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POPULATION STRUCTURE OF THE FIDDLER CRAB *UCA LEPTODACTYLA RATHBUN*, 1898 (BRACHYURA: OCYPODIDAE) IN A TROPICAL MANGROVE OF NORTHEAST BRAZIL

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Key words: ***Uca leptodactyla*, population structure, sex ratio, handedness, tropical mangrove.**

ABSTRACT

The population structure of the fiddler crab *U. leptodactyla* Rathbun, 1898 was investigated during a one-year period in a tropical mangrove forest in Northeast Brazil (3°43'S, 38°32'W). The study specifically addressed factors such as absolute density, sex ratio, population structure and handedness. Eight transects were delimited in a mangrove area of Pacoti River. Monthly, two transects were randomly selected and visited. On each transect, ten 0.25 m^2 squares were sampled during low tide periods from September 2003 to August 2004. A total of 1042 crabs was captured, of which 522 were male (50.14%) and 520 were female (49.75%). Only 4 ovigerous females were obtained during the study. There was not significant difference between the mean size of males and females. The overall size frequency distribution was unimodal, with the females being most abundant in the largest size classes, while the males in the smallest. The overall sex ratio (1:0.99) did not differ statistically from 1:1 proportion. The ratio between right-handed and left-handed males was 1:0.95 and did not differ significantly of the 1:1. The observed average density was 17 individuals/m^2, being widely found on open fields. The unimodal distribution, with juvenile being found year-round, suggests a stable population, with breeding taking place throughout the year, although the low number of ovigerous females collected didn't represent the peak of reproductive activity of *U. leptodactyla*.

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INTRODUCTION

Fiddler crabs of Genus *Uca* are a well characterized and diversified group of intertidal crabs inhabiting tropical and subtropical estuaries and mangroves of the Old and New World (Crane, 1975; Christy & Salmon, 1984).They are characterized by a great sexual dimorphism in chelae size. While females have small isomorphic claws, male fiddler crabs develop on their chelae into a major claw which is used in ritualized aggressive interactions and in mate attraction (Crane, 1975).

Recently, the number of studies on *Uca* populations has been increasing, mainly for the

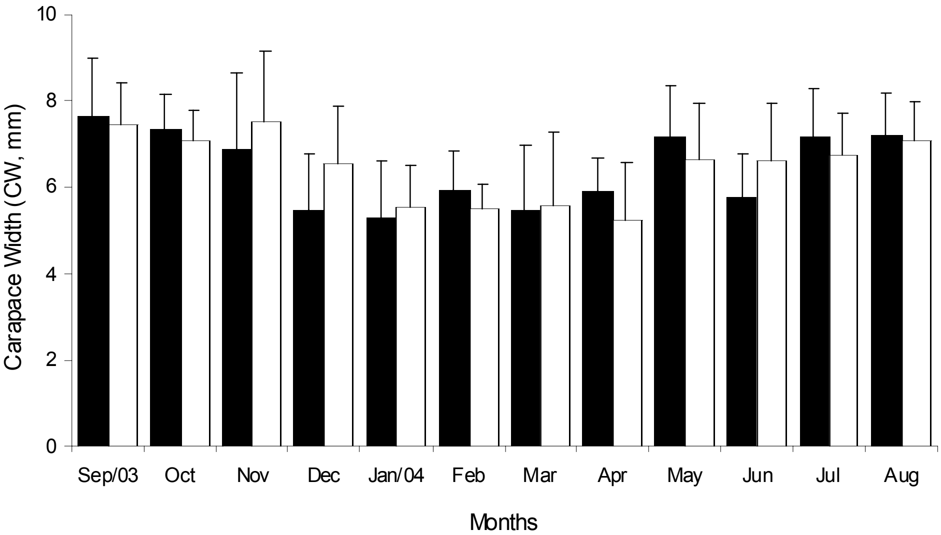

Figure 1.
Uca leptodactyla Rathbun, 1898. Medium size of individuals collected at Pacoti River mangrove, Northeast Brazil, between September 2003 and August 2004. Black bars: males; white bars: females (ovigerous and non-ovigerous).

temperate and subtropical species. This population information has been evaluated by several methods including density, size frequency distributions, spatial dispersion, sex ratio, handedness, among others (Thurman, 1985; Spivak et al., 1991; Yamaguchi, 2001). Despite the fact that fiddler crabs are abundant in the tropical areas, little attention has been directed to understanding factors regarding the population dynamics of tropical species (Litulo, 2005a, b).

Nowadays, approximately 97 species of *Uca* have been identified and described (reviewed by Rosenberg, 2001). At least 30 species are endemic to the Pacific coasts of Central and northern South America. A considerable number of species are also found throughout the Indo-West Pacific region, but only one species is found in the eastern Atlantic (Levinton *et al*., 1996).

In the tropical mangroves of Northeast Brazil, eight species of Uca have been recorded: *U. burgersi* Holthuis, 1967; *U. cumulanta* Crane, 1943; *U. leptodactyla* Rathbun, 1898; *U. maracoani* (Latreille, 1802-1803); *U. mordax* (Smith, 1870); *U. rapax* (Smith, 1870); *U. thayeri* Rathbun, 1900 and *U. vocator* (Herbst, 1804) (Melo, 1996).

Uca leptodactyla is a common resident of mangrove forests along the West Atlantic coast, from the south coast of United States (Florida and Gulf of Mexico) to Southeast Brazil (Crane, 1975; Melo, 1996). This is the smallest fiddler crab living in Atlantic, inhabiting sandy environments with seawater influence, usually flooded by high tide (Cardoso & Negreiros-Fransozo, 2004). Aspects of its physiology (Vernberg & Tashian, 1959); social behavior (Crane, 1975); allometric growth (Cardoso & Negreiros-Fransozo, 2004; Masunari & Swiech-Ayoub, 2003) and ecological aspects (Aciole *et al*., 2000) have been addressed in the last years. However, no previous studies have been published on the population biology of *U. leptodactyla*.

This contribution aimed for elucidate some aspects of population structure of *U. leptodactyla* as density, size structure, sex ratio and handedness in a tropical mangrove from Northeast Brazil.

MATERIALS AND METHODS

Site description

The fieldwork took place at Pacoti River mangrove, Ceará State, Northeast Brazil (3º43'S, 38º32'W). The climate of this region is tropical, with a maximum temperature of 34 ºC and minimum of 22 ºC. The rain season is concentrated in a fewer months of the year (average rainfall of 600 to 1000 mm). Tides

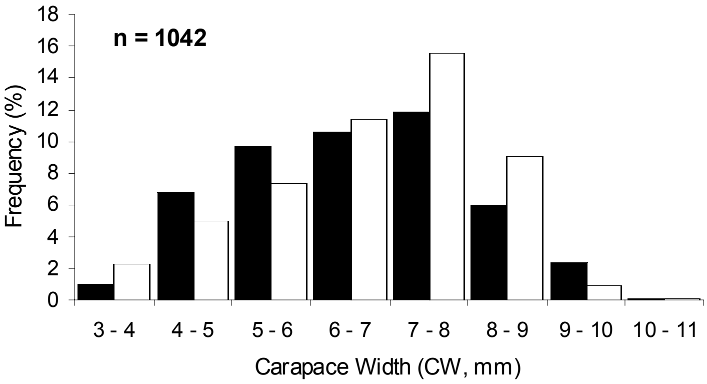

Figure 2.
Uca leptodactyla Rathbun, overall size frequency distribution of Uca leptodactyla collected at Pacoti River mangrove, Northeast Brazil, from September 2003 to August 2004. Black bars: males; white bars: females (ovigerous and non-ovigerous).

are semidiurnal, with maximum tidal amplitude of about 3.1 m and minimum of 0.9 m (Freire, 1989). The mangrove vegetation of this area is dominated by *Avicennia schaueriana* Stapf and Leechman, *Avicennia germinans* Linnaeus, *Laguncularia racemosa* Gaerth and *Rhizophora mangle* Linnaeus (Miranda *et al*., 1988).

Sampling methods

Eight transects, were delimited in the mangrove area of the Pacoti River, comprising an area of 1.2 Km^2. Monthly, two transects were selected at random and visited. On each transect, ten 50 x 50 cm (0.25 m^2) squares were sampled on a monthly basis during spring low tide periods from September 2003 to August 2004. The squares were located ran from the edge of mangrove vegetation to mud flats in the river. The squares were excavated with a corer to a depth of 30 cm and all fiddler crabs presented in the squares were bagged, labelled and preserved in 70% ethanol until further analysis.

In the laboratory, specimens were identified, sexed, checked for the presence of eggs on female pleopds and which side the males have the enlarged cheliped was anotated. The carapace width (CW) was measured using a vernier caliper (± 0.01 mm accuracy). The number of crabs on each transect was anotated.

The population size structure was analyzed as a function of the size frequency distribution of all individuals collected during the study period. Specimens were grouped in 1 mm size class intervals from 3 to 11 mm CW.

The chi-square test (x^2) and the Fisher test (z) were used to evaluate the sex ratio and the enlarged cheliped ratio. The overall size frequency distribution were tested for normality using Kolmogorov-Smirnov (KS) test (Zar, 1984). The mean size of males and females was compared using the Student *t*-test.

RESULTS

A total of 1042 individuals was collected during the study period, of which 522 were males (50.14%) and 520 (49.75%) were non-ovigerous females. Only 4 ovigerous females were sampled (Table 1). Males ranged from 3.5 to 9 mm CW (mean ± SD 6.58 ± 1.5 mm), non-ovigerous females from 3.5 to 10 mm CW (mean ± SD 6.64 ± 1.43 mm) and ovigerous females from 7 to 10 mm CW (mean ± SD 7.67 ± 1.04 mm). The crab size did not differ significantly as CW size between males and non-ovigerous females ($t = 0.62$, $p > 0.05$), males and ovigerous females ($t = 2.18$; $p > 0.05$) and between ovigerous and non-ovigerous females ($t = 2.11$; $p > 0.05$). Figure 1 shows the medium size for all sampled crabs. The ovigerous females were not included, because only one individual was collected in November (7 mm CW) and 3 in February (mean ± SD 7.9 ± 1.15 mm). Due to the low number of ovigerous females collected, the breeding season could not be determined.

Figure 2 shows the size frequency distribution for all sampled crabs. The size distribution was unimodal and differed from normality to males (KS = 0.06730, $p < 0.0001$) and females (KS = 0.08665, $p < 0.0001$).

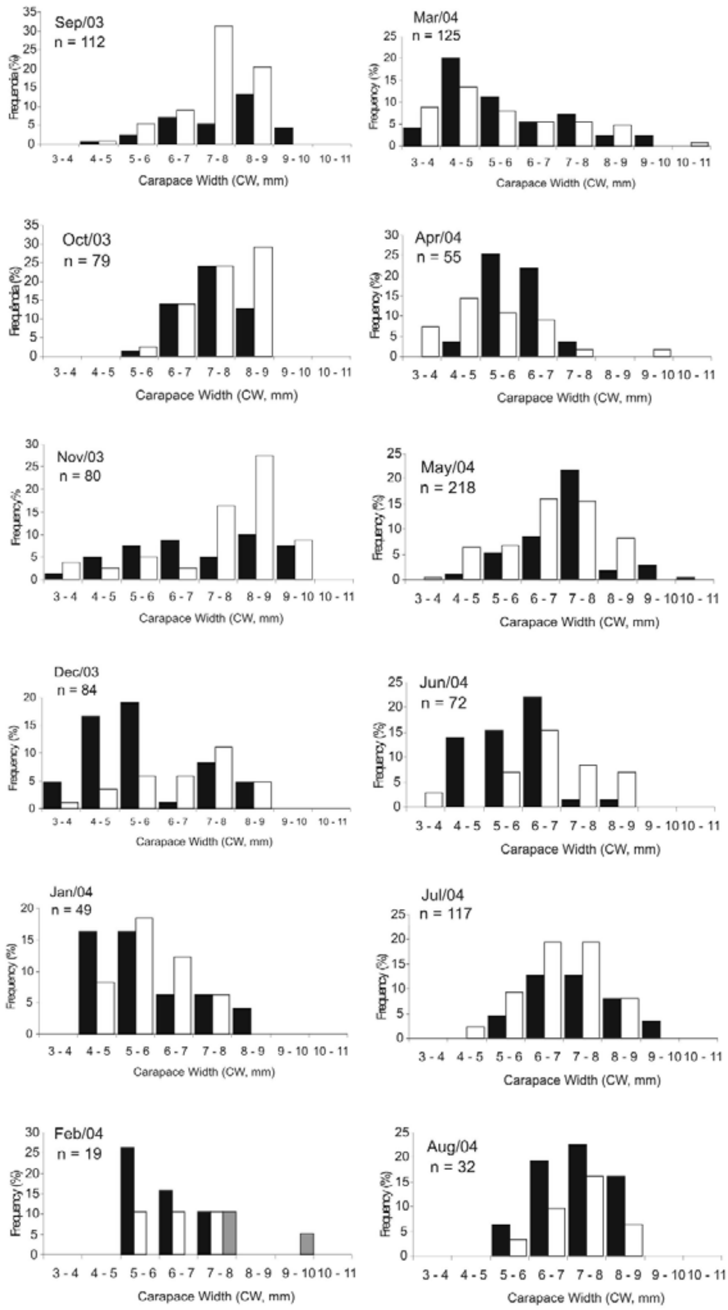

Figure 3.
Uca leptodactyla Rathbun, 1898. Monthly size frequency distributions of crabs collected at Pacoti River mangrove, Northeast Brazil. Black bars: males; white bars: non-ovigerous females and grey bars: ovigerous females.

Table 1.
Uca leptodactyla Rathbun, 1898 - total number, handedness and sex ratio of individuals collected monthly at Pacoti River mangrove, Northeast Brazil.

Month	Males					Females	Ovigerous females	Ovigerous and non-ovirgerous females	Males and females		Sexual ratio
	Right	*Left*	*Ratio*	*Total*	*%*	*Total*	*Total*	*%*	*Total*	*%*	
September*	16	22	1:1.4	38	3.65	74	-	7.1	112	10.75	1:1.95*
October	22	21	1:0.95	43	4.13	35	1	3.36	79	7.58	1:0.82
November	16	17	1:1.06	33	3.17	47	-	4.51	80	7.68	1:1.42
December	24	29	1:1.2	53	5.09	31	-	2.97	84	8.06	1:0.6
January	16	10	1:0.6	26	2.5	23	-	2.2	49	4.7	1:0.89
February***	5	4	1:0.8	10	0.96	6	3	0.86	19	1.82	1:0.9
March	33	34	1:1.03	67	6.43	58	-	5.57	125	12	1:0.87
April	20	10	1:0.5	30	2.88	25	-	2.4	55	5.28	1:0.83
May	60	45	1:0.75	105	10.08	113	-	10.85	218	20.94	1:1.08
June	17	22	1:1.3	39	3.74	33	-	3.17	72	6.91	1:0.85
July	27	30	1:1.11	57	5.47	60	-	5.76	117	11.23	1:1.05
August**	11	10	1:0.9	21	2.01	11	-	1.05	32	3.07	1:0.52**
Total	267	254	1:0.95	522	50.14	516	4	49.8	1042	100	1:0.99

* Significative deviations of the 1:1 proportion to sex ratio (x^2, $p < 0{,}05$)

** Significative deviations of the 1:1 proportion to sex ratio (z, $p < 0{,}05$)

***Male with two small chelipeds

Males were more abundant in the size classes 5-6 mm, 6-7 mm and 7-8 mm while the females size ranged from 6-7 mm, 7-8 mm and 8-9 mm CW.

Monthly size frequency distributions were in general unimodal for males and females and a fairly bimodal distribution was registered in December/2003 (Figure 3). Juvenile crabs (smaller than 4 mm CW) were recorded almost all months, except in October/2003 and February/2004.

The overall sex ratio was 1:1.07 and did not differ significantly from 1:1 proportion (x^2 test, $p > 0.05$). However, significant deviations from the 1:1 proportion were observed in September/2003 (x^2 test, $p < 0.05$) and August/2004 (z test, $p < 0.05$). The monthly sex ratio also did not differ from the Mendelian proportion (z test, $p > 0.05$). The ratio of males having the right or left chelae hypertrophied was 1:0.95 and did not differ significantly from an expected 1:1 proportion (x^2 test, $p > 0.05$). Males with 3.5 mm CW having two small chelipeds was collected in February/2004 (Table 1).

Table 2 shows the fiddler crab densities of each transect. Due the transects heterogeneity and the fact that the transects were visited in different months, it was not possible evaluate the monthly density for *U. leptodactyla*. The yearly density was of 17 individuals/m^2. The higher density was observed in the transect 8 (42.5 individuals/m^2) while transect 4 presents the lowest density (5.4 individuals/m^2).

DISCUSSION

The size frequency distribution of *Uca leptodactyla* in the Pacoti River mangrove was unimodal throughout the study period. This may suggest a stable population with continuous

Table 2. Density of each transect and total (number of individuals/m2) of Uca leptodactyla collected at Pacoti River mangrove, Northeast Brazil from September 2003 to August 2004.

Transects	Density (individuals/m^2)		Total density
	Males	Females	(Males/Females)
Transect 1	12	13.8	25.8
Transect 2	6.8	3.8	10.6
Transect 3	3.8	2.6	6.4
Transect 4	2.2	3.2	5.4
Transect 5	8.6	6	14.6
Transect 6	6.5	4.3	10.8
Transect 7	5.2	4	9.2
Transect 8	18.2	24.3	42.5
verage (individuals/ m^2)			17

recruitment, a common pattern found in tropical fiddler crabs population (MacIntosh, 1989; Litulo, 2005a, b). Most of the temperate and subtropical *Uca* populations exhibit a bi-modal frequency size distribution with seasonal breeding season (Rabalais & Cameron, 1983; Thurman, 1985; Spivak *et al*., 1991; Mounton & Felder, 1995; Yamaguchi, 2001).

In this study, it was not possible to determine the peak of reproductive events for *U. leptodactyla* population in the Pacoti River mangrove due the lower amount of ovigerous females collected. Aciole *et al.* (2000) studying the ecological aspects of *U. leptodactyla* in a tropical mangrove from Northeast Brazil, found only one ovigerous females among 351 collected females in one year-period.

The lower amount of ovigerous females collected by Aciole *et al*. (2000) and in this study may be due the fact that the ovigerous females of fiddler crabs hindering inside the deep burrows to incubate the eggs. Litulo (2005a) found ovigerous females of *U. annulipes* (H. Milne Edwards, 1837) inhabiting burrows at depths of about 30 cm and ovigerous females of *U. inversa* (Hoffman, 1874) were mostly found in burrows of about 50 cm (Litulo, 2005b).

With respect to the size at *U. leptodactyla* onset of sexual maturity, Masunari & Swiech-Ayoub (2003) studying the relative growth of *U. leptodactyla* in a subtropical mangrove population at South Brazil found that for males, the relative-growth analysis rendered an estimation of 8.35 mm of CW while for females the analysis rendered an estimation of 7.10 mm of carapace width.

In this study, only crabs smaller than 7 mm of CW were considered juvenile individuals, which were reported throughout the study period (Figure 3), showing a continuous recruitment pattern. However, the CW size in which *Uca* populations attain sexual maturity can vary with latitude (Masunari et al., 2005; Masunari & Dissenha, 2005). Therefore, allometric growth studies with *U. leptodactyla* at Pacoti River mangrove must be done to determine the size at which this fiddler attains the sexual maturity.

In relation to the mean size of fiddler crabs, sexual dimorphism has been documented in other *Uca* populations (Spivak *et al*., 1991; Johnson, 2003; Litulo 2005a, b). In general, females are smaller than males, and this may be due the fact that they concentrate their energetic budget on gonad development (Johnson,

2003) while males reach large size, once larger males have greater chances of obtaining females for copulation and win more intra-specific fights (Christy & Salmon, 1984). On the other hand, Valiela *et al*. (1974) suggests that males and females fiddler crabs have similar nutritional demands, food-processing and digestive efficiencies. However, because only the minor chaela is used for feeding, males can feed with only one chaela while females may use both, so the feeding rates of females is higher than that of males and males seem to compensate by extending the duration of feeding behavior (Valiela *et al*., 1974; Weissburg, 1992).

In this study, the carapace width size between males and females did not differ significantly and the overall size frequency distribution was non-normal, with a greater abundance of males in the smallest size classes and females in the larger ones (Figure 2). Probably *U. leptodactyla* females at Pacoti River mangrove are slightly larger than males due the fact that both expend similar time in feeding behavior. So, as females have a higher feeding rate than males, they attain larger size. *Uca leptodactyla* population with similar carapace size between males and females was registered by Aciole *et al*. (2000).

Fiddler crabs populations usually present significantly deviations of 1:1 proportion (Genoni, 1985) and Uca populations with such biased sex ratio have been recorded (Frith & Brunenmeister, 1980; Spivak *et al*., 1991; Litulo 2005a, b). Deviations of 1:1 ratio might result from sexual differences in the spatio-temporal distribution, mortality rates (Johnson, 2003), sampling methods (Montague, 1980) and differential predation on crab sex ratio (Wolf *et al*., 1975; Spivak *et al*., 1991).

Murai *et al.* (1983) stated that males of *U. vocans* (Linnaeus, 1758) spend more time away from the burrows regions. Males of the ghost crab *Ocypode gaudichaudii* Milne Edwards & Lucas, 1843 remained in the burrow area while the females were more abundant away from the burrow area than in it (Trott, 1998). So the failure to incorporate differential habitat use in the sampling methods can result in differential sex ratio. In the present study, transects ran from the edge of mangrove vegetation to mud flats on river, so the whole habitat was sampled and not only the burrow area.

According to Geisel (1972), physiologic and behaviorally homeostatic populations living in constant environments, presents a 1:1 sex ratio, or slightly male-biased while populations that inhabit inconstant environment will present deviations toward the females, to maximize the evolutionary potential due the unequal selection between male and female. Fisher (1930) predicted that in random mating populations the evolutionary stable sex ratio would be 1:1. In this study, the overall sex ratio did not differ significantly from the expected 1:1 ratio, showing that *U. leptodactyla* population at the tropical mangrove of Pacoti River is physiologic and behaviorally adapted to the habitat, besides evolutionary stable. An *U. leptodactyla* population male biased was registered by Aciole *et al*. (2000) in a tropical mangrove from Northeast Brazil, may be due the fact that females hider inside the burrows.

The major cheliped ratio was 1:0.95 and did not differ statistically from the expected 1:1 ratio. This suggest that in *U. leptodactyla* both male chelipeds (right and left) have equal chance to develop in a major one. The giant cheliped is not present in the early stages of males, but its develops enormously during the period of sexual maturation (Yamaguchi, 1977; Spivak, *et al*., 1991). Vernberg & Costlow (1966) claimed after a series of experiments that handedness is determined genetically. However, fiddler crabs populations predominantly right-handed have been reported for some Indo-West Pacific Uca population (Williams & Heng, 1981; Jones & George, 1982; Jaroensutasinee & Jaroensutasinee 2004). Males with two larger claws have been reported in the Western Atlantic *U. pugilator* (Bosc, 1802), *U. pugnax* (Smith, 1870) and the Pacific specie *U. vocans* (Linnaeus, 1758) and males with two small chelipeds were reported to Western Atlantic species *U. cumulanta* Crane, 1945 and *U. rapax* (Smith, 1870) (Mulstay, 1987).

A young male with 3.5 mm CW with two small chelipeds was collected in February/2004, but all males with the same CW size captured in the present study, already presented a differentiation between the claws. According to Yamaguchi (1977) when a young male of Uca normally loses its major chelipeds which then regenerates into a small one and the remaining cheliped develops into a giant. So, the young males captured with two small chelipeds in this study could be in the middle of the regeneration process.

The *U. leptodactyla* yearly density was of 17 individuals/m^2. This species was collected mainly at the edge of the mangrove in transects 1-7 and along the transect 8, which presented the highest density (42.5 individuals/m^2). These regions were composed by coarse sediments with lower amount of water and organic matter content and absence of vegetation, while almost all regions of the transects 1-7 were formed by muddy substratum with a high content of humidity and organic matter and by a dense *Rhizophora mangle* vegetation (Bezerra, 2005).

Bezerra (2005) stated that in Pacoti River mangrove, *U. leptodactyla* prefer inhabit sunny areas formed by coarse sand at the edge of the mangrove. Similarly, Rodriguez, (1963), Coelho, (1965) and Aciole *et al*. (2000) found *U. leptodactyla* living in sunny areas at the edge of the mangrove composed by coarse sediments with lower quantity of humidity and organic matter.

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