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Full Length Research Paper

Population dynamics and reproductive aspects of the Ghost crab *Ocypoda saratan* at Jeddah Coast, Saudi Arabia

Al-Solamy, M.A[1] and Hussein H.K[1, 2]

[1]Department of Biological Sciences, Faculty of Science, King Abdulaziz University, Jeddah, Saudi Arabia
[2]Department of Zoology, Faculty of Science, Alexandria University, Alexandria

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The population dynamics and reproductive aspects of the ghost crab, *Ocypoda saratan* were studied in Jeddah, Saudi Arabia. Crabs were randomly sampled on monthly basis during low tide periods from January to December 2011 at costal shores of Jeddah province. A total of 82 crabs was obtained, of which 37 (45.1%) were males, 24 non-ovigerous females (29.3%) and 21 (25.6%) ovigerous females, respectively. The present population presents non-normal size frequency distributions, with males reaching greater size than females. The overall sex ratio (M:F) (1:0.84) was significantly different from the 1:1 ratio. Ovigerous females were present throughout the year and the embryonic development showed synchrony with the gonadosomatic index, in which females carrying eggs close to hatching were more abundant when the gonadosomatic index reached minimum values in the population. Egg number increases with female size. Juvenile recruitment was also continuous with high proportion of young recruits being recorded in winter, probably due to the high reproductive activity displayed in summer. *Ocypoda saratan* exhibits a rapid embryonic cycle accompanied by a rapid larval development and settlement in the study area.

Keywords: Ghost crabs; Population dynamics; Sex ratio; Juvenile recruitment; Ocypoda saratan.

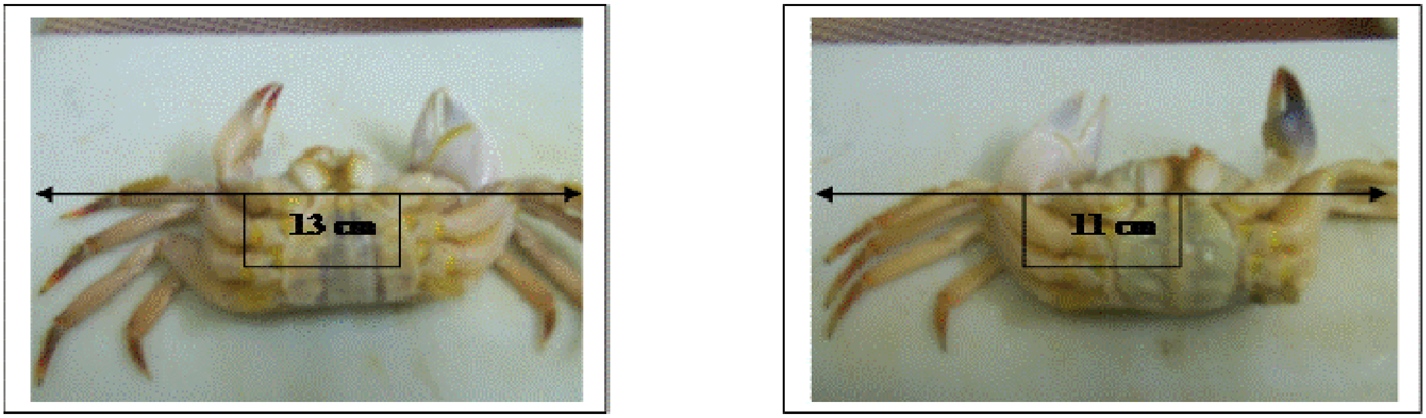
INTRODUCTION

Among the macro invertebrates commonly found in coastal regions, brachyuran crabs are one of the most important taxa with regard to number of species, density, and biomass (Lee, 1998; Hartnoll et al., 2002). They are an important component in transferring energy to both marine and terrestrial habitats since they are consumed by a large numbers of fish, birds, and invertebrates (Skov and Hartnoll, 2001; Skov et al., 2002; Litulo, 2004a).

The number of studies on crustacean populations has been increasing during the last years. Among carcinologists, this populational information has been evaluated by several methods including density, size frequency distributions, spatial dispersion, sex ratio, juvenile recruitment, reproductive season among others (e.g., Thurman, 1985; Diaz and Conde, 1989; Leme and Negreiros-Fransozo, 1998; Yamaguchi, 2001b). Moreover, comparisons between populations may constitute an important strategy to verify differences among them, as well as to understand the environment and biological constraints that are shaping them (Mantelatto et al., 1995; Oshiro, 1999; Fransozo et al., 1999).

Reproduction is the main mechanism to maintain species proliferation and continuity, and, in brachyuran crabs is extremely diversified, ultimately shaped to

*Corresponding Author E-mail: ahssan555@yahoo.com



(A) (B)

Figure 1. Dimorphism of the Ghost crab *Ocypoda saratan* showing the carapace width of male (A) is higher than female (B).

maximize egg productions, and offspring survivorship (Hartnoll and Gould, 1988; Lopez Greco et al., 2000). The determination of breeding periods is governed by a complex interaction of endogenous and exogenous factors, allowing both intra and interspecific variations regarding the duration of the reproductive season (Sastry, 1983). Generally, peaks of higher breeding activity may be associated with variations of temperature, salinity, oxygen, food availability, photoperiod, rainfall, among others (Meusy and Payen, 1988; Pinheiro and Fransozo, 2002; Costa and Negreiros-Fransozo, 2003; Mantelatto et al., 2003; Litulo, 2004a).

Ocypode crabs live in the intertidal zone of mud–sandy sediments in estuarine and sheltered areas from tropical to warm- temperate regions (Al-Solamy, 2008). They are usually characterized by their high density compared to other brachyurans inhabiting mangroves (Macia et al., 2001; Skov et al., 2002; Hartnoll et al., 2002), often building complex burrows in the substratum and displaying particular behaviour associated with burrow utilization. Most studies already carried out on their population structure and reproduction were conducted for subtropical species (e.g., Colby and Fonseca, 1984; Spivak et al., 1991; Mouton and Felder, 1995; Emmerson, 1994; Costa and Negreiros- Fransozo, 2003), while much remain unknown about tropical species (Hartnoll, 1975; Skov and Hartnoll, 2001; Litulo, 2004a, 2004b).

Other Red Sea *Ocypodidae* such as *Uca annulipes* has been the subject of a wide range of studies most of them focusing on behaviour, ecology and reproduction (Emmerson, 1994; Jennions and Backwell, 1998; Backwell and Passmore, 1996; Litulo, 2004a). Such information is fundamental to understanding the breeding patterns, which includes gonad development, breeding season, and juvenile recruitment. *Ocypoda saratan* ranges along the Red Sea, including Saudi Arabia, through an impressive range of climates (Al-Solamy, 2008). It displays the typical ocypodid behaviour of remaining burrowed at high tide, and emerging to forage only when uncovered by water at low tide. In the present study, the population structure, sex ratio, breeding biology, fecundity, and juvenile recruitment of *Ocypoda saratan* are investigated in population coastal regions along northern Jeddah.

MATERIAL AND METHODS

Kingdom of Saudi Arabia is characterized by long coast reached 4200 Km along the Red Sea and Arabian Gulf. The coastal area has good quality of water and optimum conditions such as temperature which allow reproduction of many types of crustacean which included different types of crabs.

Ocypodidae is a large family of crabs has many species, the most abundant and important one of them is *Ocypoda saratan*. This species is common in sandy shores observer dig deep holes to find bait. Males and females were differentiated morphologically by the carapace shape and width measurements (Figure 1)

Samples were taken monthly from January to December 2011 during low tides. Specimens were collected by hand during the daytime by two people over a period of approximately 1 h over the same area of about 500 m2. At each sampling occasion, 20 0.25 m2 squares were set out in the area from which 10 were randomly chosen for sampling. Each randomized square was excavated with a corer to a depth of 50 cm. All collected crabs were bagged, labeled, and stored in 70% ethanol until further analysis. In the laboratory, crabs were identified, sexed and checked for the presence of eggs on female pleopods. The carapace width (CW) was measured using a vernier caliper (±0.05 mm accuracy) (Macia et al., 2001; Litulo, 2004a).

Females were dissected under a stereomicroscope and their ovaries removed, identified, and stored with their respective females. Afterwards, both females and

Table 1. The Ghost crab O. saratan: Total number of specimens collected at Jeddah costal region from January to December 2011. n = sample size; % = percentage, CW= Carapace width, F= Females).

Month	Male			Non-ovigerous F.			Ovigerous F.			Total	Sex ratio
	n	%	CW	n	%	CW	n	%	CW		
January*	5	6.18	12.8	2	1.96	15.4	2	2.65	5.25	9	1:1.4
February*	4	4.86	24.0	2	1.59	15.7	2	2.38	17.2	8	1:1.2
March*	4	5.34	18.6	1	1.06	16.7	2	2.56	20.8	7	1:1.5
April*	2	2.21	6.65	3	3.89	13.2	1	0.53	11.4	6	1:0.5
May*	3	4.15	13.1	2	2.56	7.22	1	1.23	9.54	6	1:1.1
June*	1	0.88	23.6	1	2.38	19.7	1	0.70	17.8	3	1:0.3
July*	1	1.50	18.2	1	0.79	19.3	1	0.35	18.1	3	1:1.3
August*	2	2.56	10.3	3	4.86	17.2	2	1.23	12.8	7	1:0.4
September*	2	2.03	13.4	3	2.65	22.6	1	1.14	5.77	6	1:1.8
October*	4	4.86	23.2	2	2.21	13.9	1	1.34	16.2	7	1:0.8
November*	5	6.18	17.9	2	2.64	13.4	2	2.87	15.6	9	1:0.7
December*	4	4.94	7.88	2	2.37	10.1	5	7.16	11.3	11	1:0.49
Total	37	45.1	14.13	24	29.3	15.37	21	25.6	13.48	82	1:0.85

*Significant differences from the 1:1 ratio (*v*2 test, *P* < 0.05)

gonads were weighed using an analytical balance (0.0001 g) after drying at 70 ℃ for 12 h (Yamaguchi, 2001b). The gonadosomatic index was calculated according to the following formula: GSI =GDW⁄FDW× 100 where GDW is gonad dry weight and FDW is female dry weight, respectively.

To estimate fecundity, 20 ovigerous females with eggs at stage I were selected for egg counting. Pleopods were removed from females, placed in petri dishes filled with seawater, and eggs detached by the gradually addition of a solution of sodium hypochlorite. Bare pleopods were then discarded by gently stirring in a beaker filled with 200 ml seawater. Three 1.5 ml sub-samples were taken using a pipette, with eggs counted under a dissecting microscope. The average value obtained was then extrapolated for the whole suspension to estimate the number of eggs (Flores and Paula, 2002; Litulo, 2004b).

Statistical analysis

The population size structure was analysed as a function of the size frequency distribution of all individuals collected during the study period. Specimens were grouped in 2.0 mm size class intervals from 2.0 to 24.0 mm CW. The period of time when ovigerous females were found in the population was referred to as the breeding season and individuals (both male and female) smaller than the smallest ovigerous female captured were classified as juveniles (Wenner, 1972).

Assessment of recruitment was based on the Proportion of juveniles in the samples. The chi-square test (*v*2) was used to evaluate the sex ratio and the overall size frequency distributions were tested for normality using theKolmogorov-Smirnov (Lilliefors) (D) test (Zar, 1999). The mean size of males and females was compared using the Student *t*-test. Mean ± standard error is presented through the text.

RESULTS

Population dynamics

A total of 82 crabs was obtained, of which 37 (45.1%) were males, 24 non-ovigerous females (29.3%) and 2125.6%) ovigerous females, respectively (Table 1). Males(ranged from 6.65 to 24.0 mm CW (14.13 ± 0.243) and females from

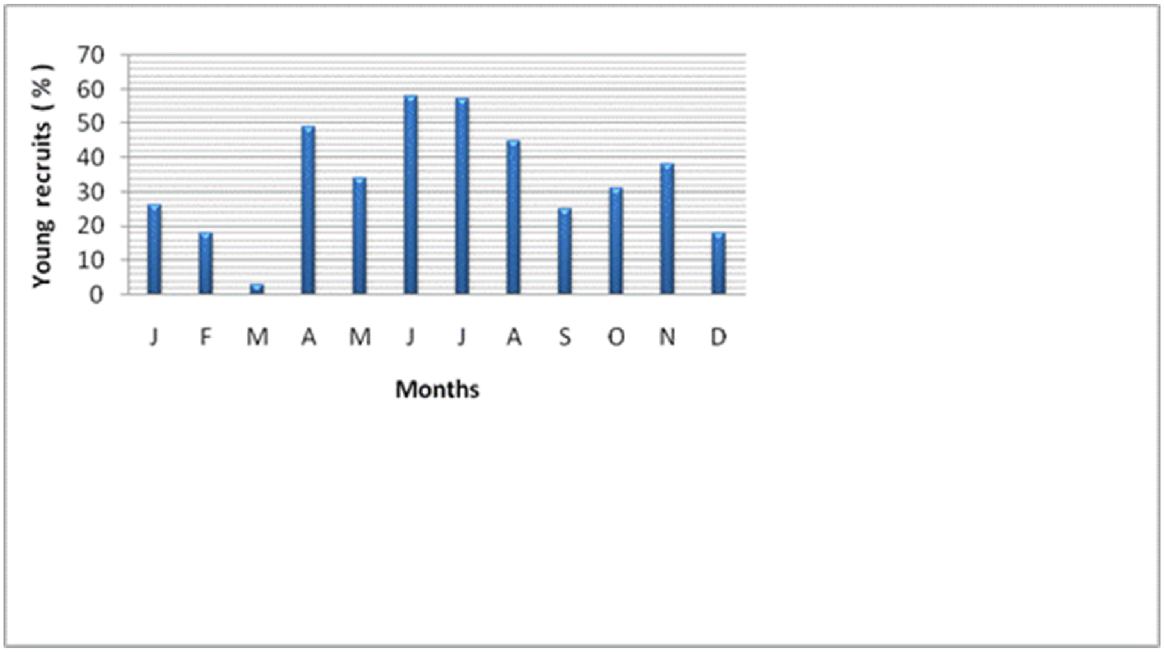


Figure 2. Temporal variation of young recruits of the Ghost crab, O saratan at Jeddah coast, Saudi Arabia. Error bars: ± standard error (SE).

5.25 to 20.8 mm CW (13.48 ± 0.144), indicating sexual dimorphism, in which males attain larger sizes than females (Student's *t*-test, $t = 9.55$, $P < 0.05$). The size frequency distributions for all sampled crabs. In both males and females, size frequency distributions differed from normality (Kolmogorov-Smirnov Liliefors test, *D* males = 0.08654, $P < 0.05$; *D* females = 0.215464, $P < 0.05$) as well as from asymmetry (*t*- test for *H*0: $c = 0$: *g* males = –0.2447, $t = 3.41$; *g* females = –0.1953, $t = 4.65$, $P < 0.05$). The size frequency histograms show a clear unimodal distribution with mean modal size is 14.13 mm CW for males, 15.37 mm CW for non-ovigerous females and 13.48 mm CW for ovigerous females, respectively. The overall sex ratio (1:0.85) was significantly different from the expected 1:1 proportion (*v*2 test, $P < 0.05$) and was male biased during most part of the study (Table 1).

The size of the smallest ovigerous female collected was 10.3 mm CW. In this way, all individuals of a smaller size than this were considered to be young recruits. Juvenile recruitment occurred with highest intensity from April to August and November and reached minimum values in February, March, and December (Figure 2).

Reproductive aspects

Figure 3 shows the patterns of gonad development in female *U. inversa* during the study period. The GSI (%) was lower in June and September whereas peaks of gonad development were observed in January, July, and December.

Fecundity ranged from 900 (CW = 10.5) to 10,000 (CW = 20.1) with a mean of 6192.83 ± 728.90 eggs. Egg number was positively correlated with female size ($b = 3.5$, *t*-test, $P < 0.05$) and the resulting scatter plot shows a curvilinear trend (Figure 4), expressed by the function $EN = 0.2839\ CW^{3.5435}$ ($R2 = 0.9783$, $n = 20$, $P < 0.0001$).

DISCUSSION

Population dynamics

The size frequency distribution of a population is a dynamic characteristic that can change throughout the year as a result of reproduction and rapid recruitment from larvae (Thurman, 1985). The global size frequency distributions for both sexes of *Ocypoda saratan* at Jeddah coast, Saudi Arabia were unimodal and skewed to the left. Similar distributions have been reported by several authors (e.g., Colby and Fonseca, 1984; Thurman, 1985; Spivak et al., 1991; Costa and Negreiros-Fransozo, 2003). This may suggest a stable population with constant recruitment and mortality rates. According to Thurman Poisson-like size frequency distributions can be found in certain situations due to seasonal mortality pulses and behavioural differences in harsh environmental conditions. Sexual dimorphism was evidenced in the present study, with males reaching larger sizes than females. Lopez Greco et al. (2000) and Mantelato et al. (2003) suggest that females may ha-ve reduced somatic growth compared to males because

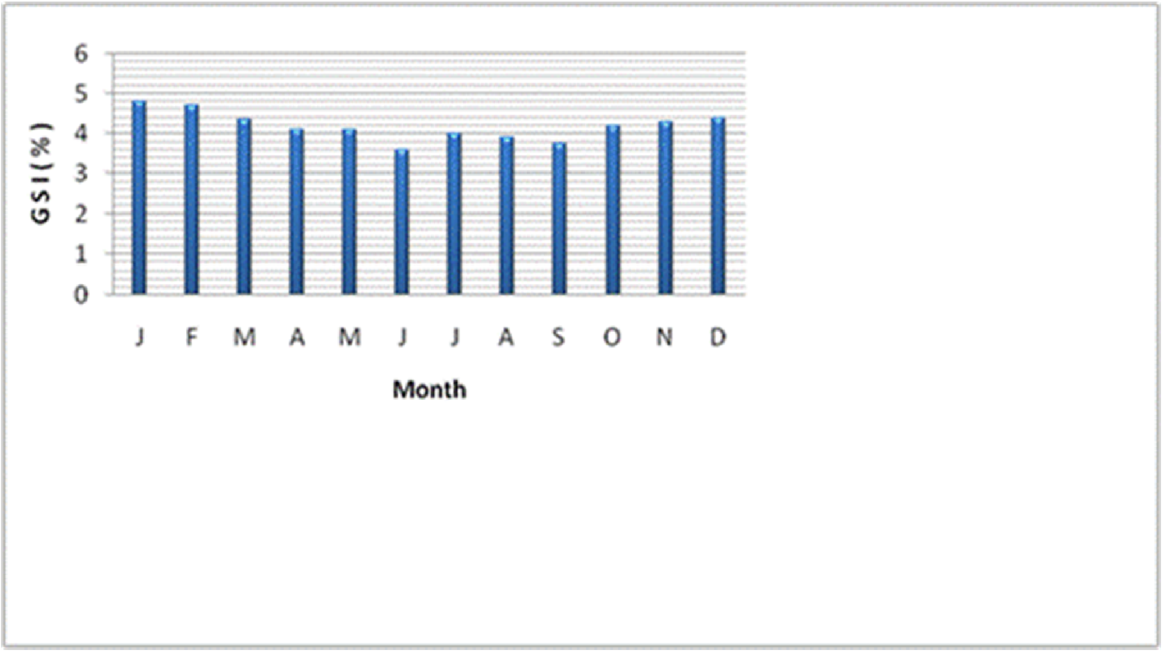


Figure 3. Temporal trends of the gonadosomatic index of the Ghost crab, *O saratan* at Jeddah coast, Saudi Arabia. Error bars ± standard error (SE).

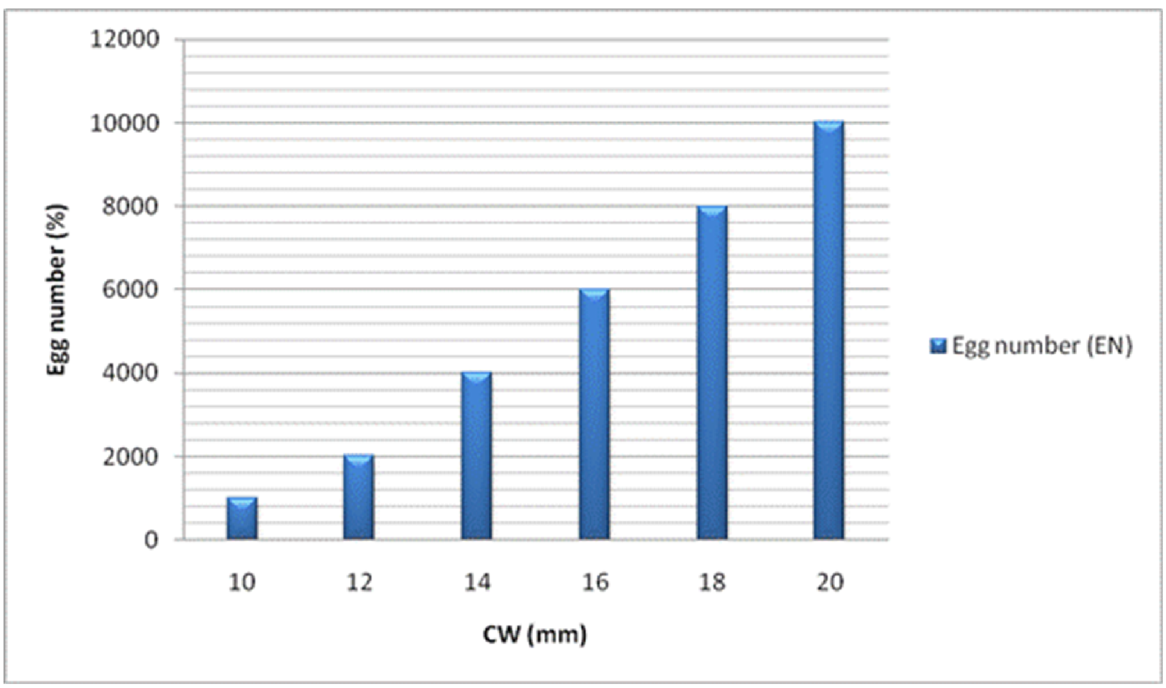


Figure 4. The relationship between number of eggs (EN) and female size (CW) in the Ghost crab, O saratan from Jeddah coast, Saudi Arabia. (EN = 0.2838 CW3.5435 R2 = 0.9783, n = 20, P< 0.0001).

they concentrate on their energetic budget for gonad development.

Moreover, males may reach larger sizes for successful competition for copulation with more than one female, since larger male ocypodid crabs may have greater chances of obtaining females for copulation and win more intraspecific fights (Henmi, 2000). In this study, the overall sex ratio was male-biased. Deviations from the 1:1 ratio might result from sexual differences in the spatio-temporal distribution and mortality of organisms

(Wada et al., 2000), differential life span,migration, longevity of each sex, food restriction, utilization of different habitats, differential production of gametes, and growth rates (Wenner, 1972; Johnson, 2003). Emmerson (1994) and Lardies et al. (2004) suggest that deviations from the 1:1 ratio can internally regulate the size of a population by affecting its reproductive potential. Additionally, lunar phases and intertidal zonation are known to be determinants of sex ratio variation in brachyuran crabs (Emmerson, 1994).

Recently, Johnson (2003) reviewed the possible sex ratio patterns among Ocypode crabs. According to this author, male-biased sex ratios may be a result of sampling artifact, which is derived from a focus on surface sampling and a failure to incorporate differential habitat use. Furthermore, ovigerous females spend prolonged periods underground and, when on the surface, often forage closer to water sources, creating spatial separation from foraging males (Macia et al., 2001).

Juvenile recruitment occurs year-round in the present population, as indicated by the presence of smaller crabs throughout the study period. Recruitment was most intense during summer (April–August) and declined in winter (December– March). Crabs recruited in winter may continue to grow and reach sexual maturity in the late winter and beginning of summer, when the presence of young recruits is low. As suggested by Emmerson (1994), González-Gordillo et al. (2003) and Gonçalves et al. (2003), juvenile recruitment occurs when concentrations of phytoplankton in estuarine areas are higher. In the case of Jeddah coast, favorable phytoplankton abundance occurs from September to November and March, due to nutrient accumulation in the rainy season.

Reproductive aspects

The study of breeding in Crustaceans can facilitate the understanding of the adaptive strategies and reproductive potential of a species and its relationship with the environment and others species. In brachyurans, the breeding patterns are a result of a trade-off between growth and reproductive are a result of a trade-off between growth and reproductive processes. During mating, brachyuran males transfer their spermatophores to female spermathecae where they are stored until fertilization (Pinheiro and Fransozo, 2002) and, after spawning, ovarian maturation resumes.

The determination of breeding period is a result of the complex interaction of endogenous and exogenous factors, allowing both inter and intra-specific variations regarding the duration of the reproductive cycle (Sastry, 1983). Peaks of higher breeding intensity may be associated with variations in temperature, salinity, food availability, rainfall, and photoperiod (Emmerson, 1994; Pinheiro and Fransozo, 2002). It is generally suggested that near the tropics reproduction occurs year round because environmental conditions are generally favorable for gonad development (Meusy and Payen, 1988; Mouton and Felder, 1995). However, both continuous and seasonal reproductive patterns are found in subtropical and tropical regions (Litulo, 2004a). In this way, it is likely to suggest that the occurrence of populations with seasonal breeding patterns in subtropical and tropical regions may be based on the population's evolutionary histories, although abiotic and biotic factors such as temperature, photoperiod, rainfall, and food availability should be taken into account when assessing the reproductive traits of a species or population.

In *O. saratan*, the gonadosomatic index suggests that reproduction is continuous, a very common pattern in tropical brachyurans (e.g., Perez, 1990; Goshima et al., 1996; Rodriguez et al, 1997; Negreiros- Fransozo, 2000; Yamaguchi, 2001b; Flores and Paula, 2002; Reigada). The major peaks of spawning occur during the summer and subsequently decline in winter. Several authors have recently reviewed the reproductive pattern of ocypode crabs (e.g., Emmerson, 1994; Yamaguchi, 2001a; Costa and Negreiros-Fransozo, 2003; Litulo, 2004a), and most of them are based on the frequency of egg-bearing females.

Few studies have analysed gonad development of females (e.g., Pilay and Nair, 1971; Mouton and Felder, 1995; Rodriguez et al., 1997). It is widely known that in brachyurans, gonad maturation is not always synchronized with ovigery condition. The examination of gonads is one of the most accurate techniques, but precise estimates rely on some previous knowledge about specific patterns of growth and reproduction to aid the interpretation of the results, as well as knowledge of short-term breeding cycles to avoid confusion between spent and immature specimens (Flores and Paula, 2002).

Among the various factors known to influence breeding activity in ocypode crabs, burrow depth is one of the most prominent. In the same study area, Litulo (2004a) studied the breeding biology of *Uca annulipes* and found that most females inhabited burrows at depths of about 30 cm, but in the present study, females of *O saratan* were mostly found much deeper (50 cm). As stated by Christy (1987), female Ocypode crabs may prefer relatively deep burrows because they provide stable thermal environments that yield constant embryonic developmental rates and do not alter precise timing of larval release. Hence, by selecting deeper burrows, they can accelerate embryonic development (Salmon, 1984, 1987; Christy and Salmon, 1984; Rabalais and Cameron, 1983; Rabalais, 1991) and reduce larvae and juvenile predation (Christy, 1982; 1989; O'connor, 1993; Moser; Macintosh, 2001 and Yamaguchi, 2001b).

This study constitutes the first account on the population ecology and reproduction of *O. saratan*. Further research on behaviour, reproductive output, larval ecology, and spatial distribution will be necessary to understand its life cycle.

REFERENCES

AL-Solamy MA (2008). Ecological and biological study aspects of the Ghost crab, Ocypoda saratan in Abo Khashaba region in the cost of the Red Sea. M. Sc. Thesis, Faculty of Oceanography, King Abdulaziz Univ., KSA.

Backwell PRY, Passmore NI (1996). Time constraints and multiple choice criteria in the sampling behaviour and mate choice of the fiddler crab, *Uca annulipes*. Behav. Ecol. Soc. 38, 407–416.

Christy JH (1982). Adaptive significance of semilunar cycles of larval release in fiddler crabs (Genus *Uca*): test of an hypothesis. Biol. Bull. 163, 251–263.

Christy JH (1987). Female choice and breeding behaviour of the fiddler crab *Uca beebei*. J. Crust. Biol. 7, 624–635.

Christy JH (1989). Rapid development ofmegalopae of the fiddler crab *Uca pugilator* reared over sediment: implications for models of larval recruitment. Mar. Ecol. Prog. Ser. 57, 259–265.

Christy JH, Salmon M (1984). Ecology and evolution ofmating systems of fiddler crabs (Genus *Uca*). Biol. Rev. 59, 483–509.

Colby DR, Fonseca MS (1984). Population dynamics, spatial dispersion and somatic growth of the sand fiddler crab *Uca pugilator*. Mar. Ecol. Prog. Ser. 16, 269–279.

Costa TM, Negreiros-Fransozo ML (2003). Population biology of *Ucathayeri* Rathbun, 1900 (Brachyura, Ocypodidae) in a subtropical South American mangrove area: results from transect and catch-per-unit-effort techniques. Crustaceana 75, 1201–1218.

Crane J (1975). Fiddler crabs of the world. *Ocypodidae*: Genus *Uca*. Princeton University Press, New Jersey.

Diaz H, Conde JE (1989). Population dynamics and life history of the mangrove crab *Aratus pisonii* (Brachyura, Grapsidae) in a marine environment. Bull. Mar. Sci. 45, 148–163.

Emmerson WD (1994). Seasonal breeding cycles and sex ratios of eight species of crabs from Mgazana, a mangrove estuary in Transkei, South Africa. J. Crust. Biol. 14, 158–168.

Flores AAV, Paula J (2002). Sexual maturity, larval release and reproductive output of two brachyuran crabs from a rocky intertidal area in central Portugal. Invert. Reprod. Develop. 42, 21–34.

Fransozo A, Bertini G, Correa MOD (1999). Population biology and habitat utilization of the stone crab *Menipe nodifrons* in the Ubatuba region, São Paulo, Brazil. Crust. Issues 12, 275–281.

Gonçalves F, Ribeiro R, Soares AMVM (2003). Comparison between two lunar situations on emission and larval transport of decapod larvae in the Mondego estuary (Portugal). Acta Oecol. 24, S183–S190.

González-Gordillo JI, Arias AM, Rodriguez A, Drake P (2003). Recruitment patterns of decapod crustacean megalopae in a shallow inlet (SW Spain) related to life history strategies. Estuar. Coast. Shelf Sci. 56, 593–607.

Goshima S, Koga T, Murai M (1996). Mate acceptance and guarding by male fiddler crabs *Uca tetragonon* (Herbst). J. Exp. Mar. Biol. Ecol. 196, 131–143.

Hartnoll RG (1975). The Grapsidae and Ocypodidae (Decapoda: Brachyura) of Tanzania. J. Zool. 177, 305–328.

Hartnoll RG, Cannicci S, Emmerson WD, Fratini S, Macia A, Mgaya YD, (2002). Geographic trends in mangrove crab abundance in East Africa.Wetl. Ecol. Manag. 10, 203–213.

Hartnoll RG, Gould P (1988). Brachyuran life history strategies and the optimization of egg production. Proc. Zool. Symp. 59, 1–9.

Henmi Y (2000). Comparisons of life history traits among populations of the ocypodid crab *Macrophthalmus japonicus* in habitats with contrasting food availability. Crust. Res. 29, 109–120.

J. Plankt. Res. 11, 2165–2178.

Jennions MD, Backwell PRY (1998). Variation in courtship routine the fiddler crab *Uca annulipes*: is it related to male attractiveness? Behav. Ecol. Soc. 9, 605–611.

Johnson PTJ (2003). Biased sex ratios in fiddler crabs (Brachyura, Ocypodidae): a review and evaluation of the influence of sampling method, size class and sex-specific mortality. Crustaceana 76, 559–580.

Lardies MA, Rojas JM, Wehrtman IS (2004). Breeding biology and population structure of the intertidal crab *Petrolisthes laevigatus* (Anomura: Porcellanidae) in central-southern Chile. J. Nat. Hist. 38, 375–388.

Lee SY (1998). Ecological role of grapsid crabs in mangrove ecosystems: a review. Mar. Freshw. Res. 49, 335–343.

Leme MHA, Negreiros-Fransozo ML (1998). Reproductive patterns *of Aratus pisonii* (Decapoda: Grapsidae) from an estuarine area of São Paulo northern coast, Brazil. Rev. Biol. Trop. 46, 673–678.

Litulo C (2004a). Reproductive aspects of a tropical population of the fiddler crab *Uca annulipes* (H.Milne Edwards, 1837) (Brachyura: Ocypodidae) at Costa do Sol Mangrove, Maputo Bay, southern Mozambique. Hydrobiologia 525, 157–173.

Litulo C (2004b). Fecundity of the Pantropical fiddler crab *Uca annulipes* (H. Milne Edwards, 1837) (Brachyura: Ocypodidae) at Costa do Sol mangrove,Maputo Bay, southern Mozambique.Western Indian Ocean J. Mar. Sci. 3, 87–91.

Lopez Greco LS, Hernández JE, Bolanos JE, Rodriguez EM, Hernández G (2000). Population features of *Microphrys bicornutus* Latreille, 1825 (Brachyura, Majidae) from Isla Margarita, Venezuela. Hydrobiologia 439, 151–159.

Macia A, Quincardete I, Paula J (2001). A comparison of alternative methods for estimating population density of the fiddler crab *Uca annulipes* at Saco mangrove, Inhaca Island (Mozambique). Hydrobiologia 449, 213–219.

Mantelatto FLM, Faria FCR, Garcia RB (2003). Biological aspects of *Mithraculus forceps* (Brachyura: Mithracidae) from Anchieta Island, Ubatuba, Brazil. J. Mar. Biol. Ass. UK 83, 789–791.

Mantelatto FLM, Fransozo A, Negreiros-Fransozo ML (1995). Population structure of *Hepatus padibundus* (Decapoda: Calappidae) in Fortaleza Bay, Brazil. Rev. Biol. Trop. 43, 265–270.

Meusy J, Payen GG (1988). Female reproduction in malacostracan Crustacea. Zool. Sci 5, 217–265.

Moser SM, Macintosh DJ (2001). Diurnal patterns of larval recruitment of brachyura into a mangrove estuary system in Ranong Province, Thailand. Mar. Biol. 138, 827–841.

Mouton EM, Felder DL (1995). Reproduction of the fiddler crabs *Uca longisignalis* and *Uca spinicarpa* in a Gulf of Mexico salt marsh. Estuaries 18, 469–481.

O'connor NJO (1993). Settlement and recruitment of the fiddler crabs *Uca pugnax* and *U. pugilator* in a North Carolina. USA salt marsh. Mar. Ecol. Prog. Ser 93, 227–234.

Oshiro LMY (1999). Aspectos reprodutivos do caranguejo guaia, *Menipe nodifrons* Stimpson (Crustacea, Decapoda, Xanthidae) da baia de Sepetiba, Rio de Janeiro, Brazil. Rev. Bras. Zool. 16, 827–834.

Paula J, Pinto I, Guambe I, Monteiro S, Gove D, Guerreiro J (1998). Seasonal cycle of planktonic communities at Inhaca, southern Mozambique.

Perez OS (1990). Reproductive biology of the sandy shore crab *Matuta lunaris* (Brachyura: Calappidae). Mar. Ecol. Prog. Ser. 59, 83–89.

Pilay KK, Nair NB (1971). The annual reproductive cycles of *Uca annulipes* and *Metapenaeus affınis* (Decapoda: Crustacea) from southwest coast of India. Mar. Biol. 11, 152–166.

Pinheiro MAA, Fransozo A (2002). Reproduction of the speckled swimming crab *Arenaeus cribrarius* (Brachyura: Portunidae) on the Brazilian coast near 23°30′S. J. Crust. Biol. 22, 416–428.

Rabalais NN (1991). Egg production in crabs with abbreviated development. In: Wenner, A., Kuris, A. (Eds.), Crustacean Egg Production.University of California, Santa Barbara, pp. 217–234.

Rabalais NN, Cameron J (1983). Abbreviated development of *Uca subcylindrica* (Stimpson, 1859) (Crustacea, Decapoda, Ocypodidae) reared in the laboratory. J. Crust. Biol. 3, 519–541.

Ramirez Llodra E (2002). Fecundity and life-history strategies in marine invertebrates. Adv. Mar. Biol. 43, 87–179.

Reigada ALD, Negreiros-Fransozo ML (2000). Reproductive cycle of

Hepatus padibundus (Herbst, 1785) (Crustacea, Decapoda, Calappidae) in Ubatuba, SP, Brazil. Rev. Bras. Biol. 60, 483–491.

Rodriguez A, Drake P, Arias AM (1997). Reproductive periods and larval abundance of the crabs *Panopeus africanus* and *Uca tangeri* in a shallow inlet (SW Spain). Mar. Ecol. Prog. Ser. 149, 133–142.

Salmon M (1984). The courtship, aggression and mating system of a primitive fiddler crab (*Uca vocans*: Ocypodidae). Trans. Zool. Soc. London. 37, 1–50.

Salmon M (1987). On the reproductive behaviour of the fiddler crab *Uca thayeri*, with comparisons to *U. pugilator* and *U. vocans*: evidence for behavioural convergence. J. Crust. Biol. 7, 25–44.

Sastry AN (1983). Ecological aspects of reproduction. In: Vernberg, F.J., Vernberg, W. (Eds.), The Biology of Crustacea, vol. 7. Environmental Adaptations. Academic Press, NewYork, pp. 179–254.

Skov MW, Hartnoll RG (2001). Comparative suitability of binocular observation, burrow counting and excavation for the quantification of the mangrove fiddler crab *Uca annulipes* (H. Milne Edwards). Hydrobiologia 449, 201–212.

Skov MW, Vannini M, Shunnula JP, Hartnoll RG, Cannicci S (2002). Quantifying the density of mangrove crabs. Ocypodidae and Grapsidae. Mar. Biol. 141, 725–732.

Spivak ED, Gavio MA, Navarro CE (1991). Life history and structure of the world's southernmost *Uca* population: *Uca uruguayensis* (Crustacea, Brachyura) in Mar Chiquita lagoon (Argentina). Bull. Mar. Sci. 48, 679–688.

Thurman CL (1985). Reproductive biology and population structure of the fiddler crab *Uca subcylindrica* (Stimpson). Biol. Bull. 169, 215–229.

Wada S, Ashidate M, Yoshino K, Sato T, Goshima S (2000). Effects of sex ratio on egg extrusion frequency and mating behaviour of the spiny king crab *Paralithodes brevipes* (Decapoda: Lithodidae). J. Crust. Biol. 20, 479–482.

Wenner AM (1972). Sex ratio as a function of size in marine Crustacea.Am. Nat. 106, 321–350.

Yamaguchi T (2001a). Breeding period of the fiddler crab *Uca lacteal* (Decapoda, Brachyura, Ocypodidae) in Japan. Crustaceana 74, 285–293.

Yamaguchi T (2001b). Incubation of eggs and embryonic development of the fiddler crab, *Uca lactea* (Decapoda, Brachyura, Ocypodidae). Crustaceana 74, 449–458.

Zar JH (1999). Biostatistical Analysis. Prentice Hall, New Jersey.