Influence of biological and environmental factors on the spatial and temporal distribution of the hermit crab *Isocheles sawayai* Forest & Saint-Laurent, 1968 (Anomura, Diogenidae)

Marina Z. Fantucci; Renata Biagi; Andrea L. Meireles and Fernando L. Mantelatto*

(MZF, RB, ALM, FLM) Laboratório de Bioecologia e Sistemática de Crustáceos, Departamento de Biologia, Faculdade de Filosofia, Ciências e Letras de Ribeirão Preto (FFCLRP), Universidade de São Paulo (USP). Avenida Bandeirantes, 3900, 14040-901, Ribeirão Preto, SP, Brasil.
E-mail: flmantel@usp.br

Abstract

The hermit crab *Isocheles sawayai* is widely distributed along the southwestern Atlantic coast, but its spatial and temporal distributions have never been investigated. For this purpose, monthly collections (July 2001 through June 2003), based on samples collected parallel to the coast at depths of 5 to 35 meters, were made with a shrimp fishing boat in the Caraguatatuba region on the northern coast of the state of São Paulo. The hermit crabs were counted, and the sex was checked. The sex ratio and reproductive period were characterized. Correlations between temporal and environmental factors and the numbers of hermit crabs were tested. The patterns of occurrence differed by month. There were significant correlations between the numbers of individuals and some environmental factors, which were negative in relation to depth and organic-matter content, and positive in relation to temperature and the proportion of sand in the sediment. This pattern is associated with the species' filtering and burrowing habits, and with the distributions of coexisting species. The environmental factors seem also to be directing some biological aspects of the species, such as the sex ratio in favor of males (1:0.23) which was related to the spatial distribution, and the seasonal reproduction which was strongly influenced by temperature. Therefore, we concluded that the distribution of *I. sawayai* is directly regulated by biological and environmental factors that influence its biology, life cycle, and interspecies relationships.

Key words: Decapoda, abiotic factors, sex ratio, interspecies relationships.

Introduction

Benthic crustaceans use the sediment as a shelter and food source (Abele, 1974), making the substrate texture a very important parameter influencing their distribution. In combination with the substrate, water conditions can also influence this aspect. Considering this, it is a consensus among researchers that the main abiotic agents acting on the distribution and abundance of marine decapods are temperature, salinity, dissolved oxygen, depth, and substrate organic-matter content and texture (Meireles *et al.,* 2006).

Some of these environmental factors fluctuate monthly and seasonally, and are affected by the local water masses. Thus, the biotic and abiotic interactions among organisms lead to different seasonal and spatial distribution patterns, the knowledge of which is essential for understanding these organisms' life cycles (Santos *et al.,* 1994).

In addition to physical variables, many other biotic factors also have an important influence on population distribution (Mantelatto *et al.,* 1995), which makes it essential to consider intra- and inter-species relationships as population variables. Particularly for hermit crabs, the availability and adequacy of gastropod shells, and the competition for this resource are additional biotic factors affecting populations (Bollay, 1964; Vance, 1972; Martinelli and Mantelatto, 1999).

In Brazil, despite the large number of hermit-crab species, systematized knowledge of their distributions focusing on the influence of abiotic factors is scanty. Recently, our study group has concentrated efforts to improve and collect data on hermit-crab species distribution (Negreiros-Fransozo *et al.,* 1997; Fransozo *et al.,* 1998; Bertini and Fransozo, 1999; Bertini *et al.,* 2004; Mantelatto *et al.,* 2004; Meireles *et al.,* 2006; Ayres-Peres and Mantelatto, 2008a), aiming to provide basic information that can contribute to further investigations.

The genus *Isocheles* Stimpson, 1858 is one of the less-studied diogenid hermit-crab genera; apart from its taxonomy, little information is available. The genus is restricted to shallow waters of tropical and subtropical American coasts, and is represented by five species (see Mantelatto *et al.,* 2009 for review). Among them, *Isocheles sawayai* Forest and Saint-Laurent, 1968 is a suspension-feeder endemic to the western Atlantic (Galindo *et al.,* 2008). Despite efforts during the last decade to improve knowledge of this sublittoral species (Mantelatto *et al.,* 2006, 2009; Fantucci *et al.,* 2008a; 2008b, 2009; Galindo *et al.,* 2008; Masunari *et al.,* 2008), its temporal and spatial distributions remain unknown. Therefore, the aim of this study was to analyze the influence of environmental and biological factors on the seasonal and spatial distribution of a population of *I. sawayai* on the southern coast of Brazil.

Material and Methods

The hermit crabs were collected monthly from July 2001 through June 2003, in the Caraguatatuba region (23°36'08"/23°47'07"S; 45°20'03"/45°08'30"W), southern coast of São Paulo, Brazil, from a fishing boat equipped with two double-rig trawl nets (20 mm mesh size in the net body and 15 mm in the cod end). The region is sheltered against the direct action of ocean waves by São Sebastião Island (Ilhabela), and is influenced by the São Sebastião Channel, resulting in moderate hydrodynamics and homogeneous morphology of the bottom (Barros *et al.,* 1997). The region is influenced by three different water masses, the South Atlantic Central Water (SACW) with low temperature and salinity, Tropical Water (TW) with high temperature and salinity, and Coastal Water (CW) with high temperature and low salinity, in different periods of the year (Castro-Filho *et al.,* 1987). The collections consisted of seven samples (trawls) parallel to the coast at 5, 10, 15, 20, 25, 30, and 35 m depths. Each trawl lasted approximately 30 minutes, at a mean speed of two knots.

Environment conditions were characterized by measuring the depth, location, temperature, and salinity of the bottom water for each sample, and seasonally by analyzing the sediment organic-matter content and grain size. The analyses followed methods previously determined by Mantelatto and Fransozo (1999) and Meireles *et al.* (2006). The latter contribution provides detailed information on the environment.

After collection, the specimens were sorted, frozen, and transported to the laboratory. There, they were removed from their shells, counted, and the sex checked according to the gonopore position and pleopod morphology. Intersex individuals (with both male and female gonopores present) were grouped with males, because the analysis of external primary (gonopores) and secondary (pleopods) sexual characters revealed a greater similarity between males and intersexes, than between intersexes and females, suggesting that intersex individuals are functional males (Fantucci *et al.,* 2008a). Individuals were measured using a caliper (0.01 mm) for cephalothoracic shield length (SL) and grouped in size classes according to Sturges (1926) ($K = 1 + \log_2 n$; K = number of classes; n = number of individuals). The sex ratio was tested by chi-square (χ^2). The reproductive period was established by the ratio between ovigerous females and the total number of females (Giese, 1959). The seasons established were: Summer – January, February, and March; Autumn – April, May, and June; Winter – July, August, and September; Spring – October, November, and December.

The relationships between each environmental factor and the number of individuals were evaluated by Pearson's Correlation. Data were analyzed statistically at the level of significance $\alpha = 0.05$ (Zar, 1996), by the program Sigma Stat Windows, Version 2.03.

Voucher specimens were deposited in the Crustacean Collection of the Department of Biology (CCDB), Faculty of Philosophy, Sciences and Letters of Ribeirão Preto (FFCLRP), University of São Paulo (USP), Brazil (accession numbers 1687-1691).

Results

During the study period, 168 samples were taken, and 307 males (82.09%, 297 normal males and 10 intersexes) and 67 females (42 non-ovigerous, 11.23% and 25 ovigerous, 6.68%) were captured. The monthly and seasonal distributions were very heterogeneous; the most individuals were caught in July 2002 (winter) and January 2003 (summer), whereas in some months no specimens or only males were captured (Fig. 1).

Spatially, all individuals were found at the 5 m depth, demonstrating a significant negative correlation between depth and the total number of individuals or among each group of interest (Tab. I). Variations on environmental factors throughout the studied period are shown (Tab. II), emphasizing temperature, salinity and organic matter content (Fig. 2A) and sediment grain size (Fig. 2B) on the depth (5m) of *I. sawayai* occurrence. There was a significant positive correlation between temperature and the number of individuals collected (Tab. I). *Isocheles sawayai* occurred in warm waters, with individuals present starting at 21°C, and predominantly between 24 and 26°C. There was no correlation between the number of individuals and salinity (Tab. I).

Hermit crabs occurred nearly always (except for five individuals) in areas with low organic-matter content (1 to 3%), with a significant negative correlation with this factor (Tab. I). There was a significant positive correlation between the proportion of sand in the substrate and the number of individuals (Tab. I).

The sex ratio was 1:0.23 in favor of males ($\chi^2 = 141.71$, $P < 0.05$). Only males occurred in the smallest size class (3.0 to 3.7 mm SL) and in the two largest classes (8.6 to 10.0 mm SL). Males predominated significantly in the size classes between 5.8 and 10.0 mm SL. Nearly equivalent numbers of both sexes were present in the initial size classes, with an increase in the prevalence of males as the size increased (Fig. 3).

Ovigerous females comprised 37.31% of the total females, and their percentage and occurrence varied widely throughout the sampling period. More ovigerous females were collected in the rainy season (spring and summer) (Fig. 4).

Discussion

Our results demonstrated that the distribution of *I. sawayai* is directly driven by biological and environmental factors, influencing its biology, life cycle, and interspecies relationships. The environmental factors seem to be directing some biological aspects of *I. sawayai,* such as the sex ratio related to the spatial distribution, and the seasonal reproduction, which is strongly influenced by temperature.

The distributional limits of a species are determined by the action of the entire environmental complex on all of the various life-history stages. Some environmental factors fluctuate more widely than others, and are commonly considered to be

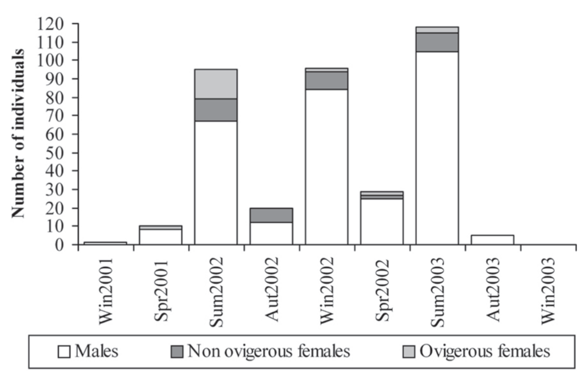

Figure 1. *Isocheles sawayai.* Seasonal distribution of the number of individuals in the Caraguatatuba region, São Paulo, from July 2001 through June 2003 (Win, winter – July, August, and September; Spr, spring – October, November, and December; Sum, summer – January, February, and March; Aut, autumn – April, May, and June).

Table I. *Isocheles sawayai.* Coefficients of Pearson's Linear Correlation between the number of sampled individuals and each environmental factor analyzed in the Caraguatatuba region, São Paulo, from July 2001 through June 2003 (*, significant correlation; α = 0.05).

Environmental factors	Non-ovigerous females	Ovigerous females	Males	Total
Temperature	0.227*	0.236*	0.168*	0.186*
Salinity	-0.046	-0.074	-0.023	-0.030
Organic matter	-0.207*	-0.163*	-0.186*	-0.194*
Depth	-0.288*	-0.245*	-0.254*	-0.267*
Gravel	-0.113	-0.099	-0.107	-0.111
Sand	0.244*	-0.199*	0.207*	0.218*
Mud	-0.154*	-0.122	-0.122	-0.130

Table II. *Isocheles sawayai.* Monthly fluctuation of the environmental factors in the Caraguatatuba region, São Paulo, from July 2001 through June 2003 (x, mean; sd, standard deviation).

Month	Depth	Temperature	Salinity	Organic matter	Gravel	Sand	Mud
July 2001	5	21.0	35.0	1.3	11.2	88.8	0.0
	10	20.0	35.0	4.6	18.7	69.5	11.5
	15	21.0	35.3	3.7	6.5	22.2	71.0
	20	21.0	35.0	8.2	11.6	13.2	75.0
	25	21.0	35.0	5.5	16.3	39.7	44.2
	30	21.5	35.0	3.0	19.0	65.0	15.7
	35	21.0	34.67	2.5	21.0	75.7	2.7
August 2001	5	21.2	35.7	1.3	11.2	88.8	0.0
	10	21.0	36.3	4.6	18.7	69.5	11.5
	15	21.2	36.7	3.7	6.5	22.2	71.0
	20	21.0	37.0	8.2	11.6	13.2	75.0
	25	21.2	37.0	5.5	16.3	39.7	44.2
	30	20.3	37.0	3.0	19.0	65.0	15.7
	35	20.2	37.0	2.5	21.0	75.7	2.7
September 2001	5	22.3	35.0	1.3	11.2	88.8	0.0
	10	21.5	35.0	4.6	18.7	69.5	11.5
	15	21.2	37.0	3.7	6.5	22.2	71.0
	20	21.0	37.0	8.2	11.6	13.2	75.0
	25	21.0	35.7	5.5	16.3	39.7	44.2
	30	20.2	36.0	3.0	19.0	65.0	15.7
	35	17.8	36.0	2.5	21.0	75.7	2.7
October 2001	5	20.5	36.0	2.5	2.8	89.5	7.7
	10	20.0	36.0	1.5	5.3	82.0	12.7
	15	19.0	36.0	2.8	7.2	37.5	55.5
	20	18.3	36.0	5.0	7.7	26.0	66.7
	25	19.0	36.0	6.0	15.0	32.5	52.5
	30	18.0	37.0	1.9	20.0	79.0	1.0
	35	18.0	37.0	2.2	22.5	77.5	0.0
November 2001	5	21.3	35.3	2.5	2.8	89.5	7.7
	10	21.2	36.0	1.5	5.3	82.0	12.7
	15	21.0	36.0	2.8	7.2	37.5	55.5
	20	19.5	36.0	5.0	7.7	26.0	66.7
	25	16.2	36.0	6.0	15.0	32.5	52.5
	30	16.8	36.0	1.9	20.0	79.0	1.0
	35	16.8	36.0	2.2	22.5	77.5	0.0
December 2001	5	24.8	35.0	2.5	2.8	89.5	7.7
	10	23.0	35.0	1.5	5.3	82.0	12.7
	15	21.2	36.0	2.8	7.2	37.5	55.5
	20	20.3	35.0	5.0	7.7	26.0	66.7
	25	19.0	35.0	6.0	15.0	32.5	52.5
	30	19.0	35.0	1.9	20.0	79.0	1.0
	35	18.7	35.0	2.2	22.5	77.5	0.0
January 2002	5	24.3	36.0	1.3	4.7	89.5	5.0
	10	24.0	36.7	2.0	5.0	73.7	20.7
	15	20.0	37.0	5.5	7.0	21.2	72.0
	20	20.2	37.0	5.9	9.5	21.7	69.0
	25	19.0	37.0	4.3	10.2	36.5	53.7
	30	20.0	37.0	1.5	17.2	83.0	0.5
	35	20.0	37.0	2.1	25.2	71.5	3.5
February 2002	5	28.0	33.0	1.3	4.7	89.5	5.0
	10	26.0	35.0	2.0	5.0	73.7	20.7
	15	23.0	35.0	5.5	7.0	21.2	72.0
	20	22.0	36.0	5.9	9.5	21.7	69.0
	25	22.0	36.0	4.3	10.2	36.5	53.7
	30	22.2	36.0	1.5	17.2	83.0	0.5
	35	20.0	36.0	2.1	25.2	71.5	3.5

Table II (Cont.). *Isocheles sawayai.* Monthly fluctuation of the environmental factors in the Caraguatatuba region, São Paulo, from July 2001 through June 2003 (x, mean; sd, standard deviation).

Month	Depth	Temperature	Salinity	Organic matter	Gravel	Sand	Mud
March 2002	5	27.0	35.0	1.3	4.7	89.5	5.0
	10	26.0	36.0	2.0	5.0	73.7	20.7
	15	22.0	36.0	5.5	7.0	21.2	72.0
	20	21.7	35.0	5.9	9.5	21.7	69.0
	25	21.5	35.0	4.3	10.2	36.5	53.7
	30	20.7	35.0	1.5	17.2	83.0	0.5
	35	20.2	35.0	2.1	25.2	71.5	3.5
April 2002	5	24.0	35.7	1.9	14.3	82.7	3.5
	10	24.0	35.0	1.3	8.0	60.3	29.5
	15	20.8	36.0	3.8	6.3	14.7	79.0
	20	20.3	37.0	4.5	12.7	31.7	55.7
	25	20.8	37.0	3.9	27.5	51.0	21.5
	30	19.2	37.0	3.7	13.0	62.7	23.7
	35	19.0	37.0	2.5	14.3	82.7	3.5
May 2002	5	25.2	34.0	1.9	14.3	82.7	3.5
	10	25.0	36.0	1.3	8.0	60.3	29.5
	15	24.2	36.0	3.8	6.3	14.7	79.0
	20	23.2	36.0	4.5	12.7	31.7	55.7
	25	23.0	36.0	3.9	27.5	51.0	21.5
	30	23.7	37.0	3.7	13.0	62.7	23.7
	35	23.2	37.0	2.5	14.3	82.7	3.5
June 2002	5	23.0	35.0	1.9	14.3	82.7	3.5
	10	23.0	35.0	1.3	8.0	60.3	29.5
	15	23.0	35.0	3.8	6.3	14.7	79.0
	20	22.3	35.0	4.5	12.7	31.7	55.7
	25	23.0	34.0	3.9	27.5	51.0	21.5
	30	22.5	33.7	3.7	13.0	62.7	23.7
	35	23.5	35.3	2.5	14.3	82.7	3.5
July 2002	5	21.8	35.0	1.3	2.7	88.5	8.8
	10	21.3	35.0	3.6	2.2	71.2	26.6
	15	22.7	36.0	3.0	0.7	34.5	64.8
	20	22.0	35.0	4.0	3.6	66.5	29.9
	25	23.0	36.0	2.5	11.7	76.5	11.8
	30	22.0	35.7	2.6	74.2	24.8	1.0
	35	21.3	34.7	1.8	51.1	44.6	4.3
August 2002	5	22.5	33.0	2.5	1.1	81.	17.5
	10	22.0	32.3	1.7	0.5	61.2	38.4
	15	22.0	32.0	7.9	5.9	32.7	61.5
	20	22.0	32.0	12.8	9.3	36.5	54.2
	25	22.0	32.0	3.5	11.3	61.3	27.4
	30	23.0	30.0	3.9	97.4	4.3	0.0
	35	21.0	35.0	4.4	53.7	38.1	8.2
September 2002	5	21.0	34.0	1.3	1.5	87.4	11.2
	10	20.5	35.0	2.4	0.7	82.0	17.2
	15	21.0	35.0	4.3	2.6	25.6	71.9
	20	21.0	35.0	6.4	5.9	53.1	41.0
	25	21.0	35.0	6.5	5.6	35.5	58.9
	30	21.0	34.0	3.7	56.7	24.0	19.3
	35	20.5	33.0	2.0	61.6	33.4	5.0
October 2002	5	26.0	35.0	1.7	0.4	3.2	96.3
	10	25.2	34.3	2.7	0.8	69.5	29.7
	15	23.2	35.0	4.3	0.8	15.9	83.3
	20	24.0	35.3	7.7	12.1	33.9	54.1
	25	20.8	36.7	3.0	71.3	15.7	13.0
	30	20.8	37.0	2.1	15.2	70.6	14.2
	35	20.0	36.3	3.7	22.5	66.6	10.9

Table II (Cont.). *Isocheles sawayai.* Monthly fluctuation of the environmental factors in the Caraguatatuba region, São Paulo, from July 2001 through June 2003 (x, mean; sd, standard deviation).

Month	Depth	Temperature	Salinity	Organic matter	Gravel	Sand	Mud
November 2002	5	27.0	34.0	1.4	0.5	95.8	3.7
	10	24.7	35.0	3.0	0.4	77.5	22.0
	15	23.3	35.0	5.0	30.6	25.8	43.6
	20	20.7	35.0	8.0	4.9	42.6	52.6
	25	22.3	35.0	2.6	13.5	77.2	9.3
	30	22.0	35.0	4.3	21.7	59.9	18.4
	35	20.0	36.0	2.8	34.4	61.4	4.2
December 2002	5	26.3	34.0	5.7	3.6	42.3	54.1
	10	24.3	34.7	2.1	1.6	25.4	73.0
	15	19.3	35.0	7.1	0.6	78.2	21.2
	20	20.3	35.3	2.9	7.7	75.9	16.4
	25	20.0	35.3	2.4	30.0	52.1	17.9
	30	20.0	35.0	1.2	93.4	4.8	1.7
	35	19.3	36.0	1.4	89.1	8.4	2.5
January 2003	5	24.5	36.0	1.2	3.1	89.8	7.1
	10	22.2	35.7	1.5	0.5	84.5	15.0
	15	19.7	35.3	2.8	2.7	45.4	51.9
	20	19.3	36.0	3.6	20.6	51.8	27.6
	25	19.3	36.0	2.3	33.3	50.3	16.4
	30	19.7	36.0	1.1	93.9	6.4	0.0
	35	18.3	36.0	8.7	75.4	18.9	5.7
February 2003	5	26.7	34.0	2.6	5.2	81.1	13.7
	10	26.3	34.0	2.6	0.4	66.9	32.8
	15	24.3	35.0	5.2	2.6	27.2	70.3
	20	21.7	35.0	6.6	5.7	39.8	54.5
	25	20.7	35.0	7.6	16.9	21.9	61.2
	30	20.0	35.0	4.3	15.4	52.4	32.2
	35	20.3	34.0	2.5	86.3	7.7	6.1
March 2003	5	28.2	35.0	1.6	4.7	84.3	11.0
	10	27.0	35.0	2.2	1.7	70.2	28.1
	15	27.2	36.0	5.4	0.5	38.4	61.1
	20	22.8	37.0	3.9	11.2	60.3	28.4
	25	22.0	37.0	5.3	16.5	55.2	28.4
	30	22.0	36.0	2.3	9.4	75.6	15.4
	35	22.0	36.0	1.7	23.0	71.8	5.1
April 2003	5	26.7	34.0	3.1	1.1	71.3	27.6
	10	26.3	35.0	2.9	1.7	72.6	25.7
	15	26.3	35.0	7.6	5.9	24.0	70.1
	20	25.2	35.0	6.5	12.4	52.1	35.5
	25	25.3	35.0	3.4	94.5	2.6	2.9
	30	25.3	35.0	6.3	66.1	20.4	13.5
	35	24.0	36.0	5.8	38.7	55.0	6.3
May 2003	5	22.7	35.0	2.0	1.0	64.6	34.5
	10	22.3	35.0	1.1	0.1	63.7	36.3
	15	23.0	36.0	4.7	0.3	49.4	50.3
	20	22.7	36.0	6.5	7.7	37.7	54.7
	25	22.7	35.0	8.6	19.4	36.9	43.6
	30	23.0	35.0	6.1	4.1	42.5	53.3
	35	22.3	35.0	1.6	4.2	84.4	11.4
June 2003	5	23.3	31.0	3.3	0.5	57.1	42.3
	10	23.3	32.0	1.9	0.2	90.1	9.7
	15	23.0	31.0	2.4	0.3	38.0	61.8
	20	24.0	32.0	4.8	3.6	29.5	66.9
	25	23.3	34.0	6.0	4.0	38.2	57.8
	30	23.3	34.0	6.3	6.8	45.6	47.6
	35	22.7	35.0	1.2	7.7	87.7	4.7

Table II (Cont.). *Isocheles sawayai.* Monthly fluctuation of the environmental factors in the Caraguatatuba region, São Paulo, from July 2001 through June 2003 (x, mean; sd, standard deviation).

Month	Depth	Temperature	Salinity	Organic matter	Gravel	Sand	Mud
x ± sd (considering the whole period)	5	24.1 ± 2.43	34.6 ± 1.15	2.0 ± 1.00	5.2 ± 4.76	79.1 ± 20.24	15.7 ± 22.08
	10	23.3 ± 2.16	35.0 ± 1.08	2.3 ± 1.08	5.1 ± 5.89	70.5 ± 12.67	24.1 ± 13.52
	15	22.2 ± 2.03	35.3 ± 1.35	4.5 ± 1.53	5.6 ± 5.99	30.1 ± 14.23	64.3 ± 13.73
	20	21.5 ± 1.61	35.4 ± 1.31	6.0 ± 2.12	9.5 ± 3.73	35.7 ± 16.87	54.8 ± 16.81
	25	21.2 ± 1.89	35.5 ± 1.15	4.7 ± 1.68	22.3 ± 20.41	41.8 ± 16.80	36.0 ± 18.71
	30	21.1 ± 1.93	35.4 ± 1.54	3.1 ± 1.57	31.8 ± 30.00	54.2 ± 26.38	14.1 ± 14.91
	35	20.4 ± 1.86	35.7 ± 1.03	2.7 ± 1.61	33.2 ± 23.84	62.5 ± 24.26	4.3 ± 2.87

limiting for a species' distribution. However, other factors, such as food or suitable habitat, may be of greater significance (Vernberg and Vernberg, 1970). In agreement with these authors, the water depth as well as sediment grain size and organic matter are the most important factors limiting the distributions of some anomurans (Negreiros-Fransozo *et al.,* 1997). These factors also seem to govern the distribution of *I. sawayai.*

All the individuals of *I. sawayai* were collected at a depth of 5 m, and 98.67% of them were found in sediment containing between 1 and 3% organic matter. Similarly, in the Ubatuba region, *I. sawayai* was observed in areas with low organic-matter content and at shallow depths (Negreiros-Fransozo *et al.,* 1997). Suspension feeders such as *I. sawayai* and *Loxopagurus loxochelis* (Moreira, 1901) have been mainly captured in areas with substrates poor in organic matter (Fransozo *et al.,* 1998).

In addition, the sediment where the species occurred was composed by more than 80% sand (Meireles *et al.,* 2006). Together with the positive correlation observed, this pattern reveals a strong preference for this kind of sediment, as is also shown by this species in the Ubatuba region (Negreiros-Fransozo *et al.,* 1997). The occurrence of *I. sawayai* on sandy bottoms is probably related to its burrowing habit (Hebling, 1978; Melo, 1999), considering that the predominance of sand could favor compaction of the bottom, allowing the animals to remain burrowed and avoiding being dragged, especially in the surf zone (Negreiros-Fransozo *et al.,* 1997).

The presence of certain species in some locations is determined not only by environmental factors, but also by biological ones such as food competition, reproductive capacity, and larval development (Mantelatto *et al.,* 1995), and shell availability in the case of hermit crabs. Among these factors, food competition probably has an important role in this species' distribution: *L. loxochelis* predominates in deeper areas, whereas *I. sawayai* is more common in shallower waters (Fransozo *et al.,* 1998). Furthermore, the spatial distribution of *I. sawayai* probably reduces competition for space, food, and shells, because other hermit-crab species that inhabit the same area, such as *Pagurus exilis* (Benedict, 1892), *Dardanus insignis* (Saussure, 1858), and *L. loxochelis* predominate at depths between 20 and 35 m (Meireles *et al.,* 2006; Meireles and Mantelatto, 2008; Ayres-Peres and Mantelatto, 2008b).

Furthermore, a significant difference in the *I. sawayai* sex ratio was observed in relation to its spatial distribution. Deviations from the expected 1:1 proportion between sexes (Fisher, 1930) are common among crustaceans (Wenner, 1972). Many such deviations favor males, as in hermit crabs such as *I. sawayai* studied here, *Petrochirus diogenes* (Linnaeus, 1758) by Bertini and Fransozo (2000), *Paguristes calliopsis* (Forest and Saint-Laurent, 1968) by Biagi *et al.* (2006), *P. exilis* by Mantelatto *et al.* (2007), and *D. insignis* by Meireles and Mantelatto (2008), all on the coast of São Paulo. Several factors including differential mortality rates between the sexes, reproductive migration, sex reversal, differential shell selection between males and females, and shell availability may contribute to an unequal proportion of males and females in a population (Wenner, 1972; Mantelatto and Meireles, 2004). Furthermore, the sex ratio can differ from the expected in species with sexual dimorphism (Wilson and Pianka, 1963) such as *I. sawayai* (Fantucci *et al.,* 2009).

Calculation of the sex ratio based on the total number of individuals may obscure the relationship between sexes within size classes (Wenner, 1972). The conventional practice is to estimate the proportion of the sexes by size class, to determine the population sex pattern. According to our analysis, *I. sawayai* exhibited an anomalous pattern of sex ratio, as found in many other hermit-crab species (Abrams, 1988). This pattern could be explained by the males and females having differential longevity, mortality and growth rates, and migration (Wenner, 1972). The last two factors probably explain the size-frequency distribution of *I. sawayai,* considering that males attain larger sizes than females (Fantucci *et al.,* 2009). In addition, the sex ratio favored males in samples from shallow waters, e.g., 5 m deep (present study; Masunari *et al.,* 2008); whereas in intertidal samples in the Ubatuba region and in Venezuela, females were more abundant than males (Pinheiro *et al.,* 1993; Galindo *et al.,* 2008). Therefore, the greater occurrence of males of *I. sawayai* found in the present study is probably associated with differential depth distribution between the sexes.

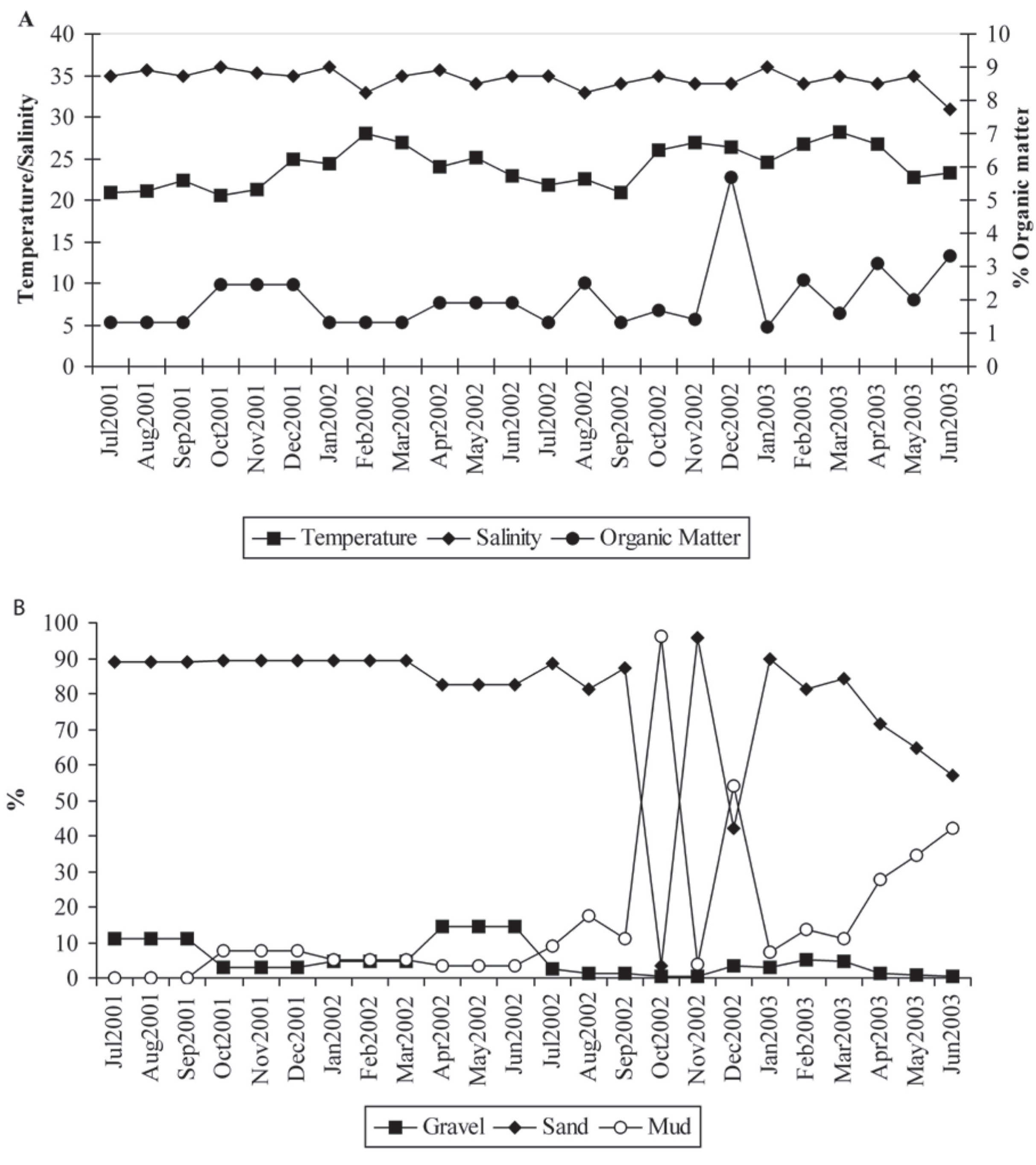

Figure 2. *Isocheles sawayai.* Monthly fluctuation of the environmental factors: A. temperature (°C), salinity (p.s.u.) and organic matter content (%); B. sediment grain size (%), on 5 m depth in Caraguatatuba region, São Paulo, from July 2001 through June 2003.

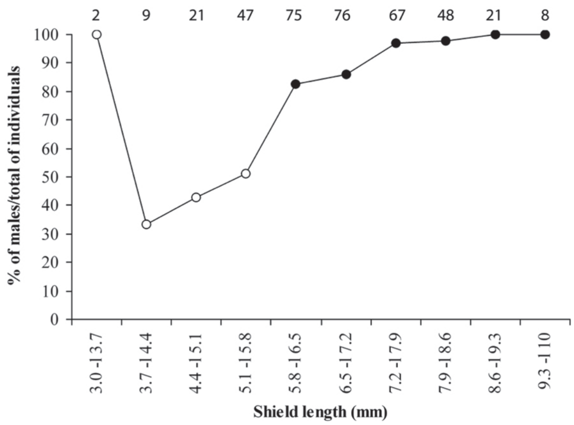

Figure 3. *Isocheles sawayai.* Percentage of males in relation to the total of individuals sampled in each size class in the Caraguatatuba region, São Paulo, from July 2001 through June 2003 (filled circles = males significantly more abundant; the numbers over each point indicate the total number of individuals in the size class).

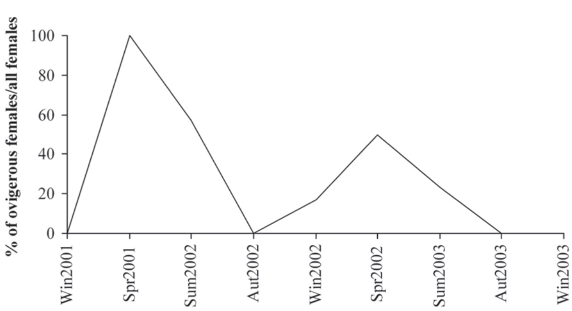

Figure 4: *Isocheles sawayai.* Ovigerous females' seasonal occurrence percentage (in relation to total of females), evidencing peaks of reproductive activity in the Caraguatatuba region, São Paulo, from July 2001 through June 2003 (Win, winter – July, August, and September; Spr, spring – October, November, and December; Sum, summer – January, February, and March; Aut, autumn – April, May, and June).

The distribution pattern related to temperature differs from those of *P. diogenes, P. exilis,* and *L. loxochelis* (Bertini and Fransozo, 1999; Meireles *et al.,* 2006; Bertini *et al.,* 2004, respectively). All these species occur more frequently in low temperatures, whereas *I. sawayai* prefers warmer waters. During the summer it is possible to find groups of *I. sawayai* in the intertidal zone of some beaches on the northern coast (FL Mantelatto, pers. obs.). This may be related to the spatial distribution, because temperature decreases with increasing depth, or may also be associated with the species' life cycle.

Temporal patterns of reproductive cycles are the result of the interaction of several factors acting on individuals in a population over time. Environmental variables interact with each other and within the population, and vary continuously throughout the year; these variations are most evident in high latitudes (Sastry, 1983). Consequently, populations that inhabit different latitudes differ in their reproductive cycles due to environmental particularities. Most species of hermit crabs that inhabit temperate regions have seasonal reproduction patterns (Asakura and Kikuchi, 1984); tropical species tend to reproduce homogeneously throughout the year (Goodbody, 1965); and species that live in subtropical regions have reproductive activity throughout the year, with peaks in warmer periods, when higher temperatures and greater food availability for larvae are favorable for their metamorphosis (Negreiros-Fransozo and Fransozo, 1992).

Continuous and seasonal reproduction are both common in tropical and subtropical regions, because in these areas there is little variation in temperature, rain, photoperiod, and nutrient supply, all factors that influence reproduction (Litulo, 2005). The *I. sawayai* population studied has seasonal reproduction with peaks in the rainy season, a reproductive strategy also shown by other hermit-crab species in the region (Fransozo and Mantelatto, 1998; Bertini and Fransozo, 2000; Garcia and Mantelatto, 2001; Miranda *et al.,* 2006). This temporal distribution can be attributed to the warmer temperatures and greater food supply for larvae at this time of year (Negreiros-Fransozo and Fransozo, 1992). The entrance of the South Atlantic Central Water (SACW) in the summer favors enrichment by nutrients, increasing phytoplankton primary production, which supports a larger biomass of herbivorous zooplankton and creates better conditions for the survival of larvae of many benthic animals (Pires-Vanin and Matsuura, 1993). These environmental variations resulting from the SACW entrance accord with the greater number of individuals in the present study, which suggests that food availability for adults and larvae is an important factor governing the seasonal population pattern of the hermit crabs (Meireles *et al.,* 2006).

The distribution pattern of *I. sawayai* led us to conclude that environmental and biotic factors act jointly on the occurrence of hermit-crab species, and can influence population characteristics, behavior, and reproduction. In this way, we demonstrated the importance of a systematized distributional study, focused on environmental factors, for improving knowledge of these hermit crabs' occurrence, interactions, and biology.

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