

Biology and Population Dynamics of Three Sympatric Talitrid Species (Crustacea: Amphipoda) from the Supralittoral Zone of Bizerte Lagoon, Northern Tunisia

Raja Jelassi^{1,2}, Mohamed Fadhel Bouslama², Hajer Khemaissia² & Karima Nasri-Ammar²

¹Institut National des Sciences et Technologies de la Mer, Salammbô

²Université de Tunis El Manar, Faculté des sciences de Tunis, Unité de Recherche de Bio-Ecologie et Systématique Evolutive El Manar II, 2092; E-mail: djelassi.raja@gmail.com

Abstract: We studied the biology, population dynamics and reproduction of three sympatric species of talitrid amphipods, *Orchestia montagui* Audouin, 1826, *O. mediterranea* Costa, 1853 and *O. gammarellus* (Pallas, 1766) from the supralittoral zone of Bizerte Lagoon. A total of 10,126 specimens were collected from July 2006 to June 2007. These species were characterised by a continuous reproduction with the presence of ovigerous females throughout the year. The average sex-ratio was male-biased in *O. montagui* and female-biased in *O. gammarellus* and *O. mediterranea*. The life span was estimated at 6-7 months, 7-8 months and 5-8 months, respectively. Cohorts born in summer tended to live longer than the ones born in winter. At the supralittoral zone of Bizerte Lagoon, *O. montagui*, *O. gammarellus* and *O. mediterranea* appeared as semiannual species, with iteroparous females which produced at least two broods per year and exhibited a bivoltine life cycle.

Key words: Supralittoral, Bizerte Lagoon, population dynamics, biology, *Orchestia montagui*, *Orchestia gammarellus*, *Orchestia mediterranea*

Introduction

The Talitridae is the only family of amphipods with truly terrestrial species, and although many are found close to the sea on the upper parts of the shore, some occur at considerable distances inland (LINCOLN 1979). It is a very large family that includes different genera (*Talitrus*, *Deshayesorchestia*, *Britorchestia*, *Orchestia* and *Platorchestia*) with about 250 species. Talitrid amphipods are important members of the wrack fauna throughout the world (PERSSON 1999). *Orchestia* is a large cosmopolitan genus comprising more than 70 recognised species which are semiterrestrial, typically living amongst intertidal stones and algae, although some are found inland, and may occur several hundred metre above sea level (LINCOLN 1979)

In Tunisia eight species of Talitridae are found in some wetlands especially in Bizerte Lagoon (JELASSI & NASRI-AMMAR 2012; JELASSI *et al.* 2012, 2013c, 2015). Owing to their ecological importance, the talitrid family has been studied worldwide us-

ing different approaches. Many studies focused on the factors influencing their spatial distribution and oriented movements on sandy beaches (EL GTARI *et al.* 2014; JELASSI *et al.* 2013c; BORGIOLO *et al.* 1999; SCAPINI *et al.* 1995). Other studied talitrid behaviour (AYARI & NASRI-AMMAR 2012a,b; JELASSI & NASRI-AMMAR 2013; JELASSI *et al.* 2013ab) and genetic determination of different behaviours (SCAPINI *et al.* 1993; SCAPINI 1997). With regard to biodiversity, talitrid populations have been compared genetically to assess inter and intra-specific variations (DE MATTHAEIS *et al.* 1995). Moreover, papers have been published on trace metals concentrations and bioaccumulation by talitrids, and on their role in biomonitoring (WEEKS 1992; FIALKOWSKI *et al.* 2000).

In Tunisia the few studies on talitrid reproduction were focused on the sandhopper *Talitrus saltator* collected from Korba (BOUSLAMA *et al.* 2007) and Zouaraa (MARQUES *et al.* 2003), *Britorchestia*

brito collected from Zouaraa (CONÇALVES 2003) and *Deshayesorchestia deshayesii* collected from Bizerte Corniche sandy beaches (AYARI-AKKARI *et al.* 2014). These authors showed that the three species were characterised by a seasonal reproduction.

Population size, reproductive strategies and potential for dispersal between habitats are usually considered to reflect evolutionary fitness (MARQUES *et al.* 2003). However, there is lack of knowledge regarding the reproductive biology and population dynamics of *Orchestia* species. To better understand the different adaptive strategies of *O. montagui*, *O. gammarellus* and *O. mediterranea*, sympatric species living in the supralittoral zone of Bizerte Lagoon, a comparative study was carried out, focusing on their main life history traits.

Materials and Methods

The Bizerte Lagoon is a coastal lagoon in north-eastern Tunisia between 37°8'-14'N and 9°46'-56'E. It is connected to the Mediterranean Sea by a canal that is 11.3 km long, 300 m wide and 13 m deep. It is also connected to the Garaet Ichkeul Lagoon through Tinja River. In winter a surplus of fresh water is discharged from the Garaet Ichkeul to Bizerte Lagoon through Tinja River, whereas during summer this river allows sea water to enter Garaet Ichkeul across the Bizerte Lagoon. Specimens were sampled within the supralittoral zone of Bizerte Lagoon, at Menzel Jmil (37°13'8"N 09°55'1"E; Fig. 1). Temperature was measured in situ using a thermo-hygrometer. It varied between 15.95°C in January and 30.98°C in August (Fig. 2). The site was divided into five sampling zones according to its plant association. These zones, together with the algal associations, were classified as:

- Zone 1: characterised by the presence of *Cymodocea* wrack mounds (or banquettes). Its width varied between 1.4 m during the summer period and 4.8 m during the winter.

- Zone 2: its vegetation was composed by *Suaeda maritima* only with width varying from 1.6 m in the autumn to 3.5 m in summer season.

- Zone 3: characterised by the association of *Suaeda maritima*, *Salicornia arabica* and *Obione portulacoides* with a distribution that did not exceed 7 m.

- Zone 4: *Obione portulacoides* was the dominant plant at this site and was present throughout the year. The width of this zone ranged between 7.8 m during the autumn and 12.6 m during the spring season.

- Zone 5: corresponds to the dry ground. The average width of this zone was about 11.6 m ± 0.5 m. In summer the increase in temperature and the

decrease of rainfall generates the drying out of the plants that appear in spring.

Orchestia montagui, *O. gammarellus* and *O. mediterranea* were collected monthly from July 2006 to June 2007. Specimens were collected by hand under *Cymodocea*, woody debris, empty bottles, and in between the roots of plants, in particular those of *Suaeda maritima*, with a sampling effort of two hours each time. Individuals were collected with their respective substratum and kept in polystyrene boxes that had been perforated to provide ventilation.

In the laboratory, specimens were preserved in 70% ethanol. Species identification was carried out using the keys of CHEVREUX & FAGE (1925) and RUFFO (1993). For each population the cephalic length (CL) of each individual was measured using a binocular microscope equipped with micrometrical ocular lens, calibrated with objective micrometers. The total length (TL) was estimated from CL using linear equations (MARQUES *et al.* 2003).

After being measured, individuals were sexed (male, female, or immature) based on the presence of copulatory appendages in the males, and presence of oostegites, with or without setae, in the females. Females with setae were considered as mature, meaning that they would carry eggs soon, or they had just been released. In the absence of any secondary sexual dimorphic features individuals were considered immature. Specimens were, therefore, classified as: (a) males, (b) resting females, (c) gravid females or (d) immature. The gravid females group included both females carrying eggs and females bearing setae on the oostegites. Eggs present in the marsupium were counted in females that did not undergo any egg loss.

It is worth noting that according to our previous results, different co-existing species occupy different niches, for example *O. montagui* was generally found closer to the shoreline than *O. gammarellus* and *O. mediterranea* (JELASSI *et al.* 2012). In addition, because of the uncertainty of the determination of juveniles their number was estimated proportionally to the number of ovigerous females only. Despite this is a rough estimation to which the risk of a misidentification has to be added, in our opinion this is the most appropriate procedure.

Furthermore, for the sex ratio, the hypothesis of 1:1 was tested using Chi square test.

Field growth rates were estimated by tracking recognisable modal distributions in the population using size frequency of distributions (0.04 mm length classes) from successive sample dates, following MARQUES *et al.* (2003) and PARDAL *et al.* (2000).

Modal distributions are assumed to result from pulses in recruitment, conventionally referred to as

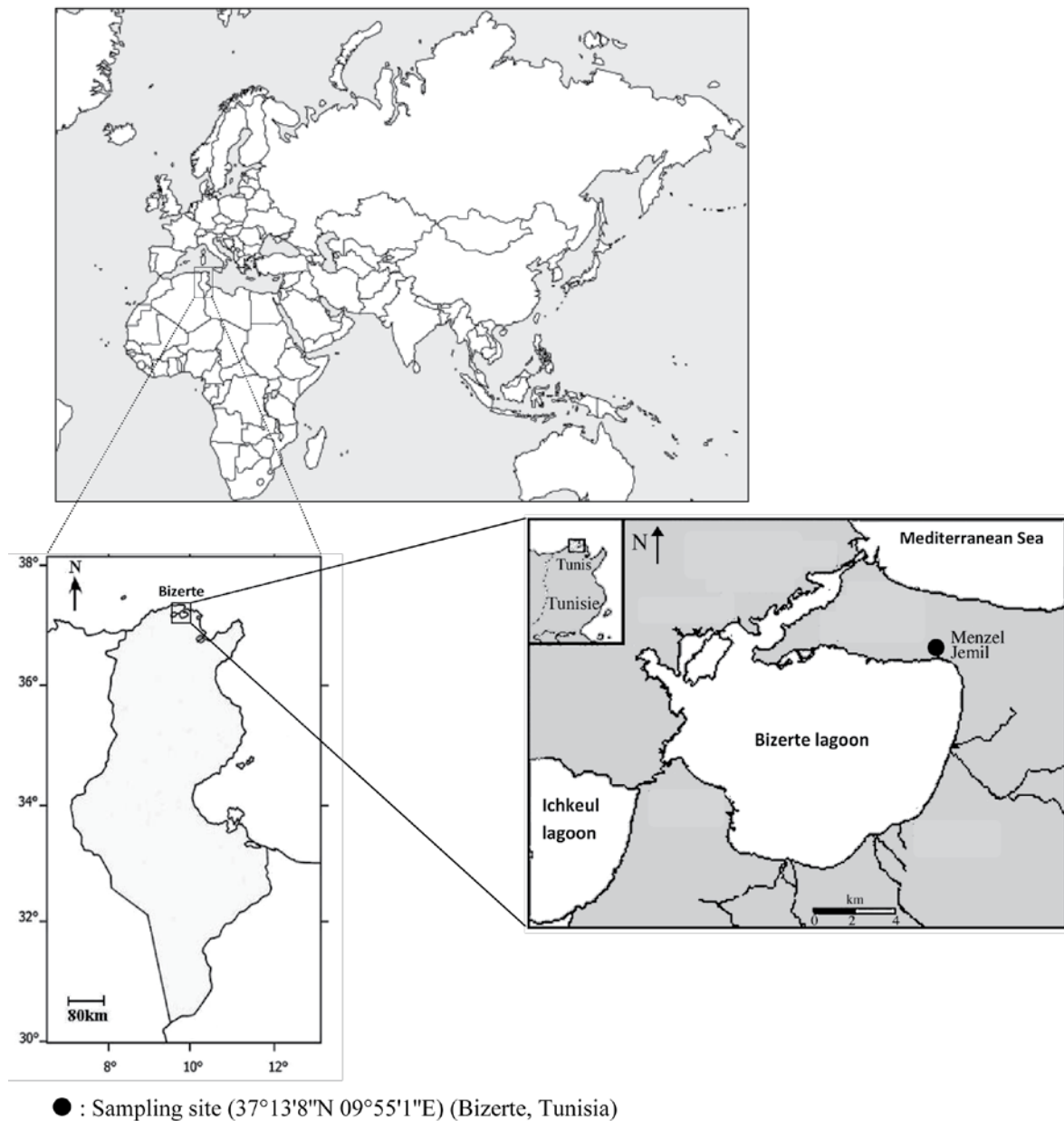


Fig. 1. Sampling locality 37°13'8" N 09°55'1"E (Bizerte, Tunisia)

cohorts. Size-frequency analysis was carried out using the probability paper method (HARDING 1949), as performed by CASSIE (1954, 1963). Computations were done with ANAMOD software (NOGUEIRA 1992), and the reliability of the distribution separation method was tested with both χ^2 and G tests ($p \leq 0.05$).

Results

Population structure

A total of 2946 specimens of *O. montagui*, 3545 of *O. gammarellus* and 3635 of *O. mediterranea* were collected.

For *O. gammarellus* the number of captured individuals ranged from 124 in October to 408 in April. A total of 996 immature specimens and 963 males were identified with the highest percentage in April (47.1%) and August (40.1%), respectively. For females, the greatest percentage of ovigerous ones was observed in July (55.3%). For females with an empty marsupium, the number of specimens varied from 1.47% in April to 28.16% in January. The overall percentage for this category was 8.6%. Concerning resting females, 144 individuals were identified with the highest percentage recorded in February (8.9%), but no individuals of this category were recorded in April (Table 1).

Table 1. Categories and sex-ratio of *Orchestia gammarellus* population in the supralittoral zone of Bizerte lagoon, Tunisia

Month	Immatures	Males	Non reproductive females	Females with empty marsupium	Ovigerous females	Sex-ratio M/F	χ^2	P
July	22	73	4	14	140	0,46	62,554	< 0,0001
August	0	97	6	29	110	0,67	19,041	< 0,0001
September	128	60	11	18	120	0,40	75,799	< 0,0001
October	14	37	5	11	57	0,51	23,564	< 0,0001
November	6	89	15	11	114	0,64	22,716	< 0,0001
December	56	102	8	32	89	0,79	6,312	0,012
January	33	105	12	78	49	0,76	9,475	0,002
February	108	77	32	53	89	0,44	74,972	< 0,0001
March	84	80	22	13	68	0,78	5,781	0,016
April	192	96	0	6	114	0,80	5,333	0,021
May	173	89	8	6	93	0,83	3,306	0,069
June	180	58	21	33	95	0,39	80,01	< 0,0001
Total	996	963	144	304	1138	0,61	304,534	< 0,0001

For *O. mediterranea*, a total of 3635 individuals were collected. The species number varied from 120 individuals in August to 437 in May. Immature and male specimens were present through the year with the highest percentage observed in April (50%) and January (53.4%), respectively. Concerning the resting females, females with empty marsupium and ovigerous females, the highest percentage of specimens was recorded in June (7.7%), January (24.3%) and November (54.3%), respectively (Table 2).

Concerning *O. montagui*, the overall number of animals collected monthly ranged between 99 in November 2006 to 388 in July 2006. The monthly change in population structure showed that immature individuals were present throughout the year except in August and in November. The overall percentage of immature individuals was 17.99% (N = 530) with the highest percentage in March 2007 (36.63%). For males, the greatest percentage was found in April (58.99%) with an overall percentage of 46.78% (N = 1378). Ovigerous females were present throughout the year with one peak of abundance observed in July (35.05%). The percentage of females with an empty marsupium varied between 2.21% and 34.55% in April and in January, respectively. Non-reproductive females were absent in December and April; their greatest percentage (26.26%) was recorded in November. For females that were either ovigerous, with an empty marsupium, or non-reproductive their overall percentages were 20.74% (N = 611), 8.93 % (N = 263), and 5.57% (N = 164), respectively (Table 3).

Relationship between cephalic length and body length

Since cephalic length (CL) is a more reliable measurement than total body length (TL) due to the curvature of the body, CL was measured for each specimen. Additionally, for each species the body and cephalic lengths of approximately 150 individuals were measured accurately to enable all CL to be converted to TL. The relationship of TL to CL was:

O. gammarellus: $TL = -0.0075 + 9.0616 * CL$.
O. mediterranea: $TL = 0.1356 + 8.7583 * CL$.
O. montagui: $TL = -0.1171 + 9.3392 * CL$.

For *O. gammarellus* mean CL of males, ovigerous females, females with an empty marsupium and non-reproductive females was 1.32 mm ± 0.16 mm, 1.3 mm ± 0.1 (0.85 – 1.875 mm), 1.29 mm ± 0.15 (0.825 – 1.8 mm) and 1.14 mm ± 0.14 (0.8 – 1.55 mm), respectively.

For *O. mediterranea* mean CL of males, ovigerous females, females with an empty marsupium and resting females was 1.27 ± 0.14 mm (0.85 - 2 mm),

1.3 ± 0.13 mm (0.825 – 1.75 mm), 1.30 ± 0.14 mm (0.875 – 1.8 mm) and 1.13 ± 0.6 mm (0.8 – 1.7 mm), respectively.

For *O. montagui*, mean CL of males, ovigerous females, females with an empty marsupium and non-reproductive females was 1.52 ± 0.13 mm (0.75 - 1.95 mm), 1.35 ± 0.15 mm (0.93 - 1.92 mm), 1.29 ± 0.17 mm (0.88 - 1.90 mm) and 1.20 ± 0.20 mm (0.75 - 1.80 mm), respectively.

Reproductive activity and sex ratio

Breeding activity was assessed by estimating the percentage of ovigerous females (number of ovigerous females divided by total number of females x 100). Breeding occurred throughout the study period, with two peaks recorded in July 2006 and April 2007 for *O. montagui* (87.7% and 86.79%, respectively) and *O. gammarellus* (88.61% and 95%, respectively). For *O. mediterranea* these two peaks were observed in November (83.22%) and in April (94.74%), suggesting a continuous reproduction of these three species during the study period (Fig. 3).

There was a clear difference in sex ratio between *O. gammarellus* and *O. mediterranea*, on one hand, and *O. montagui*, on the other. For the two first species, the sex ratio was almost always female-biased with an average of 0.61:1 and 0.78:1, respectively (Tables 1, 2). For *O. montagui* dominance of males over females in the population (1.33:1) was observed except in October, November, January and March (Table 3).

Fecundity

Fecundity was estimated from the number of eggs inside the marsupium. For *O. gammarellus* the lowest (4) and the highest (33) number of eggs were

recorded in female whose total length was equal to 12.5 mm and 14.7 mm, respectively. The average number of eggs was estimated at 18 ± 7.6 . A positive correlation between fecundity and TL of female was assessed through a linear regression model ($R^2 = 0.3876$; Fig. 4).

The number of eggs for *O. mediterranea* varied between 5 and 29 eggs recorded for females whose TL was 9.5 mm and 13.2 mm, respectively. The mean number of eggs was estimated to 15 ± 4.9 . Linear regression showed a positive correlation between fecundity and TL ($R^2 = 0.1603$) (Fig. 4).

For *O. montagui*, the lowest value of one egg was found in a female which body length was 10.50 mm, whereas the highest value (17 eggs) was observed in a female with TL= 12.50 mm. The mean number of eggs was estimated at 9 ± 5.1 . In addition, no significant correlation between fecundity and TL was found ($R^2 = 0.0074$; Fig. 4).

Field growth rates and lifespan

Size-frequency polymodal distributions were analysed for recognisable cohorts. For *O. gammarellus* six cohorts were recognised at the first sampling date and nine new cohorts were detected and tracked during the next 11 months, respectively on 03 August (cohort 7), 06 September (cohort 8), 04 October (cohort 9), 04 December (cohort 10), 09 January (cohort 11), 05 March (cohort 12), 02 April (cohort 13), 04 May (cohort 14) and 05 June (cohort 15; Fig. 5). Furthermore, the minimum average CL of new cohorts ranged from 0.35 to 0.54 mm (3.164 - 4.8836 mm TL), whereas the maximum CL varied between 1.52 and 1.64 mm (13.77 - 14.85 mm TL).

For *O. mediterranea* six cohorts were detected at the first sampling date and 11 new distributions

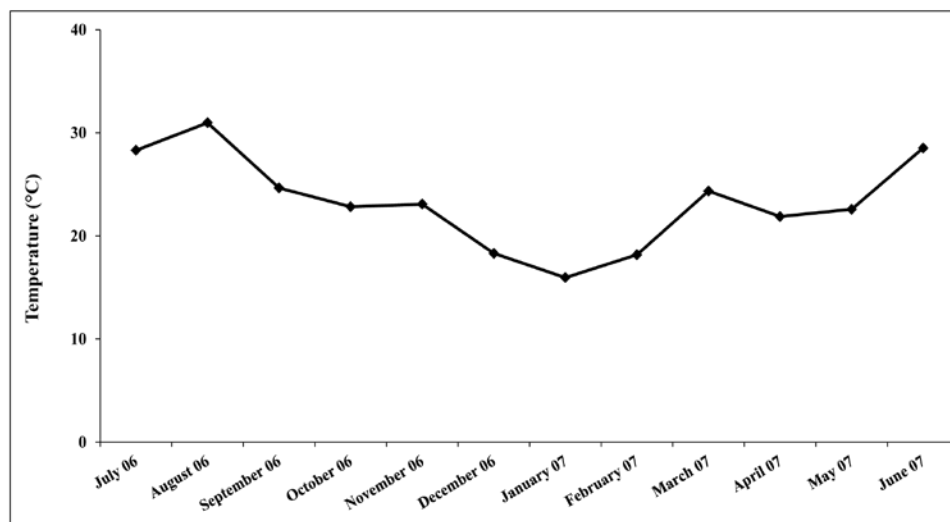


Fig. 2. Monthly variation of temperature at the sampling site during the study period

Table 2. Categories and sex-ratio of *Orchestia mediterranea* population in the supralittoral zone of Bizerte lagoon, Tunisia

Month	Immatures	Males	Non reproduc-tive females	Females with empty marsupium	Ovigerous fe-males	Sex-ratio M/F	χ^2	P
July	19	76	3	24	122	0.51	47.369	< 0.0001
August	0	60	7	13	40	1.00	0	1.000
September	120	60	10	17	116	0.42	67.872	< 0.0001
October	34	77	15	8	107	0.59	27.14	< 0.0001
November	6	70	10	14	119	0.49	50.038	< 0.0001
December	53	140	5	44	84	1.05	0.359	0.549
January	24	163	9	74	35	1.38	14.413	0.002
February	97	137	16	54	72	0.96	0.179	0.672
March	103	97	15	14	96	0.78	7.063	0.008
April	211	97	2	4	108	0.85	2.739	0.098
May	191	116	12	12	106	0.89	1.593	0.207
June	122	68	23	16	68	0.64	17.383	< 0.0001
Total	980	1161	127	294	1073	0.78	83.532	< 0.0001

Table 3. Categories and sex-ratio of *Orchestia montagui* population in the supralittoral zone of Bizerte lagoon, Tunisia

Month	Immature	Males	Non-reproductive female	Female with empty marsupium	Ovigerous female	Sex-ratio M/F	χ^2	P
July	21	212	9	10	136	1.37	17.706	< 0.0001
August	0	152	4	19	58	1.88	43.27	< 0.0001
September	74	131	25	16	59	1.31	8.32	0.004
October	11	88	32	30	29	0.97	0.101	0.751
November	0	37	26	20	16	0.60	12.626	0.000
December	17	65	0	25	30	1.18	1.667	0.197
January	20	56	14	66	35	0.49	40.713	< 0.0001
February	54	128	10	30	41	1.58	21.139	< 0.0001
March	74	50	7	11	60	0.64	12.25	0
April	77	187	0	7	46	3.53	149.633	< 0.0001
May	97	151	13	14	51	1.94	46.541	< 0.0001
June	85	121	24	15	50	1.36	9.752	0.002
Total	530	1378	164	263	611	1.33	95.695	< 0.0001

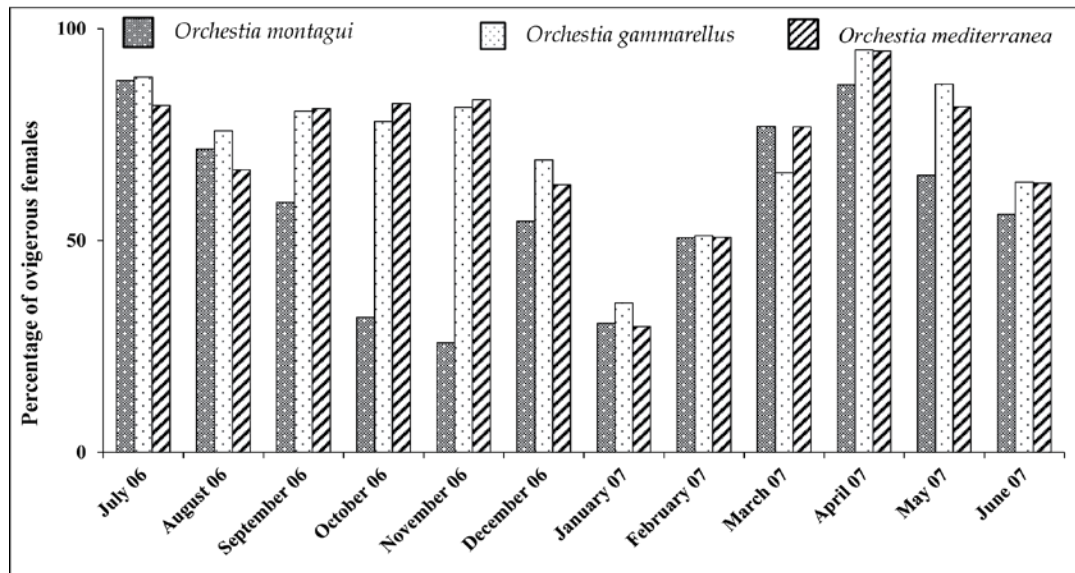


Fig. 3. Monthly variation of ovigerous females (%) of *O. montagui*, *O. gammarellus*, and *O. mediterranea* in the supralittoral zone of Bizerte lagoon

were identified during the rest of the study period, respectively, on 03 August (cohort 7), 06 September (cohort 8), 04 October (cohort 9), 04 December (cohort 10), 09 January (cohort 11), 05 February (cohort 12), 05 March (cohort 13), 02 April (cohort 14), 04 May (cohort 15 and 16) and 05 June (cohort 17; Fig. 6). The minimum average CL of new cohorts ranged from 0.28 to 0.32 mm (2.59 – 2.94 mm TL), while the maximum average CL ranged from 1.46 to 1.59 mm (12.92 – 14.06 mm TL).

Finally, for *O. montagui* six cohorts could be identified from data from the first sampling date (03 July 2006). From modal analysis, ten new cohorts were observed during the rest of the study period (Fig. 7). These new cohorts appeared on 03 August (cohort 7), 06 September (cohort 8), 04 October (cohort 9), 04 December (cohort 10), 09 January (cohort 11), 05 February (cohort 12), 05 March (cohort 13), 02 April (cohort 14), 04 May (cohort 15) and 05 June (cohort 16). The minimum average CL varied between 0.37 to 0.42 mm (3.34 - 3.81 mm TL). The maximum CL ranged from 1.62 to 1.73 mm (15.01 - 16.04 mm TL).

On average the population presenting the smallest adult was that of *O. mediterranea*, while the larger individuals came from *O. gammarellus* and *O. montagui*.

Growth was found to be continuous across the life span and varied with season. Growth rate was quicker in the early phases, and appeared to be higher, generally during summer. As a general pattern, for the three populations cohorts born during

summer tended to have a longer lifespan than those born in winter. Taking into consideration growth rate and the disappearance of cohorts, lifespan was estimated to 7-8 months for *O. gammarellus* (Fig. 8A), 5-8 months for *O. mediterranea* (Fig. 8B) and 6-7 months for *O. montagui* (Fig. 8C)

Life cycle

Size-frequency analyses allowed to determine the cohorts to which ovigerous females belonged, and thus to assess their contributions to recruitment (Fig. 9). Parental relation between existing cohorts and new arrivals in the population during the study period could therefore be interpreted, permitting the comparison of the three populations that were studied with regards to life cycle characteristics.

For *O. gammarellus*, C7 was the outcome of ovigerous females of C1, C2, C3 and C4. Cohorts C8, C9 and C10 were the offspring of C2, C3, C4 as well as C5, C6 and C7. Cohorts C1, C2 and C3 disappeared in August, September and October, respectively. Cohorts C4 and C5 merged in December 2006 and disappeared in January 2007. These two cohorts merged with those of C6, C7, C8 and C9 gave birth to C11, identified in January 2007. C12 and C13 were the outcome of ovigerous females of C6, C7, C8 and C9. C7 and C8 merged and gave birth, together with C9, C10 and C11, to the new cohort C14 in May 2007. C15, identified in June 2007, was the offspring of ovigerous females of C8, C9, C10, C11 and C12 (Fig. 9A).

Concerning *O. mediterranea* ovigerous females

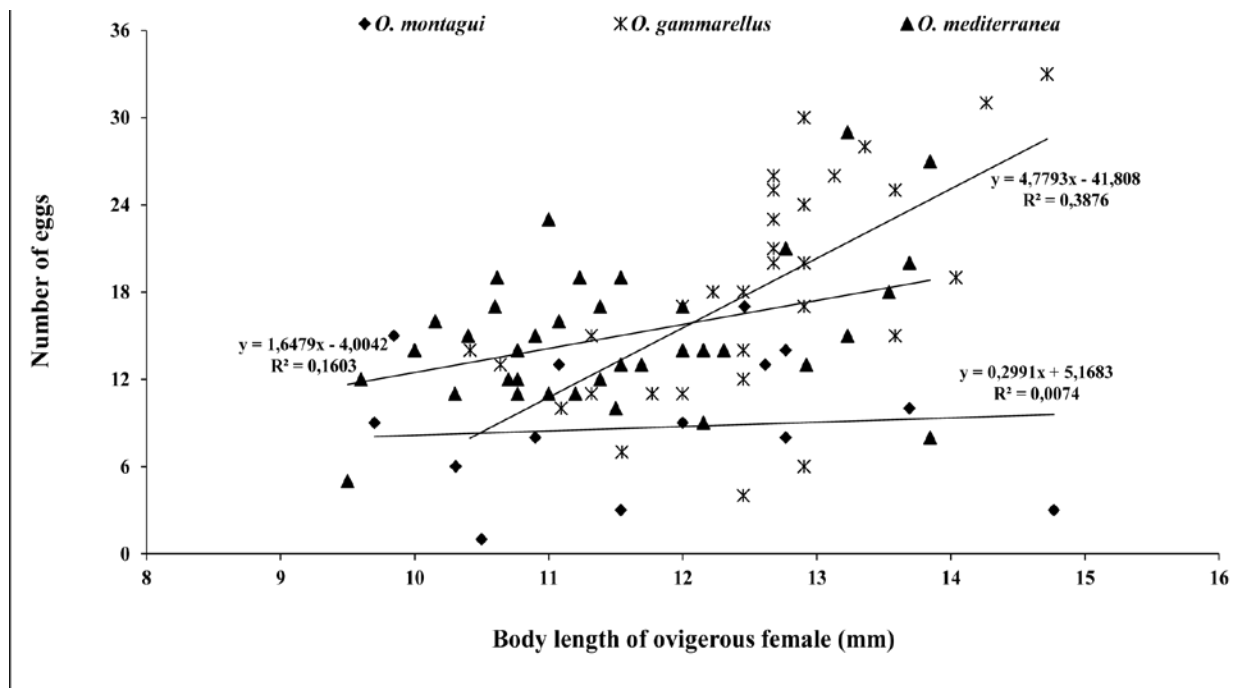


Fig. 4. Relation between number of eggs and body length of ovigerous females of *O. montagui*, *O. gammarellus* and *O. mediterranea*

of C1, C2, C3 and C4 gave birth to C7. C1 and C2 disappeared respectively in July and August. C3 and C4 contributed to the birth of C8 and gave birth to C9 with ovigerous females of C5. C3, C4 and C5 disappeared respectively in October, November and December. The C10 was the offspring of C5, C6 and C7 while the C11 comes from C6, C7 and C8. C12, identified in February 2007, was the offspring of ovigerous females of C6, C7, C8 and C9. These last cohorts (C6, C7, C8 and C9) with C10 contributed to the birth of C13. Ovigerous cohorts of C7, C8, C9 and C10 gave birth to C14. C15 was the outcome of C9, C10, C11 and C12, while C16 came from ovigerous females of C10, C11, C12 and C13 (Fig. 9B).

For *O. montagui* females of C1, C2, C3 and C4 gave birth to C7; whereas only females of C3 and C4 gave birth to C8 and also to C9 with females of C5. Then, C3, C4 and C5 disappeared in October, November and December, respectively. Cohort C10 was the outcome of ovigerous females of C5, C6 and C7, whereas, cohort C11 was the offspring of C6, C7 and C8. Ovigerous females of these cohorts (6, 7, and 8) with those of C9 and C10 gave birth to C12 and C13, respectively. Females of cohorts C7, C8, C9 and C10 gave birth to C14. Cohort C15 was the offspring of C9, C10, C11 and C12. Cohort C16 was the outcome of C10, C11, C12 and C13 (Fig. 9C).

It seems, therefore, that at the supralittoral zone of Bizerte Lagoon *O. montagui*, *O. gammarellus* and *O. mediterranea* were semiannual species (females

appear to produce two to five broods per year), with iteroparous females appearing to reproduce twice or more in their life time and have bivoltine life cycle since the populations produced two generations per year.

Discussion

Life history traits were studied in populations of three species of Talitridae, *O. montagui*, *O. gammarellus* and *O. mediterranea*, living in sympatry in the supralittoral zone of Bizerte Lagoon. We recorded continuous reproduction of all three species with ovigerous females being present throughout the year. Our findings are similar to the ones reported for *O. mediterranea* in the estuary of Bou Regreg in Morocco (ELKAÏM *et al.* 1985), for *Deshayesorchestia capensis* (Van Sensus 1988), *Platorchestia platensis* (Ciavatti 1989), *Pseudorchestoidea brasiliensis* in Brazil (CARDOSO & VELOSO 1996) and *Deshayesorchestia quoyana* in New Zealand (MARSDEN 1991). Other species in Tunisia, as well as in the world, were characterised by seasonal reproduction, i.e. *Talitrus saltator* (MARQUES *et al.* 2003, BOUSLAMA *et al.* 2007), *Britorchestia brito* (CONÇALVES *et al.* 2003) and *Deshayesorchestia deshayesii* (AYARI-AKKARI *et al.* 2014). Seasonal variation was also observed in a population of *T. saltator* from the Atlantic coast (WILLIAMS 1978), in *O. gammarellus* in the Baltic Sea (PERSSON 1999), and in *O. mediterranea* in the

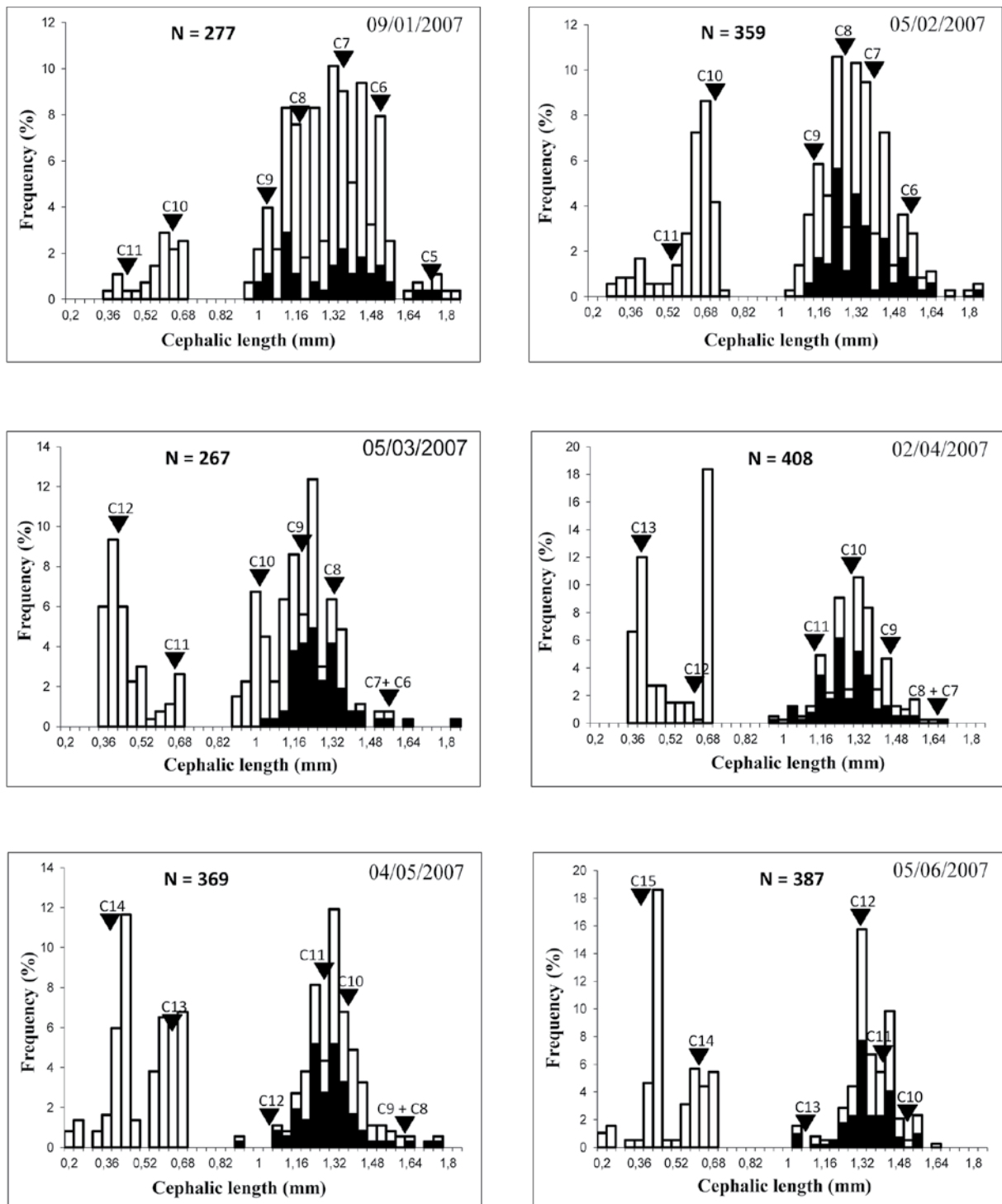


Fig. 5. Size-frequency distribution of *O. gammarellus* from the supralittoral zone. Inverted triangle indicates average CL of the numbered cohorts or groups of cohorts; Black bar indicates ovigerous females

Medway Estuary, Northern Europe. The study of Italian and Portuguese populations by MARQUES *et al.* (2003) showed that recruitment occurs over seven months, from early March to late September. Seasonal reproduction occurred from February to November for *D. deshayesii* in an Ionian sandy beach of Southern Italy (PRATO *et al.* 2009). WILLIAMS

(1978) showed that populations of *T. saltator* from the Isle of Man had a much shorter reproductive period, from May to the end of August.

Orchestia gammarellus, collected from the Smir Lagoon in Morocco, offers a good example of intraspecific plasticity. For the first time this population showed a seasonal pattern of reproduction

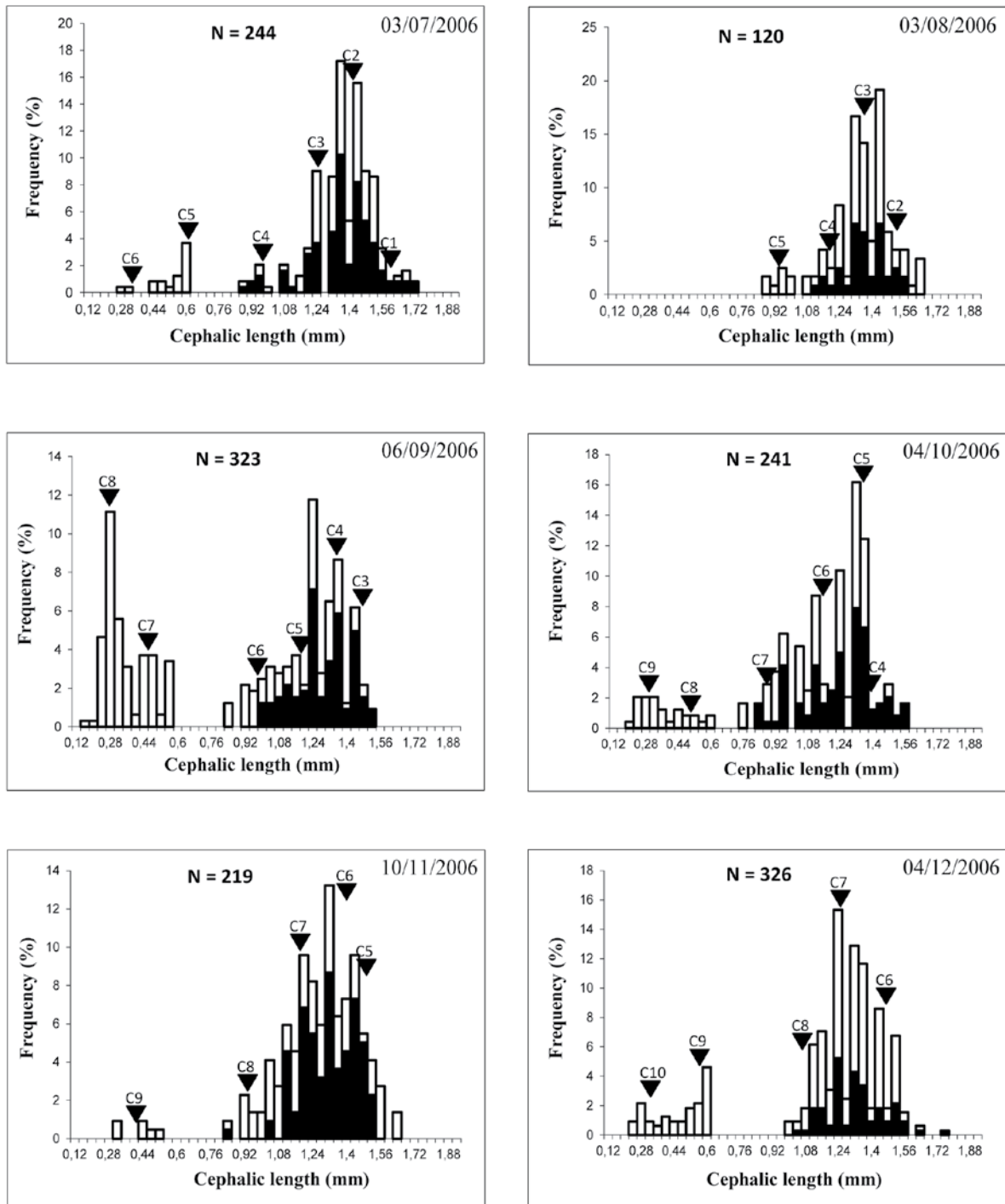


Fig. 6. Size-frequency distribution of *O. mediterranea* from the supralittoral zone. Inverted triangle indicates average CL of the numbered cohorts or groups of cohorts; Black bar indicates ovigerous females

(AKSISSOU & ELKAIM 1996) and continuous reproduction throughout the year, especially after the construction of an inland dam close to the town of Smir and Kabila port (AKSISSOU *et al.* 1998).

For these three species, *O. montagui*, *O. gammarellus* and *O. mediterranea*, breeding activity, observed throughout the year, was maintained at a minimum temperature of 15.95°C. The duration of

the reproductive period might be correlated with geographic gradient, temperature and photoperiod (WILLIAMSON 1951; MARQUES *et al.* 2003). The latter authors showed that recruitment periods were shorter in populations of *T. saltator* from the Atlantic and Northern Mediterranean areas compared to those of Southern Mediterranean coasts. According to MORRITT & STEVENSON (1993), temperature is the

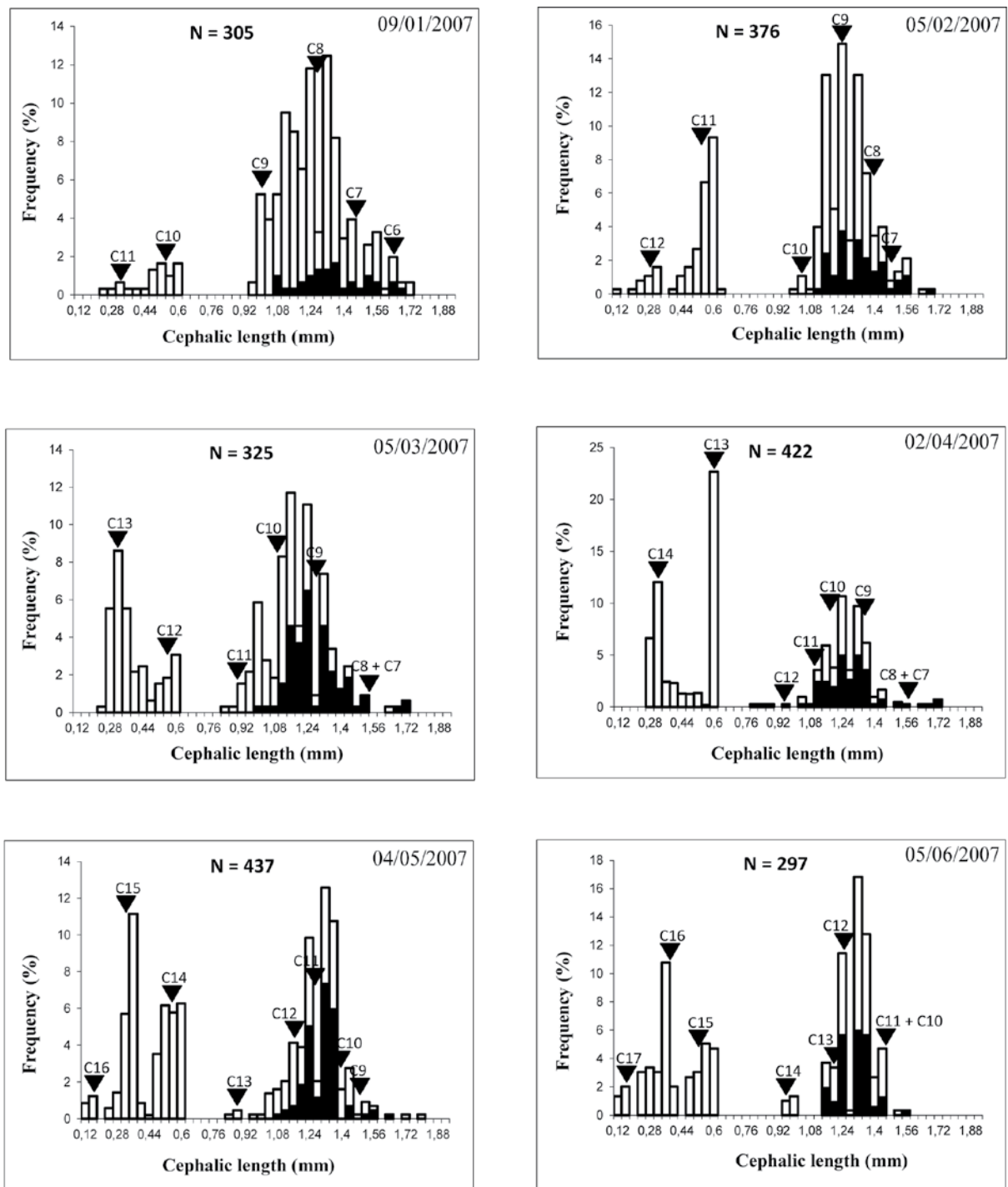


Fig. 6. Continued

main exogenous factor controlling reproduction in *O. gammarellus* and the onset is elicited when temperatures reach 10°C. Although the impact of photoperiod has not been studied in the present work, it seems that it plays an important role in reproductive activity. Indeed, WILLIAMS (1985) established a direct effect of photoperiod on the initiation of reproduction in *T. saltator*. ANASTACIO *et al.* (2003) even mentioned, in a model of population dynamics of *T. saltator*, that a photoperiod under 13:10 (light:

dark) would initiate reproduction with recruitment only taking place sometime after this value has been reached.

During the study period, sex ratio was male-biased for *O. montagui*, with a decrease in the proportion of males in the population during January and March. This result is similar to that found in a UK population of *O. gammarellus* (WILDISH 1979), and in the Atlantic (Lavos, Portugal) and Mediterranean (Collelungo, Italy) within populations of *T. sal-*

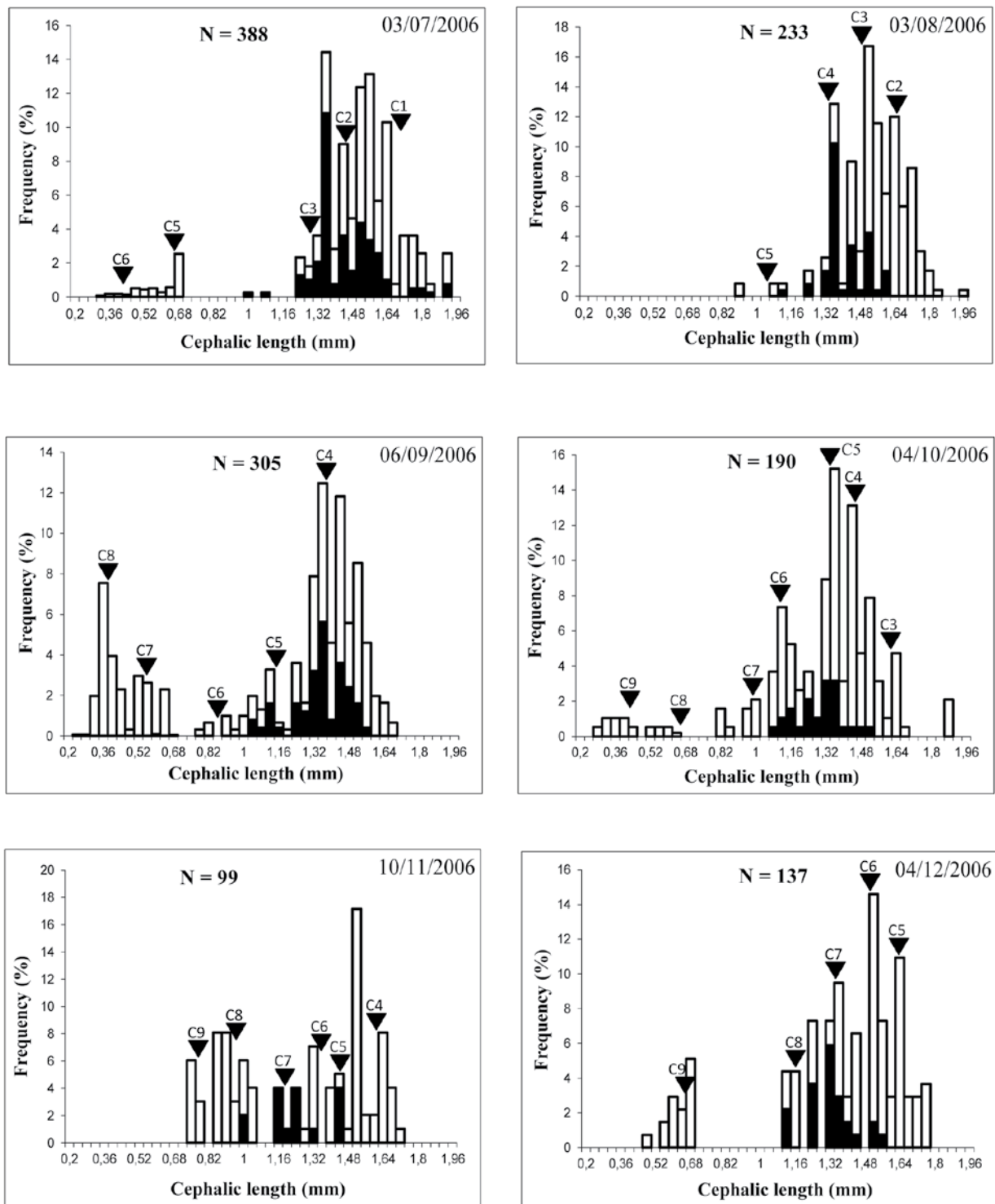


Fig. 7. Size-frequency distribution of *O. montagui* from the supralittoral zone. Inverted triangle indicates average CL of the numbered cohorts or groups of cohorts; Black bar indicates ovigerous females

tator (MARQUES *et al.* 2003), and in populations of *Britorchestia brito* occurring in the Atlantic (GONÇALVES *et al.* 2003). In addition, populations of *O. gammarellus*, *O. mediterranea* and *O. aestuarensis* from the European Atlantic and Mediterranean coasts showed a male dominance (GINSBURGER-VOGEL 1989, 1991, GINSBURGER-VOGEL, MAGNIETTE-

MARGAULT 1981). The reasons for a male-biased sex ratio remain unclear, although the presence of endoparasites has been hypothesised to explain deviation towards male dominance (GINSBURGER-VOGEL 1989, 1991, GINSBURGER-VOGEL, MAGNIETTE-MARGAULT 1981). MARQUES *et al.* (2003) showed that this result might be explained by wearing out of

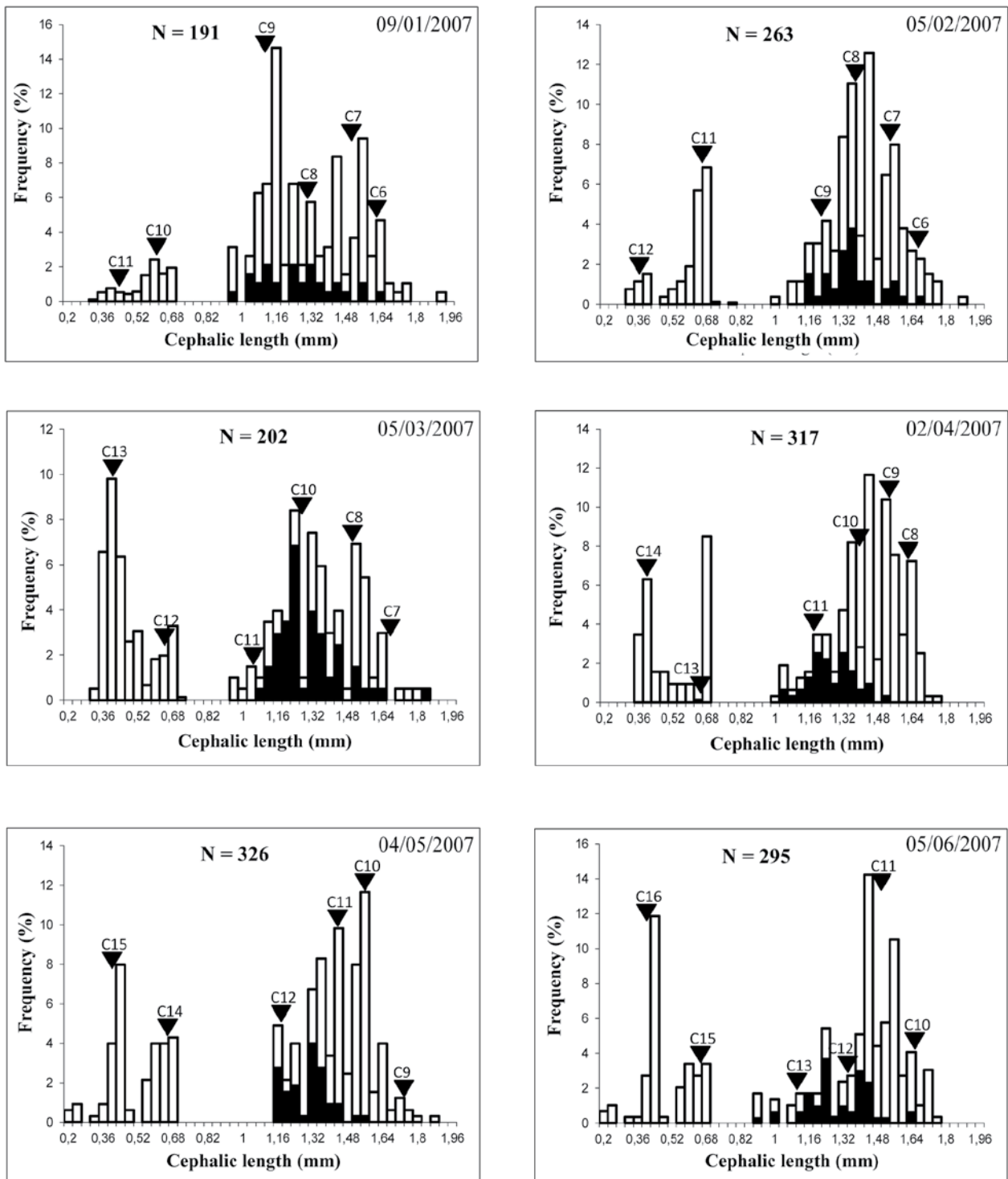


Fig. 6. Continued

males in relation to reproductive activity or by the displacement of females near the shoreline.

Furthermore, *O. gammarellus* and *O. mediterranea* were characterised by a female-biased sex ratio, which is the most common situation among talitrid populations. This is the case of *T. saltator* from Zouaraa and Korba in Tunisia (BOUSLAMA *et al.* 2007; MARQUES *et al.* 2003), of *B. brito* from Zouaraa

(GONÇALVES *et al.* 2003), *D. deshayesii* (AYARI-AKKARI *et al.* 2014), *O. mediterranea* (ELKAÏM *et al.* 1985), *O. gammarellus* (JONES & WIGHAM 1993; AKSISSOU & ELKAÏM 1996; PERSSON 1999; DIAS & SPRUNG 2004) and *Deshayesorchestia capensis* (VAN SENUS 1988). HAMILTON (1967) and WENNER (1972) showed that populations that are either male- or female-biased may be affected by factors associated

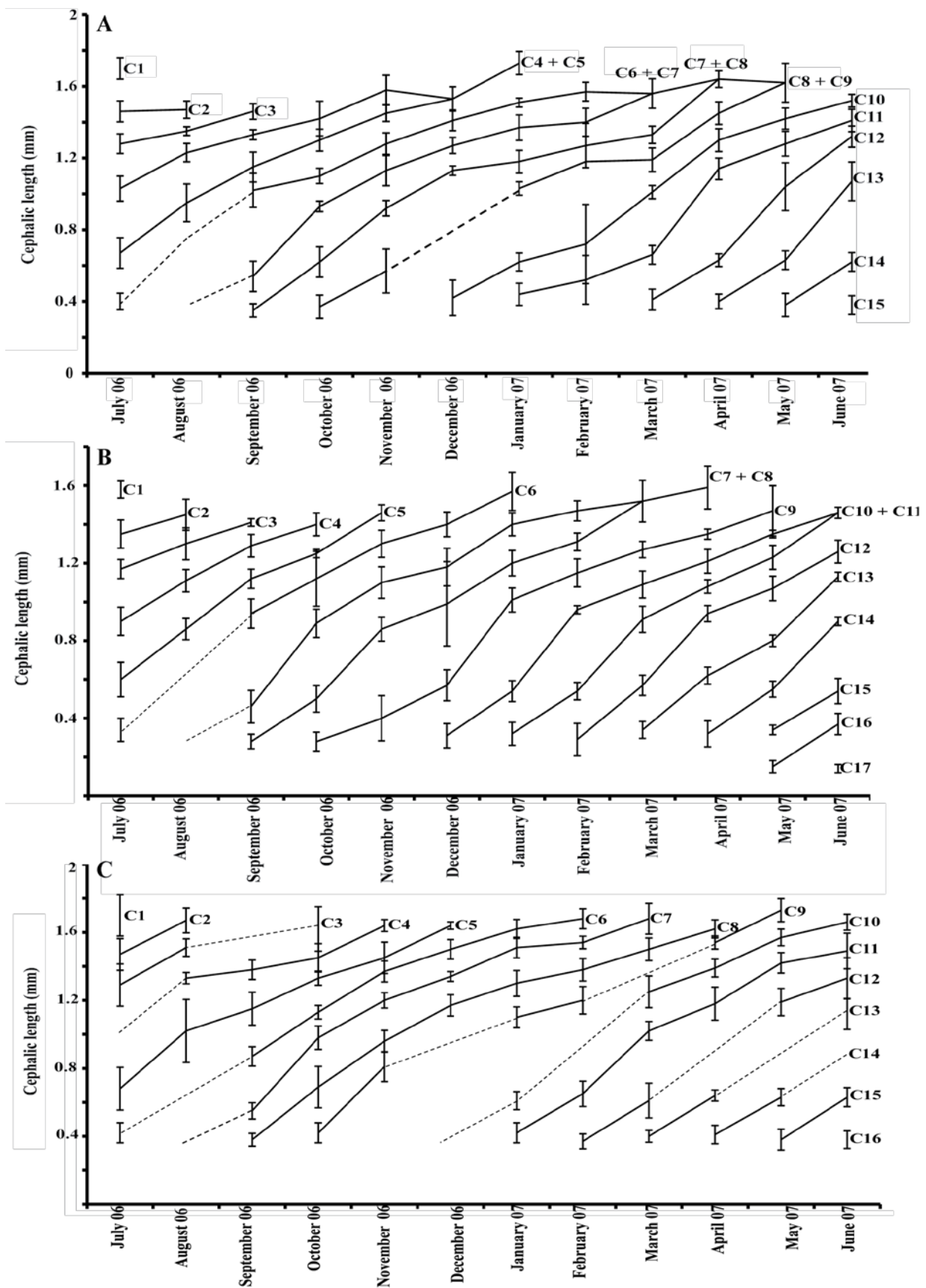


Fig. 8. Estimated growth and life span of *O. gammarellus* (A), *O. mediterranea* (B) and *O. montagui* (C) cohorts or groups of cohorts (average CL \pm standard deviation) in the supralittoral zone of Bizerte lagoon. Broken lines indicate probable cohort merging or cohort evolution in time

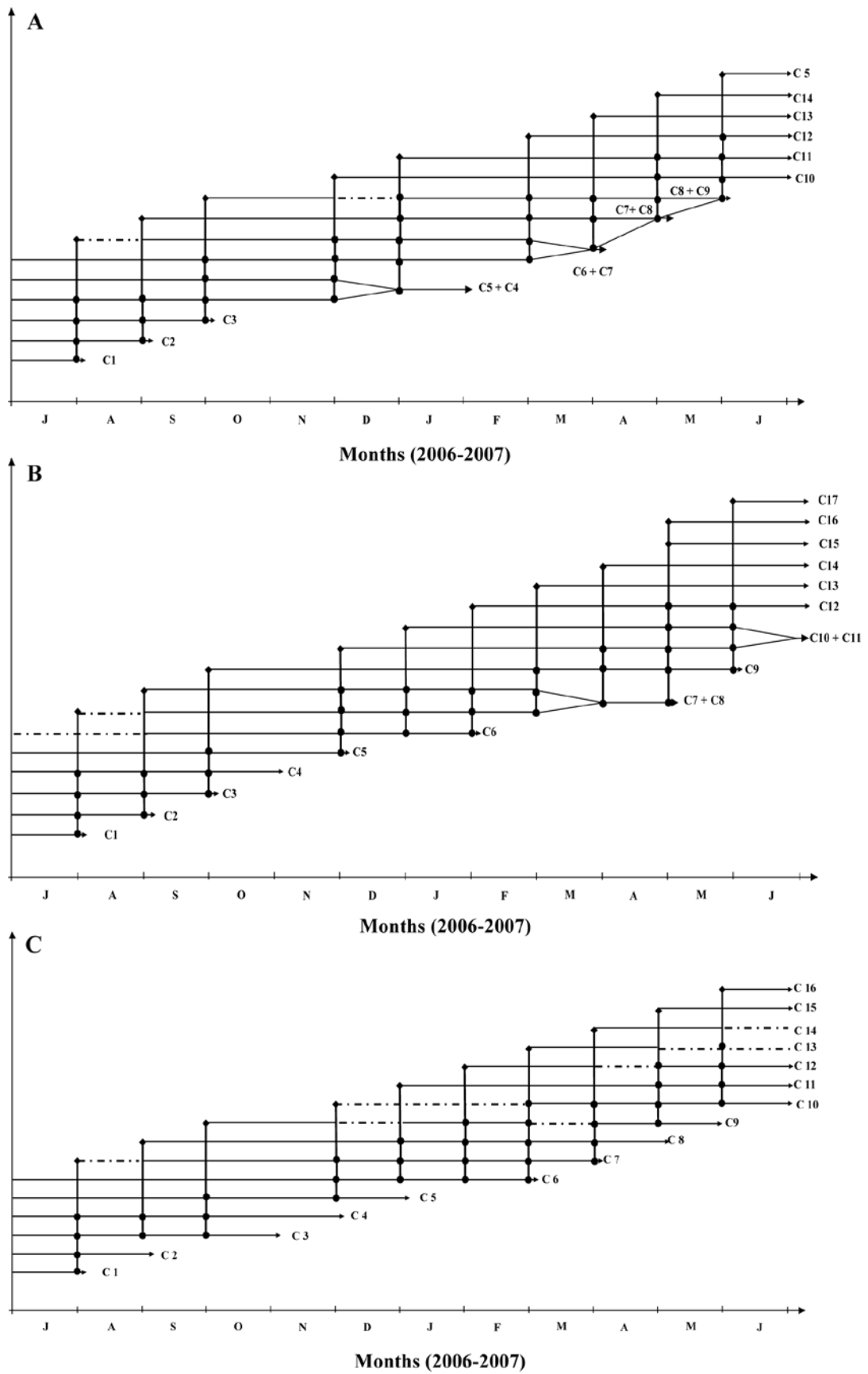


Fig. 9. Recruitment profile of *O. gammarellus* (A), *O. mediterranea* (B) and *O. montagui* (C) in the supralittoral zone of Bizerte lagoon

with their life cycle, including mortality, as well as longevity and growth rate between sexes.

The study of fecundity of *O. gammarellus* and *O. mediterranea* demonstrated a significant correlation between egg number and body length of ovigerous females in accordance to what had been observed for *T. saltator* (WILLIAMS 1978; BOUSLAMA 2009) and *Deshayesorchestia capensis* (VAN SENUS 1988). For *O. montagui* no correlation was found. Moreover, the fecundity of *O. montagui* (9 eggs) was remarkably lower than that of the two sympatric species, *O. gammarellus* (18 eggs) and *O. mediterranea* (15 eggs). These numbers were lower than that observed for *O. gammarellus* from England (19 eggs; WILDISH 1979). The lower mean egg number observed for *O. montagui* could be explained by higher survival rate of this species.

During the study period the results of the size-frequency distributions of the three analysed populations showed the presence of ten new cohorts for *O. montagui*, nine cohorts for *O. gammarellus* and 11 cohorts for *O. mediterranea*. Our results were similar to those obtained for others talitrids species: nine and eight new cohorts have been detected respectively during the first and second year of study for *T. saltator* populations from Korba, six new cohorts - for *T. saltator* from Zouaraa (Marques et al. 2003), 11 new cohorts for *D. deshayesii* from Bizerte (Ayari-Akkari et al. 2014). At Collelungo, Italy, and at Lavos, Portugal, respectively eight and five cohorts were identified (Marques et al. 2003).

The life span of these species was estimated at 6-7 months for *O. montagui*, 7-8 months for *O. gammarellus* and 5-8 months for *O. mediterranea*. A similar result of life span estimations was found for

the Mediterranean as well as for the Atlantic populations of *D. deshayesii*, (5-7 months; AYARI-AKKARI et al. 2014), of *T. saltator* (6-9 months; MARQUES et al. 2003; BOUSLAMA 2009), of *B. brito* collected from Zouaraa in Tunisia (5-8 months) and from Quiaios in Portugal (6-9 months; CONÇALVES et al. 2003), and of *O. mediterranea* in an estuary of Bou Regreg in Morocco (5-9 months; ELKAÏM et al. 1985). However, some talitrids, such as *O. gammarellus*, live as long as about 12 months (JONES, WIGHAM 1993; DIAS & SPRUNG 2004). MARQUES et al. (2003) showed that in talitrid species, there seems to be a geographical cline with life span increasing from Mediterranean populations to Northern European populations (MARQUES et al. 2003).

The three talitrid populations, characterised by continuous reproduction, were qualified as semianual species, with iteroparous females appearing to produce at least two broods per year and exhibited a bivoltine life cycle.

Conclusion

This study highlighted that *O. montagui* differed from *O. gammarellus* and *O. mediterranea* at least in some life history traits. In addition, these species do not exhibit the same temporal niches: *O. gammarellus* and *O. mediterranea* had nocturnal behaviour like the majority of supralittoral species; whereas *O. montagui* was a diurnal species (JELASSI & NASRI-AMMAR 2013; JELASSI et al. 2013b). To better understand the particularity observed for *O. montagui* it would be interesting to carry out a sequencing of mitochondrial DNA in the three species to highlight their phylogenetic relationships.

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