

Spatial and Temporal Structure of Planktonic Copepods in the Bay of Tunis (Southwestern Mediterranean Sea)

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³Hydrology and Planktonology Research Group, Tunisian Agronomic National Institute, 43 Avenue Charles Nicolle, Tunis 1082, Tunisia Fax: 216-717-99391. E-mail: dalyyahya.ons@inat.agrinet.tn

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Mohamed Néiib Daly Yahia, Sami Souissi and Ons Daly Yahia-Kéfi (2004) Spatial and temporal structure of planktonic copepods in the Bay of Tunis (southwestern Mediterranean Sea). Zoological Studies 43(2): 366-375. The community of pelagic copepods of the Bay of Tunis was studied using a grid of 14 stations regularly sampled 24 times between December 1993 and November 1995. A previously published regionalization of this bay, based on its hydrological structure leading to a description of 4 functionally different zones, was considered in this study. In the bay, copepods dominated the mesozooplankton, and spatial heterogeneity of both abundance and species composition was detected. There were 2 principal gradients: i) from coastal to offshore stations and ii) from the southwestern to the northeastern portions of the bay. In total, 52 pelagic copepod species were recorded in the bay during this study. The families of Acartiidae, Paracalanidae, Centropagidae, and Oithonidae dominated, each of which was represented by 5 species. The most abundant copepods were represented by the following species ranked according to their dominance: Oithona nana, O. helgolandica, O. plumifera, Centropages kroyeri, Clausocalanus arcuicornis, Acartia clausi, Euterpina acutifrons, and Microsetella rosea. Their contribution to total copepod abundance varied between 65% and 100% during the study. These 8 dominant species comprised the neritic community of copepods in the bay. Another community of copepods in the bay was characterized by the following oceanic species: Acartia danae, Centropages chirchiae, Mesocalanus tenuicornis, Mecynocera clausi, Candacia armata, Eucalanus crassus, and Oithona plumifera. This community was particularly evident in the central and northeastern parts of the bay, where copepod diversity was significantly higher compared to the coastal zones. http://www.sinica.edu.tw/zool/zoolstud/43.2/366.pdf

Key words: Mediterranean, Bay of Tunis, Copepod distribution, Diversity structure.

Copepods hold a key position in marine food webs as the major secondary producers of the world's oceans (Parsons et al. 1984, Huys and Boxshall 1991, Mauchline 1998). Herbivorous copepods can control different size classes of phytoplankton communities, and omnivorous and carnivorous copepods feed on micro- and mesozooplankton including early developmental stages (Ohman and Hirche 2001). They are in turn controlled by predators from the macrozooplanktonic, micronektonic, and fish communities. For example, developmental stages of copepods constitute the principal prey of such small pelagic fish species as anchovies (Tudela and Palomera 1997, Souissi et al. 2001). Even though copepods have been intensively studied experimentally and in the field, some areas still remain understudied and poorly documented. In the Mediterranean Sea, this situation is clear with most information limited to the European coasts of the northern Mediterranean, whereas the African coasts remain practically unexplored (Souissi et al. 2001). The

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northern coast of Tunisia is located between the 2 main basins of the Mediterranean Sea and is an excellent area for planktonic research. Unfortunately, until recently, plankton studies in the coastal region around Tunis have been anecdotal. Some earlier descriptive and qualitative work by Heldt (1929), Monard (1935), Rose and Vaissière (1952a b 1953), Séguin (1968), and Ktari-Chakroun (1979) were carried out. Quantitative studies were circumstantial in these areas (Bernard and Bernard 1973, Daly Yahia and Romdhane 1994).

More recently, a larger program of monitoring the Bay of Tunis (hereafter referred to as the bay) and its surrounding lagoons has been undertaken (Daly Yahia-Kéfi 1998, Daly Yahia 1998, Daly Yahia and Daly Yahia-Kéfi 1999). This considerable research effort has resulted in the development of a large spatio-temporal database of hydrology, nutrients, and phytoplankton and zooplankton species. An initial analysis based on nutrient dynamics indicated that the bay could be subdivided into 4 regions with similar hydrological regimes (Souissi et al. 2000). This global analysis was necessary to understand the functioning of this ecosystem and to choose the best locations for monitoring programs.

The main objective of this paper is to present for the 1st time a complete image of the copepod assemblages of the Bay of Tunis, their origin, and the spatial and temporal evolution of their structural diversity. These analyses are then linked to previously identified regionalization based on the hydrology of the bay. We attempted to answer the following questions: i) What is the influence of the heterogeneity of the hydrological structure on the composition and spatial distribution of the copepod community? and ii) What is the role of copepods with oceanic properties in this ecosystem?

MATERIALS AND METHODS

Sampling area

The Bay of Tunis is located between 10°17' and 11°37'E longitude and 36°42' and 36°53'N latitude (Fig. 1). It has a total area of around 361 km², and an average depth of 15 m. This bay communicates with the Gulf of Tunis on its northern side, which opens up to the Tuniso-Sicilian and Tuniso-Sardinian Straits, with the Tunis Lagoon in its southwestern area.

Seventeen stations were established for the study on the hydrological structure of the bay; however planktonic copepods were sampled with different nets at only 14 stations deeper than 2 m, monthly between Dec. 1993 and Nov. 1995. A 2-L Ruttner bottle was used to sample the surface water for chemical analyses, and phytoplanktonic and microzooplanktonic (tintinnid and rotifer) species identification and counting.

In the shallowest stations of both coastal zones (stations 1 to 8 in Fig. 1), a small plankton



Fig. 1. Location of hydrological and plankton sampling stations in the Bay of Tunis.

net (diameter, 0.4 m; length, 1.6 m; mesh size, 55 µm) was towed obliquely from a 3 m depth. At the central stations (Fig. 1), 2 vertical hauls (bottom to surface) were made with 2 different nets: a Nansen net (diameter, 0.7 m; length, 3 m; mesh size, 55 µm) and a Hensen-egg net (diameter, 0.73 m, length, 1.8 m; mesh size, 300 µm). All specimens obtained from each haul were preserved in 2% buffered formaldehyde solution for later examination in the laboratory. Specimens were identified, when possible, to species level and counted. In the central stations, the Nansen net (55 µm) was used for a quantitative study (Dauby 1985), although the Hensen-egg net is more efficient for sampling macrozooplankton and some rare large copepod adults. For phytoplankton and microzooplankton, sub-samples of 25 ml were analyzed using a Leitz inverted microscope following a sedimentation time of 48 h. Cells were counted along 2 diametric transects of the bottom plate. The entire bottom plate was also examined for scarce species (Throndsen 1995).

Analytical methods

Surface temperature and salinity were measured at each station with a WTW probe. For analyses of nutrients we used spectrophotometric methods (Beckman model 36) according to FAO (1975) methods for nitrate and phosphate.

Analysis of community structure

According to Harris et al. (2000), diversity indices were used to describe the quality of the community, which depend on the number of species and their relative abundances in a sample. In this study we used the Shannon-Wiener diversity index (Shannon and Weaver 1964), because this index is more sensitive for rare species (Krebs 1999). This index was applied to each zone and to each sampling date, so it can be interpreted as a measure of the quantity of information.

RESULTS

Spatio-temporal evolution of environmental parameters

The time evolution of surface sea temperatures showed a minimum of 13.2°C in Jan.1994 and a maximum of 28.9°C in Aug. 1994 (Fig. 2A). Vertical distribution of this parameter at station B11 reveals thermal stratification, which provided stability to the water mass between May and Oct. (Fig. 2B). Average annual salinity was about 37.42 psu with a minimum of 37.07 psu in Feb. 1994 and a maximum of 37.87 psu in Aug. 1994 (Fig. 2A).

Average annual value of the surface water nitrate concentration was about 0.50 μ Mol/l with a maximum of 1.00 μ Mol/l in Jan. 1994 and a minimum of 0.18 μ Mol/l in July 1995 (Fig. 2C). Average monthly values of phosphate concentrations fluctuated between minimums in Oct.1994 (0.04 μ Mol/l) and Apr. 1995 (0.07 μ Mol/l) and a maximum in Jan. (0.91 μ Mol/l).

Based on all nutrient data recorded in the bay, Souissi et al. (2000) showed a clear spatio-temporal heterogeneity and proposed subdividing the bay into 4 functional zones with similar nutrient



Fig. 2. Spatio-temporal distribution of main environmental factors between Dec. 1993 and Nov. 1995. A: Average water temperature and salinity variations. B: Water temperature variations at B11 station in surface and at 20m deep. C: Nitrates and phosphates time-evolution. Vertical bars represent the values of the standard deviation.

dynamics (Fig. 3): 2 coastal zones (zones I and II), a southwestern central zone (zone III), and a northeastern central zone (zone IV) which opens to the Gulf of Tunis (Fig. 3).

Taxonomic composition of pelagic copepods

Regarding species richness, planktonic copepods of the bay were the 2nd most abundant zooplanktonic group after Tintinnids (Daly Yahia et al. 2001). They were composed of 52 species of 27 genera and 20 families (Fig. 4). The Centropagidae, Acartidae, Paracalanidae, and Oithonidae were the most-highly represented families with 5 species each. Then came the Oncaeidae with 4 species and the Corycaeidae, Eucalanidae, Pontellidae, and Sapphirinidae with 3 species each. The other families were represented by only 1 or 2 species (Fig. 4).

Planktonic copepods of the bay could be classified according to their origin of distribution and their biological characteristics into 3 groups.

Neritic species

Neritic species were well represented in our sampling. According to Gaudy (1962), Mazza (1966), and Lakkis (1990), the neritic community is often considered a sea surface community. In this category we included Acartia clausi, A. latisetosa, Centropages kroyeri, C. typicus, C. violaceus, Clausocalanus arcuicornis, Cla. furcatus, Coryceus furcifer, Cor. speciosus, Euterpina acutifrons, Isias clavipes, Labidocera wollastoni, Nannocalanus minor, Oithona helgolandica, O. nana, Oncaea media, Onc. mediterranea, Paracalanus parvus, and Temora stylifera, although some of them are considered epiplanktonic because they can also proliferate in oceanic environments (Giron 1963). According to Mazza



Fig. 3. Subdivision of Tunis Bay into four functional zones of similar nutrients dynamics (according to Souissi et al. 2000).

(1961) and Ehrhardt and Bonin (1968), *Temora stylifera*, *Cla. arcuicornis*, *Cla. furcatus*, and *Paracalanus parvus* match the latter definition.

Oceanic and deep-water species

Identification of this category was based on earlier studies (Gaudy 1962, Giron 1963, Mazza 1966, Ehrhardt 1967a b, Ehrhardt and Bonin 1968, Soenen 1969 1970) and more-recent research (Dauby 1985, Lakkis 1990, Bottger-Schnack 1997). The oceanic copepod community in the bay was composed of a high number of species which were transported to the bay under typical hydrodynamic conditions (Fig. 4). However, the frequency of occurrence of oceanic species in the Bay was very low.

Species not classified or presenting mixed characters

This category included Acartia grani, A. longiremis, Cyclopina gracilis, Cyc. littoralis, Calocalanus ovalis, Microsetella norvegica, M. rosea, Macrosetella gracilis, Oithona setigera, Paroithona parvula, Oncaea minuta, Onc. venusta, Monstrilla sp., Clytemnestra rostrata, and Corycaeus clausi. Most of these species were scarce in the bay except for M. rosea. The last species may belong to the neritic community.

Spatial and temporal quantitative distribution of pelagic copepods and biotic zonation in the Bay of Tunis

The copepods regularly represented more than 20% of the total mesozooplankton and reached more than 40% during some blooms in summer and autumn (Fig. 5B, C).

The temporal dynamics of pelagic copepods were characterized in the bay by 4 periods of abundance (Fig. 5C).

The 1st period in spring occurred in May (1994) or Apr.-May (1995), after the bloom of microzooplankton in Mar. or Apr. and during the bloom of diatoms and/or dinoflagellates in May. The copepods were dominated by *O. nana*, *O. hel-golandica*, *A. clausi*, and *Euterpina acutifrons*. The 2nd period was in July during the summer blooms of diatoms, dinoflagellates, and microzooplankton; this trophic association was particularly clear in July 1995 (Fig. 5B). The major species were *C. kroyeri*, *O. nana*, *Euterpina acutifrons*, and *A. clausi*. The 3rd period occurred during Oct.-Nov.

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ORDER	FAMILIES	GENERA AND SPECIES	L	F	м	А	м	L	L	А	s	0	N	D
	CALANIDAE	Mesocalanus tenuicornis Dana, 1849 (o)												
		Namocalanus minor Claus, 1863												
		Acartia clausi Giesbrecht, 1881												
	ACARTIIDAE	Acartia danae Giesbrecht, 1889 (o, b)												
		Acartia grani Sars, 1904												
		Acartia latisetosa Krichagin, 1873												
		Acartia longiremis Lilljeborg, 1853												
		Calocalanus ovalis Shmeleva, 1968												
	PARACALANIDAE	Calocalanus pavo Dana, 1849												
		Calocalanus plumulosus Claus, 1863												
		Paracalanus aculeatus Giesbrecht, 1888 (o, b)												
		Paracalanus parvus Claus, 1863 (e)												
		Clausocalanus arcuicornis Dana, 1849 (e)												
		Clausocalanus furcatus Brady, 1883 (e)												
CALANOIDA		Centropages chirchiae Giesbrecht, 1889 (o)												
		Centropages krayeri Giesbrecht, 1892												
	CENTROPAGIDAE	Centropages typicus Kroyer, 1849												
		Centropages violaceus Claus, 1863 (o)												
		Isias clavipes Boeck, 1864												
	TEMORIDAE	Temora stylifera Dana, 1849 (e)												
		Eucalanus crassus Giesbrecht, 1888 (o, b)												
	EUCALANIDAE	Eucalanus elongatus Dana, 1849 (o, b)												
		Rhincolanus nasutus Giesbrecht, 1888 (o, b)												
	MECYNOCERIDAE	Mecynocera clausi Thompson, 1888 (o, b)												
		Labidocera brunescens Czemiavsky, 1868 (o)	ļ											
	PONTELLIDAE	Labidocera wollastoni Lubbock, 1857												
		Pontella mediterranea Claus, 1863 (o)												
	CANDACIIDAE	Candacia armata Boeck, 1872 (o, b)	ļ											
		Candacia longimana Claus, 1863 (o)												
	OITHONIDAE	Oithona helgolandica Claus, 1863	1											
		Oithona nana Giesbrecht, 1892												
		Oithona plumifera Baird, 1843 (o)											'	
CYCLOPOIDA		Oithona setigera Dana, 1849												
		Paroithona parvula Farran, 1908												
		Cyclopina gracilis Claus, 1863											'	
		Cyclopina littoralis Brady, 1872												
	ONCAEIDAE	Oncaea media Giesbrecht, 1891												
		Oncaea mediterranea Claus, 1863											<u> </u>	
		Oncaea minuta Giesbrecht,1892											<u> </u>	
		Oncaea venusta Philippi, 1843											<u> </u>	
POECILOSTOMATOIDA		Corycaeus clausi F. Dahl, 1894												
		Corycaeus furcifer Claus, 1863											!	
		Corycaeus speciosus Dana, 1849												
	SAPPHIRINIDAE	Copilia mediterranea Claus, 1863 (o, b)											\vdash	
		Copilia quadrata Dana, 1849 (o)												
	TACHYDUDAE	Sapphirina angusta Dana, 1849 (o)										- 		
	TACHIDIDAE	Euterpina acutifrons Dana, 1847			l									
HARPACTICOIDA	ECTINOSOMATIDAE	Microsetella norvegica Boeck, 1864												
	MIRACUDAE	Microsetella rosea Dana, 1847												
		pracrosetetta gracitis Dana, 1848												
		pronstritta sp											\vdash	
	CT LINKESTRIDAL	c tytennestra rostrata Brady, 1883]	1			1		<u> </u>	
(o): Oceanic species]		absent]	0 < der	nsity < 1	ind. m ⁻³	
(b) : Bathyplanktonic species SCALE					1 < den	sity < 10	ind. m ⁻³				10 < den	sity < 10	0 ind. m ⁻³	3
(e) : Epiplanktonic species				1	00 < den	sity < 10	00 ind. n	n ⁻³	<u>.</u>	10	00 < den	sity < 10	000 ind. r	m ⁻³

Fig. 4. Taxonomic composition and density range of planktonic copepods in the Bay of Tunis between Dec. 1993 to Nov. 1995 (mean annual values).

and Dec. and was dominated by *O. nana*, *O. helgolandica*, *Clausocalanus arcuicornis*, and *Euterpina acutifrons*. This period was always associated with a high development of diatoms and microzooplankton, and was a resting period characterized by low densities of adults, copepodides, and nauplii.

Monthly fluctuations in copepod nauplii followed an unimodal cycle, providing evidence of the importance of egg production during spring, summer, and autumn, whereas during the cold months of winter, especially in Jan., abundance of nauplii significantly decreased indicating low egg production during this season (Fig. 5C).

Analysis of community structure

Spatial heterogeneity of both abundance and species composition (Table 1) and the Shannon-Wiener index (H', Table 2) was determined according to the major gradients: i) from coastal to offshore stations and ii) from southwestern to northeastern portions of the bay.

Monthly variations in the relative frequency of the dominant copepods of the bay are shown in fig. 6. This community which dominated the quantitative dynamics of the bay was mainly composed of neritic and cosmopolitan species, which are long-lasting in the bay (Daly Yahia 1998). They were represented in order of decreasing abundance and throughout the period of study by *O. nana*, *Euterpina acutifrons*, *C. kroyeri*, *Cla. arcuicornis*, *A. clausi*, *M. rosea*, *O. helgolandica*, and *O. plumifera*.

From examination of table 2, 4 kinds of copepod distributions can be distinguished according to nutrient conditions (see Fig. 2C). In the coastal zone (I and II), the average density of copepods was generally low (2644 individuals/m³ in zone I and 2160 individuals/m³ in zone II) with some sudden peaks observed in summer and autumn; few copepod species were present in the community. In coastal zone I, O. *nana*, *Euterpina acutifrons*, C. *kroyeri*, and O. *helgolandica* contributed 96.42% of the total number of copepods; whereas in coastal zone II, M. *rosea*, O. *nana*, C. *kroyeri*, *Euterpina acutifrons*, and O. *helgolandica* represented 96.79%.

Copepods in the offshore stations (zones III and IV) showed approximately the same dynamics with a higher average density (3653 individuals/m³ in zone III and 3837 individuals/m³ in zone IV). In the central southwestern zone (zone III) *O. nana, Euterpina acutifrons, C. kroyeri, Cla. arcuicornis,*

A. clausi, O. helgolandica, Paracalanus parvus, Onc. mediterranea, and O. plumifera contributed 95.79% of the total number of pelagic copepods. In the central northeastern zone (zone IV) O. nana, Cla. arcuicornis, C. kroyeri, Euterpina acutifrons, A. clausi, O. helgolandica, O. plumifera, C. chirchiae, Onc. mediterranea, Nannocalanus minor, Labidocera wollastoni, Temora stylifera, and M. rosea represented 96.91% of copepods.

Table 2 and fig. 7 show the high variability of the Shannon-Wiener index (H') for copepods in the bay. The highest value of H' was observed during winter in zone IV (3.83 in Feb. 1995), while the lowest value occurred in zone I during summer (0.24 in July 1995). Temporal changes in H' in both coastal zones I and II were similar. Table 3



Fig. 5. Monthly variations of microplankton and copepods of Tunis bay between Dec. 1993 and Nov. 1995. A: Abundance of diatoms and dinoflagellates. B: Microzooplankton and meso-zooplankton evolution. C: Abundance of nauplii and adults and copepodids. Vertical bars represent the values of the standard deviation.

shows that the average value of H' increased from zones I to IV, and this reflected a more-stable copepod community in the northeastern part of the bay.

When we consider the diversity H' of the neritic and oceanic communities (Fig. 7B, C), it appears that for the neritic community, the dynamics in temporal development of H' were the same



Fig. 6. Monthly variations of the relative abundance of the dominant copepod species in the Bay of Tunis between Dec. 1993 and Nov. 1995.

as those shown in fig 7.

Results of this study allowed the Bay of Tunis to be differentiated into 2 different assemblages of copepods: 1) a neritic community composed by approximately 20 species dominated by *O. nana*, *Euterpina acutifrons*, *C. kroyeri*, *Cla. arcuicornis*, *A. clausi*, *M. rosea*, and *O. helgolandica* and 2) an oceanic community composed of 17 species dominated by *O. plumifera*, *C. chirchiae*, *Mecynocera clausi*, *A. danae*, *Mesocalanus tenuicornis*, *Eucalanus elongatus*, *C. violaceus*, and *Candacia armata*.

Table 2. Comparison of Shannon index valuesbetween inshore and offshore zones in the Bay ofTunis

Shannon-Weaver	In-S	hore	Off-Shore				
Diversity (bits/ind.)	Zone I	Zone II	Zone III	Zone IV			
H' min	0.24	0.35	1.39	1.60			
H' max	2.60	3.05	3.19	3.83			
H' mean	1.29	1.92	2.27	2.64			

 Table 1. Dominance percentage (D %) of copepod species in the Bay of Tunis (Zones I to IV) during the study period

Species (Zone I)	D(%)	Species (Zone II)	D(%)	Species (Zone III)	D(%)	Species (Zone IV)	D(%)
Oithona nana	78.41	Microsetella rosea	48.64	Oithona nana	42.34	Oithona nana	33.85
Euterpina acutifrons	8.63	Oithona nana	41.72	Euterpina acutifrons	14.64	Clausocalanus arcuicornis	12.13
Centropages kroyeri	8.22	Centropages kroyeri	2.77	Centropages kroyeri	11.79	Centropages kroyeri	11.91
Oithona helgolandica	1.16	Euterpina acutifrons	2.51	Clausocalanus arcuicornis	9.28	Euterpina acutifrons	11.36
Microsetella rosea	0.77	Oithona helgolandica	1.15	Acartia clausi	7.21	Acartia clausi	8.81
Acartia clausi	0.76	Acartia clausi	0.78	Oithona helgolandica	6.46	Oithona helgolandica	6.96
Clausocalanus arcuicornis	0.49	Oncaea mediterranea	0.35	Paracalanus parvus	1.52	Oithona plumifera	4.34
Paracalanus parvus	0.41	Oithona plumifera	0.34	Oncaea mediterranea	1.36	Oncaea mediterranea	1.60
Temora stylifera	0.21	Claucocalanus arcuicornis	0.31	Oithona plumifera	1.19	Centropages chirchiae	1.35
Centropages chirchiae	0.19	Centropages chirchiae	0.22	Temora stylifera	0.79	Nannocalanus minor	1.34
Labidocera wollastoni	0.19	Coryceus speciosus	0.20	Microsetella rosea	0.75	Temora stylifera	1.15
Oithona plumifera	0.16	Nannocalanus minor	0.20	Centropages chirchiae	0.69	Labidocera wollastoni	1.07
Nannocalanus minor	0.14	Temora sytylifera	0.20	Labidocera wollastoni	0.55	Microsetella rosea	1.04
Oncae mediterranea	0.13	Labidocera wollastoni	0.15	Nannocalanus minor	0.47	Paracalanus parvus	0.85
Others	0.15	Paracalanus parvus	0.12	Acartia latisetosa	0.22	Coryceus speciosus	0.47
		Centropages typicus	0.11	Coryceus speciosus	0.21	Centropages typicus	0.40
		Acartia latisetosa	0.11	Centropages typicus	0.12	Acartia latisetosa	0.37
		Others	0.10	Others	0.40	Mecynocera clausi	0.25
						Isias clavipes	0.14
						Calocalanus pavo	0.14
						Acartia danae	0.12
						Mesocalnus tenuicornis	0.10
						Others	0.24



Fig. 7. Monthly changes of the Shannon diversity of copepod species in the four functional zones of the Bay of Tunis. A: total copepod community. B: oceanic copepod community. C: neritic copepod community.

DISCUSSION

The species richness in the Bay of Tunis is apparently lower than those of other offshore areas of the North African coasts, where 176 copepod species have been reported to date (Rose and Vaissière 1952a b 1953). The quantitative structure of the copepod community in the bay illustrates the key role of small metazoan plankton, particularly non-calanoid copepods belonging to Cyclopoida and Harpacticoida, in Mediterranean pelagic ecosystems (Bottger-Schnack 1997).

This study on the spatial and temporal structure of the planktonic copepods of the Bay of Tunis revealed that the regularity (Frontier 1976) and diversity are higher in zone IV for 2 reasons: the relative abundances of copepods were distributed equally among species (Table 1) and the number of species reached its maximum in this area. The distribution of the neritic and oceanic copepod communities respectively indicated southwestern and northeastern gradients and seemed to be influenced by the hydrological conditions of the bay. The bay's southwestern eutrophic region and the Atlantic Current contain some indicator species considered to be an integral part of the oceanic community, such as *Mesocalanus tenuicornis*, *A. danae*, *Calocalanus pavo*, *Cal. plumulosus*, *C. chirchiae*, *C. violaceus*, *Eucalanus crassus*, *Mecynocera clausi*, and *Labidocera wollastoni* (Gaudy 1962, Giron 1963, Mazza 1966, Ehrhardt and Bonin 1968, Duran 1970, Soenen 1969 1970).

We can also consider that water stagnation in this southwestern region, which is protected from the dominant winds, and daily and seasonal fluctuations in physical and chemical factors are much stronger than in the northeastern region due to its low average depth, so fewer oceanic species were found and copepods consisted almost entirely of neritic species.

The southwestern bay communicates with Tunis Lagoon to the south (a highly polluted area) and receives polluted discharges from the Melian River, both of which enrich the nutrient content. According to Souissi et al. (2000), the high values of turbidity, nitrite, and ammonium concentrations indicate that this area is considerably polluted. The environmental conditions of the southwestern part of the bay and the influence of this anthropogenic pollution allowed differentiation of a neritic community dominated by Oithona nana, C. kroyeri, A. clausi, and Euterpina acutifrons. They are all rstrategy-type species, characterized by a high productivity and egg production rate (Hirche 1992). On the other hand, the oceanic community is composed of K-strategy-type species which are less productive and more stable, such as the species of Mes. tenuicornis, A. danae, Cal. pavo, C. chirchiae, Mec. clausi, and L. wollastoni, which are more common in the northeastern area of the Bay of Tunis (unpublished data).

The patterns of naupliar distributions are opposed to those of late developmental stages, because their highest concentrations were observed in the western and southwestern regions. This observation can be explained by the following hypotheses: 1) the passive transport of nauplii by currents generated by mesoscale and local circulations; 2) the feeding preference of nauplii (similar to other microzooplankton groups, i.e., Tintinnida and Rotatoria) based on small-sized bacterioplankton and nanophytoplankton, which are concentrated in the coastal area (Kršinic, 1995, Montanari et al. 1999); 3) exogenous origin, particularly from surrounding lagoons where densities of nauplii were higher than 120 000 individuals/m³ (unpublished data); and 4) the food of the major copepods in the bay (phytoplankton, microzooplankton) being most abundant in this zone (Souissi et al. 2000). An effect of food abundance on the rate of egg production of dominant copepod species in the northwestern Mediterranean Sea, such as C. typicus and Temora stylifera, has been documented (Razouls 1982, Abou Debs and Nival 1983, Halsband-Lenk et al. 2001, Halsband-Lenk et al. 2002). However, it appears that this high copepod production in the western part of the bay is not transferred efficiently to higher trophic levels, because predators like medusae, siphonophores, chaetognaths, and planktivorous fish like the anchovy Engraulis encrasicolus show a central and northeastern dominance (Souissi et al. 2000, Souissi et al. 2001). The functioning of this western area of the bay can be compared to the dynamics of Fukuyama Harbor in Japan (Uye and Sano 1995), where a significant portion of copepod production is lost to predation resulting in a biological cul-de-sac (Uye and Liang 1998).

In conclusion, we can say that the areal subdivision of the bay based on nutrient dynamics is confirmed by the patterns of copepod distribution. The hydrological processes affecting the bay are also characterized by certain copepod distributions and community structures. In comparison to other Mediterranean ecosystems, the Bay of Tunis is characterized by a dominant community of neritic and cosmopolitan species like in the northwestern basin (Vives 1966, Gaudy 1962 1970 1972) or in the eastern basin (Lakkis 1990) and its southern part (Dowidar and El Maghraby 1970). One of the characteristics of the bay system is the stability of its neritic community, which is regularly replenished by an oceanic community introduced by intrusions of branch currents from the Atlantic Ocean.

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REFERENCES

Abou Debs C, P Nival. 1983. Etude de la ponte et du

développement embryonnaire en relation avec la température et la nourriture chez *Temora stylifera* Dana (Copepoda: Calanoida). J. Exp. Mar. Biol. Ecol. **72:** 125-145.

- Bernard M, F Bernard. 1973. Premier examen du plancton végétal et animal des parages de l'île de Djerba. Rapp. Comm. Int. Mer Médit. 21: 503-506.
- Bottger-Schnack R. 1997. Vertical structure of small metazoan plankton, especially non-calanoid copepods. II. Deep eastern Mediterranean (Levantine Sea). Oceanol. Acta **20**: 399-419.
- Daly Yahia MN. 1998. Dynamique saisonnière du zooplancton de la baie de Tunis (Systématique, écologie numérique et biogéographie méditerranéenne). Ph.D. thesis, Univ. of Tunis.
- Daly Yahia MN, O Daly Yahia-Kéfi. 1999. Présence d'essaims à *Mysis oculata* et *Leptomysis mediterranea* (Mysidacea) dans la baie de Tunis. Vie et Milieu **49:** 193-198.
- Daly Yahia MN, O Daly Yahia-Kéfi, S Souissi, MS Romdhane. 2001. Variations spatio-temporelles du zooplancton de la baie de Tunis: composition numérique et biomasse. Rapp. Comm. Int. Mer Médit. 36: 376.
- Daly Yahia MN, MS Romdhane. 1994. Contribution à la connaissance des cycles saisonniers des Copépodes pélagiques (Mer de Bou Grara). Bull. Soc. Sci. Nat. Tunis 10: 1-10.
- Daly Yahia-Kéfi O. 1998. Le phytoplancton de la baie de Tunis: analyse systématique, biogéographique, quantitative et synécologique des Diatomées et des Dinoflagellés. Ph.D. thesis, Univ. of Tunis.
- Dauby P. 1985. Dynamique et productivité de l'écosystème planctonique du golfe de Calvi-Corse. Ph.D. thesis, Univ. of Liège, Belgium.
- Dowidar NM, AM El-Maghraby. 1970. The neritic zooplankton of the south eastern Mediterranean at Alexandria. I-Distribution and ecology of the zooplankton organisms with special reference to copepoda. Bull. Inst. Oceanogr. Fish. **1**: 227-273.
- Duran M. 1970. Sur la présence dans les eaux de Castellon de copépodes considérés comme d'origine atlantique. Rapp. Comm. Int. Mer Médit. **19:** 39-43
- Ehrhardt JP. 1967a. Contribution à l'étude du plancton superficiel et sub-superficiel du canal de sardaigne et de la mer sud-thyrrénienne. IV Le zooplancton. Cahiers Océanogr. 19: 729-781.
- Ehrhardt JP. 1967b. Contribution à l'étude du plancton superficiel et sub-superficiel du canal de sardaigne et de la mer sud-thyrrénienne. VII- Synthèse. Cahiers Océanogr. **19:** 881-921.
- Ehrhardt JP, D Bonin. 1968. Contribution à l'étude du plancton dans le canal de corse-provence. I. Le zooplancton. Cahiers Océanogr. **20:** 133-156.
- FAO. 1975. Manual of methods in aquatic environment research. Part 1-Methods for detection, measurement and monitoring of water pollution. Rome: FAO Fisheries Technical Paper FIRI/T 137.
- Frontier S. 1976. Utilisation des diagrammes rang-fréquence dans l'analyse des écosystèmes. J. Rech. Océanogr. 1: 35-48.
- Gaudy R. 1962. Biologie des copépodes pélagiques du golfe de Marseille. Rec. Trav. St. Mar. End. **27:** 93-184.
- Gaudy R. 1970. Contribution à la connaissance du cycle biologique et de la physiologie des copépodes du golfe de Marseille. Ph.D. thesis, Univ. of Marseille II.
- Gaudy R. 1972. Contribution à la connaissance du cycle

biologique des copépodes du golfe de Marseille. 2. Etude du cycle biologique de quelques espèces caractéristiques. Téthys **4:** 175-242.

- Giron F. 1963. Copépodes de la mer d'Alboran (Campagne du "président Théodore-Tissier", juin 1957). Rev. Trav. Inst. Pêches Marit. **27**: 356-402.
- Halsband-Lenk C, H Hans-Jürgen, F Carlotti. 2002. Temperature impact on reproduction and development of congener copepod populations. J. Exp. Mar. Biol. Ecol. 271: 121-153.
- Halsband-Lenk C, S Nival, F Carlotti, HJ Hirche. 2001. Seasonal cycles of egg production of two planktonic copepods, *Centropages typicus* and *Temora stylifera*, in the north-western Mediterranean Sea. J. Plankton Res. 23: 597-609.
- Harris RP, PH Wiebe, J Lenz, HR Skjoldal, M Huntley. 2000. Zooplankton methodology manual. London: Academic Press.
- Heldt H. 1929. Le Lac de Tunis (partie Nord). Résultats des pêches au filet fin. Bull. St. Océanogr. Salambô 11: 1-74.
- Hirche HJ. 1992. Egg production of *Eurytemora affinis* Effect of k-strategy. Estuar. Coast. Shelf S. **35**: 395-407.
- Huys R, GA Boxshall. 1991. Copepod evolution. London: The Ray Society.
- Krebs CJ. 1999. Ecological methodology. Menlo Park, Canada. Addison-Wesley Longman.
- Kršinic F. 1995. Changes in the microzooplankton assemblages in the northern Adriatic Sea during 1989 to 1992. J. Plankton Res. **17**: 935-953.
- Ktari-Chakroun F. 1979. Evadne nordmanni Lovén dans le golfe de Tunis: distribution et abondance. Bull. Inst. Nat. Sci. Tech. Océanogr. Pêche Salammbô 6: 123-131.
- Lakkis S. 1990. Composition, diversité et successions des copépodes planctoniques des eaux libanaises (Méditer-ranée Orientale). Oceanol. Acta **13:** 489-501.
- Mauchline J. 1998. The biology of calanoid copepods. Adv. Mar. Biol. **33:** 1-170.
- Mazza J. 1961. Remarques sur la répartition qualitative et quantitative des copépodes en Méditerrannée. Rapp. P. V. Réun. Comm. Int. Explor. Sci. Mer Médit. 16: 157-164.
- Mazza J. 1966. Les copépodes de la Méditerrannée (Bassin occidental). Rapp. P. V. Réun. Comm. Int. Explor. Sci. Mer Médit. **19**: 99.
- Monard A. 1935. Les Harpacticoides marins de la région de Salambô. Bull. St. Océanogr. Salambô **34:** 1-94.
- Montanari MP, C Pruzzo, L Pane, RR Colwell. 1999. Vibrios associated with plankton in a coastal zone of the Adriatic Sea (Italy). FEMS Microbiol. Ecol. **29**: 241-247.
- Ohman MD, HJ Hirche. 2001. Density-dependent mortality in an oceanic copepod population. Nature **412**: 638-641.
- Parsons TR, M Takahashi, B Hargrave. 1984. Biological

oceanographic processes. 3rd ed. Oxford, UK: Pergamon Press.

- Razouls S. 1982. Etude expérimentale de la ponte des Copépodes pélagiques: *Temora stylifera* et *Centropages typicus*. II. Dynamique des pontes. Vie Milieu **32**: 11-20.
- Rose M, R Vaissière. 1952a. Catalogue préliminaire des Copépodes de l'Afrique du Nord. Bull. Soc. Hist. Nat. Afr. Nord. **43:** 113-136.
- Rose M, R Vaissière. 1952b. Catalogue préliminaire des Copépodes de l'Afrique du Nord. Bull. Soc. Hist. Nat. Afr. Nord. **43:** 164-176.
- Rose M, R Vaissière. 1953. Catalogue préliminaire des Copépodes de l'Afrique du Nord. Bull. Soc. Hist. Nat. Afr. Nord. 44: 83-99.
- Séguin G. 1968. Le plancton de la côte Nord de la Tunisie (Note préliminaire). Pelagos- Bull. Inst. Océanogr. Alger. 7: 73-83.
- Shannon CE, W Weaver. 1964. The mathematical theory of communication. Urbana, IL: Univ. of Illinois Press.
- Soenen M. 1969. Contribution à l'étude du Zooplancton superficiel et profond du bassin sud-occidental-méditerranéen. Thèse de Doctorat, Faculté des Sciences de l'Université d'Aix-Marseille.
- Soenen M. 1970. Contribution à l'étude du zooplancton superficiel et profond du détroit Siculo-Tunisien. France: Toulon Naval.
- Souissi S, MN Daly Yahia, O Daly Yahia-Kéfi. 2001. Predominance of the copepod *Centropages kroyeri* (Giesbrecht, 1892) in the Bay of Tunis during the spawning period of the anchovy *Engraulis ancrasicolis*. Rapp. Comm. It. Mer Médit. **36:** 419.
- Souissi S, O Daly Yahia-Kéfi, MN Daly Yahia. 2000. Spatial characterisation of nutrient dynamics in the Bay of Tunis (south-western Mediterranean) using multivariate analyses: consequences for phyto- and zooplankton distribution. J. Plankton Res. 22: 2039-2059.
- Throndsen J. 1995. Estimating cell numbers. *In* GM Hallegraeff, DM Anderson, AD Cembella, eds. Manual on harmful marine microalgae. France, UNESCO, IOC Manuals and Guides no. 33, pp. 63-80.
- Tudela S, I Palomera. 1997. Trophic ecology of the European anchovy *Engraulis encrasicolus* in the Catalan Sea (northwest Mediterranean). Mar. Ecol.-Prog. Ser. **160**: 12-134.
- Uye SI, D Liang. 1998. Copepods attain high abundance, biomass and production in the absence of large predators but suffer cannibalistic loss. J. Mar. Syst. 15: 495-501.
- Uye SI, K Sano. 1995. Seasonal reproductive biology of the small cyclopoid copepod *Oithona davisae* in a temperate eutrophic inlet. Mar. Ecol.-Prog. Ser. **118**: 112-128.
- Vives F. 1966. Zooplancton neritico de las aguas de Castellon (Mediterraneo occidental). Inv. Pesq. **30**: 49-166.