

Breeding cycle and seasonal biochemical changes in the gonads of the North African freshwater crab *Potamon algeriense* (Bott, 1967) (Brachyura: Potamidae)

S. Fadlaoui*, M. Melhaoui

Laboratory of Water, Environment, and Sustainable Development, Department of Biology, Faculty of Sciences, Mohamed First University, Blvd Mohamed VI, PB 717, 60000, Oujda, Morocco.

** Corresponding author: soufiane.fadlaoui@gmail.com*

Soufiane Fadlaoui: ORCID 0000-0001-5280-6661

Mohammed Melhaoui: ORCID 0000-0003-0051-8822

ABSTRACT: The present study aims to determine, for the first time, the annual breeding cycle and the biochemical changes in the gonads of the North African freshwater crab, *Potamon algeriense* (Bott, 1967). Monthly collections were carried out by hand, from October 2018 to September 2019 in Oued Zegzel, a mountain stream in the Northeast of Morocco. The gonad size reached high values in the dry season (June to September) showing the maximum breeding activity during these months. By June, the gonads of most of the individuals attained full maturity where the spawning began. Spawning terminated by the end of September then the gonads entered a quiescent period. Histological observations of the gonads revealed that the ripening of the gonads started during March and extended up to May. During the maturation of the gonads, protein, fat, and glycogen contents were high, whereas, all the concentrations fell considerably reaching the minimum values at the end of the spawning period.

How to cite this article: Fadlaoui S., Melhaoui M. 2023. Breeding cycle and seasonal biochemical changes in the gonads of the North African freshwater crab *Potamon algeriense* (Bott, 1967) (Brachyura: Potamidae) // *Invert. Zool.* Vol. 20. No.1. P.97–107. doi: 10.15298/invertzool.20.1.05

KEY WORDS: breeding cycle, freshwater crabs, histology, gonadosomatic index (GSI), reproduction, spawning.

Цикл размножения и сезонные биохимические изменения в гонадах североафриканского пресноводного краба *Potamon algeriense* (Bott, 1967) (Brachyura: Potamidae)

С. Фадлауи*, М. Мельхауи

Laboratory of Water, Environment, and Sustainable Development, Department of Biology, Faculty of Sciences, Mohamed First University, Blvd Mohamed VI, PB 717, 60000, Oujda, Morocco.

** Corresponding author: soufiane.fadlaoui@gmail.com*

РЕЗЮМЕ: Цель настоящего исследования — впервые описать годовой цикл размножения и биохимические изменения в гонадах североафриканского пресноводного краба *Potamon algeriense* (Bott, 1967). Ежемесячные сборы проводились вручную с октября 2018 г. по сентябрь 2019 г. в Oued Zegzel, горном ручье на северо-востоке Марокко. Размер гонад был максимален в сухой сезон (с июня по сентябрь), что свидетельствует о максимальной активности размножения в эти месяцы. К июню гонады большинства особей достигли полной зрелости, после чего начался нерест.

Нерест заканчивался к концу сентября, после чего гонады переходили в период покоя. Гистологические исследования гонад показали, что созревание гонад началось в марте и продолжалось до мая. Во время созревания гонад содержание белка, жира и гликогена было высоким, в то время как их концентрации значительно снижались, достигая минимальных значений в конце нерестового периода.

Как цитировать эту статью: Fadlaoui S., Melhaoui M. 2023. Breeding cycle and seasonal biochemical changes in the gonads of the North African freshwater crab *Potamon algeriense* (Bott, 1967) (Brachyura: Potamidae) // *Invert. Zool.* Vol. 20. No.1. P.97–107. doi: 10.15298/invertzool.20.1.05

КЛЮЧЕВЫЕ СЛОВА: цикл размножения, пресноводные крабы, гистология, гонадосоматический индекс (GSI), размножение, нерест.

Introduction

There are more than 7200 species of brachyuran crabs distributed all over the world (Davie *et al.*, 2015). Over 1500 reported species from five families are true freshwater crabs (Robin *et al.*, 2019). Due to the ability to complete their life cycle independently from the marine environment, primary freshwater crabs have been presented as land-locked organisms (Yeo *et al.*, 2008; Cumberlidge, Ng, 2009). They have a maximum number of species as compared to the other decapod crustaceans in inland waters worldwide, therefore they are among the most ecologically important macro-invertebrate groups (Ng *et al.*, 2008; Yeo *et al.*, 2008).

Reproductive biology has a crucial role in the population dynamics and life history strategies of crustaceans. For brachyuran crabs, reproduction is tremendously variable for different species in terms of offspring survival and egg production (Lopez-Greco, Rodríguez, 1999). The determination of the breeding season is influenced by several interactions of endogenous and exogenous factors, permitting both intra and interspecific variations, dealing with the duration of the reproductive season (Sastry, 1983).

The histological observation of gonadal maturation is important for determining the phases of gonad growth and maturation status of marine and freshwater crabs (Liu, Li, 2000; Pinheiro, Lins-Oliveira, 2006; Castiglioni *et al.*, 2007; Martins *et al.*, 2007; Erkan *et al.*, 2009; Silva *et al.*, 2009; Devi, Smija, 2013; Nakhodai *et al.*, 2013; Senkman *et al.*, 2015; Sharifian *et al.*, 2017). Evaluation of the maturity is merely qualitative or may include a quantitative analysis. The gonadal index is one of the

most common and simple quantitative methods currently used in the study of the reproduction of various species (Wu *et al.*, 2007; Silva *et al.*, 2012; Magalhães *et al.*, 2012; Cilenti *et al.*, 2015; Aaqillah-Amr *et al.*, 2018; Lu *et al.*, 2018; Fazhan *et al.*, 2020; Lima *et al.*, 2021).

Potamon algeriense (Bott, 1967) is an endemic freshwater crab belonging to the family of the Potamidae, found only in three countries: Morocco, Algeria, and Tunisia (Fadlaoui *et al.*, 2019a, b). In Morocco, the species occurs in the freshwater springs located in semi-mountainous areas, it has been reported from the North in the watershed of the Oued Laou, from the North-east in the watershed of Moulouya, and from the Middle Atlas in the Oued Oum er Rbia watershed. The species inhabits springs, rivers, streams, creeks, and lakes, occurring in various types of environments, such as cracks, among branches, hollow tree trunks, under submerged stones, and piles of dead leaves, associated with aquatic macrophytes and most often in areas of stagnant water or low streamflow (Fadlaoui, Melhaoui, 2019).

Although several investigations on the reproductive biology of marine, intertidal and estuarine crabs are available (Kumar *et al.*, 2003; Lestang *et al.*, 2003; Sallam, 2005; Oh *et al.*, 2006; Henmi, Koga 2009; Lawal-Are, 2010; Sahoo *et al.*, 2011), few reports are available on the reproductive biology of freshwater, semiterrestrial or terrestrial crabs (Mansur, Hebling, 2002; Liu, Jeng, 2005; Hartnoll *et al.*, 2009, 2010; Pathre, Mina, 2010; Devi, Smija, 2013; Sharifian *et al.*, 2017; Lima *et al.*, 2021; Fadlaoui *et al.*, 2022a).

In the present study, we investigated for the first time the breeding cycle and the seasonal biochemical changes in the gonads of the en-

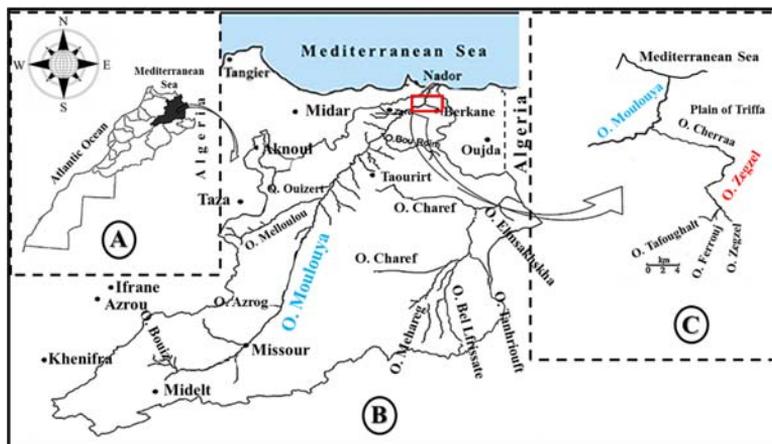


Fig. 1. Study area. Kingdom of Morocco (A), watershed of Moulouya (B), Oued Zegzel (C).
Рис. 1. Район исследования. Королевство Марокко (A), водораздел Мулуя (B), Oued Zegzel (C).

demic North African freshwater crab *P. algeriense* in Oued Zegzel, a mountain stream in Northeast of Morocco.

Material and Methods

Study area

The present study was conducted in Oued Zegzel (34°50'29.4" N, 2°21'19.8" W, 350 m above sea level), a mountain stream in the Northeast Morocco (Fig. 1). In order to determine the main phases of the breeding cycle, a 400 m² stretch of the stream was surveyed each month during October 2018 to September 2019.

Shrublands that mark the study area are composed mainly of *Eriobotrya japonica*, *Nerium oleander*, *Tamarix africana*, *Salix pedicellata*, *Rubus ulmifolius* and *Crataegus monogyna*. The stream substrata are heterogeneous and composed mainly of sandy and muddy sediments, stones, pebbles, and rocks. Stream width averages about 15 m, but usually only a small part (width 2–3 m) has a running water. Temperatures in the study area vary widely over time. The average highs of the hottest months, July and August, vary between 31 °C and 32 °C. However, the coldest months, December to February, have average lows of 3 to 4 °C (Fig. 2). Water temperature is ranged from 10 °C in winter to 27 °C in summer (Fadlaoui *et al.*, 2020; 2021). The precipitation regime during the year is homogeneous in the study area. The first rains fall at the end of October while the last come in May (Fig. 2). Like most permanent Mediterranean rivers, Oued Zegzel is characterized by irregular flow and sudden hydrological phenomena during rainy periods. Seasonal

tend is marked by a peak in March and very low flows between June and October (Fadlaoui *et al.*, 2022a, b).

Sampling methods and Measurement

Few specimens of crabs were collected every month in order to minimize the sampling pressure impact on the population. Specimens were collected manually during the daytime and over an approximate period of five hours. The crabs were placed inside iced plastic buckets and directly transported to the laboratory for further investigations. Specimens missing one of the chelipeds or one of the locomotory limbs as well as those that had just moulted were excluded from this study.

In the laboratory, sex determination of the crabs was done according to the shape of the abdomen (considerably wider in females than in males). The carapace width (CW) was measured using a Vernier caliper (± 0.01 mm) and the total body weight (TW) was measured using an electronic balance (± 0.01 g).

Several methods have been used to determine the reproductive cycle in marine invertebrates; among these, the most suitable one appears to be the measurement of the gonad index (Giese, 1969). In order to measure the gonado-somatic index (GSI), we removed the carapace using a pair of scissors, and then the gonads were weighed. The gonad index was calculated according to the formula given by Farmanfarmaian *et al.* (1958):

$$GSI = \frac{GW}{TW} \times 100;$$

where:

GW — the gonad weight, TW — the total body-weight.

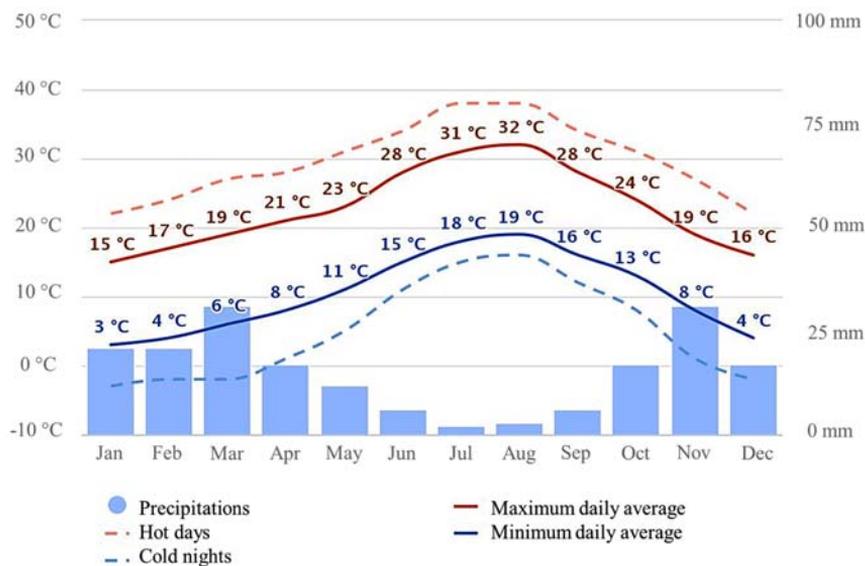


Fig. 2. Monthly total precipitations and daily average temperatures recorded in Oued Zegzel throughout the study period (2019).

Рис. 2. Месячное количество осадков и среднесуточные температуры, зарегистрированные в Oued Zegzel в течение всего периода исследования (2019).

Histological observations

For histological observations, gonads were fixed in Bouin's solution. The tissues were dehydrated in alcohol, then embedded in paraffin wax and were cut using microtome at 6–8 μ . The slices were stained with Delafield's haematoxylin and eosin.

Biochemical analysis

The biochemical changes occurring in the gonads were recorded monthly during the study period. The nitrogen was estimated by the Micro-Kjeldahl method (Hawk *et al.*, 1954). The amount of protein was calculated by multiplying the nitrogen value by the factor 6.25. The fat content was extracted from dried tissues in Soxhlet Apparatus and the percentage of fat was calculated. The glycogen was calculated according to the method recommended by Kemp *et al.* (1954) using Engel's colorimeter. The concentration of glycogen was calculated by multiplying the glucose value by the factor 0.927. All the results were expressed in percentage of the sample on a dry weight basis.

Results

Biometric parameters

A total of 84 specimens were investigated throughout the study period of which 48 were females (57.14%) and 36 were males (42.86%).

The overall sex ratio (1:0.75) was not significantly different from the expected 1:1 proportion (Chi-square test ($\div 2$); $p > 0.05$). Carapace width (CW) of males ranged from 20.11 to 55.87 mm (35.30 ± 0.67), however, the CW of females ranged from 19.24 to 46.32 mm (31.43 ± 0.54) (Fig. 3). The comparison of the carapace width means of both sexes showed significant differences (t-test; $p < 0.05$).

Gonadosomatic index (GSI)

The monthly mean values of the Gonadosomatic index were calculated and plotted in Fig. 4. The GSI of females showed a significant fluctuation compared with the results of males. The values ranged from 0.35% in September to 6.25% in June. The results indicate that the female's gonad entered a period of growth in March and reached maximum size in June. On the other hand, the GSI of males was approximately constant, where the values ranged from 3.02% in September to 3.32% in August and did not show a significant dynamics.

According to the present results, we can conclude that the breeding activity of the species as indicated by gonad indexes appears to be marked from May to September reaching a

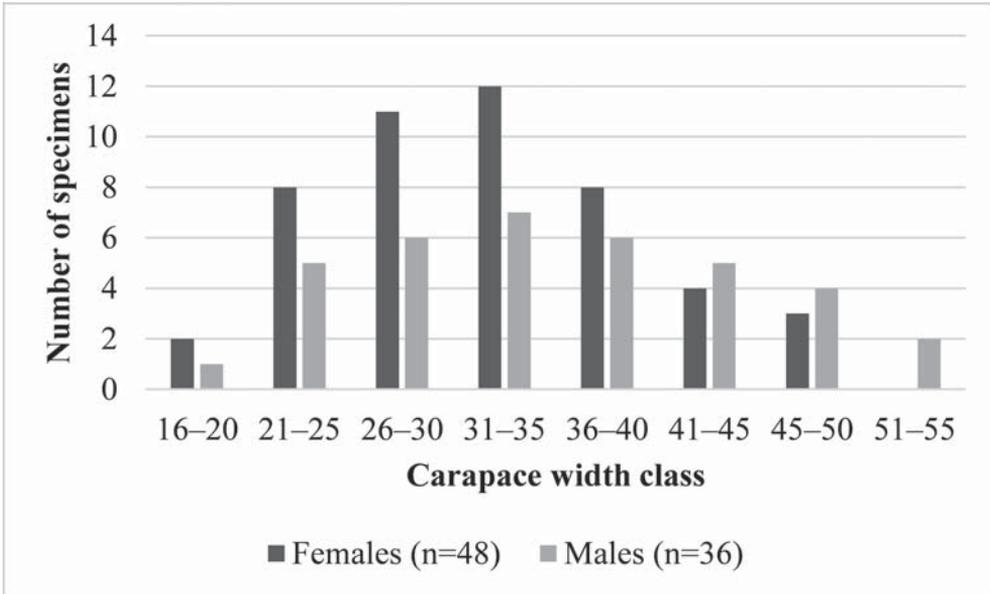


Fig. 3. Size frequency distribution of the collected population of *Potamon algeriense* recorded from October 2018 to September 2019.

Рис. 3. Размерная структура популяции *Potamon algeriense* с октября 2018 г. по сентябрь 2019 г.

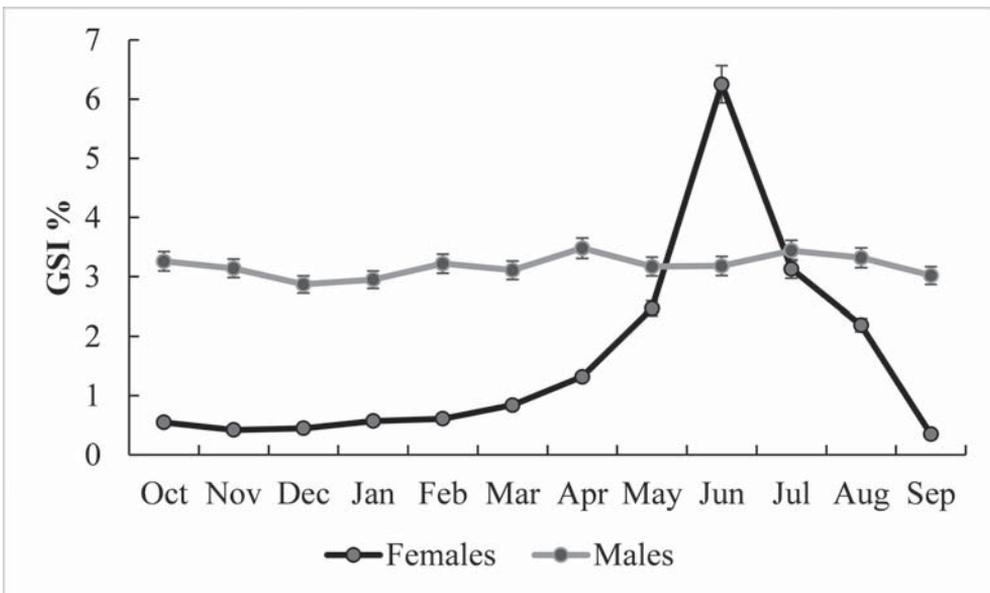


Fig. 4. Monthly dynamics of the gonadosomatic index of *Potamon algeriense* from October 2018 to September 2019.

Рис. 4. Динамика гонадосоматического индекса *Potamon algeriense* по месяцам с октября 2018 г. по сентябрь 2019 г.

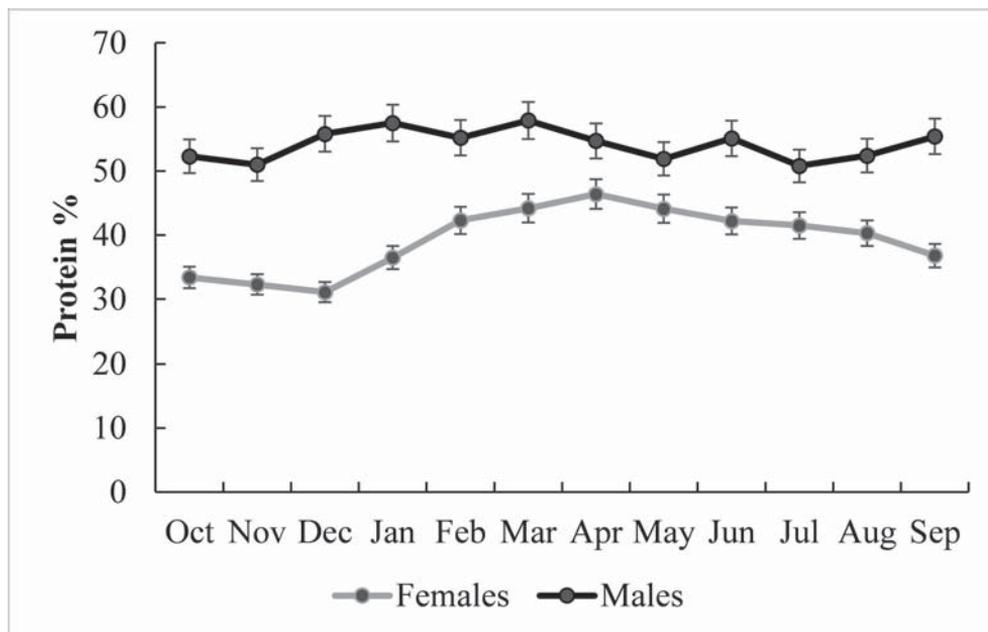


Fig. 5. Monthly dynamics of the protein content in the gonad of *Potamon algeriense* from October 2018 to September 2019.

Рис. 5. Динамика содержания протеина в гонадах *Potamon algeriense* по месяцам с октября 2018 г. по сентябрь 2019 г.

highest single peak in June. From September to February, the gonads entered a repose stage and attained minimum size. The histological observation of the gonads of both sexes throughout the year showed active sperms and mature eggs from May to September.

Biochemical analysis

The monthly mean values of the protein content in the gonads of crabs were determined and plotted in Fig. 5. The percentages of protein in the male's gonad were approximately constant, where the results ranged from 50.8% in July to 57.9% in March, whereas, the results showed a significant fluctuation in the case of females, where the values were ranging from 31.1% in December to 46.1% in May. The results showed that there is a dynamics of protein content in ovaries during different periods of the year especially in the breeding season, where a remarked fall in the protein percentage during the spawning period (May to September). On the other hand, the percentage of protein was increased during the maturation period of the gonad (March to April).

The monthly mean values of the fat content in the gonads of *P. algeriense* were determined and plotted in Fig. 6. The fat percentages in the male's gonads were approximately constant, where the results ranged from 22.9% in January to 28.1% in October, however, the results showed a significant fluctuation in the case of females ranging from 12.3% in January to 38.4% in May. The results showed a conspicuous augmentation of fat percentage in the female's ovaries during the maturation of the gonads (March to May); whereas, a steady fall of the fat content in female's gonads was observed during the spawning period.

The glycogen content in the gonads of both sexes was determined and the values were plotted in Fig. 7. The glycogen percentages in the male's gonads ranged from 0.55% in October to 0.67% in April, whereas in the female's gonads were ranged from 0.36% in September to 0.84% in April. The results showed that there is a dynamics of glycogen content in females' ovaries during different periods of the year, especially in the breeding season. There was a remarked fall in the glycogen percentage during

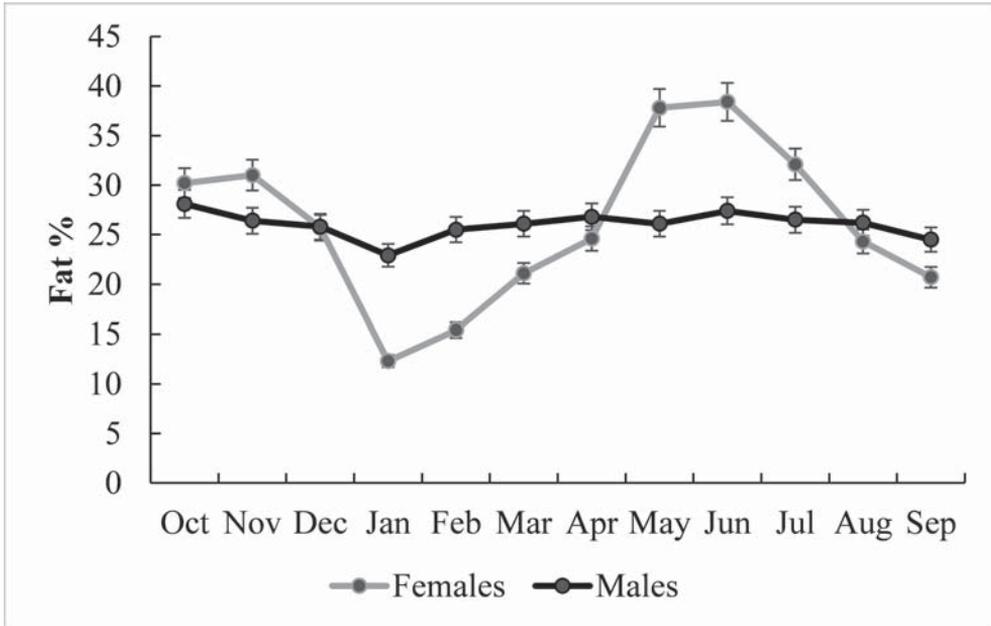


Fig. 6. Monthly dynamics of the fat content in the gonad of *Potamon algeriense* from October 2018 to September 2019.

Рис. 6. Динамика содержания жира в гонадах *Potamon algeriense* по месяцам с октября 2018 г. по сентябрь 2019 г.

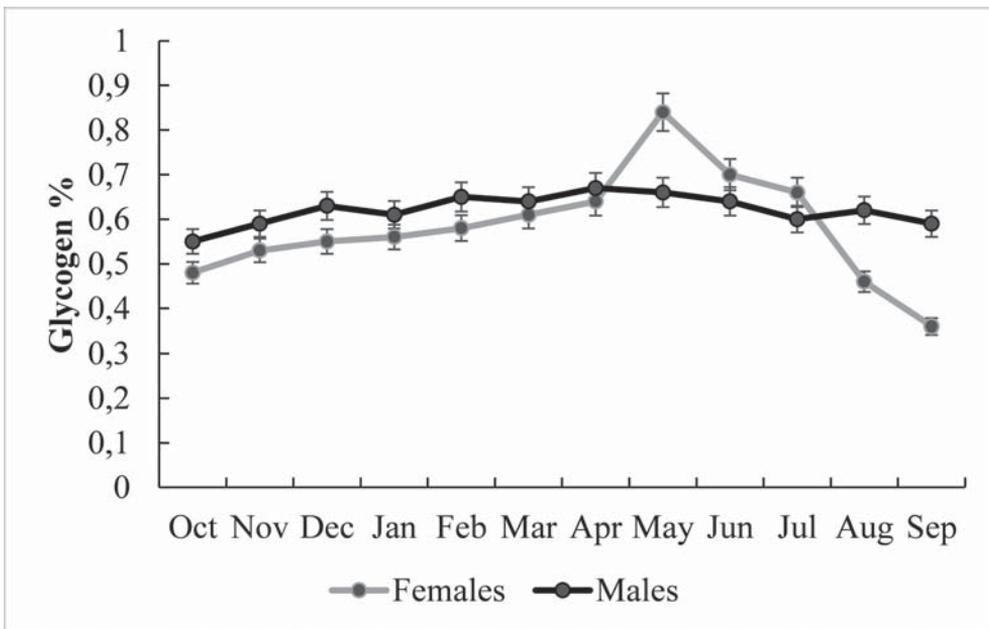


Fig. 7. Monthly dynamics of the total glycogen content in the gonad of *Potamon algeriense* from October 2018 to September 2019.

Рис. 7. Динамика содержания гликогена в гонадах *Potamon algeriense* по месяцам с октября 2018 г. по сентябрь 2019 г.

the spawning period (May to September). On the other hand, a remarked increase in the percentage of glycogen during the maturation period of the ovaries (March to April).

Discussion

Gonadal development and maturation are essential phenomena in the life history of crustaceans (Waiho *et al.*, 2017). Aside from being principally involved in reproduction, gonads are responsible for the morphological differentiation of most crustacean species, which leads to sexual dimorphism (Parvizi *et al.*, 2017; Waiho *et al.*, 2019).

The gonadosomatic index is widely used in determining the sexual maturity and reproductive period of crustaceans (Waiho *et al.*, 2017), since it has a consequent relationship with the size and weight of individuals (Magalhães *et al.*, 2012). Regarding the results of GSI, and the biochemical changes of hepatopancreas, the females of *P. algeriense* showed a rising trend during the spawning period from May to September, with a drop in September, suggesting that the freshwater crab *P. algeriense* is a single seasonal breeder. The seasonal breeding pattern has been also reported for many freshwater crabs such as *Barytelphusa cunicularis* Westwood in Sykes, 1836 (Diwan, Nagabhushnam, 1974), *Himalayapotamon koolooense* (Rathbun, 1904) (Joshi, Khana, 1982), *Sinopotamon yangtsekiense* Bott, 1967 (Tao *et al.*, 1994), *Sartoriana spinigera* (Wood-Mason, 1871) (Rahman *et al.*, 2008), *Travancoriana schirnerae* Bott, 1969 (Devi, Smija, 2013), *Sodhiana rokitanskyi* (Pretzmann, 1971) (Nakhodai *et al.*, 2013).

The annual pattern of the gonadosomatic index for males did not show, as it did for females, significant fluctuations related to reproduction. This result suggested that males showed continuous production of spermatozooids with the possibility of mating all the year-long. Similar findings were also observed in other decapods, as demonstrated by Pillay and Nair (1973), who found spermatophores in the vas deferens throughout the year in the brachyuran *Austruca annulipes* (H. Milne Edwards, 1837), *Portunus pelagicus* (Linnaeus, 1758), and shrimp *Metapenaeus affinis* (H. Milne Edwards, 1837). Koji *et al.* (1997) found that the

GSI of males of *Helicana japonica* (Sakai *et al.* Yatsuzuka, 1980) and *H. tridens* (De Haan, 1835) were relatively constant over the years. Yamaguchi (2001) studied the seasonal changes in the hepatosomatic index of *Austruca lactea* (De Haan, 1835) and noted that there was a drop in that index due not only to the reproductive period, which might be related to sexually active males throughout the year but also to the molting process of the animals.

The variability of chemical constituents of the gonads of *P. algeriense* throughout the year shows that there is a relationship between the hepatopancreas and gonad physiology in crustaceans. A striking decrease in glycogen concentrations was noticed throughout the breeding season in females. This suggests that the stored glycogen might be employed for gonadal development. Similar observations were made by Hasek & Felder (2005) on two populations of the grapsoid crabs *Armases cinereum* (Bosc, 1801) and *Sesarma reticulatum* (Say, 1817) where the carbon concentrations of hepatopancreas decrease during the ovarian maturation and subsequently, the concentrations of carbon and lipid in ovaries increase during this period.

The total fat content increased in both sexes during the maturity of the gonads, however, during the spawning period, the percentage of fat decreased. Thiele (1959) determined the total fat content of the Roman snail *Helix pomatia* Linnaeus, 1758 and found only a slight seasonal dynamics. It would appear probable that as the gonad grew it received fat from the other parts of the body and accumulated in developing gonads. Fat appeared to be one of the most important sources of energy metabolism during the breeding season. With greater catabolism of fat during the spawning period, the fat content was reduced to its minimum value. Giese (1969) found the accumulation of lipids in the ovary of *Katharina tunicata* (W. Wood, 1815) during the formation of ova preceding spawning and the lipid level remained essentially the same from month to month in the mantle, testis, and gut. Results of the present study are in agreement with the findings reported by many researchers where the gradual increase in the size of the ovarian cells has been attributed to the deposit of lipid in the ovaries during vitellogenesis (Castiglioni, Negreiros-Fransozo, 2007; Gregati *et al.*, 2010; Revathi *et al.*, 2012).

Protein concentrations showed a marked dynamics during the breeding cycle in females. Giese *et al.* (1959) while working on the organic products in the reproductive cycle of the *Strongylocentrotus purpuratus* (Stimpson, 1857), observed the increase of protein and RNA with the maturation of ovaries while the increase of DNA was proportionally less. The present observation regarding the protein level in *P. algeriense* confirms the findings of Durve and Bal (1961) in *Crassostrea graphoides* and Giese (1969) (= *Magallana cuttackensis* (Newton et E.A. Smith, 1912) in *Katharina tunicata*.

Conclusion

Data on the reproductive biology of aquatic species, including GSI, HIS, and breeding cycle, are essential for optimum management and conservation. In the present study, we found that *P. algeriense* is a single seasonal breeder, and the chemical constituents of hepatopancreas show significant antagonistic behavior in females compared to males. These results indicate an investment of the hepatopancreas' energy reserves in the ovarian development by the females, while the males use those reserves in growth and molting.

CONFLICTS OF INTEREST: The authors declare that they have no conflicts of interest.

References

- Aaqillah-Amr M.A., Hidir A., Noordiyana M.N., Ikhwanuddin M. 2018. Morphological, biochemical and histological analysis of mud crab ovary and hepatopancreas at different stages of development // *Anim. Reproduct. Sci.* Vol.195. P.274–283.
- Castiglioni D.D.S., Negreiros-Franozo M.L., Greco L.S.L., Silveira A.F., Silveira S.O. 2007. Gonad development in females of fiddler crab *Ucarapax* (Crustacea, Brachyura, Ocypodidae) using macro and microscopic techniques // *Iheringia, Ser. Zool.* Vol.97. P.505–510.
- Cilenti L., Paziienza G., Scirocco T., Fabbrocini A., D'Adamo R. 2015. First record of ovigerous *Callinectes sapidus* (Rathbun, 1896) in the Gargano Lagoons (south-west Adriatic Sea) // *Bioinvasions Rec.* Vol.4. No.4.
- Cumberlidge N., Ng P.K.L. 2009. Systematics, evolution, and biogeography of freshwater crabs // J.W. Martin, K.A. Crandall, D.L. Felder (eds.). *Decapod crustacean phylogenetics. Crustacean issues 18.* Baton Rouge: CRC Press. P.491–508.
- Da Silva G.M.F., Pantoja Ferreira M.A., Von Ledebur E.I.C.F., Da Rocha R.M. 2009. Gonadal structure analysis of *Macrobrachium amazonicum* (Heller, 1862) from a wild population: a new insight into the morphotype characterization // *Aquac. Res.* Vol.40. No.7. P.798–803.
- Davie P.J., Guinot D., Ng P.K. 2015. Anatomy and functional morphology of Brachyura // *Treatise on Zoology-Anatomy, Taxonomy, Biology. The Crustacea.* Vol.9. Part C. Brill. P.11–163.
- Devi A.S., Smija M.K. 2013. Reproductive biology of the freshwater crab, *Travancoriana schirnerae* Bott, 1969 (Brachyura: Gecarcinucidae) // *Indian J. Fish.* Vol.60. No.3. P.13–21.
- Diwan A.D., Nagabhushanam R. 1974. Reproductive cycle and biochemical changes in the gonads of the freshwater crab, *Barytelphusa cunicularis* (Westwood, 1836) // *Indian J. Fish.* Vol.21. No.1. P.164–176.
- Durve V.S., Bal D.V. 1961. Studies on the chemical composition of the oyster, *Crassostrea gryphoides* (Schlotheim) // *J. Zool. Soc. India.* Vol.13. No.1. P.70–77.
- Erkan M., Tunali Y., Balkis H., Oliveria, E. 2009. Morphology of testis and vas deferens in the xanthoid crab, *Eriphia verrucosa* (Forskål, 1775) (Decapoda: Brachyura) // *J. Crust. Biol.* Vol.29. No.4. P.458–465.
- Fadlaoui S., El Asri O., Melhaoui M. 2022a. Reproductive behaviour of the North African freshwater crab *Potamon algeriense* (Bott, 1967) (Brachyura: Potamidae) // *Invert. Reprod. Dev.* Vol.66. No.1. P.33–39.
- Fadlaoui S., Mahjoub M., El Asri O., Melhaoui M. 2019a. Allometric growth of the freshwater crab *Potamon algeriense* (Bott, 1967) (Decapoda, Brachyura, Potamidae) in Oued Zegzel, a mountain stream, in the northeast of Morocco // *Int. J. Zool.* Vol.2019. Art.5168639.
- Fadlaoui S., El Asri O., Mohammed L., Sihame A., Omari A., Melhaoui M. 2019b. Isolation and characterization of chitin from shells of the freshwater crab *Potamon algeriense* // *Prog. Chem. Appl. Chitin Deriv.* Vol.24. P.23–35.
- Fadlaoui S., Melhaoui M. 2019. Population structure of the freshwater crab *Potamon algeriense* (Bott, 1967) inhabiting oued Zegzel, (Northeast of Morocco) // *Int. J. Ecol.* Vol.2019.
- Fadlaoui S., Bouterfas M., El Asri O., El Halouani H., Melhaoui M. 2020. Contribution to the evaluation of the physico-chemical quality of the superficial waters of the Oued Zegzel (Moroccan Northeast) // *Mor. J. Chem.* Vol.8. No.1. P.8–1.
- Fadlaoui S., El Asri O., Bouterfas M., Melhaoui M. 2021. Effects of physicochemical variables of superficial waters on the abundance of the North African freshwater crab *Potamon algeriense* (Bott, 1967) // *J. Toxicol.* Vol.2021.
- Fadlaoui S., Melhaoui M. 2022b. Diet composition of the North African freshwater crab, *Potamon algeriense* (Bott, 1967) in Oued Zegzel (Northeast of Morocco) // *Mar. Freshw. Behav. Physiol.* P. 1–14.
- Farmanfarmaian A., Giese A.C., Booloottian R.A., Bennett J. 1958. Annual reproductive cycles in four species of west coast starfishes // *J. Exp. Zool.* Vol.138. No.2. P.355–367.
- Fazhan H., Waiho K., Glenner H., Moh J.H.Z., Hassan M., Ikhwanuddin M. 2020. Gonadal degeneration and hepatopancreas alteration in orange mud crab *Scylla*

- olivacea* infected with *Sacculina beauforti* (Crustacea; Rhizocephala; Sacculinidae) // *Front. Mar. Sci.* Vol.7. P.534–443.
- Giese A. 1969. A new approach to the biochemical composition of the mollusc body // *Oceanogr. Mar. Biol. Ann. Rev.* Vol.7. P.175–229.
- Giese A.C., Greenfield L., Huang H., Farmanfarmaian A., Booloitian R., Lasker R. 1959. Organic productivity in the reproductive cycle of the purple sea urchin // *Biol. Bull.* Vol.116. No.1. P.49–58.
- Gregati R.A., Fransozo V., Lopez-Greco L.S., Negreiros-Fransozo M.L. 2010. Reproductive cycle and ovarian development of the marine ornamental shrimp *Stenopus hispidus* in captivity // *Aquaculture.* Vol.306. No.1–4. P.185–190.
- Hartnoll R.G., Broderick A.C., Godley B.G., Musick S., Pearson M., Stroud S.A., Saunders K.E. 2010. Reproduction in the land crab *Johngarthia lagostoma* on Ascension Island // *J. Crust. Biol.* Vol.30. No.1. P.83–92.
- Hartnoll R.G., Broderick A.C., Godley B.G., Saunders K.E. 2009. Population structure of the land crab *Johngarthia lagostoma* on Ascension Island // *J. Crust. Biol.* Vol.29. No.1. P.57–61.
- Hasek B.E., Felder D.L. 2005. Biochemical composition of ovary, embryo, and hepatopancreas in the grapsoid crabs *Armases cinereum* and *Sesarma* nr. *reticulatum* (Crustacea, Decapoda) // *Comp. Biochem. Physiol. B, Biochem. Mol. Biol.* Vol.140. No.3. P.455–463.
- Hawk P.B., Oser B.L., Summerson W.H. 1954. *Practical Physiological Chemistry.* McGraw-Hill Book Company INC., New York.
- Henmi Y., Koga H. 2009. Growth and reproduction of the intertidal dotillid crab *Ilyoplax deschampsii* // *J. Crust. Biol.* Vol.29. No.4. P.516–522.
- Joshi P.C., Khanna S.S. 1982. Seasonal changes in the ovary of a freshwater crab, *Potamon koolooense* (Rathbun) // *Proceedings: Anim. Sci.* Vol.91. No.5. P.451–462.
- Kemp A., Van Heijningen, A.J.K. 1954. A colorimetric micro-method for the determination of glycogen in tissues // *Biochem. J.* Vol.56. No.4. P.646.
- Koji O., Keigo S., Makoto H. 1997. Life histories of sympatric mud-flat crabs, *Helice japonica* and *H. tridens* (Decapoda: Grapsidae), in a Japanese estuary // *J. Crust. Biol.* Vol.17. No.2. P.279–288.
- Kumar M.S., Xiao Y., Venema S., Hooper G. 2003. Reproductive cycle of the blue swimmer crab, *Portunus pelagicus*, off southern Australia // *J. Mar. Biol. Assoc. U.K.* Vol.83. No.5. P.983–994.
- Lawal-Are A.O. 2010. Reproductive biology of the blue crab, *Callinectes amnicola* (De Rocheburne) in the Lagos Lagoon, Nigeria // *Turkish J. Fish. Aquat. Sci.* Vol.10. No.1.
- Lestang S.D., Hall N.G., Potter L.C. 2003. Reproductive biology of the blue swimmer crab (*Portunus pelagicus*, Decapoda: Portunidae) in five bodies of water on the west coast of Australia // *Fish. Bull.* Vol.101. P.745–757.
- Lima M.C., Pereira C.A.M., Araujo M.S.L.C., Rodrigues G.G., Nicacio G. 2021. Seasonal variation in biometric parameters in a population of the endangered blue land crab (*Cardisoma guanhumi*): Indicators for assessment and management // *Reg. Stud. Mar. Sci.* Vol.45. P.101–804.
- Liu H.C., Jeng M.S. 2005. Reproduction of *Epigrapsus notatus* (Brachyura: Gecarcinidae) in Taiwan // *J. Crust. Biol.* Vol.25. No.1. P.135–140.
- Liu H.C., Li C.W. 2000. Reproduction in the fresh-water crab *Candidiopotamon rathbunae* (Brachyura: Potamidae) in Taiwan // *J. Crust. Biol.* Vol.20. No.1. P.89–99.
- López-Greco L., Rodríguez E. 1999. Annual reproduction and growth of adult crabs *Chasmagnathus granulata* (Crustacea, Brachyura, Grapsidae) // *Cah. Biol. Mar.* Vol.40. P.155–164.
- Lu Y., Liu M., Gong J., Cheng Y., Wu X. 2018. Effect of exogenous estrogen on the ovarian development and gene expression in the female swimming crab *Portunus trituberculatus* (Miers, 1876) (Decapoda: Brachyura: Portunidae) // *J. Crust. Biol.* Vol.38. No.3. P.367–373.
- Magalhães T., Mossolin E.C., Mantelatto F.L. 2012. Gonadosomatic and hepatosomatic indexes of the freshwater shrimp *Macrobrachium olfersii* (Decapoda, Palaemonidae) from São Sebastião Island, Southeastern Brazil // *Pan-Am. J. Aquat. Sci.* Vol.7. No.1. P.1–9.
- Mansur C.B., Hebling N.S. 2002. Análise comparativa entre a fecundidade de *Dilocarcinus pagei* Stimpson e *Sylviocarcinus australis* Magalhães & Türkay (Crustacea, Decapoda, Trichodactylidae) no Pantanal do Rio Paraguai, Porto Murtinho, Mato Grosso do Sul // *Rev. Bras. Zool.* Vol.19. P.797–805.
- Martins J., Ribeiro K., Rangel-Figueiredo T., Coimbra J. 2007. Reproductive cycle, ovarian development, and vertebrate-type steroids profile in the freshwater prawn *Macrobrachium rosenbergii* // *J. Crust. Biol.* Vol.27. No.2. P.220–228.
- Nakhodai S., Kamrani E., Mirzadeh M. 2013. Studies on the Morphological Aspects of the Reproductive Marsh Crab, *Sartoriana rokiatskyi*, in Geno (Southern Iran) // *Switzerland Res. Park. J.* Vol.102. P.293–299.
- Ng P.K., Guinot D., Davie P.J. 2008. *Systema Brachyurorum: Part I. An annotated checklist of extant brachyuran crabs of the world* // *Raffles Bull. Zool.* Vol.17. No.1. P.1–286.
- Oh C.W., Kim J.Y., Jeong I.J., Suh H.L., Cho Y.K. 2006. Reproduction and population dynamics of *Leptocheila gracilis* (Decapoda: Pasiphaeidae) on the western coast of Korea, Yellow Sea // *J. Mar. Biol. Assoc. U.K.* Vol.86. No.1. P.113–120.
- Parvizi E., Naderloo R., Keikhosravi A., Schubart C.D. 2017. Life history traits and patterns of sexual dimorphism in the freshwater crab *Potamon ibericum* (Bieberstein, 1809) (Decapoda: Brachyura: Potamidae) from the western Alborz Mountains, Iran // *J. Crust. Biol.* Vol.37. P.323–331.
- Pathre R.F., Patil M. 2010. Breeding cycle and fecundity of the freshwater crab, *Barytelphusa cunicularis* (Decapoda, Potamonidae) // *Worl. J. Zool.* Vol.5. No.2. P.96–102.
- Pillay K.K., Nair N.B. 1973. Observations on the biochemical changes in gonads and other organs of *Uca annulipes*, *Portunus pelagicus* and *Metapenaeus affinis* (Decapoda: Crustacea) during the reproductive cycle // *Mar. Biol.* Vol.18. No.3. P.167–198.

- Pinheiro A.P., Lins-Oliveira J.E. 2006. Reproductive biology of *Panulirus echinatus* (Crustacea: Palinuridae) from São Pedro and São Paulo Archipelago, Brazil // *Nauplius*. Vol.14. No.2. P.89–97.
- Rahman M.A., Rahman M.M., Ahmed A.T.A., Mollah A.R., Hossain M.A. 2008. A survey on the diversity of freshwater crabs in some wetland ecosystems of Bangladesh // *J. Sustain. Crop Prod.* Vol.3. P.10–17.
- Revathi P., Iyapparaj P., Munuswamy N., Krishnan M. 2012. Vitellogenesis during the ovarian development in freshwater female prawn *Macrobrachium rosenbergii* (De Man) // *Int. J. Aquat. Sci.* Vol.3. No.2. P.13–27.
- Robin N., Van Bakel B.W., Hyzny M., Cincotta A., Garcia G., Charbonnier S., Godefroit P., Valentin X. 2019. The oldest freshwater crabs: claws on dinosaur bones // *Sci. Rep.* Vol.9. No.1. P.1–14.
- Sahoo D., Panda S., Guru B.C. 2011. Studies on reproductive biology and ecology of blue swimming crab *Portunus pelagicus* from Chilika Lagoon, Orissa, India // *J. Mar. Biol. Assoc. U.K.* Vol.91. No.1. P.257–264.
- Sallam W.S. 2005. Population structure and biology of the crab *Dotilla sulcata* from Elgharqana Mangrove, South Sinai, Red Sea // *Egypt. J. Aquat. Res.* Vol.31. No.2. P.314–325.
- Sastry A.N., Vernberg F.J., Vernberg, W.B. 1983. Ecological aspects of reproduction // *Biol. Crust.* Vol.8. P.179–270.
- Senkman L.E., Negro C.L., Lopretto E.C., Collins P.A. 2015. Reproductive behaviour of three species of freshwater crabs of the family Trichodactylidae (Crustacea: Decapoda) including forced copulation by males // *Mar. Freshw. Behav. Physiol.* Vol.48. No.2. P.77–88.
- Sharifian S., Kamrani E., Dehghani M. 2017. Reproductive biology of *Sodhiana iranica* (Brachyura: Gecarcinucidae) from Southern Iran // *Rev. Biol. Trop.* Vol.65. No.1. P.365–373.
- Silva L.S., Martinelli-Lemos J.M., Ferreira M.A.P., Rocha, R. M. 2012. Gonadal development in the freshwater crab *Sylviocarcinus pictus* (H. Milne Edwards, 1853) (Brachyura: Trichodactylidae) from the Guamá River, state of Pará, Brazil // *An. Acad. Bras. Cienc.* Vol.84. P.789–798.
- Tao C., Wei L., Nan-Shan D. 1994. Growth, reproduction & population structure of the freshwater crab *Sinopotamon yangtsekiense* Bott, 1967, from zhejiang, China // *Chin. J. Oceanol. Limnol.* Vol.12. No.1. P.84–90.
- Thiele O.W. 1959. Die Lipide der Weinbergschnecke (*Helix pomatia* L.) // *Z. vergleich. Physiol.* Bd.42. H.5. S.484–491.
- Waiho K., Fazhan H., Baylon J.C., Madihah H., Noorbaiduri S., Ma H., Ikhwanuddin M. 2017. On types of sexual maturity in brachyurans, with special reference to size at the onset of sexual maturity // *J. Shellfish. Res.* Vol.36. No.3. P.807–839.
- Waiho K., Fazhan H., Zhang Y., Zhang Y., Li S., Zheng H., ... Ma H. 2019. Gonadal microRNA expression profiles and their potential role in sex differentiation and gonadal maturation of mud crab *Scylla paramamosain* // *Mar. Biotechnol.* Vol.21. No.3. P.320–334.
- Wu X., Cheng Y., Sui L., Yang X., Nan T., Wang J. 2007. Biochemical composition of pond-reared and lake-stocked Chinese mitten crab *Eriocheir sinensis* (H. Milne-Edwards) broodstock // *Aquac. Res.* Vol.38. No.14. P.1459–1467.
- Yamaguchi T. 2001. Seasonal change of the hepatopancreas index in the males of the fiddler crab, *Uca lacteal* // *Crustaceana.* Vol.74. No.7. P.627–634.
- Yeo D.C.J., Ng P.K.L., Cumberlidge N., Magalhães C., Daniels S.R., Campos M.R. 2008. Global diversity of crabs (Crustacea: Decapoda: Brachyura) in freshwater // *Hydrobiologia.* Vol.595. P.275–286.

Responsible editor A.A. Kotov