# Secondary production of *Chasmagnathus granulatus* (Crustacea; Decapoda) in a Ramsar Site from Argentina

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(With 2 figures)

#### Abstract

Secondary production of Chasmagnathus granulatus was calculated at the Refugio de Vida Silvestre Bahía Samborombón, Argentina (36° 16' S and 57° 06' W). Sampling was conducted on nine occasions between March 2001 and February 2003, crabs were collected by hand, physico-chemical variables, granulometry and organic matter contents of the sediments were registered. Crabs were classified as male, female and undifferentiated, measured (total carapace width: CW) and weighed (wet and dry weight: DW at 60 °C, during 48 hours). A correlation analysis between CW and DW was made. Morphometric growth of C. granulatus was by the application of the power function  $(y = a x^{b})$ , where the carapace width (CW) was used as an independent variable. Males, females and undifferentiated individuals were analysed separately as well as all together as a group. The data were fitted indicating a positive allometry (constant of allometry b > 3), the males showing the greatest allometric value. The individuals (n = 957 juveniles and adults) were separated in cohorts by the polymodal width-frequency distribution converted into normal curves. Three cohorts were found during the whole study period, and two cohorts coexisting in each sampling date. Ovigerous females were caught on December 2001, 2002 and February 2003. The size-frequency method was used to estimate the annual production. The major contribution to production was carried out by the mature individuals, in particular those with size between 25 and 30 mm, but on the other hand, only few individuals measuring from 10 to 20 mm were collected. The annual production of C. granulatus was estimated in 7.76 g.m<sup>-2</sup>. The biomass (expressed as total dry weight) varied between 0.55 and 1.85 g.m<sup>-2</sup>, with the greater values being registered during autumn and spring, and the lower values during summer.

Keywords: secondary production, estuarine crab, Chasmagnathus granulatus, Bahía Samborombón.

# Produção secundária de *Chasmagnathus granulatus* (Crustacea; Decapoda) em um sítio Ramsar da Argentina

#### Resumo

Foram calculadas as primeiras estimativas da produção secundária de Chasmagnathus granulatus no Refúgio da Vida Silvestre Bahía Samborombón, Argentina (36° 16' S e 57° 06' W). As amostragens foram realizadas em nove ocasiões, entre o período de março de 2001 a fevereiro de 2003. Os caranguejos foram coletados manualmente. Variáveis físico-químicas, granulometria e teor de matéria orgânica dos sedimentos foram analisados. O caranguejos (n = 957, jovens e adultos) foram classificados em: machos, fêmeas e indiferenciados; foram mensurados (Largura da Carapaça, LC) e pesados (peso úmido e seco, PS a 60 °C, 48 horas). Uma análise de correlação entre LC vs. PS foi efetuada. O crescimento morfométrico de C. granulatus foi analisado pela aplicação da função potencial (PS = a LC <sup>b</sup>), sendo que machos, fêmeas e indivíduos com sexo não diferenciado foram analisados separadamente e em conjunto. O ajuste dos dados indicou uma alometria positiva, com os machos apresentando o maior valor. Os indivíduos foram separados em coortes por meio da conversão de curvas de normalidade de uma distribuição de freqüência polimodal. Três coortes foram encontradas durante todo o período de estudo, e duas coexistindo em cada data de amostragem. Fêmeas ovígeras foram coletadas em dezembro de 2001 e 2002 e em fevereiro de 2003. Utilizou-se o método da distribuição de freqüência de tamanho para estimar a produção anual. A maior contribuição para a produção é dada pelos indivíduos sexualmente maduros, particularmente por aqueles com tamanhos entre 25 e 30 mm. A produção anual foi estimada em 7,76 g.m<sup>-2</sup>. A biomassa, expressa em peso seco, variou entre 0,55 e 1,85 g.m<sup>-2</sup>, com maiores valores registrados no outono e na primavera, e menores valores registrados no verão.

Palavras-chave: produção secundária, caranguejo estuarino, Chasmagnathus granulatus, Bahía Samborombón.

## 1. Introduction

*Chasmagnathus granulatus* Dana, 1851 (Varunidae) is an estuarine species endemic of the Neotropical region that is distributed from Rio de Janeiro (Brazil) to the Río Negro river (Argentina). Very dense populations of this species occupy the high levels of the silty or silt-sandy intertidal wetlands of Samborombón Bay, Argentina (Spivak, 1997a, 1997b; César et al., 2005), giving the landscape a special physiognomy called "cangrejales". They constitute extensive feeding areas for migratory shorebirds like "ostrero pardo" (*Haematopus palliatus* Temminck, 1820) that prey on this crab and also breeding areas for fishes of commercial and sporting interest such as the "corvina rubia" (*Micropogonias furnieri* (Demarest, 1823)) and "corvina negra" (*Pogonias cromis* (Linnaeus, 1766)).

The Samborombón Bay is a depocentre of significant magnitude, formed by sediments from the sea and the Uruguay and Paraná rivers, generating coastal plains with large marshes (Violante et al., 2001). The coast of the bay is bathed by salty waters of variable salinity corresponding to the estuarine area of the Río de la Plata River (Boschi, 1988). It represents one of the most attractive and special wetlands in the Province of Buenos Aires, declared Ramsar Site in 1997, which covers the whole extension of the bay. The vegetation in the alluvial plain is predominantly herbaceous, with "espartillo" (Spartina alterniflora Loisel. and S. densiflora (Brong.)), "pasto salado" (Distichlis scoparia (Kth.) Arech. and D. spicata (L.) Greene) and "cortadera" (Cortaderia selloana (Schult.) Asch. et Graebn.) grasslands. On the floodable area "jume" meadows (Salicornia ambigua Michx.) develop, where the very clayish soils are exposed to salinity, erosion and sediment depositions (Vervoorst, 1967).

Several papers dealing with secondary production in Crustacea have been published (e.g. Ferreira Fontoura and Buckup, 1991; Calcagno et al., 1997; Cartes and Sorbe, 1999) but only a few deal with to Brachyura (Waters, 1977; Fredete et al., 1990; Heck et al., 1995).

Despite many of the contributions on biological and physiological aspects of *C. granulatus* Argentinean populations (Anger et al., 1994; Luquet et al., 1995, 1997; Stella et al., 1996; Spivak et al., 1996; Luquet and Ansaldo, 1997; Luppi et al., 1997, 2004; López and Rodríguez, 1998, 1999; César et al., 2005), no research on secondary production have been carried out. Therefore, the aim of the present work conducted at the Refugio de Vida Silvestre Bahía Samborombón is to offer the first estimates on the secondary production of this crab.

#### 2. Material and Methods

Sampling was conducted on nine occasions between March 2001 and February 2003 at the mouth of Channel 1 at the Refugio de Vida Silvestre Bahía Samborombón. Five sampling sites were selected at  $36^{\circ} 16'$  S and  $57^{\circ} 06'$  W, two located at the intertidal of the northern

Crabs were collected by hand using a square of 5 x 5 m, with 0.5 x 0.5 m subunits. A preliminary sampling was carried out and 35 subunits were randomly taken. Based on these data, the minimum number of samples to be taken was calculated (n = 10) (Elliott, 1983). Crabs were kept in plastic bags and frozen. Samples were taken for granulometric analysis and for determination of the organic matter contents of the sediments using the Walkley-Black method (Allison, 1965). Physico-chemical variables of water were also measured: temperature (°C), pH and conductivity. In the laboratory, crabs were thawed at room temperature and fixed in 10 % formalin. Crabs were counted and classified as male, female or undifferentiated (those which did not present secondary sexual characters). They were measured (total carapace width: CW) and weighed (wet and dry weight: DW at 60 °C, during 48 hours), and the correlation analysis between CW and DW was made. The individuals captured were analysed and separated into cohorts by the polymodal width-frequency distribution converted into normal curves using a Microsoft Excel Solver macro-complement.

Morphometric growth of *C. granulatus* was studied by the application of the power function ( $y = a x^{b}$ ), where the carapace width (CW) was used as an independent variable. Males, females and undifferentiated individuals were analysed separately as well as all together as a group.

To estimate the annual production of *C. granulatus* we used the size-frequency method (Hynes and Coleman, 1968; Hamilton, 1969; Waters, 1977; Benke, 1979) and followed the procedures of Menzie (1980), Krueger and Martin (1980) and Runck and Blinn (1990, 1993):

$$P = \sum_{J=1}^{c} (N_{j} - N_{j+1}) (W_{j} \times W_{j+1})^{1/2}$$
(1)

where P is the annual production,  $N_j$  is the number of individuals that developed into the size class j during the year, c is the number of size classes and  $W_j$  is the mean weight of size class j.

As suggested by Waters (1977) for those species with life spans of more than one year, the estimate of annual production must be divided by the number of years in the life span, to obtain annual production. As a result, and taking into account the study carried out by Luppi et al. (2004), we estimate an average life span of three years by our calculations.

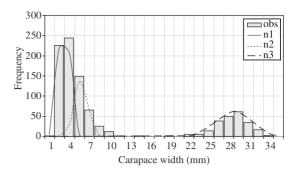
#### 3. Results

The registered physical and chemical variations would be those typical of an estuarial ecosystem.

Physical and chemical variables measured, granulometry, organic carbon and organic matter of the sediment are presented in Table 1. The organic matter and organic carbon show low to medium values with reference to soils; as for the grain-size, they are clayish. Individuals of *C. granulatus* were collected in all samplings (n = 957juveniles and adults), except in July 2002 when crabs were not found on the surface or in their burrows at to a depth of 50 cm.

Three cohorts (Figure 1) were recruited during the whole study period, and two cohorts were found coexisting in each sampling date. Ovigerous females were caught on December 2001, 2002 and February 2003.

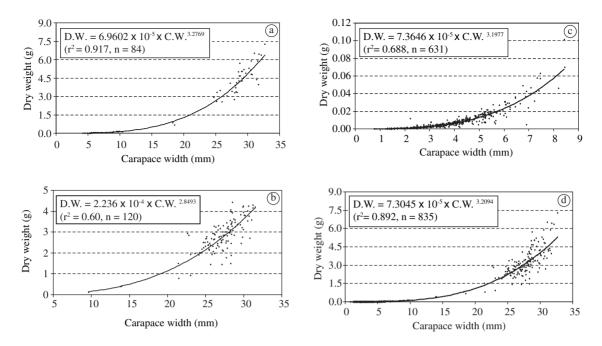
The data were fitted (Figure 2) indicating a positive allometric growth (constant of allometry b > 3), except for females. The correlation equations obtained were the



**Figure 1.** Size frequency distribution of *Chasmagnathus granulatus* in Samborombón Bay, Argentina, during the study period. Normal curves belonging to each cohort were obtained by polymodal analysis.

**Table 1.** Physical and chemical variables, granulometric characterization, organic carbon and organic matter contents measured on each site sampled in Channel 1, Samborombón Bay. The salinity values were obtained after multiplying the conductivity by 0.9.

	Date	рН	Salinity (mg.L <sup>-1</sup> )	T °C	Granulometric characterization (%)				Organic matter (%)	Organic carbon (%)
					Gravel	Sand	Silt	Clay	-	
Site 1	Mar-01	-	-	23.8	0	5.6	15.77	78.63	2.52	1.46
	Sep-01	-	-	15	-	-	-	-	-	-
	Dec-01	8.33	824.4	27	-	-	-	-	-	-
Site 1*	Jun-01	-	-	17	0	0.97	15.35	83.69	2.03	1.18
	Sep-01	-	-	15	-	-	-	-	-	-
	Dec-01	8.33	824.4	27	-	-	-	-	-	-
	Apr-02	8.76	624.6	15.7	-	-	-	-	-	-
	Oct-02	8.77	979.2	23.4	-	-	-	-	-	-
	Dec-02	7.83	842.4	27.8	-	-	-	-	-	-
	Feb-03	8.68	3303	29.6	-	-	-	-	-	-
Site 2	Jun-01	-	-	17	0	0.6	13.26	86.13	1.93	1.12
	Sep-01	-	-	14	-	-	-	-	-	-
	Dec-01	8.17	771.3	27.9	-	-	-	-	-	-
	Apr-02	8.03	866.7	16.9	-	-	-	-	-	-
	Jul-02	8.97	607.5	10	-	-	-	-	-	-
	Oct-02	7.84	877.5	19.7	-	-	-	-	-	-
	Dec-02	8.10	925.2	27.9	-	-	-	-	-	-
	Feb-03	8.47	6741	26.6	-	-	-	-	-	-
Site 3	Jun-01	-	-	17	0.15	0.76	15.25	83.85	1.29	0.75
	Sep-01	-	-	14	-	-	-	-	-	-
	Dec-01	8.17	771.3	27.9	-	-	-	-	-	-
	Apr-02	8.03	866.7	16.9	-	-	-	-	-	-
	Jul-02	8.97	607.5	10	-	-	-	-	-	-
	Oct-02	7.84	877.5	19.7	-	-	-	-	-	-
	Dec-02	8.10	925.2	27.9	-	-	-	-	-	-
	Feb-03	8.47	6741	26.6	-	-	-	-	-	-
Site 4	Oct-02	8.26	912.6	19.3	-	-	-	-	-	-
	Dec-02	7.82	936.9	30.7	-	-	-	-	-	-
	Feb-03	8.09	2889	29.2	-	-	-	-	-	-



**Figure 2.** Correlation curves in *Chasmagnathus granulatus* (carapace width vs. dry weight) collected in Samborombón Bay, Argentina. a) males; b) females; c) undifferentiated organisms; and d) all crabs grouped together.

following ones, the males showing the greatest allometric value:

- For males: DW =  $6.9602 \ 10^{-5} \ CW^{-3.2769}$  (n = 84,  $r^2 = 0.917$ , p < 0.01);
- For females: DW = 2.236 10<sup>-4</sup> CW <sup>2.8493</sup> (n = 120, r<sup>2</sup> = 0.60, p < 0.01);</li>
- For undifferentiated: DW = 7.3646 10<sup>-5</sup> CW <sup>3.1977</sup> (n = 631, r<sup>2</sup> = 0.688, p < 0.01); and</li>
- For all crabs grouped together: DW = 7.3045.10<sup>-5</sup> CW <sup>3.2094</sup> (n = 835, r<sup>2</sup> = 0.892, p < 0.01).</li>

The calculations made to obtain the annual production of *C. granulatus* are presented in Table 2, estimating 7.76 g.m<sup>-2</sup> throughout the year. According to López-Greco and Rodríguez (1999) the minimum size of functional maturity for females could be determined by the minimum size of ovigerous females from field samples. Taking into account that the smallest ovigerous female captured measured 22.76 mm, we found that the major contribution to production was carried out by the mature individuals, in particular those with size between 25 and 30 mm. On the other hand, it was notable that there were a few individuals measuring from 10 to 20 mm.

The biomass (expressed as total dry weight) varied between 0.55 and 1.85 g.m<sup>-2</sup> in the eight samplings of the collected material; the greater values were registered during autumn and spring (June 01 and October 02) and the lower values during summer (March 01, December 02 and February 03) as shown in Table 3.

#### 4. Discussion

The ecological significance of C. granulatus has been mentioned (see Introduction) as prey of several fish species of sporting and commercial value, shorebirds and also other crab species, such as Callinectes sapidus Rathbun, 1896 (Spivak, 1997b). C. granulatus builds its burrows in the intertidal of brackish wetlands, as much in the vegetated areas as in the naked one. Some populations reach high densities (i.e.: 52 to 60 ind/m<sup>2</sup>) in Bahía Samborombón (César et al., 2005; Botto and Irigoven, 1979, respectively). Its use of the habitat is complex; there is spatial segregation among sizes and reproductive stages. In the population studied in Channel 1, we found two simultaneous cohorts, with the reproduction period from spring to summer. In this population, two different sized groups sharing the habitat were registered, corresponding to undifferentiated and juvenile crabs (smaller than 12 mm) and adults (from 21 up to 33.2 mm). Other studies realized in this species, but in Mar Chiquita lagoon, distinguished two groups with 24-27 and 31-33 mm CW, respectively, although they only considered sexually mature individuals (Spivak et al., 1996, Luppi et al., 2004). The absence of individuals comprised in the 12-21 mm size interval may be caused by the spatial segregation observed in different microhabitats of the prepubescent individuals with respect to the rest, as cited by Spivak et al. (1996) and César et al. (2005).

Crabs were recruited in all samplings except in the winter of 2002. This lack of crabs on the surface could be due to the low temperatures and frosts registered during

Size class (mm)	N (ind/m <sup>2</sup> )	$\boldsymbol{N}_j - \boldsymbol{N}_{j+1}$	$W_{j}\left(g ight)$	$(W_{j} X W_{j+1})^{1/2}$	$(N_j - N_{j+1}) \times (W_j \times W_{j+1})^{1/2}$	Production
0-4.99	6.89	5.01	0.003207	0.0097170	0.0486822	0.340775
5.0-9.99	1.88	1.833	0.0294364	0.0896573	0.1634191	1.143933
10.0-14.99	0.047	0.024	0.2730780	0.4788587	0.0114926	0.080448
15.0-19.99	0.023	-0.231	0.8397075	1.2647843	-0.2921651	-2.045156
20.0-24.99	0.254	-1.579	1.9050433	2.4281296	-3.8340166	-26.838116
25.0-29.99	1.833	1.3	3.0948447	3.7250260	4.8425339	33.897737
30.0-34.99	0.533	0.533	4.4835267	4.4835267	2.3897197	16.728038
					Total Production (TP)	23.307659
					Annual production (TP/3)	7.769219

**Table 2.** Production  $(g.m^{-2} \text{ yr}^{-1})$  of *Chasmagnathus granulatus* estimated by the size-frequency method during 2001-2003 in Channel 1, Samborombón Bay. N, is the number of individuals in size class j; W, is the mean weight of size class j.

Table 3. Bioma	uss (total	dry w	eight) of	Cł	hasmagnath	ius
granulatus dur	ing the	study	period	in	Channel	1,
Samborombón B	ay, Arger	ntina.				

<i>,</i>		
Sampling date	Ν	Biomass (g.m <sup>-2</sup> )
March 01	26	0.670
June 01	220	1.853
September 01	172	1.074
December 01	79	1.097
April 02	113	1.089
October 02	157	1.569
December 02	40	0.746
February 03	150	0.554

those days in the region. The highest values in biomass were registered in June 2001 and October 2002 while the lower in March 2001 and in the summer of 2002-2003. In the sampling of June 2001, a peak of abundance was also observed with mainly the juvenile individuals constituting the biggest contribution to the biomass, although the mature sizes were also registered; the same happened in the spring of 2002. The minor values of biomass could be due to different causes, i.e.: for operative difficulties only one site was sampled in March 2001; and in February 2003, there was a great contribution of recruits. It is difficult to explain the scarcity of individuals in December 2002 taking into account that all sizes were represented. The reproductive season of C. granulatus comprises spring and summer months (September to March and even extending to April). Each female can spawn up to three or four times during the reproductive period, and thus females can produce more than one cohort during the same reproductive period (López and Rodríguez, 1998). Nevertheless, it is necessary to highlight the presence of recruits during the whole period of study. This would indicate that, although this crab presents a reproductive season during spring and summer given by the ovigerous females captured, reproduction could be more or less continuous throughout the whole year.

Weight growth of *C. granulatus* showed a positive allometry (constant of allometry b > 3) for undifferentiated individuals and males analysed separately, as well as all crabs together as a group, and the correlation equations obtained indicated that the males presented the greatest allometric value. Once sexual maturity is achieved, *C. granulatus* showed differential somatic growth between sexes, the females growing less than the males, as also noted by López and Rodríguez (1998) and D'Incao et al., (1993). It should be remembered that brachyurans females reach smaller sizes than males, because of the energy investment in reproduction and oviposition, instead of in growth.

There were reported growth differences between grapsoid populations distributed along 10° latitude (Luppi et al., 2004). Studies carried out in the growth of C. granulatus in Lagoa dos Patos (Brazil) estimated longevity from 1.7 to 2.03 years for males and females, respectively (D'Incao et al., 1993). However, López and Rodríguez (1998) concluded that this species, studied in Samborombón Bay, needed a minimum of two and a maximum of three years to reach sexual maturity from the larval stages. Luppi et al., op. cit., in the population from Mar Chiquita lagoon, found that newly settled recruits reached adulthood after only one year and estimated a lifespan of no more than three years. Since Samborombón Bay and Mar Chiquita lagoon are only 150 km apart (which would represent approximately 1.4° latitude), and in view of the fact that these populations may be genetically connected (as suggested in Luppi et al., 2004), we estimated a lifespan of three years for the calculation of annual production.

The individuals that reached reproduction size were those that made the biggest contribution to production. With regards to the annual production estimates, *C. granulatus* registered values of 77.6 kg per Ha which are comparable to those registered in the economic interest crab *C. sapidus* (i.e.: 7.7 g.m<sup>-2</sup> year<sup>-1</sup>) (Fredete et al., 1990). However, it is important to mention the biggest size in this last species with regard to the first one. Other estimations have been reached with respect

to *Orconectes virilis* (Hagen) studied in Lake Michigan (i.e.: 8.2-34.5 kg per ha) (Waters, 1977) and in the fiddler crab *Uca uruguayensis* (Nobili, 1901) (i.e.: 23 kg per ha) (Armendáriz and César, 2006), which coexists in the same habitat with the crab studied here.

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## References

ALLISON, LE., 1965. Organic carbon. In C. A Black (ed.), *Methods of soil analysis. Part 2. Chemical and Microbiological Properties*, American Society of Agronomy, Madison, Wisconsin.

ANGER, K., SPIVAK, E., BAS, C., ISMAEL, D. and LUPPI, T., 1994. Hatching rhythms and dispersion of decapod crustacean larvae in a brackish coastal lagoon in Argentina. *Helgoländer Meeresuntersuchungen*, vol. 48, p. 445-466.

ARMENDÁRIZ, LC. and CÉSAR, II., 2006. *Estimating* secondary production in Uca uruguayensis (Decapoda, Brachyura, Ocypodidae) from Samborombón Bay, Argentina. Ciencias Marinas, Ensenada, Baja California, vol. 32, no. 3, p. 551-558.

BENKE, AC., 1979. A modification of the Hynes method for estimating secondary production with particular significance for multivoltine populations. *Limnol. Oceanogr.*, vol. 24, no. 1, p. 168-171.

BOSCHI, EE., 1988. El ecosistema estuarial del Río de la Plata (Argentina y Uruguay). *An. Inst. Cienc. del Mar y Limnol. Univ. Nac. Autón. México*, vol. 15, no. 2, p. 159-182.

BOTTO, JL. and IRIGOYEN, HR., 1979. Bioecología de la comunidad del cangrejal. I. Contribución al conocimiento biológico del cangrejo de estuario, *Chasmagnathus granulata* Dana (Crustacea, Decapoda, Grapsidae) en la desembocadura del río Salado, Provincia de Buenos Aires. *Seminario Latinoamericano de Ecología Bentónica y Sedimentología de la Plataforma Continental del Atlántico Sur.* UNESCO, Montevideo, p. 161-169.

CALCAGNO, JA., LÓPEZ-GAPPA, J. and TABLADO, A., 1997. Growth and production of the barnacle *Balanus anphitrite* in an intertidal area affected by sewage pollution. *J. Crustacean Biol.*, vol. 17, no. 3, p. 417-423.

CARTES, JE. and SORBE, JC., 1999. Estimating secondary production in bathyal suprabenthic peracarid crustaceans from the Catalan Sea slope (western Mediterranean; 391-1255 m). *J. Exp. Mar. Biol. Ecol.*, vol. 239, p. 195-210.

CÉSAR, II., ARMENDÁRIZ, LC. and BECERRA, RV., 2005. Bioecology of the fiddler crac *Uca uruguayensis* and the burrowing crab *Chasmagnathus granulatus* (Decapoda, Brachyura) in the Refugio de Vida Silvestre Bahía Samborombón, Argentina. *Hydrobiologia*, vol. 545, p. 237-248.

D'INCAO, F., RUFFINO, ML., SILVA, KG., BRAGA, AC. and CUNHA-MARQUES, LH., 1993. Crescimento de *Chasmagnathus granulata* Dana, 1851, em um marisma do estuário da Lagoa dos Patos, RS (Decapoda: Grapsidae). *Rev. Bras. Biol.*, vol. 53, no. 4, p. 637-643.

ELLIOTT, JM., 1983. Some methods for the statistical analysis of simples of benthic invertebrates. Freshwater Biological Association, Scientific Publication, no. 25. 156p.

FERREIRA-FONTOURA, N. and BUCKUP, L., 1991. Biomassa e produtividade de uma população natural de *Parastacus brasiliensis* (Crustacea, Parastacidae). *Rev. Bras. Biol.*, vol. 51, no. 2, p. 289-293.

FREDETTE, TJ., DIAZ, RJ., VAN MONTFRANS, J. and ORTH, RJ., 1990. Secondary production within a seagrass bed (*Zostera marina* and *Ruppia maritima*) in Lower Chesapeake Bay. *Estuaries*, vol. 13, no. 4, p. 431-440.

HAMILTON, AL., 1969. On estimating annual production. *Limnol. Oceanogr.*, vol. 14, no. 5, p. 771-782.

HECK, KL., ABLE, KW., ROMAN, CT. and FAHAY, MP., 1995. Composition, abundance, biomass, and production of macrofauna in a New England Estuary: comparisons among eelgrass meadows and other nursery habitats. *Estuaries*, vol. 18, no. 2, p. 379-389.

HYNES, HBN. and COLEMAN, MJ., 1968. A simple method of assessing the annual production of stream benthos. *Limnol. Oceanogr.*, vol. 13, no. 4, p. 569-573.

KRUEGER, CC. and MARTIN, FB., 1980. Computation of confidence intervals for the size-frequency (Hynes) method of estimating secondary production. *Limnol. Oceanogr.*, vol. 25, no. 4, p. 773-777.

LÓPEZ, LS. and RODRÍGUEZ, EM., 1998. Somatic growth in juveniles of the estuarine crab *Chasmagnathus granulata* Dana 1851 (Brachyura, Grapsidae), under laboratory conditions. *Invest. Mar.*, vol. 26, p. 127-135.

LÓPEZ-GRECO, L. and RODRÍGUEZ, E., 1999. Size at the onset of sexual maturity in *Chasmagnathus granulatus* Dana, 1851 (Grapsidae, Sesarminae): a critical overall view about the usual criteria for its determination. *Proceedings of the Fourth International Crustacean Congress*, Leiden, p. 675-689.

LUPPI, TA., BAS, CC., SPIVAK, ED. and ANGER, K., 1997. Fecundity of two grapsid crab species in the Laguna Mar Chiquita, Argentina. *Arch. Fish. Mar. Res.*, vol. 45, p. 149-166.

LUPPI, TA., SPIVAK, ED., BAS, CC. and ANGER, K., 2004. Molt and growth of an estuarine crab, *Chasmagnathus granulatus* (Brachyura: Varunidae), in Mar Chiquita coastal lagoon, Argentina. J. Appl. Ichthyol., vol. 20, p. 333-344.

LUQUET, CM. and ANSALDO, M., 1997, Acid-base balance and ionic regulation during emersion in the estuarine intertidal crab *Chasmagnathus granulata* Dana (Decapoda Grapsidae). *Comp. Biochem. Phys.*, vol. 117 A, no. 3, p. 407-410.

LUQUET, CM., PERELLANO, G. and DE CARLO, J., 1995. Gill morphology and terrestrial adaptation in the estuarine crab *Uca uruguayensis* Nobili, 1901 (Decapoda, Brachyura). *Crustaceana*, vol. 68, no. 7, p. 882-892.

LUQUET, CM., PERELLANO, G. and ROSA, G., 1997. Salinity-induced changes in the fine structure of the gills of the semiterrestrial estuarian crab, *Uca uruguayensis* (Nobili, 1901) (Decapoda, Ocypodidae). *Tissue Cell*, vol. 29, p. 495-501.

MENZIE, CA., 1980. A note on the Hynes method of estimating secondary production. *Limnol. Oceanogr.*, vol. 25, no. 4, p. 770-773.

RUNCK, C. and BLINN, DW., 1990. Population dynamics and secondary production by *Ranatra montezuma* (Heteroptera: Nepidae). J. N. Am. Benthol. Soc., vol. 9, no. 3, p. 262-270.

-, 1993. Secondary production by *Telebasis salva* (Odonata) in a thermally constant aquatic ecosystem. *J. N. Am. Benthol. Soc.*, vol. 12, no. 2, p. 136-147.

SPIVAK, ED., 1997a. Los crustáceos decápodos del Atlántico sudoccidental (25°- 55° S) distribución y ciclos de vida. *Invest. Mar.*, vol. 25, p. 69-91.

-, 1997b. Cangrejos estuariales del Atlántico sudoccidental (25°- 41° S) (Crustacea: Decapoda: Brachyura). *Invest. Mar.*, vol. 25, p. 105-120.

SPIVAK, ED., ANGER, K., BAS, CC., LUPPI, TA. and ISMAEL, D., 1996. Size structure, sex ratio, and breeding season in two intertidal grapsid crab species from Mar Chiquita Lagoon, Argentina. *Nerítica*, vol. 10, p. 7-26.

STELLA, VS., LÓPEZ, LS. and RODRÍGUEZ, EM., 1996. Fecundity and brood biomass investment in the estuarine crab *Chasmagnathus granulatus* Dana, 1851 (Decapoda, Brachyura, Grapsidae). *Crustaceana*, vol. 69, no. 3, p. 306-312.

VERVOORST, FB., 1967. La vegetación de la República Argentina. VII. Las comunidades vegetales de la depresión del Salado (Provincia de Buenos Aires). Instituto Nacional de Tecnología Agropecuaria, Serie no. 7, 262 p.

VIOLANTE, RA., PARKER, G. and CAVALLOTTO, JL., 2001. Evolución de las llanuras costeras del este bonaerense entre la bahía Samborombón y la laguna Mar Chiquita durante el Holoceno. *Rev. Asoc. Geol. Arg.*, vol. 56, no. 1, p. 51-66.

WATERS, TF., 1977. Secondary production in inland waters. *Adv. Ecol. Res.*, vol. 10, p. 91-164.