Gulf and Caribbean Research

Volume 20 | Issue 1

2008

Shell Utilization Pattern by the Hermit Crab *Isocheles sawayai* Forest and Saint Laurent, 1968 (Anomura, Diogenidae) from Margarita Island, Caribbean Sea, Venezuela

Lee A. Galindo
Universidad de Oriente, Venezuela

Juan A. Bolanos
Universidad de Oriente, Venezuela

Fernando L. Mantelatto
University of Sao Paulo

Recommended Citation

Galindo, L. A., J. A. Bolanos and F. L. Mantelatto. 2008. Shell Utilization Pattern by the Hermit Crab *Isocheles sawayai* Forest and Saint Laurent, 1968 (Anomura, Diogenidae) from Margarita Island, Caribbean Sea, Venezuela. Gulf and Caribbean Research 20 (1): 49-57.
Retrieved from https://aquila.usm.edu/gcr/vol20/iss1/7
DOI: https://doi.org/10.18785/gcr.2001.07

Gulf and Caribbean Research Vol 20, 49-57, 2008 Manuscript received, May 5, 2007; accepted, December 11, 2007

SHELL UTILIZATION PATTERN BY THE HERMIT CRAB *ISOCHELES SAWAYAI* FOREST AND SAINT LAURENT, 1968 (ANOMURA, DIOGENIDAE) FROM MARGARITA ISLAND, CARIBBEAN SEA, VENEZUELA

Lee A. Galindo[1], Juan A. Bolaños[1], and Fernando L. Mantelatto[2]*

[1]*Laboratorio de Carcinología, Escuela de Ciencias Aplicadas del Mar, Universidad de Oriente, Apartado postal 147, Nueva Esparta, Venezuela*

[2]*Laboratory of Bioecology and Crustacean Systematics, Postgraduate Program in Comparative Biology, Department of Biology, Faculty of Philosophy, Science and Letters of Ribeirão Preto, University of São Paulo, 14040-901 Ribeirão Preto (SP), Brazil, e-mail: flmantel@usp.br*

** corresponding author*

ABSTRACT: *Isocheles sawayai* is a hermit crab that is occasionally mentioned in the literature, and recently its distribution was extended to Venezuelan waters. Because no information on the biology and shell use patterns of this species inhabiting Caribbean waters is available, we provide the first information on shell occupation patterns of *I. sawayai* from Venezuela. Specimens were collected monthly from January to December 2000 along the sandy shore of Margarita Island, Venezuela. The 942 specimens collected showed different shell use patterns between the sexes and according to the reproductive condition of the females. The gastropods *Leucozonia nassa* (37.37%), *Engoniophos unicinctus* (25.37%), *Nassarius vibex* (4.88%), *Melongena melongena* (4.25%), and *Stramonita haemastoma* (3.82%) represent 76% of the total occupied shells. Of the total of 26 different shell species occupied by *I. sawayai*, males were found occupying 21, while females were found occupying all 26 shell species. In general, both sexes most frequently occupied *L. nassa* and *E. unicinctus*. However, the percentage of females occupying these shells was significantly higher than that of the males. Regression analyses showed the best correlation between crab size, shell aperture width, and shell internal volume. The current comparative investigation, in combination with other South Atlantic populations of *I. sawayai*, provided further evidence of shell use adaptation in hermit crabs from different areas, and increases our insight into shell use of shallow-water hermit crabs.

INTRODUCTION

Hermit crabs are an interesting group from a biological and evolutionary viewpoint, especially in regard to their intriguing mechanisms of shell use. The borrowed shells of gastropods provide protection against predators and physical stress, and often constitute a limiting resource for hermit crabs (e.g., Reese 1969, Vance 1972, Fotheringham 1976a, Bertness 1981a) in terms of growth, reproduction, and social behavior.

Although many studies have been published on hermit crab shell occupation worldwide, the parameters by which a particular shell is chosen by a hermit crab are not completely known (Meireles and Mantelatto 2005). Studies on gastropod shell availability, patterns of shell use and selection, and the relationship between these factors constitute an initial part of a long-term effort undertaken to identify and clarify important parameters affecting this process (Mantelatto and Meireles 2004). The patterns of shell use vary among hermit crab populations and are influenced by several factors, such as the type and size of available shells, the inhabited area (intertidal or sublittoral area), and the hermit crabs' shell preference (Garcia and Mantelatto 2000, Mantelatto and Garcia 2000).

The genus *Isocheles* Stimpson, 1858 is known taxonomically, but there is a lack of basic biological information. For the five species in the genus reported in American tropical and subtropical waters, there are only brief references concerning their distributions (see Forest and Saint Laurent 1968, Nucci and Melo 2000, Guzmán 2004), and a recent study on molecular phylogeny (Mantelatto et al. 2006). In relation to *Isocheles sawayai* Forest and Saint Laurent 1968, the available information is restricted to data on specimens from the Brazilian coast that deals with the morphology of larval stages (Negreiros-Fransozo and Hebling 1983), shell use (Pinheiro et al. 1993, Fantucci et al. 2008), and records of intersex individuals (Fantucci et al. 2007).

Although shell use by hermit crabs has been examined in other areas of the world (see Mantelatto and Garcia 2000 for review), to our knowledge no detailed and systematic study has been carried out on the hermit crab fauna of the Caribbean or Atlantic region of Venezuela. Here we report the first observations on the patterns of gastropod shell occupation by a population of *I. sawayai* inhabiting the sandy shore of Isla Margarita, Venezuela, with emphasis on morphometric relationships between hermit crabs and their shells.

Materials and Methods

Study Area

La Restinga Beach is located in a northern cornice of Margarita Island, Venezuela on the Caribbean Sea (10°57' N - 11°03' S, 64°01' - 64°12' W; Figure 1) and is open to northwest trade winds. The beach is formed by a flat sand fringe that separates a hypersaline lagoon from the ocean, has a total surface area of about 30 km^2, and is the largest beach in Nueva Esparta Province. The mean water temperature during collections was 26 °C and the salinity was 34 ppt.

Sampling Procedures

Specimens of *I. sawayai* were collected monthly during daytime on La Restinga Beach from January to December 2000 at random locations along the beach over a distance of about 200 m. A minimum of 70 individual hermit crabs were captured by hand each month. After collection, the animals were transported to the Crustacean Laboratory of the Universidad de Oriente and preserved in a 5% solution of formalin in sea water. Each individual was removed from its occupied shell, sexed, wet weighed (WW, g), and the cephalothoracic shield length (CSL, mm) was measured to the nearest 0.05 mm using a caliper. The reproductive condition of each female (ovigerous, non-ovigerous) was also recorded.

Shell Study

Shell species were identified according to the descriptions in Warmke and Abbott (1962), Abbott (1974), and Morris (1975), and confirmed by a specialist. The measurements were made according to Imafuku and Ando (1999) and Mantelatto and Garcia (1999): Total Shell Length (TSL, mm); Shell Maximum Width (SMW, mm); and Shell Dry Weight (SDW, g). Shell Internal Volume (SIV, cc^3) was measured by the method suggested by Bertness (1981b), and involved determining the volume of sand (known weight) required to fill an empty shell. Shell Angle Tip (SAT, degree) was measured according to Asakura (1995). An empirical scale was used to evaluate the physical state of shell condition, from 1 for perfect shell condition to 6 for severely damaged.

Data Analysis

To determine correlations among hermit crab dimensions and shell variables, regressions $Y = a \bullet X^b$ and correlation coefficients were calculated. The percentage of occupied gastropod shells was estimated based on the total number of individuals collected. The Shannon-Weaver Diversity Index (Margalef 1974), based on the number of gastropod species

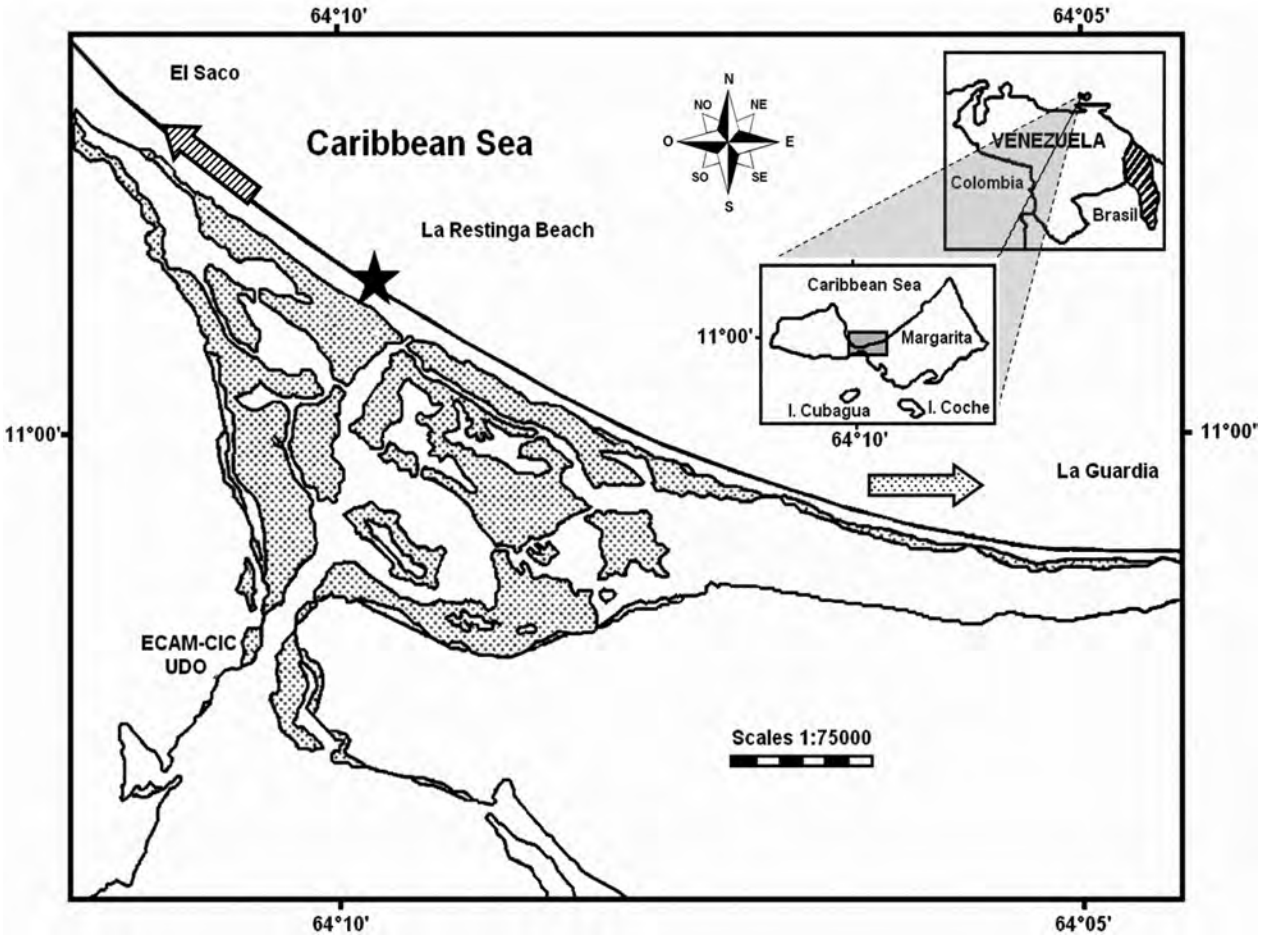

Figure 1.
Map showing the sampling location (star) at an exposed sandy beach at La Restinga, Margarita Island, Venezuela (10°57'N - 11°03'S, 64°01'- 64°12'W). Potential sources of shells: La Guardia (dotted arrow) and El Saco (striped arrow).

TABLE 1. *Species, number, and percentage (monthly and total) of gastropod shells used by Isocheles sawayai from January to December 2000 at La Restinga Beach, Venezuela. Occurrence is expressed as the number of shells found per number of collections.*

Shell Species	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Total	Occurrence	%
Leucozonia nassa	52	39	23	14	31	29	26	30	30	42	21	15	352	12/12	37.37
Engoniophos unicinctus	9	13	11	12	15	26	18	22	17	32	38	26	239	12/12	25.37
Nassarius vibex	-	1	4	1	1	5	5	11	2	4	10	2	46	11/12	4.88
Melongena melongena	3	2	5	8	6		5	3	3	2	1	2	40	11/12	4.25
Stramonita haemastoma	10	3	6	5	3	4	1	1	2	1	-	-	36	10/12	3.82
Stramonita rustica	-	6	6	2	-	2	2	1	3	4	2	1	29	10/12	3.08
Natica canrena	2	6	2	3	4	1	4	-	3	1	1	2	29	11/12	3.08
Bursa granularis	4	4	2	2	2	1	2	3	2	2	2	1	27	12/12	2.87
Pisania tincta	5	-	-	2	2	1	-	3	-	5	2	-	20	7/12	2.12
Clathrodrillia gibosa	3	3	3	1	-	-	3	1	-	2	1	1	18	9/12	1.91
Murex chrysostoma	1	3	2	1	1	1	3	-	-	3	-	3	18	9/12	1.91
Turritella variegata	1	-	-	1	1	-	-	3	3	2	3	3	17	8/12	1.80
Conus spp.	-	-	1	-	2	1	2	-	5	-	-	-	11	5/12	1.17
Chicoreus brevifrons	2	-	1	1	1	1	1	-	-	-	1	1	9	9/12	0.96
Marginella prunum	1	-	2	1	1	1	-	1	-	-	1	1	9	8/12	0.96
Others[1]	7	3	1	5	5	3	3	3	2	3	3	4	42	-	4.46
Total number of species per month	**17**	**13**	**14**	**18**	**15**	**15**	**15**	**13**	**12**	**15**	**14**	**14**	**17**		

[1]Species and % occurrence included in Other category: *Fusinus closter* (0.74%), *Cancellaria reticulata* (0.53%), *Olivia reticulatus* (0.42%), *Terebra cinerea* (0.32%), *Fasciolaria tulipa* (0.21%), *Ancilla tankervilli* (0.11%), *Cymatium parthenopeum* (0.11%), *Murex* spp. (0.11%), *Ceritium eburneum* (0.11%), *Conus jaspideus* (0.11%), and *Tegula lividomaculata* (0.11%), 2 unidentified (1.58%).

used by *I. sawayai*, was also calculated. The occupancy of shell species by hermit crabs (males, non-ovigerous females, and ovigerous females) was tested by the chi-square test and the mean size of both sexes was compared by Mann-Whitney U-test (Zar 1996). The level of significance was 0.05 for all tests.

Results

Of 942 hermit crabs collected, 171 were males (18.15%), 164 were non-ovigerous females (17.41%), 600 were ovigerous females (63.69%), and the sex of 7 was undetermined (0.74%). Males and females had a CSL ranging from 1.70 to 7.35 mm and from 2.15 to 8.75 mm, respectively. Males were significantly larger than non-ovigerous ($U = 17167.6$, $p < 0.01$) and ovigerous females ($U = 18985.3$, $p < 0.01$).

Isocheles sawayai occupied shells of 26 gastropod species. *Leucozonia nassa, Engoniophos unicinctus, Nassarius vibex, Melongena melongena*, and *Stramonita haemastoma* represented 75.69% of the total shells obtained. The great majority of hermit crabs (95.55%) occupied 15 of the 26 shell species (Table 1). The shell species used least frequently were *Fusinus closter* (0.74%), *Cancellaria reticulata* (0.53%), *Olivia reticulatus* (0.42%), *Terebra cinerea* (0.32%), *Fasciolaria tulipa* (0.21%), *Ancilla tankervilli* (0.11%), *Cymatium parthenopeum* (0.11%), *Murex* spp. (0.11%), *Ceritium eburneum* (0.11%), *Conus jaspideus* (0.11%), and *Tegula lividomaculata* (0.11%). These 9 species of infrequently used shells plus 2 unidentified ones were designated as "others."

The number of shell species occupied per month by *I. sawayai* ranged from 12 (September) to 18 (April). *Leucozonia nassa*, *S. haemastoma*, and *Stramonita rustica* showed the highest frequency of occurrence (12/12) during the study period (Table 1). Of the total shells analyzed, 16% were covered externally by epibionts (bryozoans in most cases), 50% were generally damaged, and only 34% were in a perfect state of condition.

Morphometric relationships between hermit crabs and used shells were statistically significant, but with low correlation coefficients (Table 2, Figure 2). Of these, the relationships SMW versus CSL and SIV versus CSL turned out to best describe the association between hermit crabs and their shells. Although significant, SAT versus CSL ($r = 0.29$) did not seem to generate much information concerning the population.

Males and females ($\chi^2 = 90.71$; $p < 0.001$; permutation test = 0) as well as ovigerous and non-ovigerous females ($\chi^2 = 30.59$; $p < 0.001$; permutation test = 0) showed different shell use patterns (Figure 3). Males were found occupying 21 of the 26 collected gastropod shells, whereas females (ovigerous

as well as non-ovigerous) used all the shell species collected. The mean Shannon-Weaver diversity (H') of shells occupied by *I. sawayai* was 1.67 ± 0.16 bit/ind and ranged from 1.51 to 2.07 bit/ind. High values of H' indicate the population occupied a wider variety of shell species. In general, males and females of *I. sawayai* inhabit *L. nassa* (19% ♂; 42% ♀, respectively) and *E. unicinctus* (16% ♂; 28% ♀, respectively) most frequently; the percentage of females using these two shells was significantly higher than that of males ($\chi^2 = 25.23$; $p < 0.001$; permutation = 0.006 and $\chi^2 = 14.92$; $p < 0.01$; permutation = 0.05; respectively). The use of *E. unicinctus* by ovigerous and non-ovigerous females was statistically different ($\chi^2 = 16.49$; $p < 0.01$; permutation = 0.01). However, there was no evidence of a difference between the reproductive state of females and their occupation of *L. nassa* ($\chi^2 = 7.09$; $p < 0.31$; permutation = 0.34). The variability of shell species used decreased as the hermit crab size increased (Figure 4). However, in the smallest size class of hermit crab the shell variability was limited by the availability of small shells.

Discussion

In general, *I. sawayai* occupied a wider variety of shell species compared with other hermit crabs from tropical and subtropical areas (Table 3). Although shell availability was not evaluated, intense occupancy of some species of gastropod shells would indicate active selection behavior in *I. sawayai* in the field. *Isocheles sawayai* is a medium-sized hermit crab; this size may increase the possibility of finding adequate shells compared to larger crabs that are forced to look for larger shells.

Judging from the large number of shell species used, it could be expected that high gastropod shell diversity is available at La Restinga Beach; however, neither living gastropods nor empty shells were found in the field during the present study. The present study revealed a high variation of shell use in this hermit crab population. Generally, when there is good availability of resources (*i.e.*, empty shells, live

TABLE 2. *Shell dimensions of gastropods occupied by Isocheles sawayai from January to December 2000 at La Restinga Beach, Venezuela. TSL = Total Shell Length; SMW = Shell Maximum Width; SDW = Shell Dry Weight; SIV = Shell Internal Volume; SAT = Shell Angle Tip; N = Number of Shells; Min = Minimum Value; Max = Maximum Value; $\bar{X}$ = Mean; sd = Standard Deviation; CV = Coefficient of Variation.*

	N	Min	Max	$\bar{X}$	sd	CV
TSL (cm)	941	0.005	0.729	0.235	0.068	28.80
SMW (cm)	938	0.019	0.441	0.143	0.043	29.68
SDW (g)	942	0.07	16.90	1.72	1.46	85.01
SIV (cm^3)	899	0.02	8.12	0.69	0.86	124.48
SAT (°)	937	12	135	60.60	18.70	30.90

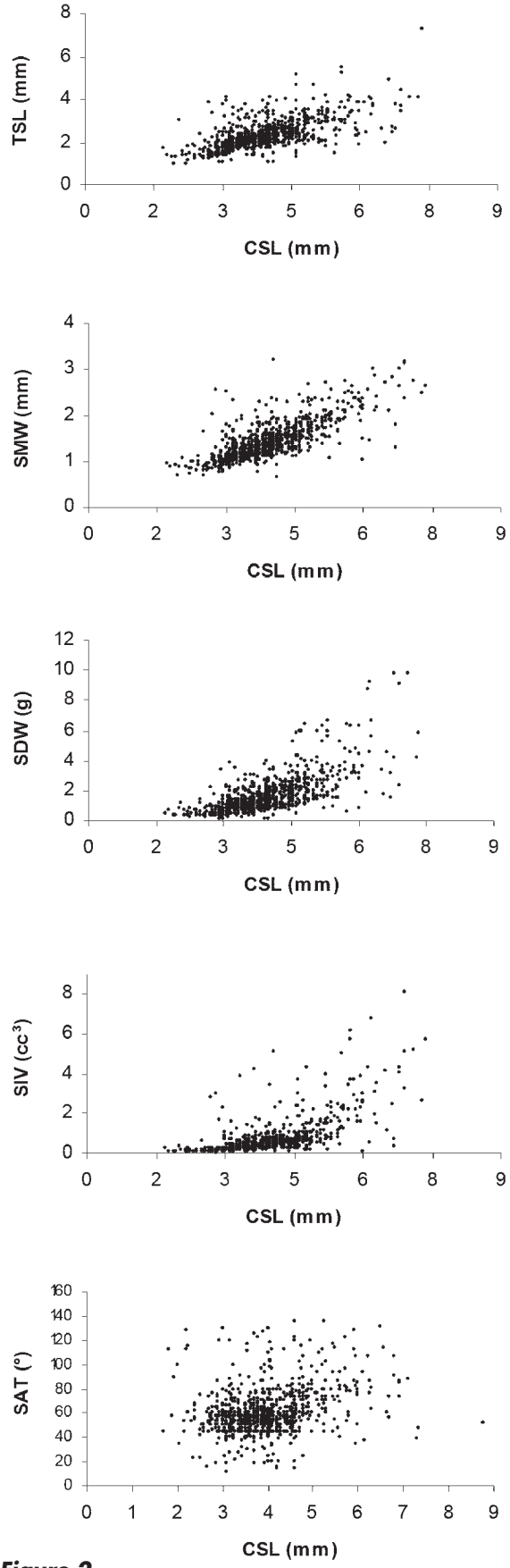

Figure 2.
Regression plots between cephalothoracic shield length (SL) of Isocheles sawayai and total shell length (TSL), shell maximum width (SMW), shell dry weight (SDW), shell internal volume (SIV), and shell angle tip (SAT).

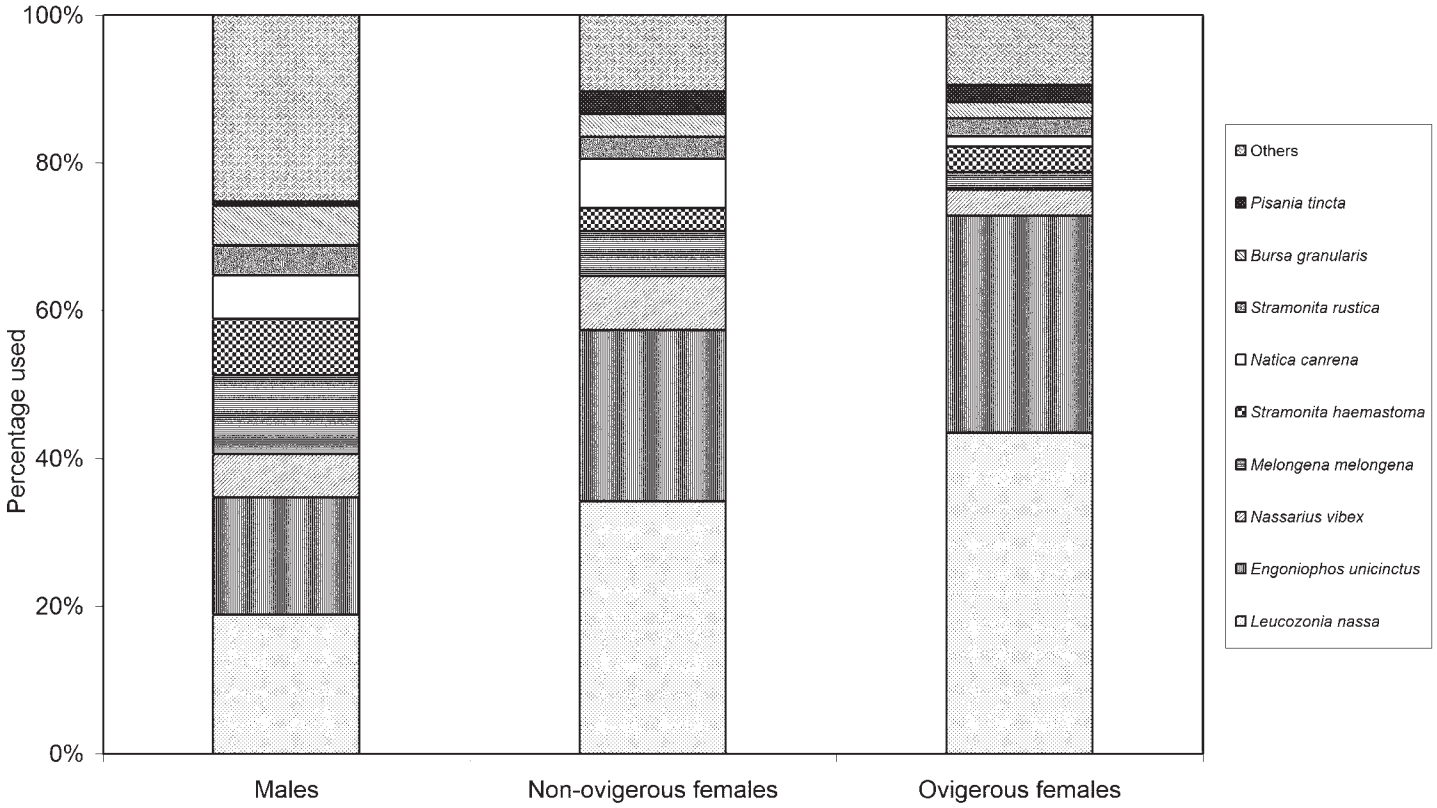

Figure 3.
Percent use by Isocheles sawayai of different species of gastropod shells by demographic category.

gastropods, and high diversity of occupied shells), the most common pattern observed is an occupation of adequate and undamaged shells by the hermit crabs (Mantelatto and Meireles 2004). However, this condition was not observed in the population studied: a large number (76%) of damaged shells were found, and no preference for occupation of these shells by either sex or ovigerous females was observed. A similar pattern has been described for other hermit crabs from different areas worldwide (Vance 1972, Bach et al. 1976, Martinelli and Mantelatto 1999, Mantelatto and Meireles 2004). According to Scully (1979), the occupation of damaged shells increases the probability of interactions and shell exchanges within a population, affecting both protection and reproduction of the resident hermit crabs. For example, in situations where shell availability is limited, we expect to find a greater use of damaged shells (Hazlett 1966, 1970, Childress 1972, Bertness 1981b). Specimens of *I. sawayai* need heavy shells to survive the strong waves on an exposed sandy beach. The observed pattern of occupation of damaged shells suggests that competition for shell resources made occupation of inadequate shells essential. The natural occurrence of hermit crabs in specific gastropod shells may be a consequence of a preference for such shells and of their relative abundance in the appropriate size range with respect to crab abundance (Conover 1978). We can conclude that the population of *I. sawayai* at La Restinga Beach most probably displays intense shell exchange mechanisms.

One intriguing question arising from this study is, where does *I. sawayai* obtain shells? The crabs may obtain their shells from several different sources: 1) empty shells could be available from El Saco to the West via migratory movements parallel to shore (see Figure 1); 2) the action of waves and currents have an important role in shell transportation from different areas (rocks, mud sediments, and lagoons) such as northwest of La Guardia Bay to the east (see Figure 1), where the most frequently available shells are those more susceptible to physical action (waves and currents); 3) shells may come from older shells deposited in the sediments in the area; and 4) shells may come from intraspecific exchanges. These factors may influence shell availability at La Restinga Beach.

Provenzano (1959) reported a high occupation rate of *Stramonita* gastropod shells by *I. wurdemanni* in Bermuda. Similar results were reported for *I. wurdemanni* in *Stramonita floridana* shells (95.6% occupancy; Caine 1978) in Florida, and in Brazil (49.9% occupancy; Fantucci et al. 2008). The genera *Stramonita, Leucozonia,* and *Cymatium* occur over a wide latitudinal range, and their shells are commonly occupied in noticeably high percentages by pagurid and diogenid hermit crabs (Grant and Ulmer 1974, Bertness 1982, Negreiros-Fransozo et al. 1997, Mantelatto and Garcia 1999); thus it is not surprising that they would also be suitable for the hermit crab population studied here.

The presence of live individuals of *Stramonita* and *Leucozonia* in the rocky shore regions of El Saco and La Guardia peripheral to the study area (see Figure 1) can be considered as potential sources of shells appropriate for *I. sawayai*, although proper studies have yet to be done. The genera *Terebra*, *Murex*, and *Melongena* are frequent, but not abundant, in some other reports of shell use by tropical hermit crabs (Provenzano 1959, Fotheringham 1976a, Caine 1978, Bertness 1982), reflecting a similar pattern found in the population studied here. Unfortunately, there are no data or detailed studies available on gastropod species in this area for comparative analysis.

From the results obtained here, we can infer that *I. sawayai* inhabits a wide variety of shell species, but tend to occupy shells of specific species (*L. nassa* and *E. unicinctus*). From published reports it is evident that, in nature, each species of hermit crab preferentially occupies one or a few species of shells, as reported for *Paguristes tortugae* by Mantelatto and Dominciano (2002), *Calcinus tibicen* by Garcia and Mantelatto (2000), *Pagurus brevidactylus* by Mantelatto and Meireles (2004), and *I. sawayai* by Fantucci et al. (2008). These patterns of occupation are related to preferences for specific shells and/or the abundance of appropriate shells in the habitat. However, in the case of *I. sawayai*, the reasons cannot be precisely determined by the study methods used, so further experimental studies dealing with these questions are necessary.

Differences in shell weight are known to encourage use patterns and may affect reproduction of hermit crabs. According to Fotheringham (1976a), shell weight directly affects the amount of energy available for reproduction; crabs carrying heavier shells must shift energy to activities such as locomotion and the search for food. Males of *I. sawayai* were found occupying heavier shells than females and juveniles, probably because of their larger size as well as their numerical dominance or status in the population (Garcia and Mantelatto 2000). Furthermore, larger shells are less subject to displacement by water movements. Larger males preferentially occupied *M. melongena*, probably because of both its ornamental shape (triangular-ovate body and triangular aperture) and medium size. Ovigerous females clearly preferentially occupied *L. nassa* and *E. unicinctus*, but only up to 6.5 mm CSL. Males also showed a higher diversity of shells used (2.27 bit/ind) compared with non-ovigerous females only (1.66 bit/ind). It is possible that males change shells more frequently as a consequence of their faster growth (Mantelatto et al. 2005) as they increase in size and require new and larger shells.

For females, the tendency to occupy larger and heavier shells is related to the space available to contain more eggs (Mantelatto and Garcia 1999). Ovigerous females < 4.7 mm CSL clearly preferred *L. nassa* and *E. unicinctus* shells compared to non-ovigerous females. These observations are supported by Bach et al. (1976), Fotheringham

TABLE 3. *Comparative data on gastropod shell species occupation in hermit crab species of the family Diogenidae from tropical and subtropical zones.*

Hermit species	Number of shell species	Locality	Reference
Calcinus seurati	5	Hawaii, USA	Hazlett (1989)
Calcinus tibicen	21	Randolf Reef, Panama	Bertness (1982)
Calcinus tibicen	7	Ubatuba, Brazil	Mantelatto and Garcia (2000)
Calcinus tubularis	15	Mediterranean Sea, Italy	Pessani et al. (2000a)
Clibanarius albidigitus	7	Golfo Dulce, Costa Rica	Childress (1972)
Clibanarius antillensis	22	Randolf Reef, Panamá	Bertness (1982)
Clibanarius tricolor	18	Florida, USA	Bach et al. (1976)
Clibanarius vittatus	8	Texas, USA	Fotheringham (1976a)
Clibanarius zebra	> 9	Hawaii, USA	Hazlett (1989)
Dardanus insignis	7	Ubatuba, Brazil	Negreiros-Fransozo et al. (1997)
Diogenes nitidimanus	26	Kyushu, Japan	Asakura (1995)
Diogenes pugilator	10	Ligurian Sea, Italy	Pessani et al. (2000b)
Isocheles sawayai	4	Ubatuba, Brazil	Negreiros-Fransozo et al. (1997)
Isocheles sawayai	17	Ubatuba, Brazil	Fantucci (2008)
Isocheles sawayai	26	La Restinga, Venezuela	Present study
Loxopagurus loxochelis	6	Ubatuba, Brazil	Martinelli and Mantelatto (1999)
Paguristes tortugae	21	Ubatuba, Brazil	Mantelatto and Dominciano (2002)
Petrochirus diogenes	12	Ubatuba, Brazil	Bertini and Fransozo (2000)

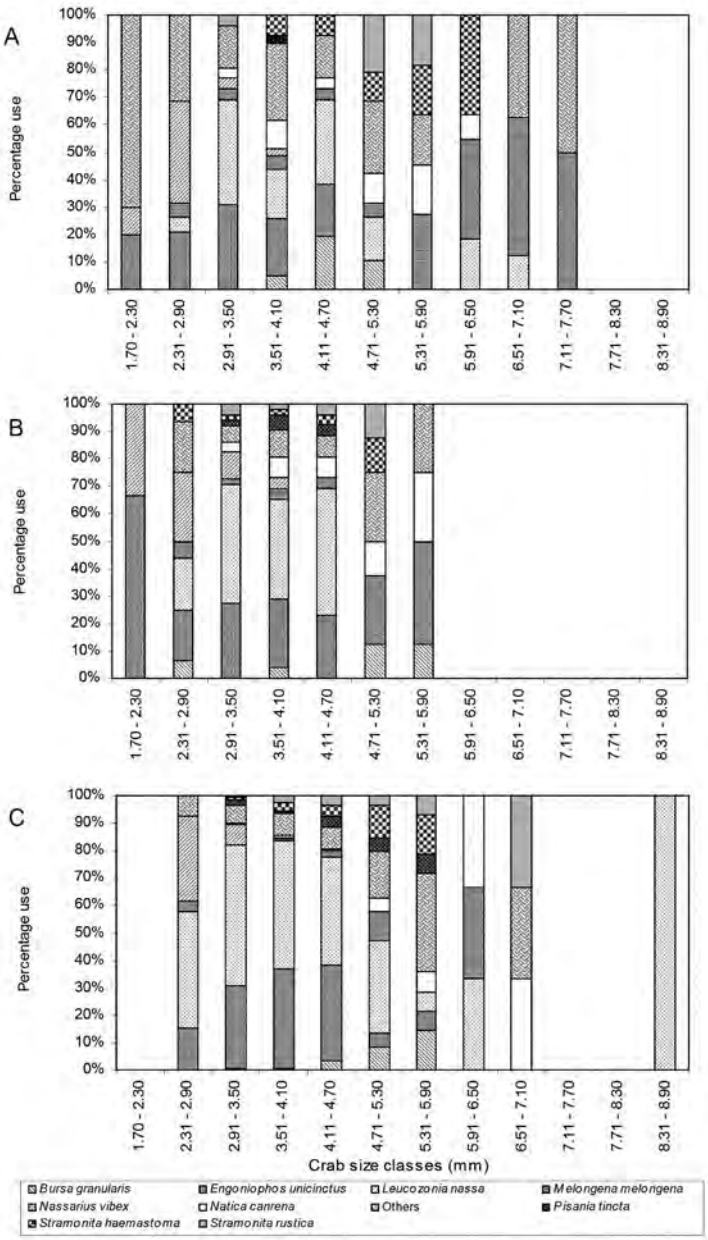

Figure 4.
Percent use of gastropod species shells by Isocheles sawayai in each size class and demographic category.
A. Males.
B. Non-Ovigerous females.
C. Ovigerous females.

(1976b), and Mantelatto and Garcia (1999, 2000). We infer that ovigerous females of *I. sawayai* are more selective regarding shell use in order to 1) reach optimal shell size, 2) use a shell shape that provides a better fit for the crab body shape/size, and 3) allows a better space to carry their broods, as observed in other pagurids of similar size (Dominciano and Mantelatto 2004). In other words, non-ovigerous females may go through a transition period when they look for the appropriate shell to brood their eggs.

In conclusion, we postulate that *I. sawayai* in the La Restinga Beach area shows intense competition for appropriate shells through shell exchange, but concentrated on two gastropod species. The shell use pattern of this species varies between the sexes and the reproductive condition of females. In general, the population inhabits shells of *L. nassa* and *E. unicinctus*, but this occurs mainly for all the ovigerous females. There was a significant size relationship between the hermit crab and its shell, principally with respect to shell width and internal volume.

Acknowledgements

Special thanks go to those who collaborated during the course of this study, especially J.C. Capelo for helping in shell identification and the fishermen for support during field activities. FLM received direct support from the Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) for an ongoing research fellowship and during the International Cooperative Project - CNPq - Prosul Program (490340/2004-0), which provided financial support to FLM and JCB during a Brazil-Venezuela visiting program. We are also thankful to A.L. Meireles, R. Biagi, two anonymous reviewers, and the editorial committee for their criticism and suggestions on an early version of the manuscript. Janet W. Reid (Virginia Museum of Natural History) revised the English text.

Literature Cited

Abbott, R.T. 1974. American Seashells. 2nd ed., Van Nostrand Reinhold Company, Princeton, NJ, USA, 663 p.

Asakura, A. 1995. Sexual differences in life history and resource utilization by the hermit crab. Ecology 76:2295-2313.

Bach, C.B., B. Hazlett, and D. Rittschof. 1976. Effects of interspecific competition on fitness of the hermit crab *Clibanarius tricolor*. Ecology 57:579-586.

Bertini, G. and A. Fransozo. 2000. Patterns of shell utilization in *Petrochirus diogenes* (Decapoda: Anomura: Diogenidae) in the Ubatuba region, São Paulo, Brazil. Journal of Crustacean Biology 20:468-473.

Bertness, M.D. 1981a. The influence of shell type on the growth rates and clutch sizes of hermit crabs. Crustaceana 40:197-205.

Bertness, M.D. 1981b. Seasonality in tropical hermit crab reproduction in the Bay of Panama. Biotropica 13:292-300.

Bertness, M.D. 1982. Shell utilization, predation pressure, and thermal stress in Panamanian hermit crabs: an interoceanic comparison. Journal of Experimental Marine Biology and Ecology 64:159-187.

Caine, E.A. 1978. Habitat adaptations of *Isocheles wurdemanni* Stimpson (Crustacea; Anomura: Diogenidae) and seasonality of occurrences in northwestern Florida. Contributions in Marine Science 21:117-123.

Childress, J.R. 1972. Behavioral ecology and fitness theory in a tropical hermit crab. Ecology 53:960-964.

Conover, M.R. 1978. The importance of various shell characteristics to the shell-selection behavior of hermit crabs. Journal of Experimental Marine Biology and Ecology 32:131-142.

Dominciano, L.C.C. and F.L. Mantelatto. 2004. The influence of shell species and size on the shell selection pattern of *Paguristes tortugae* (Decapoda, Diogenidae) from Anchieta Island (Ubatuba, Brazil). Iheringia, Série Zoologia, 94:425-428.

Fantucci, M.Z., R. Biagi, and F.L. Mantelatto. 2008. Shell occupation by the endemic western Atlantic hermit crab *Isocheles sawayai* (Diogenidae) from Caraguatatuba, Brazil. Brazilian Journal of Biology 68(4):in press

Fantucci, M.Z., R. Biagi, and F.L. Mantelatto. 2007. Record of intersexuality in the western Atlantic hermit crab *Isocheles sawayai* (Anomura, Diogenidae). Journal of the Marine Biological Association of the United Kingdom 2, Biodiversity records 5735: 1-3. Published online (http://www.mba.ac.uk/jmba/pdf/5735.pdf) (accessed 7 January 2008).

Forest, J. and M. De Saint Laurent. 1968. Campagne de la Calypso au large des côtes atlantiques de l'Amérique du Sud (1961-1962). 6. Crustacés Décapodes: Pagurides. Annales de l´Institut océanographique 45:47-169.

Fotheringham, N. 1976a. Population consequences of shell utilization by hermit crabs. Ecology 57:570-578.

Fotheringham, N. 1976b. Hermit crab shells as a limiting resource (Decapoda: Paguridae). Crustaceana 31:193-199.

Garcia, R.B. and F.L. Mantelatto. 2000. Variability of shell occupation by intertidal and infralittoral *Calcinus tibicen* (Anomura, Diogenidae) populations. Nauplius 8:99-105.

Grant, W.C. and K.M. Ulmer. 1974. Shell selection and aggressive behaviour in two sympatric species of hermit crabs. Biological Bulletin 146:32-43.

Guzmán, G. 2004. *Isocheles aequimanus* (Dana, 1852) (Decapoda, Anomura, Paguroidea): revalidación para la carcinofauna chilena. Investigaciones Marinas 32:129-132.

Hazlett, B.A. 1966. The social behaviour of the Paguridae and Diogenidae of Curaçao. Studies on the Fauna of Curaçao and Caribbean Islands 88:1-143.

Hazlett, B.A. 1970. The effect of shell size and weight on the agonistic behavior of a hermit crab. Zeitschrift für Tierpsychologie 27:369-374.

Hazlett, B.A. 1989. Mating success of male hermit crabs in shell generalist and shell specialist species. Behavioural Ecology and Sociobiology 25:119-128.

Imafuku, M. and T. Ando. 1999. Behaviour and morphology of pagurid hermit crab (Decapoda: Anomura) that live in tusk shells (Mollusca, Scaphopoda). Crustaceana 72:129-144.

Mantelatto, F.L. and L.C.C. Dominciano. 2002. Pattern of shell utilization by the hermit crab *Paguristes tortugae* (Diogenidae) from Anchieta Island, Southern Brazil. Scientia Marina 66:265-272.

Mantelatto, F.L. and R.B. Garcia. 1999. Reproductive potential of the hermit crab *Calcinus tibicen* (Anomura) from Ubatuba, São Paulo, Brazil. Journal of Crustacean Biology 19:268-275.

Mantelatto, F.L. and R.B. Garcia. 2000. Shell utilization pattern of the hermit crab *Calcinus tibicen* (Diogenidae) from southern Brazil. Journal of Crustacean Biology 20:460-467.

Mantelatto, F.L. and A.L. Meireles. 2004. The importance of shell occupation and shell availability in the hermit crab *Pagurus brevidactylus* (Stimpson, 1859) (Paguridae) population from Southern Atlantic. Bulletin of Marine Science 75:27-35.

Mantelatto, F.L., R.A. Christofoletti, and W.C. Valenti. 2005. Population structure and growth of the hermit crab *Pagurus brevidactylus* (Anomura: Paguridae) from the northern coast of São Paulo, Brazil. Journal of the Marine Biological Association of the United Kingdom 85:127-128.

Mantelatto, F.L., R. Robles, R. Biagi, and D.L. Felder. 2006. Molecular analysis of the taxonomic and distributional status for the hermit crab genera *Loxopagurus* Forest, 1964, and *Isocheles* Stimpson, 1858 (Decapoda, Anomura, Diogenidae). Zoosystema 28:495-506.

Margalef, R. 1974. Ecología. Omega, Barcelona, Spain. 951 p.

Martinelli, J. and F.L. Mantelatto. 1999. Shell utilization by the hermit crab *Loxopagurus loxochelis* (Diogenidae) in Ubatuba Bay, Brazil. In: F.R. Schram and J.C. Vaupel Klein, eds. Crustaceans and the Biodiversity Crisis. Proceedings of the Fourth International Crustacean Congress, Vol. 1, Koninklijke Brill NV, Leiden, The Netherlands, p. 719-731.

Meireles, A.L. and F.L. Mantelatto. 2005. Shell use by *Pagurus brevidactylus* (Anomura, Paguridae): a comparison between laboratory and field conditions. Acta Zoologica Sinica 51:813-820.

Morris, P.A. 1975. A Field Guide to Shells of the Atlantic and Gulf Coasts and the West Indies. 3rd ed. Houghton Mifflin Company, Boston, MA., USA, 330 p.

Negreiros-Fransozo, M.L., A. Fransozo, F.L. Mantelatto, M.A.A. Pinheiro, and S. Santos. 1997. Anomuran species (Crustacea: Decapoda) and their ecological distribution at Fortaleza Bay sublittoral, Ubatuba, São Paulo, Brazil. Iheringia, Série Zoologia 83:181-186.

Negreiros-Fransozo, M.L. and N.J. Hebling. 1983. Desenvolvimento pós-embrionário de *Isocheles sawayai* Forest & Saint Laurent, 1967 (Decapoda, Diogenidae) em laboratório. Papéis Avulsos de Zoologia 35:41-53.

Nucci, P.R. and G.A.S. Melo. 2000. Range extensions for eight species of western Atlantic hermit crabs (Crustacea, Paguroidea). Nauplius 8:141-147.

Pessani, D., M.T. Damiano, G. Maiorana, and T. Tirelli. 2000a. The biology of the hermit crab *Calcinus tubularis* (Decapoda, Diogenidae) in nature and in the laboratory. In: F.R. Schram and J.C. Vaupel Klein, eds. Crustacean Issues 12.

Crustaceans and the Biodiversity Crisis. Proceedings of the Fourth International Crustacean Congress, Vol. 2. Brill, Leiden, Netherlands, p. 377-383.

Pessani, D., M. Dappiano, T. Tirelli, and C. Cerrano. 2000b. The biology of a population of the hermit crab *Diogenes pugilator* (Decapoda, Diogenidae) in the Ligurian Sea. In: F.R. Schram and J.C. Vaupel Klein, eds. Crustacean Issues 12. Crustaceans and the Biodiversity Crisis. Proceedings of the Fourth International Crustacean Congress, Volume 2, Brill, Leiden, Netherlands, p. 323-329.

Pinheiro, M.A.A., A. Fransozo, and M.L. Negreiros-Fransozo. 1993. Seleção e relação com a concha em *Isocheles sawayai* Forest and Saint Laurent, 1967 (Crustacea: Anomura: Diogenidae). Arquivos de Biologia e Tecnologia 36:745-752.

Provenzano, A.J. Jr. 1959. The shallow water hermit crabs of Florida. Bulletin of Marine Science of the Gulf and Caribbean 9:349-420.

Reese, E.S. 1969. Behavioural adaptations of intertidal hermit crabs. American Zoologist 9:343-355.

Scully, E.P. 1979. The effects of shell availability on intraspecific competition in experimental populations of the hermit crab, *Pagurus longicarpus* Say. Journal of Experimental Marine Biology and Ecology 71:221-236.

Vance, R.R. 1972. The role of shell adequacy in behavioral interactions involving hermit crabs. Ecology 53:1075-1083.

Warmke, G.L. and R.T. Abbott. 1962. Caribbean Sea Shells. Livingston Publishing Company, Narberth, PA, USA, 450p.

Zar, J.H. 1996. Biostatistical Analysis. Prentice-Hall, Upper Saddle River, NJ, USA, 907p.