

What are the factors leading to the success of small planktonic copepods in the Gulf of Gabes, Tunisia?

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*An oceanographic cruise conducted during June 2008 in the Gulf of Gabes revealed the existence of different water masses; the Modified Atlantic Waters (MAW) circulated in the upper 100 m in the offshore area, the Mixed Mediterranean Water (MMW) was confined to the inshore region and the Ionian Water (IW) was in deep offshore water. The thermal stratification was indicated by the vertical profiles of temperature generated from a coast-offshore section. Phosphorus limitation was induced by the thermal stratification as shown by the high N/P ratio. Heterotrophic and mixotrophic dinoflagellates were the major contributors to total phytoplankton biomass. Ciliates were less abundant and dominated by tintinnids. Small planktonic copepods (≤ 1.45 mm) contributed to 93.64% of total copepod abundance in the inshore area as a result of the high density of *Oithona similis*, *Oithona nana*, *Clausocalanus furcatus* and *Euterpina acutifrons* in this area characterized by warm and salty MMW. In fact, small copepods were significantly correlated to both temperature and salinity. Small copepod fraction prevailed also in the MAW contributing to 71.05% of total copepod abundance as a result of the dominance of *O. nana* and *C. furcatus*. Nonetheless, the large copepod *Nannocalanus minor* was more adapted to the deep IW where it contributed to 44.05% of total copepod abundance. Invasive species were encountered in the offshore region intruded by the Atlantic waters. The Atlantic copepods were scarce and less abundant reflecting the weakening of the Atlantic flow in the eastern basin of the Mediterranean.*

Keywords: small copepods, dinoflagellates, tintinnids, invasive species, Modified Atlantic Waters, Mixed Mediterranean Water, Ionian Water

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INTRODUCTION

Metazooplankton communities have a pivotal role in the functioning and evolution of marine ecosystems (Beaugrand & Ibanez, 2004). Copepods have colonized the pelagic realm in both inshore and open sea waters (Kjørboe, 2011). They have a key role in the marine food webs by transferring the primary production to higher trophic levels (Tiselius *et al.*, 2013). Meanwhile, the diversity and size spectrum of copepods reflect the physical and chemical properties of the water column (Richardson, 2008) as well as the availability of their prey, mainly phytoplankton and ciliates. Small planktonic copepods involving developmental stages (nauplii and copepodites) are important intermediaries between larger and microbial components of the marine pelagic food webs (Turner, 2004). Their role is mainly important in oligotrophic ecosystems characterized by a relatively small size of primary producers and the dominance of microbial components

(Agawin *et al.*, 2000). Besides, heterotrophic and mixotrophic dinoflagellates are ubiquitous components of microzooplankton due to their successful feeding behaviour and their ability to overcome the lack of nutrients (Calbet, 2008; Jeong *et al.*, 2010). In addition to dinoflagellates, ciliates also constitute an important microzooplankton group (Hannachi *et al.*, 2008). They are the main components of the copepod diet in oligotrophic ecosystems (Calbet & Saiz, 2005) characterized by a low autotrophic biomass produced by nano- and picoplankton which are rarely consumed by copepods (Calbet *et al.*, 2000). In combination with trophic conditions, the physical properties of water masses have a major influence on the abundance and spatial distribution of planktonic copepods (Beaugrand *et al.*, 2002), which are thus considered as good biological indicators for water masses exchange (Bonnet & Frid, 2004).

In the Gulf of Gabes, copepods have been reported to be the main contributors to total zooplankton (Drira *et al.*, 2014), while picoplankton and small flagellates have become the major component of the autotrophic biomass (Bel Hassen *et al.*, 2008). Therefore, mesozooplankton communities are affected by the prevalence of small phytoplankton fractions.

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They are also dependent on the water masses circulation which is strongly linked to the general circulation of the Mediterranean Sea (Hattour *et al.*, 2010). Previous studies have shown the presence of a salinity minima zone resulting from the propagation of the Atlantic waters off the Gulf of Gabes (Bel Hassen *et al.*, 2008, 2009). Mediterranean and Atlantic mesozooplankton communities represent several similarities exhibiting temperate and tropical influences (Champalbert, 1996). Endemic species are scarce and restricted to inshore waters (Furnestin, 1979). The influence of the Atlantic flow is important in the Alboran Sea and in the south-western basin contributing to higher biodiversity and abundance than in the Catalan Sea (Furnestin, 1968). Atlantic mesozooplankton are then transferred through the Sicilo-Tunisian Strait; their abundance decreases eastward (Champalbert, 1996; Nowaczyk *et al.*, 2011) due to the bifurcation of the Atlantic vein in this strait (Poulain & Zambianchi, 2007).

We are aiming, through this work, to study the spatial distribution of planktonic copepods in relation to phytoplankton, microzooplankton and physical properties of the water column, to highlight the importance of small planktonic copepods and their trophic interaction with microzooplankton, mainly heterotrophic dinoflagellates and ciliates, in the oligotrophic waters of the Gulf of Gabes.

MATERIALS AND METHODS

Study site

The study was conducted in the Gulf of Gabes, in the south-east of Tunisia (Figure 1). This important marine ecosystem expands over 700 km along the Tunisian coasts from Chebba to the Tunisian–Libyan border. The immense

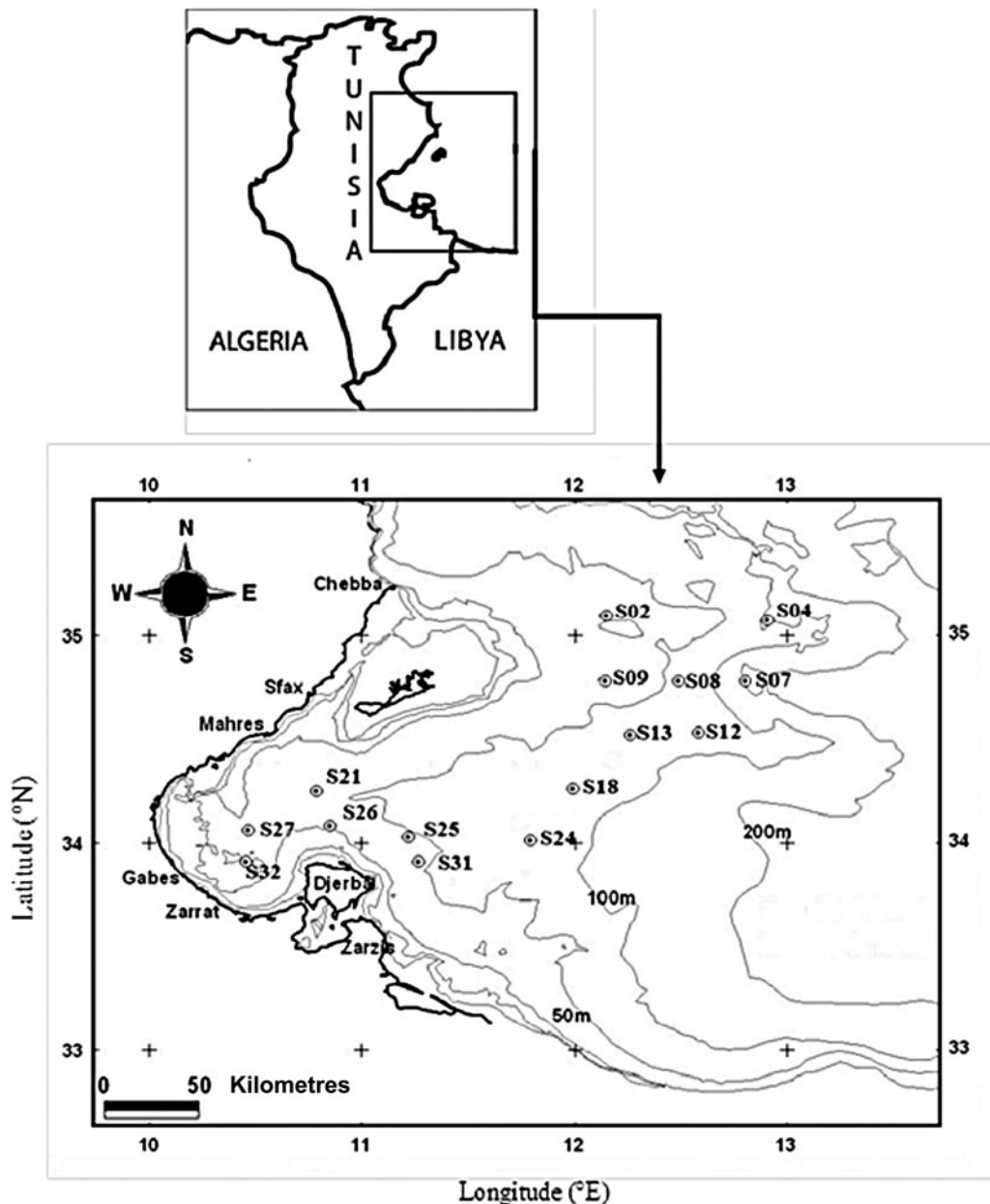


Fig. 1. Map of the sampled stations in the Gulf of Gabes during a summer cruise in June 2008 and the isobaths 50, 100 and 200 m.

continental shelf (250 km) and the low slopes make the main features of this region (Hattour *et al.*, 2010). The tide in the Gulf of Gabes is semi-diurnal. It is the highest in the Mediterranean with a maximum of 2 m resulting from resonance phenomena (Sammari *et al.*, 2006). The climate in this region is arid to semi-arid. The shallow waters run around Kerkennah, Djerba islands, and the lagoons of Boughrara and El Bibane (Hattour *et al.*, 2010). As the Gulf of Gabes is located between the eastern and western parts of the Mediterranean Sea, the dynamics of its water masses is strongly linked to the general circulation of the Mediterranean Sea. To the north of the Italian island Lampedusa, the current of Atlantic origin is divided into two veins: the first one goes to the south-east while the second turns southward and feeds the circulation in the Gulf of Gabes (Poulain & Zambianchi, 2007). The flow of the Atlantic waters through the Sicilo-Tunisian Strait undergoes an obvious seasonal variability (Ben Ismail *et al.*, 2012). The intensity of this Atlantic vein is subject to fluctuations that affect the circulation of water masses along the Gulf of Gabes (Bel Hassen *et al.*, 2009). Salinity in this region is high (37.5–39.25 psu). The existence of salinity minima in the Gulf of Gabes is attributed to the Atlantic waters (Sammari *et al.*, 1999).

Sampling

An oceanographic cruise was conducted during the summer, from 13 June to 16 June 2008 aboard the RV 'Hannibal', with 15 sampling stations in the Gulf of Gabes (Figure 1). In each station, values of temperature, salinity, dissolved oxygen and sigma-t were determined with a conductivity-temperature-depth profiler (CTD: SBE 9, Sea-bird Electronics, USA) equipped with a 12 Niskin bottle rosette sampler lowered from the surface to near the bottom. Water samples for chemical analysis, phytoplankton and ciliate examination were collected from three depths (surface, middle of the water column and near the bottom) in inshore stations less than 50 m in depth (S32, S27, S21, S26, S25, S31 and S09) and from five depths (surface, -20, -50, -75, near bottom) in offshore stations where the depth exceeded 50 m (S02, S25, S04, S07, S12, S13, S18 and S18). Samples for nutrient analyses (120 ml) were immediately preserved upon collection (-20°C, in the dark). For phytoplankton and ciliate enumeration, 1 litre was preserved in a Lugol (4%) iodine solution (Bourrelly, 1985) and stored in the dark at a low temperature (4°C) until analysis.

Chlorophyll-a samples (1000 ml) were filtered by vacuum filtration onto Whatman GF/F glass fibre filters. Filters were then immediately stored at -20°C.

Zooplankton were collected using a cylindro-conical net (30 cm aperture, 100 cm height and 100 m mesh size) equipped with a Hydro-Bios flowmeter. The net was towed obliquely from a depth near the bottom to the surface in each station at a mean speed of 1 m s⁻¹ during 10 min. After collection, zooplankton samples were rapidly preserved in a 2% buffered formaldehyde solution. They were stained with rose Bengal to identify internal tissues of the different zooplankton species and also to facilitate the dissection of copepods.

Nutrient and chl-a analyses

The nutrients (nitrate, ammonium, orthophosphate and silicate) were analysed with a Bran and Luebbe type 3 autoanalyser.

Chlorophyll-a was analysed using the HPLC method fully described in Bel Hassen *et al.* (2008).

Phytoplankton and ciliates enumeration

Sub-samples (50 ml) were counted under an inverted microscope after settling for 24–48 h. The identification of phytoplankton taxa was made according to various keys (Dodge, 1985; Tomas, 1996). Tintinnids were identified relying on the lorica morphology and species description made by Aboud-Abi Saab (2008). Naked ciliates were identified following the works of Alder (1999) and Strüder-Kypke & Montagnes (2002). Biovolumes were calculated from length and width measurements and converted to carbon biomass using the conversion factor for phytoplankton proposed by Menden-Deuer & Lessard (2000), with 1 µm³ = 0.216 × 10⁻⁶ µg C for all phytoplankton taxa except diatoms (1 µm³ = 0.288 × 10⁻⁶ µg C). For ciliate species, we used the conversion factor proposed by Putt & Stoecker (1989): 1 pg C = 1 µm³ × 0.19.

Zooplankton enumeration

Zooplankton samples, especially planktonic copepods, were identified according to Rose (1933) and Bradford-Grieve *et al.* (1999) and sorted into four demographic classes (nauplii, copepodites, adult males and adult females). Miscellaneous mesozooplankton such as Doliolida, Cladocera, Appendicularia and Siphonophora, were also counted according to Tregouboff & Rose (1957). Enumeration was performed under a vertically mounted deep-focus dissecting microscope (Olympus TL 2). The zooplankton density was expressed as: $X = N/(\pi r^2 s)/3$, where N = number of individuals sampled, r = 15 cm: half of the diameter of the plankton net and s = turn numbers shown by the flowmeter. The diversity of the phytoplankton, ciliates and copepods was determined using the Shannon–Weaver index (Shannon & Weaver, 1949).

Data analysis

Diagrams and contour plots were made using Ocean Data View (ODV) software, version 4.2.1, R. Schlitzer, <http://odv.awi-bremerhaven.de/>, 2009.

Pearson coefficients were calculated to detect significant correlations between the studied parameters. One-way analysis of variance (ANOVA) was performed to detect significant differences between inshore and offshore regions for the physico-chemical and biological parameters. Canonical correspondence analysis (CCA) was applied to different physical (temperature, salinity, water density and dissolved oxygen), chemical (nitrate, orthophosphate, ammonium and silicate) and biological parameters (Dinoflagellate biomass, diatom biomass, ciliate biomass, chl-a) in relation with the densities of the most dominant copepod species. All the analyses were performed using the X L-Stat software.

RESULTS

Physico-chemical parameters

The temperature–salinity diagram revealed the presence of different water masses (Figure 2). The deep and cool waters (>100 m depth) correspond to the Ionian Waters (IW)

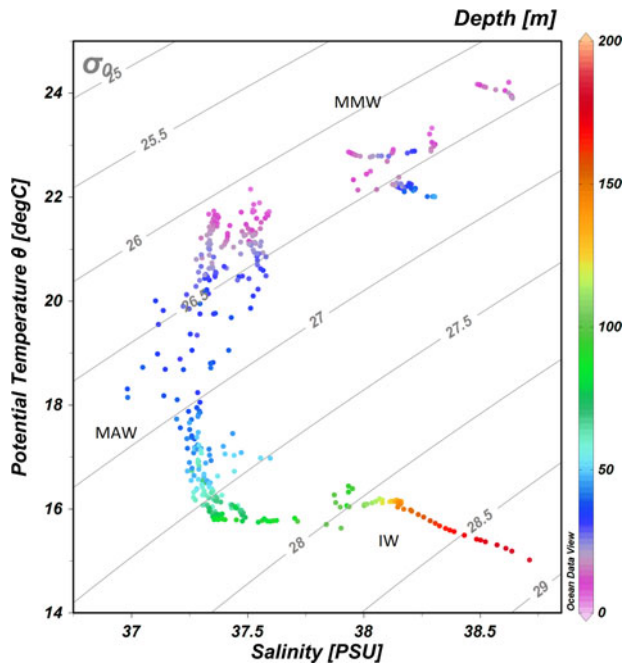


Fig. 2. Temperature-salinity diagram showing the presence of different water masses in the Gulf of Gabes during a summer cruise in June 2008. (Ocean Data View (ODV) software, version 4.2.1, R. Schlitzer, <http://odv.awi-bremerhaven.de/>, 2009).

characterized by high salinity intruding mainly to the stations S07 and S04 in the offshore region. The intermediate depth (<100 m) and cool waters correspond to the Modified Atlantic Waters (MAW) intruding mainly to the stations S25, S04, S12, S13, S18 and S18. These waters are further recognized by their low salinity (<37.5 psu). The shallow salty and warm waters correspond to the Mixed Mediterranean Water (MMW) confined to the inshore region (<50 m depth; stations S32, S27, S21, S26, S25, S31 and S09). Nonetheless, the IW and MAW are encountered in the offshore region.

Contour plots of temperature revealed a decreasing water temperature from surface to bottom and from inshore to open sea regions (Figure 3A). Significant differences were found between the inshore and offshore regions (ANOVA, $F=32.38$, $P<0.001$). Inshore waters were the warmest reaching 24°C with an average of $22.06 \pm 1.43^{\circ}\text{C}$. In the open sea region, water temperature decreased considerably with depth recording 15°C near the bottom. Therefore this quick diminution of temperature with depth led to the establishment of a thermocline (Figure 3A). The vertical distribution of salinity showed the presence of a salinity minimum (<37.5 psu) in the offshore region. The deep offshore waters were distinguished by high salinity and low temperature corresponding to the IW. Nonetheless, the inshore region of the Gulf of Gabes was characterized by salty Mediterranean waters (MMW) exceeding 38 psu (Figure 3B).

Nutrient concentrations were low, despite higher nitrate concentration at the surface in the offshore region (with a maximum of $3.75 \mu\text{M}$) (Figure 4A). Ammonium and orthophosphate did not exceed 1.5 and $0.1 \mu\text{M}$ respectively (Figure 4B, C). Silicate concentrations increased in the deep offshore region. They reached $6 \mu\text{M}$ near 200 m isobath (Figure 4D). Phosphorus limitation was underlined by the

high N/P ratio (Figure 4E). Chlorophyll-a concentrations were very low ($<0.3 \mu\text{g C l}^{-1}$) suggesting an oligotrophic ecosystem. A deep chl-a maximum ($0.25 \mu\text{g C l}^{-1}$) was recorded between 80 and 120 m depth in the offshore area (Figure 4F).

Phytoplankton and ciliates

Total phytoplankton density ranged from $2.27 \times 10^3 \pm 1.45 \times 10^3 \text{ cells l}^{-1}$ in the deep offshore IW to $15.87 \times 10^3 \pm 12.34 \times 10^3 \text{ cells l}^{-1}$ in the MMW (Figure 5A, Table 1). The obvious proliferation of heterotrophic and mixotrophic dinoflagellates was the distinctive feature of this summer cruise.

They contributed to 52% of total phytoplankton abundance in the MMW where the maximum of abundance was recorded ($8.16 \times 10^3 \pm 7.51 \times 10^3 \text{ cells l}^{-1}$) due to the important proliferation of *Protoperidinium ovatum*. Dinoflagellate density was positively correlated to both temperature ($r=0.772$; $N=71$; $P=0.05$) and salinity ($r=0.765$; $N=71$; $P=0.05$) suggesting a good adaptation of this group to the warm and salty MMW waters in the inshore region. Diatom density showed positive correlation to both temperature ($r=0.726$; $N=71$; $P=0.05$) and salinity ($r=0.654$; $N=71$; $P=0.05$) in the MMW. Silicoflagellates were restricted to the MMW (Table 1). Cyanobacteria were obviously more abundant in the MMW (Table 1). Despite the low values of chl-a, total phytoplankton biomass was high especially in the MMW reaching a mean value of $8.57 \times 10^2 \pm 3.77 \times 10^2 \mu\text{g C l}^{-1}$ (Table 1, Figure 5B).

Dinoflagellates were the main contributors to the total phytoplankton biomass during the whole cruise (99%). Dinoflagellate biomass was the highest in the MMW in the inshore region (Figure 5C) due to the proliferation of large taxa such as *Noctiluca scintillans* ($400 \mu\text{m}$), *Neoceratium pentagonum* ($218 \mu\text{m}$) and *Protoperidinium depressum* ($50 \mu\text{m}$). *Noctiluca scintillans* contributed to 47.23% of total dinoflagellate biomass in the MMW (Figure 5D).

Ciliate density was obviously higher in the MMW (mean \pm SD = $1.56 \times 10^3 \pm 0.46 \times 10^3 \text{ cells l}^{-1}$) (Table 1). They were characterized by the prevalence of tintinnids which exceeded total naked ciliates either in abundance or in biomass. Both temperature ($r=0.701$; $N=71$; $P=0.05$) and salinity ($r=0.642$; $N=71$; $P=0.05$) were positively correlated to Tintinnida.

Zooplankton

The spatial distribution of the mesozooplankton communities revealed a high total mesozooplankton density in the inshore area intruded by salty and warm MMW (mean \pm SD = $1033 \times 10^3 \pm 886 \times 10^3 \text{ individuals m}^{-3}$) (Figure 6A). Copepods were the most abundant mesozooplankton group; their density ranged from 50×10^3 to $1450 \times 10^3 \text{ individuals m}^{-3}$ (Figure 6B). Meanwhile, small copepods (total length 0.4–1.45 mm including all developmental stages) obviously prevailed in the MMW.

The highest copepod density was recorded in the MMW ($1450 \times 10^3 \text{ individuals m}^{-3}$ at S27) mainly driven by small copepods (Figure 6C). Larger copepod taxa did not exceed $76 \times 10^3 \text{ individuals m}^{-3}$ (Figure 6D). The important proliferation of Oithonidae in the inshore region led to the prevalence of small planktonic copepods accounting for 93.64% of total copepod abundance in the MMW (Table 2).

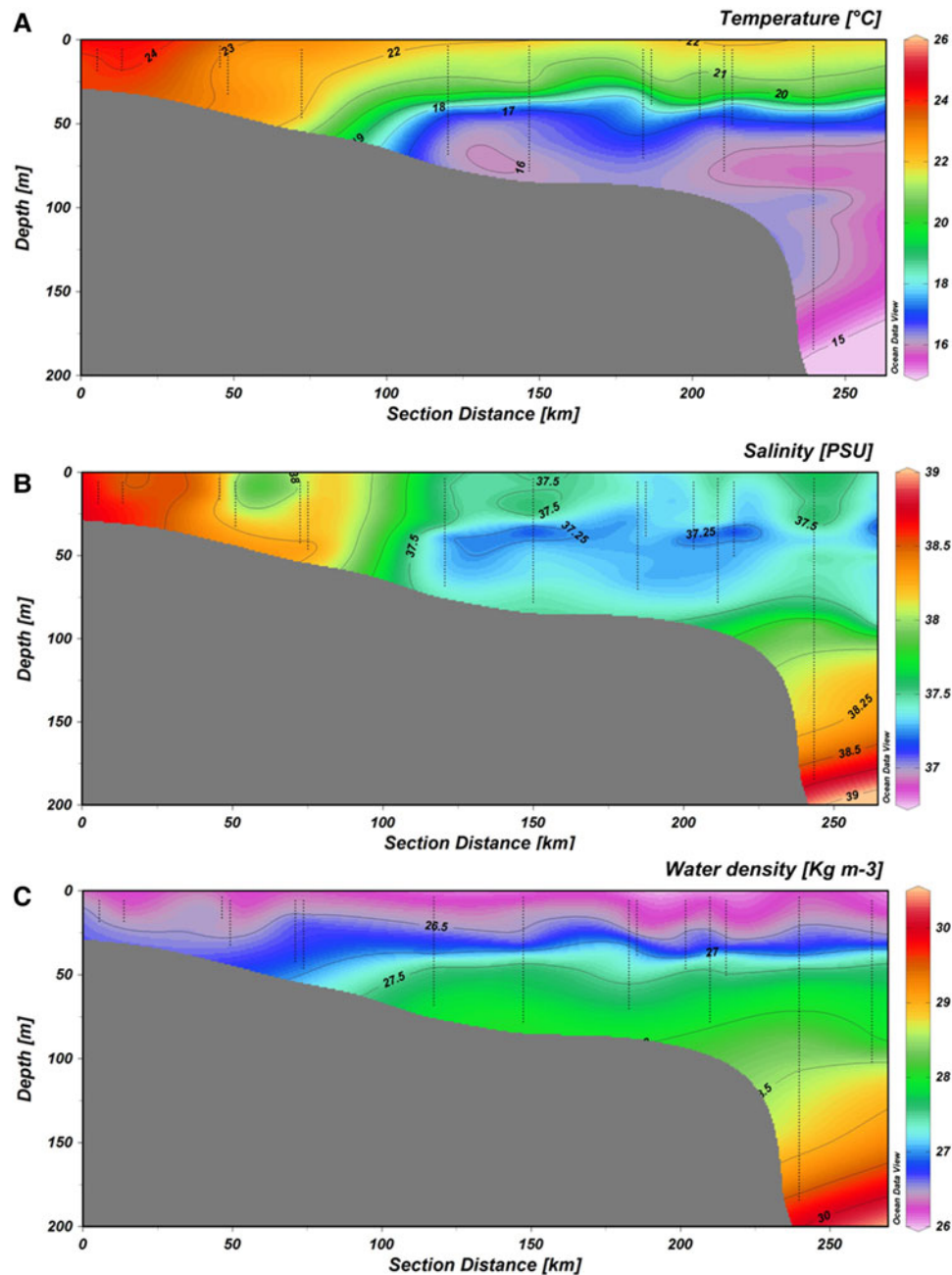


Fig. 3. Vertical profiles of (A) temperature, (B) salinity, and (C) water density during a summer cruise in June 2008 in the Gulf of Gabes according to the coast gradient. Distance on the x-axis is scaled in kilometres from the starting point of the section: First station ($10.46^{\circ}\text{E } 33.91^{\circ}\text{N}$). The end of the section is located at the most distant station ($12.91^{\circ}\text{E } 35.09^{\circ}\text{N}$). Black dots represent sampling points.

Oithona similis and *O. nana* were the most abundant species contributing to 39.61 and 23.49% of total copepod abundance in the MMW respectively (Table 2). The prevalence of small copepods was also recorded in the MAW where they contributed up to 71.05% of total copepod abundance (Table 2). In addition to Oithonidae, this water mass was also distinguished by the proliferation of clausocalanids. In fact, *O. nana*, *Clausocalanus furcatus* and *O. similis* were the most dominant species in the MAW contributing to 15.49, 11.93 and 10.43% respectively in this water mass. Meanwhile, the deep offshore IW was characterized by the dominance of larger copepod fractions (total length 1.45–2.5mm) as a result of the proliferation of *Nannocalanus minor* (44.05% of total copepod abundance in the IW).

During this cruise, the small *C. furcatus* was revealed to be a permanent component of the offshore copepod communities of the Gulf of Gabes in the IW as well as in the MAW. In fact, this species contributed up to 15.08% of total copepod abundance in the IW (Table 2).

Small planktonic copepods included cyclopoids, harpacticoids, poecilostomatoids and small calanoid genera (*Acartia*, *Metacalanus*, *Paracalanus*, *Clausocalanus* and *Calocalanus*) (Table 2). Oithonids were numerically dominant contributing to the high cyclopoid density (Figure 7A). The latter was significantly correlated with temperature ($r = 0.736$, $N = 71$, $P = 0.05$) and salinity ($r = 0.738$, $N = 71$, $P = 0.05$). Therefore the small cyclopoids represented the best adapted group to the MMW.

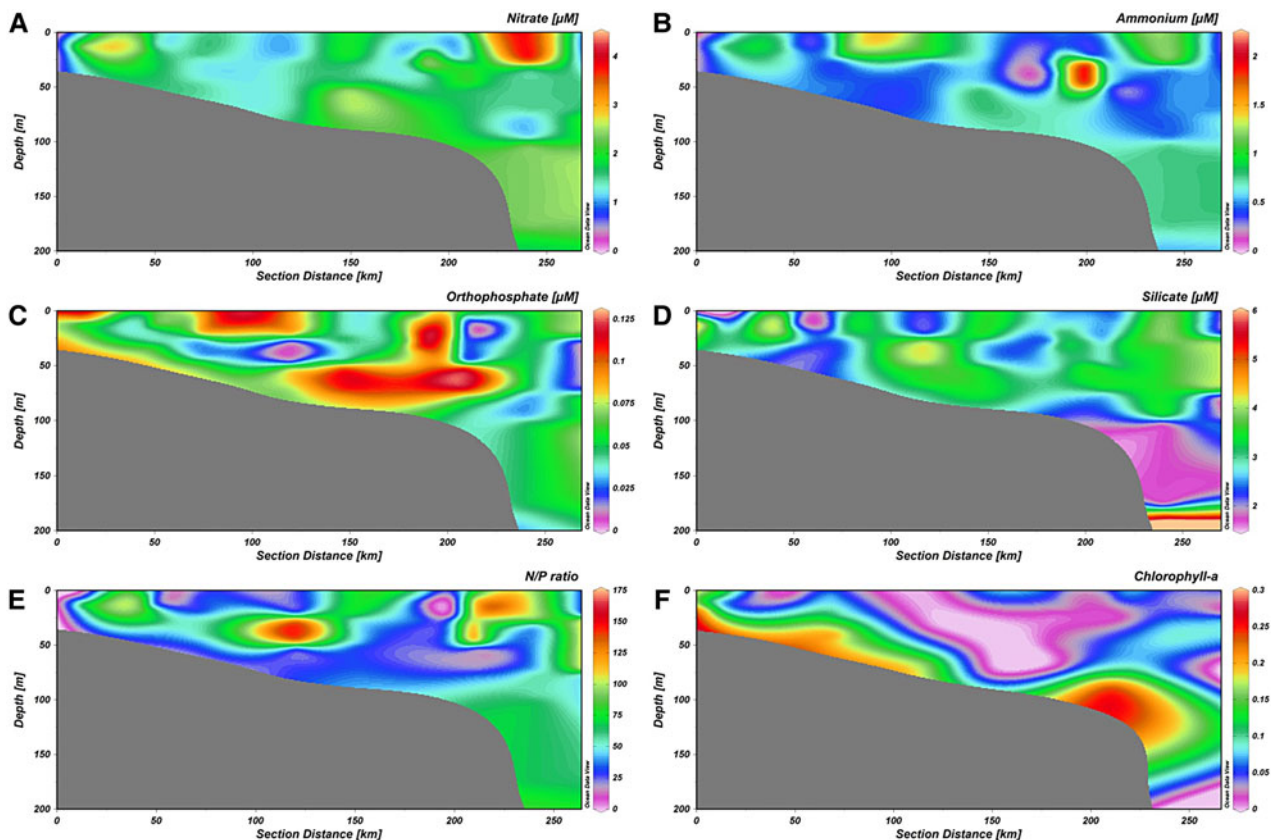


Fig. 4. Vertical profiles of (A) nitrate, (B) ammonium, (C) orthophosphate, (D) silicate, (E) N/P ratio and (F) chlorophyll-*a* ($\mu\text{g C l}^{-1}$) during a summer cruise in June 2008. Details of the section are the same as in Figure 3.

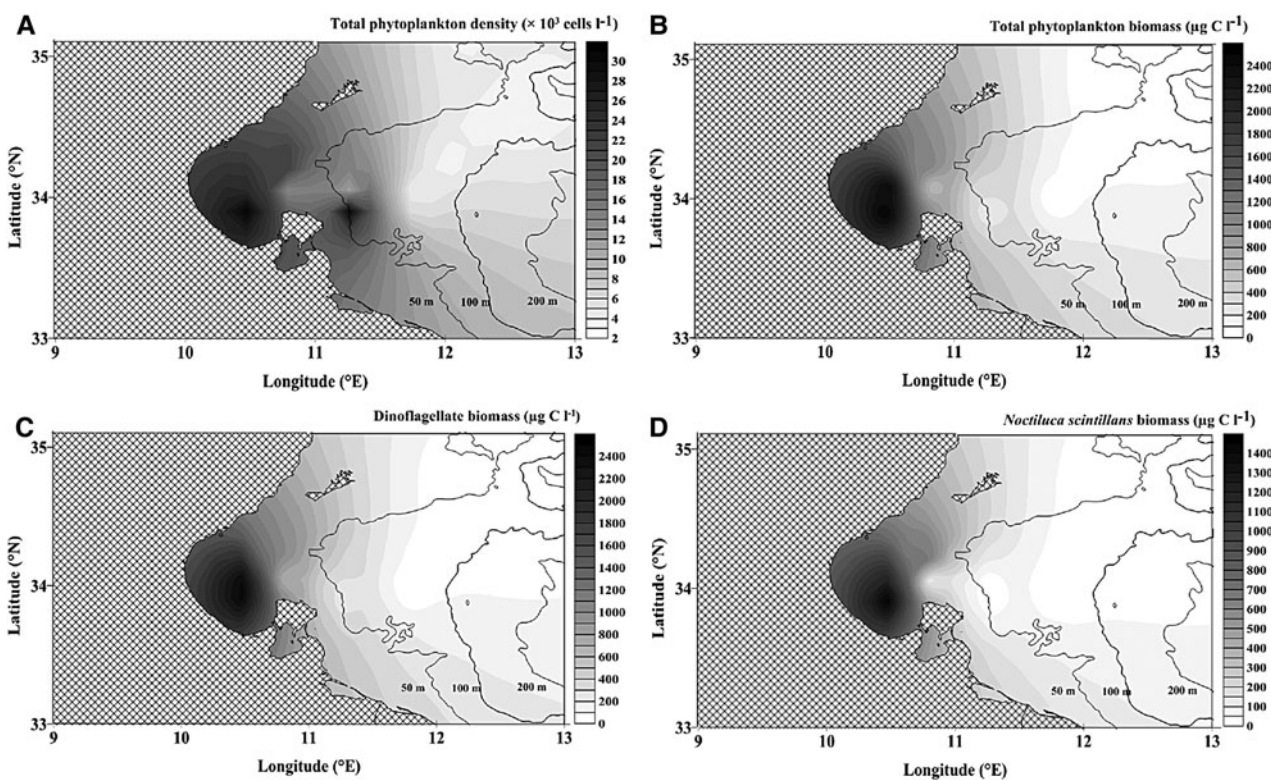


Fig. 5. Spatial distribution of (A) total phytoplankton density, (B) total phytoplankton biomass, (C) dinoflagellate biomass and (D) the heterotrophic dinoflagellate *Noctiluca scintillans* biomass, during a summer cruise in June 2008.

Table 1. Densities and biomass of the major microplankton groups encountered in the three water masses of the Gulf of Gabes during a summer cruise in June 2008.

	MMW	MAW	IW
Total phytoplankton ($\times 10^3$ cells l^{-1})	15.87 \pm 12.34	2.44 \pm 2.26	2.27 \pm 1.45
Total phytoplankton biomass ($\times 10^2$ μ g C l^{-1})	8.57 \pm 3.77	0.41 \pm 0.45	0.94 \pm 0.00
Dinoflagellate density ($\times 10^3$ cells l^{-1})	8.16 \pm 7.51	1.55 \pm 2.14	0.65 \pm 0.494
Dinoflagellate biomass ($\times 10^2$ μ g C l^{-1})	8.46 \pm 0.54	0.38 \pm 0.43	0.003 \pm 0.00
Diatom density ($\times 10^3$ cells l^{-1})	2.64 \pm 2.18	0.46 \pm 0.25	0.75 \pm 0.55
Cyanobacteria density ($\times 10^3$ cells l^{-1})	2.64 \pm 2.18	0.42 \pm 0.29	0.36 \pm 0.17
Silicoflagellate density ($\times 10^3$ cells l^{-1})	2.4 \pm 2.94	0.00	0.00
Total ciliate density ($\times 10^3$ cells l^{-1})	1.56 \pm 0.46	0.24 \pm 0.01	0.10 \pm 0.00
Total ciliate biomass (μ g C l^{-1})	8.92 \pm 5.04	0.45 \pm 0.60	0.81 \pm 0.00

Harpacticoid density ranged from 20×10^3 to 320×10^3 individuals m^{-3} (Figure 7B). The abundance of harpacticoids was the result of the important proliferation of *Euterpina acutifrons* which was highly correlated with temperature ($r = 0.695$, $N = 71$, $P = 0.05$) and salinity ($r = 0.742$, $N = 71$, $P = 0.05$). Therefore, the occurrence of harpacticoids was mainly neritic enhanced by the warm and salty MMW (Figure 7B). Small calanoid families such as Acartiidae, Clausocalanidae and Paracalanidae contributed to the proliferation of small calanoids (Figure 7C). These small calanoids involved three Atlantic invasive species such as *Calocalanus contractus*, *Acartia bifilosa* and *A. tonsa* (Table 2). In contrast to other small copepods, the spatial distribution of Poecilostomatoida showed a preference to the MAW in the offshore area (Figure 7D). In fact, this order included two invasive Atlantic species, namely *Corycaeus amazonicus* and *Pachos tuberosum* (Table 2).

In addition to adults, small planktonic copepods also included copepodites and nauplii of almost all genera.

Nauplii density was very low (mean \pm SD = $13 \times 10^3 \pm 9.85 \times 10^3$) (Figure 8A). Meanwhile, the remaining developmental stages were characterized by the numerical dominance of copepodites (Figure 8B) (mean \pm SD = $409.33 \times 10^3 \pm 407 \times 10^3$) and adults (mean \pm SD = $407 \times 10^3 \pm 286 \times 10^3$) (Figure 8C).

As opposed to the copepod density, there was an obvious increase in diversity in the offshore region (mean \pm SD = 1.13 ± 0.11 bits $cell^{-1}$) (Figure 9A). During our survey, rare species such as invasive Atlantic copepods were mainly encountered in the offshore region where hydrography is governed by the propagation of an Atlantic vein. The distribution of the total copepod diversity was not strongly linked to those exhibited by ciliates and phytoplankton (Figure 9B, C).

Cladocerans, siphonophores, chaetognaths and appendicularians were also permanent components of the holoplankton in the Gulf of Gabes (Table 3). Meroplankton was made up essentially of larval stages such as bivalve larvae (Table 3).

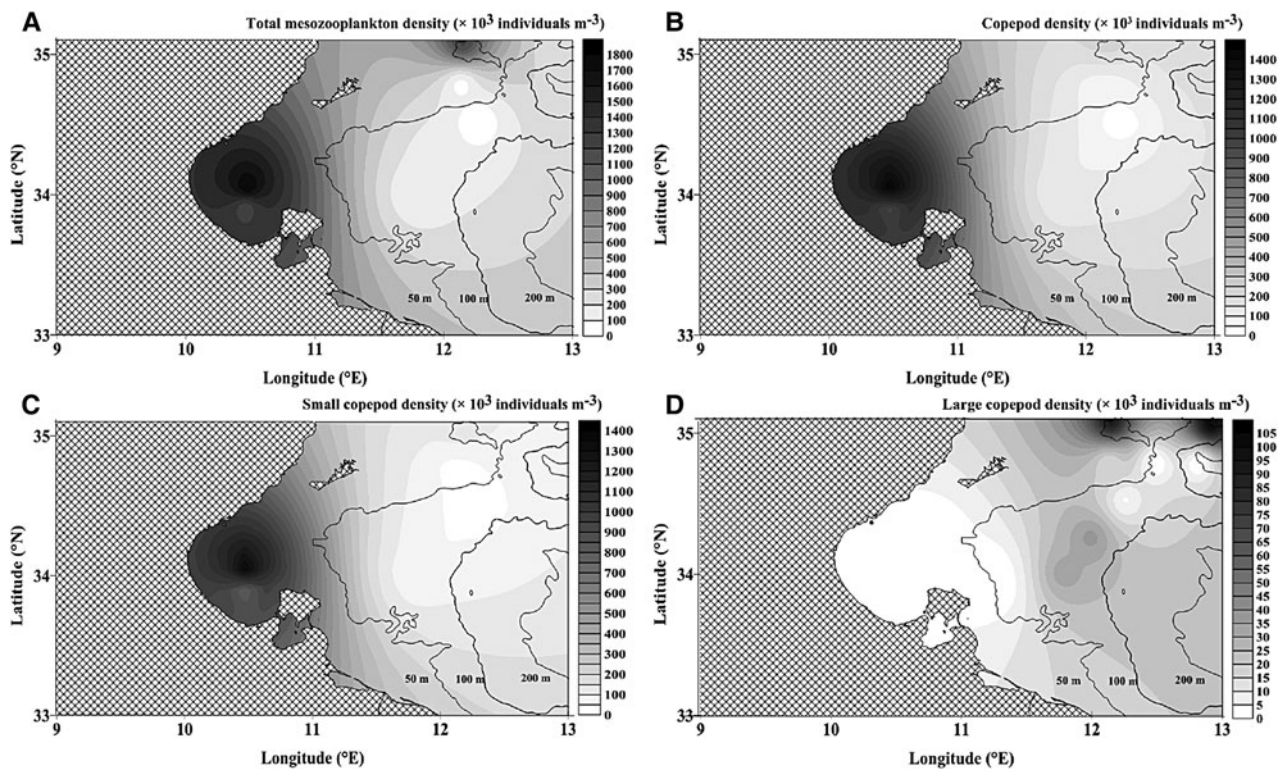
**Fig. 6.** Spatial distribution of (A) total mesozooplankton, (B) total copepods, (C) small copepods and (D) large copepods in the Gulf of Gabes during a summer cruise in June 2008. Small copepods included species with total length of adult ≤ 1.45 mm.

Table 2. Small and large copepod species classified along an increasing gradient of total body length (TL) and their relative abundance in the three major water masses of the Gulf of Gabes in June 2008 (^A copepod species of Atlantic origin referring to Rose, 1933). The highest abundances are in bold.

Copepod taxa	T L (mm)	Relative abundance (%)		
		MMW	MAW	IW
0.4–1.45 mm (Small copepods)		93.64	71.05	45.63
<i>Euterpina acutifrons</i> (Dana, 1852)	0.40	13.54	0.16	0.00
<i>Oithona similis</i> (Claus, 1866)	0.49	39.61	10.43	6.35
<i>Metacalanus inaequicornis</i> ^A (Sars, 1902)	0.57	0.00	0.32	0.00
<i>Microsetella norvegica</i> (Boeck, 1864)	0.64	0.05	0.16	0.00
<i>Oithona nana</i> (Giesbrecht, 1892)	0.65	23.49	15.49	0.00
<i>Microsetella rosea</i> (Dana, 1852)	0.67	0.06	0.32	0.00
<i>Oncaea venusta</i> (Philippi, 1843)	0.68	0.02	0.13	0.00
<i>Farranula rostrata</i> (Claus, 1863)	0.72	0.15	3.11	0.79
<i>Corycaeus latus</i> (Dana, 1849)	0.75	0.23	0.16	0.00
<i>Oncaea mediterranea</i> (Claus, 1863)	0.76	0.05	3.79	0.00
<i>Clausocalanus furcatus</i> (Brady, 1883)	0.78	4.58	11.93	15.08
<i>Calocalanus contractus</i> ^A (Farran, 1926)	0.78	0.09	0.12	1.19
<i>Oncaea clevei</i> (Früchtl, 1923)	0.81	0.29	0.78	0.79
<i>Corycaeus ovalis</i> (Claus, 1863)	0.87	0.09	0.38	0.00
<i>Calocalanus styliremis</i> (Giesbrecht, 1889)	0.95	0.05	0.00	0.00
<i>Corycaeus speciosus</i> (Dana, 1849)	0.99	0.84	2.63	0.00
<i>Acartia bifilosa</i> ^A (Giesbrecht, 1881)	0.99	1.88	1.90	0.00
<i>Oithona linearis</i> (Giesbrecht, 1891)	1.00	0.00	0.65	4.76
<i>Acartia clausi</i> (Giesbrecht, 1889)	1.08	3.05	3.68	2.78
<i>Paracalanus parvus</i> (Claus, 1863)	1.08	0.00	2.07	1.98
<i>Acartia discaudata</i> (Giesbrecht, 1881)	1.10	0.76	0.65	1.59
<i>Rhincalanus nasutus</i> (Dana, 1848)	1.16	0.02	0.16	1.19
<i>Macrosetella gracilis</i> (Dana, 1852)	1.20	0.00	0.16	0.79
<i>Acartia longiremis</i> (Lilljeborg, 1853)	1.24	2.47	3.96	3.17
<i>Acartia tonsa</i> ^A (Dana, 1848)	1.26	0.77	0.00	0.00
<i>Corycaeus clausi</i> (F. Dahl, 1894)	1.28	0.40	3.35	0.00
<i>Oithona plumifera</i> (Baird, 1843)	1.42	1.16	4.55	5.16
1.45–2.5 mm (Large copepods)		6.36	28.95	54.37
<i>Centropages typicus</i> (Krøyer, 1849)	1.45	2.02	3.11	1.19
<i>Centropages kroyeri</i> (Giesbrecht, 1892)	1.46	0.30	3.17	1.98
<i>Centropages hamatus</i> (Lilljeborg, 1853)	1.47	0.06	2.74	0.00
<i>Pleuromamma xiphias</i> ^A (Giesbrecht, 1889)	1.49	0.34	0.26	0.00
<i>Centropages ponticus</i> (Karavaev, 1894)	1.49	0.34	1.13	1.59
<i>Temora stylifera</i> (Dana, 1848)	1.54	0.51	2.58	2.38
<i>Centropages chierchiae</i> (Giesbrecht, 1889)	1.70	0.00	0.97	0.00
<i>Calanus helgolandicus</i> (Claus, 1863)	1.82	0.06	3.91	3.17
<i>Labidocera brunescens</i> (Czerniavsky, 1868)	1.83	0.02	0.13	0.00
<i>Pachos tuberosum</i> ^A (Giesbrecht, 1891)	2.00	0.00	0.28	0.00
<i>Nannocalanus minor</i> (Claus, 1863)	2.15	2.42	10.43	44.05
<i>Candacia armata</i> (Boeck, 1872)	2.50	0.29	0.26	0.00

Canonical Correspondence Analysis (CCA) showed that F1 and F2 axes explained 87.52% of the variance (Figure 10A). The small copepod species *O. nana*, *O. similis* and *Euterpina acutifrons* showed a close link to the temperature and salinity at the inshore stations (S26, S27) intruded by MMW. The large calanoid *N. minor* was more sensitive to the availability of nutrients (nitrate, silicate, ammonium) in the offshore stations (S04, S07) involving the IW. The density of the small calanoid *C. furcatus* and chl-a concentration were higher in the MAW. The spatial distribution of the calanoids *Acartia clausi*, *A. longiremis*, *Centropages typicus* and *Centropages kroyeri* was linked to the biomass of ciliates, diatoms and chl-a. *Clausocalanus furcatus* and *Oithona plumifera* was associated to nutrients (orthophosphate, ammonium, silicate and nitrate). Water density was the major physical parameter governing the abundance and the distribution of these two species. Canonical Correspondence Analysis applied using the sampled stations and the physical parameters showed both increasing

temperature and salinity in the inshore stations S31, S32, S25, S21, S27 and S26 (Figure 10B). Therefore, these stations were likely to be intruded by the MMW.

DISCUSSION

Physical and trophic context during summer stratification in the Gulf of Gabes

Our study during this summer cruise in the Gulf of Gabes showed the existence of three different water masses associated with Mediterranean (MMW and IW) and Atlantic (MAW) origins as already described in previous studies (Bel Hassen *et al.*, 2008; Ben Ismail *et al.*, 2012). The salinity minimum zone resulted from the propagation of Atlantic waters and was evidence of the existence of MAW in the offshore region of the Gulf of Gabes. The propagation of this

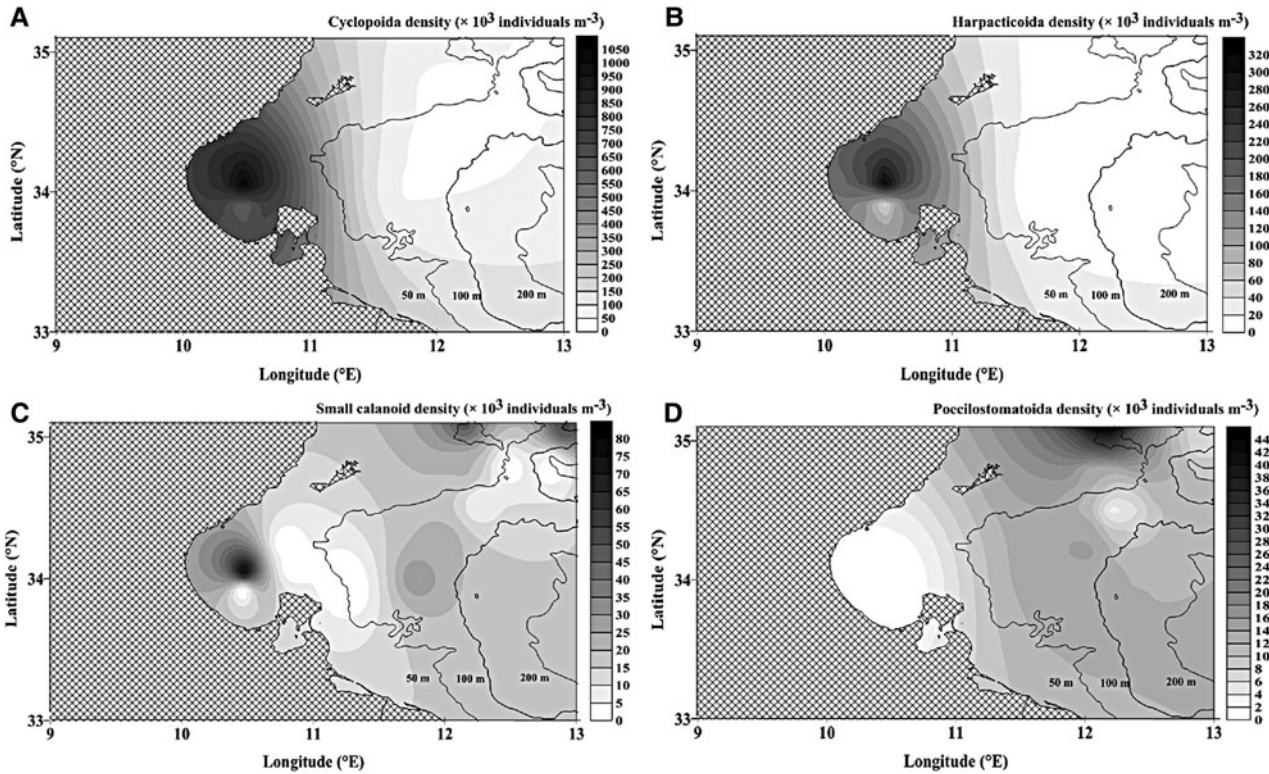


Fig. 7. The spatial distribution of the main orders making up small copepod communities in the Gulf of Gabes during a summer cruise in June 2008: (A) Cyclopoida, (B) Harpacticoida, (C) small calanoids and (D) Poecilostomatoida.

Atlantic vein participated in fertilizing the offshore region with nutrients as shown by higher nitrate concentrations found at the surface in the offshore region. Conversely, the

shallow inshore waters were intruded by saltier, warmer and nutrient-depleted MMW waters. Dinoflagellates and diatoms proliferated mainly in the MMW of the Gulf of

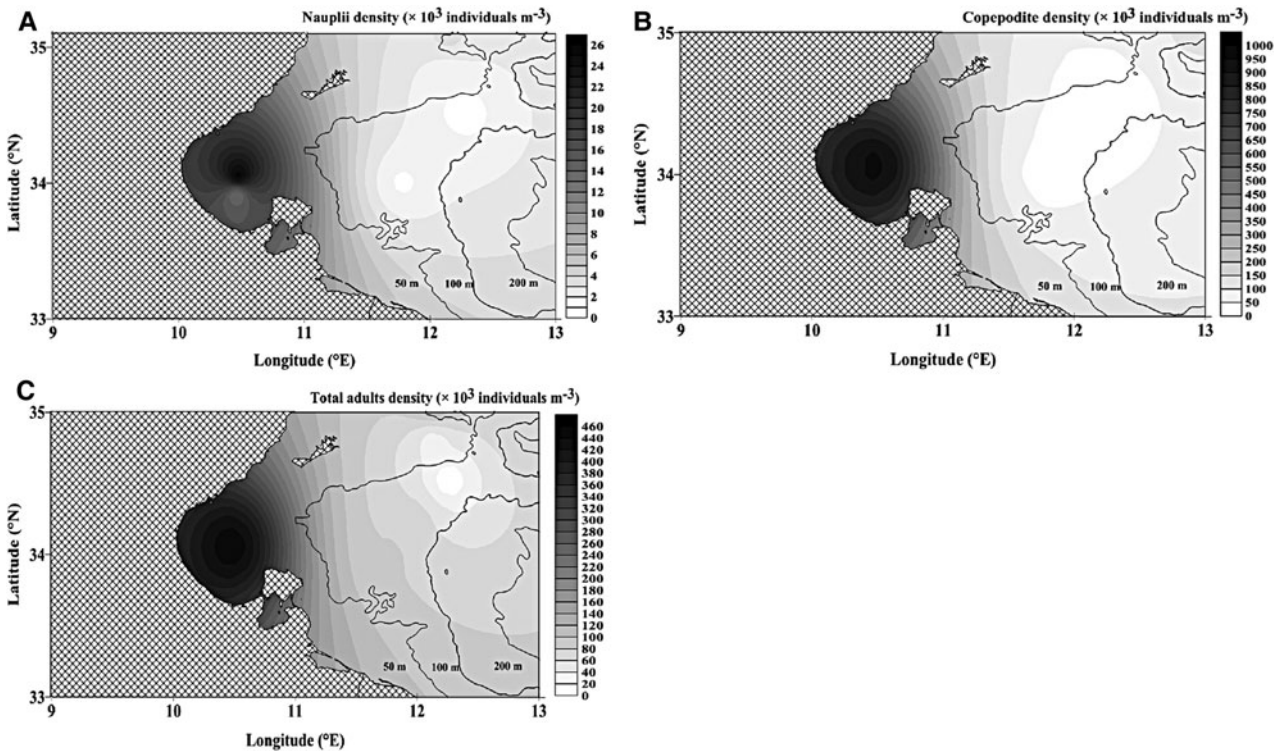


Fig. 8. The spatial distribution of copepod developmental stages communities in the Gulf of Gabes during a summer cruise in June 2008: (A) nauplii, (B) copepodites and (C) adult.

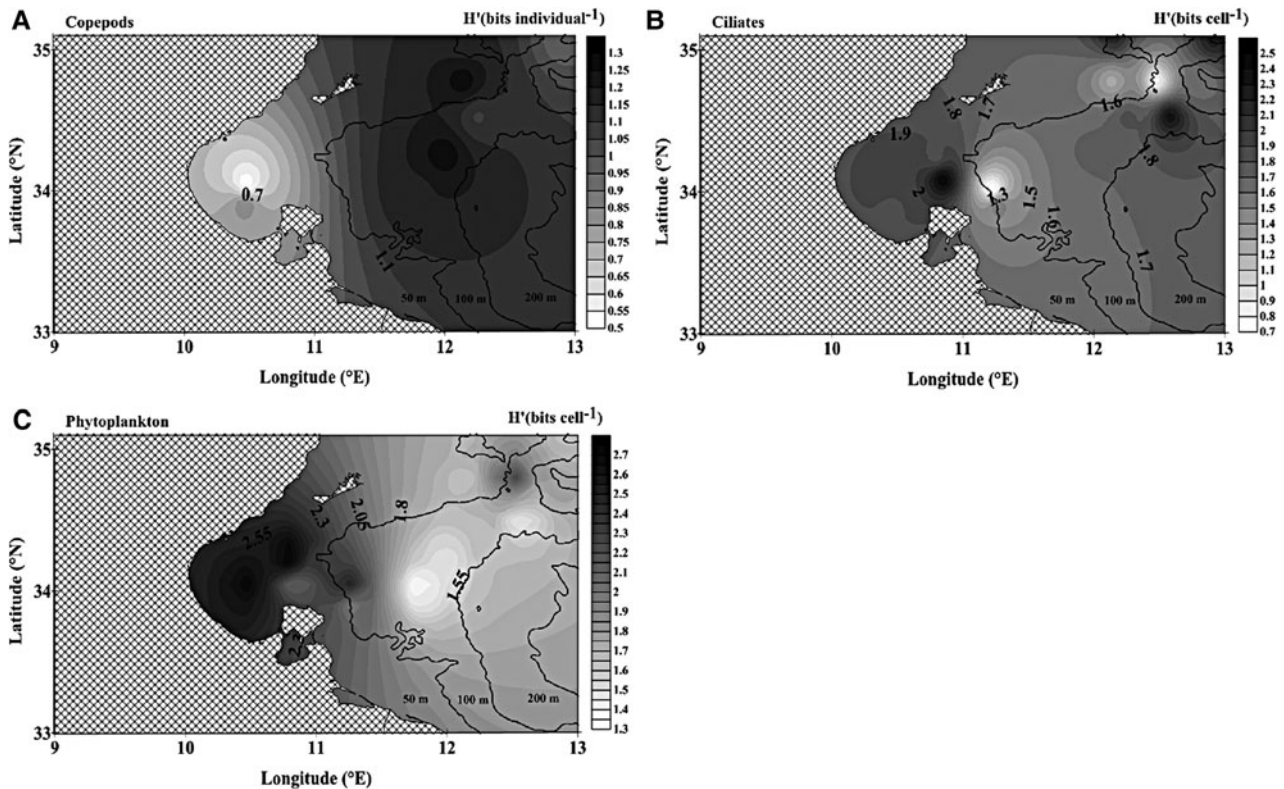


Fig. 9. The spatial distribution of the diversity index H' of (A) total copepods, (B) total ciliates and (C) total phytoplankton in the Gulf of Gabes during a summer cruise in June 2008.

Gabes characterized by higher temperature and salinity and by low and phosphorus-limited nutrients. The dominance of dinoflagellates is usually encountered during stratification in the Mediterranean Sea (Gómez & Gorsky, 2003). In fact, they prefer a stable water column and warm temperature (Lasternas *et al.*, 2011). Thus, the stability of the water column during summer stratification provides the opportunity to take full advantage of these abilities. Their proliferation, despite the establishment of a thermocline limiting the replenishment of the euphotic layer with nutrients, may be linked to their motility and their ability to move and migrate vertically in the water column in search of nutrients and light (Ross & Sharples, 2007). Besides, they can overcome the lack of nutrients by diversifying their trophic modes (autotrophic,

mixotrophic and heterotrophic) (Jeong *et al.*, 2010). Dinoflagellates are ubiquitous in marine ecosystems. They are also very abundant in the Gulf of Gabes as found by Bel Hassen *et al.* (2008) who proved that the nano- and picophytoplankton were the major contributors to the autotrophic biomass in the gulf. About half of dinoflagellate species in marine plankton are deprived of chloroplasts (Sherr & Sherr, 2007). Mixotrophic and heterotrophic dinoflagellates exhibit several feeding mechanisms (pallium-feeding, peduncle-feeding and direct engulfment) (Jeong *et al.*, 2010). Several *Protoperidinium* species are able to feed on diatoms (Sherr & Sherr 2007), autotrophic dinoflagellates, eggs and early naupliar stages (Jeong *et al.*, 2010). *Protoperidinium* species may be in competition with mesozooplankton to feed on other dinoflagellates and diatoms. Due to the low values of chl-a and the high biomass of heterotrophic dinoflagellates and ciliates, the Gulf of Gabes had a heterotrophic microplankton standing stock feeding on a large variety of prey ranging from picoplankton to diatoms (Bel Hassen *et al.*, 2008).

During the study period, the ciliate biomass was very low, revealing a possible predation by copepods and even by heterotrophic dinoflagellates (Jeong *et al.*, 2010). Copepods represent an important mesozooplankton group able to complete a top-down control on ciliate populations (Zervoudaki *et al.*, 2007). In fact, ciliates are considered as a rich protein food source for copepods (Gifford & Dagg, 1991). In the eastern Mediterranean Sea, similar results reported the strong top-down control of copepods in regulating ciliate populations (Siokou-Frangou *et al.*, 2002). Furthermore, the subsistence of tintinnids on behalf of aloricate ciliates may be explained by their ability to escape grazing due to the presence of a protective lorica (Abboud-Abi Saab, 2008).

Table 3. Miscellaneous zooplankton groups and their relative abundance in the major water masses encountered in the Gulf of Gabes in June 2008.

Miscellaneous zooplankton	MMW	MAW	IW
Cladocera	11.81	30.97	9.52
Decapoda	6.61	4.22	7.14
Chaetognatha	9.39	9.97	9.52
Appendicularia	6.45	4.63	7.14
Siphonophora	21.70	9.75	19.05
Gastropoda larvae	8.38	9.35	14.29
Bivalvia larvae	6.81	10.25	7.14
Ophiuroidea larvae	5.21	1.62	4.76
Polychaeta larvae	11.71	7.77	9.52
Scaphopoda larvae	3.27	5.25	2.38
Fish larvae	6.16	4.13	7.14
Doliolida	2.48	2.11	2.38
Foraminifera	0.03	0.00	0.00

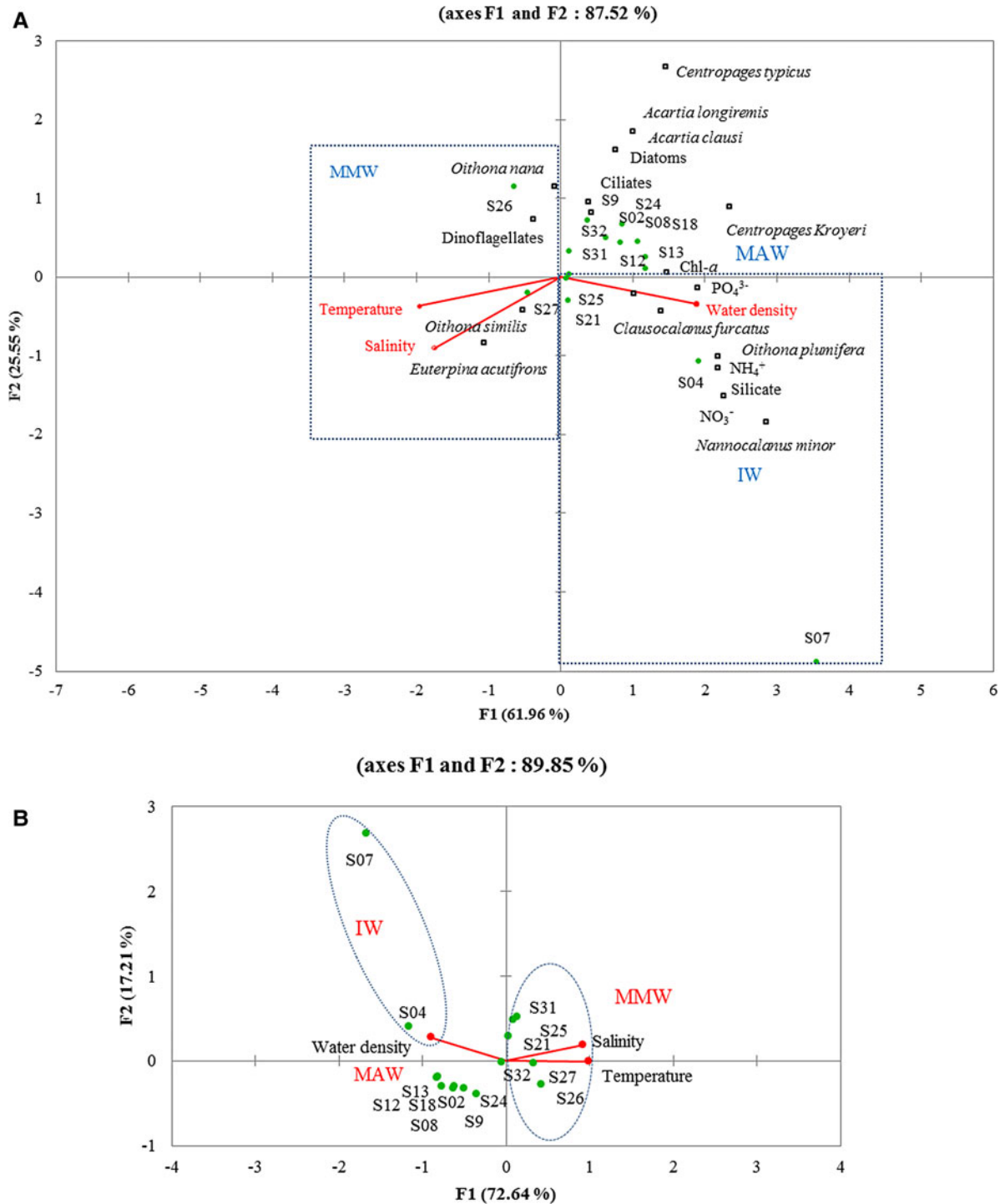


Fig. 10. Canonical Correspondence Analysis applied on the biomass of phytoplankton, ciliates, the abundance of copepod orders and the most dominant copepod species (A) and between stations and physical parameters (B) during a summer cruise in June 2008 in the Gulf of Gabes.

Copepod communities: dominance of small copepods in the MMW in the inshore area and in the MAW in the offshore area

During this summer cruise, small copepods, particularly oithonids, were found to largely dominate copepod communities in both MMW and MAW. This appears to be a common feature in the neritic region of the Gulf of Gabes intruded by the MMW, as it was also reported in four previous cruises

(July 2005, May–June 2006, September 2006 and March 2007) by Drira *et al.* (2014). During these cruises, as well as what was observed during our study, oithonids recorded very high abundances with *O. similis* (10^3 to $>10^5$ ind m^{-3}) and *O. nana* (10^4 to $>10^5$ ind m^{-3}) being the most abundant species. The dominance of small copepods, particularly oithonids, in warm and salty coastal waters (similar to the MMW) has also been reported in the north of Tunisia (bay of Tunis; Daly Yahia *et al.*, 2004) and on the Algerian coast (Hafferssas

& Seridji, 2010) as well as in other sites all over the Mediterranean: the Balearic Sea (Fernandez de Puelles *et al.*, 2003), the bay of Toulon (Jamet *et al.*, 2005), the Gulf of Naples (Mazzocchi & Ribera d'Alcalà, 1995), the Adriatic Sea (Vidjak *et al.*, 2007), the Aegean Sea (Zervoudaki *et al.*, 2007) and the Northern Levantine basin (Uysal & Shmeleva, 2012). Most of these studies reported a very high contribution of small copepods (>80%) to the copepod community, comparable to our results (93% in the MMW).

Oithona similis has been recognized as the most ubiquitous copepod species in the world ocean (Gallienne & Robins, 2001). It was reported to record very high densities in the neritic temperate seas. This may explain its prevalence in the Gulf of Gabes as a semi-arid Mediterranean site (Nakamura & Turner, 1997). This small cyclopoid revealed clear eurythermal and euryhaline distribution. In fact, the abundance of *O. similis* was positively correlated with temperature ($r = 0.712$; $N = 71$; $P = 0.05$) and salinity ($r = 0.712$, $N = 71$, $P = 0.05$) explaining its abundance in this inshore region under the influence of salty and warm Mediterranean waters (MMW) (Bel Hassen *et al.*, 2008). In addition, this copepod is omnivorous feeding on phytoplankton, heterotrophic protists and naupliar stages of copepods, showing a preference for heterotrophic dinoflagellates and ciliates (Nakamura & Turner, 1997; Turner, 2004). Furthermore, this species revealed clear preference for motile over non-motile prey (Castellani *et al.*, 2008). In fact, *O. similis* selects ciliates to diatoms of similar size and shape (Castellani *et al.*, 2008). This goes hand in hand with our results in the Gulf of Gabes characterized by an obvious proliferation of dinoflagellates accounting for the most important part of phytoplankton biomass.

The small cyclopoid *O. nana* (0.48–0.8 mm) significantly contributed to total copepod abundance (23.49%) in the inshore region intruded by salty and warm MMW. It recorded high densities at the stations S32 and S27 located in the south of the Gulf of Gabes. This area is characterized by an arid climate accompanied by a higher temperature enhancing the development of this small Oithonidae (Drira *et al.*, 2014), also shown by a positive correlation with temperature ($r = 0.619$, $N = 71$, $P = 0.05$). *Oithona nana* exhibits a certain ability to endure the environmental perturbations relying on its low respiratory rate and omnivorous diet (Gallienne & Robins, 2001). Several studies proved that *O. nana* was able to proliferate in fluctuating ecosystems (Williams & Muxagata, 2006). The monitoring of the zooplankton communities and mainly of *O. nana* is considered as a useful biological indicator aiming to assess the evolution of marine ecosystems (Siokou-Frangou *et al.*, 1998). The semi-enclosed region of Gabes is subject to industrial discharge from cities (Gabes, Sfax), harbours and several chemical manufacturers. Transport of petrol through Skhira port may also be a source of pollution to the Gulf of Gabes as well as an uncontrolled phosphogypsum dumpsite. The link between phosphogypsum impact and the abundance of oithonids was shown in a previous study in the Gulf of Gabes (Rekik *et al.*, 2012).

In the open sea region of the Gulf of Gabes, where exchange of water masses is active and under the influence of the Atlantic, oithonid density declined significantly giving place to offshore copepod species. The copepod community there was characterized by lower abundance but higher diversity. The large calanoid *N. minor* dominated in this offshore region. In fact, this calanoid is omnivorous, feeding on small

phytoplankton and ciliates. It reveals a quick response when productivity in the water column increases by undergoing a rapid population expansion. Furthermore this copepod is able to maintain continuous reproduction, producing 2–5 generations/year (Ashjian & Wishner, 1993).

During our survey, the small calanoid *C. furcatus* proliferated well in the offshore region intruded by the MAW and IW. This widespread copepod species is considered as an indicator of temperate offshore waters (Fragopoulou & Lakkis, 1990). It has an epipelagic distribution above the thermocline (Paffenhöfer & Mazzocchi, 2003). Previous studies reported high summer and autumn densities of this small calanoid regardless of the low phytoplankton biomass in the Gulf of Naples (Ribera d'Alcalà *et al.*, 2004) and in the highly oligotrophic eastern Mediterranean (Siokou-Frangou *et al.*, 1997) confirming thus that this species is able to accomplish its metabolic needs even at a low autotrophic biomass. This was demonstrated by *in situ* feeding experiments conducted by Mazzocchi & Paffenhöfer (1998). These authors confirmed that *C. furcatus* is the only species of the genus *Clausocalanus* that inhabits epipelagic waters during summer confirming a preference for the warmer waters. However other species belonging to the same genus migrate towards deep layers below the thermocline (Peralba & Mazzocchi, 2004). Therefore *C. furcatus* showed a wider tolerance to the increasing temperature during summer stratification in the Gulf of Gabes.

What are the factors leading to the success of small planktonic copepods in the Gulf of Gabes?

Despite the intensive predation by diverse meroplankton larvae or by other holoplankton such as chaetognaths, appendicularians and large copepods, small planktonic copepods succeed in recuperating from losses caused by predation. In fact, these zooplankters are able to perform a successful reproductive strategy. Cyclopoids, harpacticoids, poecilostomatoids and some small calanoids are egg-carrying, while the majority of large calanoids are free spawning (Huys & Boxshall, 1991). This strategy was mainly encountered with cyclopoids in oligotrophic marine ecosystems (Satapoomin *et al.*, 2004). The advantage of the small species bearing egg sacs is to protect eggs against predators until they hatch and produce nauplii. Therefore they reduce the mortality rate by generating a higher number of juveniles (Zervoudaki *et al.*, 2007). In addition it was shown that egg viability of small egg-carrying copepods was roughly conserved after fish larval gut passage (Saint-Jean & Pagano, 1995). This agrees with the advantage of egg-carrying copepods in coastal waters under strong predation pressure by fish larvae and juveniles. In the Gulf of Gabes, where fish larvae are very abundant in relation to active fishery (65% of the national fish production; Commissariat Général des Pêches, 1996), this reproductive strategy, by lowering the effects of predation by fish larvae, should favour the dominance of small egg-carrying copepods in the neritic waters.

It is evident that certain small copepods behave as predators of heterotrophic and mixotrophic protists rather than of autotrophic phytoplankton (Paffenhöfer, 1998; Turner, 2000). This is the case of *Acartia* adults (Gifford & Dagg, 1988), *Oithona* (Graneli & Turner, 2002), *Paracalanus* (Suzuki *et al.*, 1999) and even nauplii of *Calanus* spp. (Turner *et al.*, 2001). The small fractions, mainly developmental stages, were revealed

to feed on bacterioplankton while adult copepods are not able to consume picoplankton due to its very small size (Roff *et al.*, 1995). They are both carnivorous and detritivorous, preying upon other mesozooplankton and organic aggregates. Poecilostomatoids such as *Corycaeus* species are described as predators of copepod nauplii (Landry *et al.*, 1985). Omnivorous diet of small copepods belonging to the genera *Paracalanus*, *Acartia*, *Oncaea*, *Corycaeus* and *Oithona* was also deduced from the contents of their faecal pellets including diatom frustules, dinoflagellate thecae and tintinnid loricae (Turner, 1991). Zervoudaki *et al.* (2007) highlighted the combined influence of low metabolic needs and omnivorous diet (based on phytoplankton, heterotrophic flagellates and ciliates) in sustaining the high production of small copepods in the northern Aegean Sea.

Tolerance to heavy pollution, as observed in the Gulf of Gabes, may also explain the high proliferation of oithonid species such as *O. nana*, as observed in the Bay of Toulon (north-west Mediterranean) by Jamet *et al.* (2001) who suggested that this species may be used as a biological indicator of such perturbed systems.

The adoption of a successful reproductive strategy combined with an omnivorous diet, lower metabolic needs and tolerance to pollution (*O. nana*) are certainly behind the prominence of small planktonic copepods in the oligotrophic waters of the Gulf of Gabes.

Copepods as indicators of water masses exchange

In addition to their role in the marine pelagic food web, planktonic copepods have been regarded as good indicators of water masses exchange (Hsieh *et al.*, 2004). In fact, the strait of Gibraltar is a natural aperture that connects the Mediterranean Sea to the Atlantic Ocean. Seven invasive Atlantic copepod species (*Calocalanus contractus*, *C. tenuis*, *Acartia bifilosa*, *A. tonsa*, *Corycaeus amazonicus*, *Metacalanus inaequicornis* and *Pachos tuberosum*) were recorded mainly in the offshore region of the Gulf of Gabes showing that hydrology and water masses exchange are certainly influenced by the Atlantic Tunisian Current.

CONCLUSION

The summer spatial distribution of zooplankton in the Gulf of Gabes revealed the prevalence of small planktonic copepods. The latter benefited from the remarkable dominance of heterotrophic microplankton, mainly dinoflagellates and tintinnids. Small oithonids such as *Oithona similis* and *O. nana* revealed very high densities in the inshore region intruded by salty and warm MMW. The MAW was also distinguished by the prevalence of small planktonic copepods such as *Oithona nana* and *Clausocalanus furcatus*. However, the large calanidae *Nannocalanus minor* dominated in the deep offshore region characterized by the presence of IW. The propagation of the Atlantic waters off the Gulf of Gabes was followed by the presence of invasive copepod species.

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REFERENCES

- Aboud-Abi Saab M. (2008) *Tintinnids of the Lebanese coastal waters (Eastern Mediterranean)*. Lebanon: CNRS-Lebanon/UNEP/MAP/RAC/SPA.
- Agawin N.S.R., Duarte C. and Agustí S. (2000) Nutrient and temperature control of the contribution of picoplankton to phytoplankton biomass and production. *Limnology and Oceanography* 45, 591–600.
- Alder V.A. (1999) Tintinninoidea. In Boltovskoy D. (ed.) *South Atlantic zooplankton*. Leiden: Backhuys Publishers, pp. 321–384.
- Ashjian C.J. and Wishner K.F. (1993) Temporal and spatial changes in body size and reproductive state of *Nannocalanus minor* (Copepoda) females across and along the Gulf Stream. *Journal of Plankton Research* 15, 67–98.
- Beaugrand G. and Ibanez F. (2004) Monitoring marine plankton ecosystems. II: Long-term changes in North Sea calanoid copepods in relation to hydro-climatic variability. *Marine Ecology Progress Series* 284, 35–47.
- Beaugrand G., Ibanez F., Lindley J.A. and Reid P.C. (2002) Diversity of calanoid copepods in the North Atlantic and adjacent seas: species associations and biogeography. *Marine Ecology Progress Series* 232, 179–195.
- Bel Hassen M., Drira Z., Hamza A., Ayadi H., Akrouf F. and Issaoui H. (2008) Summer phytoplankton pigments and community composition related to water mass properties in the Gulf of Gabes. *Estuarine Coastal and Shelf Science* 77, 645–656.
- Bel Hassen M., Drira Z., Hamza A., Ayadi H., Akrouf F., Messaoudi S., Issaoui H., Aleya L. and Bouaïn A. (2009) Phytoplankton dynamics related to water mass properties in the Gulf of Gabes: ecological implications. *Estuarine Coastal and Shelf Science* 75, 216–226.
- Ben Ismail S., Sammari C., Gasparini G.P., Béranger K., Brahim M. and Aleya L. (2012) Water masses exchanged through the Channel of Sicily: evidence for the presence of new water masses on the Tunisian side of the Channel. *Deep-Sea Research (Part I, Oceanographic Research Papers)* 63, 65–81.
- Bonnet D. and Frid C. (2004) Seven copepod species considered as indicators of water-mass influence and changes: results from a Northumberland coastal station. *ICES Journal of Marine Science* 61, 485–491.
- Bourrelly P. (1985) *Les Algues d'eau douce. Initiation à la systématique. Tome II. Les Algues bleues et rouges. Les Euglénins, Peridiniens et Cryptomonadines*. Paris: Société Nouvelle des Editions Boubée.
- Bradford-Grieve J.M., Markhaseva E.L., Rocha C.E.F. and Abiahy B. (1999) Copepoda. In Boltovskoy D. (ed.) *South Atlantic zooplankton*. Leiden: Backhuys Publishers, pp. 869–1098.

- Calbet A. (2008) The trophic roles of microzooplankton in marine systems. *ICES Journal of Marine Science* 65, 325–331.
- Calbet A., Landry M.R. and Scheinberg R.D. (2000) Copepod grazing in a subtropical bay: species-specific responses to a midsummer increase in nanoplankton standing stock. *Marine Ecology–Progress Series* 193, 75–84.
- Calbet A. and Saiz E. (2005) The ciliate-copepod link in marine ecosystems. *Aquatic Microbial Ecology* 38, 157–167.
- Commissariat Général des Pêches (1996) Annuaire des statistiques des pêches en Tunisie. Tunis: Ministère de l'agriculture.
- Castellani C., Irigoien X., Mayor D.J., Harris R.P. and Wilson D. (2008) Feeding of *Calanus finmarchicus* and *Oithona similis* on the microplankton assemblage in the Irminger Sea, North Atlantic. *Journal of Plankton Research* 30, 1095–1116.
- Champalbert G. (1996) Characteristics of zooplankton standing stock and communities in the Western Mediterranean Sea: relations to hydrology. *Scientia Marina* 60, 97–113.
- Daly Yahia M.N., Souissi S. and Daly Yahia Kefi O. (2004) Spatial and temporal structure of planktonic copepods in the Bay of Tunis (south-western Mediterranean Sea). *Zoological Studies* 43, 366–375.
- Dodge J.D. (1985) *Atlas of dinoflagellates. A scanning electron microscope survey*. London: Farrand Press.
- Drira Z., Bel Hassen M., Ayadi H. and Aleya L. (2014) What factors drive copepod community distribution in the Gulf of Gabes, Eastern Mediterranean Sea? *Environmental Science and Pollution Research* 4, 2918–2934.
- Fernandez de Puelles M.L., Gras D. and Hernandez Leon S. (2003) Annual cycle of zooplankton biomass, abundance and species composition in the neritic area of the Balearic Sea, Western Mediterranean. *Marine Ecology Pubblicazioni Della Stazione Zoologica Di Napoli I* 24, 123–139.
- Fragopoulou N. and Lakkis J. (1990) Vertical distribution and nocturnal migration of zooplankton in relation to the development of the seasonal thermocline in Patraikos Gulf. *Marine Biology* 104, 381–387.
- Furnestin M.L. (1968) Le zooplancton de la Méditerranée (Bassin occidental). Essai de synthèse. *Journal du Conseil/Conseil Permanent International pour l'Exploration de la Mer* 32, 25–69.
- Furnestin M.L. (1979) Aspects of the zoogeography of the Mediterranean plankton. In van der Spoel S. and Pierrot-Bults A.C. (eds) *Zoogeography and diversity of plankton*. New York, NY: Halsted Press (Wiley), pp. 191–253.
- Gallienne C.P. and Robins D.B. (2001) Is *Oithona* the most important copepod in the world's oceans? *Journal of Plankton Research* 23, 1421–1432.
- Gifford D.J. and Dagg M.J. (1988) Feeding of the estuarine copepod *Acartia tonsa* Dana: carnivory vs herbivory in natural microplankton assemblages. *Bulletin of Marine Science* 43, 458–468.
- Gifford D.J. and Dagg M.J. (1991) The microzooplankton-mesozooplankton link: consumption of planktonic protozoa by the calanoid copepods *Acartia tonsa* Dana and *Neocalanus plumchrus* Murukawa. *Aquatic Microbial Ecology* 5, 161–177.
- Gómez F. and Gorsky G. (2003) Annual microplankton cycles in Villefranche Bay, Ligurian Sea, NW Mediterranean. *Journal of Plankton Research* 25, 323–339.
- Graneli E. and Turner J.T. (2002) Top-down regulation in ctenophore-copepod-ciliate-diatom-phytoflagellate communities in coastal waters: a mesocosm study. *Marine Ecology Progress Series* 239, 57–68.
- Hafferssas A. and Seridji R. (2010) Relationships between the hydrodynamics and changes in copepod structure on the Algerian coast. *Zoological Studies* 49, 353–366.
- Hannachi I., Drira Z., Belhassen M., Hamza A., Ayadi H. and Bouain A. (2008) Abundance and biomass of the ciliate community during a spring cruise in the Gulf of Gabès. *Acta Protozoologica* 47, 293–305.
- Hattour M.J., Sammari C. and Ben Nassrallah S. (2010) Hydrodynamics of the Gulf of Gabes deduced from the observations of currents and water levels. *Revue Paralia*, 3, 1–12.
- Hsieh C.H., Chiu T.S. and Shih C.T. (2004) Copepod diversity and composition as indicators of intrusion of the Kuroshio Branch Current into the northern Taiwan Strait in spring 2000. *Zoological Studies* 43, 393–403.
- Huys R. and Boxshall G.A. (1991) Copepod evolution. *Royal Society Publication* 159, 1–468.
- Jamet J.-L., Bogé G., Richard S., Geneys C. and Jamet D. (2001) The zooplankton community in bays of Toulon area (northwest Mediterranean Sea, France). *Hydrobiologia* 457, 155–165.
- Jamet J.L., Jean N., Bogé G., Richard S. and Jamet D. (2005) Plankton succession and assemblage structure in two neighbouring littoral ecosystems in the north-west Mediterranean Sea. *Marine and Freshwater Research* 56 (1), 69–83.
- Jeong H.J., Yoo Y.D., Kim J.S., Seong K.A., Kang N.S. and Kim T.H. (2010) Growth, feeding and ecological roles of the mixotrophic and heterotrophic dinoflagellates in marine planktonic food webs. *Ocean Science Journal* 45, 65–91.
- Kiorboe T. (2011) What makes pelagic copepods so successful? *Journal of Plankton Research* 33, 677–685.
- Landry M.R., Lehner Fournier J.M. and Fagerness V.L. (1985) Predatory feeding behavior of the marine cyclopoid copepod *Corycaeus anglicus*. *Marine Biology* 85, 163–169.
- Lasternas S., Tunin-Ley A., Ibanez F., Andersen V., Pizay M.D. and Lemée R. (2011) Short-term dynamics of microplankton abundance and diversity in NW Mediterranean Sea during late summer conditions (DYNAPROC 2 cruise; 2004). *Biogeosciences*, 8, 743–761.
- Mazzocchi M.G. and Paffenhöfer G.A. (1998) First observations on the biology of *Clausocalanus furcatus* (Copepoda, Calanoida). *Journal of Plankton Research* 20, 331–342.
- Mazzocchi M.G. and Ribera d'Alcala M. (1995) Recurrent patterns in zooplankton structure and succession in a variable coastal environment. *ICES Journal of Marine Science* 52, 679–691.
- Menden-Deuer S. and Lessard E.J. (2000) Carbon to volume relationships for dinoflagellates, diatoms, and other protist plankton. *Limnology and Oceanography* 45, 569–579.
- Nakamura Y. and Turner J.T. (1997) Predation and respiration by the small cyclopoid copepod *Oithona similis*: how important is feeding on ciliates and heterotrophic flagellates? *Journal of Plankton Research* 19, 1275–1288.
- Nowaczyk A., Carlotti F., Thibault-Botha D. and Pagano M. (2011) Distribution of epipelagic metazooplankton across the Mediterranean Sea during the summer BOUM cruise. *Biogeosciences* 8, 2159–2177.
- Paffenhöfer G.A. (1998) Heterotrophic protozoa and small metazoa: feeding rates and prey-consumer interactions. *Journal of Plankton Research* 20, 121–133.
- Paffenhöfer G.A. and Mazzocchi M.G. (2003) Vertical distribution of subtropical epipelagic copepods. *Journal of Plankton Research* 25, 1139–1156.
- Peralba A. and Mazzocchi M.G. (2004) Vertical and seasonal distribution of eight *Clausocalanus* species (Copepoda: Calanoida) in oligotrophic waters. *ICES Journal of Marine Science* 61, 645–653.
- Poulain P. and Zambianchi E. (2007) Near surface circulation in the central Mediterranean Sea as deduced from Lagrangian drifters in the 1990s. *Continental Shelf Research* 27, 981–1001.

- Putt M. and Stoecker D.K.** (1989) An experimentally determined carbon: volume ratio for marine oligotrichous ciliates from estuarine and coastal waters. *Limnology and Oceanography* 34, 1097–1104.
- Rekik A., Drira Z., Guermazi W., Elloumi J., Maalej S., Aleya L. and Ayadi H.** (2012) Impacts of an uncontrolled phosphogypsum dumpsite on summer distribution of phytoplankton, copepods and ciliates in relation to abiotic variables along the near-shore of the southwestern Mediterranean coast. *Marine Pollution Bulletin* 64, 336–346.
- Ribera d'alcalá M., Conversano F., Corato F., Licandro P., Mangoni O., Marino D., Mazzocchi M.G., Modigh M., Montresor M., Nardella M., Saggiomo V., Sarno D. and Zingone A.** (2004) Seasonal patterns in plankton communities in a pluriannual time series at an inshore Mediterranean site (Gulf of Naples): an attempt to discern recurrences and trends. *Scientia Marina* 68, 65–83.
- Richardson A.J.** (2008) In hot water: zooplankton and climate change. *ICES Journal of Marine Science* 65, 279–295.
- Roff J.C., Turner J.T., Webber M.K. and Hopcroft R.R.** (1995) Bacterivory by tropical copepod nauplii: extent and possible significance. *Aquatic Microbial Ecology* 9, 165–175.
- Rose M.** (1933) Copépode pélagiques. In *Faune de France* 26. Paris: Office Central de Faunistique, pp. 372.
- Ross O.N. and Sharples J.** (2007) Phytoplankton motility and the competition for nutrients in the thermocline. *Marine Ecology Progress Series* 347, 21–38.
- Saint Jean L. and Pagano M.** (1995) Egg mortality through predation in egg-carrying zooplankters. Studies on *Heterobranchius longifilis* larvae fed on copepods, cladocerans and rotifers. *Journal of Plankton Research* 17, 1501–1512.
- Sammari C., Koutitonsky V.G. and Moussa M.** (2006) Sea level variability and tidal resonance in the Gulf of Gabes, Tunisia. *Continental Shelf Research* 26, 338–350.
- Sammari C., Millot C., Taupier-Letage I., Stefani A. and Brahim M.** (1999) Hydrological characteristics in the Tunisia–Sardinia–Sicily area during spring 1995. *Deep-Sea Research (Part I, Oceanographic Research Papers)* 46, 1671–1703.
- Satapoomin S., Nielsen T.G. and Hansen P.J.** (2004) Andaman Sea copepods: spatio-temporal variations in biomass and production, and role in the pelagic food web. *Marine Ecology Progress Series* 274, 99–122.
- Shannon C.E. and Weaver G.** (1949) *The mathematical theory of communication*. Urbana, IL: University of Illinois Press.
- Sherr E.B. and Sherr B.F.** (2007) Heterotrophic dinoflagellates: a significant component of microzooplankton biomass and major grazers of diatoms in the sea. *Marine Ecology Progress Series* 352, 187–197.
- Siokou-Frangou I., Bianchi M., Christaki U., Christou E.D., Giannakourou A., Gotsis O., Ignatiades L., Pagou K., Pitta P., Psarra S., Souvermezoglou E., Van Wambeke F. and Zervakis V.** (2002) Carbon flow in the planktonic food web along a gradient of oligotrophy in Aegean Sea (Mediterranean Sea). *Journal of Marine Systems* 33, 335–353.
- Siokou-Frangou I., Christou E.D., Fragopoulou N. and Mazzocchi M.G.** (1997) Mesozooplankton distribution from Sicily to Cyprus (Eastern Mediterranean) .1. General aspects - .2. Copepod assemblages. *Oceanologica Acta* 20, 537–548.
- Siokou-Frangou I., Papatheassiou E., Lepretre A. and Frontier S.** (1998) Zooplankton assemblages and influence of environmental parameters on them in a Mediterranean coastal area. *Journal of Plankton Research* 20, 847–870.
- Strüder-Kypke M.C. and Montagnes D.J.S.** (2002) Development of web based guides to planktonic protists. *Aquatic Microbial Ecology* 27, 203–207.
- Suzuki K., Nakamura Y. and Hiromi J.** (1999) Feeding by the small calanoid copepod *Paracalanus* sp. on heterotrophic dinoflagellates and ciliates. *Aquatic Microbial Ecology* 17, 99–103.
- Tiselius P., Saiz E. and Kjørboe T.** (2013) Sensory capabilities and food capture of two small copepods, *Paracalanus parvus* and *Pseudocalanus* sp. *Limnology and Oceanography* 58, 1657–1666.
- Tomas C.R.** (1996) *Identifying marine phytoplankton*. San Diego, CA: Academic Press.
- Tregouboff G. and Rose M.** (1957) *Manuel de planctologie méditerranéenne*. Paris: Centre National de la Recherche Scientifique, vol. 1, 587 pp.; vol. 2, 207 pls.
- Turner J.T.** (1991) Zooplankton feeding ecology: do co-occurring copepods compete for the same food? *Reviews in Aquatic Sciences* 5, 101–195.
- Turner J.T.** (2000) Feeding ecology of marine copepods: an overview of recent studies and emerging issues. Proceedings of the International Symposium on Marine Biology in Taiwan- Crustacean and Zooplankton Taxonomy, Ecology and Living Resources, 26–27 May 1998. *National Taiwan Museum Special Publication Series* 10, 37–57.
- Turner J.T.** (2004) The importance of small planktonic copepods and their roles in pelagic marine food webs. *Zoological Studies* 43, 255–266.
- Turner J.T., Levensen H., Nielsen T.G. and Hansen B.W.** (2001) Zooplankton feeding ecology: grazing on phytoplankton and predation on protozoans by copepod and barnacle nauplii in Disko Bay, West Greenland. *Marine Ecology Progress Series* 221, 209–219.
- Uysal Z. and Shmeleva A.A.** (2012) Species composition, abundance and biomass of copepoda in plankton of the Northern Levantine basin (Eastern Mediterranean Sea). *Crustaceana* 85, 909–935.
- Vidjak O., Bojanic N., Kuspilic G., Gladan Z.N. and Ticina V.** (2007) Zooplankton community and hydrographical properties of the Neretva channel (eastern Adriatic Sea). *Helgoland Marine Research* 61, 267–282.
- Williams J.A. and Muxagata E.** (2006) The seasonal abundance and production of *Oithona nana* (Copepoda : Cyclopoida) in Southampton Water. *Journal of Plankton Research* 28, 1055–1065.
- and
- Zervoudaki S., Christou E.D., Nielsen T.G., Siokou Frangou I., Assimakopoulou G., Giannakourou A., Maar M., Pagou K., Krasakopoulou E., Christaki U. and Moraitou Apostolopoulou M.** (2007) The importance of small-sized copepods in a frontal area of the Aegean Sea. *Journal of Plankton Research* 29, 317–338.

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