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Research Article

Sexual maturity of the deep-sea red crab *Chaceon notialis* Manning & Holthuis, 1989 (Brachyura: Geryonidae) in southern Brazil

Rodrigo Sant'Ana[1] & Paulo Ricardo Pezzuto[1]
[1]Universidade do Vale do Itajaí, Centro de Ciências Tecnológicas da Terra e do Mar
Rua Uruguai 458, CEP 88.302-202, Itajaí, SC, Brazil

ABSTRACT. The red crab *Chaceon notialis* is one of the three deep-sea crab species currently exploited in Brazil. The red crab fishery started in 1998 with foreign vessels that, as of 2000, have been extensively monitored by observers and tracked by satellite. A management plan implemented in 2005 was based only on biomass dynamics, as biological knowledge of the resource was limited at that date. Samples taken aboard were used to determine size at first sexual maturity for males and females by studying the allometric growth of the chelae and abdomen in relation to the carapace width (CW), the proportion of females with opened vulvae and eggs in the pleopods, and males showing copula marks on the first ambulatory legs. Morphometric maturity was attained, on average, at 8.9 cm CW (males) and 8.8 cm CW (females). The $CW_{50\%}$ was estimated to be 6.9 and 9.7 cm CW for females, considering the vulva condition and eggs in the pleopods, respectively, and 8.4 cm CW for males. The maximum estimated proportions of ovigerous females and males with copula marks by size class were 0.8 and 0.7, respectively, suggesting an annual reproductive cycle for the species, both at the populational and individuals levels. The size composition analysis showed that up to 97% of the females caught in the fishery were immature. Given these results, enhancing trap selectivity and minimizing the mortality of ovigerous females should be considered as new and immediate goals for the management of the resource.

Keywords: reproduction, trap fisheries, relative growth, sexual maturity, Geryonidae, *Chaceon notialis,* Brazil.

Madurez sexual del cangrejo rojo de profundidad *Chaceon notialis* Manning & Holthuis, 1989 (Brachyura: Geryonidae) al sur de Brasil

RESUMEN. El cangrejo-rojo *Chaceon notialis* corresponde a una de las tres especies de cangrejos de profundidad que actualmente se explotan en Brasil. La pesca de cangrejo-rojo comenzó en el año 1998 por barcos extranjeros que, desde 2000 fueron intensamente vigilados por observadores y rastreados por satélites. En el año de 2005 se implementó un plan de manejo, considerando solamente el estudio de la dinámica de la biomasa del recurso, ya que el conocimiento biológico todavía era limitado. A partir de muestras obtenidas a bordo de los barcos de pesca, se estimó la talla de primera madurez de machos y hembras mediante la utilización del crecimiento alométrico de la quela y el abdomen, con respecto al ancho del caparazón (CW), proporción de hembras con vulvas abiertas y huevos en los pleópodos y machos con marcas de cópula en las primeras patas ambulatorias. La madurez morfométrica para los machos fue obtenida en promedio a 8,9 cm de CW y para las hembras a 8,8 cm de CW. El $CW_{50\%}$ fue estimado en 8,4 cm para machos y para hembras, tomando en cuenta la condición de la vulva o los huevos en los pleópodos, en 6,9 y 9,7 cm respectivamente. Las máximas proporciones estimadas de hembras ovígeras y machos con marcas de cópula por talla fueron de 0,8 y 0,7 respectivamente, lo que sugiere que el ciclo reproductivo a nivel poblacional e individual es anual. El análisis de la composición de tallas indicó que el 97% de las hembras capturadas, eran inmaduras. A partir de estos resultados se consideró un aumento en la selectividad de las trampas y la disminución de las hembras ovígeras en las capturas como objetivos nuevos e inmediatos para el mejor manejo de este recurso.

Palabras clave: reproducción, pesca con trampas, crecimiento relativo, madurez sexual, Geryonidae, *Chaceon notialis,* Brasil.

Corresponding author: Paulo Ricardo Pezzuto (pezzuto@univali.br)

INTRODUCTION

The red crab *Chaceon notialis* is one of two geryonid crabs known from the southwestern Atlantic Ocean. The species inhabits slope grounds off Brazil, Uruguay, and Argentina, between 120 and 1000 m depth (Manning & Holthuis, 1989; Pezzuto *et al.*, 2002; Delgado & Defeo, 2004).

In the late 1970s, investigations undertaken by the National Fishery Institute identified a potentially harvestable stock of the species in Uruguay (Niggermeyer *et al.*, 1990). Red crab assessments conducted in the middle 1980s along the Uruguayan EEZ estimated an exploitable biomass of nearly 22,000 ton, corresponding to one of the highest geryonid stocks known in the whole world ocean (Defeo *et al.*, 1991). A directed fishery for the species emerged in that country as of 1995, attaining annual landings of up to 4,102 ton since (Delgado & Defeo, 2004).

In Brazil, the first commercial exploitation of red crabs dates from 1984 and 1985, when an exploratory fishery was conducted by two Japanese vessels near the border of the Brazilian and Uruguayan EEZs (Lima & Lima-Branco, 1991). Only after 1998 did the species become the target of a fully developed fishery carried out by another Japanese vessel (F/V Kinpo Maru 58) in the same region. Completely export oriented, this fishery yielded a total of 7,347 ton (live weight) between 1998 and 2006, with annual landings varying between 303 and 1,378 ton (Pezzuto *et al.*, 2006b).

This vessel was intensively monitored by observers and satellite vessel monitoring systems (VMS), producing a large fishery-based data set that was used to identify the species distribution and to generate preliminary estimates of stock biomass and maximum sustainable yield (Pezzuto *et al.*, 2002, 2006b). A management plan for the red crab fishery was established in May 2005, based mostly on the biomass dynamics of the stock, including a total allowable catch (TAC) (1,050 ton live weight year^{-1}, corresponding to the Maximum Sustainable Yield), maximum number of permits (two vessels), and minimum mesh size in the traps (100 mm stretched). Biological measures such as minimum legal sizes, closed areas/seasons, or sex-selective harvest strategies would have been considered in the plan but no life-cycle parameters were available for the species at the time, even though biological data had been intensively collected aboard by the observers.

At the present time, information about the species is relatively scarce and includes biomass assessments (Defeo *et al.*, 1991; Pezzuto *et al.*, 2002), fishing dynamics (Defeo & Masello, 2000a, 2000b; Athiê & Rossi-Wongtschowski, 2004), contributions to the feeding of demersal fishes (Peres & Haimovici, 2003), management (Pezzuto *et al.*, 2006a), diet (Domingos *et al.*, 2007), and size at the onset of morphological and functional maturity of females caught in Uruguayan waters (Delgado & Defeo, 2004). No information about the maturity of females is available for the Brazilian part of the stock or for males exploited anywhere.

Given their high value and k-strategist life-traits, geryonid crabs are expected to be highly vulnerable to overexploitation, requiring severe fishing regulations for their sustainability (see review by Hastie, 1995). Like biomass estimates and population structure data, knowledge about reproductive features can give the necessary support to develop management tactics intended to ensure appropriate biomass renewal rates for these fragile crabs. Size-at-maturity is, therefore, one of the most important biological parameters used for management purposes and has been widely studied in several Geryonid stocks (*e.g.* Haefner, 1977; Beyers & Wilke, 1980; Erdman & Blake, 1988; Attrill *et al.*, 1991; Fernández-Vergaz *et al.*, 2000; Delgado & Defeo, 2004; Pezzuto & Sant'Ana, 2009).

Considering the need to improve the red crab management plan with biological reference points, this paper investigates the sexual maturity of *C. notialis* vulnerable to a directed fishery in southern Brazil and analyzes the annual size-structure of the catches, quantifying the contribution of immature and mature individuals to the fishery.

MATERIAL AND METHODS

Data source and sampling

Maturity analyses were carried out with biological data collected by observers during 19 commercial trips conducted between 2001 and 2005 by the F/V Kinpo Maru 58, a 63-m-long factory vessel. This vessel fished in Brazilian waters from September 1999 to November 2007. It operated four sets of ground lines simultaneously; 450 ± 16 (SD) cylindrical-conical traps were attached to each line. The traps were spaced regularly at 18 m and measured 140 cm (Ø) at the base, 73 cm (Ø) at the top, and 65 cm in height; they were rigged with a 100-mm (stretched) mesh. The mean soak time was 38 h (Pezzuto *et al.*, 2002, 2006a).

Observers recorded, for all hauls, the date, position, depth, number of traps line^{-1}, soak time, catch haul^{-1} (kg), and the mean number of crabs trap^{-1}. During the study period, nearly 41,000 crabs were sampled aboard within the main fishing ground of the species (*i.e.* 31^{o} to 35°S and 100 to 1,000 m depth) (Table 1, Fig. 1).

Biological sampling was carried out on hauls especially selected by the observers in order to cover different depths and latitudes according to the commercial fishing strategy used by the vessel's captain. The maximum interval between successive samplings was 48 h. All crabs caught in randomly selected traps positioned in the beginning, middle, and end sections of the main ground line were examined. The sex was determined and the carapace width (CW; distance between the fifth antero-lateral spine tips) was measured to the nearest millimeter. Males were classified according to the presence or absence of copula marks (blackened areas in the merus of the second pereiopods - (see Melville-Smith, 1987) for 125 hauls. The vulva condition (*i.e.* closed/immature or opened/mature; Delgado & Defeo, 2004) and the presence of eggs in the pleopods were recorded for females sampled from 285 and 180 hauls, respectively. The number of hauls on which such biological features were observed differed due to female-biased sex ratios in the catches and seasonal reproduction.

Besides the data collected aboard, additional biological samples (frozen crabs) were regularly obtained by the observers for detailed laboratory analyses concerning the relative growth of body parts, as logistical constraints precluded taking new measurements in the field. In the laboratory, these crabs were measured (carapace width), sexed, and examined for copula marks, vulva condition, and the presence of eggs in the pleopods following the same procedures adopted aboard. In addition, detailed measurements of body parts were also obtained for relative growth analyses of secondary sexual characteristics (Hartnoll, 1974, 1982). Measurements were conducted with sliding calipers to the nearest 0.5 mm and included the abdomen width (AW, measured between the 4th and 5th abdominal somites), left and right cheliped lengths (LChL and RChL, maximum length of the upper portion of the propodus), and left and right maximum cheliped height (LChH and RChH, maximum height of the propodus measured on its exterior face) for males and females.

Data analysis

According to Hartnoll (1974, 1982), most brachyuran crabs exhibit changes in the relative growth of their secondary sexual characteristics along their ontogeny. Such changes define the transition between different growth phases (*i.e.* pre- and post-pubertal growth) that occur at the puberty molt. In this paper, the morphometric maturity of *C. notialis* was studied by analyzing the relative growth of 512 crabs processed in the laboratory (266 males, 246 females). An allometric equation ($Y = a\ CW^{b}$) was fitted to the data by least squares regression and the transition points (*i.e.* changes in slope and/or elevation) were iteratively searched by a specific routine of the software Regrans (Pezzuto, 1993). The routine seeks the CW value where the data could be split into two subsets resulting in the lowest combined residual sum of squares. A statistical test for coincidental regressions was conducted in order to check the validity of the transition points. The test compared the difference between the global sum of squares (*i.e.* calculated from a single model fitted to the data) and the pooled residual sum of squares (*i.e.* from the subsets located to the left and right sides of the transition point) (Zar, 1996). If a significant difference was found, an ANCOVA ($\alpha = 0.05$) was used to test the difference between the elevations and slopes of the two regressions (Zar, 1996), which were assumed to correspond to the pre- and post-pubertal growth phases (sensu Hartnoll, 1974).

The relative growth pattern (*i.e.* negative allometric, isometric, positive allometric) of each body dimension and phase (pre- and post-pubertal) was identified by testing the allometric coefficient (slope) against the reference value "1" (Zar, 1996).

Functional/sexual maturity was also studied by estimating the mean sizes ($CW_{50\%}$) at which males and females were able to copulate and reproduce. Proportions of males showing copula marks and females with opened vulvae and eggs in the pleopods

Table 1. *Chaceon notialis*. Number of trips, hauls, and crabs sampled aboard the F/V Kinpo Maru 58 on the slope of southern Brazil for the size at maturity analysis.

Tabla 1. *Chaceon notialis*. Número de viajes, lances de pesca y cangrejos muestreados a bordo del F/V Kinpo Maru 58 en el sur de Brasil para el análisis de la madurez sexual.

Year	Trips	Hauls	Males	Females	Total	Depth range (m)
2001	4	85	5,379	16,097	21,447	326 - 830
2002	4	83	2,156	4,842	6,999	182 - 970
2003	4	99	1,268	2,865	4,134	357 - 844
2004	4	112	2,073	4,183	6,257	264 - 901
2005	3	74	867	2,042	2,909	325 - 835
Total	19	451	11,744	30,030	41,774	182 - 970

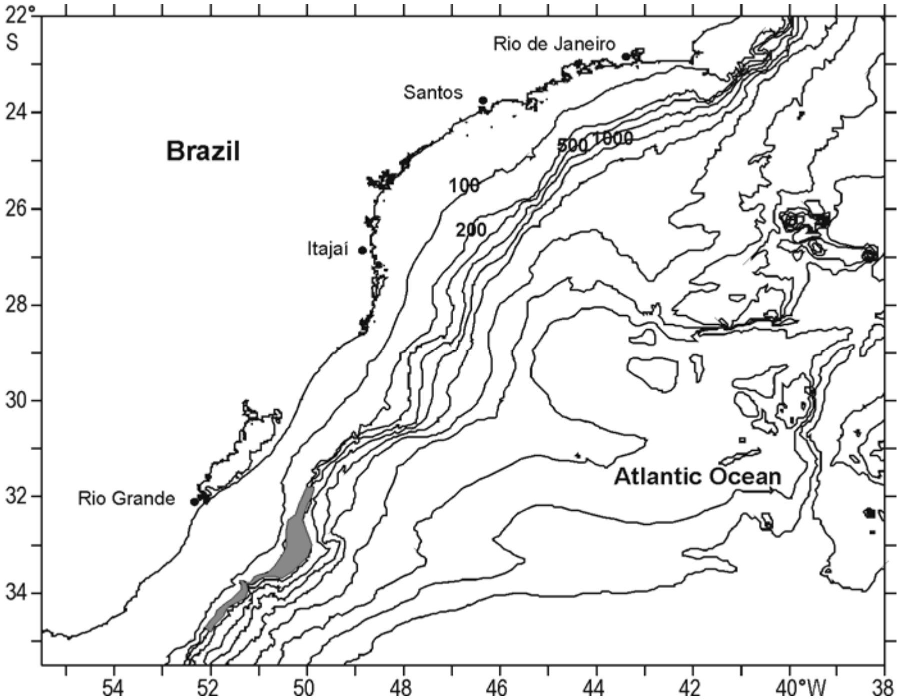

Figure 1. Map showing the main fishing area of *Chaceon notialis* in southern Brazil during the study period (gray area). Isobaths of 100, 200, 500, and 1000 m are indicated.

Figura 1. Mapa de la área principal de pesca de *Chaceon notialis* en el sur de Brasil durante el período de estudio (área gris). Se indican las isóbatas de 100, 200, 500 y 1000 m.

were calculated for 1-cm size (CW) classes, considering the total number of individuals caught during the hauls sampled aboard. The total numbers in the catches were previously estimated by multiplying the numbers in the samples by the ratio between the total catch weight and the sample weight. Proportions of ovigerous females were analyzed only for trips carried out between July and December, the main reproductive season of the species (Pezzuto *et al.*, 2006b).

A non-linear minimum squares estimation procedure was then used to fit a generalized logistic model (Restrepo & Watson, 1991) to the data as follows:

$$P_{CW} = \frac{\beta}{1+e^{(\alpha_1-\alpha_2 CW)}} \qquad (1)$$

where P_{CW} is the proportion of individuals in each size class and $\alpha 1$, $\alpha 2$, and β are parameters. In this model, β is a more general parameter that allows for the asymptotic proportion of the model to be lower or equal to 1. Therefore, a penalty function for $\beta \leq 1$ was included in the parameter estimation procedure. This is of special interest for management purposes as it can indicate the maximum theoretical proportion of individuals presenting the maturity criteria in the largest size classes in a given period/study area. Size at 50% maturity was given by the equation:

$$CW_{50\%} = \frac{\alpha_1}{\alpha_2} \qquad (2)$$

Confidence intervals for $CW_{50\%}$ were estimated by a bootstrap procedure in which frequency distributions of individuals with copula marks, opened vulvae, and eggs in the pleopods were randomly resampled 250 times, resulting in a corresponding number of logistic curves for each case. Given the asymmetrical distribution of the results, the medians of the 250 $CW_{50\%}$ estimates were calculated and the 2.5 and 97.5% percentiles used as 95% confidence intervals (CI) (Haddon, 2001).

The size-structure of the global catches was studied using information collected by the observers during all trips. It was analyzed by sex in terms of the proportion of mature and immature individuals fished per year and considering the total number of individuals sampled aboard in the period. Before pooling the data from several trips and hauls, numbers sampled by size class and sex were raised to the total caught in the respective hauls following the same procedure described in the functional/sexual maturity analysis.

Weighted averages (and the respective 95% CI) of the CW for ovigerous females were calculated by year following Defeo *et al.* (1992). Increasing or decreasing trends in mean sizes with time were tested by fitting a linear minimum squares regression to the data and testing the slope significance against 0 (Zar, 1996).

RESULTS

Morphometric maturity

The relative growth of males showed significant changes along the ontogeny for all selected dimensions ($p < 0.05$). Transitions occurred between 8.2 and 10.6 CW (mean = 8.9 ± 0.9 SD) and several dimensions showed different relative growth patterns before and after their transition points (Table 2, Fig. 2). Allometry in ChH was first isometric ($b = 1$) and then changed to allometric positive after the respective transition points. The allometry was also positive for ChL in larger sizes but was preceded by an isometric and allometric growth phase in the right and left chelae, respectively (Table 2, Fig. 2).

As observed in males, relative growth in females was also characterized by significant changes along the ontogeny. For both chelae, the transition points in height and length occurred within a narrower range of CW values (8.5 to 9.5 cm) than in the abdomen, where growth changes were observed in comparatively smaller sizes (7.6 cm) (Table 2, Fig. 3). In all dimensions, relative growth was first allometric positive, changing to allometric negative for ChL (left and right) and ChH (right) and to isometric for AW and ChH (left) (Table 2, Fig. 3). Considering all the dimensions examined in females, the transition points of females occurred, on average, at 8.8 ± 0.8 cm CW.

Functional/sexual maturity

The smallest male observed with copula marks was an individual of 6.3 cm CW. A value of 0.68 was estimated for the parameter β of the logistic function, as the proportion of males with darkened areas on their legs never reached 100% for any size class (Fig. 4a). The onset of sexual maturity in males ($CW_{50\%}$) occurred at 8.4 cm (Table 3, Fig. 4a).

The smallest female with opened vulvae measured 5.0 cm and all individuals larger than 10 cm showed this condition, resulting in an estimate of the size of functional maturity of 6.9 cm (CW) (Table 3, Fig. 4b). The presence of eggs in the pleopods was first observed in a female measuring 7.0 cm CW. Based on this characteristic, we estimated sexual maturity to occur at 9.7 cm, and the maximum theoretical proportion of individuals carrying eggs during the main reproductive period (β parameter) was 0.8 (Table 3, Fig. 4c).

Size-structure

The global size structure of red crab catches examined between 2001 and 2005 revealed that males were relatively larger than females, ranging from 4.9 to 17.5 cm and 3.5 to 14.3 cm, respectively. Both sexes showed normally distributed size frequencies, but males exhibited a fairly asymmetric distribution for smaller sizes (Fig. 5a). The size catch-composition analysis indicated different scenarios depending on the maturity criterion considered.

Table 2. *Chaceon notialis*. Potential regressions ($Y = a X^b$) fitted between carapace width (CW) (independent variable) and abdomen width (AW), left chelae length (LChL), left chelae height (LChH), right chelae length (RChL), and right chelae height (RChH) by sex. t-value: tests for H_0: b = 1; *: $p < 0.05$; **: $p < 0.01$; D.F. degrees of freedom.

Tabla 2. *Chaceon notialis*. Regresiones potenciales ($Y = a X^b$) ajustadas entre el ancho del caparazón (CW) (variable independiente) y ancho del abdomen (AW), largo de la quela izquierda (LChL), altura de la quela izquierda (LChH), largo de la quela derecha (RChL) y altura de la quela derecha (RChH), por sexo. Valor de t: test para H_0: b = 1; *: p < 0,05; **: p < 0,01. DF: grados de libertad.

Sex	Body dimension	Transition point (CW, cm)	Subset	a	b	r^2	t-value	DF
Male	AW	10.6 cm	Left	0.2065	1.1360	0.906	4.4812**	147
			Right	0.6700	0.6562	0.218	-2.9893**	119
	LChL	8.7 cm	Left	0.1517	1.2764	0.870	3.7573**	47
			Right	0.1813	1.2166	0.830	5.4830**	196
	LChH	8.2 cm	Left	0.1724	1.1352	0.882	1.3055	18
			Right	0.1108	1.3857	0.857	9.6353**	202
	RChL	8.5 cm	Left	0.2243	1.1162	0.873	1.700	41
			Right	0.1720	1.2738	0.815	6.3229**	199
	RChH	8.4 cm	Left	0.2488	0.9968	0.796	-0.0355	34
			Right	0.111	1.4200	0.842	9.7315**	205
Female	AW	7.6 cm	Left	0.111	1.6762	0.894	9.3888**	66
			Right	0.3984	1.0642	0.787	1.5456	180
	LChL	8.5 cm	Left	0.2105	1.0624	0.925	2.355*	132
			Right	0.3524	0.8328	0.499	-1.9526*	97
	LChH	9.5 cm	Left	0.1427	1.2061	0.947	10.3876**	210
			Right	0.1745	1.1035	0.511	0.3951	19
	RChL	9.4 cm	Left	0.2313	1.0542	0.911	2.2516*	190
			Right	1.3287	0.288	0.060	-3.3214**	30
	RChH	9.2 cm	Left	0.1833	1.1180	0.926	5.0042**	182
			Right	0.6631	0.5562	0.246	-2.6597**	36

Virtually all females caught during the study period (99%) were functionally mature (Table 4). However, a radically opposed scenario emerged when considering the morphometric (i.e. mean value of the CW transition points) and sexual maturity criteria, in which cases the proportion of immature females in the catches attained, on average, 67.9% and 96.7%, respectively (Table 4). Contrary to that observed in females, the contribution of immature males in the catches was always reduced (< 12%), irrespective of the maturity criteria chosen for analysis (Table 4).

Weighted mean sizes (CW) of ovigerous females caught in the fishery tended to decrease along the years of exploitation from 8.6 cm in 2001 to 8.1 cm in 2005, but this trend was not significant (b = -0.0967; p = 0.12; t-value = -2.16) (Fig. 5b).

DISCUSSION

In this work, size at maturity estimates for *C. notialis* were obtained by taking into account a scenario of indeterminate growth, *i.e.* not considering the existence of a terminal molt in the species. This approach follows the arguments of Pezzuto & Sant'Ana (2009), which examined the maturity of the royal crab *Chaceon ramosae* in Brazil. The authors revealed that, whereas some controversy does exist, at present, few if any concrete bases can be found in the literature to support the hypothesis of deterministic growth in geryonids.

In a recent paper, Delgado & Defeo (2004) studied the sexual maturity of *C. notialis* females in Uruguay considering either the presence or absence of a terminal molt in the species. The estimates produced in the present study were strikingly close to their results (obtained under the assumption that females continue to grow after the pubertal molt). The CW$_{50\%}$ estimated from females with opened vulvae were virtually identical in both studies (6.9 cm in Brazil; 7.0 in Uruguay) and very similar to the size at maturity calculated by Delgado & Defeo (2004) from the percentages of females with gonads in an advanced developmental

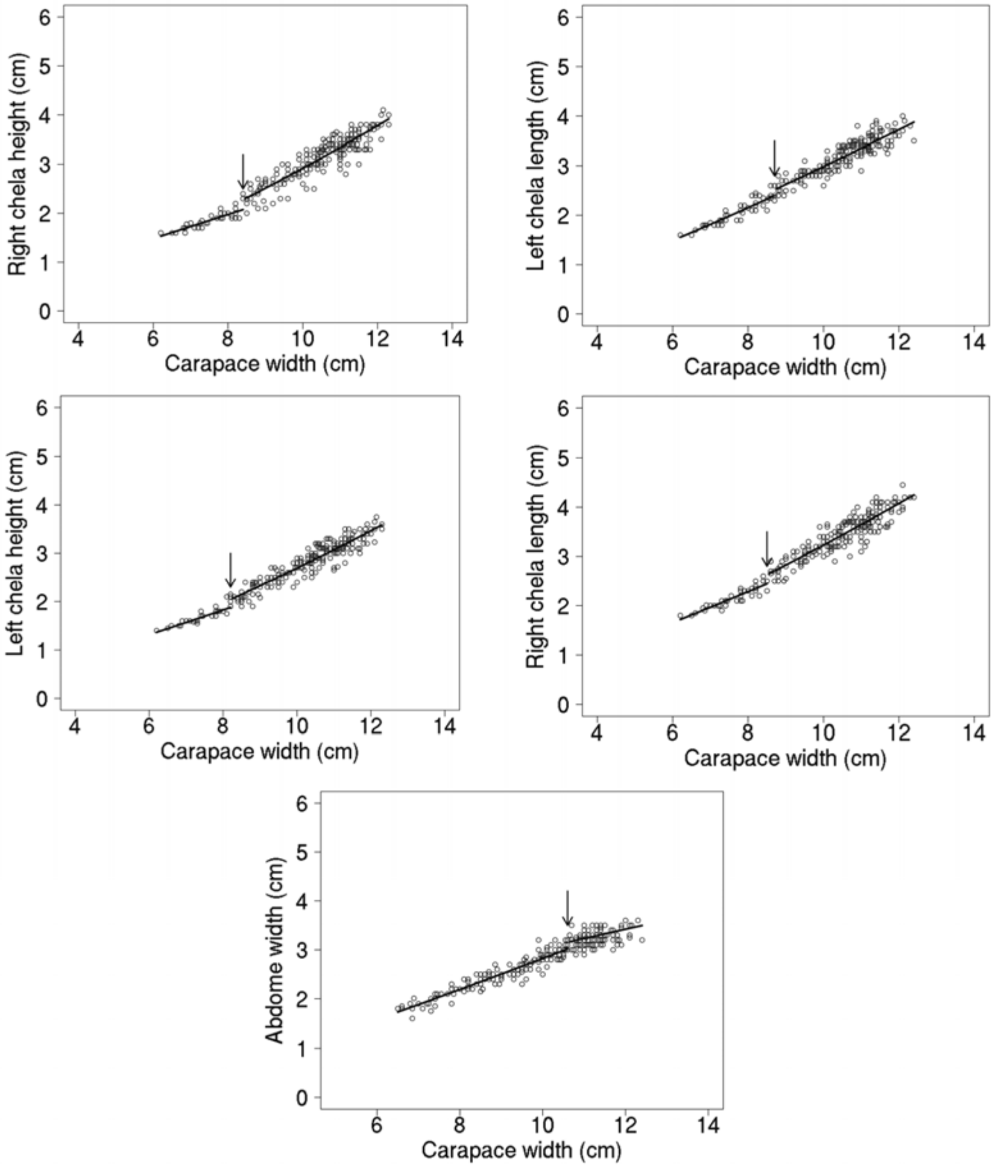

Figure 2. *Chaceon notialis*. Plots of relative growth of chelipod and abdomen dimensions for males. Arrows indicate transition points between different growth phases.

Figura 2. *Chaceon notialis.* Relaciones de crecimiento relativo de las dimensiones de la quela y abdomen para machos. Las flechas indican los puntos de transición entre las diferentes fases de crecimiento.

stage (7.2 cm). In addition, the $CW_{50\%}$ estimated in Brazil from ovigerous females (9.7 cm) matched the mean size of females with mature gonads taken from Uruguayan waters (~9.1 cm). The similarity among these results reinforces the suspicion that *C. notialis* may constitute a shared stock between Brazil and Uruguay (Lima & Lima-Branco, 1991; Defeo *et al.*, 1992; Pezzuto *et al.*, 2006a).

As observed in most geryonids (Hastie, 1995), *C. notialis* males attain larger sizes than females (Niggemeyer *et al.*, 1990). Melville-Smith (1989), who found a similar pattern in *C. maritae*, argued that females would undergo smaller size increments per molt than males because of their higher reproductive investment. As a consequence of the larger sizes attained by males and their specialized copulatory behavior, which involves forming a protective cage around the receptive female by using their locomotory legs (Elner *et al.*, 1987; Erdman & Blake, 1988), males also tend to mature at larger sizes (see review in Pezzuto

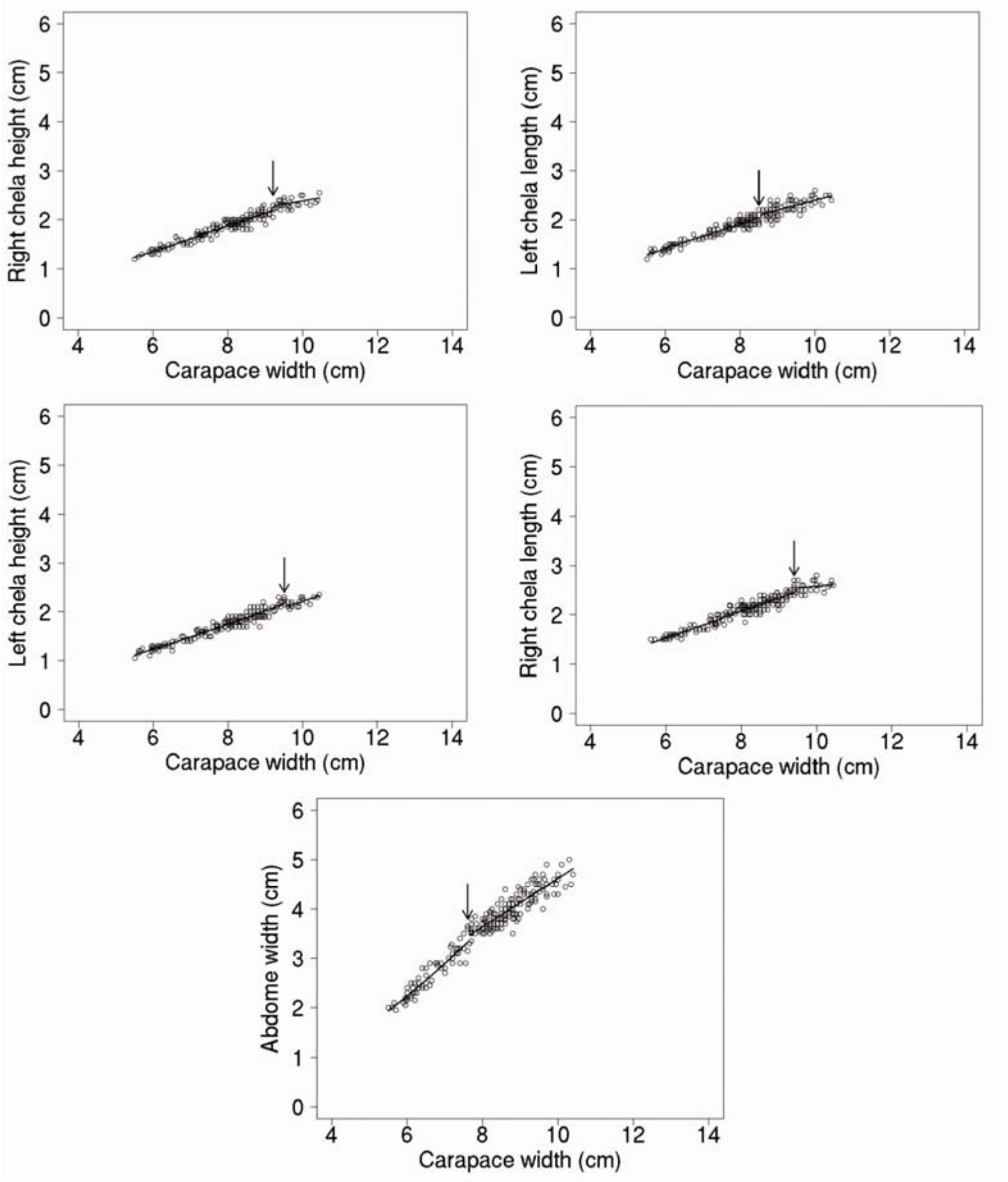

Figure 3. *Chaceon notialis*. Plots of relative growth of chelipod and abdomen dimensions for females. Arrows indicate transition points between different growth phases.

Figura 3. *Chaceon notialis.* Relaciones de crecimiento relativo entre la quela y abdomen en hembras. Las flechas indican los puntos de transición entre las diferentes fases de crecimiento.

Sant'Ana, 2009). Therefore, it is noteworthy that *C. notialis* males seem to mature at relatively smaller sizes than females, as suggested in the present paper. In the northeast Atlantic, a similar result was found for an exploited population of *C. affinis*, whose males and females were found to mature at 94 mm and 109 mm, respectively (Robinson, 2008). However, as expected for the group, males of the same species mature at larger sizes than females in the Canary Islands, where no fishery for the species exists (Fernández-Vérgaz *et al.*, 2000).

Three hypotheses can be raised to explain this very unexpected result: (i) morphological and sexual sizes at maturity calculated in the present work for males of *C. notialis* are, in fact, underestimated; (ii) female sizes at sexual maturity (based on the proportion of ovigerous females in the catches) are overestimated; and (iii) all estimates are correct and a deviation does exist in the actual population structure of the species. The first hypothesis seems to be largely improbable as both morphological and sexual sizes at maturity were very similar despite being supported by completely

Table 3. *Chaceon notialis.* Parameters (α1, α2, and *β*) of the logistic curves (± C.I. 95%) fitted to the proportion of females with opened vulvae, ovigerous females and males showing copula marks by size class and the corresponding size at maturity ($CW_{50\%}$) estimated by the bootstrap procedure.

Tabla 3. *Chaceon notialis*. Parámetros (α1, α2 y *β*) del modelo logístico (± I.C. 95%) ajustados a la proporción de hembras con vulvas abiertas, hembras ovígeras y machos con marcas de cópula por clases de talla y las correspondientes tallas de primera madurez ($CW_{50\%}$), estimadas por bootstrap.

Parameters	Female				Male	
	Opened vulvae		Ovigerous		Copula marks	
	Mean	CI (95%)	Mean	CI (95%)	Mean	CI (95%)
B	0.98	0.95-1.00	0.80	0.31-1.29	0.68	0.58-0.77
α1	12.75	10.55-14.95	6.89	4.05-9.72	11.79	4.98-18.60
α2	1.96	1.54-2.18	0.69	0.28-1.10	1.41	0.57-2.24
$CW_{50\%}$ (cm)	6.85		9.98		8.36	
Bootstrap	Median	CI (2.5-97.5%)	Median	CI (2.5-97.5%)	Median	CI (2.5-97.5%)
$CW_{50\%}$ (cm)	6.85	6.53-7.13	9.73	7.29-11.01	8.40	7.95-10.0

distinct data, methods, and assumptions. On the other hand, the second hypothesis could be supported by the fact that sizes at maturity estimated from size-specific proportions of ovigerous females in the catches might be influenced by the catch composition, which might vary according to the abundance of mature and immature individuals in the fishing areas and/or due to differential attractiveness of the traps and vulnerability of females to these during the breeding phase (Melville-Smith, 1987). However, using fishing-based data collected in the middle 1990s, Defeo & Masello (2000a) reported a marked reduction in the mean individual weight of males in comparison with the original size-structure observed before the development of the commercial fishery in Uruguay. The authors considered this finding to be a first sign of overexploitation, especially because, this is a male-centered fishery, *i.e.*, only males are retained in that country (Delgado & Defeo, 2004). As with the change in the male size structure, the recent tendency toward lower mean sizes of ovigerous females and the occurrence of smaller average females in Brazil with opened vulvae (6.8 cm) than observed from morphological analyses (8.9 cm) suggest that the third hypothesis could, in fact, be true. In this case, the population would be experiencing an adjustment in its reproductive parameters as a response to the overexploited condition of the stock.

Not all mature males exhibited copula marks on their legs (maximum observed and predicted proportions of individuals showing this feature were 0.74 and 0.68, respectively). Pezzuto & Sant'Ana (2009) observed similar results for *C. ramosae*, with a slightly lower *β* parameter (0.58) in the logistic function. The authors pointed out that such a pattern might emerge from three main situations: a) if a proportion of the recently paired males molted before being caught; b) if abrasion marks are not necessarily formed in 100% of the recently paired males; and c) if not all mature males copulate during each reproductive season. Molting in *C. notialis* has not been investigated yet. Therefore, we are not able to test whether the first hypothesis could be valid for this species. However, given the low growth rates attributable to geryonid crabs and the increasing intermolt periods expected for large individuals (Lux *et al.*, 1982; Melville-Smith, 1989; Arana, 2000), it seems quite improbable that nearly 30% of adult males had molted (*i.e.* eliminating the respective copula marks along with their old shells) between the last copula and being caught, as should be the case for supporting the first hypothesis. On the other hand, the second hypothesis seems to be highly plausible. The proportion of males with copula marks was not constant in the largest size classes used in the analysis but showed a slight reduction in the 12-cm size class. In addition, 28 males measuring between 13 and 16.5 cm CW were also sampled during the study and did not show any copula marks on their legs. These specimens were not included in the analysis given their smaller sample sizes as compared to the numbers available for the other size classes. Both facts support the idea that the probability of developing copula marks could be lower from some threshold size in mature individuals of this species. In fact, a similar pattern was reported by Melville-Smith (1987) for *C. maritae*: males larger than 12 cm CW did not exhibit any marks on their legs. In this species, damage to the integument of large-sized males is not produced because their merus do not chafe against the female

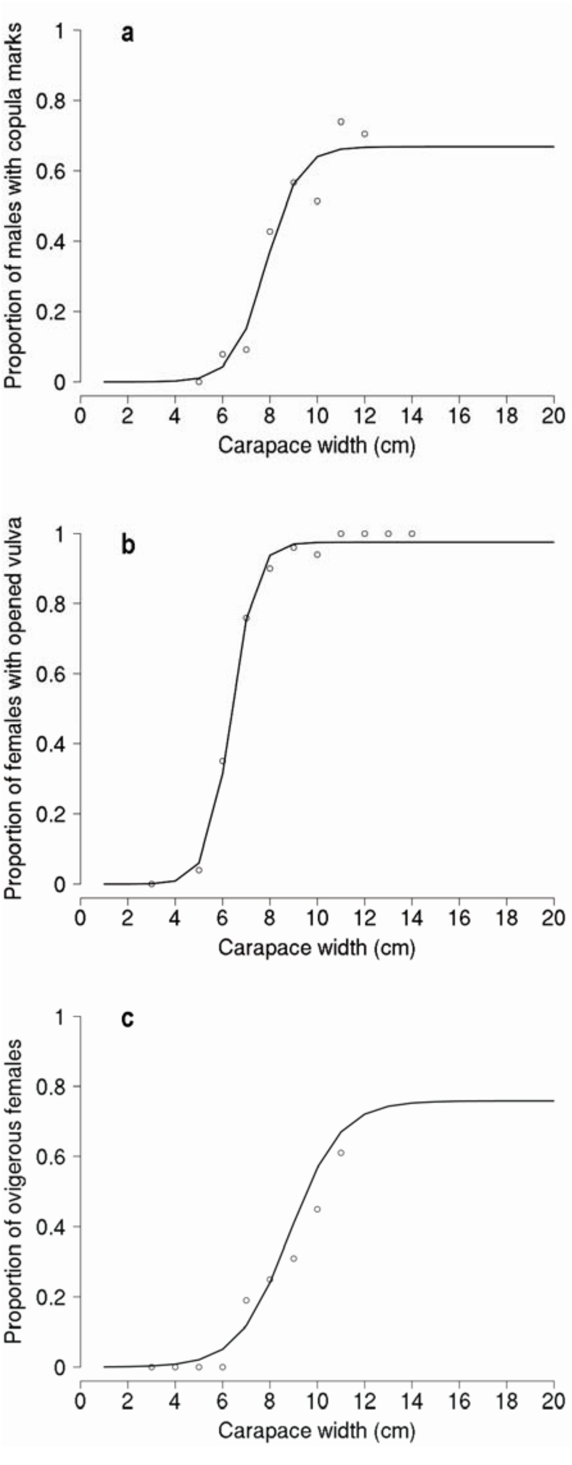

Figure 4. *Chaceon notialis*. Logistic model (solid line) fitted to the observed proportion (points) of males showing copula marks (a) and females with opened vulva (b) and eggs in the pleopods (c).

Figura 4. *Chaceon notialis.* Modelo logístico (línea continua) ajustado a la proporción observada (puntos) de machos con marcas de cópula (a); hembras con vulvas abiertas (b); y huevos en los pleópodos (c).

carapace during the pre-copulatory embrace and mating (Melville-Smith, 1987). It is possible, therefore, that *C. notialis* behave in a similar way, with most mature males copulating in each reproductive period but not necessarily producing copula marks. Besides supporting said hypothesis, our results concerning the maximum proportion of ovigerous females by size (see below) also offer little if any support to the third hypothesis that individual males do not tend to reproduce each year.

According to the logistic model fitted to the data, the maximum theoretical proportion of ovigerous females by size class was 80% ($\beta = 0.8$). β values near 1 (100%) are considerably high and suggest that reproduction in this species takes place on an annual basis, both at the populational and individual levels, as also found for *C. maritae* off Namibia (Melville-Smith, 1987). On the other hand, the same does not occur with the royal-crab *C. ramosae* in Brazil, which has been exploited between 19 and 31°S (farther north than the *C. notialis* fishing grounds; see Figure 1 in Pezzuto & Sant'Ana, 2009). Catches of ovigerous royal-crab females are concentrated in the first semester of each year (Pezzuto *et al.*, 2006b), but individual males and females seem to reproduce on a bi-annual basis only (Pezzuto & Sant'Ana, 2009). Bi-annual cycles were suggested for other geryonids and have been interpreted as a consequence of the food-limited characteristic of the deep-water environment (Erdman & Blake, 1988; Erdman *et al.*, 1991; Pinho *et al.*, 1998 in López-Abellán *et al.*, 2002). In the case of *C. notialis*, an annual reproductive strategy would imply a significant energetic investment that should be compensated by comparatively higher food availability. In fact, the species occurs along subtropical/temperate latitudes strongly influenced by highly productive water masses including Subantarctic Water carried out by the Malvinas Current, the Subtropical Convergence formed between the Malvinas and Brazil currents, and discharge from La Plata River (Garcia & Garcia, 2008). Therefore, higher biological production levels should be expected to occur along the *C. notialis* distributional range than in the tropical waters under which *C. ramosae* occurs (see review on primary productivity along southeastern and southern Brazil in Gaeta & Brandini, 2006). These processes also seem to influence the biomass of the respective stocks. Defeo *et al.* (1991) concluded, based on surveys conducted in the middle 1980s, that *C. notialis* shows one of the highest biomasses estimated for geryonid crabs in the world, even considering only the portion of the stock found in Uruguay and northern Argentina.

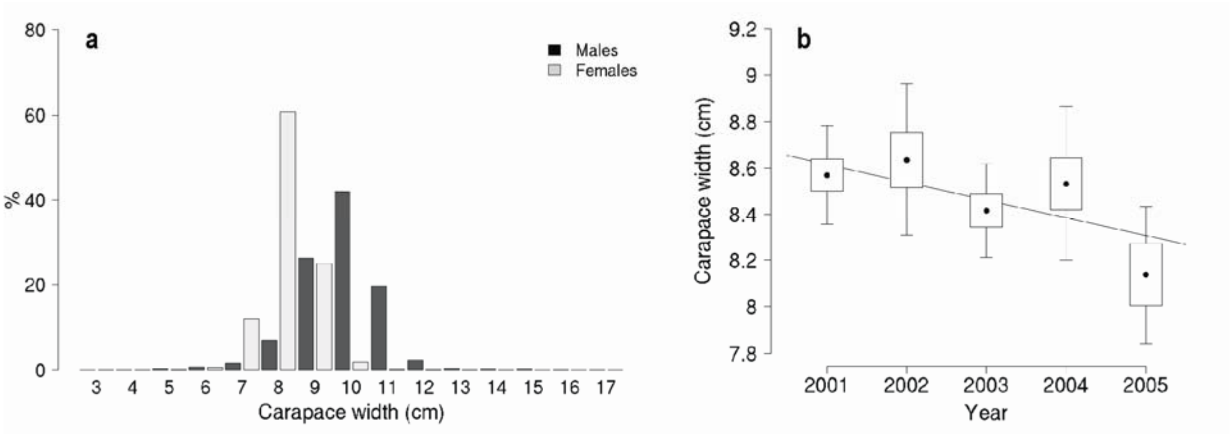

Figure 5. *Chaceon notialis*. Size-frequency distribution of males and females (a) and variation of mean sizes of ovigerous females (b) caught in commercial fisheries in southern Brazil between 2001 and 2005. In (b), boxes and bars are, respectively, confidence intervals (95%) and standard deviations.

Figura 5. *Chaceon notialis*. Distribución de frecuencia de tallas de machos y hembras (a) y variación de los tamaños promedios de las hembras ovígeras (b) capturadas por la pesca comercial en el sur de Brasil entre 2001 y 2005. En (b) se presentan los intervalos de confianza al 95% (cajas) y las desviaciones estándar.

Table 4. *Chaceon notialis.* Percentages of immature and mature individuals in the commercial catches by sex and year, according to the different criteria for determining sexual maturity. SD: standard deviation.

Tabla 4. *Chaceon notialis.* Porcentaje de individuos inmaduros y maduros en las capturas comerciales por sexo y año según los distintos criterios de determinación de la madurez sexual. SD: desviación estándar.

Year	Females						Males			
	Relative growth (8.8 cm)		Opened vulvae (6.9 cm)		Eggs in the pleopods (9.7 cm)		Relative growth (8.9 cm)		Copula marks (8.4 cm)	
	Immature (%)	Mature (%)	Immature (%)	Mature (%)	Immature (%)	Mature (%)	Immature (%)	Mature (%)	Immature (%)	Mature (%)
2001	59.9	40.1	0.0	100.0	94.9	5.1	3.4	96.6	1.2	98.9
2002	64.8	35.2	1.3	98.7	93.2	6.8	12.4	87.6	6.0	94.0
2003	67.8	32.2	0.2	99.8	98.5	1.5	8.3	91.7	2.9	97.1
2004	68.4	31.6	2.5	97.5	97.4	2.6	17.2	82.8	11.0	89.0
2005	78.4	21.6	0.8	99.3	99.6	0.4	17.7	82.3	10.3	89.7
Mean	67.9	32.1	0.9	99.1	96.7	3.3	11.8	88.2	6.3	93.7
SD	6.8	6.8	1.0	1.0	2.6	2.6	6.1	6.1	4.4	4.4

In spite of the relatively high value obtained for the maximum theoretical proportion of ovigerous females by size class, it must be stressed that, at present, the observed values peaked at a much lower level (0.61). Delgado & Defeo (2004) investigated the sexual maturity of the same species in Uruguay and observed that 65% of the morphologically mature females showed marks of mating. In addition, most of them lacked seminal contents in their reservoirs. Delgado & Defeo (2004) suggested that, due to the selective exploitation of males, the sperm supply might have become a limiting resource for the population. A similar concern was raised by Wahle *et al.* (2008) for the northwest Atlantic red crab *C. quinquedens* fishery, where the abundance of large males declined by 42% after three decades of selective harvesting. Our results could support the Delgado & Defeo (2004) hypothesis, considering that most *C. notialis* males caught in Brazil (supposedly in much lower numbers than in the original population structure) have shown signs of reproductive activity (copula marks), but a proportionally smaller portion of the females seem to have been effectively fertilized. Examining the temporal series of sex-ratio and ovigerous females caught by reproductive season (available at least for the Brazilian portion of the stock) could provide more support to test this hypothesis in the future.

Analyzing the percentages of immature crabs in the commercial catches reveals distinct scenarios depending on the sex and maturity criteria analyzed. In Brazil, the participation of immature males in the catches, although higher in 2004 and 2005, has been quite low. On the contrary, most females caught in Brazil could be classified as immature, considering both morphometric and sexual sizes at maturity. Taking into account that a) contrary to the situation in Uruguay, the Brazilian fishery has been predominantly sustained by females, b) enforcement in Brazil has not been completely successful as catches have also surpassed the maximum estimated sustainable yield in most years and minimum mesh sizes restrictions have not been observed, c) mean sizes of ovigerous females seem to be declining over the years, and d) the stock biomass in the Brazilian EEZ was reduced by 30% in 2005 (Pezzuto *et al.*, 2006b), the excessively high mortality levels imposed on immature females could contribute to a much more severe impact on the stock.

This scenario points to a biologically unsustainable condition that should be changed by modifying and including new measures in the management of the *C. notialis* fishery in Brazil. These measures should emphasize enhancing trap selectivity (Tallack, 2007) and the implementation of spatial and temporal restrictions on effort allocation in order to reduce catches of immature and ovigerous females by the fleet. Based on the results from this paper and from Pezzuto *et al.* (2006b), the present management of the *C. notialis* fishery in Brazil has been changed recently, incorporating, *inter alia*, a 30% reduction in the TAC, an increase in the permitted minimum mesh size in the traps (from 100 to 120 mm stretched), and the closure of the spawning areas < 600 m depth to the fishery from 1 August to 31 December each year. As the vessels targeting *C. notialis* should be obligatorily monitored by observers on 100% of their trips, biological data will be available in order to verify the efficacy of these changes and to refine them, if necessary, in a continuous process of adaptive management. On the other hand, the establishment of collaborative efforts between Brazilian and Uruguayan fishing authorities and scientists should be encouraged in the near future in order to confirm the shared status of the stock and implement global management measures intended to ensure the biological sustainability of *C. notialis*.

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