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Factors affecting *Oithona nana* and *Oithona similis* along a salinity gradient

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Abstract

Spatial and temporal variations of reproduction variables of the two cyclopoid copepods *Oithona nana* Giesbrecht, 1893 and *Oithona similis* Claus, 1866 were evaluated monthly from September 2007 to August 2008 in four ponds at different salinities in the solar saltern of Sfax, Tunisia, under hypersaline conditions. Along the salinity gradient the abundance of *O. nana* and *O. similis* declined from 14,900 ± 15,200 ind. m^{-3} (A1) to 6,800 ± 7,200 (C31) and from 13,800 ± 17,100 ind. m^{-3} (A1) to 3,700 ± 5,800 (C31), respectively. The findings showed that the abundance of these *Oithona* species, particularly the ovigerous females, was positively correlated with the abundance of Diatomeae, and negatively correlated with salinity. The egg production rate (EPR), the egg diameter, the clutch size, as well as the cephalothorax length of mature females, were all negatively correlated with salinity and positively correlated with the abundance of Diatomeae. Along the existing salinity gradient, the EPR decreased from 4.7 ± 0.39 (A1) to 3.2 ± 0.13 (C31) eggs $female^{-1}$ day^{-1} and from 5.19 ± 0.46 (A1) to 3.66 ± 0.05 (C31) eggs $female^{-1}$ day^{-1} for *O. nana* and *O. similis*, respectively, and this could mainly be attributed to the hypersaline conditions. The positive relationship between the abundance of Diatomeae with all traits shows, that these may be a vital component of the diet for the investigated species. The reduction of body size of *Oithona* along the salinity gradient demonstrates that such a character could mainly be due to a network of causes, related with the confinement and not only to salinity.

Keywords: Copepoda; Cyclopoida; *Oithona*; Reproduction variables; Salinity; Solar saltern.

Introduction

Oithonidae are among the most successful free-living small-sized Cyclopoida in the marine epipelagic (Temperoni *et al*., 2011) and *Oithona* Baird, 1843, is a widely distributed neritic genus representing common copepods in the oceans world-wide, thus being a significant contributor to secondary production (Paffenhöfer, 1998; Porri *et al*., 2007; Temperoni *et al*., 2011). *Oithona* species show a wide geographical distribution, from the poles to the equator (Nishida, 1985; Letterio & Ianora, 1995). The wide distribution of this genus in coastal areas is due to the euryhaline and eurythermal physiology of its species (Torres-Sorando *et al*., 2003; Hansen *et al*., 2004; Turner, 2004), in addition to their relatively low energy expenditure for respiration (Paffenhöfer, 1998; Castellani *et al*., 2005) and reproduction (Zamora-Terol & Saiz, 2013).

Oithona spp. play a key role in neritic marine food webs, feeding on phytoplankton and other microbial components and, in turn, being prey for larger zooplankton and several forms of pelagic ichthyoplankton (Castro *et al*., 2010; Spinelli *et al*., 2011; Rakhesh *et al*., 2013; Van Noord *et al*., 2013). *Oithona* spp. are thought to prefer motile preys and in particular Protozoa (Atkinson, 1995; Lonsdale *et al*., 2000; Castellani *et al*., 2005; Castellani *et al*., 2008), although Chromista (Diatomeae and Dinophyta) are also ingested (Pond & Ward, 2011). Furthermore, *Oithona* species feed on a wider size range of food compared to other copepods, and this might be a major factor influencing population abundance and/or success (Lampitt & Gamble, 1982). In addition, studies mentioning coprophagy also help to explain the wide ecological success of *Oithona*, as faecal pellets of plankton organisms are a universal source of food in the sea (González & Smetacek, 1994).

Despite the high contribution and the important ecological role of *Oithona* spp. in the functioning of marine ecosystems, little is known about their biology and ecology, especially in the Mediterranean Sea. *Oithona nana* Giesbrecht, 1893 and *Oithona similis* Claus, 1866 are two cosmopolitan species that also dominate the Mediterranean neritic ecosystems (Mazzocchi & Ribera d'Alcalà, 1995; Siokou-Frangou *et al*., 1997; Annabi-Trabelsi *et al*., 2005; Kršinić *et al*., 2007; Rekik *et al*., 2012; Ben ltaief *et al*., 2015; Ben Salem *et al*., 2015) as well as other parts of the world's oceans (Williams & Muxagata, 2006; Wang *et al*., 2017).

Cyclopoida, among Copepoda, is the second most abundant zooplankton group in the solar saltern of Sfax (salinity, 41 - 71 psu), and dominate during winter, spring, and summer at pond A5 (salinity = 46.4 psu), and during autumn, winter, and summer at pond A16 (salinity = 67.6 psu) (Kobbi-Rebai *et al*., 2013). *Oithona nana* and *O. similis* are classified as thallassophilic species (species which prefer salinity of marine origin – in contrast with other hypersaline habitats where salt is not of marine origin). The solar saltern of Sfax is an environment that offers a unique water habitat with high salinity (Khemakhem *et al*., 2010). In this hyperhaline ecosystem, salinity and the microhabitat, in terms of food availability, were found to be essential factors in arranging the population dynamics and reproduction variables of the Calanoida species *Paracartia grani* Sars G.O., 1904 (Annabi-Trabelsi *et al*., 2018) and the Harpacticoida *Canuella perplexa* Scott T. & Scott A., 1893 and *Bryocamptus* sp. (Kobbi-Rebai *et al*., 2020).

Little is known on the reproduction variables of *Oithona*, especially no information is available about this subject at extreme salinities (38-86 psu), like the solar saltern of Sfax, (south-eastern Tunisia). The goal was to characterise the effect of some environmental parameters (temperature, salinity, suspended matter, chlorophyll-*a*, abundance of both phytoplankton, and Ciliophora) on the adult dynamics, and especially the reproduction variables (clutch size, ovisac length, egg diameter, cephalotorax length of ovigerous females, sex ratio, and egg production rate) of two Cyclopoida: *Oithona nana* and *O. similis*.

Material and Methods

Study area

The Sfax Solar Saltern (central-eastern coast of Tunisia, located at about 34.3901° N, 10.4235° E) is an artificial system formed of consecutively connected ponds (reservoir, evaporation, concentration, and crystallization), extending over a total area of 1,500 ha along the southern coast of Sfax. This ecosystem is separated from the sea by an artificial seawall of red silt (Fig. 1). The ponds are shallow (depth range: 20-70 cm), with a salinity range of 40-400 psu (Ayadi *et al*., 2004).

Sampling

Samples were collected monthly from September 2007 to August 2008 in four ponds of the saltern, indicated as A1, A5, A16, and C31 (Fig. 1). Temperature was measured immediately after sampling, using a mercury glass thermometer graduated in 0.1°C. Salinity was estimated using a refractometer (Zuzi C39545). The con-

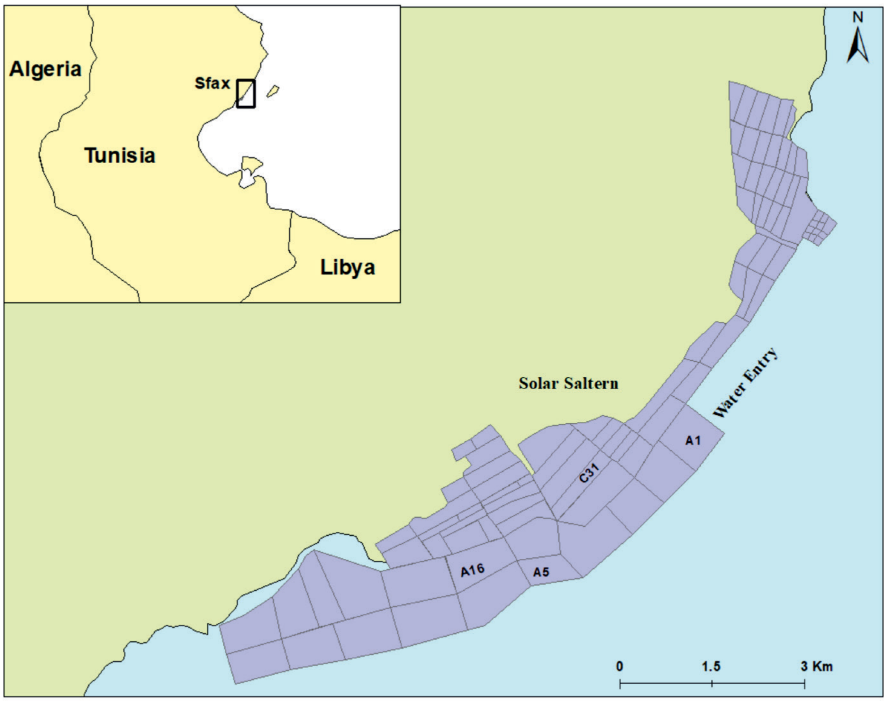

Fig. 1: Map of the location of the study area and the sampling ponds in the Sfax Solar Saltern: A1, A5, A16, and C31.

centration of suspended matter was determined from surface water samples by measuring the dry weight of the residue after water filtration through a Whatman GF/C membrane (APHA, 1992).

Surface water samples (1 L), were collected in duplicate for analysing phytoplankton and Ciliophora, fixed with acid Lugol's iodine (1% final concentration), and stored in the dark at 4°C until further analysis. Phytoplankton and Ciliophora were counted under a Leica (model number DMi1) inverted microscope (×400) using Utermöhl's (1958) method. Chlorophyll *a* (Chl-*a*) was extracted using 10 ml of acetone and determined spectrophotometrically after filtering a 0.15 – 1L sample through a Whatman GF/C filter. Concentrations were then calculated according to the equations of Strickland and Parsons (1968).

Zooplankton samples were collected with a Niskin bottle, and 50 L of water were filtered through a 50-μm mesh net, then transferred to a 125 ml flask and fixed with formaldehyde (2%). The adults of both *Oithona* species were rapidly isolated. Ovisacs were detached from gravid females and the number of eggs per clutch was noted. Twenty to thirty ovigerous females of each species (if available) were secured on each date and their prosome length from the anterior point of the rostrum to the posterior end of the last prosome somite, were measured with the aid of an eyepiece micrometer adjusted to a Leica MS5 stereomicroscope.

Egg production rate (EPR, eggs female^{-1} day^{-1}) for *O. nana* was calculated using the egg-to-female ratio (E/F) as estimated from the preserved samples and the embryonic time (ET, days): EPR = (E/F) (1/ET)

ET was estimated from the equation reported by Temperoni *et al*. (2011) by using the mean temperature of the water column (T, °C): $ET = 4.694\ (T-8)^{-0.462}$.

Egg production rate (EPR, eggs female^{-1} day^{-1}) for *O. similis* was determined using the egg-to-female ratio (E/F) and hatching time (HT) according to Edmondson (1971):

EPR = (E/F) (1/HT)

Hatching time (HT, days) was calculated using the equation of Nielsen and Andersen (2002):
$HT = 1504.5\ (T+7.6998)^{-2.05}$, where T = water temperature (°C).

Statistics

The data were analysed using one-way ANOVA, applied to examine the difference of physicochemical factors and biological factors among the ponds. In addition, Pearson's correlation analysis was adopted to evaluate potential relationships between the abundance and reproduction variables of the *Oithona* spp. in this study on the one hand, and the abiotic and biotic variables, on the other. A principal component analysis (PCA) based on a correlation coefficient matrix among parameters at each pond was used to reveal relationships between physicochemical and biological parameters. SPSS statistical software version 1.0.0.1406 was used to conduct all statistical analyses.

Results

Physico-chemical parameters

Water temperature showed a typical annual profile similar in all ponds, varying between a maximum value of 30°C in pond A16, and a minimum value of 11.5° C in pond A1 (Fig. 2). The annual mean values of temperature in the four ponds were 20.7 ± 5.5 (A1), 21.1 ± 5.5 (A5), 20.9 ± 5.8 (A16) and 21.2 ± 6.1° C (C31). Salinity showed a significant difference between the four ponds during the sampling period (F = 129.62, ANOVA, $p < 0.001$). The salinity exhibited marked differences between seasons, varying between a minimum of 38 psu in pond A1 (April 2008) and a maximum of 86.1 psu in pond C31 (December 2007) (Fig. 2). Low values of salinity during summer and spring compared to winter could be due to the opening of water gates by the saltern managers only during summer and spring to feed the ponds with seawater (extremely lower salinity than the water in the solar saltern), thus contrasting excess evaporation. The annual mean values of salinity in the ponds were 41.5 ± 2.3 psu (A1), 46.4 ± 5.2 psu (A5), 67.6 ± 7.2 psu (A16) and 77.0 ± 4.3 psu (C31). The concentration of suspended matter (SM) fluctuated from 0.1×10^3 mg L^{-1} in pond A5 during March 2008, to 4.2×10^3 mg L^{-1} in pond A5 during June 2008 (Fig. 2). The annual mean values of SM were 1.1 ± 0.5, 1.2 ± 1.1, 1.1 ± 0.9 and 1.3 ± 0.5 × 10^3 mg L^{-1} in ponds A1, A5, A16 and C31, respectively.

Seasonal and spatial distribution of phytoplankton and Ciliophora

A shift was observed from Diatomeae to Dinophyta dominance, along the increasing salinity gradient. The salinity gradient from ponds A1 to C31 showed a negative correlation with the abundance of Diatomeae (r = - 0.719, $p < 0.05$), while it was positively correlated with the abundance of Dinophyta (r = 0.571, $p < 0.05$). Both groups displayed a distinctive pattern of seasonal variation (Fig. 3). The Diatomeae abundance varied between a maximum of 102,400 cells L^{-1} (September 2007) in pond A1 and a minimum of 5,000 cells L^{-1} (July 2008) in pond A16 (Fig. 3). Dinophyta maximum abundance was observed in pond C31 (September 2007, 113,000 cells L^{-1}) (Fig. 3). Diatomeae and Dinophyta were the most abundant groups in all ponds, however, Cyanobacteria, Euglenophyta, and Silicoflagellata were also present but in very small numbers not exceeding 5% of the total phytoplankton community.

The concentration of Chl-*a* ranged from 55.5 mg L^{-1} during June 2008 (pond A1) to 187.0 mg L^{-1} during June 2008 (pond C31) (Fig. 3). The annual mean values of Chl-*a* concentrations were 94.9 ± 26.7, 103.2 ± 15.3, 110.9 ± 28.7 and 102.4 ± 34.5 psu in ponds A1, A5, A16 and C31, respectively. As for Ciliophora, their abundance varied from 500 cells L^{-1} (A1, June 2008) to 186,000 cells L^{-1} (A5, January 2008) (Fig. 4).

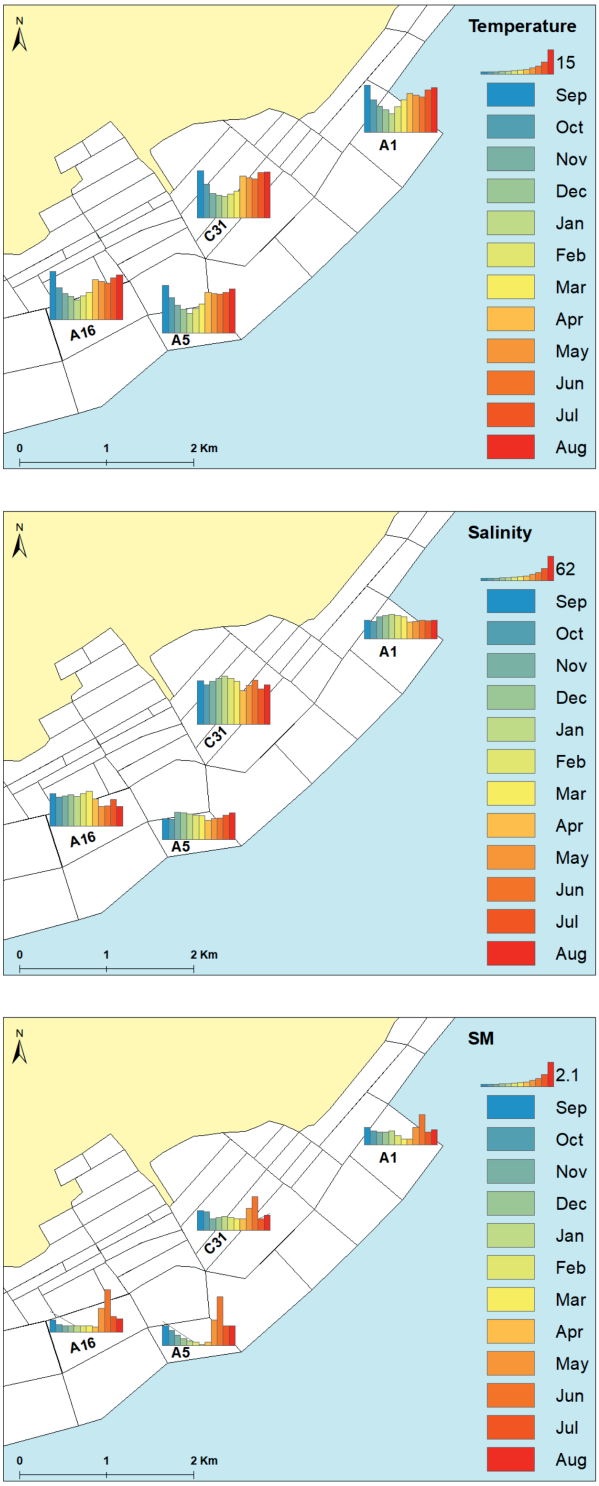

Fig. 2: Monthly variations of physicochemical variables (temperature (°C), salinity (psu), and suspended matter (SM) (×10^3 mg L^{-1}) in ponds A1, A5, A16, and C31 of the Sfax Solar Salterns.

Cyclopoida community

The Cyclopoida community of the Sfax Solar Saltern contained four thalassophilic species: *Oithona nana*, *Oithona similis*, *Triconia conifera* Giesbrecht, 1891, and *Oncaea mediterranea* Claus, 1863 (Kobbi-Rebai *et al.*, 2013). The last-mentioned species was totally absent from C31.

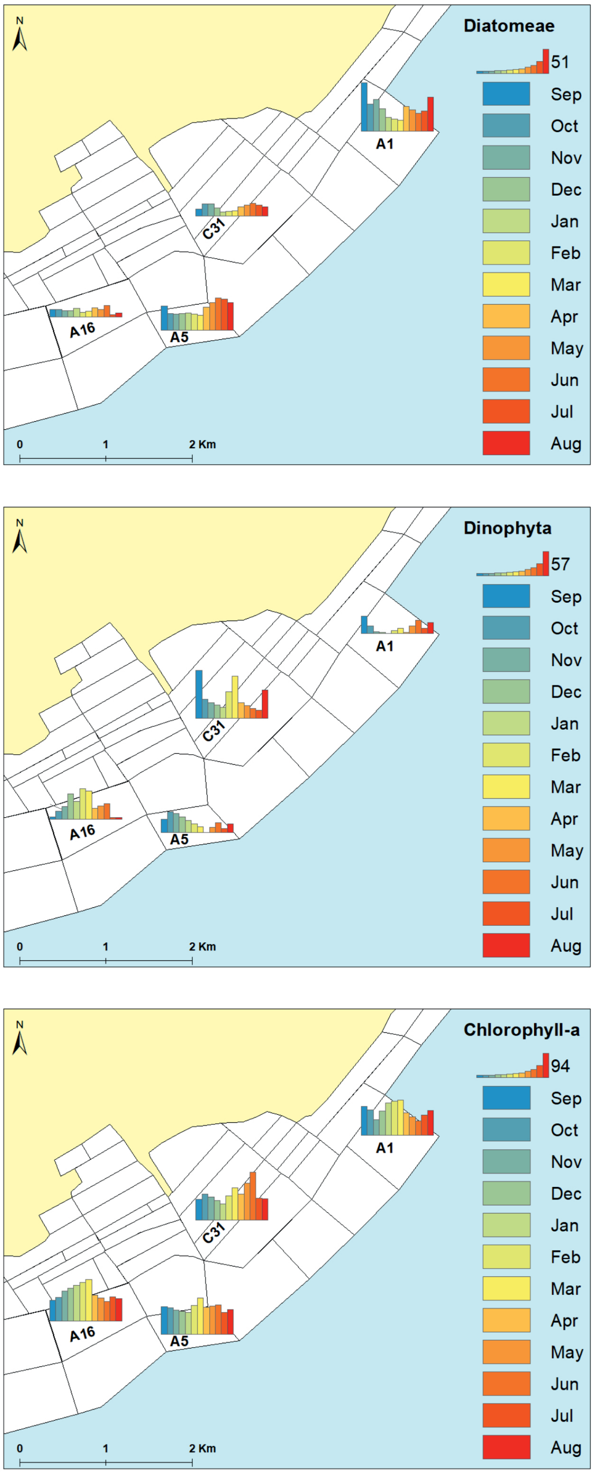

Fig. 3: Monthly variations of phytoplankton variables (Diatomeae (× 10^3 cells L^{-1}), Dinophyta (× 10^3 cells L^{-1}) and Chlorophyll-*a* (mg L^{-1}) in ponds A1, A5, A16, and C31 of the Sfax Solar Salterns.

The total annual mean of the abundance of adult Cyclopoida decreased along the salinity gradient, ranging from 31,670 ± 33,220 to 11,070 ± 12,780 ind. m^{-3} in ponds A1 and C31, respectively (Fig. 5). Cyclopoida showed a negative correlation with salinity ($r = -0.294$, $p < 0.05$), and a negative correlation with temperature ($r = -0.362$, $p < 0.05$). *Oithona nana* dominated the Cyclopoida community in all ponds, and its contribution increased with

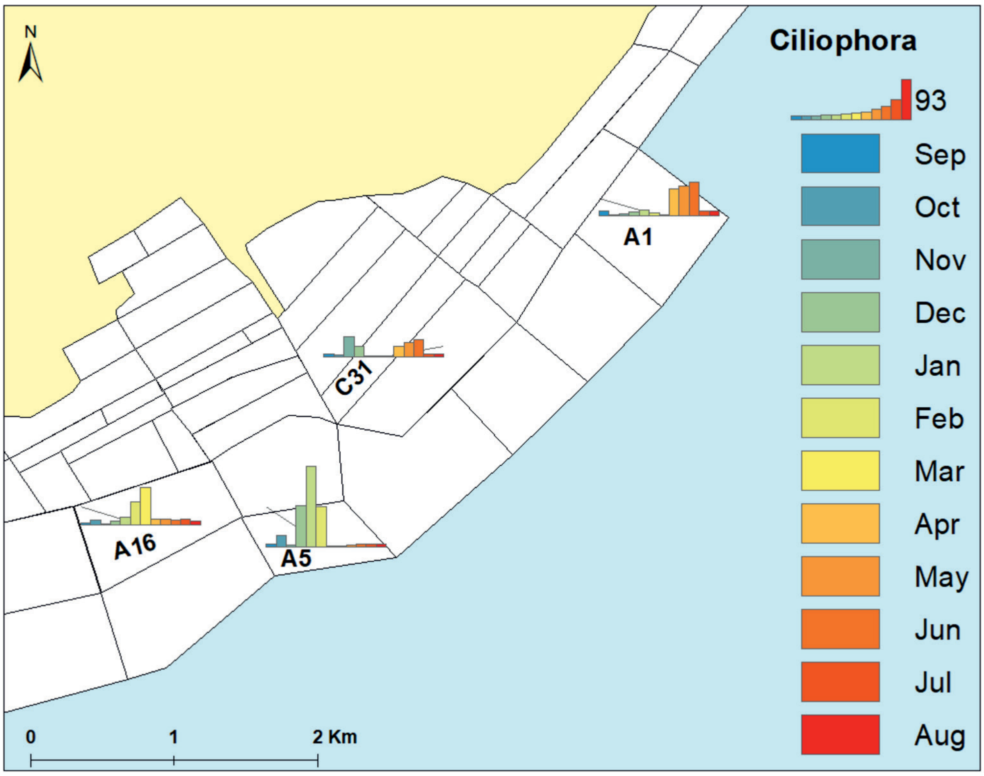

Fig. 4: Monthly variations of Ciliophora (× 10^3 cells L^{-1}) in ponds A1, A5, A16, and C31 of the Sfax Solar Salterns.

the general decrease of Cyclopoida along the increasing salinity. *Oithona nana* represented 47% of Cyclopoida in A1 and 62% in C31 (Fig. 5), while *O. similis* formed 43% and 33% of the adult cyclopoid copepods in ponds A1 and C31, respectively (Fig. 5).

Oithona nana **Giesbrecht, 1893**

The average annual abundance of males of *O. nana* varied between 1,720 ± 1,940 ×10^3 ind. m^{-3} in C31 and 3,690 ± 4,170 ind. m^{-3} in A1 (Table 1, Fig. 6), while females of *O. nana* showed their maximum abundance in pond A1 (average, 2,240 ± 2,300 ind. m^{-3} with 8,000 ind. m^{-3} in autumn, 13 September 2007) and a minimum abundance of 970 ± 1,050 ind. m^{-3} in C31 (Table 1, Fig. 6). Both sexes of this species showed a positive correlation with Diatomeae abundance ($p < 0.01$) and did not differ significantly among the ponds (ANOVA, $p < 0.05$) (Table 1).

The percentage of ovigerous females of *O. nana* varied between 0% and 50% of the total abundance of females (maximum observed on 6 June 2008 in pond A1) (Fig. 6). Significant differences in numbers of total ovigerous females were found between all ponds (ANOVA, F = 2.44, $p < 0.05$) (Table 1). A negative correlation was observed between ovigerous females and salinity (r = -

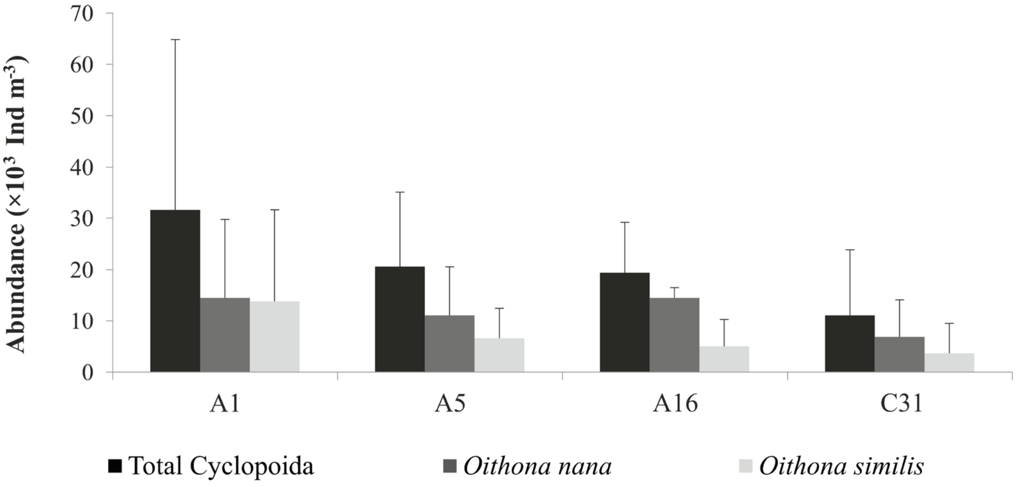

Fig. 5: Spatial variations of the adult mean annual abundance of total Cyclopoida, *Oithona nana* Giesbrecht, 1893 and *Oithona similis* Claus, 1866 in ponds A1, A5, A16, and C31.

Table 1. Annual mean (±SD) abundance of adults (males and females), copepodites, adult males, adult females, ovigerous females, sex ratios (n. males/n. females), and number of eggs for two copepod communities *Oithona nana* Giesbrecht, 1893 and *Oithona similis* Claus, 1866 in ponds A1, A5, A16, and C31. In the last column, results of one-way ANOVA analyses are given as *F values* between-groups mean square/within-groups mean square: *$p < 0.05$; **$p < 0.01$; ***$p < 0.001$, significant differences between sampled ponds.

Ponds	A1	A5	A16	C31	*F-values*
		Oithona nana			
Adults+copepodites (×10^3 ind m^{-3})	14.9 ± 15.2	11.1 ± 9.5	10.8 ± 5.7	6.8 ± 7.2	1.03
Adult males (×10^3 ind m^{-3})	3.69 ± 4.17	2.68 ± 2.87	2.54 ± 1.31	1.72 ± 1.94	0.93
Adult females (×10^3 ind m^{-3})	2.24 ± 2.30	1.49 ± 1.48	1.46 ± 0.81	0.97 ± 1.05	1.30
Sex ratio (n. males/n. females)	1.56 ± 0.27	1.77 ± 0.34	1.76 ± 0.22	1.79 ± 0.39	1.30
Ovigerous females (×10^3 ind m^{-3})	0.68 ± 0.75	0.43 ± 0.55	0.33 ± 0.39	0.10 ± 0.23	2.44*
Prosome of ovigerous females (mm)	0.39 ± 0.010	0.38 ± 0.015	0.32 ± 0.006	0.27 ± 0.010	98.63***
Clutch size (eggs fem^{-1})	17.77 ± 1.13	17.85 ± 0.83	18.16 ± 0.89	18.50 ± 0.50	0.49
EPR (eggs $female^{-1}$ day^{-1})	4.70 ± 0.39	3.86 ± 0.21	3.34 ± 0.10	3.20 ± 0.13	36.08***
Ovisac length (mm)	0.44 ± 0.05	0.40 ± 0.01	0.40 ± 0.01	0.39 ± 0.01	5.89*
Egg diameter (mm)	0.043 ±0.002	0.042 ± 0.001	0.040 ± 0.001	0.039 ± 0.002	16.53***
		Oithona similis			
Adults+copepodites (×10^3 ind m^{-3})	13.8 ± 17.9	6.6 ± 5.8	5.8 ± 5.3	3.7 ± 5.8	2.15*
Adult males (×10^3 ind m^{-3})	2.91 ± 3.13	1.74 ± 1.72	1.33 ± 1.44	0.85 ± 1.34	2.05*
Adult females (×10^3 ind m^{-3})	1.42 ± 1.66	1.09 ± 1.02	0.92 ± 1.01	0.62 ± 1.09	0.8
Sex ratio (n. males/n. females)	2.23 ± 0.21	1.55 ± 0.21	1.54 ± 0.22	1.51 ± 0.29	2.6
Ovigerous females (×10^3 ind m^{-3})	0.12 ± 0.27	0.11 ± 0.13	0.08 ± 0.14	0.10 ± 0.22	0.07
Prosome of ovigerous females (mm)	0.47 ± 0.009	0.43 ± 0.015	0.36 ± 0.008	0.31 ± 0.007	134.7***
Clutch size (eggs fem^{-1})	20.50 ± 0.57	21.17 ± 0.58	20.55 ± 0.75	21.33 ± 0.58	1.78
EPR (eggs $female^{-1}$ day^{-1})	5.19 ± 0.64	4.43 ± 0.25	3.78 ± 0.37	3.66 ± 0.05	14.88***
Ovisac length (mm)	0.45 ± 0.06	0.44 ± 0.02	0.43 ± 0.03	0.41 ± 0.01	4.82*
Egg diameter (mm)	0.043 ± 0.001	0.042 ± 0.002	0.041 ± 0.001	0.040 ± 0.002	23.13***

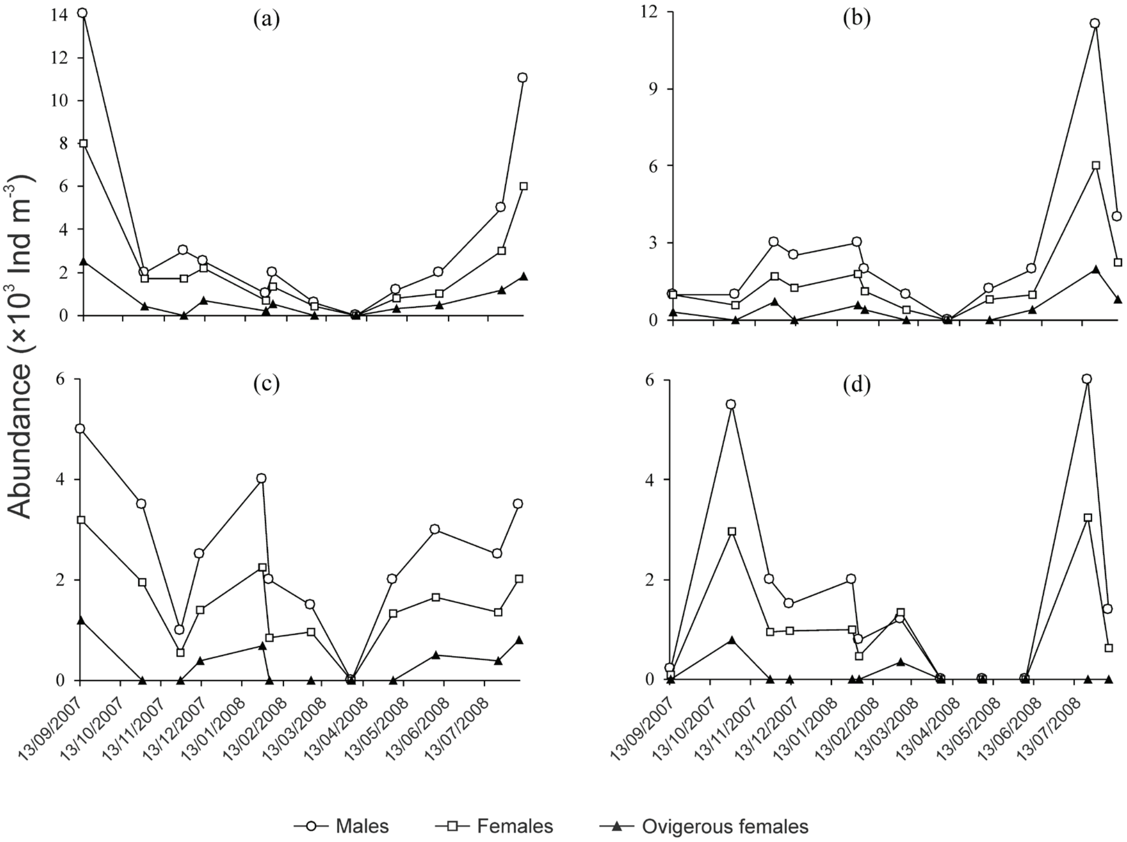

Fig. 6: Temporal and spatial variations of males, females, and ovigerous females' abundances of *Oithona nana* Giesbrecht, 1893 in ponds A1 (a), A5 (b), A16 (c), and C31 (d) in the Sfax Solar Saltern.

0.302, $p < 0.05$). The abundance of ovigerous females was positively correlated with Diatomeae ($r = 0.549$, $p < 0.01$) and temperature ($r = 0.301$, $p < 0.05$). *O. nana* adults (males + females) were completely absent on 4 April 2008 in ponds A1, A5 and A16, and from 4 April 2008 to 6 June 2008 in pond C31 (Fig. 6). The highest salinity associated with *O. nana* adults was 86.1 psu on 12 December 2007 in pond C31.

Ovigerous females were observed in pond C31 only on 29 October 2007 and 4 March 2008 (Fig. 6). The sex ratio (n. males/n. females) was highly skewed towards males in all ponds with the highest value of 1.79 ± 0.39 in pond C31 (Table 1).

The annual mean prosome length of ovigerous females ranged between 0.39 ± 0.010 and 0.27 ± 0.007 mm in ponds A1 and C31, respectively (Table 1). It was negatively correlated with salinity ($r = - 0.895$, $p < 0.01$) and positively correlated with Diatomeae ($r = 0.630$, $p < 0.01$). The clutch size varied slightly between females (maximum 20, minimum 16 eggs fem^{-1}). The annual mean values of clutch size ranged between 17.77 ± 1.13 eggs fem^{-1} in A1 and 18.50 ± 0.50 eggs fem^{-1} in C31.

The egg production rate (EPR) fluctuated between 3.2 eggs female^{-1} day^{-1} recorded on 6 June 2008 (pond A16), 29 October 2007 and 4 March 2008 (pond C31), and 5.5 eggs female^{-1} day^{-1} on 28 January 2008 (pond A1) (Fig. 7). EPR showed a positive correlation with Diatomeae ($r = 0.430$, $p < 0.05$) and negative correlations with salinity ($r = -0.716$, $p < 0.01$) and Dinophyta ($r = -0.402$, $p < 0.05$).

The annual mean of ovisac length of *O. nana* varied significantly between 0.39 ± 0.01 mm for the population in C31 and 0.44 ± 0.05 mm for the population in A1 (Table 1). The egg diameter varied between 0.039 ± 0.002 mm in C31 and 0.043 ± 0.002 mm in A1 (Table 1). The egg diameter ($r = -0.542$, $p < 0.01$) and the ovisac length ($r = -0.530$, $p < 0.01$) showed negative correlations with salinity.

Oithona similis Claus, 1866

The annual abundance of males of *O. similis* varied between 850 ± 1,340 m^{-3} in C31 and 2,910 ± 1,340 ind. m^{-3} in A1 (Table 1, Fig. 8). The maximum abundance of males (6,000 ind. m^{-3}) was observed on 13 September 2007 in pond A1. The abundance of males differed significantly between ponds (ANOVA, $p < 0.05$). The abundance of males showed a positive correlation with Diatomeae ($r = 0.416$, $p < 0.01$) and a negative correlation with salinity ($r = -0.307$, $p < 0.01$). Females of *O. similis* varied in abundance between 620 ± 1,090 ind. m^{-3} in C31 and 1,420 ± 1,660 ind. m^{-3} in pond A1 (Table 1, Fig. 8). No significant differences in the variation of number of adult females of this species were found between the ponds (Table 1). However, the adult females showed a positive correlation with Diatomeae ($r = 0.382$, $p < 0.01$).

The percentage of ovigerous females of *O. similis* varied between 0% and 22.22% of the total abundances of females (maximum observed on 13 September 2007 in pond C31) (Fig. 8). Ovigerous females showed their maximum abundance in pond A1 with 1,000 ind. m^{-3} on

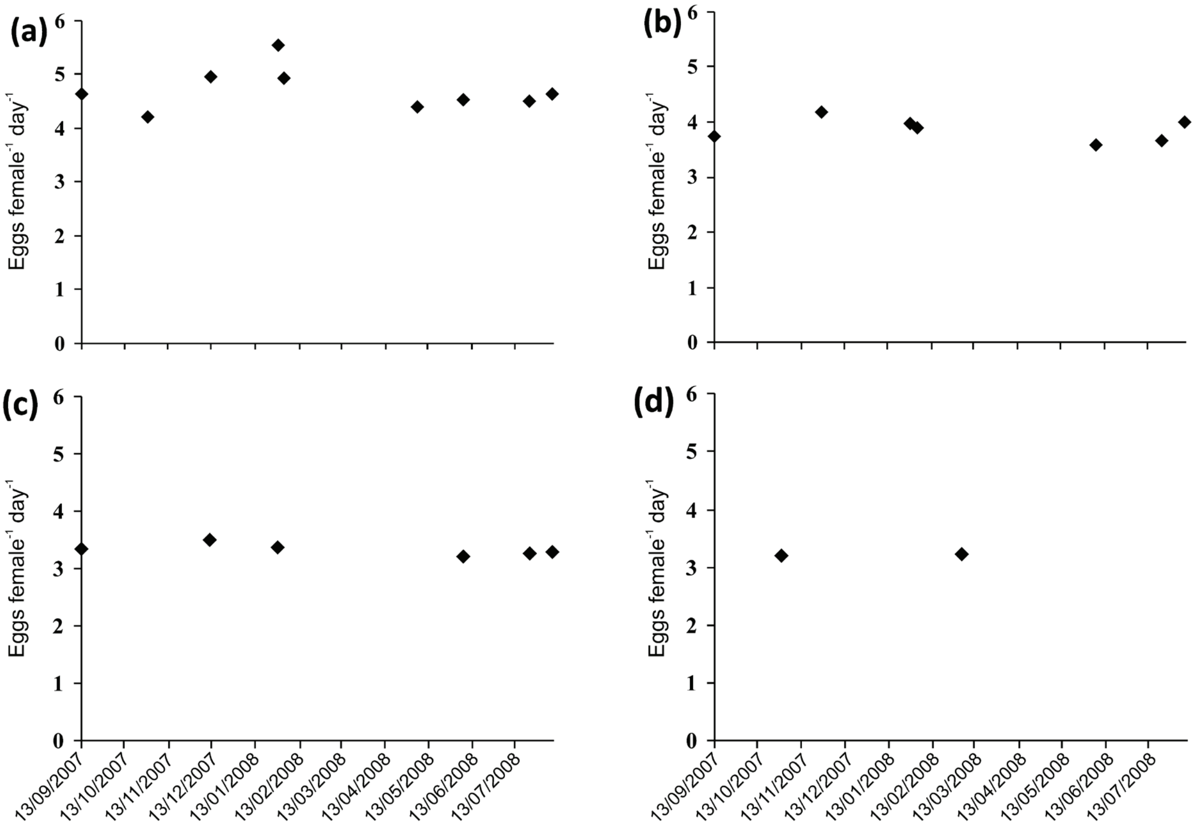

Fig. 7: Spatial and temporal variation of *Oithona nana* Giesbrecht, 1893 egg production rate (EPR) in ponds A1 (a), A5 (b), A16 (c), and C31 (d) in the Sfax Solar Saltern.

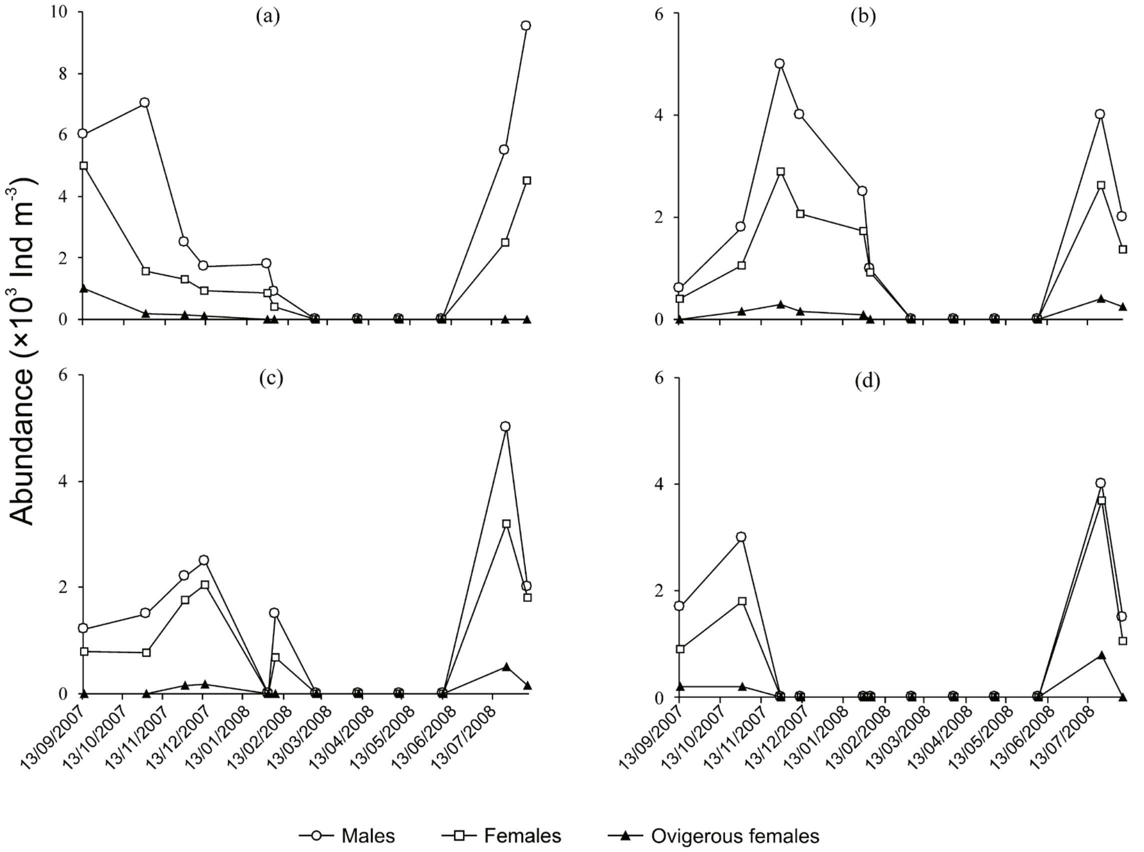

Fig. 8: Temporal and spatial variations of males, females, and ovigerous females' abundances of *Oithona similis* Claus, 1866 in ponds A1 (a), A5 (b), A16 (c), and C31 (d) in the Sfax Solar Saltern.

13 September 2007. The abundance of ovigerous females of *O. similis* was positively correlated with Diatomeae ($r = 0.333$, $p < 0.01$) and temperature ($r = 0.285$, $p < 0.05$). *O. similis* adults (males + females) were totally absent from 4 March to 6 June 2008 in ponds A1, A5, and A16, and from 27 October 2007 to 6 June 2008 in pond C31 (Fig. 8). The highest salinity in which *O. similis* adults were found was 80 psu, on 8 August 2008 (pond C31).

The sex ratio (n. males/n. females) was highly skewed towards males in all ponds (Table 1). The annual mean prosome length of ovigerous females ranged between 0.47 ± 0.009 and 0.31 ± 0.007 mm in ponds A1 and C31, respectively (Table 1). It was negatively correlated with salinity ($r = - 0.940$, $p < 0.01$) and positively correlated with Diatomeae ($r = 0.795$, $p < 0.01$). The clutch size did not vary significantly between ponds (Table 1). The annual mean values ranged between 20.50 ± 0.577 eggs fem^{-1} in A1 and 21.33 ± 0.57 eggs fem^{-1} in C31 (maximum 22 eggs fem^{-1} and a minimum 20 eggs fem^{-1}). *O. similis* clutch size showed positive correlations with suspended matter ($r = 0.498$, $p < 0.05$) and temperature ($r = 0.495$, $p < 0.05$).

The egg production rate (EPR) varied between 3.60 eggs female^{-1} day^{-1} (recorded on 13 September 2007 in pond C31) and 5.93 eggs female^{-1} day^{-1} (on 27 October 2007 in pond A1) (Fig. 9). EPR showed a positive correlation with Diatomeae ($r = 0.625$, $p < 0.01$) and a negative correlation with salinity ($r = -0.730$, $p < 0.01$). The ovisac length and egg diameter of *O. similis* varied significantly between ponds (Table 1), since both traits showed negative correlations with salinity ($r = -0.642$, $p < 0.01$) and ($r = -0.740$, $p < 0.01$), respectively.

Principal components analysis

The principal components analysis (PCA) was characterized by 59.80 % (axis-F1) and 27.55% (axis-F2) of total variance in reproduction variables of two copepod species and environmental variables of the Solar Saltern, respectively (Fig. 10). The positive end of the first axis accounted for the major part of the reproduction variables which are coupled at first level by Diatomeae (strong correlation) and Ciliophora (not strong correlation). While temperature, salinity, suspended matter, Chl-*a*, Dinophyta and Clutch size exhibited high negative loadings on PCA II. The PCA confirmed that the reproduction variables of the two Cyclopoida species are higher in ponds A1 and A5, associated with higher abundance of Diatomeae. While temperature and salinity were negatively correlated with the reproduction variables of *Oithona nana,* they were positively correlated with the clutch size of *Oithona similis* in ponds A16 and C31.

Discussion

The present study is the first contribution, to the best of our knowledge, to evaluate some of the factors that drive the adult population and reproduction variables of

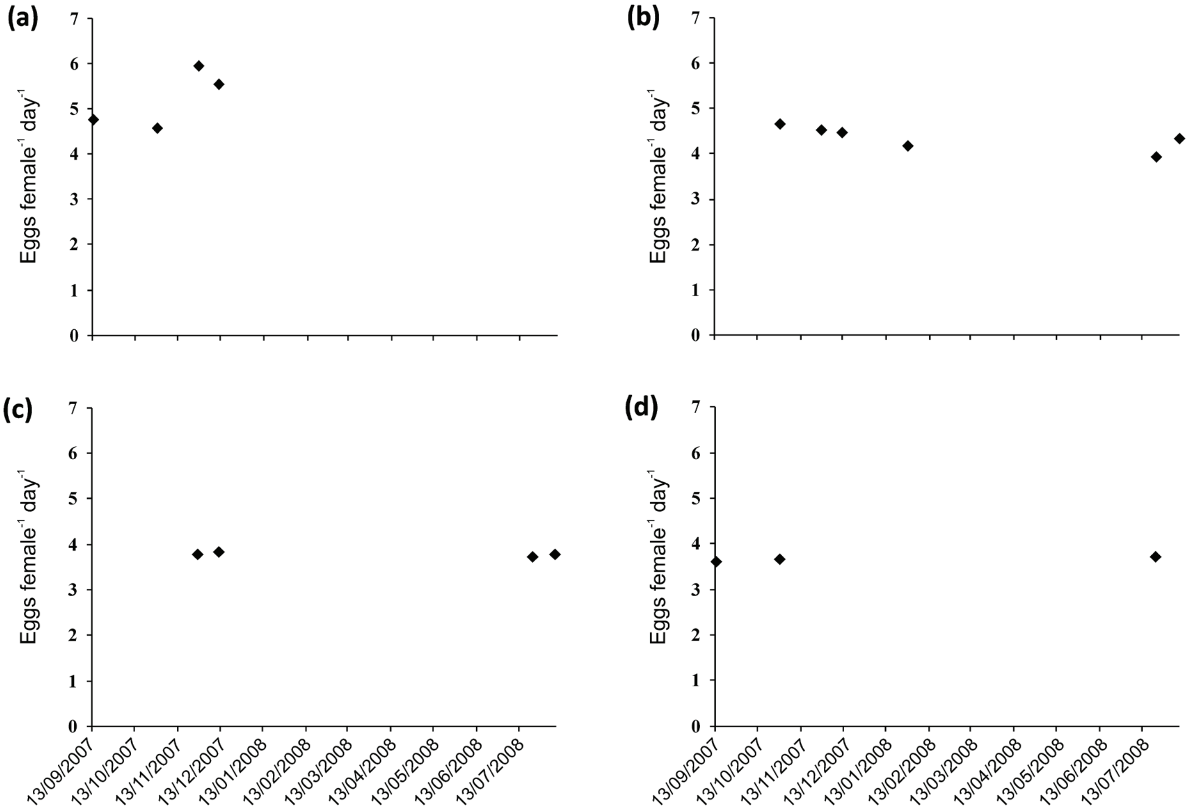

Fig. 9: Spatial and temporal variation of *Oithona similis* Claus, 1866 egg production rate (EPR) in ponds A1 (a), A5 (b), A16 (c), and C31 (d) in the Sfax Solar Saltern.

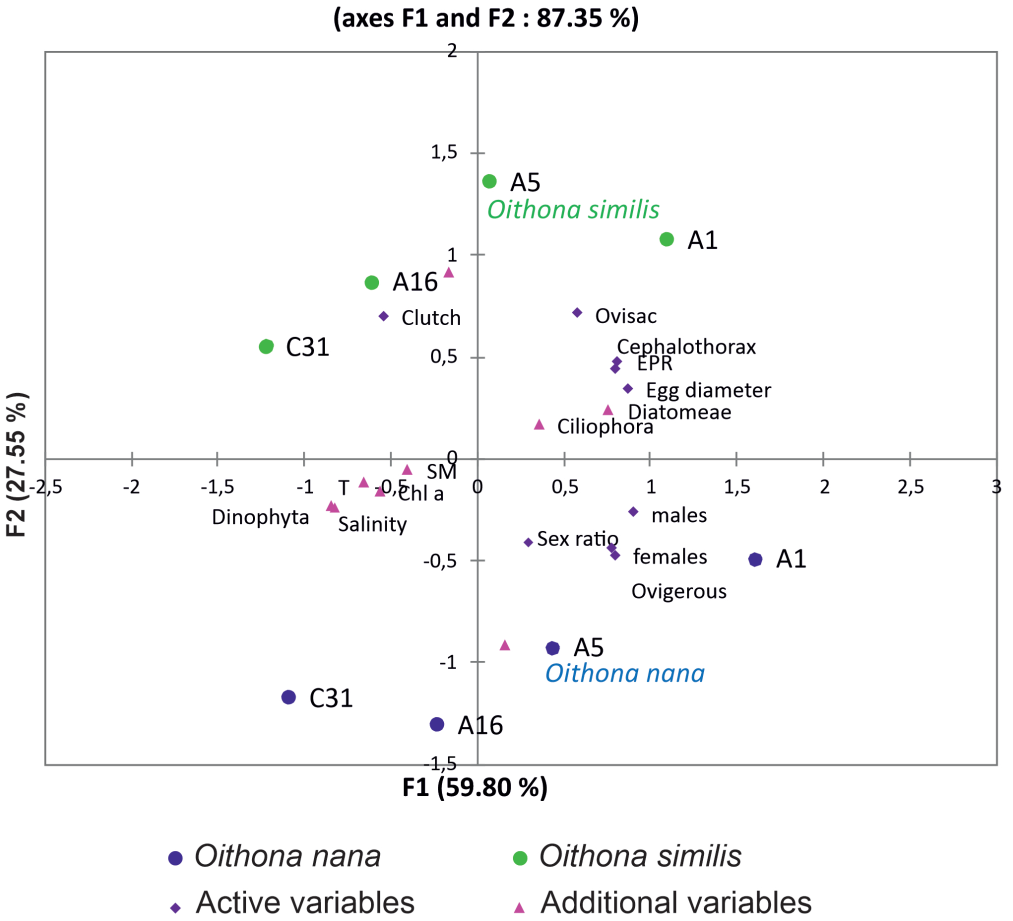

Fig. 10: Biplot of Principal Components Analysis (PCA) with simultaneous representations of variables and observations; for further explanations, see text.

two *Oithona* species; *O. nana* and *O. similis*, in high salinity environments (from 38 to 86 psu). Both species are typical, euryhaline marine species found under various salinity regimes worldwide varying for *O. similis* from 7 to 16 psu in the Baltic Sea (Hansen *et al*., 2004) to 38.8 psu in the southern Adriatic Sea (Miloslavić *et al*., 2012), while *O. nana* has been recorded in salinities ranging between 9 and 43.8 (Vieira *et al*., 2003; Annabi-Trabelsi *et al*., 2005; Williams & Muxagata, 2006; Miyashita *et al*., 2009; Cepeda *et al*., 2015). In the present study these two species showed a great ability to survive at high salinities (up to 80 for *O. similis* and up to 86.1 for *O. nana*), higher that the salinity values recorded so far. Such findings broaden our understanding of the ecological niche of these two cosmopolitan Cyclopoida species in relation to their reproduction as well as to their survival under hypersaline conditions.

This wide range of tolerance of *O. similis* (present study: 38.8-80.0 psu) and *O. nana* (present study: 38.8 – 86.1 psu) for salinity represents an explanation for their wide geographic distribution under different conditions, while it allows them to settle in extreme environments, which are normally hostile to other copepods. However, the increasing salinity had a negative impact on ovigerous females, which were only sporadically observed in pond C31 (the saltiest pond in this study).

Species of the genus *Oithona* have a wide range of diets and several feeding strategies are known (González & Smetacek, 1994; Atkinson, 1996; Nakamura & Turner, 1997; Calbet *et al*., 2000; Svensen & Kiørboe, 2000; Paffenhöfer & Mazzocchi, 2002). Males, females, and ovigerous females of both *Oithona* species in this study showed strongly positive correlations with Diatomeae. The abundance of *Oithona* inhabiting ponds A1 and A5 of the Sfax Solar Saltern had a positive correlation with the abundance of Diatomeae, which could indicate feeding preference on these phytoplankton elements. Compared to other marine coastal and oceanic regions, *Oithona* spp. generally feed on motile prey, especially Protozoa (Atkinson, 1995; Lonsdale *et al*., 2000; Castellani *et al*., 2005; Castellani *et al*., 2008). However, their most abundant prey was *Nitzschia longissima* (Diatomeae), which is considered of a small-sized compared to other Diatomeae, in this study. Both *Oithona* species can feed on such small-sized prey (Khemakhem *et al*., 2010) in these ponds, especially in the lower abundance of Protozoa and other phytoplankton. Thus, *Oithona* species are logically able to exploit a high availability of small Diatomeae in the ponds of the Sfax Solar Saltern. In fact, the large and robust maxillipeds of *Oithona* indicate that this genus has adaptations that facilitate the ingestion and processing of Diatomeae, since the frustules of this group can be extremely robust and require considerable force to be broken (Hamm *et al*., 2003; Smetacek *et al*., 2004). A similar situation was observed in Antarctic waters, where females *O. similis* contained the highest levels of Diatomeae fatty acid biomarkers (Pond & Ward, 2011). According to Ward and Hirst (2007), abundances of all developmental stages of *O. similis* are correlated with both temperature and Chl-*a* concentrations.

Food also assists in the accumulation of large amounts of lipids, which are essential for Copepoda to maintain neutral buoyancy (Campbell & Dower, 2003; Breteler *et al*., 2004; Boissonnot *et al*., 2016; Jónasdóttir, 2019). The bodies of the majority of copepods are denser than the seawater in which they live, despite the level of salinity (Mauchline, 1998). The absolute coincidence of body and water densities is an extremely rare phenomenon (Campbell, 2004). The body density changes proportionally to the salinity and density of water. Hence, within the salinity tolerance range, changes in density, sinking speed, and energy losses for the maintenance at a required depth are constant in these species (Svetlichny *et al*., 2012). There are such critical situations when the moving capabilities of Copepoda would be insufficient to maintain buoyancy in the water column. That is why copepods should possess neutral buoyancy by accumulating large amounts of lipids (Campbell & Dower, 2003). Fatty acid biomarker analysis has indicated that Diatomeae are an important food source for the genus *Oithona* (Pond & Ward, 2011). The results of the present study indicate that feeding on Diatomeae by both *Oithona* species could have occurred in order to accumulate lipids for buoyancy especially at pond A1 (lowest salinity). It is also important to note that Diatomeae are rich in lipids compared to other phytoplankton (Jónasdóttir, 2019).

In this investigation, sex ratios favoured males over females in both species. Male-biased sex-ratio results in females becoming more selective when they have a greater opportunity to choose mates (Balshine-Earn, 1996) and males tend to compete more intensively for females due to the presence of more potential competitors (Jormalainen *et al*., 1994; Dick & Elwood, 1996). According to Boyer (2012), the dominance of males over the dominance of females optimizes mating success. In some environments with visual predation pressures (Castonguay & Fitz Geralt, 1990, Ludovisi *et al*., 2008) and in some populations at low densities (Schmitt *et al*., 2008), the sex ratio is in favour of males. However, in the same ecosystem, it has been reported that sex ratio favoured females over males for the calanoid copepod *Paracartia grani* (cf. Annabi-Trabelsi *et al*., 2018) and for two harpacticoid copepods, *Canuella perplexa* and *Bryocamptus* sp. (Kobbi-Rebai *et al*., 2020). The dominance of females over males is a common trait in the communities of Copepoda (Hicks & Coull, 1983; Gusmão & McKinnon, 2009). Also, it has been reported that salinity tolerance was found to be unequal in favour of females over males at each life cycle stage in the different sexes (Damgaard & Davenport, 1994). In *Oithona* spp., the maintenance of the population during unfavourable periods appears to depend on the abundance of females and sex-ratio, since this species does not produce resting eggs during its life cycle (Temperoni e*t al*., 2011). In the case reported herein, it seems also to depend on the percentage of ovigerous females and sex ratio, but this needs further investigation.

Significant spatial variations in female prosome length were observed between ponds for *O. nana* and *O. similis* in this study. The presence of smaller females under increasing salinity gradient in the ponds of the Sfax

Solar Saltern has also been observed in estuarine conditions for *Oithona* spp. (Cepeda *et al*., 2015). As for other copepods, Belmonte and Cavallo (1997) found that the body size of female *Acartia* (*Acartiura*) *margalefi* Alcaraz, 1976 (a species adapted to variable environments) was strongly and inversely correlated with confinement. According to Uye (1994), the general shift to small-sized copepods in a progressive enhancement of confinement could be due to changes in the composition of food particles (replacement of diatoms by much smaller prey). It is well known that plankton of confined environments is of smaller size than that of the open sea (Uye, 1994; Belmonte *et al*., 2013). Even the same species has a smaller body size in confined environments (Belmonte & Cavallo, 1997). This well-known result is generally correlated with salinity (lower salinity, smaller body size, and *vice versa*). In the present study, however, there is an evident inverse correlation with salinity (higher salinity, smaller body size). This could suggest that salinity was not the only factor responsible for the planktonic copepods' body size. Guelorget and Perthuisot (1992) proposed to put together confined environments (either brackish or hypersaline) on the basis of the confinement grade (changing time of the water, trophic status, oxygen depletion due to organic matter decomposition).

The present study was not only concerned with the description of the presence of *Oithona* spp. in highly saline environments, but also shows that there could be other factors beside salinity affecting the reproduction variables. Experimental reports on *Dioithona rigida* (Giesbrecht, 1896) (formerly *Oithona rigida* Giesbrecht, 1896) demonstrate that low salinity causes slower development, mainly because of osmoregulation costs, which reduces the final size of the copepods (Santhanam & Perumal 2012).

The EPR for *O. nana* and *O. similis* in the study herein ranged between 3.2 and 5.5 eggs female^{-1} day^{-1} and between 3.60 and 5.93 eggs female^{-1} day^{-1}, respectively. These values of EPR fall within the range of previously reported values from field studies of *Oithona* spp. (Sabatini *&* Kiørboe, 1994; Zamora-Terol & Saiz, 2013; Zamora-Terol *et al*., 2014; Cepeda *et al*., 2015). However, the percentage of ovigerous females in this study was generally low (0-50% for *O. nana* and 0-22% for *O. similis*) and the maximum EPR did not reach values reported in previous investigations regarding other *Oithona* species (Uye & Sano, 1995; McKinnon & Klumpp, 1998) and that could mainly be attributed not only to the extreme salinity but also to the effect of food.

Conclusion

In the present study, the increasing salinity gradient was found to be correlated with morphological and reproduction variables of *Oithona nana* and *O. similis*. Salinity was negatively correlated with the prosome length of ovigerous females, EPR, egg diameter, and ovisac length for both species, but they were positively correlated to the abundance of Diatomeae. *O. nana* and *O. similis* abundances were reduced in the saltiest pond because of a mix of high salinity and a decrease in the Diatomeae densities. The EPR of both Cyclopoida in the study herein, was generally within the range of other *Oithona* spp. and the maximum EPR in this study was lowest compared to previous studies about *Oithona* spp. In addition, the percentage of ovigerous females for both Cyclopoida in this investigation was low. The maintenance of the populations of the studied *Oithona* spp. in the Sfax Solar Saltern seems to depend on the percentage of ovigerous females and sex-ratio.

The availability of copepods in these environments conveniently allows to utilize them as live-food for larval fish in aquaculture, and also, quite differently, to use them for laboratory experiments in relation to climate change, including acidification. Furthermore, additional studies about the seasonality and the feeding ecology of these Cyclopoida (as well as other copepods) in relation to season, salinity, and abundance of Diatomeae, should be performed in order to confirm the present data about the diet choice of these species and about the mechanisms permitting them to survive such extreme saline conditions.

The reduction of *Oithona* ovigerous female prosome length along the salinity gradient of the present study was also reported from confined brackish water (with low salinity values) and demonstrates that such a character is due to a network of causes related with the confinement (Guelorget & Perthuisot, 1992) and not to salinity *per se*. Also, the observations of this study, particularly about size and abundance are very important to understand the size spectra (relationship between mass and abundance) as well as the marine food web interactions and food web structure (Werner & Gilliam, 1984; Werner, 1988; Williams & Martinez, 2000; Dunne *et al*., 2002; Woodward & Hildrew, 2002; Hartvig *et al*., 2011; Jacob *et al*., 2011; Blanchard *et al*., 2014, 2017; Clegg *et al*., 2018) in such extremely saline ecosystem.

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