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COMPARATIVE STUDY ON THE LIFE-HISTORIES AND REPRODUCTION OF TWO SYMPATRIC SANDY-BEACH AMPHIPODS: *TALITRUS SALTATOR* AND *DESHAYESORCHESTIA DESHAYESII* (CRUSTACEA: TALITRIDAE) FROM BIZERTE BEACH (NORTH OF TUNISIA)

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POPULATION DYNAMICS
REPRODUCTIVE SEASON
LIFE CYCLE
COHORTS
TALITRIDAE
TALITRUS SALTATOR
DESHAYESORCHESTIA DESHAYESII

ABSTRACT. – The life history and reproductive activity of the two sympatric Amphipods *Deshayesorchestia deshayesii* (Audouin, 1826) and *Talitrus saltator* (Montagu, 1808) were studied through 18 months in Bizerte beach (37°19'17.1"N; 09°51'57.3"E). During this period, 6255 and 2152 specimens, respectively, of *Deshayesorchestia deshayesii* and *Talitrus saltator* were identified. The reproductive season extended from April to November for *D. deshayesii* and from March to November for *T. saltator*, with a sexual rest period during winter for both species. During the study period, three cohorts were identified on the first sampling date for *T. saltator* and twelve new cohorts were detected later, while *D. deshayesii* has presented six cohorts on the first sampling date and twelve new cohorts were detected during the study period. The life span was estimated at 4 to 10 months and at 5 to 7 months depending on the time of birth, respectively, for *D. deshayesii* and *T. saltator*. These results suggest that the two species can be considered as a semiannual species, with iteroparous females.

INTRODUCTION

Talitrid Amphipods are important members of the wrack fauna in the world (Persson 1999). They present an important ecological role as decomposers, and likewise they can be considered as a potential bio-indicator for the quality of sandy beaches (Ketmaier *et al*. 2003). This family is very large and includes 80 genera with about 512 species (Horton *et al*. 2018), that several has been studied worldwide us using different approaches. In Tunisia, the distribution, orientation, locomotor rhythm and biology of many Talitridae have been studied in different Tunisian sandy beaches and banks lagoons: Bizerte Corniche (Ayari & Nasri-Ammar 2012a, b), Bizerte lagoon (Jelassi *et al*. 2012, Jelassi & Nasri-Ammar 2013), Barkoukech beach (Nasri-Ammar & Morgan 2006), Zouaraa beach (Charfi-Cheikhrouha *et al*. 2000, Scapini *et al*. 2002, Marques *et al*. 2003, Bouslama 2009), Korba beach (Nasri-Ammar & Morgan 2005, Bouslama *et al*. 2007) and Gabes beach (Ayari & Nasri-Ammar 2011a, b). Moreover, the limited studies on reproduction were focused on *Talitrus saltator* collected from Korba Zouaraa (Marques *et al*. 2003, Bouslama *et al*. 2007), *Deshayesorchestia deshayesii* collected from Bizerte Corniche sandy beaches (Ayari-Akkari *et al*. 2014), *Britorchestia brito* collected from Zouaraa (Gonçalves *et al*. 2003), and *Orchestia montagui*, *O. mediterranea* and *O. gammarellus* from the supralittoral zone of Bizerte Lagoon (Jelassi *et al*. 2017). However, the present study aims to improve the knowledge regarding the reproductive biology and population dynamics on the talitrid family.

In this study, *Talitrus saltator* (Montagu, 1808) and *Deshayesorchestia deshayesii* (Audouin, 1826), detritivorous Amphipoda, which occupy the supralittoral zone on some Tunisian beaches (Williams 1982, Ayari & Nasri-Ammar 2008), have received special attention. The first one inhabits non-permanent burrows in sand (Scapini *et al*. 1992, Weslawski *et al*. 2000), while the second buries in the *Posidonia* banks, associated with some other macrophytes where it avoids desiccation (Scapini 1999) by burrowing between the fronds that constitute the banks themselves. These Talitridae are the most abundant Amphipods living in Bizerte beach with three other talitrids, *Orchestia gammarellus*, *O. mediterranea* and *O. montagui* (Ayari *et al*. 2011).

The present study was carried out to estimate the period of reproduction activity and biological parameters such as sex ratio and fecundity, in order to compare the annual cycle of growth of the two sympatric populations of *Talitrus saltator* and *Deshayesorchestia deshayesii* at Bizerte beach.

MATERIALS AND METHODS

Study area and field sampling: The study site, Bizerte beach, located in northern of Tunisia in the littoral area (37°19'17.1"N; 09°51'57.3"E) (Fig. 1), is characterized by the presence of benches of *Posidonia oceanica* and some algae such as *Ulva* sp., *Padina* sp., *Cymodocea nodosa*. that run parallel to the coast, as well as by non-significant tidal movements. This beach measures 9.5-19.5 m in width depending on the season (Table I).

Fieldwork was conducted each month, from June 2007 to December 2008, in the supra-littoral zone. Specimens of both species were collected by hand during the morning and sampling effort varied from 1 to 2 hours. Aside from the species of *Deshayesorchestia deshayesii*, that is one of the subject of this study, other talitrid species, *Orchestia gammarellus*, *O. mediterranea* and *O. montagui,* were collected within the bench of the vegetation near the shoreline, while *Talitrus saltator* were collected from their burrows in the sand in the same supra-littoral zone. Samples were transported to the laboratory in plastic boxes containing sand from the collection site. During the sampling, temperature and moisture of both air and sand were measured using a thermo-hygrometer.

Laboratory protocols: In the laboratory, with using a binocular microscope equipped with a micrometrical ocular lens, calibrated with objective micrometers, specimens collected were identified via the keys of Chevreux & Fage (1925) and Bellan-Santini (1993). After being identified, individuals were measured (cephalic and body lengths), counted and sexed for different categories: non-sexually differentiated juveniles, adult males, young females, non-reproductive females, reproductive females (with setae or with eggs/embryos) (Table I). Both animals and eggs were preserved in tubes containing 70° ethanol.

The total length (TL) was estimated from CL using linear equations (Marques *et al*. 2003).

The sex ratio was estimated by the ratio of males to females. The observed and expected values were compared using a χ^2 test.

Statistical analyses: Comparisons among mean total body size of the reproductive females and mean number of eggs was done through a one-way analysis of variance (ANOVA) using the XLSTAT 7.5.2 Software. The difference in cephalic length (CL) and total body length (TL) of all individuals were also tested between the two sympatric species.

The modal distributions were tracked in successive sample dates by means of size-class (0.04 mm) frequency analysis, which was carried out using the probability paper method (Harding 1949), as performed by Cassie (1954, 1963). Distributions are assumed to result from pulses in recruitment, conventionally referred to as cohorts. Computations used the ANAMOD software (Nogueira 1992), and the reliability of the distribution separation method was tested with both the χ^2 and G tests ($p \leq 0.05$).

Fig. 1. – Sampling sites.

Table I. – Structure and taxonomic composition of the Amphipod population from the supra-littoral zone of the Bizerte beach (June 2007-December 2008). YF: young female; NRF: non-reproductive female; RF: reproductive female.

		Deshayesorchestia deshayesii				*Talitrus saltator*				*Orchestia gammarellus*				*Orchestia mediterranea*				*Orchestia montagui*				
		♂	♀			♂	♀			♂	♀			♂	♀			♂	♀			
	Juveniles		YF	NRF	RF		YF	NRF	RF		YF	NRF	RF		YF	NRF	RF		FJ	NRF	RF	Total
Jun-07	290	113	103	31	158	1	1	4	12	5	1	7	26	8	4	4	1	2	0	0	0	771
Jull-07	304	103	168	69	128	0	0	0	4	0	0	2	0	1	0	0	0	1	0	1	0	781
Aug-07	26	37	23	45	55	0	0	0	3	2	0	2	0	0	0	0	0	4	0	8	0	205
Sept-07	130	80	102	13	48	31	20	31	7	0	0	0	0	0	0	0	0	0	1	0	0	463
Oct-07	356	90	108	0	138	33	4	13	3	1	1	1	0	0	0	0	0	0	0	0	0	748
Nov-07	445	47	291	61	62	47	44	9	4	5	24	5	0	0	0	2	0	1	0	0	0	1047
Dec-07	32	0	50	19	0	6	14	2	0	1	0	2	0	0	0	0	0	0	0	0	0	126
Jan-08	448	31	246	172	0	20	53	45	0	6	27	19	0	0	0	0	0	0	0	0	0	1067
Feb-08	50	9	43	28	0	9	11	19	0	1	1	1	0	0	0	0	0	0	0	0	0	172
Mar-08	21	13	78	33	0	4	9	19	1	2	1	2	0	0	0	0	0	0	0	0	0	183
Apr-08	0	94	91	74	56	22	5	27	2	0	0	0	0	0	0	0	0	0	0	0	0	371
May-08	153	58	98	27	107	108	15	7	17	1	0	3	2	0	0	0	0	0	0	0	0	596
Jun-08	361	61	94	49	123	38	28	27	13	6	1	3	10	0	0	0	0	4	0	1	0	819
Jull-08	10	13	5	19	10	20	34	42	3	1	0	0	1	0	0	0	0	0	0	0	0	158
Aug-08	2	15	14	14	24	60	9	21	6	5	0	5	1	0	0	0	0	2	0	5	1	184
Sept-08	197	47	38	8	55	84	8	23	13	0	0	0	0	0	0	0	0	0	0	0	0	473
Oct-08	18	7	15	6	23	26	37	21	2	3	2	2	1	0	0	0	0	0	0	0	0	163
Nov-08	83	7	45	11	1	55	67	47	1	1	0	2	0	0	0	0	0	0	0	0	0	320
Dec-08	23	4	40	5	0	23	13	22	0	0	0	0	0	0	0	0	0	0	0	0	0	130
Total	2949	829	1652	684	988	587	372	379	91	40	58	56	41	9	4	6	1	14	1	15	1	8777

RESULTS

Description of the sampling site

The sampling lasted 18 months from June 2007 until December 2008. Each time, temperature and relative moisture of both sand and air were measured. Figures 2 and 3 show that, throughout the study period, the air temperature was higher than that of the sand, while the reverse is true for the relative moisture.

Population structure

Table I summarizes the structure, taxonomic composition and number of the different Talitridae categories at the sampling dates (June 2007-December 2008) from the supra-littoral zone of the Bizerte beach. The number of animals collected monthly ranged from 130 to 1067 and the total number of all species was 8777 individuals.

The study of the structure of populations of *Deshayesorchestia deshayesii* and *Talitrus saltator* showed that the

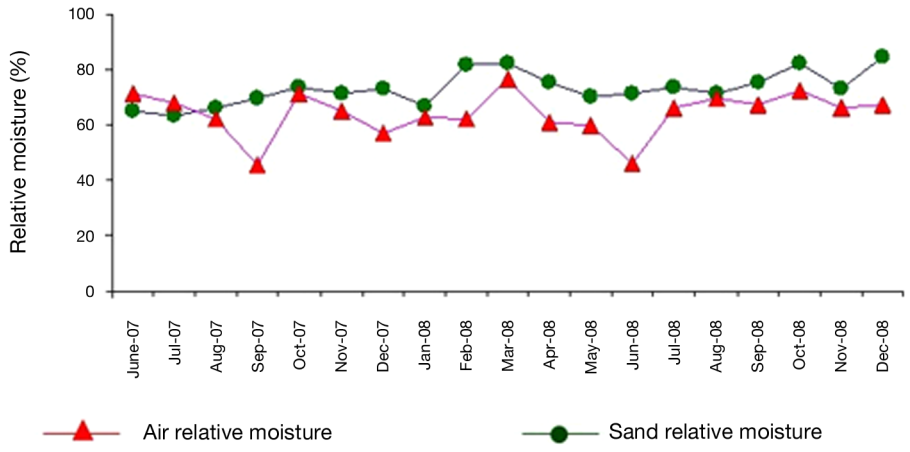

Fig. 2. – Monthly variation of air and sand moisture during the study period.

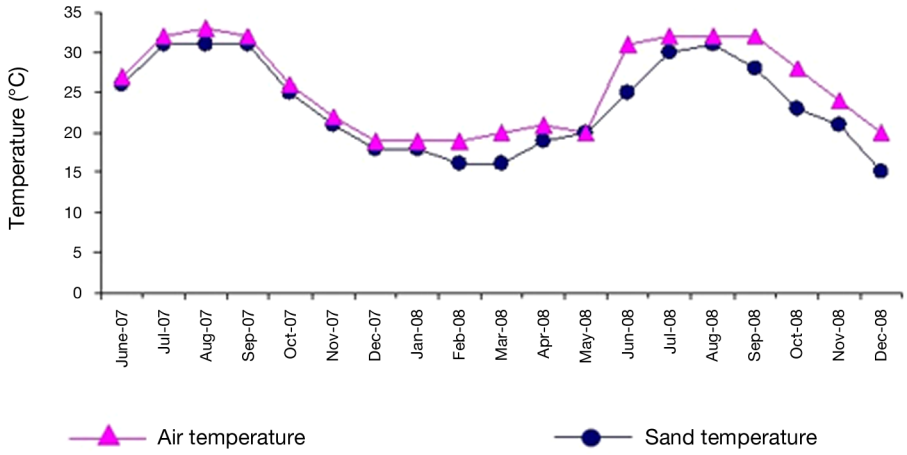

Fig. 3. – Monthly variation of air and sand during the study period.

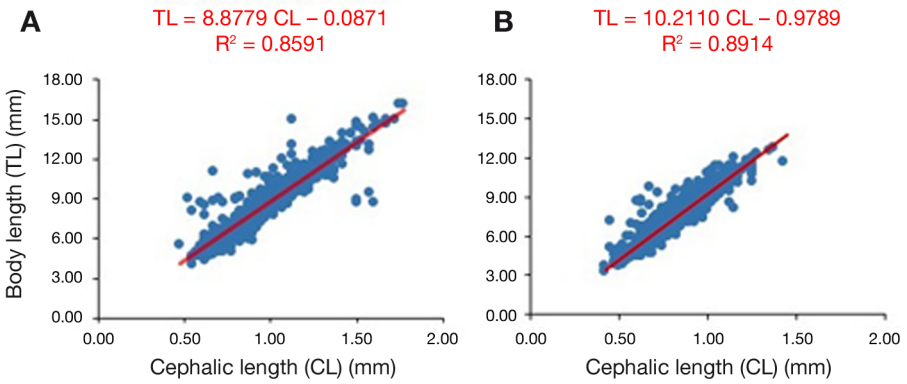

Fig. 4. – Relation between body length (BL) and cephalic length (CL) of *Talitrus saltator* (**A**) and *Deshayesorchestia deshayesii* (**B**) on Bizerte beach.

first species was present with 6255 specimens distributed in 13.3 % of males, 53.1 % of females with all categories (young females, non-reproductive females and reproductive females) and 33.6 % juveniles; 2152 individuals were identified as *T. saltator* and divided into 27.2 % males, 39.1 % females with all categories and 33.7 % undifferentiated (Table I).

Moreover, the monitoring of the Amphipods structure and composition (Table I) highlighted the presence of five species belonging to the Talitridae family namely: *D. deshayesii*, *T. saltator*, *Orchestia gammarellus*, *O. montagui* and *O. mediterranea*. These last two species are qualified, respectively, as accessory and rare species, while the first three ones are called common species among which *D. deshayesii* and *T. saltator* are the most dominant (Table II).

Table II. – Frequency and constancy of the studied species.

	Frequency (%)	Constancy
Deshayesorchestia deshayesii	100	common species
Talitrus saltator	100	common species
Orchestia gammarellus	83	common species
Orchestia montagui	39	accessory species
Orchestia mediterranea	17	rare species

Relationship between cephalic length and body length

Since that cephalic length (CL) was a more reliable measurement than body length (TL) due to the curvature of the body, the CL was measured for each specimen, while the TL was measured for 682 and 1541 specimens, respectively, for *T. saltator* and *D. deshayesii*. In fact, the body and cephalic lengths were measured accurately to allow all CL to be converted to TL.

The relationship between TL and CL was:
for *T. altator*: TL = 8.8779 CL – 0.0871 (Fig. 4);
for *D. deshayesii*: TL = 10.2110 CL – 0.9789 (Fig. 4).

Sex ratio

The structure of the population of *Deshayesorchestia deshayesii* and *Talitrus saltator* showed, respectively, a total number of females equal to 3324 and 842 individuals (including all categories) and only 829 and 587 male individuals. The sex ratio revealed a clear difference between the two sympatric species.

Consequently, for *D. deshayesii,* the sex ratio was strongly biased in favor of female throughout the study period (18 months) and the overall sex-ratio was equal to 0.21. For *T. saltator*, we revealed the dominance of males over females in the population during six months of the

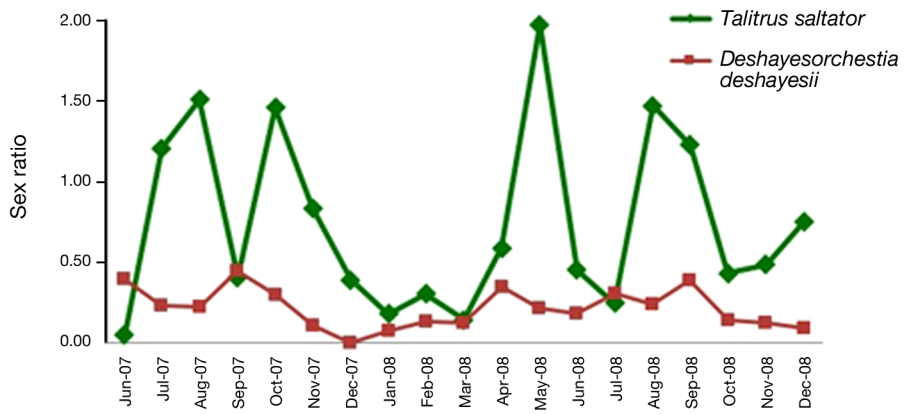

Fig. 5. – Monthly variation of the sex ratio of *Talitrus saltator* and *Deshayesorchestia deshayesii* during the study period.

study period: July, August and October of 2007 and May, August and September of 2008 and the overall sex-ratio was equal to 0.74. (Fig. 5).

Fecundity

Egg number per brood pouch was counted and the development state of eggs was determined for each ovigerous female for both species. Only ovigerous females during the earlier stages of development of eggs were considered to be sure that they did not have a loss. Thus, fecundity varied between 2 and 12 eggs and the total body length of these females between 7.5 and 11 mm for *T. saltator*, while it varied between 4 and 17 eggs and the body length between 4.6 and 10.7 mm for and *D. deshayesii*.

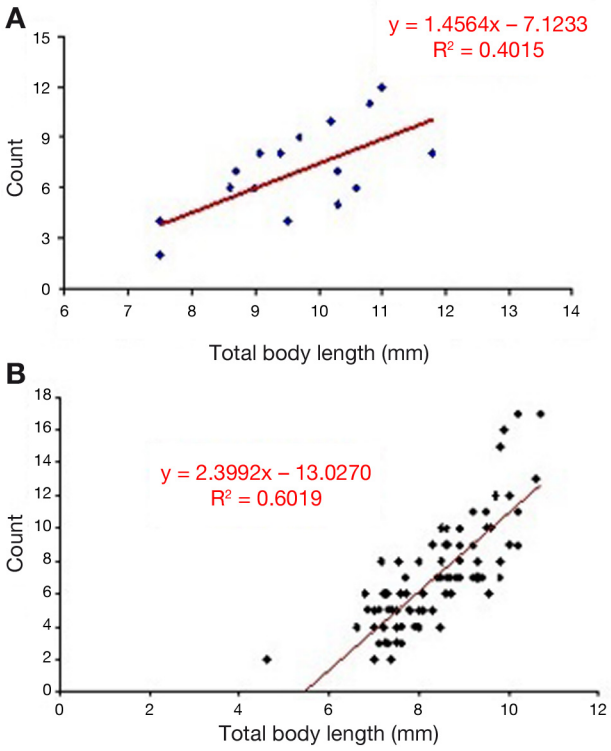

Fig. 6. – Relationship between the number of eggs in the brood pouch and total body length of females (mm) in *Talitrus saltator* (**A**) and *Deshayesorchestia deshayesii* (**B**) on Bizerte beach.

Fecundity estimated by the number of eggs inside the marsupium for both species was positively correlated with female total body length ($p < 0.0001$) for *T. saltator* ($r^2 = 0.4015$) and *D. deshayesii* ($r^2 = 0.6019$) (Fig. 6).

Growth and life span

Size-frequency distributions were estimated for the recognition of cohorts in two sympatric sandy-beach from the Bizerte beach. During the first sampling in June 2007, three and six cohorts were recognized, respectively, for *T. saltator* and *D. deshayesii* and twelve new distributions were detected along the study period for both species. Moreover, these 12 new cohorts appeared monthly; beginning of July 1, 2007.

On the one hand, for *T. saltator*, the minimum average cephalic length (CL) of new cohorts ranged from 0.35 and 0.63 mm corresponding, respectively, to a total body length (TL) varying between 2.25 mm and 5.00 mm. Whereas, the maximum values of CL ranged from 1.03 to 1.49 mm correspondingly to a TL between 12.90 to 16.20 mm (Fig. 7A). On the other hand, for *D. deshayesii*, the minimum average cephalic length (CL) of new cohorts ranged from 0.34 to 0.53 mm corresponding, respectively, to a total body length (TL) varying between 2.25 mm and 5.00 mm. Whereas, the maximum values of CL ranged from 0.93 to 1.24 mm correspondingly to a TL between 8.80 to 12.00 mm (Fig. 7B). Statistical analysis revealed a highly significant difference between the all values of TL of the two sympatric species ($p < 0.0001$).

Furthermore, growth appeared to be continuous over the life span for the two species. Thus, seasonality was observed in this growth and individuals had a life expectancy of 4 to 10 months and 5 to 7 months, corresponding respectively to *T. saltator* and *D. deshayesii* (Fig. 7A, B).

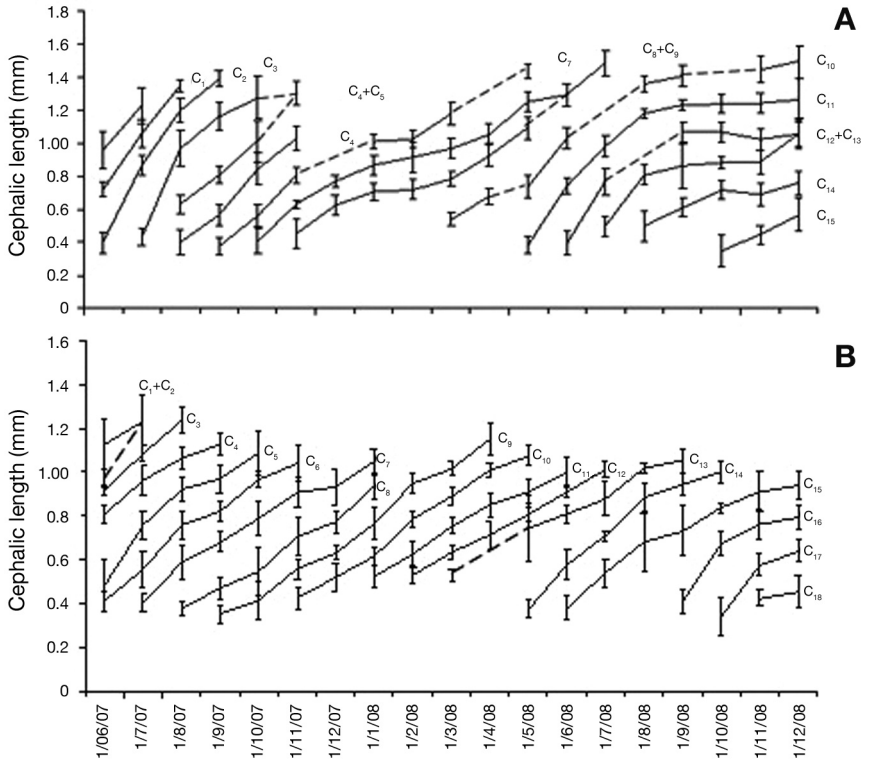

Fig. 7. – Estimated growth and life span (field growth data) of the cohorts or groups of cohorts at Bizerte beach (average cephalic length (mm) ± standard deviation) during the study period in *Talitrus saltator* (**A**) and *Deshayesorchestia deshayesii* (**B**). Broken lines indicate probable cohort merging or cohort development over time.

Life cycle

To identify the male and ovigerous female belonged cohorts and their contribution in recruitment, frequency size analysis was performed for the two sympatric species. For *D. deshayesii*, cohorts born early at the reproductive period, such as cohorts 13 and 14, tend to have a shorter life than those born at the end of this period, corresponding to late fall/early winter, as cohorts 9 and 10. In fact, these last cohorts survive the winter and bred in the next reproductive period (Fig. 8A). While, for *T. saltator*, cohorts born during the late winter/early spring breeding season, such as the C10 cohort, will continue to breed in the same season, but probably would not survive winter. Contrarily to those born in the late summer/early fall, such as the C7 and C8 cohorts surviving the winter, from which they will survive longer, and reach sexual maturity in the following spring (Fig. 8B).

Therefore, both species are described as a semi-annual species, with iteroparous females having the ability to reproduce twice or more in their lifetime. Furthermore, as well for *T. saltator* as for *D. deshayesii* from Bizerte beach, their population produces two generations per year. In fact, they are considered species with bivoltine life cycle.

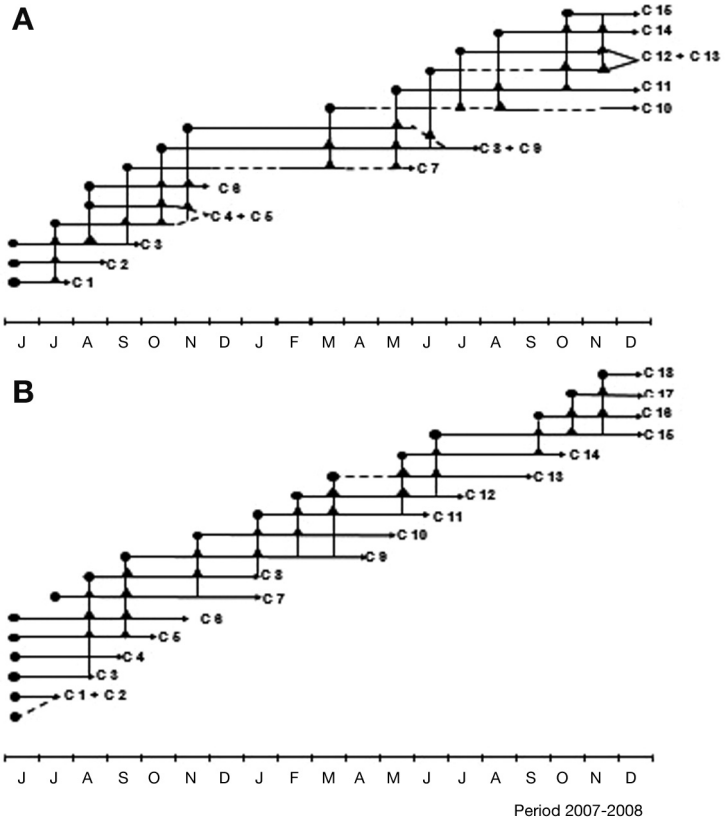

Fig. 8. – Analysis of the recruitment pattern of the population of two sympatric sandy beach *Talitrus saltator* (**A**) and *Deshayesorchestia deshayesii* (**B**). The horizontal arrows represent the period during which the cohort was followed in the study period, starting in the solid circles. The assumed contributions of each cohort or group of cohorts are indicated (triangles). Contributions of the various cohorts to recruitment are indicated.

DISCUSSION AND CONCLUSION

Talitrid Amphipods have been extensively studied along Mediterranean coasts (Scapini *et al*. 1992, Fallaci *et al*. 1999, Bouslama 2009, Ayari *et al*. 2011, Jelassi *et al*. 2017). *Talitrus saltator* and *Deshayesorchestia deshayesii* are nocturnal, detritivorous Amphipoda, which occupy the supralittoral zone on some Tunisian beaches (Ayari & Nasri-Ammar 2008). The first species, considered as special type, was widely studied in the world while the second presented a paucity of information.

The monitoring of the structure and composition of the Amphipods at Bizerte beach was carried out monthly from June 2007 to December 2008. During this study period, *T. saltator* and *D. deshayesii* are the most dominant in this ecosystem (Ayari & Nasri-Ammar 2011a). Indeed, the very high abundance of *D. deshayesii* in comparison with *T. saltator* is probably related to the characteristics of their biotopes: *D. deshayesii* live under benches of *Posidonia oceanica* where the humidity is constant, the dangers of predation and desiccation are limited and the food is abundant, while *T. saltator* dig their burrows on sand where sunshine and predation are greater, suggesting that population abundance depends on their biotope.

Results corresponding to the total and cephalic length of individuals of both species revealed, on the one hand, that the total length and the cephalic length of the undifferentiated varied, respectively, between 2.25-5.00 mm and 0.20-0.60 mm. On the second hand, that the specimens sexually differentiated of *T. saltator* presented larger sizes than those of *D. deshayesii* and this regardless of sex. Thus, the total length of *T. saltator* and *D. deshayesii* males and females varied between 4.70-16.20 mm, 4.60-14.30 mm, 4.70-12 mm and 3.80-11 mm, respectively. Concerning the cephalic length, it was between 0.6-1.7 mm, 0.5-1.6 mm, 0.7-1.4 mm and 0.5-1.5 mm, respectively. In fact, these previously mentioned differences in the two sympatric species *D. deshayesii* and *T. saltator* are at the origin of a variability between the genetic structures of each species as demonstrated by De Matthaeis *et al*. (2000). These morphological differences also existed between populations of the same species, accentuated with the geographical temperature gradient as well as the ecological characteristics of the biotope. Moreover, Scapini (1999) revealed morphological differences between Mediterranean and Atlantic populations of *T. saltator* without correlating them to a geographical gradient, but rather to the local ecological characteristics specific to the two environments.

The study of the sex ratio of *Deshayesorchestia deshayesii*, from Bizerte beach, showed that it was biased in favor of females throughout the study period (18 months). However, for *Talitrus saltator*, we highlighted a different result where the imbalance was reversed in favor of males during the months of July, August and October (2007) and May, August and September (2008). In fact, males of *T. saltator* were present in greater numbers during the reproduction season. A female-biased sex ratio is very common in Amphipods as has been described for *Orchestia gammarellus* (Jones & Wigham 1993, Persson 1999, Dias & Sprung 2004, Jelassi *et al*. 2017), *Peudorchestoidea brasiliensis* (Cardoso & Veloso 1996), *Talorchestia capensis* (Van Senus 1988), *Orchestia mediterranea* (Jelassi *et al*. 2017) and also in *T. saltator* and *Talorchestia brito* from Zouaraa beach (Charfi-Cheikhrouha *et al*. 2000). This substantial difference between males and females can be explained by a significant mortality of older males contributing to the coupling or by the presence of a feminizing bacteria *Wolbachia*-type revealed in several species of isopods (Rigaud *et al*. 1997) and in some species of Amphipods as *D. deshayesii* and *O. gammarellus* (Cordaux *et al*. 2001). *Wolbachia* are intracellular maternally inherited alpha-proteobacteria infecting a wide range of arthropods, that can convert genetically males into functional females, which typically produce, in turn, female-biased progenies (Rigaud *et al*. 1997). Moreover, a sex-ratio biased in favor of males was revealed in the populations of *T. saltator* from Collelungo beach (Italy) and Lavos beach (Portugal) (Marques *et al*. 2003).

Additionally, a positive correlation between the fecundity and the body length of ovigerous females was established. This result confirms those observed in *T. saltator* at the Atlantic coast (Williams 1978), in *Neohaustorius schmitzi* at the North of Carolina (Dexter 1971), in *T. saltator* from Korba beach in Tunisia (Bouslama 2009) and in *O. gammarellus* and *O. mediterranea* from Bizerte lagoon (Jelassi *et al*. 2017)

During the study period, we have noticed, for both sympatric species *T. saltator* and *D. deshayesii*, that the two populations are characterized by a seasonal reproductive period. Thus, for *T. saltator*, reproductive and recruitment activity extends from March to November with a three-month rest period from December to February. Whereas, for *D. deshayesii,* this rest period is about four months from March to December and the reproductive period and recruitment extends from April to November. In fact, seasonal reproduction is also observed in several populations of Amphipods such as the population of *O. mediterranea* from the Medway estuary in Great Britain, characterized by a period of sexual rest spanning from October to mid-April (Wildish 1979) and populations from Languedoc ponds in southern France with a rest period from November to mid-March (Louis 1977). In addition, Marsden (1991), Williams (1978) and Persson (1999) have showed that this type of reproduction is revealed respectively in *Talorchestia quoyana* (New Zealand), *T. saltator* (Atlantic coast) and *O. gammarellus* (Baltic Sea). Otherwise, other populations of Amphipods are characterized by a continuous reproductive cycle with the presence of ovigerous females throughout the year, as in the populations of *O. gammarellus*, *O. montagui* and *O. mediterranea*

collected from the banks of Bizerte lagoon (Jelassi *et al*. 2017). These results suggest that the strategy of reproduction, either seasonal or continuous, seems to be correlated with the geographic gradient, the temperature and also the photoperiod. Marques *et al*. (2003) have shown in populations of Italian and Portuguese *T. saltator* that recruitment periods were shorter in the north and much longer in the south.

In conclusion, the analysis of the life history of the two sympatric Amphipods, *Deshayesorchestia deshayesii* and *Talitrus saltator* from the supralittoral of the Bizerte beach showed a reproductive period followed by sexual rest with more or less similar durations. Both species are described as a semi-annual species, with iteroparous females having the ability to reproduce twice or more in their lifetime. Furthermore, as well for *T. saltator* as for *D. deshayesii*, their population produces two generations per year. In fact, they are considered species with bivoltine life cycle and fecundity was positively correlated with female size.

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REFERENCES

Ayari A, Nasri-Ammar K 2008. Étude expérimentale comparative du rythme locomoteur de deux Amphipodes supralittoraux sympatriques de la plage de Bizerte (Tunisie) : *Talitrus saltator* et *Talorchestia deshayesii*. *Bull Soc Zool Fr* 133: 159-167.

Ayari A, Nasri-Ammar K 2011a. Distribution and biology of Amphipods on two geomorphologically different sandy beaches in Tunisia. *Crustaceana* 84: 591-599.

Ayari A, Nasri-Ammar K 2011b. Locomotor rhythm phenology of *Talitrus saltator* from two geomorphologically different beaches of Tunisia: Bizerte (North of Tunisia) and Gabes Gulf (South of Tunisia). *Biol Rhythm Res* 43: 113-123.

Ayari A, Nasri-Ammar K 2012a. Seasonal variation of the endogenous rhythm in two sympatric Amphipods: *Talitrus saltator* and *Talorchestia deshayesii* from Bizerte beach (northern Tunisia). *Biol Rhythm Res* 43:515-526.

Ayari A, Nasri-Ammar K 2012b. Locomotor rhythm phenology of *Talitrus saltator* from two geomorphologically different beaches of Tunisia: Bizerte (North of Tunisia) and Gulf of Gabes (South of Tunisia). *Biol Rhythm Res* 43:113-123.

Ayari A, Bohli D, Nasri-Ammar K 2011. Population dynamics and structure of Talitrid Amphipods from Bizerte beach (North of Tunisia). *In* Bayed A ed, Sandy Beaches and Coastal Zone Management. Fifth Int Symp on Sandy Beaches, 2009 Oct 19-23, Morocco (Rabat): *Trav Inst Sci* Rabat 6: 15-19.

Ayari-Akkari A, Jelassi R, Khemaissia H, Nasri-Ammar K 2014. Life history of the sandy beach Amphipod *Deshayesorchestia deshayesii* (Crustacea: Talitridae) from Bizerta beach (North of Tunisia). *Invert Reprod Develop* 58(4): 269-277.

Bellan-Santini D, Karaman G, Krapp-Schickel G, Ledoyer M, Ruffo S 1993. The Amphipoda of Mediterranean. Part III: Gammaridea (Melphidippidae to Talitridae), Ingolfiellidae, Caprellidae. *Mém Inst Océanogr Monaco* 13: 813 p.

Bouslama MF 2009. Étude comparative de la dynamique et de la génétique de populations de quelques espèces de Talitridés en Tunisie (Crustacea, Amphipoda). Thèse de doctorat Université de Tunis, Tunisie: 208 p.

Bouslama MF, Neto JM, Charfi-Cheikhrouha F, Marques JC 2007. Biology, population dynamics and secondary production of *Talitrus saltator* (Amphipoda, Talitridae) at Korba beach (east coast of Tunisia). *Crustaceana* 80: 1103-1119.

Cardoso RS, Veloso VG 1996. Population biology and secondary production of the sandhopper *Pseudorchestoidea brasiliensis* (Amphipoda: Talitridae) at Prainha Beach. *Brazil*. *Mar Ecol Progr Ser* 142: 111-119.

Cassie RM 1954. Some uses of probability paper in the analysis of size-frequency distributions. *Aust J Mar Freswh Res* 3: 513-522.

Cassie RM 1963. Tests of significance for probability paper analysis. *N Z Sci Rev* 6: 474-482.

Charfi-Cheikhrouha F, El Gtari M, Bouslama MF 2000. Distribution and reproduction of two sandhoppers, *Talitrus saltator* and *Britorchestia brito* from Zouaraa (Tunisia). *Polsk Arch Hydrobiol* 43: 621-629.

Chevreux E, Fage L 1925. Faune de France : Amphipodes. Office Central de Faunistique de la Fédération Française des Sociétés de Sciences Naturelles (Ed), Paris 9: 488 p.

Cordaux R, Michel-Salzat A, Bouchon D 2001. *Wolbachia* infection in crustaceans: novel hosts and potential routes for horizontal transmission. *J Evol Biol* 14: 237-243.

De Matthaeis E, Ketmaier V, Davolos D, Schembri PJ 2000. Patterns of genetic diversity in Mediterranean supralittoral Amphipods (Crustacea, Amphipoda). *Polsk Arch Hydrobiol* 47: 473-487.

Dexter DM 1971. Life history of the sandy-beach Amphipod *Neohaustorius schmitzi* (Crustacea: Haustoriidae). *Mar Biol* 8: 232-237.

Dias N, Sprung M. 2004. Population dynamics and production of the Amphipod *Orchestia gammarellus* (Talitridae) in a Ria Formosa saltmarsh (Southern Portugal). *Crustaceana* 76: 1123-1141.

Fallaci M, Aloia A, Audoglio M, Colombini I, Scapini F, Chelazzi L 1999. Differences in behavioural strategies between two sympatric talitrids (Amphipoda) inhabiting an exposed sandy beach of the French Atlantic coast. *Estuar Coast Shelf Sci* 58: 469-482.

Gonçalves SC, Marques JC, Pardal MA, Bouslama MF, El Gtari M, Charfi-Cheikhrouha F 2003. Comparison of the biology, dynamics, and secondary production of *Britorchestia brito* (Amphipoda, Talitridae) in Atlantic (Portugal) and Mediterranean (Tunisia) populations. *Estuar Coast Shelf Sci* 58: 901-916.

Harding JP 1949. The use of probability paper for the graphical analysis of polymodal frequency distributions. *J Mar Biol Ass U K* 28: 141-153.

Horton T, Lowry J, De Broyer C, Bellan-Santini D, Coleman CO *et al*. 2018. World Amphipoda Database. *Talitridae Rafinesque*, 1815. Accessed through: World Register Mar Spec at: http://www.marinespecies.org/aphia.php?p=taxdetails&id=101411 on 2018-08-30.

Jelassi R, Nasri-Ammar K 2013. Seasonal variation of locomotor activity rhythm of *Orchestia montagui* in the supralittoral zone of Bizerte lagoon (North of Tunisia). *Biol Rhythm Res* 44:718-729.

Jelassi R, Khemaissia H, Nasri-Ammar K 2012. Intra-annual variation of the spatiotemporal distribution and abundance of Talitridae and Oniscidea (Crustacea, Peracarida) at Bizerte Lagoon (northern Tunisia). *Afr J Ecol* 50: 381-392.

Jelassi R, Bouslama MF, Khemaissia H, Nasri-Ammar K 2017. Biology and population dynamics of three sympatric talitrid species (Crustacea: Amphipoda) from the supralittoral zone of Bizerte Lagoon, Northern Tunisia. *Acta Zool Bulg* 69(1):71-88.

Jones MB, Wigham GD 1993. Reproductive biology of *Orchestia gammarellus* Crustacea: Amphipoda living in a sewage treatment works. *J Mar Biol Ass U K* 73: 405-416.

Ketmaier V, Scapini F, De Matthaeis E 2003. Exploratory analysis of talitrid population genetics as an indicator of the quality of sandy beaches. *Estuar Coast Shelf Sci* 58(S): 159-167.

Louis M 1977. Étude des populations de Talitridae des étangs littoraux Méditerranéens I. variations des effectifs au sein des différentes phases et interprétation. *Bull Ecol* 8: 63-74.

Marques JC, Gonçalaves SC, Pardal MA, Chelazzi L, Colombini I, Fallaci M, Bouslama MF, El Gtari M, Charfi-Cheikhrouha F, Scapini F 2003. Comparison of *T. saltator* (Amphipoda, Talitridae) biology, dynamics and secondary production in Atlantic (Portugal) and Mediterranean (Italy and Tunisia) populations. *Estuar Coast Shelf Sci* 58: 127-148.

Marsden ID 1991. Kelp-sandhopper interactions on a sand beach in New Zealand. II. Population dynamics of *Talorchestia quoyana* (Milne-Edwards). *J Exp Mar Biol Ecol* 152: 75-90.

Nasri-Ammar K, Morgan E 2005. Variation saisonnière du rythme de l'activité locomotrice de *Talitrus saltator* issu de la plage de Korba (Cap Bon, Tunisie). *Bull Soc Zool Fr* 130: 19-29.

Nasri-Ammar K, Morgan E 2006. Seasonality of the endogenous activity rhythm in *Talitrus saltator* (Montagu) from a sandy beach in northeastern Tunisia. *Biol Rhythm Res* 37: 479-488.

Nogueira A 1992. ANAMOD – Extracção dos componentes modais de distribuições de frequências de variáveis biométricas. Coimbra : Trabalho de Síntese, Provas de Aptidão Pegagógicae de Capacidade Científica, Universidade de Coimbra: 1-67.

Persson LE 1999. Growth and reproduction in two brackish water populations of *Orchestia gammarellus* (Amphipoda: Talitridae) in the Baltic Sea. *J Crustacean Biol* 19: 53-59.

Rigaud T, Antoine D, Marcade I, Juchault P 1997. The effect of temperature on sex ratio in the isopod *Porcellionides pruinosus*: environmental sex determination or by-product of cytoplasmic sex determination. *Evol Ecol* 11: 205-215.

Scapini F 1999. Tendances initiales et ajustement des systèmes d'orientation chez les Talitres. Paris: Hermes Science Publications: 426 p.

Scapini F, Chelazzi L, Colombini I, Fallaci M 1992. Surface activity, zonation and migration of *Talitrus saltator* on a Mediterranean beach. *Mar Biol* 112: 573-581.

Scapini F, Aloia A, Bouslama MF, Chelazzi L, Colombini I, El Gtari M, Fallaci M, Marchetti GM 2002. Multiple regression analysis of the source of variation in orientation of two sympatric sandhoppers, *Talitrus saltator* and *Talorchestia brito*, from an exposed Mediterranean beach. *Behav Ecol Sociobiol* 51: 403-414.

Van Senus P 1988. Reproduction of the Sandhopper, *Talorchestia Capensis* (Dana) (Amphipoda, Talitridae). *Crustaceana* 55: 93-103.

Weslawski JM, Stanek A, Siewert A, Beer N 2000. The sandhopper (*Talitrus saltator* Montagu, 1808) on the Polish Baltic Coast. Is it a victim of increased tourism? *Oceanol Stud* 29: 77-87.

Wildish DJ 1979. Reproductive consequences of the terrestrial habit in *Orchestia* (Crustacea: Amphipoda). *Int J Invertebr Reprod* 1: 9-20.

Williams JA 1978. The annual pattern of reproduction of *Talitrus saltator* (Crustacea: Amphipoda: Talitridae). *J Zool Lond* 184: 231-244.

Williams JA 1982. Environmental influence on the locomotor activity rhythm of the sand shore Amphipod, *Talorchestia deshayesii*. *Mar Biol* 69: 69-71.

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