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Research Article

Sexual maturity of the deep-sea royal crab *Chaceon ramosae* Manning, Tavares & Albuquerque, 1989 (Brachyura: Geryonidae) in southern Brazil

Paulo Ricardo Pezzuto[1] & Rodrigo Sant'Ana[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 royal crab *Chaceon ramosae* is one of the three species of deep-sea crabs currently exploited in Brazil. The royal crab fishery started in 2001 with foreign vessels that were 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 use of allometric growth of chelae and abdomen in relation to 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 12.1 cm (males) and 10.7 cm (females). The $CW_{50\%}$ was estimated to be 10.9 cm and 12.2 cm for females, respectively considering the vulva condition and eggs in the pleopods, and 13.6 cm for males. By size class, the maximum estimated proportions of ovigerous females by size class was 0.4 and of males with copula marks was 0.6, suggesting a bi-annual reproductive cycle for individuals of the species. The size composition analysis showed that immature individuals may comprise up to 70% of the catches. These results indicate the need to consider enhanced trap selectivity and lower mortality of ovigerous females as new and immediate goals to improve resource management.

Keywords: deep-water resources, reproduction, trap fisheries, relative growth, sexual maturity, Geryonidae, *Chaceon ramosae*, continental slope, Brazil.

Madurez sexual del cangrejo real *Chaceon ramosae* Manning, Tavares & Albuquerque, 1989 (Brachyura: Geryonidae) en el sur de Brasil

RESUMEN. El cangrejo real *Chaceon ramosae* corresponde a una de las tres especies de cangrejos de profundidad que actualmente se explotan en Brasil. La pesca de cangrejo real comenzó en el año 2001 por barcos extranjeros que eran intensamente supervisados 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 a través de 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 de los machos fue obtenida en promedio a 12,1 cm CW y en las hembras a 10,7 cm CW. El $CW_{50\%}$ fue estimado en 13,6 cm en machos y, en hembras considerando la condición de la vulva o los huevos en los pleópodos, en 10,9 y 12,2 cm respectivamente. La máxima proporción estimada de hembras ovígeras y machos con marcas de cópula por talla fueron de 0,4 y 0,6 respectivamente, lo que sugiere que el ciclo reproductivo a nivel individual es bi-anual. El análisis de la composición de tallas evidenció que individuos inmaduros componen hasta el 70% de las capturas. A partir de estos resultados, se consideró incrementar el efecto selectivo de las trampas y disminuir la captura de hembras ovígeras, como objetivos nuevos e inmediatos para mejorar el manejo de este recurso.

Palabras clave: recursos de profundidad, reproducción, pesca con trampas, crecimiento relativo, madurez sexual, Geryonidae, *Chaceon ramosae*, talud continental, Brasil.

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

INTRODUCTION

Geryonid crabs are widely distributed around the continental slopes of the world ocean (Hastie, 1995) and sustain commercial fisheries on both sides of the Atlantic. *Chaceon maritae* is fished for along southwestern Africa (Melville-Smith, 1988); *C. quinquedens* is targeted from Canada throughout the southeastern United States, where a fishery for *C. fenneri* also takes place (Erdman & Blake, 1988; NEFMC, 2002); and *C. notialis* has been exploited in Uruguayan waters since the 1990s (Defeo & Masello, 2000; Delgado & Defeo, 2004).

Following the worldwide expansion of industrial fisheries to deep-water areas (Morato *et al.*, 2006), since the end of the 1990s, the formerly coastal-based Brazilian fishing industry has directed longline, gillnet, trawl, and trap operations to previously unexploited grounds on the slope and seamounts, searching for new and valuable bottom resources, including deep-water crabs (Peres & Haimovici, 1998; Perez *et al.*, 2002, 2003; Pezzuto *et al.*, 2006a, 2006b; Haimovici *et al.*, 2007; Carvalho *et al.*, 2009).

Revealed by trap vessels in 2001, commercial concentrations of the endemic deep-sea royal crab *Chaceon ramosae* (Manning *et al.*, 1989) soon became the target of up to eight foreign processor vessels chartered by national companies. The species was also the most abundant and valuable by-catch item for several gill-netters and trawlers that targeted other deep-sea resources, namely monkfish (*Lophius gastrophysus*) and aristeid shrimps, in the same areas (Perez & Wahrlich, 2005; Pezzuto *et al.,* 2006b). Annual royal crab landings (live weight) recorded between 2001 and 2005 ranged from 495 to 1,252 tons (mean = 789 ton yr^{-1}), including both directed and incidental catches.

The intense monitoring of trap vessels by observers and vessel monitoring systems (VMS) has resulted in a large fishery-based data set that was used to identify the species distribution and generate preliminary estimates of stock biomass and maximum sustainable yields (Pezzuto *et al.*, 2002, 2006a). A management plan for the royal crab fishery was established in May 2005, based mostly on the biomass dynamics of the stock, including total allowable catch (600 ton live weight year^{-1}, corresponding to the maximum sustainable yield), maximum number of permits (3 vessels), maximum number of traps per vessel (900 units), and minimum mesh size in 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 by the onboard observers.

Given their high value and k-strategist life-traits, geryonid crabs are expected to be highly vulnerable to over-exploitation, requiring severe fishing regulations for their sustainability (see review by Hastie, 1995). Given the need to improve the royal crab management plan with biological reference points, this paper investigates the sexual maturity of *C. ramosae* that are vulnerable to a directed fishery in southern Brazil and analyses the annual size structure of the catches, quantifying the contribution of “immature” and “mature” individuals in the fishery.

MATERIAL AND METHODS

Data source

The maturity analysis was carried out with biological data collected by observers during 21 commercial trips conducted between 2002 and 2005 by the F/V Royalist. Measuring 35.7 m total length, this factory vessel operated in Brazilian waters from May 2001 to June 2006. During the study period, nearly 19,200 crabs were sampled at the main fishing ground of the species (*i.e.* 25° to 31°S and 300 to 1,100 m depth) (Table 1, Fig. 1).

The size structure of the global catches, totaling 33,238 individuals, was studied using information collected simultaneously by observers on another seven commercial vessels operating in the same areas.

Besides the data collected aboard, biological samples (frozen crabs) were regularly obtained for laboratory analysis. Nearly 50% of these specimens were collected aboard the F/V Royalist and the remaining came from the other vessels. Detailed information on most vessels and traps used in the royal crab fishery are available in Pezzuto *et al.* (2006a).

Sampling

Observers recorded the date, position, depth, number of traps line^{-1}, soaking time, catch haul^{-1} (kg), and mean number of crab trap^{-1} for all hauls. Biological sampling was carried out on hauls selected by the observers in order to cover different depths and latitudes, according to the fishing strategy used by the vessel’s captain. Most vessels worked simultaneously with four trap lines. The maximum interval between successive samplings was 48 h and the mean soaking time of each line was 42.3 h (± 6.9 h). Crabs were randomly selected from traps positioned in the beginning, middle and end sections of the main line. Their sex was determined and their carapace width (CW, distance between the fifth antero-lateral spine tips)

Table 1. *Chaceon ramosae.* Number of trips, hauls, and crabs sampled annually aboard the F/V Royalist in southern Brazil for size-at-maturity analysis.

Tabla 1. *Chaceon ramosae*. Número de viajes, lances de pesca y muestreo de cangrejos a bordo del F/V Royalist en el sur de Brasil para el análisis de la madurez sexual.

Year	Trips	Hauls	Males	Females	Total	Depth range (m)
2002	4	60	1,916	454	2,370	504 – 1,010
2003	7	142	4,880	1,380	6,260	508 – 947
2004	6	149	5,067	2,281	7,348	435 – 1,020
2005	4	82	1,991	1,158	3,149	345 – 918
Total	21	433	13,854	5,273	19,127	-

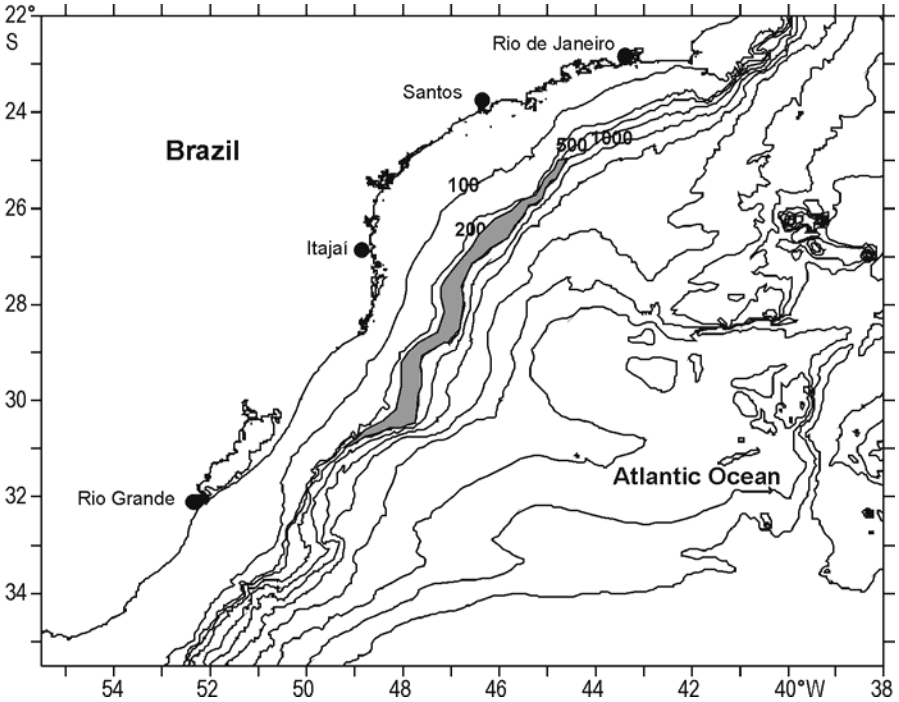

Figure 1. Map showing the main fishing area for *Chaceon ramosae* in southern Brazil during the study period (gray area). The 100, 200, 500, and 1000 m isobaths are indicated.

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

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) on 125 hauls. 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.

Frozen crabs were processed in the laboratory according to the same procedures used aboard, but detailed measurements of body parts were also obtained for the relative growth analysis of secondary sexual characteristics (Hartnoll, 1982). Measurements were conducted with sliding calipers to the nearest 0.5 mm and included: 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 in its exterior face).

Data analysis

Morphometric maturity was studied by analyzing the relative growth of 1,090 crabs processed at the laboratory (511 males, 579 females). A visual examination of scatter plots for several body parts versus CW (reference dimension) showed no clearly identifiable transition points in the data associated with morphometric maturity (Hartnoll, 1982). Therefore, an allometric equation ($Y = a\ X^b$) was fitted to the data by least squares regression and the transition points were iteratively searched by a specific routine of the software Regrans (Pezzuto, 1993). This routine seeks the CW value where the data could be split in 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 compares 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.* of the subsets located to the left and right sides of the transition point) (Zar, 1996). If a significant difference was found, ANCOVA ($\alpha = 0.05$) was used to test the difference between the elevation and slopes of the two regressions, corresponding to the pre and post-pubertal growth phases (Zar, 1996).

The relative growth pattern (*i.e.* negative allometric, isometric, or 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 studied by estimating the mean sizes ($CW_{50\%}$) at which males and females are able to copulate and reproduce. Proportions of males showing copula marks and females with opened vulvae and eggs in the pleopods 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 only analyzed on trips carried out between January and June, the main reproductive season of the species (Pezzuto *et al.*, 2006c).

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

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

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 than 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/area of study. Size at 50% maturity was given by the equation:

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

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 median of the 250 $CW_{50\%}$ estimates were calculated and the 2.5 and 97.5% percentiles were used as 95% confidence limits (Haddon, 2001).

The size-structure of the global catches was analyzed by sex in terms of the proportion of mature and immature individuals fished per year, considering all the individuals sampled aboard the eight vessels targeting *C. ramose* in the period. Before pooling the data from these vessels, trips, and hauls, the numbers sampled by size class and sex were raised to the total caught in the respective hauls following the same procedure described for the fuctional/sexual maturity analysis.

RESULTS

Morphometric maturity

The relative growth of males showed significant transition points at 12.1 cm (CW) for all dimensions but AW, whose relationship with CW was described by a single model (Table 2, Fig. 2). Allometry in the growth of the chelae was always positive ($b > 1$) irrespective of the dimension (width or height) or subset considered (pre or post-pubertal phase), but the regressions calculated for crabs larger than 12.1 cm revealed a significant increase in their elevation (suggesting a sudden increase in chelae size) and a reduction in their slopes (Table 2, Fig. 2).

Compared to the males, the females had more variable relative growth patterns. Transition points were found for all variables (including AW) and fluctuated mostly between 10.7 and 11.0 cm CW (Table 2, Fig. 3). Allometry was always positive before the transition points (pre-pubertal phase). However, in the post-

Table 2. *Chaceon ramosae*. 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 *Ho:* b = 1 *: $p < 0.05$; **: $p < 0.01$, DF: degrees of freedom.

Tabla 2. *Chaceon ramosae*. Regresiones ($Y = a X^b$) 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 *Ho:* b = 1 *: $p < 0,05$; **: $p < 0,01$, DF: grados de libertad.

Sex	Body dimension	Transition point (CW, cm)	Subset	a	b	r²	t-value	DF
Males	AW	-	Total	0.1835	1.1432	0.975	17.365**	501
	LChL	12.1	Left	0.1629	1.1981	0.958	12.656**	256
			Right	0.2202	1.1054	0.866	3.556**	217
	LChH	12.1	Left	0.1279	1.2483	0.959	15.238**	254
			Right	0.1892	1.1183	0.856	3.767**	216
	RChL	12.1	Left	0.1770	1.1904	0.958	12.252**	257
			Right	0.2309	1.1053	0.867	3.545**	215
	RChH	12.1	Left	0.1542	1.2018	0.955	12.275**	253
			Right	0.2039	1.1125	0.833	3.295**	215
Females	AW	10.7	Left	0.1303	1.4701	0.962	20.956**	172
			Right	0.2051	1.3009	0.784	8.136**	344
	LChL	11.0	Left	0.1830	1.1193	0.965	7.696**	193
			Right	0.3048	0.9122	0.655	- 2.146*	264
	LChH	10.7	Left	0.1477	1.1600	0.968	9.536**	162
			Right	0.2311	0.9777	0.716	- 0.613	289
	RChL	11.0	Left	0.1934	1.1178	0.963	7.481**	195
			Right	0.3410	0.8856	0.598	- 2.522*	259
	RChH	9.8	Left	0.1648	1.1424	0.949	5.602**	111
			Right	0.2441	0.9779	0.761	- 0.738	339

pubertal phase, the growth pattern of females became isometric for ChH and negative for ChL, yet remained positive for AW (Table 2, Fig. 3).

Functional/sexual maturity

The smallest male exhibiting copula marks measured 9.3 cm CW. A value of only 0.58 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. 4). The onset of sexual maturity in males ($CW_{50\%}$) occurred at 13.6 cm with a confidence interval distinctly skewed to the bigger sizes (12.8-15.8 cm) (Table 3).

The smallest female with opened vulvae was 7.4 cm CW. The proportion of individuals in this condition increased continuously with size, attaining 100% in females larger than 13 cm (β = 1) (Fig. 4). The $CW_{50\%}$ estimated by bootstrap was 10.9 cm with a narrow and almost symmetrical confidence interval (Table 3). Compared to the vulva condition, the presence of eggs in the pleopods suggested that sexual maturity in females was attained at larger sizes. The carapace width of the smallest ovigerous female was 8.0 cm and the respective $CW_{50\%}$ increased from 10.9 cm (opened vulvae) to 12.2 cm (Table 3, Fig. 4). Additionally, despite that fact that more than 90% of the females larger than 12.2 cm presented opened vulvae, the proportion of females carrying eggs during the main reproductive period did not surpass 0.41 (Table 3, Fig. 4).

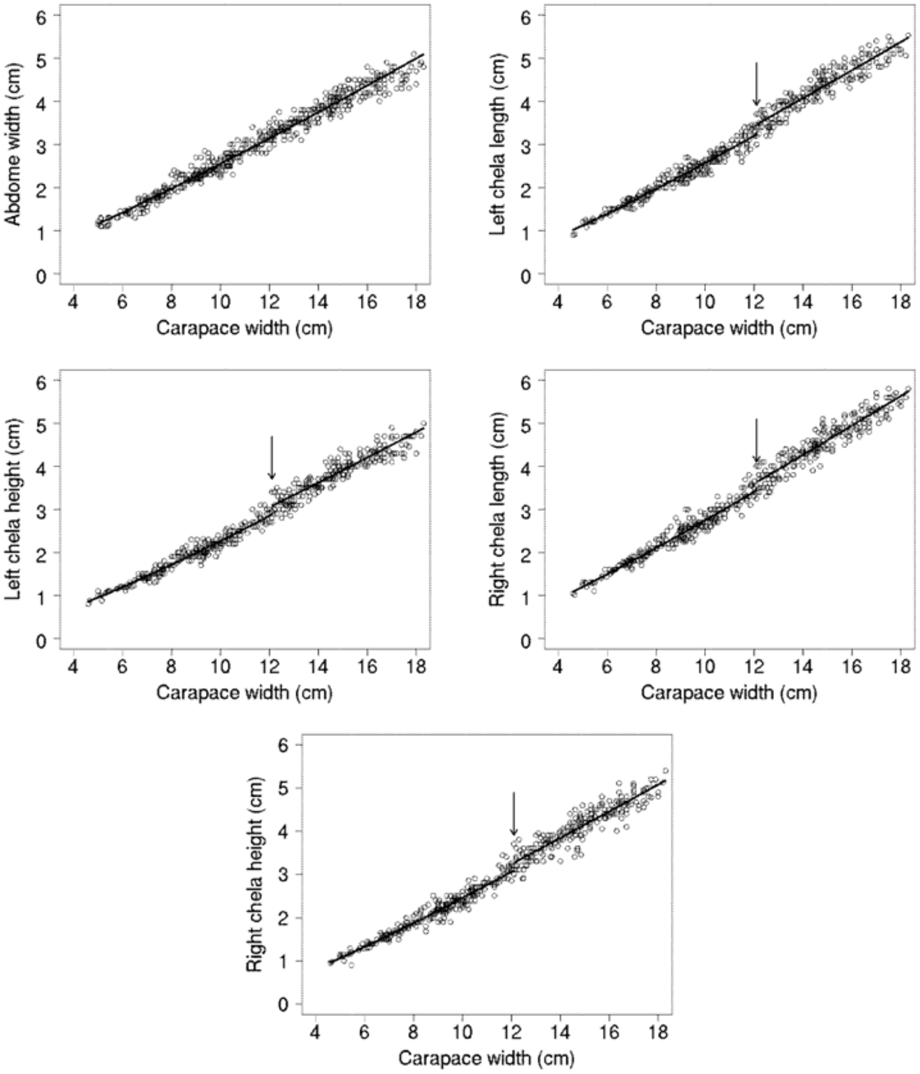

Figure 2. *Chaceon ramosae.* Plots of relative growth of chelipod and abdomen dimensions for males. Arrows indicate transition points between different growth phases.

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

Size-structure

Figure 5 shows the global size structure of the royal crab catches recorded between 2002 and 2005. Males (3.9-19.2 cm) were larger than females (4.9-17.0 cm). The size frequency distribution of males was bimodal, peaking at 11.25 and 14.25 cm, whereas females displayed a narrower distribution with a single mode at 12.25 cm. In both sexes, the catches were slightly asymmetrical for the smaller individuals.

The size catch composition analysis pointed out different scenarios depending on the maturity criterion considered. Throughout all the study period, the mean percentage of immature females in the catches varied from 15.9% (morphometric maturity) to 63.9% (functional maturity). For males, the participation of immature individuals fluctuated in a much narrower interval, varying from 33.1% to 54.8% (Table 4). On the other hand, the incidence of juveniles in the catches during the course of the fishery showed an inverse pattern for the sexes, irrespective of the maturity criterion chosen for the analysis. Whereas the amount of immature females decreased from 2002 to 2004, the numbers of undersized males increased continuously in the same period. Both functionally immature males and females peaked in 2005, with 66% and 70%, respectively (Table 4).

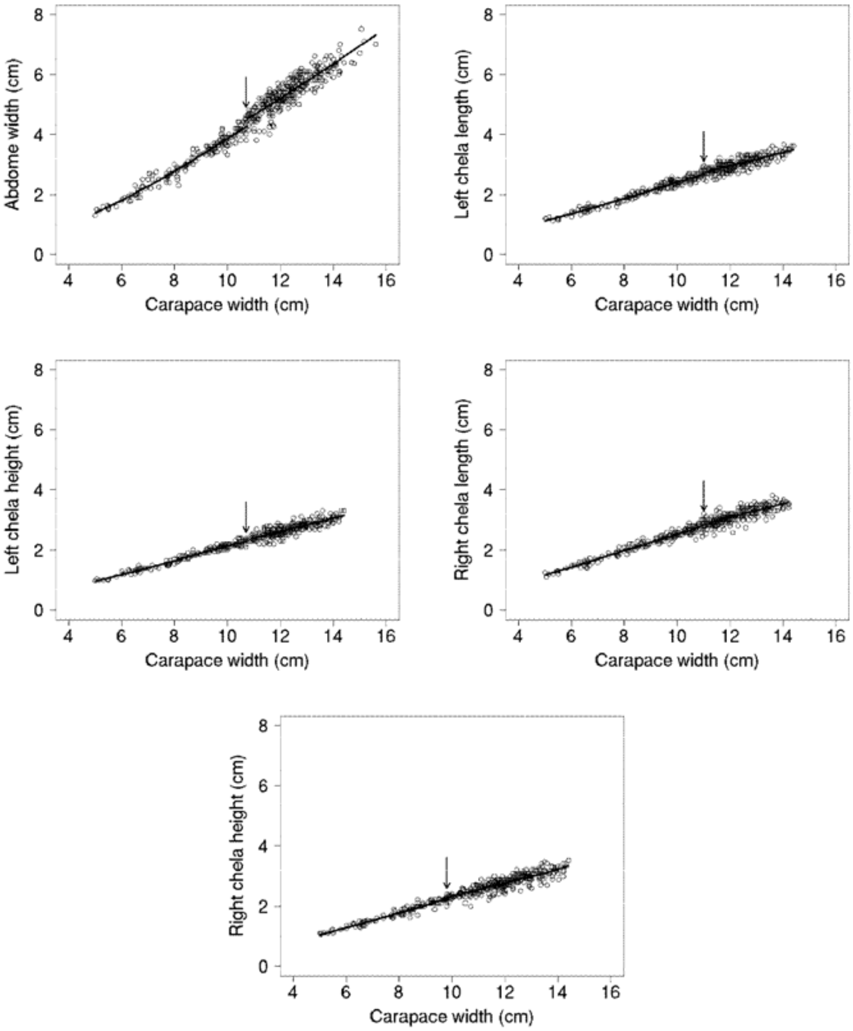

Figure 3. *Chaceon ramosae.* Plots of relative growth of chelipod and abdomen dimensions for females. Arrows indicate transition points between different growth phases.

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

Table 3. *Chaceon ramosae.* Parameters (α1, α2, and β) of the logistic curves (± CI 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 ramosae*. Parámetros (α1, α2 y β) del modelo logístico (± CI 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 un procedimiento *bootstrap*.

Parameters	Females				Males	
	Opened vulvae		Ovigerous		Copula marks	
	Mean	CI (95%)	Mean	CI (95%)	Mean	CI (95%)
β	1.00	0.97-1.06	0.40	0.37-0.44	0.58	0.55-0.62
α1	14.55	11.39-17.71	11.56	8.58-14.53	12.93	10.51-15.35
α2	1.32	1.03-1.61	0.94	0.69-1.19	0.95	0.77-1.14
Bootstrap	Median	CI (2.5-97.5%)	Median	CI (2.5-97.5%)	Median	CI (2.5-97.5%)
$CW_{50\%}$ (cm)	10.94	10.59-11.11	12.24	10.55-15.83	13.61	12.83-15.79

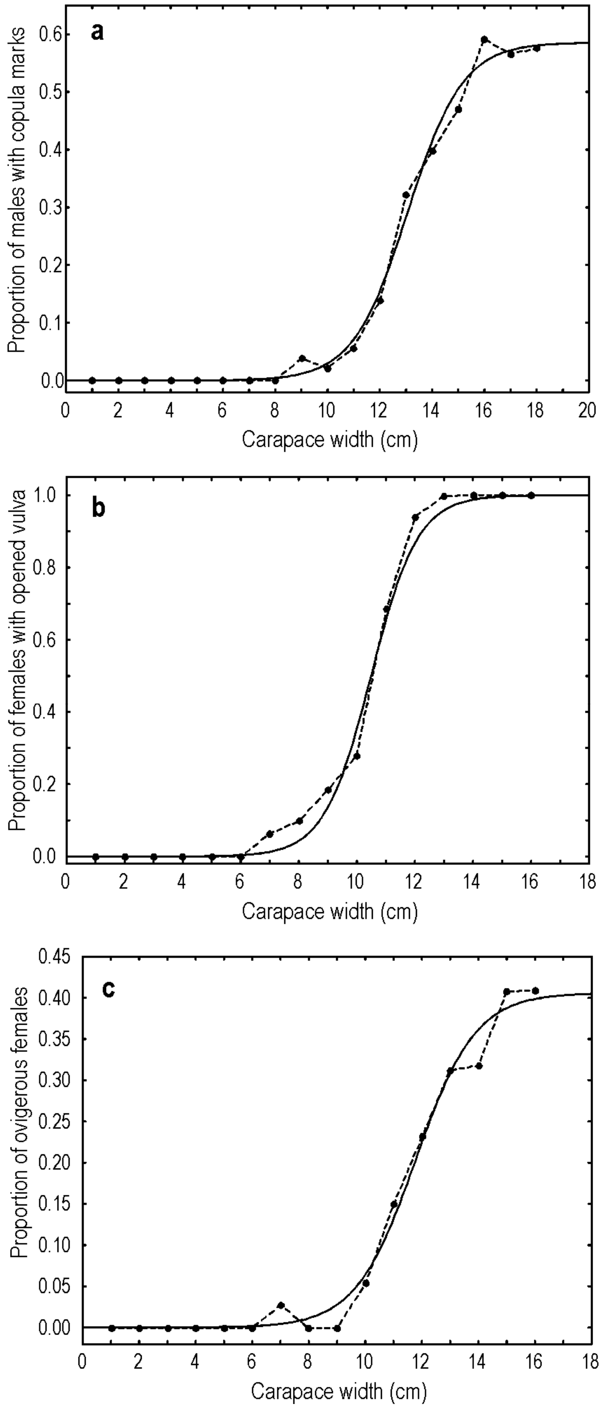

Figure 4. *Chaceon ramosae.* a) Logistic model (solid line) fitted to the observed proportion (dashed line) of males showing copula marks, b) females with opened vulva, and c) eggs in the pleopods. Note the differences among Y-axis values.

Figura 4. *Chaceon ramosae.* a) Modelo logístico (línea continua) ajustado a la proporción observada (línea discontinua) de machos con marcas de cópula, b) hembras con vulvas abiertas, c) huevos en los pleópodos. Note las diferencias entre los valores de los ejes Y.

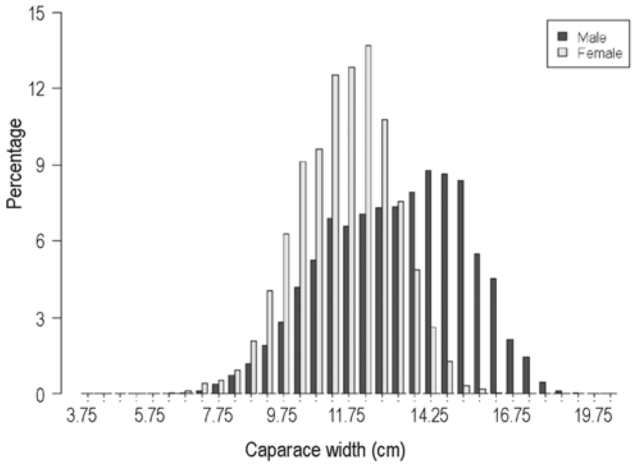

Figure 5. *Chaceon ramosae.* Size-frequency distribution of males and females caught in commercial fisheries in southern Brazil between 2002 and 2005.

Figura 5. *Chaceon ramosae.* Distribución de frecuencia de tallas de machos y hembras capturados por la pesca comercial en el sur de Brasil entre 2002 y 2005.

DISCUSSION

In this paper, the determination of size at maturity considered a scenario of indeterminate growth for *C. ramosae*, *i.e.* a non-terminal pubertal moult. In a recent paper, Delgado & Defeo (2004) estimated size-at-maturity for females of *C. notialis* under hypotheses of indeterminate and determinate growth, as Melville-Smith (1987) suggested the existence of a terminal moult for *C. maritae* females. In addition, Steimle *et al.* (2001) considered determinate growth for *C. quinquedens* based on evidence supposedly obtained by Lux *et al.* (1982) and Lawton & Duggan (1998).

In spite of some controversy in the literature, we agree with Hines (1990): there is no real evidence to support a true terminal moult in the group. Melville-Smith's (1987) assertion for *C. maritae* (see page 270) was preliminary and not based on any explicitly demonstrated data. In fact, in a seminal paper on the growth and age of the species (Melville-Smith, 1989), the author was categorical that: "a small number or recaptured females (three or 1.6 per cent) did moult after being tagged as mature animals. It therefore appears that mature females are capable of moulting more than once, but that there is probably a lengthy interval between moults. The longest period over which a mature female remained unmoulted was 1,217 days (3.3 years). The fact that few females reach 110 mm CW, suggests that it is unlikely that they moult more than twice after maturity". In another paper dealing with mark-and-recapture techniques, Lux *et al.* (1982) found that some *C. quinquedens* females were

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

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

Year	Females						Males			
	Relative growth (10.7 cm)		Opened vulvae (10.9 cm)		Eggs in the pleopods (12.3 cm)		Relative growth (12.1 cm)		Copula marks (13.6 cm)	
	Immature (%)	Mature (%)	Immature (%)	Mature (%)	Immature (%)	Mature (%)	Immature (%)	Mature (%)	Immature (%)	Mature (%)
2002	16.6	83.4	23.7	75.4	64.6	27.4	26.6	73.5	48.0	52.0
2003	16.0	84.0	23.3	74.9	62.4	31.1	30.5	69.5	52.7	47.4
2004	11.1	89.0	18.8	80.9	58.2	34.9	30.6	69.4	52.8	47.2
2005	19.9	80.1	31.5	70.3	70.3	34.8	44.8	55.2	65.6	34.4
Mean	15.9	84.1	24.3	75.4	63.9	32.0	33.1	66.9	54.8	45.2
SD	3.6	3.6	5.3	4.3	5.0	3.6	8.0	8.0	7.6	7.6

recaptured as ovigerous, mostly up to three years after being released although, two individuals were recaptured after five and seven years. These authors concluded that sperm stored since the last pretagging moult would remain viable for several years in the species and that, as found by Melville-Smith (1989), intermoult periods increase with age. However, a terminal moult was never suggested. On the contrary, they suggested that immature females mate after the pubertal moult and that mature females mate again after a subsequent moult (Lux *et al.*, 1982). Attrill *et al.* (1991) discussed in detail the possibility of a terminal ecdysis in *G. trispinosus* and concluded that evidence for this is inconclusive but that it is possible that males and females stop growth two and four instars after the pubertal moult, when they are significantly larger than their respective sizes at maturity. Finally, although explicitly indicating a terminal moult for *C. quinquedens*, Lawton & Duggan (1998) do not clearly demonstrated any data in their paper that support this. It seems, therefore, that much more data on Geryonidae reproduction and growth patterns are necessary to better develop and support a terminal moult hypothesis for the group.

Table 5 summarizes maximum sizes and sexual maturity data available for several Geryonidae species. The sizes at maturity estimated for both sexes (12.1-13.6 cm for males and 10.7-12.3 cm for females) as well as the range of sizes observed for ovigerous females in this study (8.0-16.2 cm) coincide with the general values reported for the group. In fact, estimates produced for *C. ramosae* were closer to those found for *C. affinis*, C. *fenneri*, and *C. granulatus*, which are all among the largest species in the family.

Sizes at morphometric maturity are attained before the individuals of both sexes are functionally mature. In fact, relative growth changes occurred in males at 12.1 cm, whereas sexual activity revealed by copula marks was identified, on average, only at 13.6 cm. In females, both allometric changes and opened vulvae were observed at CWs 1.3 cm smaller than the $CW_{50\%}$ estimated for ovigerous females. Because gonadal development was not investigated in this study, we were not able to conclude whether physiological and morphometric maturity are synchronous or not in the species. Physiological maturity seems to be correlated with changes in the relative growth pattern of secondary sexual traits and/or the vulvae condition, at least in *C. quinquedens*, *C. maritae*, *C. fenner, C. chilensis*, and *C. notialis* (Haefner Jr.; 1977; Melville-Smith, 1987; Erdman & Blake, 1988; Delgado & Defeo, 2004; Guerrero & Arana, 2009). On the other hand, first gonadal development is attained before (males) or after (females) morphometric maturation in *C. affinis* (Fernández-Vergaz *et al.*, 2000). Whatever the size of *C. ramosae* at physiological maturity, the finding that morphometric maturity is attained before males copulate and females are able to oviposit and incubate eggs indicates that changes in form should play a role in the reproductive success of the species. Notwithstanding, it is noteworthy that changes in relative growth patterns in the morphometric maturity of *C. ramosae* were much more difficult to identify than in many other Brachyura such as, for instance, Majidae, Ocypodidae, and Pinnotheridae (*e.g.* Carmona-Suárez, 2003; Negreiros-Fransozo *et al.*, 2003; Alves *et al.*, 2005). In fact, changes in allometry patterns in Geryonidae have been found to be very subtle or even in

Table 5. Summary of size-at-maturity values estimated for male and female geryonid crabs. When available, overall size ranges (including mature and/or immature individuals) of the samples are included for comparison among the species. Except for *C. bicolor, C. chilensis* and *G. trispinosus*, which were measured in terms of carapace length (CL), all values refer to carapace width, in centimeters. Methods of analysis are indicated as: a) morphometric data/relative growth, b) vulva condition, c) visual examination of abdomen development, d) smallest ovigerous female, e) gonadal development, f) mean size of ovigerous females, g) percentage of ovigerous females by size class, and h) copula marks; ?: not specified.

Tabla 5. Resumen de tallas de primera madurez estimadas para machos y hembras de cangrejos gerionídeos. Cuando estaban disponibles, los rangos de tallas (incluyendo individuos maduros y/o inmaduros) en las muestras fueron incluidos para efecto de comparación entre las especies. Todas las medidas se refieren al ancho del caparazón, en centímetros, con excepción de *C. bicolor, C. chilensis* y *G. trispinosus*, cuyas medidas fueron el largo del caparazón (CL). Los métodos de análisis están indicados como: a: datos morfométricos/crecimiento relativo, b: condición de la vulva, c: examen visual del desarrollo del abdomen, d: hembra ovígera de menor tamaño, e: desarrollo gonadal, f: talla promedia de hembras ovígeras, g: porcentaje de hembras ovígeras por clase de talla, h: marcas de cópula, ?: no especificado.

Species	Females			Males		Source
	Size-at-maturity	Ovigerous size range	Overall size range	Size at maturity	Overall size range	
Chaceon affinis	9.9^{a} ; 10,8$^{c, e}$; 11,3^{b}	> 12.0	6.1 - 16.5	12.9^{a}	6.5 – 18.9	Fernández-Vergaz *et al.* (2000)
	10.2 – 11.8^{b}; 11.4^{f}	9.8 – 13.2	5.5 – 16.5	-	5.0 – 19.0	Pinho *et al.* (2001)
	13.2^{f}	11.5 – 16.5	6.1 – 16.5	-	5.2 – 18.9	López-Abellán *et al.* (2002)
Chaceon bicolor	-	-	-	9.4 (CL)^{e}	5.9-16.3 (CL)	Hall *et al.* (2006)
Chaceon chilensis	-	-	-	10.0(CL)^{a}	4.6-19.0	Guerrero & Arana (2009)
Chaceon fenneri	9.7$^{b, e}$	-	8.5 – 17.0	-	8.8 – 19.3	Wenner *et al*. (1987)
	8.5 - 10.0$^{b, e, g}$	9.7 - 14.7	8.9 - 15.6	-	-	Erdman & Blake (1988)
	-	11.0 – 14.3	-	-	-	Hines (1988)
Chaceon granulatus	-	13.4 – 17.0	11.4 – 17.4		12.4 – 17.9	Hastie & Sounders (1992)
Chaceon maritae	> 6.2^{d}	6.2 – 10.2	6.0 – 10.4	-	6.5 – 16.4	Beyers & Wilke (1980)
	8.3^{a}	-	-	-	-	Gaertner & LaLoé (1986)
	8.4 – 10.0^{b}	-	-	7.6 – 8.0$^{e, h}$		Melville-Smith (1987)
	6.5$^{?}$	-	-	-	-	Diop & Kojemiakine (1995)
Chaceon notialis	7.0 – 9,1$^{a, b, e}$	-	4.6 – 11.4	-	-	Delgado & Defeo (2004)
Chaceon quinquedens	8.0 - 9.1$^{a, b, e, g}$	9.7 - 13,1	-	-	-	Haefner (1977)
	10.3^{f}	-	7.0 – 13.1	-	6.0 – 16.3	McElman & Elner (1982)
	-	9.0 – 11.8	-	-	-	Hines (1988)
Chaceon ramosae	10.7-12.3$^{a, b, f, g}$	8.0 – 16.2	4.9 – 16.8	12.1^{a}; 13.6^{h}	3.9 – 19.0	This study
Chaceon sp. (= *C. poupini*)	8.2^{a} ; > 9.0^{b}	-	4.6 – 15.3	-	5.1 – 17.4	Poupin & Buat (1992)
Geryon trispinosus	1.2 – 1.5 (CL)$^{a;e}$	> 2.0 (CL)	~ 0.5 – 5.0 (CL)	3.5 (CL)^{a}	~ 0.5 – 7.5 (CL)	Attrill *et al.* (1991)

existent under visual or statistical analyses (*e.g.* Haefner, 1977; Gaertner & Laloé, 1986; Fernández-Vergaz *et al.*, 2000; Pinho *et al.*, 2001; Delgado & Defeo, 2004; Hall *et al.*, 2006), rendering morphometric data very limited for estimating size at the onset of morphometric maturity in this group. The small geryonid *Geryon trispinosus* is probably an exception as its pubertal moult is characterized by significant changes in the relative growth of the abdomen and right chelae of females and males, respectively (Attrill *et al.*, 1991).

It is possible that the absence of remarkable allometric changes in Geryonidae result from constraints associated with mating behavior and survival in deep-water environments. Laboratory observations demonstrate that mating is a relatively prolonged process in Geryonidae. Males display a pre-copulatory behavior, forming a protective cage around the receptive female by using their locomotory legs. Pre-ecdysis is then initiated in the female, lasting several days, and mating starts just after her ecdysis. The copulatory embrace lasts 7 to 11 days, during which the male actively protects the vulnerable soft-shelled female (Elner *et al.*, 1987; Erdman & Blake, 1988). A similar behavior was described by Hartnoll (1969) as a common pattern in aquatic members of Cancridae and Portunidae, which recognize individuals for mating relying mostly on chemical and tactile stimuli (Type I). On the contrary, copula in several other Brachyura, including semi-terrestrial members of Grapsidae and Ocypodidae, is conducted with hard-shelled females and lasts only some minutes. A brief courtship occurs and recognition between individuals is based mostly on visual, tactile, and even auditory stimuli (Type II) (Hartnoll, 1969), in which we expect secondary sexual traits to play a very significant role for sexual attraction and selection.

Christy (1987) distinguished eight kinds of mating associations in brachyuran crabs based on apparent modes of competition among males for mates. According to this classification, behaviors similar to those described above for Geryonidae should be expected in aquatic species in which receptive females are relatively uncommon, dispersed, mobile, and mate infrequently. In these cases, males tend to search for receptive females that release pheromones and defend them from other competing males; this seems to agree with the general knowledge about mating in Geryonidae. Considering this "search-and-defend" strategy (*sensu* Christy, 1987) and the opportunistic scavenging/predatory behavior reported for geryonid crabs (Hastie, 1995; Kitsos *et al.*, 2005; Domingos *et al.*, 2007, 2008), the increase in general body size might play a more significant role in the survivorship and reproductive success of the group than, for instance, disproportionate chelae growth. Investing in a bigger body should improve the locomotory ability of the crabs and, consequently, their capacity to locate mates and food resources that are dispersed widely over the sea-bed. In addition, a larger size should reduce the costs of body maintenance, as less energy should be spent per unit biomass, a key advantage in an oligotrophic environment (Gage & Tyler, 1991).

In a recent article, Bonduriansky (2007) argued that strong positive allometries in secondary sexual traits might even be exceptions in nature, especially in traits not totally dedicated to reproductive activities but primarily involved in individual maintenance (*e.g.* locomotory and sensorial appendices). In these cases, the gains obtained with disproportionate growth of the allometric trait, in terms of sexual selection, can be surpassed by viability costs of exaggeration, which might interfere with the general performance of the individual (*e.g.* movement, food acquisition). A similar reasoning was used by Attrill *et al.* (1991) to explain the relative reduction of the chela size in *G. trispinosus* males at the pubertal moult. As the male needs to carry the female for mating, the optimal outcome for the individuals could be a maximal increase in body size at maturity to allow successful courtship, making chela growth a lower priority. It is likely, therefore, that the lack of strong changes in allometry in the chelae of Geryonid males could reflect an absence or weakness of selective pressures for sexual selection in the group.

The maximum theoretical proportion of males exhibiting copula marks (parameter β of the logistic function) was only 0.58 in *C. ramosae*. Three hypotheses can be posed to explain this relatively small value: a) abrasion marks are not necessarily formed on all recently paired males; b) a proportion of the recently paired males may have moulted before being caught; and c) not all mature males copulate in each reproductive season. The first hypothesis could be supported by Melville-Smith's (1987) finding that no copula marks are found on very large males of the red crab *C. maritae* (CW > 120 mm), as their merus do not chafe against the female carapace when she is carried during the pre-copulatory embrace and mating. However, in *C. ramosae*, even the largest individuals exhibited copula marks on their legs. In addition, Melville-Smith's findings on the disappearance of copula marks on large-sized red crabs did not explain why only 60% of the mature *C. ramosae* individuals of intermediate sizes had damaged shells, assuming that they all should have been abraded if mating had occurred. Moulting details are not known for the royal crab, precluding testing of the second hypothesis. On the other hand, the low growth rates attributable to geryonids and the increasing intermoult periods expected for large individuals (Lux *et al.*, 1982; Melville-Smith, 1989; Arana, 2000) render improbable the moulting of nearly 40% of the adult males (*i.e.* eliminating the respective copula marks along with their old shells) between the last copula and their catch. The hypothesis that not all mature males copulate during each reproductive season will be analyzed in conjunction with the female pattern of sexual activity and maturity.

The maximum theoretical proportion of ovigerous females in any size class did not surpass 40% in *C. ramosae*. Proportions smaller than 100% would be expected: a) if the catchability of breeding females is reduced due to behavioral limitations (*e.g.* reduced activity, difficulty for climbing the traps), and/or availability on the fishing grounds (Melville-Smith, 1987; Hastie & Saunders, 1992; Poupin & Baut, 1992) and/or, inevitably, b) if breeding among individuals in the population is not simultaneous during the reproductive season, such that some adult females are bearing eggs whereas others are not at the moment of being caught. The latter condition would be easily satisfied if females produced more than a single batch per season, since some time interval would occur between batches. In this case, only a fraction of the whole reproductively active population would be ovigerous at any time, resulting in a β parameter of the logistic model that is smaller than 1. However, evidence in the literature suggests that geryonid crabs have long breeding periods lasting 6 to 9 months (Hinsch, 1988; Erdman & Blake, 1988; Attrill *et al.*, 1991; Erdman *et al.*, 1991). Under this scenario, a maximum of 40% of the ovigerous *C. ramosae* females in any size class of the catch would characterize its reproduction as annual at the population level, as spawning takes place from January to June in areas shallower than 700 m (Pezzuto *et al.*, 2006c), but would be nearly bi-annual at the individual level; this would also agree with the relatively small proportion of mature males exhibiting copula marks. Although this hypothesis should be better investigated, it is important to keep in mind that bi-annual cycles were suggested for *C. affinis, C. fenneri* and *C. quinquedens*, and were interpreted by some authors to be a consequence of the food-limited characteristic of deep-water environments (Erdman & Blake, 1988; Erdman *et al.*, 1991; Pinho *et al.*, 1998; López-Abellán *et al.*, 2002). If confirmed, this bi-annual strategy would render the royal crab stock extremely vulnerable to the overfishing of recruits.

Analyzing the percentages of immature crabs in the commercial catches reveals very distinct scenarios depending on the criteria used for determining size at sexual maturity. Considering the sizes at morphological maturity for both sexes and the vulva condition in females, commercial fleet operations are characterized by a relatively small proportion of immature individuals. More conservatively, however, when determining maturity through data on ovigerous females and males with copula marks, more than 50% of the catches between 2002 and 2005 corresponded to sexually immature individuals, with a severe peak of more than 70% in 2005. The excessively high and certainly biologically unsafe proportions of immature crabs in the catches were similar between the sexes, suggesting at least a relatively uniform impact of the fishery on the population structure of the resource.

Global landings of *C. ramosae* exceeded the estimated maximum sustainable yield (MSY) in most years (Pezzuto *et al.*, 2006c) and included ovigerous females whose catches are not yet limited. This fact, combined with the actual size composition of the catches and the hypothesis of a bi-annual reproductive cycle for the species, renders the fishery highly unsustainable. Therefore, the current management regime of the royal crab fishery should be improved by incorporating new regulations based on biological considerations. The new regulations should emphasize enhanced trap selectivity and the implementation of spatial-temporal restrictions on effort allocation in order to diminish the participation of immature individuals of both sexes and ovigerous females in the catches, contributing to the biological sustainability of the resource. In fact, based on the results of this paper and those of Pezzuto *et al.* (2006c), the management of the royal crab fishery has been changed very recently, incorporating, *inter alia*, an increased permitted minimum mesh size in the traps (from 100 to 120 mm stretched) and the annual closure of the spawning areas < 700 m depth from January 1 to June 30. As the vessels engaging in the fishery should be obligatorily monitored by observers on all trips, biological data will soon be available in order to verify the efficacy of these changes and to refine them, if necessary, in a continuous process of adaptive management.

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