

## Copepoda in the shallow hypersaline Bardawil coastal lake (Egypt): Are there long-term changes in composition and abundance?

by

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### Abstract

Coastal Lake Bardawil (Egypt) is one of the largest hypersaline lakes in the world. In 2009–2010, the authors studied composition, distribution and seasonal dynamics of copepods at 12 sites. A total of 10 species of copepods were recorded in zooplankton during the study period, including 5 Calanoida, 2 Cyclopoida and 3 Harpacticoida. *Oithona nana* was the most common and most abundant species. All copepods in the lake can be divided into three groups: 1) planktic species that form stable populations, 2) species of Mediterranean plankton incidentally entering the lake from the adjacent sea area, 3) benthic Cyclopoida and Harpacticoida that can be abundant in plankton. Two species – *Acartia tonsa* and *A. danae* were recorded here for the first time. The total abundance of copepods in the lake was significantly higher (90 times on average) compared to that observed in 2008–2009 in the waters of the Egyptian Mediterranean Sea. Since 1967, the complex of common and dominant copepod species in the lake has changed significantly. The total average annual copepod abundance varied: in 2002 – it was about 4000 ind. m<sup>-3</sup>, in 2004 – 152 000 ind. m<sup>-3</sup>, in 2005 – about 25 300 ind. m<sup>-3</sup>, and in 2009–2010 – about 56 000 ind. m<sup>-3</sup>.

**Key words:** Copepoda, hypersaline, coastal lakes, species richness, abundance, long-term changes

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## Introduction

Copepods play an important functional role in different marine ecosystems (Huys & Boxshall 1991; Schminke 2007; Anufrieva 2015; 2016). Individual species of copepods, representing various trophic levels, are often the key players that determine the structure of trophic webs and the rate of biogenic element cycling. Knowledge of the plankton copepod species structure and the patterns of its dynamics is necessary to understand the functioning of marine ecosystems and to predict their possible changes.

Coastal lakes/lagoons are an important component of the World Ocean. They cover 13% of the coastal areas around the world and significantly affect the productivity of coastal zones, the land-ocean interactions and support large human populations (Mee 1978; Pérez-Ruzafa et al. 2012). Lagoons are characterized by very high diversity, including also salinity. Most lagoons have marine or brackish salinity, only a small number of lagoons on different continents are hypersaline (salinity > 35 PSU) (Por 1972; Post et al. 1983; Orihuela et al. 1991; Lamptey & Armah 2008). The largest of them are the Sivash (The Sea of Azov, area 2560 km<sup>2</sup>), Laguna Ojo de Liebre (the Pacific coast of Baja California, 850 km<sup>2</sup>), Bardawil Lagoon (Egypt, 600 km<sup>2</sup>) and Lagoa de Araruama (the Atlantic coast of Brazil, 220 km<sup>2</sup>) (Postma 1965; Kjerfve et al. 1996; Abd Ellah & Hussein 2009; Shadrin et al. 2017).

The climatic prerequisite of lagoon salinization and hypersalinity incorporates several geophysical factors (Kjerfve et al. 1996; Shadrin 2017). Hypersalinity of lagoons is a result of arid or semi-arid climatic conditions, and a relatively small drainage basin. The evaporation in a hypersaline lagoon exceeds precipitation, the water influx (sea water and terrestrial runoff) will not compensate for the difference as usually. The energy of coastal sea/ocean waves supplies into the lagoons by filtering the seawater through the sand/gravel barrier and/or seawater flux into the channels connecting the lagoon-to-sea. An important factor for lagoons is the storm winds that sharply raise the sea level – huge waves moving through sand spits and the rising sea level substantially increase the filtration rate into a lagoon, which receives a greater seawater influx (Kjerfve et al. 1996; Shadrin & Anufrieva 2013).

Features of thermal and oxygen regimes in the hypersaline lagoon contribute to their polyextremality (Shadrin 2017). The specific heat capacity decreases as the salinity increases. This leads to faster heating and cooling of hypersaline waters with higher day and lower night temperatures compared to freshwater, brackish or marine lagoons. The range of daily

temperature fluctuations in water bodies increases. Thermal conductivity also decreases with increasing salinity, and this leads to stronger spatial gradients of temperature and salinity in the water column of shallow lagoons (Shadrin 2017). Thermal stratification was observed in hypersaline lagoons with a depth below 2 m. Temperature differences in the water column with a depth of 1 m may reach 14°C. The development of floating mats of filamentous algae leads to an increase in the vertical temperature gradient. The solubility of oxygen decreases with increasing water temperature and salinity. The oxygen diffusion coefficient decreases with increasing salinity, which contributes to strong daily fluctuations of oxygen concentration and its spatial gradients in hypersaline waters. Strong fluctuations – from 200% of saturation (daytime) to zero (nighttime) were observed in the lagoons (Shadrin 2017). This contributes to the formation of near-bottom anoxic zones, which are common features of different hypersaline lagoons/coastal lakes (Shadrin & Anufrieva 2013; Shadrin et al. 2016). The coastal lagoons are continuously transformed by the variability in precipitation and temperature regimes, winds, natural and anthropogenic hydrological factors (siltation, erosion and dredging of channels) as well as other factors. Ecosystems of hypersaline lagoons generally exist in a precarious balance and demonstrate high variability, which adds to the already extreme habitable conditions.

The severity of habitat conditions and high seasonal and long-term variability of various abiotic parameters, significantly exceeding the ranges of variability in other types of marine ecosystems, make the hypersaline lagoons convenient model objects to study the role of variability of various factors in biotic composition changes. Despite the severity of their environment, hypersaline lagoons often demonstrate the highest biological productivity (Shadrin et al. 2015a). This surprising phenomenon has not yet been fully explained, but the hypothesis has been suggested that wide gradients of key abiotic factors in a microscale (e.g. Eh, pH, O<sub>2</sub>, H<sub>2</sub>S, light energy) and their short-term variability (hours) facilitate the optimal coupling between different types of metabolism, while maximizing energy and fluxes of biogenic elements in hypersaline lagoon ecosystems (Shadrin et al. 2015a). It is assumed that halotolerant and abundant copepods may contribute to high productivity in such lagoons/lakes (Mageed 2006; Lamptey & Armah 2008; Shadrin & Anufrieva 2013; Anufrieva 2015; Shadrin et al. 2017).

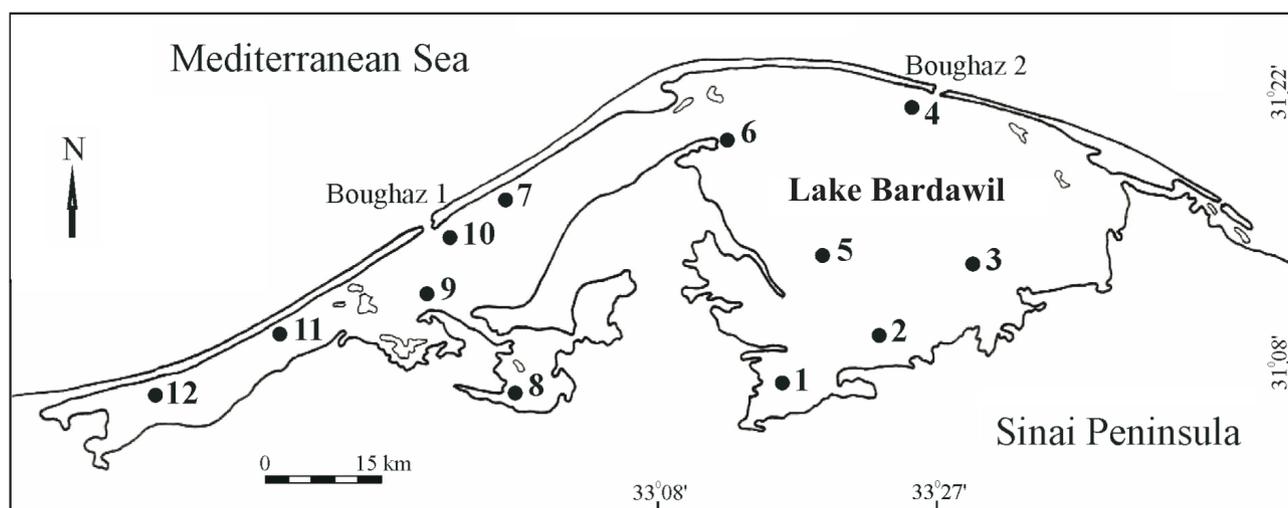
There are more than 100 coastal lakes/lagoons in the Mediterranean Sea, and only a few of them are hypersaline (Pérez-Ruzafa et al. 2012), including Lake Bardawil. It is located in the central

part of the Mediterranean coast of Sinai, which is an arid, semi-desert area, characterized by very low precipitation, with the average annual value ranging from 80 to 90 mm, and recharged mainly by seawater intrusions (Krumgalz et al. 1980; Abd Allah & Hussein 2009). The lake is characterized by hypersaline conditions (from 39 to 100 PSU) and has tectonic origin. The tidal effect, wind direction and speed can cause changes in the water inflow from the Mediterranean Sea, determining the variability of abiotic environmental factors and biotic composition in the lagoon. This coastal lake may serve as a good model system to assess the spatial and temporal variability of the copepod diversity and abundance, and the influence of different factors on these characteristics under hypersaline conditions. So far, several studies have been carried out on copepods in the lagoon (Kimor 1975; Por & Ben-Tuvia 1981; Fouda et al. 1985; El-Shabrawy 2006; Mageed 2006; El-Shabrawy & Gohar 2008). Based on the collected data, the authors hypothesized that: 1) long-term changes occur in the species composition of copepods and their abundance; 2) the salinity fluctuation is not the only factor responsible for these changes; 3) *Acartia tonsa* Dana, 1849 invaded Lake Bardawil as well as other Mediterranean and Black Sea coastal lakes/lagoons. In 2009–2010, the authors studied composition, distribution and seasonal dynamics of copepods in the coastal lake. The new results are presented in this paper. The new data together with the previously published data enable us to assess the long-term changes in the species composition and abundance of copepods in the lagoon and the factors affecting them.

## Materials and methods

### Study area

The studied coastal lake is situated at 32°40'E to 33°30'E and 31°03'N to 31°14'N (Krumgalz et al. 1980; Touliabah et al. 2002; Abd Allah & Hussein 2009) (Fig. 1). Its length from east to west is about 90 km, the average width is 10 km, and the maximum width is about 22 km at Nahal Yam or Mitzifzaq. The lake surface area is more than 600 km<sup>2</sup> when all its branches are filled with water. This area fluctuates throughout the year, while ponds and lakes are separated in summer time. The salinity varies from the lowest value of 38 PSU to the highest one – over 70 PSU. The maximum depth is 6.5 m (in the western arm), the minimum depth is 0.3 m and the average depth is 1.2 m. A sand barrier of varying width (from 300 to 2000 m) separates the lake from the Mediterranean Sea, having only one natural opening at the far eastern end. Since 1927, two artificial openings (narrow channels connecting the lagoon with the sea), Boughaz I and II, have been established to reduce the salinity through water exchange with the sea (Fig. 1). This allows the migration of commercial fish from the sea (Ben-Tuvia 1979). The regional arid climate has low precipitation restricted mostly to winter when wind-driven seawater intrusion occurs, and high evaporation during summer. There are two seasons in the region: the rainy season (November to April) and the dry season (from May to October). High air temperatures with scarce rainfall and a high rate of evaporation are observed in dry months. The rainy season is characterized by low air temperatures, strong winds and precipitation.



**Figure 1**

Distribution of the sampling sites in the hypersaline Bardawil coastal lake

The precipitation fluctuates on average between 72 mm (December) and 246 mm (July). The prevailing wind direction in the area is mostly from the north but winds may come from all directions. The tidal events, wind direction and speed are among the main causes of the variability in abiotic factors and biotic composition, especially near and between three openings named Boughazes on the northern side of the lake (Touliabah et al. 2002; Mageed 2006). Lake Bardawil has high productivity; its water is often oversaturated with oxygen due to high photosynthetic activity of phytoplankton and bottom macro- and microalgae dwelling in the lake (Krumgalz et al. 1980; Touliabah et al. 2002; El-Shabrawy 2006; El-Kassas et al. 2016). Tintinnina (Ciliophora) and Foraminifera are also abundant in plankton (El-Shabrawy et al. 2018). It is the least polluted Egyptian coastal lake and an important fishing area of high economic value. A large number of migratory birds use this area, which is listed as a Ramsar site since 1988 (El-Shabrawy & Gohar 2008; El-Kassas et al. 2016).

### Sampling and processing

Zooplankton and water samples were collected at 12 sites in Lake Bardawil in August and November 2009, and in February and May 2010 (Fig. 1, Table 1). Zooplankton was collected by filtration of 50 l of water through a plankton net (0.3 m diameter) with a mesh size of 55  $\mu\text{m}$ . Samples were fixed with 4% buffered formalin solution in situ and analyzed using an Olympus SZ-ST stereo microscope and Olympus BX50 compound microscope. Copepod species were identified according to the literature (Lang 1948; Newell & Newell 1977; Nishida 1985; Bradford-Grieve 1994; 1999; Huys et al. 1996; Wells 2007; Prusova et al.

2011). Species names are given in accordance with the World Register of Marine Species database (<http://www.marinespecies.org/index.php>).

Water samples for chemical analyses were collected by a 1 l bathometer. Water turbidity was measured in situ using a black and white Secchi disk with a 0.3 m diameter, while pH and water temperature ( $^{\circ}\text{C}$ ) were measured by Hydrolab (Multi Set 430i WTW). Salinity (PSU) was evaluated as total dissolved solids by filtrating through a glass microfiber filter (GF/C) and a known volume of filtrate was evaporated at  $180^{\circ}\text{C}$ . Dissolved oxygen ( $\text{mg l}^{-1}$ ) was determined using a modified Winkler method.

### Statistical analysis

Data were processed using standard statistical methods (Sokal & Rohlf 1995). The variability of parameters was evaluated by the coefficient of variability (CV). Parameters of regression equations and pair coefficients of correlation (R) were calculated in MS Excel. The Student's t-test was used to evaluate the significance of differences in average values. The confidence level of correlation coefficients (p) was determined by comparison with critical values of parameters (Müller et al. 1979).

## Results

Spatial and seasonal variability of abiotic parameters in Lake Bardawil in 2009–2010 is presented in Table 2. The studied parameters fluctuated in similar ranges to those observed in other years (El-Shabrawy 2006; Mageed 2006; El-Shabrawy & Gohar 2008). A total of 10 species of copepods were recorded in zooplankton during the study period, including 5 Calanoida, 2 Cyclopoida and 3 Harpacticoida (Table 3). Only 4 species were present in all seasons, and 3 species were recorded in only one season. *Oithona nana* Giesbrecht, 1893 was the most common species – in three seasons, it was found in all samples, and in one season in 75% of the samples. Six species of copepods were recorded in summer samples, while their number varied at different sites: 1 and 4 species were observed at only one site, 2 species at six sites, 3 species at two sites. Only 6 species were recorded in autumn, including 2 species at three sites, 3 species at two sites and 4 species at seven sites. In winter, 7 species of adult copepods were present in the plankton, including 3 species at three sites, 2 species at one site, 3 and 4 species at one site, 5 species at two sites, and no adult copepod was observed at site N1. In spring, there were also 7 species in total: 2 species at four sites,

**Table 1**

Coordinates and depth of the sampling sites in Lake Bardawil in 2009–2010

Sites	Latitude ( $^{\circ}\text{N}$ ); Longitude ( $^{\circ}\text{E}$ )	Depth (m)
1	31 $^{\circ}$ 04'37"; 33 $^{\circ}$ 13'36"	1.40
2	31 $^{\circ}$ 05'58"; 33 $^{\circ}$ 15'03"	1.50
3	31 $^{\circ}$ 07'03"; 33 $^{\circ}$ 16'51"	1.10
4	31 $^{\circ}$ 12'15"; 33 $^{\circ}$ 15'41"	2.00
5	31 $^{\circ}$ 08'35"; 33 $^{\circ}$ 15'40"	1.50
6	31 $^{\circ}$ 11'47"; 33 $^{\circ}$ 09'20"	1.00
7	31 $^{\circ}$ 11'26"; 33 $^{\circ}$ 05'54"	1.40
8	31 $^{\circ}$ 03'50"; 33 $^{\circ}$ 00'02"	1.00
9	31 $^{\circ}$ 06'28"; 32 $^{\circ}$ 56'49"	1.60
10	31 $^{\circ}$ 08'01"; 32 $^{\circ}$ 55'47"	2.50
11	31 $^{\circ}$ 04'55"; 32 $^{\circ}$ 49'17"	2.10
12	31 $^{\circ}$ 03'51"; 32 $^{\circ}$ 46'75"	1.50

**Table 2**

Abiotic characteristics at the sampling sites (Lake Bardawil; 2009–2010). TB = transparent to the bottom; CV = the coefficient of variability

Parameter	Sites												Average	CV
	1	2	3	4	5	6	7	8	9	10	11	12		
Summer 2009														
Temperature, °C	27.0	27.2	28.1	28.8	28.6	29.5	29.3	27.1	27.7	27.1	27.2	28.3	28.0	0.03
Salinity, PSU	57.7	51.0	57.4	46.2	53.2	48.2	48.7	54.3	44.5	39.5	53.2	67.7	51.8	0.14
Dissolved oxygen, mg l <sup>-1</sup>	8.8	8.8	9.1	9.3	8.5	8.3	9.1	7.7	8.5	8.5	7.5	8.3	8.5	0.06
pH	8.42	8.56	8.66	8.40	8.50	8.50	8.46	8.11	8.24	8.33	8.33	8.43	8.43	0.02
Transparency, m	1.25	1.25	0.70	1.50	0.60	0.60	0.60	0.70	1.20	2.00	2.00	1.00	1.17	0.46
Autumn 2009														
Temperature, °C	17.3	17.5	17.2	18.5	17.6	16.7	17.0	16.4	16.7	17.6	16.4	15.9	17.1	0.04
Salinity, PSU	54.1	56.1	49.4	49.4	40.0	48.9	42.4	50.0	44.3	39.8	45.4	52.1	47.7	0.11
Dissolved oxygen, mg l <sup>-1</sup>	8.1	9.1	9.5	9.6	9.8	9.2	9.8	11.9	9.6	10.2	12.0	10.9	10.0	0.11
pH	8.33	8.37	8.50	8.31	8.35	8.20	8.28	8.11	8.19	8.30	8.18	8.22	8.28	0.01
Transparency, m	TB	TB	TB	TB	TB	TB	TB	TB	TB	TB	TB	TB	–	–
Winter 2010														
Temperature, °C	20.7	20.3	20.1	19.4	20.9	18.4	20.2	22.1	21.3	19.4	21.5	21.6	20.5	0.05
Salinity, PSU	49.0	48.6	45.8	38.8	42.4	40.4	41.1	47.4	39.7	38.6	45.9	52.9	44.2	0.10
Dissolved oxygen, mg l <sup>-1</sup>	7.1	5.6	6.2	7.3	6.3	5.3	5.8	8.4	7.4	7.2	6.3	8.0	6.7	0.14
pH	7.95	8.17	8.04	8.20	8.01	8.16	8.14	8.04	8.26	8.36	8.06	8.19	8.13	0.01
Transparency, m	0.5	TB	TB	TB	TB	TB	0.4	TB	TB	TB	TB	TB	–	–
Spring 2010														
Temperature, °C	23.6	23.7	23.8	24.3	26.2	25.6	25.4	25.3	25.4	25.0	24.9	24.3	24.8	0.03
Salinity, PSU	56.2	52.8	46.4	40.5	49.9	48.2	46.9	51.8	42.6	39.9	49.5	59.1	48.7	0.12
Dissolved oxygen, mg l <sup>-1</sup>	5.8	8.4	8.6	7.0	6.8	8.8	6.4	6.8	6.6	8.4	5.9	6.4	7.2	0.15
pH	8.07	8.08	8.07	8.20	8.20	8.40	8.31	8.01	8.19	8.15	8.17	8.20	8.17	0.01
Transparency, m	TB	TB	TB	TB	TB	TB	0.6	TB	TB	TB	TB	TB	–	–

**Table 3**

Copepoda species in plankton of Lake Bardawil in 2009–2010. A = frequency of occurrence (%); B = average abundance (ind. m<sup>-3</sup>)/the coefficient of variability; C = relative abundance (%)

Species	2009				2010				Annual average/CV
	August		November		February		May		
Calanoida									
	A	B	A	B	A	B	A	B	B
<i>Acartia (Acanthacartia) tonsa</i> Dana, 1849	36	364/1.39	0	0	0	0	0	0	91/2.00
<i>Acartia (Acartia) danae</i> Giesbrecht, 1889	0	0	42	767/1.67	25	267/1.95	50	1545/1.09	679/1.05
<i>Clausocalanus furcatus</i> (Brady, 1883)	0	0	0	0	0	0	17	182/2.14	46/2.00
<i>Lucicutia flavicornis</i> (Claus, 1863)	0	0	0	0	0	0	25	364/1.79	91/2.00
<i>Paracalanus parvus</i> (Claus, 1863)	9	182/3.32	67	433/1.08	25	200/1.81	50	727/1.07	255/0.66
Cyclopoida									
<i>Oithona nana</i> Giesbrecht, 1893	100	4455/0.87	100	3833/0.62	75	867/0.73	100	4273/0.64	1680/0.39
<i>Oithona plumifera</i> Baird, 1843	0	0	9	67/3.46	9	67/3.46	0	0	34/1.16
Harpacticoida									
<i>Euterpina acutifrons</i> (Dana, 1847)	33	364/1.85	92	3233/1.11	50	1533/1.38	83	3273/0.98	1414/0.67
<i>Harpacticus littoralis</i> Sars G.O., 1910	55	727/1.39	25	133/1.95	33	267/1.48	50	727/1.33	309/0.67
<i>Microsetella norvegica</i> (Boeck, 1865)	9	91/3.32	0	0	17	133/2.34	0	0	67/1.20
Nauplius	100	39 455/0.36	100	51 500/0.05	100	18 733/0.63	100	45 364/0.79	14 230/0.37
Cyclopoid copepodids	100	13 000/0.49	100	7567/0.36	100	2067/0.65	100	10 917/0.64	8388/0.57
Calanoid copepodids	45	1000/2.10	83	2267/1.30	25	667/2.45	75	2636/1.09	956/0.58
Total copepodids	100	14 000/0.45	100	9833/0.38	100	2733/0.77	100	13 333/0.66	9975/0.52
Total adults	100	7182/0.79	100	8467/0.70	92	3333/1.00	100	10 417/0.50	7350/0.41
Total of all stages	100	59 636/0.34	100	69 800/0.41	100	24 800/0.54	100	69 833/0.60	56 017/0.38
Total metazoan zooplankton	100	69 727/0.33	100	78 200/0.42	100	35 133/0.41	100	23 2917/0.64	10 3994/0.85
	C		C		C		C		C
Percentage of all copepod stages in total metazoan zooplankton abundance, %	85		90		68		35		70
Percentage of <i>O. nana</i> abundance in the total number of adult copepods, %	62		45		26		41		44
Percentage of <i>E. acutifrons</i> abundance in the total number of adult copepods, %	5		38		46		31		30
Percentage of <i>A. danae</i> abundance in the total number of adult copepods, %	0		9		8		15		8

4 and 7 species were found at one site, and 5 species were recorded at four sites.

The maximum total abundance of copepods was recorded in autumn and spring (Table 3), when copepods accounted for 68 to 90% of the total abundance of metazoan zooplankton in three seasons, and only 35% in spring. In addition to Copepoda, Rotifera, Pteropoda, Appendicularia, Chetognata, and larvae of benthic fauna were present in the metazoan plankton, which will be analyzed in another work prepared by the authors. The average annual contribution of *O. nana* to the total abundance of adult copepods was 44%, and it was the dominant copepod species in all seasons (from 41 to 62%) except winter, when the contribution of *Euterpina acutifrons* (Dana, 1847) was higher (46%). The third most abundant species was *Acartia danae* Giesbrecht, 1889, with the highest contribution in spring – 15%, and the annual average of 8%. The age structure of the taxocene varied throughout the year (total number of nauplii/total number of copepodids) (Table 3). The naupliial stages contributed significantly to the total abundance of copepods in all seasons, fluctuating during the year from 24 800 to 68 833 ind. m<sup>-3</sup>.

The distribution of the total abundance of copepods was close to random in the coastal lake, while the spatial distribution of adults and copepodid stages of individual species varied from random to aggregated. The distribution of the total abundance of nauplii in particular seasons varied from close to homogeneous (autumn) to random (spring). Abiotic factors did not significantly affect the distribution of the total abundance of copepods, nauplii and copepodids, or the abundance of individual species. The salinity significantly influenced the abundance of nauplii only in autumn ( $R = 0.615$ ,  $p = 0.01$ ). A significant negative effect of salinity on the

abundance of *E. acutifrons* ( $R = -0.790$ ;  $p = 0.03$ ) was observed in autumn, while in the case of *A. danae* ( $R = -0.761$ ;  $p = 0.04$ ) such correlation was recorded in spring. Of the 10 copepod species found, 8 species can normally develop in salinity above 50 PSU (Table 4). It is believed that temperature above 26°C can reduce the development of three copepod species (Table 4). The abundance of different common copepod species did not correlate with each other.

## Discussion

To date, 30 copepod species have been found in the lake (Table 5). A total of 561 species of planktic copepods were recorded in the Mediterranean Sea (Razouls et al. 2005–17; Zakaria et al. 2016), of which no more than 2% were able to adapt to the habitat conditions of a shallow hypersaline coastal lake. *Centropages calaninus* (Dana, 1849) has never been recorded in the Mediterranean Sea (Razouls et al. 2005–17), but it was found the lake in 1985 (Fouda et al. 1985). The authors of this paper are not in a position to assess the correctness of this identification. Two reviews of the copepod species inhabiting hypersaline waters worldwide have been made to date (Anufrieva 2015; 2016). According to those reviews, there are only 46 copepod species that may dwell in hypersaline waters, including 26 species that may live in waters with salinity above 100 PSU. Por (1972) wrote that 100 PSU is a “natural” limit for marine hypersaline fauna.

All copepods found in the lake can be divided into three groups: 1) plankton species that form stable populations, 2) species of Mediterranean plankton incidentally entering the lake from the adjacent sea area, 3) benthic Cyclopoida – *Neocyclops salinarum* (Gurney, 1927) (found only in 1985; see Table 5) and Harpacticoida – *Harpacticus littoralis* Sars G.O., 1910, which can be abundant in plankton. Fifteen benthic species of highly halotolerant Harpacticoida and Cyclopoida occur in Lake Bardawil, including the most halotolerant copepod *Cletocamptus retrogressus* Schmankevitch, 1875 (Por 1972; 1973). In hypersaline waters, most benthic animals live in the water column, including a number of harpacticoid species found in the lake (Por 1973; Belmonte et al. 2012; Shadrin & Anufrieva 2013; Shadrin et al. 2017).

The total copepod abundance in the lagoon was significantly higher (90 times on average) compared to that observed in 2008–2009 in the waters of the Mediterranean Sea off the coast of Egypt (Zakaria et al. 2016). The greatest differences were observed in spring, when the number of copepods in the lake was on average 93 times higher than in the sea.

**Table 4**

Salinity and temperature limits for copepod species occurrence in Lake Bardawil (2009–2010)

Species name	Temperature, °C		Salinity, PSU	
	min.	max	min.	max
<i>Acartia (Acanthacartia) tonsa</i>	27.1	28.6	39.5	54.3
<i>Acartia (Acartia) danae</i>	16.4	25.6	38.8	52.1
<i>Clausocalanus furcatus</i>	25.0	25.3	39.9	51.8
<i>Euterpina acutifrons</i>	15.9	29.3	38.6	59.1
<i>Harpacticus littoralis</i>	17.3	29.5	39.7	57.4
<i>Lucicutia flavicornis</i>	23.8	25.4	39.9	46.4
<i>Microsetella norvegica</i>	18.4	27.7	38.6	44.5
<i>Oithona nana</i>	15.9	29.5	38.6	59.1
<i>Oithona plumifera</i>	19.4	19.4	38.6	38.6
<i>Paracalanus parvus</i>	15.9	27.7	38.6	52.1

Table 5

## Copepoda species found in Lake Bardawil in 1967–2010

Species	1967 <sup>a</sup>	1981 <sup>b</sup>	1985 <sup>c</sup>	2002–2003 <sup>d</sup>	2005 <sup>e</sup>	2006 <sup>f</sup>	2009–2010 <sup>g</sup>
<b>Calanoida</b>							
<i>Acartia (Acartiura) clausi</i> Giesbrecht, 1889	–	+	+	+	+	+	–
<i>Acartia (Acartia) danae</i> Giesbrecht, 1889	–	–	–	–	–	+	+
<i>Acartia (Acanthacartia) tonsa</i> Dana, 1849	–	–	–	–	–	–	+
<i>Archescocleithrix auropecten</i> (Giesbrecht, 1893)	–	–	+	–	–	–	–
<i>Calanus</i> sp.	–	–	+	–	–	–	–
<i>Centropages calaninus</i> (Dana, 1849)	–	–	–	–	–	+	–
<i>Centropages kroyeri</i> Giesbrecht, 1893	+	–	–	–	–	–	–
<i>Centropages ponticus</i> Karavaev, 1895	–	–	–	+	+	–	–
<i>Clausocalanus furcatus</i> (Brady, 1883)	–	–	+	+	+	+	+
<i>Eurytemora affinis</i> (Poppe, 1880)	–	–	+	+	+	–	–
<i>Isias clavipes</i> Boeck, 1865	–	–	+	–	–	–	–
<i>Lucicutia flavicornis</i> (Claus, 1863)	–	–	+	–	–	+	+
<i>Lucicutia ovalis</i> (Giesbrecht, 1889)	–	–	+	–	–	–	–
<i>Paracalanus parvus</i> (Claus, 1863)	–	–	+	+	+	+	+
<i>Paracartia latisetosa</i> (Krichagin, 1873)	–	+	+	+	+	–	–
<i>Parapontella brevicornis</i> (Lubbock, 1857)	–	–	+	–	–	–	–
<i>Parvocalanus crassirostris</i> (Dahl F., 1894)	–	–	–	–	–	+	–
<i>Temora longicornis</i> (Müller O.F., 1785)	–	–	+	–	–	–	–
<b>Cyclopoida</b>							
<i>Neocyclops salinarum</i> (Gurney, 1927)	–	–	+	–	–	–	–
<i>Oithona nana</i> Giesbrecht, 1893	–	–	–	+	+	+	+
<i>Oithona plumifera</i> Baird, 1843	–	–	–	+	+	–	+
<b>Harpacticoida</b>							
<i>Bryocamptus (Echinocamptus) spp.</i>	–	–	+	–	–	–	–
<i>Canuella</i> sp.	–	–	–	+	+	+	–
<i>Euterpina acutifrons</i> (Dana, 1847)	–	+	+	+	+	+	+
<i>Harpacticus littoralis</i> Sars G.O., 1910	–	–	–	+	+	+	+
<i>Metis jousseaumei</i> (Richard, 1892)	–	–	–	+	+	–	–
<i>Microsetella norvegica</i> (Boeck, 1865)	–	–	+	+	+	+	+
<b>Poecilostomatoida</b>							
<i>Corycaeus clausi</i> Dahl F., 1894	–	–	+	–	–	–	–
<i>Sapphirina angusta</i> Dana, 1849	–	–	+	–	–	–	–
<i>Sapphirina opalina</i> Dana, 1849	–	–	+	–	–	–	–
<i>Triconia conifera</i> (Giesbrecht, 1891)	–	–	–	–	–	+	–

a – Kimor 1975; b – Por and Ben-Tuvia 1981; c – Fouda et al. 1985; d – El-Shabrawy 2006; e – El-Shabrawy and Gohar 2008; f – Mageed 2006; g – authors' data

The smallest differences were recorded in winter – the average abundance in the lake was only 58 times higher. In general, the nature of seasonal changes in the abundance of copepods in the sea and the lake was the same. However, the amplitude of seasonal changes in the average total abundance of copepods was significantly higher in the lake, and it was 2.8 times higher in spring than in winter, while in the sea this ratio was 1.2. The age structure of copepod taxocenes in the sea also differed from that in the lake. The contribution of nauplii and copepodid stages to the total number of copepods in the lake varied from 65 to 76% and from 8 to 22%, respectively. In the sea, these values varied from 25 to 39% and from 36 to 40%, respectively. Such high proportion of nauplii in the

total number of copepods in the lake (from 53 to 79%) was also observed in 2002–2005 (El-Shabrawy 2006; Mageed 2006; El-Shabrawy & Gohar 2008). Probably these differences can be explained by the shorter lifespan of adult stages in the lake, higher fertility and/or higher mortality of copepodids and adults.

Such high abundance and a large proportion of nauplii indicate a high productive potential of the copepod taxocene in the lake. This contributes to the intensification of nutrient cycling and supports high primary productivity in the lake. An increase in zooplankton grazing on phytoplankton usually causes a greater nutrient input, which is important for the productivity of oligotrophic lakes/lagoons. There is a nutrient limitation of primary production in Lake

Bardawil – N-limitation in spring and summer and P-limitation in summer and autumn (Touliabah et al. 2002). To discuss this issue in greater depth, we need information on trophology and ecophysiology of copepods in the lake.

In spring, *O. nana* was the dominant species in the lake and in the sea. It contributed 13% to the total adult copepod abundance in the sea (Zakaria et al. 2016) and 41% in the lake. In summer, *Nannocalanus minor* (Claus, 1863) was the dominant species in the sea – 13% of the total number of copepods, while *O. nana* – 7% (Zakaria et al. 2016). *O. nana* dominated in the lake (62%). In winter, *Farranula rostrata* (Claus, 1863) (7.8% of the total adult copepods), *O. nana* (7.3%) and *Clausocalanus arcuicornis* (Dana, 1849) (6.7%) were the most abundant species in the sea (Zakaria et al. 2016), while *E. acutifrons* (46%), *O. nana* (26%) and *A. danae* (15%) were the most abundant copepod species in the lake. A similar pattern was observed previously in the lake – *O. nana* averaged from 48 to 78% of the total number of adult copepods in 2002–2005 (El-Shabrawy 2006; Mageed 2006; El-Shabrawy & Gohar 2008).

Since 1967, the complex of common and dominant copepod species in the lake has changed significantly (Table 5). Only the harpacticoid *E. acutifrons* was a common subdominant species in all the study periods, but not throughout the seasons. *Paracalanus parvus* (Claus, 1863) was the common but not abundant species in all years. *O. nana* was found in 1967 but was not recorded between 1980 and 1985. In 2002–2010, the species again became the most abundant copepod. To explain this, we need to refer to history. Due to the Arab-Israeli wars (1967–1973), the two openings from the sea into the lake were completely blocked by the accumulated sand between 1969 and 1971. As a result, the salinity in the lake increased considerably, reaching 100 PSU in the main part of the lake, and in some isolated basins – up to 170 PSU (Ben-Tuvia 1979; Abd Allah & Hussein 2009). To thrive in such conditions, crustacean species need to have resting stages. Such stages are known in harpacticoid species and *Acartia* spp., but the authors cannot find information about dormant stages of *Oithona* spp. (Marcus 1996; Moscatello & Bemonte 2009; Anufrieva & Shadrin, 2014; Shadrin et al. 2015b). The upper salinity limit for *O. nana* is about 60–80 PSU (Anufrieva 2015; 2016; Ghannay et al. 2015). That is why *Oithona* disappeared from the lake when salinity increased to higher values. The accumulated sand was removed in the 1980s, when the exchange with the sea resumed (Touliabah et al. 2002). The salinity decreased gradually after dredging and re-opening of the two channels. It reached about 78 PSU in the 1990s, and varied between 54 and 68 PSU in 2000,

and between 38.5 PSU (Boughaz II area) and 74.5 PSU (at the most western part of the lake) in 2002–2010 (Mageed 2006; El-Shabrawy & Gohar 2008; Abd Allah & Hussein 2009). With the decreasing salinity, *Oithona* was able to recolonize the lake and again became the abundant dominant species. *Acartia clausi* Giesbrecht, 1889 was recorded in the period from 1967 to 2005 (Table 5). In 1985, it was the dominant copepod species throughout the year, while *O. nana* was absent (Fouda et al. 1985). In 2002–2005, however, it ceased to be dominant or even present for most of the year. It was not found in our study, but two new species of *Acartia* – *Acartia tonsa* Dana, 1849 and *A. danae* Giesbrecht, 1889 were recorded in the lake (Table 3). *A. danae*, a circumtropical species that was not found in shallow coastal lakes/lagoons previously (Belmonte & Potenza 2001), has become abundant in all seasons except summer, contributing 9–15% to the total adult copepod density. *A. tonsa*, an alien species in the Mediterranean and Ponto-Caspian basins (Belmonte et al. 1994; Belmonte & Potenza 2001; Shadrin 2013), was observed only in summer when it accounted for 5% of the total number of adult copepods. Currently, *A. tonsa* has become a widespread abundant species in the new region. The species was also found in the coastal lakes/lagoons, including hypersaline ones (Cervetto et al. 1999; Marques et al. 2007; Shadrin & Anufrieva 2013). It can live in the lake in salinity up to 80–90 PSU (Hedgpeth 1967; Debenay et al. 1989). *Paracartia latisetosa* (Krichagin, 1873) also disappeared from the plankton. It is possible that its resting egg bank is preserved in the bottom sediments and that sporadic outbreaks of the species may still occur (Belmonte 1992).

The total average annual copepod abundance fluctuated (El-Shabrawy 2006; Mageed 2006; El-Shabrawy & Gohar 2008; present study): in 2002 – about 4000 ind. m<sup>-3</sup>, in 2004 – more than 152 000 ind. m<sup>-3</sup>, in 2005 – 25 300 ind. m<sup>-3</sup>, and in 2009–2010 – 56 000 ind. m<sup>-3</sup>. We do not have enough data to look for regularities of the long-term variability in copepod abundance. It can be considered that salinity in coastal lakes/lagoons is one of the most important factors affecting organisms (Reid & Wood 1976). The new data together with the previously published works (Jorcin 1999; Shadrin & Anufrieva 2013; El-Shabrawy et al. 2015; Shadrin et al. 2017) have led us to an assumption that changes in salinity are not the main cause of the spatial and temporal variability in the abundance of copepods in the lake in 2002–2010. Fluctuations in the water and species exchange between the lake and the sea are likely to contribute more to the variability in plankton composition and abundance. In general, it is very difficult to relate the

total marine zooplankton changes in some areas to changes in one or two environmental parameters. As an example, a plankton time series (1988–2007) has been conducted at the monitoring station in the Western Channel off Plymouth (UK), and the analysis of these data demonstrated that long-term changes in the overall mesozooplankton community structure and abundance over a period of 20 years cannot be strongly linked to environmental descriptors (Eloire et al. 2010). Taking into account all available information, we may assume that different irregularities and the chance are among the main drivers of the spatial, seasonal and long-term variability of the copepod taxocene in the studied coastal lake. We cannot understand the dynamics of plankton without accounting for the above drivers or benthos-plankton interactions. Lack of knowledge about the above as well as some other neglected factors and associations limit our understanding of the lake ecosystem as a whole. For this reason, we do not attempt to explain spatial and temporal variability and patterns in this work, as significantly more information is needed to do this.

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