

*Research Article*

## Importance of biogenic substrates for the stone crab *Menippe nodifrons* Stimpson, 1859 (Brachyura: Eriphioidea)

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**ABSTRACT.** In order to better understand the ecology of the different growth phases of the stone crab, *Menippe nodifrons*, and provide information for conservation of the natural stocks, this study describes the utilization of different biogenic substrates by this species in the intertidal zone. Sampling was carried out by hand at Ubatuba, State of São Paulo, Brazil. Crabs were captured among rocks or in association with three different biogenic substrates: *Phragmatopoma lapidosa*, *Sargassum cymosum* and *Schizoporella unicornis*. In the laboratory, the substrates were sorted and scanned for specimens of *M. nodifrons*, which were separated and measured at their maximum carapace width (CW), and classified as juvenile or adult specimens. Sex ratio and size distribution of crabs were analyzed for each of the substrate types. A total of 686 specimens of *M. nodifrons* were obtained during the sampling, ranging in size between 2.4 and 82.5 mm CW. Different mean sizes were recorded in the different substrates ( $P < 0.05$ ). The high prevalence of juveniles in the samples suggests that these microhabitats are fundamental for the juvenile development of *M. nodifrons*, as they provide refuge, protection and probably food for juveniles.

**Keywords:** intertidal, life cycle, recruitment, spatial dynamic, substrate, *Menippe nodifrons*.

## Importancia de los sustratos biogénicos para el cangrejo de piedra *Menippe nodifrons* Stimpson, 1859 (Brachyura: Eriphioidea)

**RESUMEN.** Para comprender mejor la ecología de las diferentes fases de crecimiento de los cangrejos de piedra, *Menippe nodifrons*, y proporcionar información para la conservación de sus poblaciones naturales, se describe la utilización de los diferentes sustratos biogénicos, para esta especie en la zona intermareal. El muestreo se efectuó en Ubatuba, Estado de São Paulo, Brasil. Los cangrejos fueron capturados entre las rocas o en asociación con tres diferentes sustratos biogénicos: *Phragmatopoma lapidosa*, *Sargassum cymosum* y *Schizoporella unicornis*. En el laboratorio, los sustratos se clasificaron y analizaron en busca de especímenes de *M. nodifrons*, que fueron separados y medidos en el ancho máximo del caparazón (CW), y se clasificaron como juveniles o adultos. La proporción de sexos y la distribución de tamaño de los cangrejos se analizó para cada uno de los tipos de sustrato. Se obtuvo un total de 686 ejemplares de *M. nodifrons*, que variaron entre 2,4 y 82,5 mm CW. Se registraron tamaños medios significativamente diferentes en los distintos sustratos ( $P < 0,05$ ). El alto número de juveniles en las muestras sugiere que estos microhábitats son fundamentales para el desarrollo juvenil de *M. nodifrons*, ya que proporcionan refugio, protección y, probablemente, alimentación para estos juveniles.

**Palabras clave:** intermareal, ciclo de vida, reclutamiento, dinámica espacial, sustrato, *Menippe nodifrons*.

## INTRODUCTION

The genus *Menippe* De Haan, 1833 contains seven described species. According to Ng *et al.* (2008) it belongs to the superfamily Eriphoidea Macleay, 1838, and family Menippidae Ortmann, 1893. Some species of this genus are used as a fishery resource; for instance, *Menippe mercenaria* (Say, 1818) and *Menippe adina* Williams & Felder, 1986, are exploited in the southeastern of the United States (Gerhart & Bert, 2008). Popularly known in Brazil as “Guaiá”, *Menippe nodifrons* Stimpson, 1959, has a wide geographical distribution in the western Atlantic, from Florida to southern Brazil, and with records for the eastern Atlantic, from Cabo Verde to the Angola coast (Melo, 1998). It occurs mainly on rocky shores, from the intertidal to 10 m deep, in rocky crevices or in association with biogenic substrates (Melo, 1998; Fransozo *et al.*, 2000; Alves *et al.*, 2013).

*Menippe nodifrons* is large in size compared to other brachyurans from rocky shores on the Brazilian coast, reaching 130 mm carapace width (Williams, 1984), and showing well developed muscles in the chelipeds (Melo, 1998). This crab is also used as a fishery resource along the Brazilian coast (Fransozo *et al.*, 2000). Thus, information on its life cycle, habitats and feeding is important for the maintenance of its natural stocks.

Several studies have been published on the biology of *M. nodifrons*: Scotto (1979) described the larval development; Fransozo *et al.* (1988) described the juvenile development under laboratory conditions; Oshiro (1999) studied the reproductive aspects of a population on the southeastern Brazilian coast; Fransozo *et al.* (2000) studied its population biology and the utilization of the polychaete *Phragmatopoma lapidosa*: (Kinberg, 1867) as its habitat; Madambashi *et al.* (2005) investigated its natural diet; Oliveira *et al.* (2005) studied its fecundity; Bertini *et al.* (2007) provided information on its relative growth and sexual maturity; and Santana *et al.* (2009), investigated its predatory behavior on mollusks. However, there is little information on the occupation of different substrates by this species.

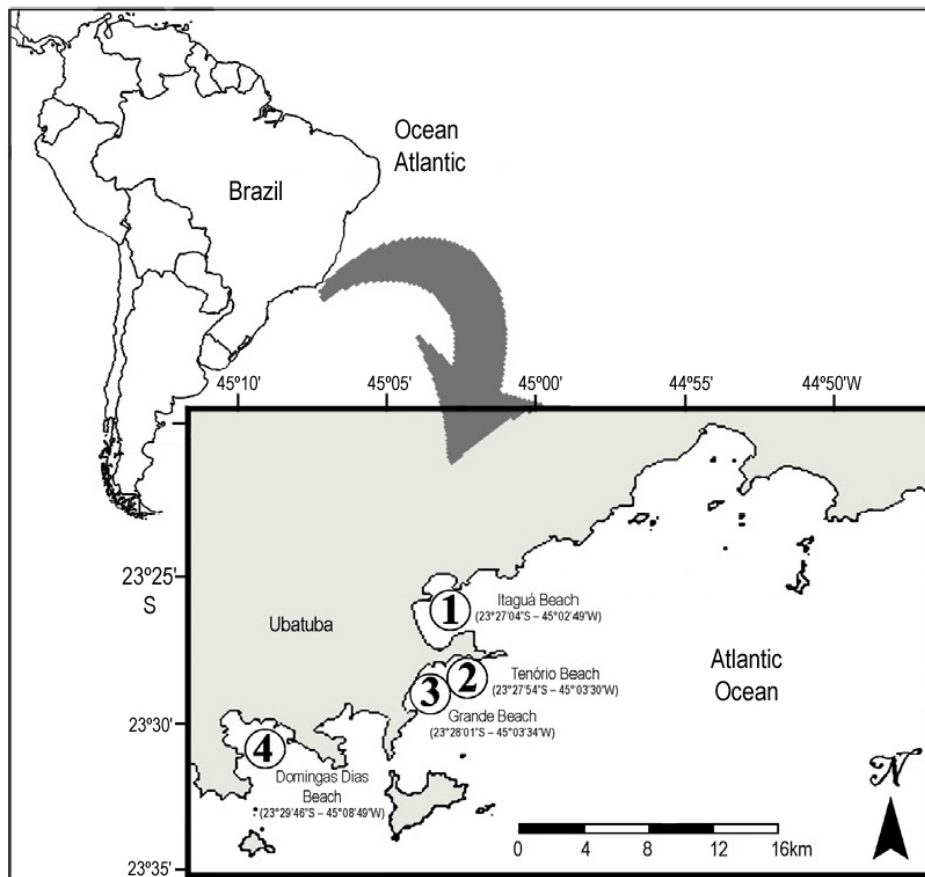
Studies have shown that many species of crabs can non-randomly occupy the available substrates and that the selection of a preferred substrate can be made by larvae (Moksnes, 2002), juveniles (Moksnes & Heck, 2006) or adults (Lindberg *et al.*, 1990). In addition, inter- or intraspecific interactions such as competition, cannibalism and predation may determine the emergence of non-random patterns of substrate use by decapod crustaceans (Smith & Herrnkind, 1992; Fernández *et al.*, 1993).

In summary, three factors interact within populations after the recruitment of young: selection of settlement habitat by competent larvae; habitat-specific post-settlement mortality; and active secondary dispersal among habitats by juveniles. The relative importance of these factors, likely affecting abundance and habitat distribution patterns, can vary depending on the ecological and life-history traits of the target species in a given environment (Pardo *et al.*, 2007). Consequently, determining why these specific patterns of substrate use emerge is a complex task, and it is usually achieved through experimental studies (*e.g.*, Hedvall *et al.*, 1998; Moksnes & Heck, 2006; Webley *et al.*, 2009). However, it is known that young, benthic, vagile individuals are often found in higher concentrations on substrates with higher structural complexity, which can provide refuge for them (Moksnes & Heck, 2006; Webley *et al.*, 2009).

Knowing that *M. nodifrons* normally occupies rocky substrates, yet it can also be found in biogenic substrates such as *P. lapidosa*. A few questions arose: is there a non-random pattern for the distribution of *M. nodifrons*? Are young individuals found in greater concentrations in biogenic substrates? Is the size of *M. nodifrons* important for the occupation of a certain substrate? This study described the utilization of different biogenic substrates on rocky shores by *M. nodifrons*, in order to evaluate the dynamics of the spatial occupation of this crab during its ontogenetic development. A better knowledge of habitat occupation by *M. nodifrons* could provide useful information for its monitoring and conservation.

## MATERIALS AND METHODS

All sampling was carried out in the intertidal zone of rocky shores of Ubatuba, northern coast of the State of São Paulo, Brazil (Fig. 1). Colonies of *Phragmatopoma lapidosa* (Polychaeta: Sabellariidae), were collected at Tenório Beach (23°27'54"S, 45°03'30"W). Algae banks of *Sargassum cymosum* C. Agardh, 1820 (Phaeophyceae: Fucales), were sampled at Grande Beach (23°28'01"S, 45°03'34"W), and Domingas Dias Beach (23°29'46"S, 45°08'49"W). Colonies of *Schizoporella unicornis* (Johnston, 1874) (Bryozoa, Gymnolaemata) were sampled at Itaguá Beach (23°27'04"S, 45°02'49"W). At the collection site, the crabs were removed from the biogenic substrates by hand. The crabs that were not associated with biogenic substrates were sampled on or under rocks and in rock crevices by hand at Grande Beach (23°27'54"S, 45°03'30"W). All sampling was carried out bi-monthly, during two years, in low-tide periods, with a catch per unit effort of two persons during 2 h each



**Figure 1.** Map of Brazil, northeastern coast of São Paulo, detail of Ubatuba region. 1: Itaguá Beach, 2: Tenório Beach, 3: Grande Beach, 4: Domingas Días Beach.

month, totaling 4 h of catch effort per month and per substrate. The biogenic substrates used in this study were chosen based on previous studies, such as those of Fransozo *et al.* (2000); Barros-Alves (2009) and Alves *et al.* 2013.

In the laboratory, the maximum carapace width (CW) of crabs was measured with a vernier caliper (0.1 mm). Crab sex was determined by observing the external morphology of the abdomen (in males the abdomen is triangular, and in females it is oval), and number of pleopods (males with 2 pairs and females with 4 pairs of pleopods).

The juveniles for which we could find no sign of sex differentiation were classified as undetermined sex (UN). Determination of the juvenile and adult conditions was based on the size at sexual maturity of *M. nodifrons* described by Bertini *et al.* (2007), for the same region. Thus, female crabs smaller than 29.7 mm CW were considered as juvenile females, and male crabs smaller than 31.6 mm CW were considered as juvenile males.

For each biogenic substrate type, the distribution of proportions by size class and sex ratio was determined, and tested by  $\chi^2$  ( $P < 0.05$ ). The mean size of specimens on each substrate type was compared by means of the Kruskal-Wallis test (Zar, 2010). The tests were chosen only after the premises of normality and homoscedasticity were satisfied (Zar, 2010).

A correspondence analysis (CA) was used to analyze the relations: crab size vs substrate type, and crab demographic category vs substrate type (Lepš & Šmilauer, 2003). In this analysis, we used the proportion values, considering each substrate type as an independent set of data, in order to minimize the influence of sampling design.

## RESULTS

We obtained 686 specimens of *M. nodifrons*: 134 associated with *P. lapidosa*, 285 with *S. cymosum*, 80 with *S. unicornis*, and 187 in rock crevices or neighboring areas. There were 306 juvenile males, 25

adult males, 244 juvenile females, 33 adult females, one ovigerous female, and 77 undetermined individuals (for details, see Table 1).

Among the different substrates, the crabs' size ranged from 2.4 to 82.5 mm CW (mean =  $13.1 \pm 12.5$  mm), recorded for *S. cymosum* and rocks, respectively (Table 1). The smallest mean size was also recorded for *S. cymosum* (mean =  $7.2 \pm 3.0$  mm) (Table 1). The mean size of males and females did not differ significantly ( $U = 44,279.00$ ;  $P = 0.380$ ). The mean size of individuals of *M. nodifrons* from rocks showed significant differences with respect to other substrates ( $P < 0.001$ ) (Table 2).

The crabs were distributed in 11 size classes with 8 mm amplitude. The size-frequency distribution of crabs was unimodal (Fig. 2). In *P. lapidosa* and *S. unicornis*, individuals reached up to size class 26-34 mm CW (Figs. 2a-2c); in *S. cymosum* individuals reached up to size class 18-26 mm CW (Fig. 2b); and in the rocks, crabs from all size classes were found, with the highest frequency in the 10-18 mm CW size class (Fig. 2d).

A deviation from the expected 1:1 sex ratio was observed only for individuals associated with algae (*S. cymosum*), in favor of males (1:0.64;  $\chi^2 = 11163.00$ ;  $P = 0.001$ ) (Table 3).

The correspondence analysis (CA) indicated a major correspondence between individuals of size classes 2-10 and 10-18 with the substrates *S. cymosum*, *S. unicornis* and *P. lapidosa*. Additionally, specimens of size classes 18-26 to 82-90 were associated with rocks. Although *P. lapidosa* was closer to *S. cymosum* and *S. unicornis* than to rocks, when one observe the "x" axis, the *P. lapidosa* group is the most distant from the other groups (see "y" axis) (Fig. 3). The CA also revealed a higher correspondence of the biogenic substrates with the immature crabs; and of rocks with adult crabs of *M. nodifrons* (Fig. 4).

## DISCUSSION

The utilization of certain habitats by marine organisms is commonly mentioned in the literature, showing its biological adaptive advantages. For instance, the

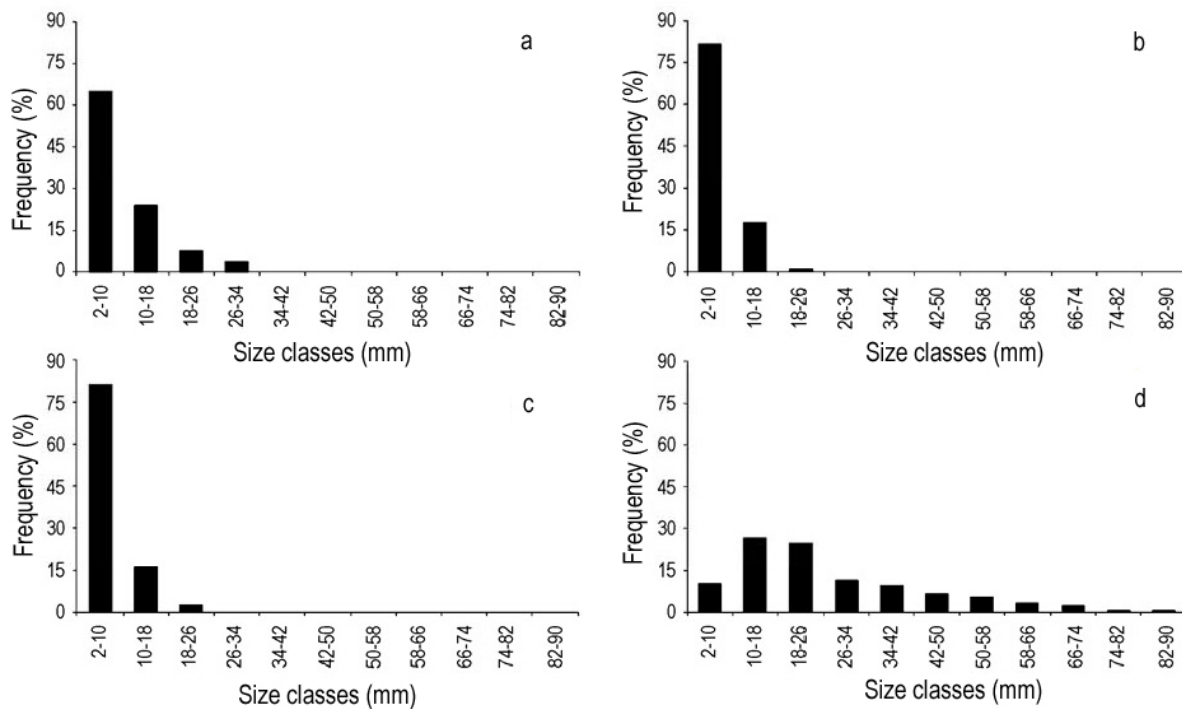
**Table 1.** Descriptive statistics of the stone crab *Menippe nodifrons* in different substrates. Number of individuals (n), minimum (Min.) and maximum sizes (Max.), and mean size (x) by demographic category and substrate. CW: carapace width, SD: standard deviation, UN: undetermined, JM: juvenile male, AM: adult male, JF: juvenile female, AF: adult female, OF: ovigerous females.

Substrate	Demographic category	n	CW (mm)		
			Min.	Max.	x $\pm$ SD
<i>Sargassum cymosum</i>	UN	52	2.6	9.1	$5.1 \pm 1.6$
	JM	142	2.4	15.4	$7.4 \pm 3.0$
	JF	91	3.2	23.5	$8.0 \pm 3.0$
	Total	285	2.4	23.5	$7.2 \pm 3.0$
<i>Schizoporella unicornis</i>	UN	2	3.6	4.0	$3.8 \pm 0.3$
	JM	33	2.5	24.8	$8.9 \pm 5.3$
	JF	45	3.1	15.2	$7.0 \pm 2.6$
	Total	80	2.5	24.8	$7.7 \pm 4.1$
<i>Phragmatopoma lapidosa</i>	UN	23	2.6	4.7	$3.7 \pm 0.6$
	JM	51	5.0	28.9	$11.7 \pm 5.8$
	AM	1			31.7
	JF	59	3.6	28.8	$10.4 \pm 5.9$
	Total	134	2.6	31.7	$9.9 \pm 6.3$
Rocks	JM	80	6.2	28.9	$16.9 \pm 6.5$
	AM	24	30.8	67.1	$40.1 \pm 8.2$
	JF	49	8.4	31.1	$19.3 \pm 6.4$
	AF	33	32.0	82.5	$51.8 \pm 12.0$
	OF	1			70.1
	Total	187	6.2	82.5	$26.9 \pm 16.2$

**Table 2.** Comparison ( $P$  values) of the mean size of *Menippe nodifrons* captured in different substrates (Kruskal-Wallis,  $P < 0.05$ ).

	<i>Phragmatopom lapidosa</i>	<i>Sargassum cymosum</i>	<i>Schizoporella unicornis</i>	Rocks
<i>Phragmatopoma lapidosa</i>	-	0.004*	0.189	< 0.001*
<i>Sargassum cymosum</i>	0.004*	-	1.000	< 0.001*
<i>Schizoporella unicornis</i>	0.189	1.000	-	< 0.001*
Rocks	< 0.001*	< 0.001*	< 0.001*	-

\*Significant values

**Figure 2.** Size-frequency distribution of *Menippe nodifrons* by type of substrate. a) *Phragmatopoma lapidosa*, b) *Sargassum cymosum*, c) *Schizoporella unicornis*, d) rocks.

provision of refuge against adverse environmental conditions (Abele, 1974), predators (Wieters *et al.*, 2009), and the availability of food (Amarasekare, 2003). Jones *et al.* (1994) and Chintiroglou *et al.* (2004) termed the sessile fauna of rocky shores “ecosystem engineers”, capable of increasing the heterogeneity and tridimensionality of the environment, providing new microhabitats.

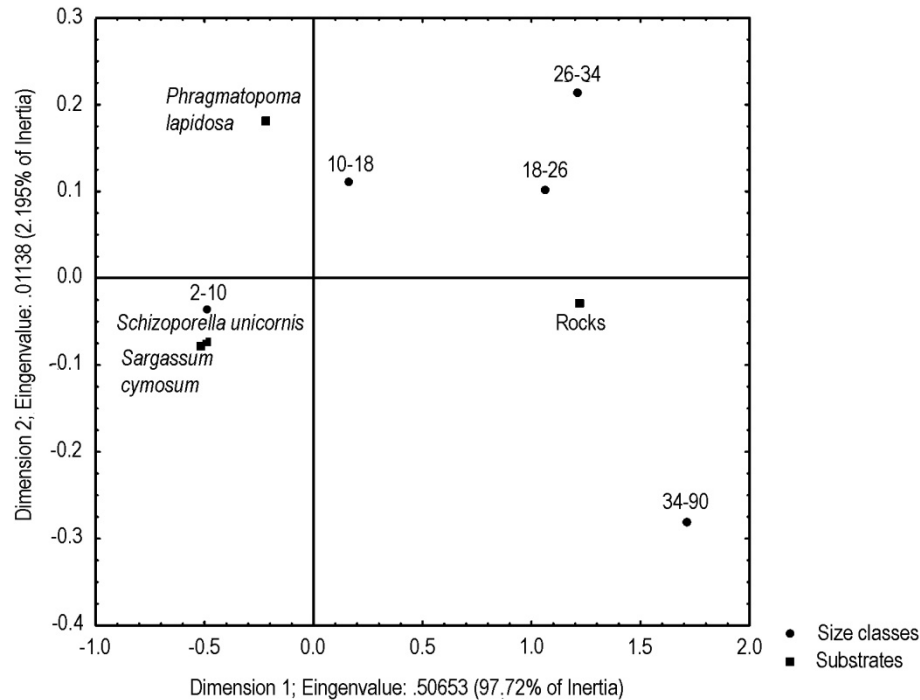
The biogenic substrates evaluated here are sessile species and generate favorable internal spaces for exploitation by vagile organisms, which search for the benefits described above. Thus, the high proportion of juveniles of *M. nodifrons* in these biogenic substrates

might be the consequence, mainly of the availability of refuge sites at the millimeter scale, as well as food availability (*e.g.*, other small-sized invertebrates and algae), and to minimize competition with larger crabs for available resources. Furthermore, the smaller proportion of juveniles of *M. nodifrons* recorded on rocks may be a consequence of a lower recruitment rate in that habitat. This can be caused by tactile or chemical identification of a “favorite” substrate, or also by a higher mortality rate through predation of young *M. nodifrons* on rocks, since this is one of the factors responsible for the occurrence of non-random distribution patterns in young benthic organisms

**Table 3.** Sex ratios of *Menippe nodifrons* captured in different substrates.

	Males	Females	M:F	$\chi^2$	P
<i>Phragmatopoma lapidosa</i>	52	59	1:1.13	0.441	0.569
<i>Sargassum cymosum</i>	142	91	1:0.64	11163	0.001*
<i>Schizoporella unicornis</i>	33	45	1:1.36	1846	0.213
Rocks	105	83	1:0.79	2574	0.126

\* Significant values

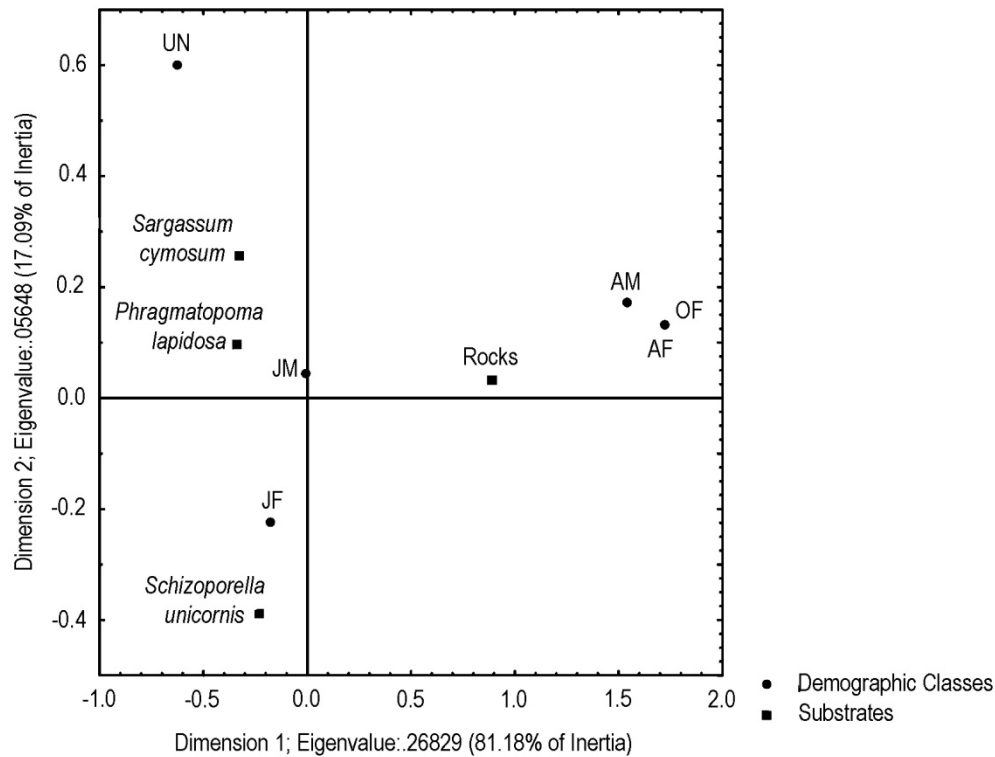
**Figure 3.** Correspondence analysis (CA) between the numbers of *Menippe nodifrons* crabs caught by size class (mm) (2-10, 10-18, 18-26, 26-34, 34-90) and type of substrate.

(Smith & Herrnkind, 1992; Fernández *et al.*, 1993). Rocky habitats have lower structural complexity compared to biogenic substrates, which may lead to a higher mortality rate caused by predation in those environments (Dittel *et al.*, 1996; Moksnes *et al.*, 1998).

In addition to the low proportion of young crabs, a few individuals of the first size class (2-10 mm) were also obtained on rocks. There are probably some refuges on rock substrates also, but in a lower proportion, since these small crabs represented only about 10% of the total individuals found there. This may be associated with the existence of a larger number of refuges for large crabs and fewer refuges of millimeter scale for small crabs. Another hypothesis is that in rocks, the greater occurrence of adult

individuals may increase competition and cannibalism. The smaller individuals are threatened in these intraspecific relationships, given that cannibalism is considered one of the main contributors to the mortality of juvenile crabs in high-density locations (Fernández *et al.*, 1993; Moksnes *et al.*, 1998).

The results of the correspondence analysis and the size comparison by substrate type indicated the predominance of juvenile crabs of *M. nodifrons* in colonies of *S. unicornis*, *P. lapidosa* and algae banks of *S. cymosum*. Those substrates are important microhabitats for the development of immature individuals. In contrast, the predominance of adult individuals only on rocks, suggests that individuals with a carapace width of 18 mm or more disperse actively among the substrates, most likely due to a



**Figure 4.** Correspondence analysis (CA) between the number of crabs caught by demographic category and type of substrate. UN: undetermined, JM: juvenile males, AM: adult males, JF: juvenile females, AF: adult females, OF: ovigerous females.

lower risk of predation in association with a larger body size and greater defensive ability (Smith & Herrnkind, 1992).

The utilization of different microhabitats by individuals in different phases of the life cycle has been reported for many species (Werner & Gilliam, 1984; Olson, 1996; Hjelm *et al.*, 2000; Moksnes & Heck, 2006). Among crustaceans, habitat partitioning during the course of ontogeny is common (*e.g.*, Beck, 1995; Flores & Negreiros-Fransozo, 1999; Micheletti-Flores & Negreiros-Fransozo, 1999; Díaz *et al.*, 2001; Pardo *et al.*, 2007). This partitioning suggests a selective pressure for space, modulating the adaptations for shelter and refuge against predation, which are more critical in the initial benthic life phase (MacArthur & Levins, 1967; Santelices *et al.*, 1982; Edgar, 1983; Schoener, 1983; Corona *et al.*, 2000; Guisande *et al.*, 2003).

The sex ratio in favor of males, as observed in this study, among the alga *S. cymosum*, is common in many populations of marine crustaceans. This may be a consequence of the limitations imposed by several factors, such as mortality, behavior and differential

migration between the sexes (Wenner, 1972). It could be hypothesized that there is a natural deviation toward males in this species, since *S. cymosum* was the substrate with the highest rate of recruitment for *M. nodifrons*, in view of the relatively large number of specimens of undetermined sex and small mean size captured there.

Knowledge of the distribution and life cycle of species exploited as fishery resources is fundamental for the sustainability of natural populations. This study provided new information about *M. nodifrons*, from which a non-random pattern of distribution can be suggested, where body size seems to be the most important factor influencing the distribution of individuals among the substrates. However, future studies are needed, especially experimental ones, to investigate whether the observed pattern is a consequence of a preference of smaller individuals for a specific habitat, or also whether a greater availability of refuges in certain habitats ensures a higher survival rate. We reinforce the need for conservation of these natural substrates, not only for conservation itself but also for their visitors and inhabitants, in order to maintain the natural stocks.

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## REFERENCES

- Abele, L.G. 1974. Species diversity of decapod crustaceans in marine habitats. *Ecology*, 55: 156-161.
- Alves, D.F.R., S.P. Barros-Alves, D.J.M. Lima, V.J. Cobo & M.L. Negreiros-Fransozo. 2013. Brachyuran and anomuran crabs associated with *Schizoporella unicornis* (Ectoprocta, Cheilostomata) from southeastern Brazil. *An. Acad. Bras. Ciênc.*, 85(1): 245-256.
- Amarasekare, P. 2003. Diversity-stability relationships in multitrophic systems: an empirical exploration. *J. Anim. Ecol.*, 72: 713-724.
- Barros-Alves, S.P. 2009. Biodiversidade de caranguejos braquiuros (Crustacea, Decapoda) associada a bancos da alga *Sargassum cymosum* (C. Agardh, 1820) na região de Ubatuba, litoral norte paulista. Dissertação de Mestrado, Universidad Estadual Paulista, Sao Paulo, 87 pp.
- Beck, M.W. 1995. Size-specific shelter limitation in stone crabs: a test of demographic bottleneck hypothesis. *Ecology*, 76: 968-987.
- Bertini, G., A.A. Braga, A. Fransozo, M.O.D.A Corrêa & F.A.M. Freire. 2007. Relative growth and sexual maturity of the stone crab *Menippe nodifrons* Stimpson, 1859 (Brachyura, Xanthoidea) in southeastern Brazil. *Braz. Arch. Biol. Techn.*, 50(2): 259-267.
- Chintiroglou, C.C., P. Damianidis, C. Antoniadou, M. Lantzouni & D. Vafidis. 2004. Macrofauna biodiversity of mussel bed assemblages in Thermaikos Gulf (northern Aegean Sea). *Helgol. Mar. Res.*, 58: 62-70.
- Corona, A., L.A. Soto, & A.J. Sánchez. 2000. Epibenthic amphipod abundance and predation efficiency of the pink shrimp *Farfantepenaeus duorarum* (Burkenroad, 1939) in habitats with different physical complexity in a tropical estuarine system. *J. Exp. Mar. Biol. Ecol.*, 253: 33-48.
- Díaz, D., M. Marí, P. Abelló & M. Demestre. 2001. Settlement and juvenile habitat of the European spiny lobster *Palinurus elephas* (Crustacea: Decapoda: Palinuridae) in the western Mediterranean Sea. *Sci. Mar.*, 65(4): 347-356.
- Dittel, A., C.E. Epifanio & C. Natunewicz. 1996. Predation on mud crab megalopae, *Panopeus herbstii* H. Milne Edwards: effect of habitat complexity, predator species and postlarval densities. *J. Exp. Mar. Biol. Ecol.*, 198: 191-202.
- Edgar, G.J. 1983. The ecology of south-east Tasmanian phytal animal communities. IV. Factors advecting the distribution of amphipod amphipods among algae. *J. Exp. Mar. Biol. Ecol.*, 70: 205-225.
- Fernández, M., O. Iribarne & D. Armstrong. 1993. Habitat selection by young-of-the-year dungeness crab *Cancer magister* and predation risk in intertidal habitats. *Mar. Ecol. Prog. Ser.*, 92: 171-177.
- Flores, A.A.V. & M.L. Negreiros-Fransozo. 1999. On the population biology of the mottled shore crab *Pachygrapsus transversus* (Gibbes, 1850) (Brachyura, Grapsidae) in a subtropical area. *Bull. Mar. Sci.*, 65(1): 59-73.
- Fransozo, A., M.L. Negreiros-Fransozo & C.M. Hiyodo. 1988. Développement juvénile de *Menippe nodifrons* Stimpson, 1859 (Crustacea, Decapoda, Xanthidae) au laboratoire. *Rev. Hydrobiol. Trop.*, 21: 297-308.
- Fransozo, A., G. Bertini & M.O.D. Corrêa. 2000. Population biology and habitat utilization of the stone crab *Menippe nodifrons* Stimpson, 1859 (Decapoda, Xanthidae) in Ubatuba region, Brazil. In: J.C. Vaupel-Klein J.C. & F.R. Schram (eds.). *The biodiversity crisis and Crustacea. Crustacean Issues*, A.A. Balkema/Rotterdam, pp. 275-281.
- Gerhart, S.D. & T.M. Bert. 2008. Life-history aspects of stone crabs (Genus *Menippe*): size at maturity, growth, and age. *J. Crust. Biol.*, 28(2): 252-261.
- Guisande, C., F. Bartumeus, M. Ventura & J. Catalan. 2003. Role of food partitioning in structuring the zooplankton community in mountain lakes. *Oecologia*, 136: 627-634.
- Hedvall, O., P.O. Moksnes & L. Pihl. 1998. Active habitat selection by megalopae and juvenile shore crabs *Carcinus maenas*: a laboratory study in an annular flume. *Hydrobiologia*, 375/376: 89-100.
- Hjelm, J., L. Persson & B. Christensen. 2000. Growth, morphological variation and ontogenetic niche shifts in perch (*Perca fluviatilis*) in relation to resource availability. *Oecologia*, 122: 190-199.
- Jones, C.G., J.H. Lawton & M. Shachak. 1994. Organisms as ecosystem engineers. *Oikos*, 69: 373-386.
- Lepš, J. & P. Šmilauer. 2003. Multivariate analysis of ecological data using CANOCO. Cambridge University Press, Cambridge, 269 pp.



- Lindberg, W.J., T.K. Frazer & G.R. Stanton. 1990. Population effects of refuge dispersion for adult stone crabs (Xanthidae, *Menippe*). *Mar. Ecol. Prog. Ser.*, 66: 239-249.
- MacArthur, R.H. & R. Levins. 1967. The limiting similarity, convergence, and divergence of coexisting species. *Am. Nat.*, 101: 377-385.
- Madambashi, A.M., R.A. Christofolletti & M.A.A. Pinheiro. 2005. Natural diet of the crab *Menippe nodifrons* Stimpson, 1859 (Brachyura, Menippidae) in Paranapuã Beach, São Vicente (SP), Brasil. *Nauplius*, 13(1): 77-82.
- Melo, G.A.S. 1998. Malacostraca-Eucarida. Brachyura. Oxyrhyncha and Brachyrhyncha. In: P.S. Young (ed.). *Catalogue of Crustacea of Brazil*. Museu Nacional (Série Livros N°6) Rio de Janeiro, pp. 455-515.
- Micheletti-Flores, C.V. & M.L. Negreiros-Fransozo. 1999. Porcellanid crabs (Crustacea, Decapoda) inhabiting sand reefs built by *Phragmatopoma lapidosa* (Polychaeta Sabellaridae) at Paranapuã Beach, São Vicente, SP, Brazil. *Rev. Bras. Biol.*, 59(1): 63-73.
- Moksnes, P.O., L. Pihl & J. Van Montfrans. 1998. Predation on postlarvae and juveniles of the shore crab *Carcinus maenas*: importance of shelter, size and cannibalism. *Mar. Ecol. Prog. Ser.*, 166: 211-225.
- Moksnes, P.O. 2002. The relative importance of habitat-specific settlement, predation and juvenile dispersal for distribution and abundance of young juvenile shore crabs *Carcinus maenas* L. *J. Exp. Mar. Biol. Ecol.*, 271: 41-73.
- Moksnes, P.O. & K.L. Heck. 2006. Relative importance of habitat selection and predation for the distribution of blue crab megalopae and young juveniles. *Mar. Ecol. Prog. Ser.*, 308: 165-181.
- Ng, P.K.L., D. Guinot & P.J.F. Davie. 2008. Systema brachyurorum: Part I. An annotated checklist of extant brachyuran crabs of the world. *Raffles Bull. Zool.*, 17: 1-208.
- Oliveira, D.A.F., G.Y. Hattori & M.A.A. Pinheiro. 2005. Fecundity of *Menippe nodifrons* Stimpson, 1859 (Brachyura, Menippidae) in the Parnapuã Beach, SP, Brazil. *Nauplius*, 13(2): 167-174.
- Olson, M.H. 1996. Ontogenetic niche shifts in largemouth bass: variability and consequences for first-year growth. *Ecology*, 77: 179-190.
- Oshiro, L.M.Y. 1999. Aspectos reprodutivos do caranguejo guaiá, *Menippe nodifrons* Stimpson (Crustacea, Decapoda, Xanthidae) da Baía de Sepetiba, Rio de Janeiro, Brasil. *Rev. Bras. Zool.*, 16(3): 827-834.
- Pardo, L.M., A.T. Palma, C. Prieto, P. Sepulveda, I. Valdivia & P. Ojeda. 2007. Processes regulating early post-settlement habitat use in a subtidal assemblage of brachyuran decapods. *J. Exp. Mar. Biol. Ecol.*, 344: 10-22.
- Santana, G.X., A.A.F. Filho, L.E.A. Bezerra & H. Matthews-Cascon. 2009. Comportamento predatório *ex-situ* do caranguejo *Menippe nodifrons* Stimpson, 1859 (Decapoda, Brachyura) sobre moluscos gastrópodes. *PanamJAS*, 4(3): 326-338.
- Santelices, B., J.C. Castilla, P. Schmiede & J. Cancino. 1982. Comparative ecology of *Lessonia nigrescens* and *Durvillaea antarctica* (Phaeophyta) in Central Chile. *Mar. Biol.*, 59: 119-132.
- Schoener, T.W. 1983. Field experiments on interspecific competition. *Am. Nat.*, 122: 240-285.
- Scotto, L.E. 1979. Larval development of the Cuban stone crab, *Menippe nodifrons* (Brachyura, Xanthidae), under laboratory conditions with notes on the status of the Family Menippidae. *Fish. Bull.*, 77(2): 359-386.
- Smith, K.N. & W.F. Herrnkind. 1992. Predation on early juvenile spiny lobster *Panulirus argus* (Latreille): influence of size and shelter. *J. Exp. Biol. Ecol.*, 157: 3-18.
- Webley, J.A.C., R.M. Connolly & R.A. Young. 2009. Habitat selectivity of megalopae and juvenile mud crabs (*Scylla serrata*): implications for recruitment mechanism. *Mar. Biol.*, 166: 891-899.
- Wenner, A.M. 1972. Sex ratio as a function of size in marine Crustacea. *Am. Nat.*, 106: 321-350.
- Werner, E.E. & J.F. Gilliam. 1984. The ontogenetic niche and species interactions in size-structured populations. *Annu. Rev. Ecol. Syst.*, 15: 393-425.
- Wieters, E.A., E. Salles, S.M. Januario & S.A. Navarrete. 2009. Refuge utilization and preferences between competing intertidal crab species. *J. Exp. Mar. Biol. Ecol.*, 374: 37-44.
- Williams, A.B. 1984. Shrimps, lobsters, and crabs of the Atlantic coast of the Eastern United States, Maine to Florida. Smithsonian Institution Press, Washington, XVIII+ 550 pp.
- Zar, J.H. 2010. Biostatistical analysis. Prentice-Hall, Upper Saddle River, 944 pp.

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