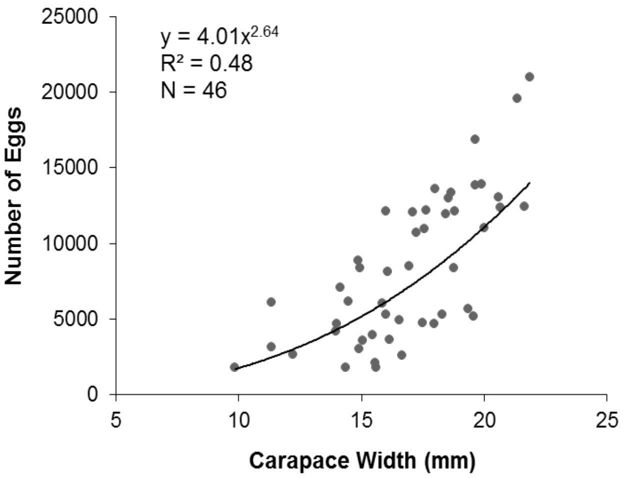

Figure 6. Relationship between number of eggs and carapace width for *Aratus pisonii* collected from February 1999 to February 2000 in the Iguape region.

In tropical regions, sex ratio records for *A. pisonii* were female-biased and a continuous reproduction pattern was recorded all year round (Warner 1967, Diaz & Conde 1989, Conde & Diaz 1989a,b). According to Warner (1967) females living in the inside areas of mangroves would need to migrate seaward for larval release increasing this way female proportion in the population. Anyway, this is not a consensus, since Dìaz & Conde (1989a), states that *A. pisonii* is a sedentary crab. Thereafter, Leme (2002) did not record active females during the winter on the north coast of São Paulo state; rather, she found inactive females, hiding under tree trunks, probably in response to the lower temperatures recorded there (Alvarez *et al*. 2013). In this study, the reproductive pause and the female-biased sex ratio in the dry winter suggest that females of *A. pisonii* are optimizing their nutritional state when the environmental conditions are unfavorable for producing eggs (Henmi 1989, 2003). Probably, this nutritional input be the factor improving the reproductive output at the end of the dry season, which could explain our finding of no difference in fecundity between dry and rainy seasons.

This study well demonstrated the reproductive plasticity and the response pattern of this species to climate conditions and local productivity. An understanding of spatial and temporal variability in the development of biological traits of species is necessary to improve stock assessment and management model in several kinds of environments, including mangrove forests where the current and future temporal changes can have important management's implications.

Acknowledgments

The authors acknowledge the 'Fundação de Amparo à Pesquisa do Estado de São Paulo' (FAPESP) for awarding financial support to MAAP (# 1998/6055-0). To Gustavo Y. Hattori that aided during the monthly captures, and Gustavo Pinheiro for helping with the figures of this article. MAAP is also grateful to CNPq for the research fellowship. Capture of the specimens was formally authorized with a permanent license to collect zoological material and to organize field expedition (# 13.585-1) by SISBIO (ICMBio-MMA). MAAP is also grateful to CNPq for the research fellowship.

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Received July 2014
Accepted December 2014
Published online December 2014