

Research Article

Abundance and distribution of the deep-sea crab *Chaceon ramosae* (Decapoda: Geryonidae) in southern Brazil: contribution to the fishing regulation

Harry Boos^{1,2} & Paula Beatriz Araujo²

¹Centro Nacional de Pesquisa e Conservação da Biodiversidade Marinha do Sudeste e Sul-CEPSUL
Instituto Chico Mendes de Conservação da Biodiversidade-ICMBio, Itajaí, Santa Catarina, Brazil

²Programa de Pós-Graduação em Biologia Animal, Instituto de Biociências
Universidade Federal do Rio Grande do Sul-UFRGS, Porto Alegre, Rio Grande do Sul, Brazil

Corresponding author: Harry Boos (harry.boos-junior@icmbio.gov.br)

ABSTRACT. The deep-sea crab *Chaceon ramosae* occurs at 350-1200 m depth in the southeast and south of Brazil. Here we evaluated the latitudinal, bathymetric, and seasonal abundance of *C. ramosae* in southern Brazil obtained during several research cruises. We also obtained populational data to evaluate the effectiveness of the fishing regulations for *C. ramosae*. Five sampling cruises were carried out in 2009-2010 and the sampling effort comprised 32 fishing hauls with four pots per mainline. In total, 195 individuals were caught, 128 males and 67 females, of which 17 were ovigerous. The highest catch per unit effort occurred between 29°03' and 29°05'S at 800-1000 m in depth. The highest abundance occurred in winter, and almost all ovigerous females were captured in this season. The size at the onset of sexual maturity was estimated at 120 mm carapace width. Depth was the most critical environmental factor explaining *C. ramosae* distribution. The largest individuals, as well as the mature ones, were mainly captured in shallower regions (400-600 m). Our results confirm the need for prohibiting the fishing for *C. ramosae* at depths lesser than 500 m.

Keywords: *Chaceon ramosae*, sexual maturity, deep-water resources, continental slope, southern Atlantic.

INTRODUCTION

Deep-sea crabs of the family Geryonidae Colossi, 1923 (Decapoda: Brachyura) inhabit muddy and sandy-mud substrates from 50 to 2800 m depth, where temperatures range from 12 to 4°C (Wigley *et al.*, 1975; Haefner, 1978; Manning & Holthuis, 1989). Studies about their growth and longevity are scarce, but they probably exhibit the common traits of most deep-sea species: high longevity, late maturation, slow growth, and non-annual reproduction (Melville-Smith, 1989). These traits often result in populations with low biomass production, and therefore, with slow recovery when intensely exploited (Rogers *et al.*, 2008; Groeneveld *et al.*, 2013).

Four Geryonidae species occur along the Atlantic coast of South America, and all belong to the genus *Chaceon* Manning & Holthuis, 1989: *C. eldorado* Manning & Holthuis, 1989 (Colombia, Venezuela, Trinidad Tobago, French Guyana); *C. linsi* Tavares & Pinheiro, 2011 (northeastern Brazil); *C. ramosae* Manning, Tavares & Albuquerque, 1989 (southeastern

and southern Brazil); and *C. notialis* Manning & Holthuis, 1989 (southern Brazil, Uruguay and Argentina) (Tavares & Pinheiro, 2011). Molecular analyses suggested that *C. notialis* might be a species complex, whereas the taxonomic status of the other three species was confirmed (Mantelatto *et al.*, 2014). Recently, *C. gordonae* (Ingle, 1985) was reported in Brazil at the St. Peter and St. Paul Archipelago (Ferreira *et al.*, 2016).

The first fishing cruises targeting deep-sea crabs in southern Brazil at more than 400 m depth, occurred in 1984-1985 between latitudes 25° and 34°S (Lima & Lima-Branco, 1991; Haimovici *et al.*, 2007). After the launch of a governmental program to develop deep-sea fisheries in 1998, the continental slope of southern Brazil and Uruguay became a profitable fishing region (Perez & Wahrlich, 2005; Pezzuto *et al.*, 2006a, 2006b). However, the deep-sea fauna remains sparsely studied in Brazil, and new species are still being discovered, mainly as bycatch of the industrial fishing (Mincarone & Anderson, 2008).

Along the Brazilian coast, *C. ramosae* occurs from Espírito Santo to Rio Grande do Sul, at depths of 350-1200 m (Manning *et al.*, 1989; Melo, 1996). Nowadays, according to the National Program of Fishing Vessel Monitoring by Satellite (PREPS), there is no fishing activity targeting the deep-sea crab (*C. ramosae*). However, between 1999 and 2009, it was captured almost 585 t y⁻¹ of this species. Only in 2004, the total of capture reached 1742 t (Univali/CTTMar, 2010). Due to inefficient management and biological attributes such great longevity and slow-growth, fisheries targeting deep-sea species usually follows a pattern of a fast increase in catches, followed by an abrupt decline, driving species to overfishing (Rogers *et al.*, 2008; Clark *et al.*, 2016). In recent assessments of extinction risk, it was estimated that in the last 45 years the population of *C. ramosae* decreased by nearly 50%. However, this species was categorized as "Near Threatened," as its bathymetric and latitudinal distribution is wider than the range exploited by the industrial fishing fleet (Instituto Chico Mendes, 2016; Pezzuto *et al.*, 2016).

The small number of research vessels in operation limits the knowledge of the Brazilian marine fauna, especially in regions deeper than 200 m. The existing information about these regions comes mainly from the industrial fishing. In these cases, however, the estimation of distribution and abundance might be biased because the industrial fishing has a typical non-random search mode towards their target species (Walters, 2003). Although marine fauna inventories have been done previously in Brazil, mainly focusing the southeast and extreme south, some of them occurred more than three decades ago and were sporadic and irregular (Haimovici *et al.*, 2007). However, despite being provided by industrial fishing vessels, Pezzuto *et al.* (2002) did analyze unbiased data, once deep-sea crabs were caught during an exploratory phase of the fishery when almost none were known about occurrence and abundance of their stocks. Conversely, the evaluation of the effectiveness of deep-sea fisheries management measures are recommended by FAO (2009), which establishes that countries should monitor the implementation of their fisheries management plans, and periodically review the plans using the best data available.

In this sense, the aim of the study was to verify the validity of two restriction measures present in the normative which regulates the fishing of *C. ramosae* in Brazilian waters: i) the minimum fishing depth of 500 m, and ii) prohibition of fishing, during summer and autumn, at depths lesser than 700 m. In order to achieve this, we sought to identify the patterns of the bathymetric, latitudinal and seasonal distribution of *C.*

ramosae in southern Brazil and, also, to analyze the reproductive period, proportion and sexual maturity from samples obtained in five research cruises.

MATERIALS AND METHODS

Study area

Low nutrient concentrations and low productivity characterize the Brazilian Economic Exclusive Zone (EEZ). However, the Subtropical Convergence (SC) contributes to increasing its productivity (Rossi-Wongtschowsky *et al.*, 2006; Castello *et al.*, 2012). The SC ($38 \pm 2^\circ\text{S}$) is formed by the encounter of the Brazilian and Falklands currents in the southeastern and southern regions (Olson *et al.*, 1988). The continental shelf between Cape of São Tomé (22°S) and Chuí ($34^\circ34'\text{S}$) is more extensive in the central part and narrower next to Cabo Frio (23°S) and Cape Santa Marta Grande ($28^\circ40'\text{S}$), furthermore it is also characterized by a very gentle slope less than 2 m km^{-1} . In the upper continental slope, the slope is about 20 m km^{-1} , except between Rio Grande and Chuí, where it is $80\text{-}130 \text{ m km}^{-1}$, and north of Cabo Frio, where it is 100 m km^{-1} . The shelf break, where the continental slope begins, occurs at depths between 160 and 190 m (Zembruscki *et al.*, 1972; Haimovici *et al.*, 2007).

Sampling

Five research cruises were conducted in 2009 (winter and spring) and 2010 (summer, autumn, and winter), aboard the R/V Soloncy Moura. This vessel belongs to the "Centro Nacional de Pesquisa e Conservação da Biodiversidade Marinha do Sudeste e Sul do Brasil" (CEPSUL), of the Brazilian Ministry of Environment. The sampling stations were distributed off the southwestern Brazilian coast between 400 and 1000 m depth, along with the upper continental slope from 26° to 29°S . This area was divided into five latitudinal sectors: north ($26^\circ14'\text{-}26^\circ18'\text{S}$), central-north ($26^\circ50'\text{-}26^\circ51'\text{S}$), central ($27^\circ15'\text{-}27^\circ46'\text{S}$), central-south ($28^\circ31'\text{-}28^\circ45'\text{S}$), and south ($29^\circ03'\text{-}29^\circ05'\text{S}$) (Fig. 1).

The bathymetry was grouped using intervals of 200 m depths, and the samples of each cruise were grouped seasonally: winter and spring'2009 and summer, autumn and winter'2010. The total sampling effort was approximately 265 hours (Table 1).

To capture the crabs, we carried out 32 fishing operations with four pots per the main line, baited with skipjack tuna, *Katsuwonus pelamis* (Linnaeus, 1758). The pots were of a beehive pot type with a conical iron frame (Japanese model for deep-sea crab fishing) (Slack-Smith, 2001). On the upper face of the frame, there was a plastic entrance with 30 cm of diameter, and

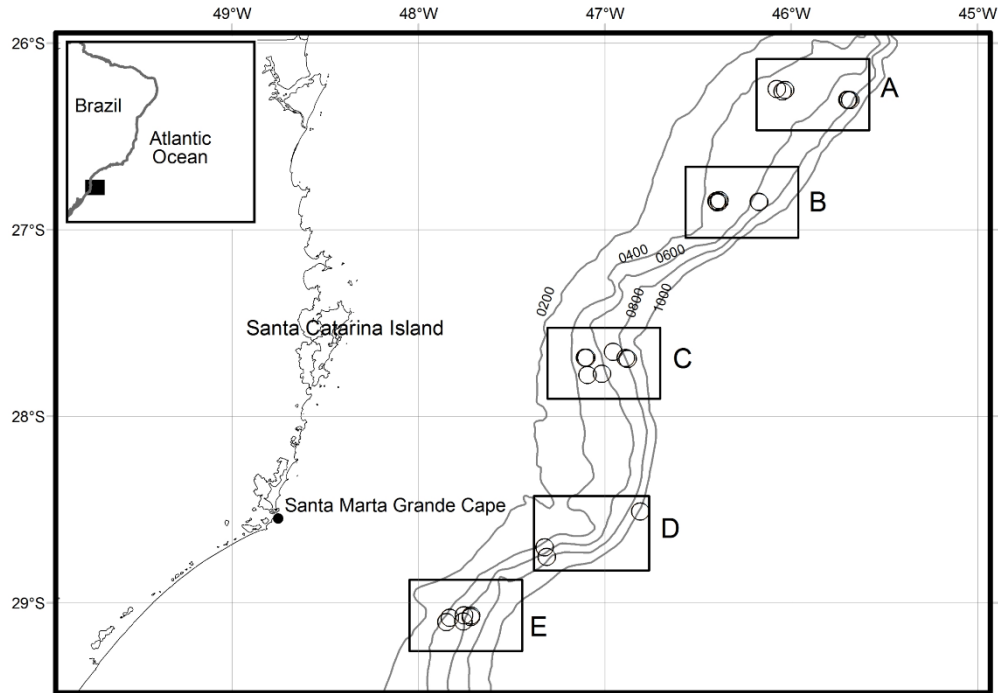


Figure 1. Sampling area conducted in 2009 (winter and spring) and 2010 (summer, autumn, and winter), aboard the R/V Soloncy Moura/CEPSUL. Circles indicate the sampling stations and rectangles indicate the latitudinal sectors: A: north ($26^{\circ}14'-26^{\circ}18'S$), B: north-central ($26^{\circ}50'-26^{\circ}51'S$), C: central ($27^{\circ}15'-27^{\circ}46'S$), D: south-central ($28^{\circ}31'-28^{\circ}45'S$), and E: south ($29^{\circ}03'-29^{\circ}05'S$).

the covering surface was nylon netting with a mesh size of 20 mm. Each pot was fixed to a secondary line of 2 m long, which was attached to the main line. The distance between pots was 30 m (Fig. 2).

These pots have been the main fishing device used to capture deep-sea crabs in Brazil (*Chaceon* spp.) (Athiê & Rossi-Wongtschowski, 2004).

Biometry

The carapace width (CW) of all crabs was measured to the nearest 0.1 mm using vernier caliper, as the maximum transversal distance at the midline of the carapace, including the dorsolateral spines. The sex was determined upon the presence of secondary sexual characters: the shape of the abdomen and absence of gonopods. As from the identification of copula evidence in males and females, the animals were grouped in five categories: i) males without mating marks; ii) males with mating marks (dark spots on the ventral side of the coxae, ischia, and meri); iii) females with closed vulvae (gonopores near thoracic sternal suture 5/6); iv) females with opened vulvae and v) ovigerous females (with eggs attached to pleopods) (Elnor *et al.*, 1987; Melville-Smith, 1987; Biscoito *et al.*, 2015) (Fig. 3).

Identification and vouchers

The animals were identified according to Manning *et al.* (1989) and Melo (1996). Some of the sampled animals were cryo-anesthetized and subsequently fixed and preserved in 95% ethanol. Vouchers were deposited in the Biological Collection of CEPSUL (N°168-175, 177, 178, 183, 186) and the samplings were authorized by the Brazilian authority (SISBIO/ICMBio License N°16886-2).

Data analysis

The analysis of variation in the distribution and abundance of collected *C. ramosae* (sex and age groups categories) was undertaken from the calculation of Catch per Unit Effort (CPUE, in a number of individuals per 6 h captured in fishing operations with four pots per main line). Since CPUE variances of the depth intervals were not homogeneous, they were compared with the non-parametric Kruskal-Wallis test. However, CPUEs among the latitudinal sectors were compared by analysis of variance (ANOVA) (Ayres *et al.*, 2007; Borcard *et al.*, 2011). A cluster analysis (Unweighted Pair-Group Method using arithmetic Averages-UPGMA) was used to verify how the categories are related (males without marks, males with

Table 1. Date, hauling number, start latitude/longitude, latitudinal sector, depth (m) and duration of hauling time (h). The fishing hauls where pots were not collected are stated as "lost," and then, these hours were not counted for the total sampling effort.

Date	N° of haul	Start Lat.	Start Log.	Sector	Initial depth	Duration
14/08/2009	1	29°06.17'S	47°51.078'W	South	570	11:12
16/08/2009	2	27°46.67'S	47°05.659'W	Central	500	09:30
16/08/2009	3	27°46.24'S	47°00.993'W	Central	530	11:00
25/10/2009	4	26°50.41'S	46°23.205'W	North-central	430	02:52
25/10/2009	5	26°51.03'S	46°10.344'W	North-central	750	06:45
26/10/2009	6	27°39.35'S	46°52.497'W	Central	750	lost
26/10/2009	7	27°41.11'S	47°06.405'W	Central	530	09:28
27/10/2009	8	28°42.09'S	47°19.403'W	South-central	580	06:56
27/10/2009	9	29°05.96'S	47°45.597'W	South	560	09:26
27/02/2010	10	26°14.95'S	46°02.026'W	North	460	14:55
27/02/2010	11	26°18.23'S	45°41.09'W	North	750	15:20
28/02/2010	12	26°50.93'S	46°10.483'W	North-central	620	06:20
28/02/2010	13	26°50.73'S	46°24.138'W	North-central	433	07:05
12/03/2010	14	29°04.78'S	47°49.979'W	South	457	10:40
12/03/2010	15	29°03.95'S	47°45.365'W	South	600	09:10
13/03/2010	16	28°30.58'S	46°48.669'W	South-central	970	12:50
13/03/2010	17	28°33.83'S	47°04.522'W	South-central	400	lost
14/03/2010	18	27°41.24'S	46°53.359'W	Central	772	05:45
04/06/2010	19	27°41.1'S	47°06.007'W	Central	536	12:10
09/06/2010	20	27°41.48'S	46°52.729'W	Central	774	13:10
08/06/2010	21	26°14.63'S	46°04.712'W	North	436	12:58
08/06/2010	22	26°18.15'S	45°41.98'W	North	711	15:30
08/06/2010	23	26°50.65'S	46°10.483'W	North-central	616	lost
09/06/2010	24	26°51.16'S	46°23.875'W	North-central	433	08:40
30/06/2010	25	29°04.05'S	47°43.051'W	South	600	07:30
01/07/2010	26	28°31.68'S	47°52.301'W	South-central	749	lost
11/08/2010	27	26°15.42'S	46°02.826'W	North	721	06:00
11/08/2010	28	26°18.09'S	45°41.665'W	North	455	06:23
21/08/2010	29	26°51.04'S	46°23.3'W	North-central	438	08:18
22/08/2010	30	27°39.25'S	46°57.358'W	Central	703	06:37
23/08/2010	31	28°45.21'S	47°18.742'W	South-central	816	06:11
24/08/2010	32	29°04.55'S	47°43.205'W	South	650	06:27

marks, females with closed vulvae, female with opened vulvae and ovigerous females) according to the variation of latitude, bathymetry and seasons (Legendre & Legendre, 1998; Borcard *et al.*, 2011). A Principal Component Analysis (PCA) was used to verify how the males and females categories were distributed along the latitudinal, bathymetric, and seasonal gradients. The importance of each variable and their contribution to the pair of axes was analyzed from the circle of equilibrium contribution (Borcard *et al.*, 2011). The relationship between female carapace width (mm) and depth (m) was analyzed by linear regression.

Female size at the onset of sexual maturity was estimated from the size class containing 50% of mature

females (ovigerous or with open vulvae) (Santos, 1978; Vazzoler, 1981). Male size at sexual maturity was estimated based on the presence of mating marks (Melville-Smith, 1987; Pezzuto & Sant'Ana, 2009). The dispersion of points was adjusted to the sigmoid model ($y = 1/1 + e^{(LC-LC50)}$), adapted from Fontelhes-Filho (1989) and Vazzoler (1996). The sex ratio was compared between the bathymetric, latitudinal, and seasonal gradients, using a chi-square test with Yates' correction or G-test with Williams' correction, with a 5% significance level. The presence of ovigerous females determined the reproductive period.

The R (R Development Core Team, 2014) was used for the estimation of size at the onset of sexual maturity.

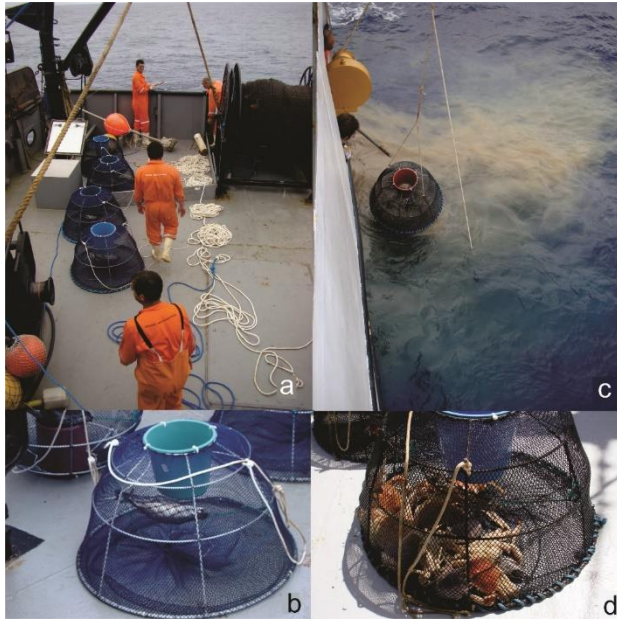


Figure 2. a) Main line with a series of four pots ready to haul, b) pot with bait before to be hauling, c) hauling the pot to a surface, d) pot with prays after fishing.

The software Statistica 7.1 (StatSoft Inc., 2005) was used for the UPGMA and PCA.

RESULTS

In total, 195 individuals were captured: 128 males and 67 females (17 ovigerous). The highest CPUE occurred in the Southern sector (CPUE = 9.9) and between 801 and 900 m depth (CPUE = 36.8). However, the CPUE was not significantly different among latitudinal sectors (ANOVA: $P = 0.3474$) or depths intervals (Kruskal-Wallis: $P = 0.0814$) (Fig. 4). Most individuals, and especially the ovigerous females, were captured during winter, and almost all ovigerous females ($n = 16$) were captured in the Central sector and between 501 and 600 m (Table 2).

Fifty percent of males and 67% of females were captured between 600 and 800 m depth. There was a clear bathymetric pattern in the distribution of females: females with a closed vulva occurred in the deepest areas, those with an open vulva occurred in intermediate depths, and ovigerous females were only captured in the shallowest areas, within 400-600 m of depth. A similar relationship was observed in males: immature (without marks) males were mainly captured in deeper regions, whereas mature ones were captured in shallower areas (Table 2).

The UPGMA relating the abundances to the bathymetric, latitudinal, and seasonal gradients showed

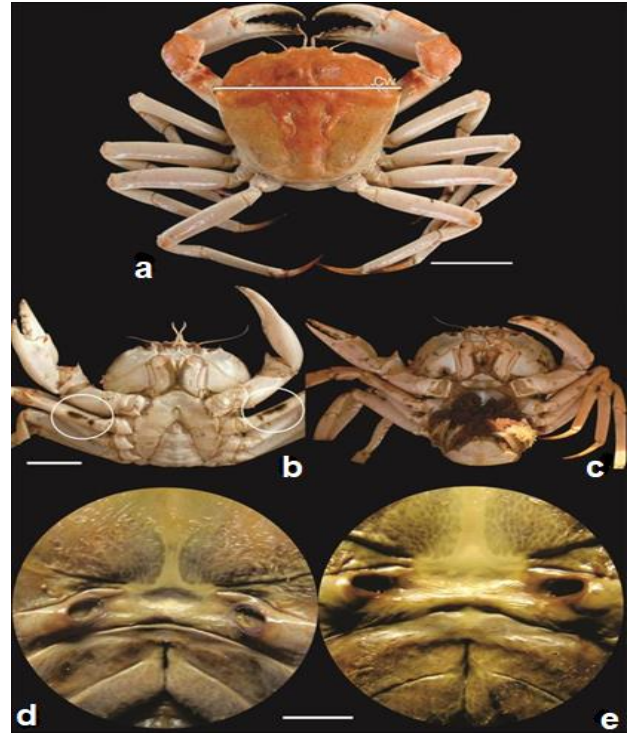


Figure 3. *Chaceon ramosae*. a) Carapace width (CW) (scale = 10 cm), b) male showing mating marks (circles) (scale = 5 cm), c) ovigerous females, d) female with closed vulvae (scale = 1 cm), e) female with opened vulvae (scale = 1 cm).

two main groups (distance = 98.6), one formed by males without mating marks, and another formed by the other four categories. The latter group, in turn, was formed by two subgroups (distance = 31.2), one consisting of males with mating marks and ovigerous females, and the other consisting of females with open and closed vulvae (Fig. 5). The PCA indicated that ovigerous females, females with an open vulvae and males with mating marks were similarly distributed along the gradients. The two first axes explained 78.6% of the total variation (Fig. 6). Latitudinal sectors (Axis 1) and depth (Axis 2) were the two variables which contributed more to this distribution.

The largest male and female measured reached 176.1 mm and 147.9 mm CW, respectively. In general, the largest individuals of both sexes (140.6 mm CW on average) were captured in shallow areas, between 400 and 600 m depth. The size was significantly different along the bathymetric gradient (Kruskal-Wallis, $P = 0.0495$), and an increase in size with the decrease in depth was evident in the females (Fig. 7).

The smallest and largest ovigerous females were 115 and 142 mm CW, respectively. The smallest male with mating marks was 123 mm and the largest, 166 mm CW. The size at the onset of sexual maturity of

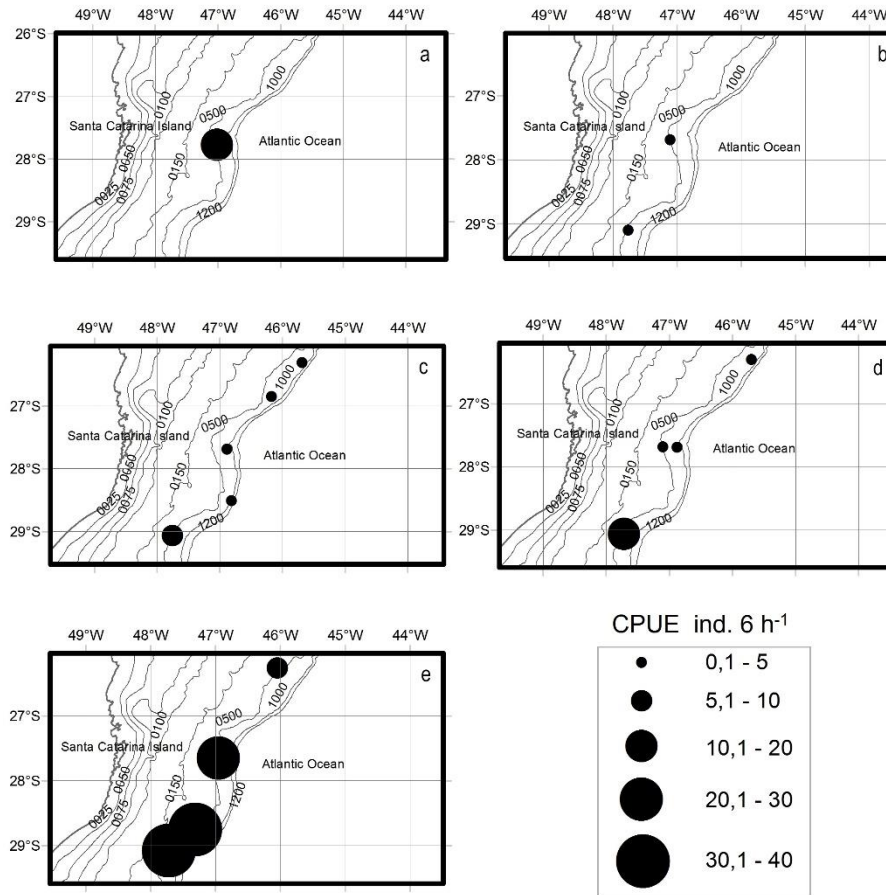


Figure 4. Catch per unit effort (ind 6 h⁻¹) per season. a) winter 2009, b) spring, c) summer, d) autumn, e) winter 2010 in the sampling stations during the research cruises aboard the R/V Soloncy Moura/CEPSUL.

males and females was estimated at 140 mm and 120 mm CW, respectively (Fig. 8).

The sex ratio favored males in almost all seasons and latitudinal sectors. Along the bathymetric gradient, however, the sex ratio was biased towards females in the shallowest region (401-700 m), and towards males in the deeper regions (701-900 m) (Table 3).

DISCUSSION

The high CPUE of *C. ramosae* recorded in the south of Cape Santa Marta Grande (29°19'S), and the presence of most ovigerous females between 27°15' and 27°46'S (central sector), can be explained by some oceanographic processes in the region. One process is the Subtropical Convergence (SC), already mentioned, which increases productivity (Emilson, 1961; Carvalho *et al.*, 1998; Amaral & Jablonski, 2005; Rossi-Wongtschowsky *et al.*, 2006). A second one is the upwelling of the South Atlantic Central Water during the northeasterly winds. This upwelling occurs especially in spring and summer and increases the local

primary production. Consequently, the primary productivity favors the survival of plankton and the reproduction of the benthic fauna (Pires-Vanin & Matsuura, 1993; Matsuura, 1995). In addition, the distribution of fish larvae in the southern portion of the continental shelf of southern Brazil is influenced by the Plata Plume Water (Macedo-Soares *et al.*, 2014), which is an important source of carbon of continental origin, particularly during periods of El Niño Southern Oscillation (ENSO) (Piola *et al.*, 2005). Over the winter, the Plata Plume Water occupies a coastal band several tens of kilometers wide, nearly reaching our North-central latitudinal sector (26°14'-26°18'S) (Piola *et al.*, 2008).

Another process that can influence the distribution of animals is the formation of frontal zones due to the encounter of water masses with different properties (temperature, salinity, etc.). These frontal zones, when associated with divergent water masses, generate upwelling events that bring nutrients up to the euphotic region. The inflow of nutrients favors the growth of phytoplankton, which favors the growth of other

Table 2. Catch per unit effort (ind 6 h⁻¹) of males and females per season (winter and spring'2009; summer, autumn and winter'2010), along the latitudinal (north 26°14'-26°18'S, north-central 26°50'-26°51'S, central 27°15'-27°46'S, south-central 28°31'-28°45'S, and south 29°03'-29°05'S) and bathymetric gradients.

Variables	Males		Females		
	Without marks	With marks	Closed vulvae	Open vulvae	Ovigerous
Winter'09	1.1	0.2	0	0	3
Spring	0.1	0.4	0	0.4	0
Summer	1.4	0.4	0.1	0.1	0
Autumn	1	1	0	0.3	0.1
Winter'10	10.4	0.3	2.3	3.3	0
North	1.3	0.3	0	0	0
North-central	0.1	0	0	0.1	0
Central	3.2	0.3	0	0.4	1.3
South-central	5.7	0	1.8	0.2	0
South	2.8	2.5	0.9	3.4	0.1
401-500 m	0	0	0	0.1	0
501-600 m	1.2	1.4	0	0.4	1.3
601-700 m	5.2	0.9	2.8	9.4	0
701-800 m	4.1	0.4	0	0.2	0
801-900 m	28.2	0	7.8	1	0
901-1000 m	0.9	0	0.9	0	0

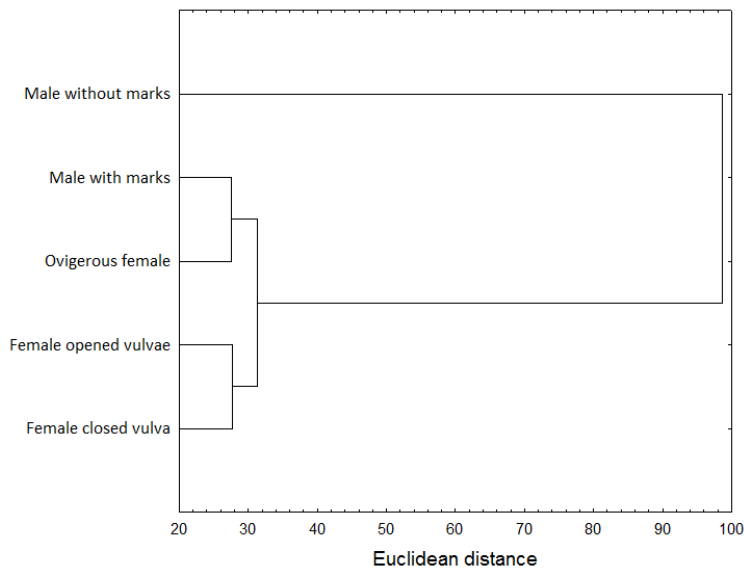


Figure 5. Cluster analysis (UPGMA) of males and females along the latitudinal (north 26°14'-26°18'S, north-central 26°50'-26°51'S, central 27°15'-27°46'S, south-central 28°31'-28°45'S, and south 29°03'-29°05'S), bathymetric (between 400 and 1000 m depth) and seasonal gradients (winter and spring'2009; summer, autumn and winter'2010).

organisms. On the other hand, when the water masses converge, organisms with less swimming abilities are aggregated and passively dragged down to the bottom (Bakun, 2006). In the bottom, they can be preyed by opportunistic carnivores such as *C. ramosae* (Domingos *et al.*, 2008). These phenomena have been identified as responsible for the fluctuation in the biomass of deep-water populations in south Brazil (Fischer, 2012). These two processes, upwelling and sinking, create feeding opportunities and influence many organisms in different life stages. These food sources may benefit fast-growing species with high mortality, as well as the

slow-growing species with low mortality (Bakun, 2006; Fischer, 2012), such as *C. ramosae*.

The presence of ovigerous females in shallow regions (500-600 m) of the continental slope may promote the survival of larvae released there. At these depths, the temperatures range from 4°C to 10°C, and the primary and secondary productivity is higher than in deeper regions, due to the SC (Gutiérrez *et al.*, 2011). In Uruguay, most ovigerous females of *C. notialis* occurred at 300-400 m depth (Gutiérrez *et al.*, 2011), whereas in the Madeira archipelago and the Canary Islands, ovigerous females were mainly found at 800-

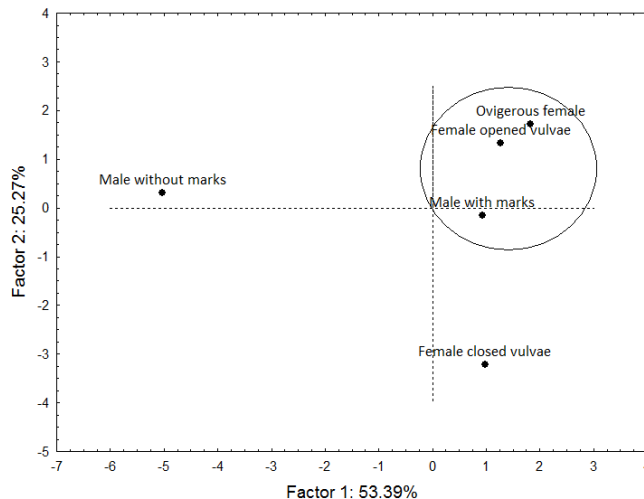


Figure 6. Ordination (PCA) of the abundance of males and females along the latitudinal, (north $26^{\circ}14' - 26^{\circ}18'S$, north-central $26^{\circ}50' - 26^{\circ}51'S$, central $27^{\circ}15' - 27^{\circ}46'S$, south-central $28^{\circ}31' - 28^{\circ}45'S$, and south $29^{\circ}03' - 29^{\circ}05'S$), bathymetric (between 400 and 1000 m depth) and seasonal gradients (winter and spring'2009; summer, autumn and winter'2010). Axes 1 and 2 explained 78.6% of total variation.

1000 m depth. In the latter case, the absence of females in shallow areas may be due to competition with other crab species (Biscoito *et al.*, 2015). In addition to ovigerous females, larger and sexually mature individuals were also more abundant in shallower regions (500-700 m), indicating that depth is the main environmental factor influencing distribution. Males with mating marks, and females with open vulvae and ovigerous formed a distinct group in this region. A similar trend was observed in most geryonid crab populations, in *C. affinis* in the North Atlantic, where the size of both sexes decreased with depth (Biscoito *et al.*, 2015). These results confirm precopulatory mate guard behavior (Elner *et al.*, 1987) associated with mating-related migration to lower depths. The reproduction of *C. ramosae* is not only dependent on satisfactory conditions to maturity individuals, with higher energy costs due to the reproductive behavior, but also favorable conditions to the larvae survival.

Seasonal reproductive cycles are usually triggered by environmental changes, such as day length and temperature. In the deep sea, none of these stimuli can trigger reproduction (Melville-Smith, 1987). However, the absence of seasonal changes in these environments has been disproved recently (Morales-Nin & Panfili, 2005; Danovaro *et al.*, 2014). The seasonal food supply that reaches the deeper regions, in the form of particulate organic carbon, is used by the benthic fauna for maintenance (respiration) and growth (Rowe, 2013),

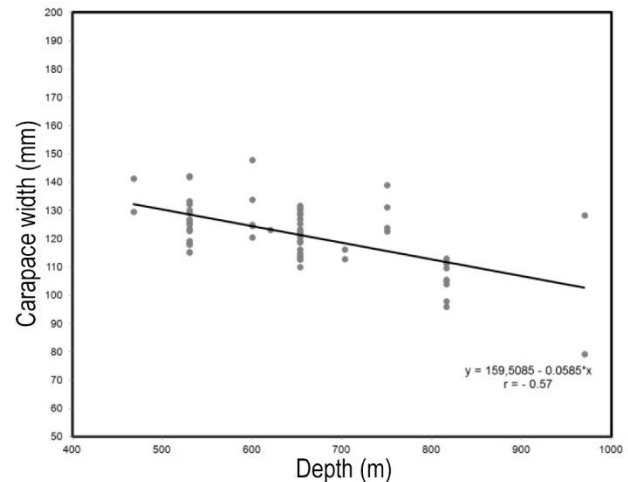


Figure 7. Relationship between female (n = 67) carapace width (mm) and depth ($F = 31,3967$; $P < 0.0001$).

and sexual maturation is influenced by and synchronized with, food availability (Rosa & Nunes, 2003). Besides, the sinking of carcasses, by natural death or discards by industrial fishing, constitutes an important food source for animals of large size and high mobility, such as *C. ramosae*.

Nonetheless, oceanographic processes that provide water exchange between two currents (*e.g.*, eddies) also contribute to the nutrients fluxes and have been identified as responsible for biomass fluctuations of deep-sea populations (Fischer, 2012). Unlike *C. affinis* in the Canary Islands, where ovigerous females were found throughout the year (Biscoito *et al.*, 2015), ovigerous females of *C. ramosae* were only found in autumn and winter, suggesting a seasonal reproductive pattern in the studied area. Contrary to what occurs in most brachyuran species, evidence of seasonal reproduction in geryonid crabs is scarce (Wigley *et al.*, 1975; Haefner, 1978; Lux *et al.*, 1982; Melville-Smith, 1987). The reproductive cycle of *C. ramosae* is probably regulated by the seasonal availability of food, as already observed for other species (George & Menzies, 1968; Barradas-Ortiz *et al.*, 2003; Rose & Nunes, 2003). However, the synergy among the oceanographic processes involved in the regulation of food availability, in the southeast and south of Brazil, and its influence on the life cycle of deep-sea populations, still needs to be better understood. However, the highest seasonal variation of CPUEs, between winter 2009 and 2010, it is probably explained by the different sampling depths and not by the different environment condition of the seasons. In 2009, the research cruiser sampled regions between 500 and 600 m depth, and in the winter of 2010 regions between 400 and 800 m.

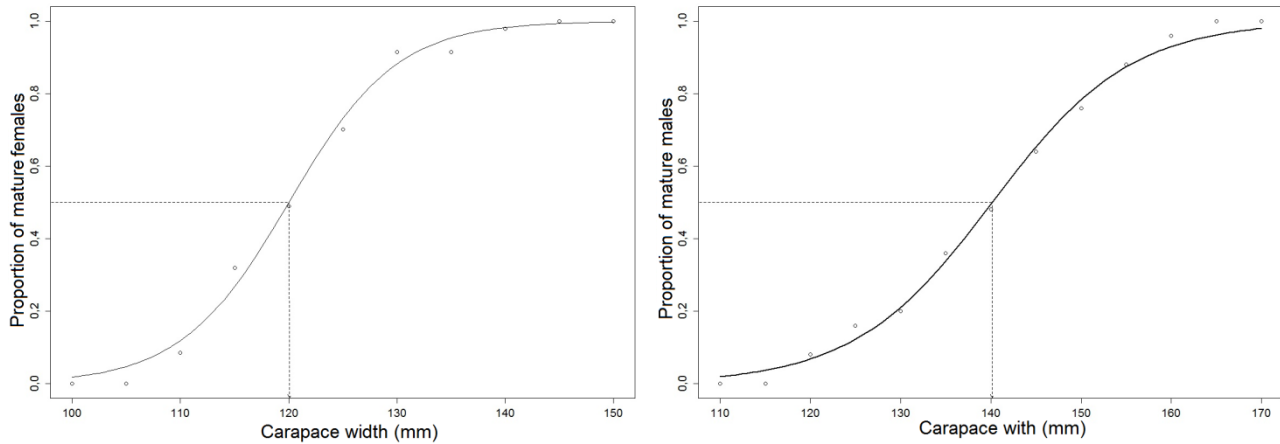


Figure 8. a) Cumulative frequency of mature females (ovigerous or with open vulvae) per size class (carapace width in mm). The L_{50} is 120 mm, b) Cumulative frequency of mature males (with mating marks) per size class (carapace width in mm). The L_{50} is 140 mm.

Table 3. Sex ratio (males/females) along the seasonal, latitudinal, (north 26°14'-26°18'S, north-central 26°50'-26°51'S, central 27°15'-27°46'S, south-central 28°31'-28°45'S, south 29°03'-29°05'S) and bathymetric gradients (m). ^achi-square test with Yates' correction, ^bG-test with Williams' correction, *Significant F.

Variables	Males	Females	Sex ratio (m/f)	P
Winter'09	7	16	0.4	0.0953 ^a
Spring	4	3	1.3	0.0542 ^b
Summer	25	3	8.3	< 0.0001*
Autumn	24	5	4.8	0.0008*
Winter'10	71	37	1.9	0.0015*
North	19	0	-	-
North-central	1	1	1	0.0261 ^b *
Central	45	21	2.1	0.0046*
South-central	31	11	2.8	0.0034*
South	36	30	1.2	0.5383
401-500 m	0	2	-	-
501-600 m	33	22	1.5	0.1775
601-700 m	13	26	0.5	0.0547
701-800 m	55	2	27.5	< 0.0001*
801-900 m	29	9	3.2	0.0021*
901-1000 m	2	2	1	0.0249 ^b

The size at onset of sexual maturity estimated here for females and males, 120 mm and 140 mm CW, respectively, was very similar to those estimated by Pezzuto & Sant'Ana (2009): 122 mm and 136 mm. In their study, the crabs were captured by industrial fishing vessels and the sample size was larger than in our study (511 males and 579 females).

Regarding the validity of the current *C. ramosae* fishing regulation in Brazil (SEAP Normative Instruc-

tion # 21, December 1, 2008), our results do confirm the need to prohibit the capture in areas less than 500 m depth, since ovigerous females were only recorded at depths of 600 m or less. The uncontrolled capture along this area, allowing ovigerous females to be captured, does put reproduction in risk, with immediate negative implications to population recruit-ment. Moreover, the prohibition of fishing during summer and autumn at depths lesser than 700 m can perhaps be reviewed, since ovigerous females were mainly collected during winter and always at depths lesser than 600 m. However, it should be considered that only a total of 17 ovigerous females were sampled on our cruises. Reductions in conservation measures to *C. ramosae*, elaborated from monitoring of catches made by industrial vessels leased in the early 2000s, can only be made when new research cruises, using a bigger sampling effort, capture more ovigerous females. In conclusion, the maintenance and recovery of the *C. ramosae* population are ensured by the current national fishing regulation.

ACKNOWLEDGMENTS

The authors wish to express their gratitude to the Centro Nacional de Pesquisa e Conservação da Biodiversidade Marinha do Sudeste e Sul (CEPSUL) staff, Roberta Aguiar dos Santos, Felipe Farias Albanez, Elisabeth Michelletti and Luiz Fernando Rodrigues. To the undergraduate students of UFSC, UNIVALI and FURB that helped with sampling; to the crew of the R/V Soloncy Moura/CEPSUL; to Karin Schacht, Allan Scalco, Bernardo Cerantola, and Paula Salge, for suggestions and support in drafting the manuscript; and to CNPq for grants given to PBA. This research was

supported by the Instituto Chico Mendes de Conservação da Biodiversidade (ICMBio), and Comissão Interministerial para os Recursos do Mar (CIRM) through Avaliação, Monitoramento e Conservação da Biodiversidade Marinha (REVIMAR). The authors also would like to thank the anonymous reviewers for their valuable contributions.

REFERENCES

- Amaral, A.C.Z. & S. Jablonski. 2005. Conservation of marine and coastal biodiversity in Brazil. *Conserv. Biol.*, 19: 625-631.
- Athiê, A.A.R. & C.L.B. Rossi-Wongtschowski. 2004. Os caranguejos-de-profundidade na Zona Econômica Exclusiva da Região Sudeste-Sul do Brasil: análise das operações de pesca e das capturas do N/P Kimpo Maru nº58. Instituto Oceanográfico-USP, São Paulo, 64 pp.
- Ayres, M., M. Ayres Júnior, D.L. Ayres & A.D.A. Santos. 2007. Aplicações estatísticas nas áreas das ciências bio-médicas. Instituto Mamirauá, Belém, 364 pp.
- Bakun, A. 2006. Fronts and eddies as key structures in the habitat of marine fish larvae: opportunity, adaptive response and competitive advantage. *Sci. Mar.*, 70: 105-122.
- Barradas-Ortiz, C., P. Briones-Fourzan & E. Lozano-Alvarez. 2003. Seasonal reproduction and feeding ecology of giant isopods *Bathynomus giganteus* from the continental slope of the Yucatan Peninsula. *Deep-Sea Res. I*, 50: 495-513.
- Biscoito, M., M. Freitas, J.G. Pajuelo, R. Triay-Portella, J.I. Santana, A.L. Costa, J. Delgado & J.A. González. 2015. Sex-structure, depth distribution, intermoult period and reproductive pattern of the deep-sea red crab *Chaceon affinis* (Brachyura, Geryonidae) in two populations in the north-eastern Atlantic. *Deep-Sea Res. I*, 95: 99-114.
- Borcard, D., F. Gillet & P. Legendre. 2011. Numerical ecology with R. Springer Science & Business Media, New York, 306 pp.
- Carvalho, J.L.B., C.A.F. Schettini & T.M. Ribas. 1998. Estrutura termohalina do litoral Centro-Norte catarinense. *Notas Téc. FACIMAR*, 2: 181-197.
- Castello, J.P., M. Haimovici, C. Odebrecht & C.M. Vooren. 2012. The Continental shelf and slope. In: U. Seeliger C. Odebrecht & J.P. Castello (eds.). Subtropical convergence environments: the coast and sea in the southwestern Atlantic. Springer Science & Business Media, Berlin, pp. 171-178.
- Clark, M.R., F. Althaus, T.A. Schlacher, A. Williams, D.A. Bowden & A.A. Rowden. 2016. The impacts of deep-sea fisheries on benthic communities: a review. *ICES J. Mar. Sci.*, 73: 51-69.
- Danovaro, R., P.V.R. Snelgrove & P. Tyler. 2014. Challenging the paradigms of deep-sea ecology. *Trends Ecol. Evol.*, 29: 465-475.
- Domingos, S.S., A.A.R. Athiê & C.L.B. Rossi-Wongtschowski. 2008. Diet of *Chaceon ramosae* (Decapoda, Brachyura) on the southern brazilian exclusive economic zone. *Braz. J. Oceanogr.*, 56: 59-63.
- Elner, R.W., S. Koshio & G.V. Hurley. 1987. Mating behavior of the deep-sea red crab, *Geryon quinquedens* Smith (Decapoda, Brachyura, Geryonidae). *Crustaceana*, 52(2): 194-201.
- Emilson, I. 1961. The shelf and coastal waters off southern Brazil. *Bol. Inst. Oceanogr.*, 11: 101-112.
- Ferreira, R.C.P., D.M. Nunes, R.A. Shinozaki-Mendes, A.M.A. Pires & F.H.V. Hazin. 2016. First record and preliminary information on the biology of the deep-sea African crab, *Chaceon gordonae* (Ingle, 1985) (Brachyura: Geryonidae) in Saint Peter and Saint Paul Archipelago, Brazil. *Lat. Am. J. Aquat. Res.*, 44(2): 392-400.
- Fischer, L.G. 2012. Distribuição, biomassas e ecologia de Macrouridae (Teleostei, Gadiformes) no talude continental do sul do Brasil, com ênfase em *Coelrorinchus marinii* Hubbs 1934 e *Malacocephalus occidentalis* Goode & Bean 1885. Ph.D. thesis. Universidade Federal de Rio Grande, Rio Grande, 266 pp.
- Fonteles-Filho, A.A. 1989. Recursos pesqueiros. Biologia e dinâmica populacional. Imprensa Oficial do Ceará, Fortaleza, 296 pp.
- Food and Agriculture Organization (FAO). 2009. International guidelines for the management of deep-sea fisheries in the high seas. FAO, Rome, 73 pp.
- George, R.Y. & R.J. Menzies. 1968. Further evidence for seasonal breeding cycles in deep sea. *Nature*, 220: 80-81.
- Groeneveld, J.C., B.I. Everett, S.T. Fennessy, S.P. Kirkman, J. Santos & W.D. Robertson. 2013. Spatial distribution patterns, abundance and population structure of deep-sea crab *Chaceon macphersoni*, based on complementary analyses of trap and trawl data. *Mar. Freshwater Res.*, 64: 507-517.
- Gutiérrez, N.L., A. Masello G. Uscudun & O. Defeo. 2011. Spatial distribution patterns in biomass and population structure of the deep sea red crab *Chaceon notialis* in the Southwestern Atlantic Ocean. *Fish. Res.*, 110: 59-66.
- Haefner, P.A. Jr. 1978. Seasonal aspects of the biology, distribution and relative abundance of the deep-sea red crab *Geryon quinquedens* Smith, in the vicinity of the

- Norfolk Canyon, western North Atlantic. Proc. Natl. Shellfish Assoc., 68: 49-62.
- Haimovici, M., A.O.A. da Silva, L.V. de Miranda & S. Klippel. 2007. Prospecção na Região Sudeste-Sul. In: M. Haimovici (ed.). A prospecção pesqueira e abundância de estoques marinhos no Brasil nas décadas de 1960 a 1990: Levantamento de dados e avaliação crítica. Ministério do Meio Ambiente, Brasília, pp. 35-73.
- Instituto Chico Mendes. 2016. Avaliação do risco de extinção dos crustáceos no Brasil: 2010-2014 –World Wide Web electronic publication, accessible at [http://www.icmbio.gov.br/cepsul/images/stories/biblioteca/download/trabalhos_tecnicos/pub_2016_avaliacao_crustaceos_2010_2014.pdf]. (Reviewed: 12 October 2016).
- Legendre, P. & L. Legendre. 1998. Numerical ecology. Elsevier, Amsterdam, 852 pp.
- Lima, J.H.M. & R. Lima-Branco. 1991. Análise das operações de pesca do caranguejo de profundidade (*Geryon quinquedens* Smith, 1879) por barcos japoneses arrendados na região sul do Brasil- 1984/85. Atlântica, 13: 179-187.
- Lux, F.E., A.R. Ganz & W.F. Rathjen. 1982. Marking studies on the red crab *Geryon quinquedens* Smith off Southern New England. J. Shellfish Res., 2: 71-80.
- Macedo-Soares, L.C.P., C.A.E. Garcia, A.S. Freire & J.H. Muelbert. 2014. Large-scale ichthyoplankton and water mass distribution along the South Brazil Shelf. PLoS One, 9: e91241.
- Manning, R.B. & L.B. Holthius. 1989. Two new genera and nine new species of geryonid crabs (Crustacea, Decapoda, Geryonidae). Proc. Biol. Soc. Wash., 102: 50-77.
- Manning, R.B., M. Tavares & E.F. Albuquerque. 1989. *Chaceon ramosae*, a new deep-water crab from Brazil (Crustacea: Decapoda: Geryonidae). Proc. Biol. Soc. Wash., 102: 646-650.
- Mantelatto, F.L., P.R. Pezzuto, A. Masello, C.L.D.B. Rossi-Wongtschowski, A.W.S. Hilsdorf & N. Rossi. 2014. Molecular analysis of the commercial deep-sea crabs *Chaceon ramosae* and *Chaceon notialis* (Brachyura, Geryonidae) reveals possible cryptic species in the South Atlantic. Deep-Sea Res. I, 84: 29-37.
- Matsuura, Y. 1995. Exploração Pesqueira. In: Ministério do Meio Ambiente (eds.). Os ecossistemas brasileiros e os principais macrovetores de desenvolvimento. Ministério do Meio Ambiente, Brasília, pp. 40-46.
- Melo, G.A.S. 1996. Manual de identificação dos Brachyura (caranguejos e siris) do litoral brasileiro. Plêiade/FAPESP, São Paulo, 603 pp.
- Melville-Smith, R. 1987. The reproductive biology of *Geryon maritae* (Decapoda, Brachyura) off South West Africa/Namibia. Crustaceana, 53: 259-275.
- Melville-Smith, R. 1989. A growth model for the deep-sea red crab (*Geryon maritae*) off South Africa/Namibia (Decapoda, Brachyura). Crustaceana, 56: 279-292.
- Mincarone, M.M. & M.E. Anderson. 2008. A new genus and species of eelpout (Teleostei: Zoarcidae) from Brazil. Zootaxa, 1852: 65-68.
- Morales-Nin, B. & J. Panfili. 2005. Seasonality in the deep sea and tropics revisited: what can otoliths tell us? Mar. Freshwater Res., 56: 585-598.
- Olson, D.B., G.P. Podestá, R.H. Evans & O.B. Brown. 1988. Temporal variations in the separation of Brazil and Malvinas Currents. Deep-Sea Res., 35(12): 1971-1990.
- Perez, J.A.A. & R. Wahrlich. 2005. A bycatch assessment of the gillnet monkfish *Lophius gastrophysus* fishery off southern Brazil. Fish. Res., 72: 81-95.
- Pezzuto, P.R. & R. Sant'Ana. 2009. Sexual maturity of the deep-sea royal crab *Chaceon ramosae* Manning, Tavares & Albuquerque, 1989 (Brachyura: Geryonidae) in southern Brazil. Lat. Am. J. Aquat. Res., 37(3): 297-312.
- Pezzuto, P.R., J.A.A. Pérez, R. Wahrlich, W.G. Vale & F.R.A. Lopes. 2002. Análise da pescaria dos caranguejos-de-profundidade no Sul do Brasil - Anos 2001-2002. [http://gep.acad.univali.br/download/relatorios/relatorio_chaceon.pdf] Reviewed: 17 August 2017.
- Pezzuto, P.R., J.A.A. Pérez & R. Wahrlich. 2006a. Deep-sea shrimps (Decapoda: Aristeidae): new targets of the deep-water trawling fishery in Brazil. Braz. J. Oceanogr., 54(2/3): 123-134.
- Pezzuto, P.R., J.A.A. Perez & R. Wahrlich. 2006b. O ordenamento das pescarias de caranguejos-de profundidade (*Chaceon* spp.) (Decapoda: Geryonidae) no sul do Brasil. Bol. Inst. Pesca, 32(2): 229-247.
- Pezzuto, P.R., A.P. Pinheiro & H. Boos. 2016. Avaliação dos caranguejos gerionídeos (Decapoda: Geryonidae). In: M.A.A. Pinheiro & H. Boos (Org.). Livro Vermelho dos Crustáceos do Brasil: Avaliação 2010-2014. Sociedade Brasileira de Carcinologia-SBC, Porto Alegre, pp. 192-202.
- Piola, A.R., O.O. Möller Jr., R.A. Guerrero & E.J.D. Campos. 2008. Variability of the subtropical shelf front off eastern South America: winter 2003 and summer 2004. Cont. Shelf Res., 28: 1639-1648.
- Piola, A.R., R.P. Matano, E.D. Palma, O.O. Möller Jr. & E.J.D. Campos. 2005. The influence of the Plata River discharge on the western South Atlantic shelf. Geophys. Res. Lett., 32: L01603.
- Pires-Vanin, A.M. & Y. Matsuura. 1993. Estrutura e função do ecossistema de plataforma continental da

- região de Ubatuba, Estado de São Paulo: uma introdução. Publ. Esp. Inst. Oceanogr., 10: 1-8.
- R Development Core Team. 2014. R: a language and environment for statistical computing (Version 3.1.1) -World Wide Web electronic publication, accessible at [https://www.r-project.org]. Reviewed: 8 December 2016.
- Rogers, A.D., M.R. Clark, J.M. Hall-Spencer & K.M. Gjerde. 2008. The science behind the guidelines: a scientific guide to the FAO draft international guidelines (December 2007) for the management of deep-sea fisheries in the high seas and examples of how the guidelines may be practically implemented. IUCN, Switzerland, 44 pp.
- Rosa, R. & M.L. Nunes. 2003. Biochemical compositions of deep-sea decapods crustaceans with two different benthic life strategies off the Portuguese south coast. Deep-Sea Res. I, 50: 119-130.
- Rossi-Wongtschowsky, C.L.D.B., J.L. Valentin, S. Jablonski, A.C.Z. Amaral, F.H.V. Hazin & M. El-Robrini. 2006. O Ambiente Marinho. In: Ministério do Meio Ambiente. Programa REVIZEE: avaliação do potencial sustentável de recursos vivos na zona econômica exclusiva: relatório executivo. Ministério do Meio Ambiente, Brasília, pp. 21-75.
- Rowe, G.T. 2013. Seasonality in deep-sea food webs -A tribute to the early works of Paul Tyler. Deep-Sea Res. II, 92: 9-17.
- Santos, E.P. 1978. Dinâmica de populações aplicada à pesca e piscicultura. HUCITEC/EDUSP, São Paulo, 129 pp.
- Slack-Smith R.J. 2001. Fishing with traps and pots. FAO, Rome, 62 pp.
- StatSoft Inc. 2005. Statistica (data analysis software system), version 7.1.
- Tavares, M. & A. Pinheiro. 2011. A new species of *Chaceon* Manning & Holthuis, 1989, from the southwestern Atlantic, with a key to the western Atlantic species (Crustacea, Decapoda, Geryonidae). Zootaxa, 3086: 57-68.
- Univali/CTTMar. 2010. Boletim estatístico da pesca industrial de Santa Catarina-Ano 2009 e panorama 2000-2009: programa de monitoramento e avaliação da atividade pesqueira industrial no sudeste e sul do Brasil. Universidade do Vale do Itajaí, Itajaí, 97 pp.
- Vazzoler, A.E.A.M. 1981. Manual de métodos para estudos biológicos de populações de peixes: reprodução e crescimento. CNPq, Brasília, 106 pp.
- Vazzoler, A.E.A.M. 1996. Biologia da reprodução de peixes Teleósteos: teoria e prática. EDUEM, Maringá, 169 pp.
- Walters, C. 2003. Folly and fantasy in the analysis of spatial catch rate data. Can. J. Fish. Aquat. Sci., 60: 1433-1436.
- Wigley, R.L., R.B. Theroux & H.E. Murray. 1975. Deep-sea red crab, *Geryon quinqueedens*, survey off the northeastern United States. Mar. Fish. Rev., 37(8): 1-21.
- Zembruski, S.G., H.T. Barreto, C.J. Palma & J.D. Milliman. 1972. Estudo preliminar das províncias geomorfológicas da margem continental brasileira. In: Congresso Brasileiro de Geologia. Belém, pp. 187-209.

Received: 17 March 2017; Accepted: 29 August 2018