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Abundance and distribution of Portunidae larval phases (Crustacea: Brachyura) in the estuarine and coastal region of the Patos Lagoon, southern Brazil

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ABSTRACT: The abundance and distribution of larval phases of the Portunidae found in the estuary of the Patos Lagoon and the coastal region were studied during two years (1995 and 1999). A conical net (165 cm long, 60 cm mouth, and 330 µm mesh) equipped with a flowmeter was towed for three minutes at 2 knots at six stations within the estuary and four stations in the coastal region. Samplings were carried out on the surface and near the bottom. At each sampling location, the salinity and temperature were also recorded. In 1995, the zoeae of Arenaeus cribrarius (Lamarck, 1818), Callinectes sapidus Rathbun, 1896 and Achelous spinicarpus Stimpson, 1871 were caught, resulting in a total abundance of 121.98 ind.100 m⁻³ (90.95 ind.100 m⁻³ on the surface and 31.03 ind.100 m⁻³ near the bottom). A total of 452.27 ind.100 m⁻³ were caught in the megalopa phase (13.49 ind.100 m⁻³ on the surface and 438.78 ind.100 m⁻³ near the bottom). In 1999, only zoeae of *C. sapidus* were caught, resulting in a total abundance of 419.78 ind.100 m⁻³ (386.98 ind.100 m⁻³ on the surface and 32.8 ind.100 m⁻³ near the bottom). Megalopae of these three species were caught, resulting in a total abundance of 179.91 ind.100 m⁻³ (25.38 ind.100 m⁻³ on surface and 154.53 ind.100 m⁻³ near the bottom). Summer was the season with the highest abundance of larvae in both years. During spring and summer, spawning was observed in the estuarine region of the Patos Lagoon.

Key words: Achelous spinicarpus, Arenaeus cribrarius, Callinectes sapidus, crab larvae, meroplankton.

Introduction

Estuaries are important regions for many estuarine and coastal invertebrate and vertebrate species because they are used as growth and feeding areas during larval and juvenile phases. Decapod larvae are an important segment of estuarine meroplankton and their coastal regions, and they play an important role in the food chain, as they are a food resource mostly for fish larvae (Drake and Arias, 1993). The early life stages of most marine species are affected by environmental factors such as temperature, salinity and currents that transport larvae horizontally over long distances (at km scale) because advection exceeds the capacity of larval

swimming (Archambault and Bourget, 1999; Calderon-Aguilera *et al.*, 2003). Many estuarine invertebrates developed behavioral mechanisms that increased the retention of larvae in the estuary; others exported their larvae to coastal waters, where development occurred (Epifanio, 1988). Many species of Brachyura Linnaeus, 1758 are present in estuarine regions during their complete life cycle. However, Portunidae Rafinesque, 1815 zoeal stages are transported to the coastal adjacent areas to complete their zoeal development and return to estuarine habitat during their megalopa phase (McConaugha *et al.*, 1983; Johnson *et al.*, 1984; Epifanio, 1988; 1995; McConaugha, 1988;

Epifanio *et al.*, 1989; Goodrich *et al.*, 1989; Little, 1990; Blanton *et al.*, 1995; Lochmann *et al.*, 1995).

The Patos Lagoon is located in southern Brazil between 30°S and 32°S. It occupies an area of approximately 10,000 km² and is the largest choked coastal lagoon in the world (Kjerfe, 1986). The estuarine area of the Patos Lagoon is 971 km² and it is connected to the Atlantic Ocean in the southern portion by a single channel 20 km long, with a width between 0.5 km and 3 km. The estuarine area, together with the coastal region, stands out among the coastal environments of the Southwest Atlantic for their ecological and social-economic importance (Asmus and Tagliani, 1998; Garcia et al., 2001). In addition, it is also an important nursery area for several invertebrate and vertebrate species. Meteorological processes, mostly wind, control the water exchange between the estuary and the continental shelf near the Patos Lagoon and are responsible for the transport of holoplanktonic and meroplanktonic species (Costa et al., 1988; Muelbert and Weiss, 1991; Abreu and Castello, 1998). Although many studies were conducted in this region (for review see Seeliger et al., 1998), few studies were performed on zooplankton (Montú, 1980; Duarte et al., 2014) and meroplankton (Rieger and D'Incao, 1991; Calazans, 2002).

Several studies on the Brazilian coast have focused on the biology, ecology, larval and juvenile development, genetics, distribution and occurrence of species belonging to the genera Arenaeus Dana, 1851, Callinectes Stimpson, 1860 and Achelous De Haan, 1833: Coelho and Ramos Porto (1995); Avila and Branco (1996); Mantelatto and Fransozo (1996; 1997; 1999a; 1999b); Barros *et al.* (1997); Teixeira and Sá (1998); Mantelatto and Martinelli (1999); Negreiros-Fransozo et al. (1999; 2007); Sankarankutty et al. (1999); Barutot et al. (2001); Chacur and Negreiros-Fransozo (2001); Mantelatto and Christofoletti (2001); Mantelatto et al. (2002; 2009); Pinheiro and Fransozo (2002); Weber et al. (2003); Baptista-Metri et al. (2005); Oliveira et al. (2006); Bolla Júnior et al. (2008); Almeida et al. (2010); Rodrigues *et al.* (2011); Araújo *et al.* (2012); Pardal-Souza and Pinheiro (2013); Rodrigues and D'Incao (2014). However, no studies focused on the distribution and abundance of larvae.

The goal of the present study was to determine the larval abundance and distribution of *Achelous spinicarpus* Stimpson, 1871, *Arenaeus cribrarius* (Lamarck, 1818) and *Callinectes sapidus* Rathbun, 1896 collected on the surface and the bottom of the estuarine and coastal regions of the Patos Lagoon during 1995 and 1999.

MATERIAL AND METHODS

Sampling design

Daytime samples were collected in the navigation channel of the Patos Lagoon and coastal region fortnightly during 1995 and 1999. In 1995, samples were taken from five points within the estuary [Saco do Retiro (SR), São José do Norte (SJ), Pier Copesul (PC), Pier da Marinha (PA) and Entre bóias 7 and 8 (EB)] and three in the coastal region [Ponta dos Molhes (PO), Terminal Turístico (TT) and 1 Milha Leste (MI)]. In 1999, samples were taken from four points within the estuary [SJ, PC, Tecon (TC) and EB] and three in the coastal region [PO, Paralelo aos Molhes (PR) and TT] (Fig. 1).

At each point, horizontal hauls were performed at the surface and near the bottom with a conical net that was 165 cm long, 60 cm diameter and 330 µm mesh with flowmeter. The net was towed for three minutes at a speed of two knots. In the bottom hauls, after three minutes, the net was closed with a manual closing device and raised. The sampled material was immediately preserved with 4% formaldehyde solution. At each sampling point, the surface and bottom temperatures and salinities were obtained with a thermosalinometer.

Samples analysis

The Portunidae larvae were separated from the other larvae in the samples under a stereoscopic microscope. A Nomarski microscope and camcorder were used to observe and identify the species. The identification followed Vieira and Calazans (2010).

For the purposes of relative seasonal abundance and distribution, the samples were grouped for summer (January, February and March), autumn (April, May and June), winter (July, August and September) and spring (October, November and December).

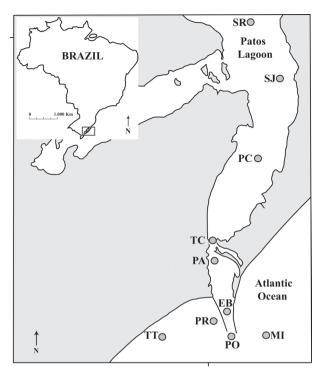


Figure 1. Positions of the sampling points within the estuary of the Patos Lagoon: Saco do Retiro (SR), São José do Norte (SJ), Pier Copesul (PC), Tecon (TC), Píer da Marinha (PA) and Entre Bóias 7 and 8 (EB). Points in the coastal region of the Patos Lagoon: Ponta dos Molhes (PO), Paralelo aos Molhes (PR), Terminal Turístico (TT) and 1 Milha Molhe Leste (MI).

Larval abundance was expressed as ind.100 m⁻³. For distribution, a geometric progression of base 3 was used to allow a rapid interpretation of the abundance categories contours. The abundance magnitude, established in this way, provided a scale as follows: absent [0]; 1 extremely rare]0,1]; 2 very rare]1,3]; 3 rare]3,9]; 4 normal]9,27]; 5 abundant]27,81]; 6 very abundant]81,243] and 7 extremely abundant]243,729] (Nichols and Thompson, 1988).

Statistical analysis

The level of significance for tests was a=0.05, and the results were considered statistically significant when the p value was less than 0.05 (p<0.05). A non-parametric Kruskall-Wallis (Zar, 1999) analysis was used to test the larval stages abundance against the following factors: depth (surface and bottom) and seasons of the year.

The sites "EB" and "1 MI" performed in the first year and "PR" in the second year were not included in the statistical analysis because they were performed only in one season.

RESULTS

Temperature and salinity

During the two years of sampling, the surface and bottom mean temperatures were not significantly different for the same period of the year (Tab. 1). Surface temperature was slightly higher than the bottom temperature, except in autumn 1995. The seasonal variations are shown in Tab. 1.

The average salinity during 1995 and 1999 increased towards the bottom. The seasonal variations are shown in Tab. 2. In both years, the mean salinity values were lower in the points located within estuary than in the points located in the coastal region (Figs. 2 and 3).

Species composition – 1995

All zoeae collected were in first stage. The total abundance was 121.98 ind.100 m⁻³ and zoeae of *C. sapidus* were the most abundant (97%). For megalopae, the abundance was 452.27 ind.100 m⁻³ and the most abundant species was *C. sapidus* (63%).

Zoea phase

On the surface, the total abundance of zoeae was 90.95 ind.100 m⁻³ and belonged to A. spinicarpus and C. sapidus that were caught in three seasons of the year. In summer, C. sapidus was the most abundant species, with 53.97 ind.100 m⁻³ caught in three points within the estuary and two points in the coastal region (Fig. 4A). Achelous spinicarpus had an abundance of 4.05 ind.100 m⁻³ in the summer, and all of the individuals were caught in one site within the estuary (Fig. 4D). During autumn, all of the identified zoeae were C. sapidus caught at one site on the coastal region, and the abundance was 13.18 ind.100 m⁻³ (Fig. 4B). In winter, no zoeae were collected. In spring, only C. sapidus zoeae were collected in three sites within the estuary and at one site in the coastal region, and the abundance was of 19.75 ind.100 m⁻³ (Fig. 4C). For zoeae caught on the surface, the summer was significantly different from the other seasons of the year for zoeae of C. sapidus (Tab. 3). When we analyzed the zoeae of all of the species together, we verified that the summer and spring were significantly different from the other seasons (Tab. 3).

Table 1. Mean values of temperatures (°C) on the surface and the bottom in the estuary and coastal region of the Patos lagoon, southern Brazil, during 1995 and 1999. MM, monthly means; SM, seasons means, ± standard deviation.

		<u> </u>				
YEARS			SURFACE		ВОТ	TOM
	SEASONS	MONTHS	MM	SM	MM	SM
		January	24.2±1.78		23±4.72	
	SUMMER	February	24.4±0.86	23.9±1.39	23.5±0.45	23±3.17
		March	22.7±0.62		22.6±0.51	
		April	19.1±1.10		18.4±4.44	
	AUTUMN	May	16±1.22	16.4±2.30	16.1±0.39	20.9±2.88
1995		June	14.6±1.51		14.3±1.30	
		July	13.6±0.45		13.5±0.65	
	WINTER	August	13.8±2.15	13.9±1.72	13.4±1.90	12.9±1.25
		September	15.7±1.47		14.3±0.48	
		October	18.6±1.29		18.1±1.36	
	SPRING	November	22.5±4.16	21.5±3.54	19.0±1.79	20.9±2.47
		December	23.0±1.86		22.5±1.68	
		January	23.8±0			
	SUMMER	February	24.6±1.02	24.6±1.36	24.1±0.57	24.1±0.86
		March	27.6±1.6		24.3±0.98	
		April	20.1±2.49		20.0±2.61	
	AUTUMN	May	18.6±0.39	18.6±2.57	18.5±0.22	18.5±2.62
1999		June	14.7±0.38		14.6±0.38	
		July	13.7±0.42		13.4±0.18	
	WINTER	August	11.5±0.37	14±1.64	11.3±0.17	13.3±1.03
		September	15.5±0.93		13.9±0.58	
		October	_		_	
	SPRING	November	21.6±2.08	22.4±1.60	21±1.45	21.8±1.29
		December	23.3±0.48		22.6±0.19	

Table 2. Mean values of salinity on the surface and the bottom in the estuary and coastal region of the Patos lagoon, southern Brazil, during 1995 and 1999. MM, monthly means; SM, seasons means, ± standard deviation.

			SURFACE		BOT	TOM
YEARS	SEASONS	MONTHS	MM	SM	MM	SM
		January	15.1±11.67		25.8±7.07	
	SUMMER	February	17.0±15.37	18.6±14.12	33±1.53	28.9±6.09
		March	22.4±16.01		29.8±2.53	
		April	22.8±4.42		24.1±3.83	
	AUTUMN	May	17.1±6.40	18.9±7.61	21±3.83	20.9±7.69
1995		June	16.8±8.89		18.3±8.98	
		July	5.4±2.54		10.7±8.03	
	WINTER	August	3.7±2.94	7.0±5.52	6.6±10.45	12.9±10.67
		September	8.2±7.90		23.75±0.92	
		October	16.3±9.81		10.6±1.34	
	SPRING	November	13±15.48	15.2±11.80	24.3±4.40	20.9±10.85
		December	26.8±2.81		27.4±2.07	
		January	28.6±2.12		_	
	SUMMER	February	21.7±10.99	20.9±11.71	25.9±9.5	27.7±10.16
		March	22.7±13.35		29.1±10.73	
		April	17±8.44		22.8±10.19	
	AUTUMN	May	24.3±11.81	18.6±10.91	31.9±0.09	26.7±10.60
1999		June	12.4±14.49		13.1±14.14	
		July	7.1±8.85		20.5±9.76	
	WINTER	August	14.1±6.05	10.3±9.63	24.7±6.28	23.1±17.66
		September	8.1±10.77		27.7±1.15	
		October	_		_	
	SPRING	November	29±4.43	30±4.92	31.6±1.21	31.7±1.84
		December	30.3±5.56		31.1±2.32	

In the bottom samples, the total abundance of zoeae was 31.03 ind.100 m⁻³. They all belonged to *C. sapidus* and were caught during summer and spring. In summer, the abundance was 11.48 ind.100 m⁻³, the zoeae were caught at two sites within the estuary and two sites in the coastal region

(Fig. 4E). In spring, the abundance was 19.55 ind.100 m⁻³, and the zoeae were caught in three sites within the estuary (Fig. 4F). There was no significant difference (p>0.05) among seasons of the year for the zoea stage of each species caught on the bottom (Tab. 3). However, when the zoeae

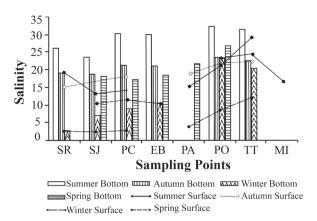


Figure 2. Mean values of salinities on the surface and the bottom at each sample point during 1995. Points within the estuary of the Patos Lagoon: Saco do Retiro (SR), São José do Norte (SJ), Pier Copesul (PC), Entre bóias 7 and 8 (EB), Pier da Marinha (PA). Points in the coastal region of the Patos Lagoon: Ponta dos Molhes (PO), Terminal Turístico (TT) and 1 Milha Leste (MI).

of all of the species were combined, the summer and spring were significantly different from the others seasons (Tab. 3).

There were no significant differences (p>0.05) between the surface and the bottom (Tab. 3) for the zoea stage of each species caught. Additionally, there was no significant difference between the surface and bottom when we analyzed all of the species together (Tab. 3).

Megalopa phase

On the surface, megalopae of *C. sapidus* and *A. cribrarius* were captured only in summer with a total abundance of 13.49 ind.100 m⁻³. The most abundant species was *C. sapidus* (7.71 ind.100 m⁻³), caught in one site within the estuary (PC) and one site in the coastal region (TT). The abundance of *A. cribrarius* was 5.78 ind.100 m⁻³, and all were caught at one site within the estuary (PC). For the seasons of the year, the summer was significantly different from the other seasons (Tab. 3).

In the bottom samples, the total abundance of megalopae was 438.78 ind.100 m⁻³ and belonged to all the three species, all caught during the summer. The abundance of *A. cribrarius* was 106.75 ind.100 m⁻³, caught in four sites within the estuary and one site in the coastal region (Fig. 5A). *Callinectes sapidus* was the most abundant species with 279.6 ind.100 m⁻³ caught in four sites within the estuary and one site in the coastal region (Fig. 5B). The abundance of *A. spinicarpus* was 53.43 ind.100

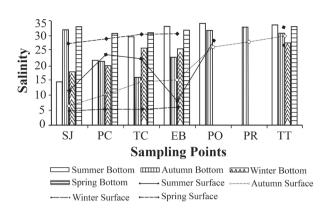


Figure 3. Mean values of salinities on the surface and the bottom at each sample point during 1999. Points within the estuary of the Patos Lagoon: São José do Norte (SJ), Pier Copesul (PC), Tecon (TC), Entre bóias 7 and 8 (EB). Points in the coastal region of the Patos Lagoon: Ponta dos Molhes (PO), Paralelo aos Molhes (PR) and Terminal Turístico (TT).

m⁻³ caught in two sites within the estuary (SR and PA) and one site in the coastal region (PO). For the megalopa stage of each species caught on the bottom, the summer was significantly different (p<0.05) from the other seasons for *A. cribrarius* and *C. sapidus* (Tab. 3). For the total abundance of the megalopae of all species caught on the bottom, the summer was significantly different (p<0.05) from the other seasons (Tab. 3).

There was a significant difference (p<0.05) in the megalopa stage of A. *cribrarius* between the surface and bottom (Tab. 3). When we analyzed all of the species together, we verified that there was a significant difference (p<0.05) between the surface and bottom (Tab. 3).

Species composition 1999

All zoeae collected were first stage of *C. sapidus*, and the total abundance was 419.78 ind.100 m⁻³. Megalopae of all three portunid were collected and the total abundance was 179.91 ind.100 m⁻³.

Zoea phase

On the surface, the total abundance of zoeae was 386.98 ind.100 m⁻³, and they were all caught during the summer at one site within the estuary and one site in the coastal region (Fig. 6A). For the zoeae caught on the surface, the summer was significantly different (p<0.05) from the other seasons (Tab. 4).

In the bottom samples, the abundance was 32.80 ind. 100 m⁻³ for those caught in summer at one site

Table 3. Results of Kruskall-Wallis (p<0.05) abundance of larval phase (zoea and megalopa) in each stratum (surface and bottom) in the estuary and coastal region of the Patos lagoon, southern Brazil, and among the seasons of the year (1995). Surface (Sur.); Bottom (Bot); not significant (ns); significant (#); Summer (Su); Autumn (Au); Winter (Wi) and Spring (Sp).

c ·	Phase -	Stratum	Seasons	
Species	Phase –	Sur x Bot	Su Au Wi Sp	
	Zoea Sur.		ns	
	Zoea Bot.		ns	
Arenaeus cribrarius Lamarck, 1818	Total Zoea	ns	ns	
	Megalopa Sur.		ns	
	Megalopa Bot.		Su#Au=Wi=Sp	
	Total Megalopa	Sur x Bot	Su#Au=Wi=Sp	
	Zoea Sur.		ns	
	Zoea Bot.		ns	
Callinectes sapidus Rathbun, 1896	Total Zoea	ns	Su#Au=Wi=Sp	
	Megalopa Sur.		ns	
	Megalopa Bot.		Su#Au=Wi=Sp	
	Total Megalopa		Su#Au=Wi=Sp	
	Zoea Sur.		ns	
	Zoea Bot.		ns	
Achelous spinicarpus Stimpson, 1871	Zoea Total	ns	ns	
	Megalopa Sur.		ns	
	Megalopa Bot.		ns	
	Total Megalopa	ns	ns	
	Zoea Sur.		Su#Au=Wi=Sp	
	Zoea Bot.		Su#Au#Wi=Sp	
Portunidae Rafinesque, 1815 (all species)	Total Zoea	ns	Su=Sp#Au=Wi	
	Megalopa Sur.		ns	
	Megalopa Bot.		Su#Au=Wi=Sp	
	Total Megalopa	#	Su#Au=Wi=Sp	

within the estuary and one site at the coastal region (Fig. 6B). For the zoeae caught on the bottom, the summer was significantly different (p<0.05) than the other seasons (Tab. 4).

There were no significant differences (p>0.05) between the zoeae caught on the surface and the bottom (Tab 4). Additionally, there was no significant difference (p>0.05) between the surface and bottom when we analyzed all of the species together (Tab. 4).

Megalopa phase

On the surface, all of the megalopae collected were *C. sapidus*. The abundance was of 25.38 ind.100 m⁻³, and all were caught during the summer in one site within the estuary (SJ) and one site at the coastal region (PO). For the megalopa caught on the surface, there was no significant difference (p>0.05) among the seasons (Tab. 4).

The abundance on the bottom was 154.53 ind.100 m⁻³ caught in three seasons of the year. In summer, the abundance was 111.83 ind.100 m⁻³, and they belonged to two species: *A. cribrarius* (92.82 ind.100 m⁻³), caught in only site in the coastal region (Fig. 7A), and *A. spinicarpus* (19.01 ind.100 m⁻³), caught at one point in the coastal

region (Fig. 7B). In autumn, the total abundance of megalopae was of 2.94 ind.100 m⁻³, and all belonged to C. sapidus, caught at one point in the coastal region (PR). During winter, no megalopae were caught. In spring, the abundance was 39.76 ind.100 m⁻³, and all belonged to C. sapidus caught at one point within the estuary (PC). For the megalopa stage of each species caught on the bottom, the summer was significantly different (p<0.05) from the other seasons for the megalopae of A. cribrarius (Tab. 4). However, for the total abundance of the megalopae of all of the species combined and caught on the bottom, there was no significant difference (p>0.05) among the seasons (Tab. 4). Additionally, there was no significance difference between the surface and bottom (Tab. 4) for megalopae caught for both strata.

DISCUSSION

After fertilization, the female of *Callinectes sapidus* returns to more saline waters in the lower estuary, where spawning usually occurs on an ebbing tide in the spring, summer and autumn (Perry and Stuck, 1981; Steele and Perry, 1990, Rodrigues and D'Incao, 2014) and behavioral adaptations during larval phases allow for the dispersion from coastal

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Figure 4. Spatial and seasonal distribution of zoea caught on the surface at different sampling points during 1995. A–C, *Callinectes sapidus* (Rathbun, 1896); D; *Achelous spinicarpus* Stimpson, 1871. Spatial and seasonal distribution of zoeae caught near the bottom at different sampling points during 1995. E–F, *Callinectes sapidus*. (0) absent; (1) extremely rare; (2) very rare; (3) rare; (4) normal; (5) abundant; (6) very abundant and (7) extremely abundant.

Table 4. Results of Kruskall-Wallis (p<0.05) abundance of larval phase (zoea and megalopa) in each stratum (surface and bottom) and among the seasons of the year (1999). Surface (Sur); Bottom (Bot); not significant (ns); significant (#); Summer (Su); Autumn (Au); Winter (Wi) and Spring (Sp).

		Stratum	Seasons
Species	Phase	Sur x Bot	Su Au Wi Sp
-	Zoea Sur.		ns
	Zoea Bot.		ns
Arenaeus cribrarius Lamarck, 1818	Total Zoea	ns	ns
	Megalopa Sur.		ns
	Megalopa Bot.		Su#Au=Wi=Sp
	Total Megalopa	ns	ns
	Zoea Sur.		Su#Au=Wi=Sp
	Zoea Bot.		Su#Au=Wi=Sp
Callinectes sapidus Rathbun, 1896	Total Zoea	ns	Su#Au=Wi=Sp
	Megalopa Sur.		ns
	Megalopa Bot.		ns
	Total Megalopa	ns	ns
	Zoea Sur.		ns
	Zoea Bot.		ns
Achelous spinicarpus Stimpson, 1871	Total Zoea	ns	ns
	Megalopa Sur.		ns
	Megalopa Bot.		ns
	Total Megalopa	ns	ns
	Zoea Sur.		Su#Au=Wi=Sp
	Zoea Bot.		Su#Au#Wi=Sp
Portunidae Rafinesque, 1815 (all species)	Total Zoea	ns	Su=Sp#Au=Wi
	Megalopa Sur.		ns
	Megalopa Bot.		ns
	Total Megalopa	ns	ns

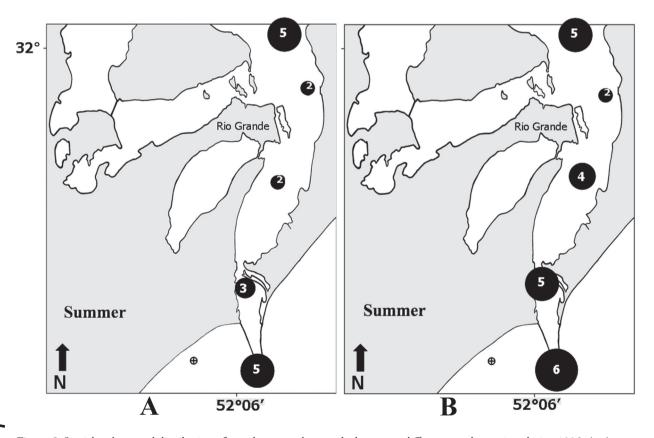


Figure 5. Spatial and seasonal distribution of megalopae caught near the bottom at different sampling points during 1995. A, *Arenaeus cribrarius* (Lamarck, 1818); B, *Callinectes sapidus* (Rathbun, 1896). (0) absent; (1) extremely rare; (2) very rare; (3) rare; (4) normal; (5) abundant; (6) very abundant and (7) extremely abundant.

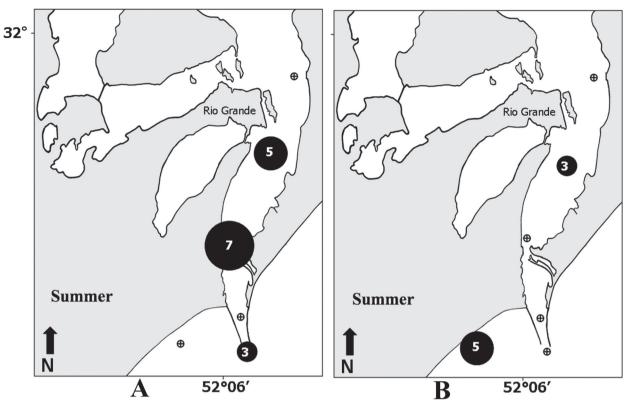


Figure 6. Spatial and seasonal distribution of *Callinectes sapidus* (Rathbun, 1896). A, zoea caught on the surface at different sampling points during 1999; B, zoea caught near the bottom at different sampling points during 1999. (0) absent; (1) extremely rare; (2) very rare; (3) rare; (4) normal; (5) abundant; (6) very abundant and (7) extremely abundant.

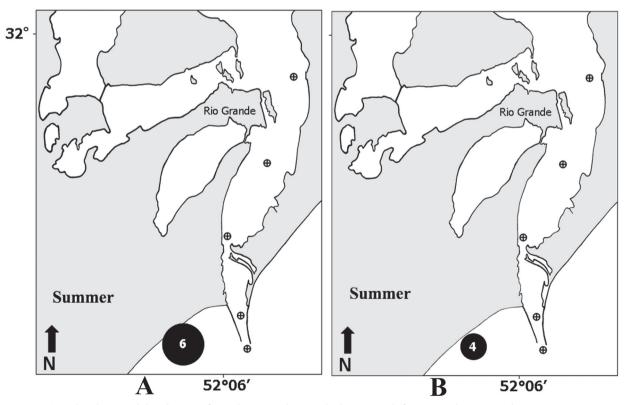


Figure 7. Spatial and seasonal distribution of megalopae caught near the bottom at different sampling points during 1999. A, *Arenaeus cribrarius* (Lamarck, 1818); B, *Achelous spinicarpus* (Stimpson, 1871). (0) absent; (1) extremely rare; (2) very rare; (3) rare; (4) normal; (5) abundant; (6) very abundant and (7) extremely abundant.

spawning areas and recruitment back to the estuary (Sulkin *et al.*, 1980; Sulkin and Van Heukelem, 1982). The zoeae of *C. sapidus* caught within the estuary of the Patos Lagoon on the surface were due to the spawnning that occurred inside the estuary. According to Sulkin (1984) and Epifanio *et al.* (1989), the first stage of zoea had negative geotaxis and high barokinesis and remained near the surface, and the zoeae were transported seaward to complete their development.

The zoeae of *Achelous spinicarpus* within the estuary caught in summer (mean temperature of 23.9°C and salinity of 18) were rare, because juveniles and adults inhabit only the coastal areas (Dumont and D'Incao, 2011). The bottom currents transported zoeae to the upper estuary, away from their parental habitat, where they would not complete their larval development. Bookhout and Costlow (1974) showed that zoeae of *A. spinicarpus* reared in laboratory completed the zoeal development (composed by seven stages) to megalopa phase when the temperature was above 20°C and salinity was greater than 30.

The absence of *Arenaeus cribrarius* zoeal stages within the estuary could be explained by: a) adults living in the coastal area and b) larvae dispersed by surface currents to the continental shelf, where salinity was higher. In laboratory conditions, *A. cribrarius* larval stages needed salinity of least 25 to complete development in two months (Stuck and Truesdale, 1988).

The highest zoeal abundance of *C. sapidus* during summer was due to a greater abundance of ovigerous females with eggs in all of the developmental stages (Rodrigues et al., 2011). Zoeae caught in one site of the coastal region in early autumn were from ovigerous females from late summer. During autumn, the low salinity and temperature (the temperature average was below 18°C) did not allow changes for the later stages, which was corroborated by laboratory studies performed by Costlow and Bookhout (1959), who noted that all larvae died at temperatures lower than 20°C. By late spring, the zoeal phase has probably completed its development until the megalopa phase and would be able to settle. In the Chesapeake Bay and Delaware, USA, ovigerous females synchronized the release of zoeae with the period with higher temperatures (Provenzano *et al.*, 1983; Epifanio *et al.*, 1989). This fact was also observed for some planktonic species in the estuarine region of the Patos Lagoon (Montú, 1980) and in larval stages of decapod species of the coastal zone, such as the hermit crab *Loxopagurus loxochelis* (Moreira, 1901) (Rieger and D'Incao, 1991).

The occurrence of *A. cribrarius* megalopae during the summer in a site located within the estuary was probably due to the transport of megalopae by bottom currents. However, these megalopae would not likely change to the juvenile phase because the juveniles and adults are not found inside the estuary. On the contrary, megalopae of *A. cribrarius* and *A. spinicarpus* in the adjacent coastal region had a better chance to develop to the adult phase because the salinity was higher in that area than in the estuarine area, and it is the place where the adults are found.

The highest abundance of megalopa of *C. sapidus* was located within the estuary because the zoeae stages dispersed to the continental shelf, and according to Emilsson (1961), the southern Brazilian continental shelf of Rio Grande do Sul was covered by shallow tropical waters of the current of Brazil transporting water with temperatures above 20°C and a salinity of 36. These were favorable conditions for the development of zoeal phases of *C. sapidus* and their return to the estuary by bottom currents during the megalopa phase.

The role that physical transport processes play in shaping the population demographics of marine species with planktonic larval stages has been well established (e.g., McConnaughey et al., 1992; Olmi, 1995; Archambault and Bourget, 1999; Hsieh et al., 2010; Daigle and Metaxas, 2011; Pan et al., 2011). Both pre and post-settlement processes are important determinants of the levels of harvestable adults. Pre-settlement processes affecting the recruitment success include both biotic (fecundity, behavior and predation) and abiotic factors (currents, winds, tides, lunar phase and water quality parameters); however, abiotic factors are thought to be the initial regulators of year class strength (Johnson and Perry, 1999). Wind stress is an especially attractive abiotic factor for inclusion

in population predictive models because it plays a significant role in forcing surface currents over the shallow shelf regions and it is relatively easy to monitor (Johnson and Perry, 1999).

Many mechanisms were proposed for the reinvasion of megalopae into estuaries. Litlle (1990) and Johnson and Hess (1990) used a dispersal and recruitment numerical simulation and found that a 29% average of larvae dispersal in the Chesapeake Bay would return passively by surface currents. Scheltema (1975) studied the estuaries of the South Atlantic and Mid-Atlantic Bight and found that if the megalopae became demersal on the continental shelf, they were passively transported by bottom currents to the estuary. Sulkin and Van Heukelem (1982) proposed a model for offshore recruitment based on the behavioral traits of C. sapidus larvae. They noted that radical behavior changes occurred in the megalopa phase, which resulted in a depth regulatory mechanism of high precision. Late-stage megalopae (near settlement) develop vertical migratory behavior that support shoreward transport. Another study suggested that this change in megalopa migratory behavior is mediated by chemical cues associated with settlement sites (Forward and Rittschof, 1994). Olmi (1995) noted that changes in megalopa behavior as they approached estuarine waters was reflected in their distributions in the water column: from a surface orientation offshore to tidally related vertical migration within the estuary. Another mechanism for reinvasion was related to wind periods toward the shore causing a positive anomaly in the water volume. King (1971) worked on the Texas coast and reported that the abundance was significantly related to the wind direction. In the estuary of the Patos Lagoon, reinvasion was probably related to wind patterns because during the low fluvial discharge (e.g., summer/autumn), onshore SE and SW winds force seawater through the inlet into the estuary and occasionally as far as 150 km into the lagoon (Garcia, 1998).

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