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REVIEW ARTICLE

Diversity and distribution of gelatinous zooplankton in the Southwestern Mediterranean Sea

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Abstract

Gelatinous zooplankton species composition, distribution and abundance were investigated in the bay and the lagoon of Bizerte (North Tunisian coast) from January 2004 to December 2005. In total, 48 species were identified in the study area: 24 medusae, 11 siphonophores, four appendicularians, six chaetognaths, two pteropods and one doliolid. The hydromedusa *Eutima mira* was recorded for the first time in the Western Mediterranean Sea. The diversity in the Bay of Bizerte was greater than the diversity in the Bizerte lagoon. There was a loss of species diversity. Siphonophores were the most sensitive group to anthropogenic discharge. Only two species of siphonophores were recorded in the lagoon. Four species of gelatinous zooplankton, *Muggiaea kochi*, *Lensia conoidea*, *Oikopleura longicauda* and *Podocorynoides minima* were the most frequent species in the lagoon and may benefit from eutrophication. Appendicularians were numerically the most dominant group in the bay and the lagoon of Bizerte. Mesozooplankton density declined significantly in autumn and winter of 2004 and 2005 in relation to the dense aggregations of the scyphomedusae *Pelagia noctiluca*. Statistical analysis divided the study area into three zones: lagoon zone, bay zone and channel zone.

Introduction

Gelatinous animals have long been known to be widespread inhabitants of the world's oceans (Pugh 1975; Gamulin & Krsinie 1993). The gelatinous component of plankton 'mysteriously' appears (and disappears) at unpredictable times and is usually considered to represent the dark side of ecology (Benovic *et al.* 1987; Boero & Mills 1997; Graham *et al.* 2001). Although the role of gelatinous plankton is attracting increasing attention, the bulk of scientific literature has focused on phytoplankton, crustacean zooplankton and their relationships.

Gelatinous zooplankton represent one of the driving forces of marine ecosystems. Their components undergo seasonal pulses in response to favourable conditions and rapidly produce biomass that sustains the marine food chain (Boero *et al.* 2008).

Gelatinous filter feeders play a key role in the rapid transfer of energy toward higher trophic levels through the filtering of large quantities of nanoplankton and picoplankton (Flood *et al.* 1992; Deibel 1998; Gorsky & Fenaux 1998; Hopcroft & Roff 1998; Hopcroft *et al.* 1998). Due to their fast sinking rate, fecal pellets of salps and the houses of appendicularians may transfer a significant amount of organic matter from the surface down to the benthic compartment during the productive season (Bone 1998). Gelatinous carnivores may substantially affect pelagic food webs by exerting top–down control on their ecosystems (Deason & Smayda 1982; Greve 1994).

These organisms play an important role in zooplankton structure and dynamics due to the heavy impact of their predatory activity (Matsakis & Conover 1991; Purcell 1997). When abundant, gelatinous predators can have profound effects on the plankton community through direct predation and competition for food (Behrends & Schneider 1995; Matsakis & Conover 1991; Nicholas & Frid 1999; Malacic *et al.* 2007; Doyle *et al.* 2008) as well as cascading trophic effects (Verity & Smetacek 1996).

Gelatinous carnivores are ubiquitous in coastal ecosystems and can prey voraciously on zooplankton and ichthyoplankton (Suchman *et al.* 2008). Their potential importance as both predators and competitors of fish is of particular interest to humans (Purcell & Arai 2001 Brodeur *et al.* 2002; Sabates *et al.* 2010).

Recent studies show a steady increase in the population of gelatinous organisms in diverse marine areas (Mills 2001; Brodeur *et al.* 2002; Richardson *et al.* 2009; Touzri *et al.* 2010). Swarms of plankton medusae may interfere with fisheries by clogging fishing nets and can impact tourism negatively by causing medical problems for swimmers (Burnett 2001; Purcell *et al.* 2007).

Studies on gelatinous plankton are quite scarce in the Southwestern Mediterranean. However, some information on hydromedusae and scyphomedusae has been collected along the Tunisian coast of Bizerte (Addad *et al.* 2008; Touzri *et al.* 2010).

The aim of this study is to provide a comprehensive description of gelatinous zooplankton diversity, distribution and abundance, comparing seasonal dynamics in the bay and the lagoon of Bizerte (north coast of Tunisia).

Methods

Study area

Knowledge about the circulation in the Southwestern Mediterranean is restricted largely to the circulation of the surface Modified Atlantic Water (MAW) and the boundary currents (Millot 1987). This study took place off the North Tunisian coast (South Mediterranean) in the bay of Bizerte, which is under the influence of the MAW. The bay of Bizerte communicates with Bizerte lagoon through the channel of Bizerte (Fig. 1). The tidal regime of this area is dominated by a semi-diurnal cycle and is characterized by low amplitude that rarely reaches 15 cm during spring tide (Harzallah 2003). Although tidal activity is low in this region, the highest current velocities recorded in the middle of the channel can reach 1 m s^{-1} (Harzallah 2003). The survey was carried out from January 2004 to December 2005 in the stations indicated in Fig. 1.

Water and zooplankton sampling

Hydrological parameters such as temperature (°C) and salinity (psu) were measured from surface-water samples using a multiparameter WTW 340i probe. Monthly zooplankton samples were collected in the bay and the lagoon of Bizerte using a double WP2 net fitted with two

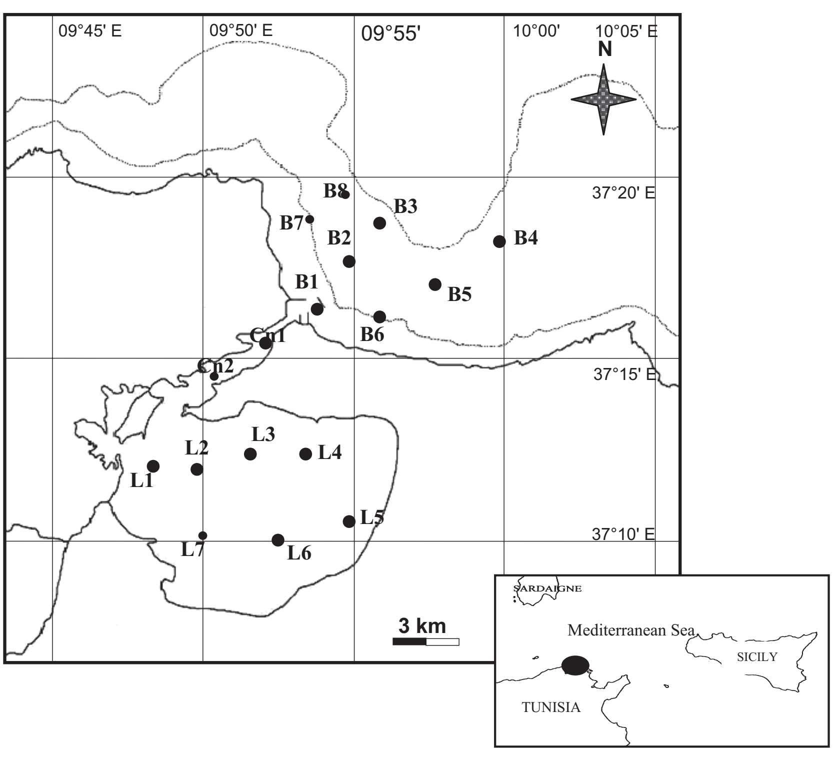

Fig. 1. Map of the study area showing the location of sampling stations in the bay and the lagoon of Bizerte.

mesh sizes (70 and 200 μm). For estimates of zooplankton density, oblique tows were taken from the bottom to the surface at each station; catches were pooled and preserved with buffered formaldehyde (2%) for further analysis. Only the gelatinous zooplankton were identified and counted.

Estimates of scyphomedusa density were obtained by counting the specimens collected in an estimated water volume of 1000 m^3 obtained by towing a hand net between 0 and 5 m depth from a small boat (6 m).

Statistical analyses

Multivariate statistical analyses were performed using PRIMER 5 software. Principal component analysis (PCA) was used to describe the relationships between species and environmental variables. Based on the abundance of the main species, multidimensional scaling ordination (MDS) was used to identify different groups of stations. Cluster analysis using complete linkage and Bray–Curtis similarity was used to separate different species assemblages. The analysis of similarities (ANOSIM) was used to test whether the assemblages were significantly different. The Shannon-Wiener index and Margalef index were used to investigate the changes in the diversity of the gelatinous zooplankton community.

Results

Environmental conditions

Sea surface temperature (SST) showed high values in the summer season and low values in the winter season for the 2 years of study, fluctuating between 13.85 and 26.25 °C in 2004 and between 11.05 and 28.28 °C in 2005 in Bizerte Bay. In the lagoon (including channel stations), temperature reached high values in the summer season: 27.61 °C in 2004 and 28.19 °C in 2005 (Fig. 2A).

In the bay, sea surface salinity (SSS) ranged from 34.48 psu in winter to 37.81 psu in summer 2004. In 2005, values varied from 36.33 to 37.77 psu. Values were lower in the lagoon than in the bay and fluctuated between 31.81 psu in winter and 37.71 psu in summer 2004, and between 36.47 and 37.38 psu in 2005 (Fig. 2B).

Salinity varied significantly between the winter and summer seasons in the bay and the lagoon and these variations are probably influenced by fresh water recharge from rivers into the lagoon.

Overall Chl-*a* concentrations were significantly different between the sites (bay and lagoon) and reflected the direct effect of anthropogenic eutrophication on the lagoon. The Chl-*a* concentrations in the bay ranged between 0.67 and 2.4 $\mu g \cdot l^{-1}$. In the lagoon, three peaks of Chl-*a* concentration occurred during the autumn, spring

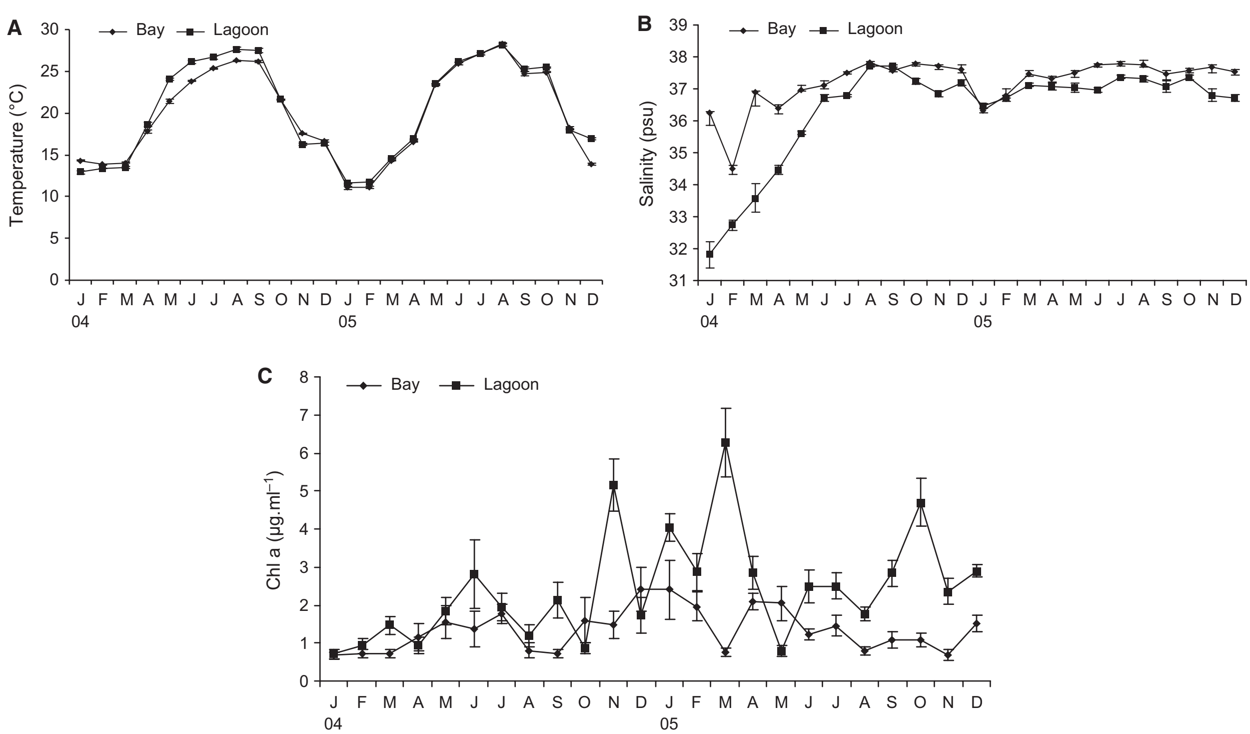

Fig. 2. Monthly evolution of sea surface temperature (A), salinity (B) and Chl-*a* concentration (C) in the bay and the lagoon of Bizerte.

and summer seasons. The highest value was observed in the lagoon in early spring 2005 (6.27 $\mu g \cdot l^{-1}$); this could be the result of phytoplankton growth in the lagoon (Fig. 2C). The increase of Chl-*a* concentrations in the lagoon is related to the increase of nutrients (N and P) released from anthropogenic discharge.

The lagoon showed a high influx of nutrients. Nitrates fluctuated between 1.54 μM in June and 20.11 μM in October 2004 and reached 43.01 μM in the bay in February 2005. In the lagoon, concentrations were higher in the winter season and reached 32.58 μM in January 2004, 79.46 μM in January 2005 and 49.94 μM in February 2005 as a result of anthropogenic discharge and fresh water outflow from rivers (Fig. 3A). Phosphate concentrations were also high in the lagoon, especially in the summer season of 2004 and 2005, 15.49 and 18.81 μM, respectively (Fig. 3B), related to the high summer temperature. However, in 2005, concentrations fluctuated between 2.25 and 3.63 μM in the lagoon. The highest concentration of ammonia was recorded in the lagoon (19.88 μM) in October 2004 (Fig. 3C).

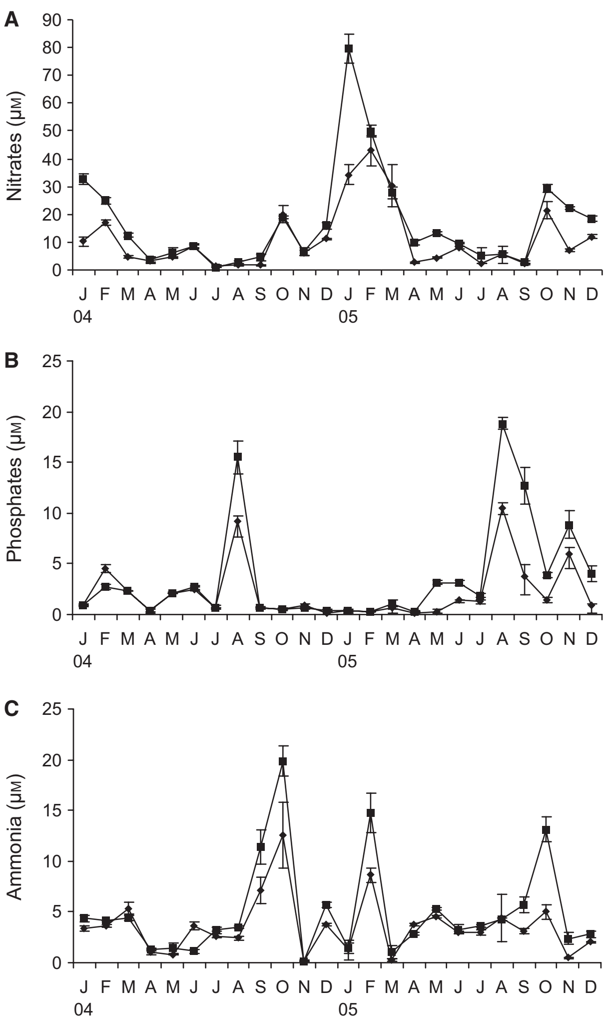

Fig. 3. Monthly fluctuation of nutrients in the bay and the lagoon of Bizerte (A: nitrates; B: phosphates; C: ammonia).

Abundance and distribution of gelatinous zooplankton

The group with the highest contribution to total abundance was Appendicularians (up 95% in the bay and the lagoon of Bizerte) (Fig. 4). These were more dominant in the bay (Table 1). Chaetognaths were less represented in the bay and the lagoon; maximum densities of 17.58 and 5.31 $ind \cdot m^{-3}$ respectively were recorded in the bay in March 2004 and in the lagoon in August 2004 (Fig. 5). The highest medusa density was recorded in the lagoon of Bizerte in July 2004 (Fig. 5). Siphonophores showed higher abundance in winter season in the bay (January 2004 and 2005): 8 and 10 $ind \cdot m^{-3}$ respectively; in the lagoon, the density was very low (3.47 $ind \cdot m^{-3}$ in January

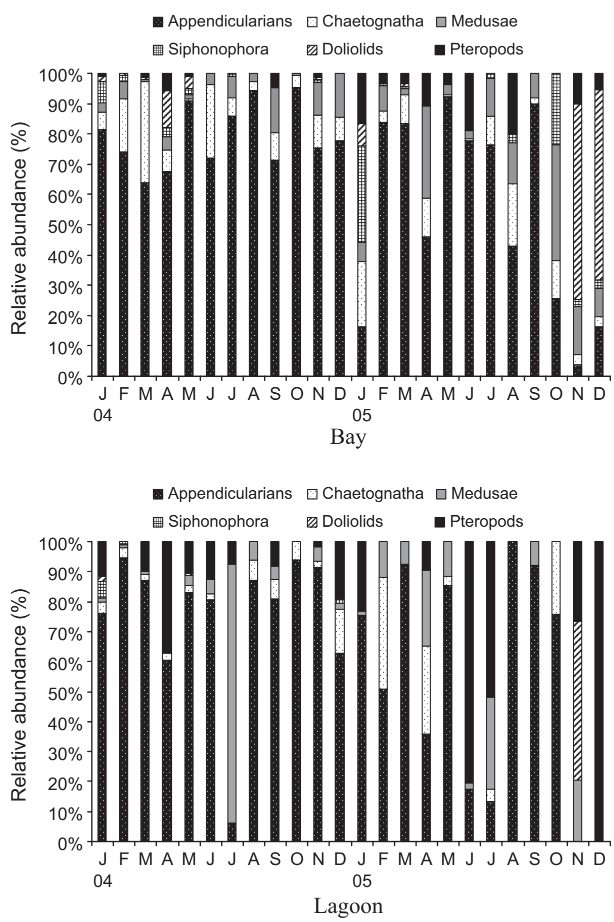

Fig. 4. Percentage contribution of each gelatinous zooplankton group to total abundance in the bay and the lagoon of Bizerte.

Table 1. Seasonal abundance of the different gelatinous groups.

Groups	Winter 2004	Spring 2004	Summer 2004	Autumn 2004	Winter 2005	Spring 2005	Summer 2005	Autumn 2005
Appendicularians								
Bay	89.6 ± 38.9	320.6 ± 89.86	80.8 ± 32.5	93.3 ± 71.5	34.3 ± 13.1	64.3 ± 24.5	110.1 ± 42	37.3 ± 14.2
Lagoon	50.7 ± 16.9	94 ± 31	14.2 ± 4.7	64 ± 21	18.3 ± 6.3	6.2 ± 2.1	2.8 ± 0.9	1.3 ± 0.4
Chaetognaths								
Bay	6.4 ± 2.4	17.6 ± 6.7	7.5 ± 2.8	10.6 ± 4	6.8 ± 2.6	7.3 ± 2.8	13.7 ± 5.2	13.1 ± 4.9
Lagoon	2.3 ± 0.8	2.5 ± 0.8	1.1 ± 0.4	5.3 ± 1.8	2.1 ± 0.7	5 ± 1.7	0.84 ± 0.2	0.2 ± 0.09
Medusae								
Bay	3.1 ± 1.1	4.4 ± 1.6	4.6 ± 1.7	10.7 ± 4.1	3.5 ± 1.3	16.4 ± 6.3	18.1 ± 6.8	7.6 ± 2.9
Lagoon	1.1 ± 0.4	1.1 ± 0.4	63 ± 21	3.5 ± 1.2	0.66 ± 0.2	4.3 ± 1.4	6.8 ± 2.1	0.3 ± 0.09
Siphonophora								
Bay	8.1 ± 3.1	6.8 ± 2.6	0.6 ± 0.2	1.2 ± 0.4	10.1 ± 3.8	0.4 ± 0.1	2.3 ± 0.8	3.7 ± 1.4
Lagoon	3.5 ± 1.2	–	–	0.1 ± 0.05	–	–	–	–
Doliolids								
Bay	1.8 ± 0.4	14.9 ± 5.6	–	0.5 ± 0.2	2.3 ± 0.8	0.31 ± 0.1	–	30.8 ± 11.7
Lagoon	1.2 ± 0.4	0.16 ± 0.1	–	–	–	–	–	0.8 ± 0.2
Pteropods								
Bay	1.2 ± 0.4	5.6 ± 2.1	–	2.8 ± 1.1	5.25 ± 2	5.6 ± 2.1	13.9 ± 5.3	4.8 ± 1.86
Lagoon	7.7 ± 2.6	10.8 ± 3.6	5.5 ± 1.8	6.5 ± 2.2	5.6 ± 1.9	1.7 ± 0.8	10.8 ± 3.6	0.33 ± 0.1

2004) (Fig. 5). Doliolids were more abundant in the bay of Bizerte. Pteropods were dominant in the lagoon (Fig. 5).

Species composition

Altogether, 48 species of gelatinous zooplankton were identified (table 2): 24 medusae, 11 siphonophores, four appendicularians, six chaetognaths, one doliolid and two pteropods. In the bay, 48 species were recorded, whereas only 22 species were recorded in the lagoon.

The most common species were *Aglaura hemistoma*, *Rhopalonema velatum*, *Clytia* spp., *Eucheilota paradoxica, Obelia* spp., *Oikopleura longicauda*, *Oikopleura dioica*, *Eudoxoides spiralis*, *Sagitta setosa*, *Sagitta inflata* and *Limacina inflata*.

The diversity index was higher in the bay of Bizerte; the highest values were recorded in January, April and August 2005. The Shannon–Wiener index varied between 0.96 bits per individual and 2.52 bits per individual throughout the study period (Fig. 6). In the lagoon, the species richness was generally low and the diversity index did not exceed 1.7 bits per individual (Fig. 6).

In the bay of Bizerte, the largest number of species (24) was found in April 2004 and the lowest number (five) in December 2004. In the lagoon, the largest number of species (10) was observed in January 2004. Margalef's species richness index fluctuated between 5 and 1.96 in Bizerte Bay in 2004 and between 4.64 and 1.75 in 2005. In the lagoon, this index varied between 3.24 and 1.14 in 2004 and between 6.19 and 1.1 in 2005 (Fig. 6).

Abundance and distribution of the main species

The monthly fluctuation of the most frequent and abundant species of carnivorous zooplankton are presented in Fig. 7. The most abundant hydromedusae in the bay of Bizerte were *Aglaura hemistoma* and *Rhopalonema velatum*. *Aglaura hemistoma* peaked in July 2005 (16 ind$\cdot$m^{-3}), with a maximum in oceanic stations. In the lagoon, this species appeared sporadically and was generally less abundant than in the bay. *Rhopalonema velatum* was present throughout the year only in the bay, where it showed two peaks, one in April 2005 (6.5 ind$\cdot$m^{-3}) and one in December 2005 (6 ind$\cdot$m^{-3}) (Fig. 7). The scyphomedusa *Pelagia noctiluca* appeared in high numbers in winter and autumn; high densities of 552 and 512 ind$\cdot$1000 m^{-3} were observed in December 2004 and November 2005, respectively, in the bay of Bizerte. In the lagoon, densities of *Pelagia noctiluca* reached as high as 580 ind$\cdot$1000 m^{-3} in November 2005 (Fig. 7). The invasion of *P. noctiluca* might have affected the mesozooplankton density, which declined significantly and reached 342 ind$\cdot$m^{-3} (Fig. 7).

Podocorynoides minima with a maximum abundance of 63 ind$\cdot$m^{-3}, recorded in July 2004, was the only hydromedusa with high densities in the lagoon of Bizerte (Fig. 7).

Muggiaea kochi was the dominant calycophorae in the bay of Bizerte. It was more abundant in winter 2004 and 2005 (4.48 and 4.25 ind$\cdot$m^{-3}, respectively) (Fig. 7). The most abundant and frequent chaetognaths were *Sagitta setosa* and *Sagitta inflata. Sagitta setosa* appeared throughout the year and the maximum densities were observed in March 2004 and August 2005 (5 ind$\cdot$m^{-3}); however, three

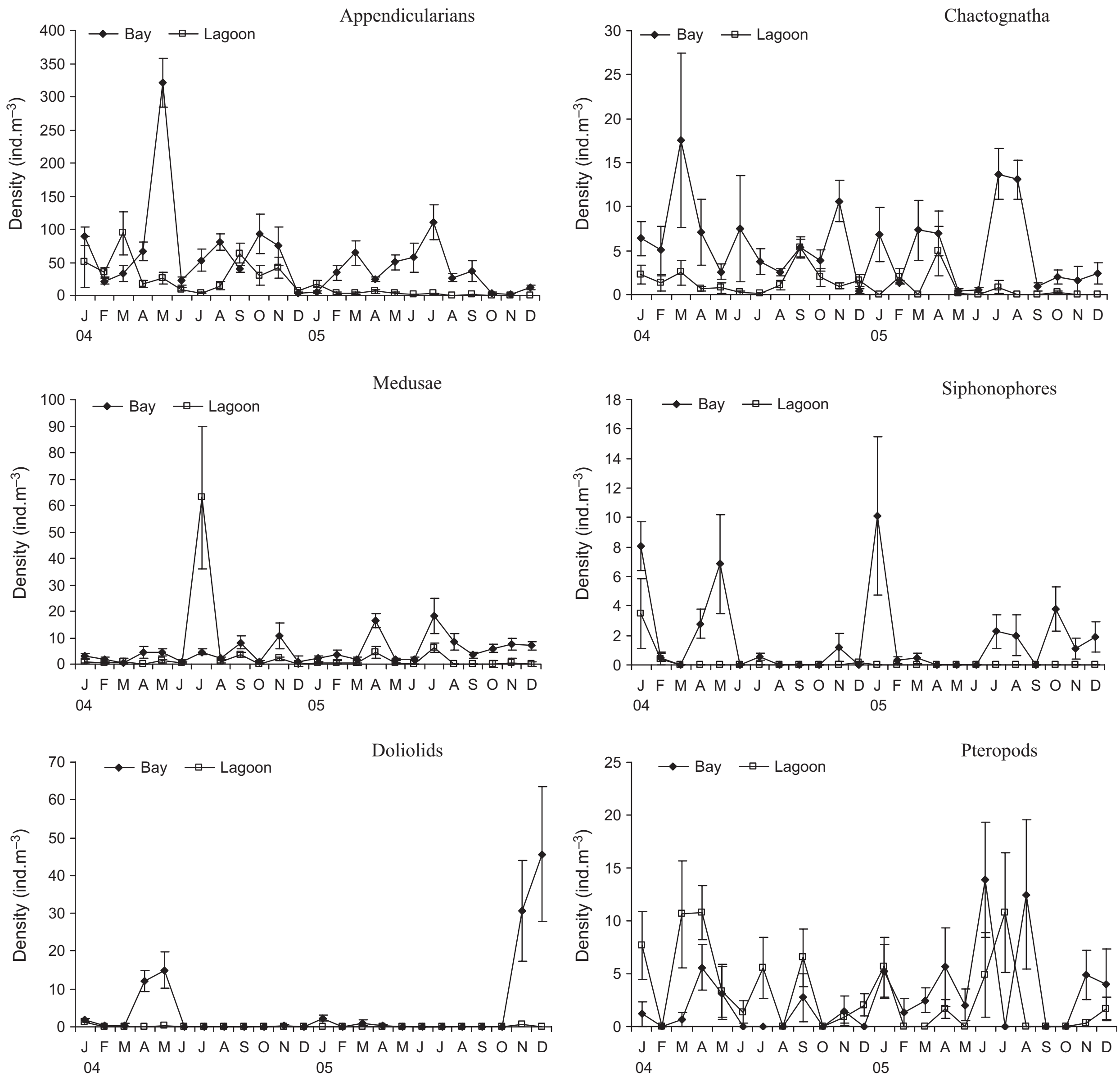

Fig. 5. Monthly fluctuation of gelatinous zooplankton group densities.

peaks were observed in the lagoon (Fig. 7). A high abundance of *Sagitta inflata* was found from January to December 2004, with a maximum of 10 ind·m^{-3} in March 2004. In the lagoon, this species was frequent throughout the year and predominant in April 2004.

Oikopleura longicauda was the most abundant species in the bay and the lagoon of Bizerte, the maximum density being recorded in the bay in spring (199 ind·m^{-3}) (Fig. 8). Pteropods were represented by two species: *Limacina inflata* and *Creseis acicula*. The two species occurred in high numbers in the bay and lagoon of Bizerte (Fig. 8).

Doliolum nationalis was more frequent and abundant in the bay of Bizerte than in the lagoon; the increase of this species in May 2004 (15 ind·m^{-3}) was followed by a rapid decrease. High densities were observed in November and December 2005: 31 and 46 ind·m^{-3}, respectively (Fig. 8).

Statistical analysis

Cluster analysis in the bay of Bizerte (Fig. 9A) revealed four groups. Group 1 is composed of perennial species in the bay that are frequent in neritic stations, such as *Clytia* spp., *Obelia* spp., *Eucheilota paradoxica*, *Podocorynoides*

Table 2. List of gelatinous species off the bay and the lagoon of Bizerte.

	bay	lagoon
Medusae		
Amphinema dinema (Peron & Lesueur, 1809)	+	–
Corymorpha nutans M. Sars, 1835	+	+
Euphysa aurata Forbes, 1848	+	+
Eucodonium brownei Hartlaub, 1907	+	–
Paragotoea bathybia Kramp, 1942	+	+
Podocorynoides minima (Trinci, 1903)	+	+
Lizzia blondina Mayer, 1900	+	–
Coryne eximia (Allman, 1859)	+	–
Aequorea aequorea (Forskall, 1775)	+	+
Eucheilota paradoxica (Mayer, 1900)	+	+
Clytia spp. (Lamoureux, 1812)	+	+
Clytia hemisphaerica (Linnaeus, 1767)	+	+
Clytia mccradyi (Brooks, 1888)	+	–
Eutima gracilis (Forbes & Goodsir, 1851)	+	–
Eutima mira Mc Crady, 1857	+	–
Obelia spp. Peron & Lesueur, 1810	+	+
Aglaura hemistoma Peron & Lesueur, 1810	+	+
Liriope tetraphylla Chamisso & Eysenhardt, 1828	+	–
Rhopalonema velatum Gegenbaur, 1857	+	–
Solmundella bitentaculata Quoy & Gaimard, 1833	+	–
Aurelia aurita Linne, 1858	+	–
Pelagia noctiluca Forskal, 1775	+	+
Cotylorhiza tuberculata Macri, 1778	+	–
Rhizostoma pulmo Macri, 1778	+	–
Siphonophores		
Abylopsis tetragona (Otto, 1823)	+	–
Bassia bassensis (Quoy & Gaimard, 1833)	+	–
Chaelophyes appendiculata (Eschscholtz, 1829)	+	–
Ceratocymba sagitata (Quoy & Gaimard, 1827)	+	–
Diphyes chamissonis Huxley, 1859	+	–
Eudoxoides mitra Huxley, 1859	+	–
Eudoxoides spiralis Bigelow, 1911	+	–
Lensia conoidea (Keferstein & Ehlers, 1860)	+	+
Muggiaea atlantica Cunningham, 1829	+	–
Muggiaea kochi Will, 1844	+	+
Sphaeronectes gracilis (Claus, 1873–1874)	+	–
Appendicularians		
Oikopleura longicauda Vogt, 1854	+	+
Oikopleura fusiformis Fol, 1872	+	+
Oikopleura dioica Fol, 1872	+	+
Fritillaria pellucida Busch, 1851	+	+
Chaetognaths		
Sagitta setosa Muller, 1847	+	+
Sagitta inflata Grassi, 1881	+	+
Sagitta minima Grassi, 1881	+	–
Sagitta elegans Verril, 1873	+	–
Sagitta decipiens Fowler, 1905	+	–
Sagitta planctonis Steinhaus, 1896	+	–
Doliolids		
Doliolum nationalis Borgert, 1901	+	+
Pteropods		
Limacina inflata d'Orbigny, 1836	+	+
Creseis acicula Rang, 1828	+	+

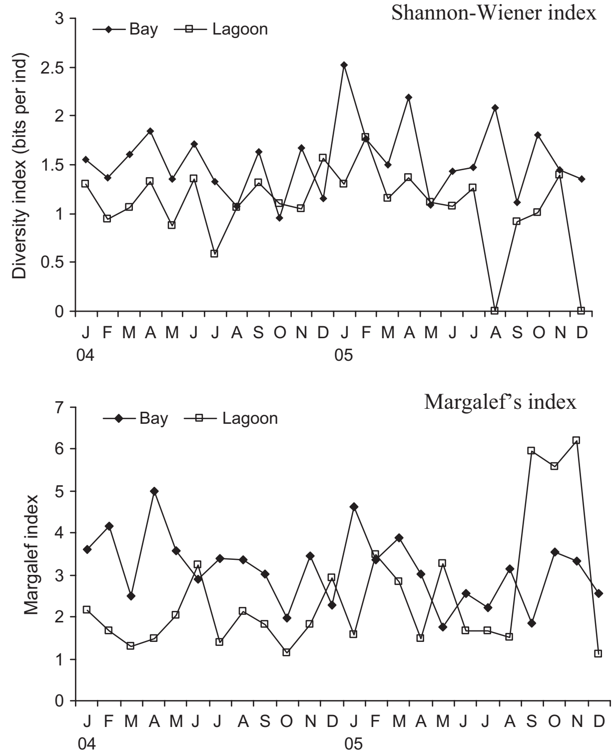

Fig. 6. Monthly fluctuation of diversity indexes in the bay and the lagoon of Bizerte.

minima and *Pelagia noctiluca*. Group 2 is composed of *Muggiaea atlantica* and occurred in the winter season. Group 3 comprised species which occurred in the bay with high densities and Group 4 comprised species widely distributed in the study area.

In the lagoon, three groups were identified: the first one comprising species such *as Aglaura hemistoma*, *Obelia* spp., *Sagitta setosa* and *Pelagia noctiluca* that occurred in low densities in the lagoon; the second one composed by *Muggiaea kochi*; the third one comprising *Limacina inflata*, three *Oikopleura* species, *Podocorynoides minima*, *Creseis acicula* and *Sagitta inflata*. All these species occurred in high numbers and may profit from the eutrophication (Fig. 9B).

Multidimensional scaling ordination analysis clearly showed three main groups of stations: Group (A) composed of marine stations (B1, B2, B3, B4, B5, B6, B7 and B8); Group (B) composed of lagoon stations that were generally under anthropogenic impact (L1, L2, L3, L4, L5, L6 and L7) and group (C) composed of stations that received mixed marine and lagoon water (Fig. 10). ANOSIM showed a significant difference between groups A, B and C ($R = 0.2$; $P < 0.001$).

The PCA (Fig. 11) revealed three groups of variables. Group 1 is composed of *Podocorynoides minima*, nitrates, nitrites and Chl-*a*, indicating that the development of this

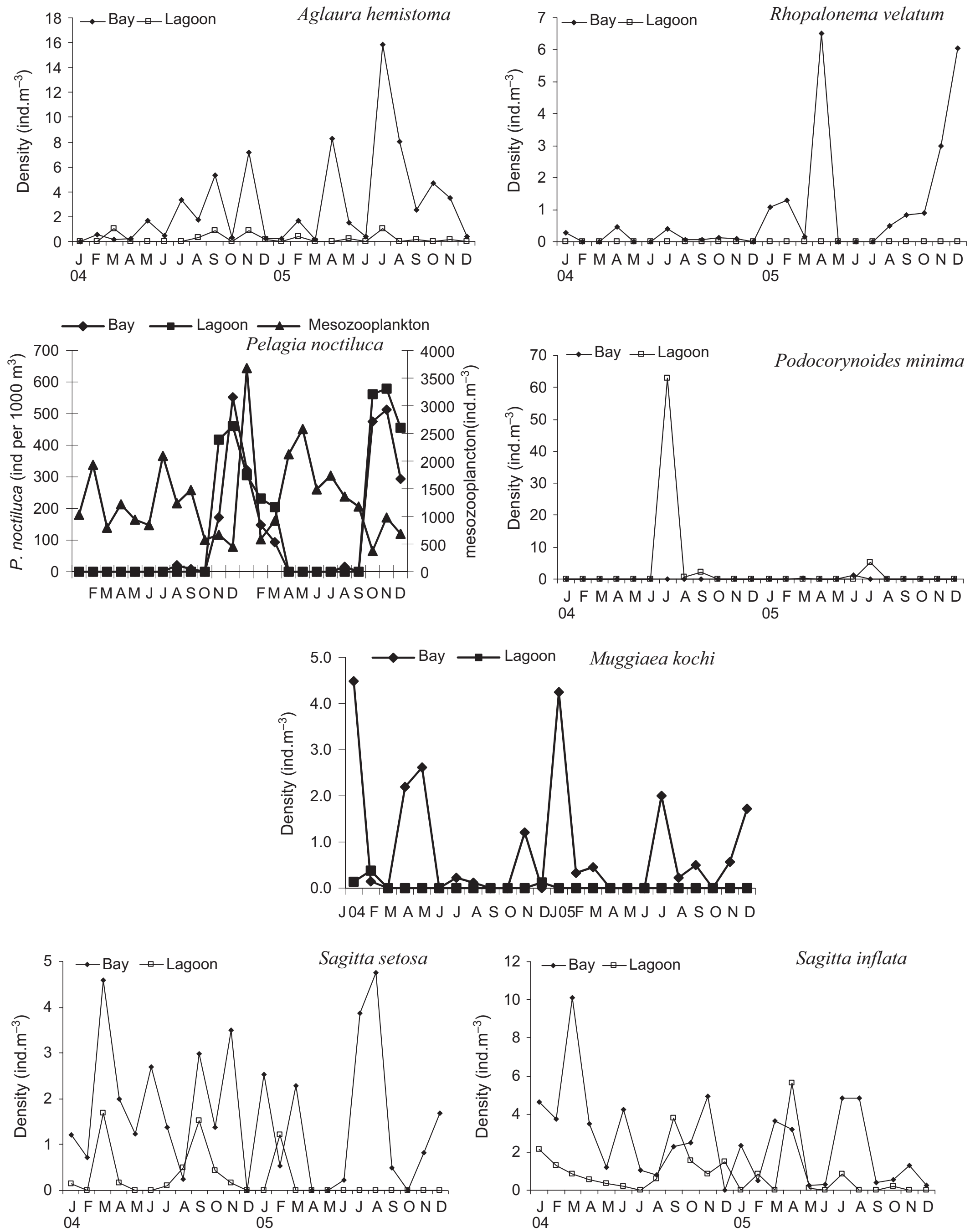

Fig. 7. Distribution of most abundant species of gelatinous carnivores in the bay and the lagoon of Bizerte.

species is associated with high concentrations of nutrients and Chl-*a*. Group 2 comprises the maximum number of species, *e.g. Sagitta inflata*, *Aglaura hemistoma*, *Oikopleura longicauda*, *Sagitta setosa*, *Pelagia noctiluca*, *Doliolum nationalis*, *Oikopleura dioica and Muggiaea kochi*; those species are positively associated with salinity and are characteristic of the bay of Bizerte. The third group contains the pteropods *Creseis acicula*, *Limacina inflata* and is associated with temperature.

Discussion

The present study provides basic information on the seasonal variability of gelatinous zooplankton in a neritic

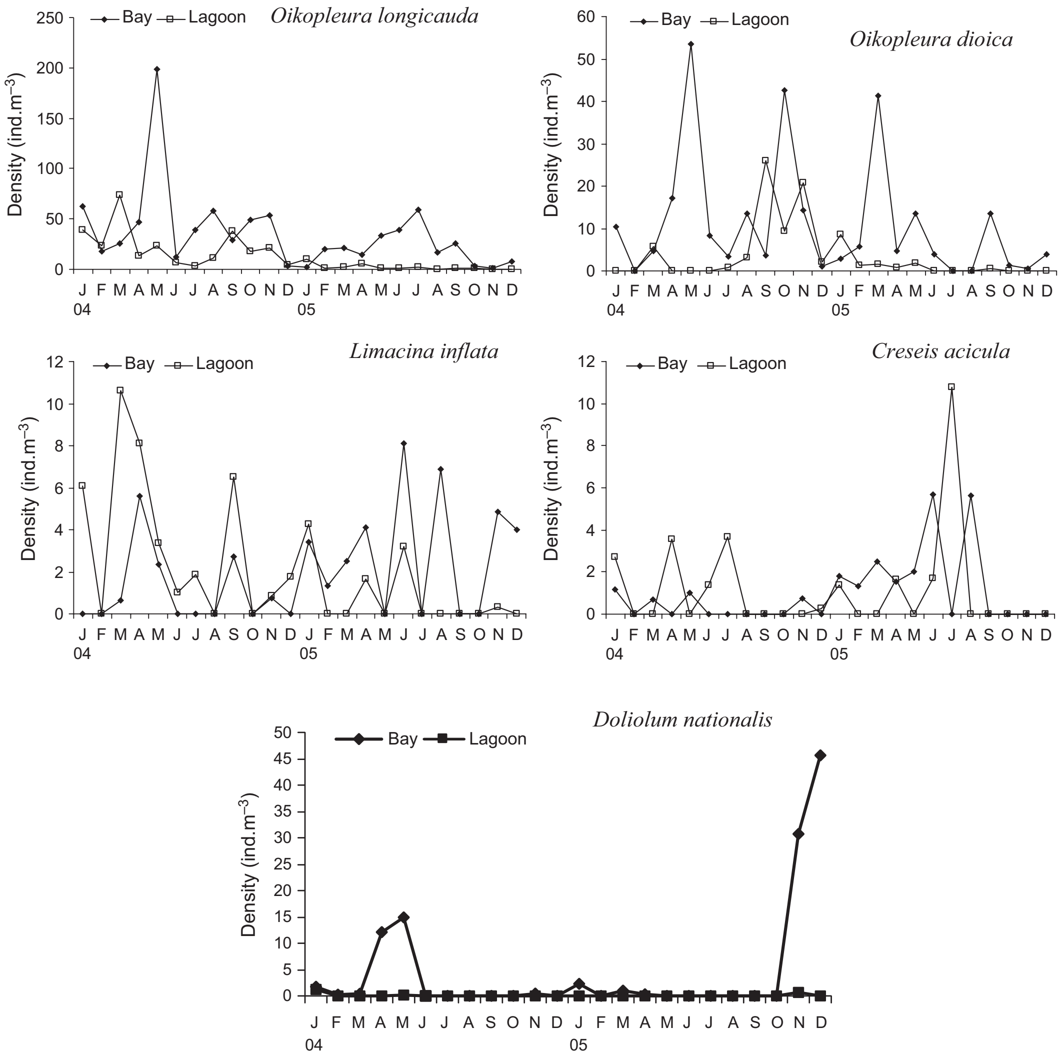

Fig. 8. Distribution of most abundant filter feeders species in the bay and the lagoon of Bizerte.

area in the Southwestern Mediterranean Sea, describing the diversity and distribution of a community in the bay and in the lagoon of Bizerte (North Tunisia).

With 48 species, the bay of Bizerte appeared to be more diverse than the lagoon, where only 22 species were found. Such a difference is likely due to a limited adaptability of the taxa to the unstable environmental conditions that characterized the brackish and eutrophic waters of the lagoon.

The diversity of the gelatinous zooplankton population as described by the Shannon-Wiener and Margalef indices was higher in the bay than in the lagoon, typically in spring, a period of transition in which temperature reaches relatively high values owing to reproduction of most gelatinous species. The high number of taxa recorded in the lagoon in January could be related to circulation patterns that can transport marine species from the sea into the lagoon. The low diversity recorded in autumn probably reflects the end of the productive season that follows the decrease of water temperature.

Some species which occurred in high numbers in the lagoon, such as *Oikopleura longicauda*, *Creseis acicula*, *Limacina inflata* and *Podocorynoides minima*, seemed to profit from such eutrophic environment. In particular, *P. minima* was very abundant at L4, where its polyp could settle on the oyster rafts. Overall, meroplanktonic medusae such as *P. minima* dominated in the lagoon, whereas holoplanktonic medusae such as *Aglaura hemistoma* and *Rhopalonema velatum* were dominant in the bay of Bizerte. This is in agreement with Goy (1991) who

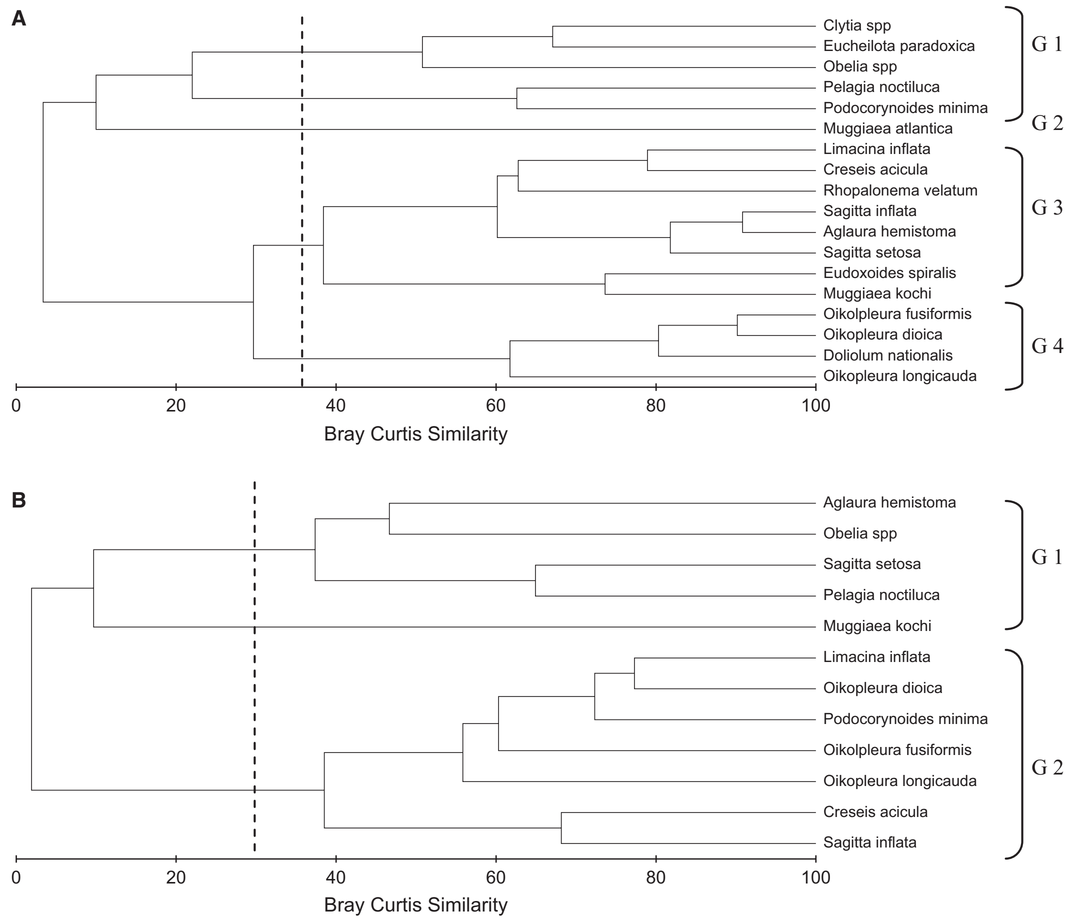

Fig. 9. Dendrogram showing species similarity in the bay (A) and the lagoon (B) of Bizerte.

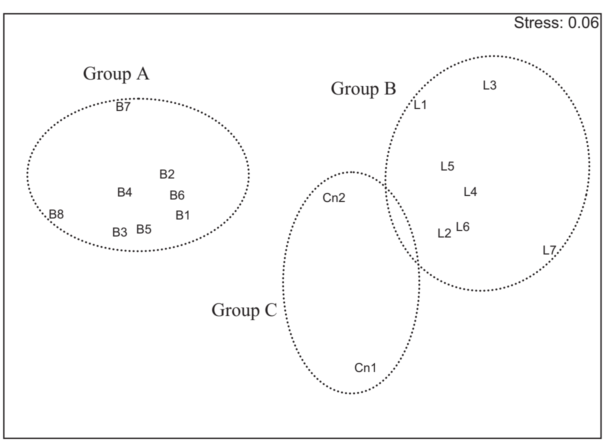

Fig. 10. Multidimensional scaling ordination of stations of the bay and the lagoon of Bizerte based on Bray–Curtis similarity coefficient.

pointed out the dominance of holoplanktonic medusae in environments characterized by stable hydrological conditions such as the bay of Bizerte.

Siphonophores were the most sensitive group to anthropogenic discharge. Of the 11 species that were recorded in the bay of Bizerte, only two species, *Muggiaea kochi* and *Lensia conoidea*, were recorded in the lagoon and in the channel. *Muggiaea kochi* was the dominant siphonophore in Tunisian waters. This region does not seem to be a suitable environmental for *Muggiaea atlantica*, which is progressively expanding its distribution in the Mediterranean (Licandro *et al.* 2008).

Oikopleura longicauda and *Oikopleura dioica* were the dominant appendicularians in the bay and the lagoon of Bizerte. *Oikopleura dioica* was previously reported as the dominant taxon in eutrophic coastal waters (Nomura & Murano 1992; Uye & Ichino 1995), as this species seems to have a higher food requirement than other appendicularians (Tomita *et al.* 2003). In the region off Bizerte the most common gelatinous zooplankton species were *A. hemistoma*, *Rhopalonema velatum*, *P. minima*, *Obelia* spp., *Eucheilota paradoxica*, *O. longicauda*, *O. dioica, M. kochi, Eudoxoides spiralis*, *C. acicula* and *L. inflata*. On

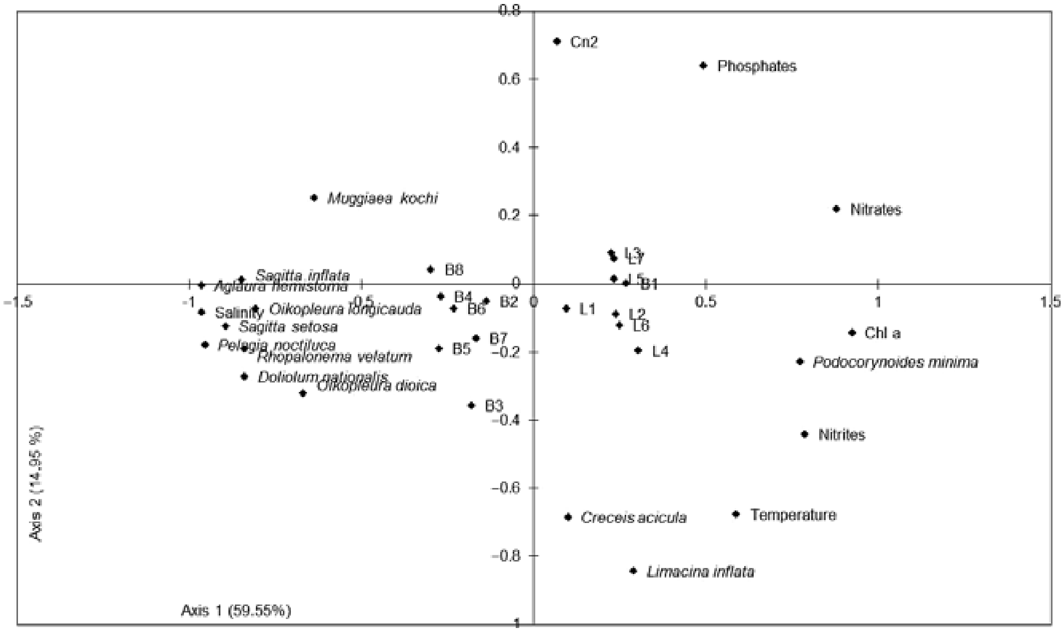

Fig. 11. Principal component analysis (PCA) showing the relationships between gelatinous species and environmental variables.

average, the highest densities were recorded in spring and summer. This is in agreement with previous studies that reported high densities of gelatinous zooplankton, in particular medusae, during summer in the bay of Sousse (Touzri *et al.* 2004) and the bay of Tunis (Daly Yahia *et al.* 2003), and along the Egyptian coast (Zakaria 2004).

The seasonal distribution of gelatinous species in the bay and the lagoon of Bizerte can be affected by environmental factors such as temperature, salinity, Chl-*a* and nutrients. *Podocorynoides minima* showed high densities in the eutrophic environment, where concentrations of Chl-*a*, nitrates and nitrites were high. The distribution of other species (*M. kochi*, *S. inflata*, *A. hemistoma*, *O. hemistoma*, *O. longicauda*, *Sagitta setosa*, *Pelagia noctiluca*, *R. velatum*, *Doliolum nationalis* and *O. dioica*) is likely associated with high salinity. The increase of temperature could affect the seasonal occurrence of pteropods such as *C. acicula* and *L. inflata*.

Several studies in the Mediterranean showed that high abundances of gelatinous zooplankton are usually associated with variations in water masses, in particular with high salinity and warm temperatures (Goy *et al.* 1989; UNEP, 1991; Daly Yahia *et al.* 2003; Batistic *et al.* 2004, 2007; Touzri *et al.* 2004, 2010; Molinero *et al.* 2005; Purcell *et al.* 2009).

The scyphomedusa *P. noctiluca*, which is known to be an efficient predator consuming fish eggs and larvae as well as crustaceans such as copepods (Goy *et al.* 1989; Giorgi *et al.* 1991; Purcell & Arai 2001), occurred in high number in the bay and the lagoon of Bizerte in the autumn and winter season. This species had a significant ecological impact on mesozooplankton that sharply decreased in autumn and winter.

Multidimensional scaling ordination clearly distinguished three groups of stations: group A including bay stations, group B comprising lagoon station directly influenced by anthropogenic discharge, and group C comprising transitional stations between the bay and the lagoon of Bizerte; however, the distribution of gelatinous zooplankton divided the study area into three zones according to differences in the species composition.

Climate plays a key role in the oceanographic regime and consequently has a direct influence on plankton community production (Fernandez de Puelles & Molinero 2007). During the last decades, an interest in the effects of climate variability on biological processes has emerged. Reports have shown that climate interacts with population densities (Molinero *et al.* 2005). The North Atlantic Oscillation (NAO) may affect zooplankton variability, as shown by Fromentin & Planque (1996); thus long-term SST and circulation in the Western Mediterranean Sea have been related to the NAO (Vignudelly *et al.* 1999).

In our study, species diversity in the bay and the lagoon of Bizerte was low; the majority of gelatinous species found in the present study have been recorded in the bay of Tunis (Daly Yahia *et al.* 2003, 2004) and the bay of Sousse (Touzri *et al.* 2004). Some species were newly recorded in the study area. Some of the species can be considered characteristic of Tunisian coasts, *e.g. Obelia* spp., *Clytia* spp., *Rhizostoma pulmo*, *A. hemistoma*, *R. velatum*, *O. longicauda*, *O. dioica*, *D. nationalis*, *C. acicula*, *L. inflata, S. setosa, S. inflata, L. conoidea, Chelophyes appendiculata, Lensia conoidea et Eudoxoides spiralis.*

Species found in this study have been previously recorded in the Western Mediterranean Sea (Goy 1972; Goy *et al.* 1991; Benovic & Lucic 1996; Mills *et al.*, 1996; Licandro & Ibanez 2000; Daly Yahia *et al.* 2003; Fernandez de Puelles *et al.* 2003; Batistic *et al.* 2007). However, this is the first recording of *Eutima mira* in the Western Mediterranean Sea.

The species richness of Tunisian bays was low in comparison with species composition recorded in the Mediterranean Sea off the Lebanese coast (71 species, Goy *et al.* 1991), Marseille Bay (35 species, Berhaut 1969), the Ligurian Sea (59 species, Goy 1972) and the Adriatic Sea (66 species Batistic *et al.* 2007).

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References

Addad S., Daly Yahia M.N., Belgith H., Zamamouch S., Goy J., Daly Yahia-Kefi O. (2008) Analyse taxinomique, écologique et caractérisation biochimique des scyphoméduses de la baie de Bizerte et de Tunis (Juillet-Décembre 2004). *Bulletin de la Société Zoologique de France*, **133**, 33–41.

Batistic M., Krsinic F., Jasprica N., Caric M., Vilicic D., Lucic D. (2004) Gelatinous invertebrate zooplankton of the south Adriatic: species composition and vertical distribution. *Journal of Plankton Research*, **26**, 459–474.

Batistic M., Jasprica N., Caric M., Lucic D. (2007) Annual cycle of the gelatinous invertebrate zooplankton of the eastern south Adriatic coast (NE Mediterranean). *Journal of Plankton Research*, **29**, 671–686.

Behrends G., Schneider G. (1995) Impact of *Aurelia aurita* medusa (cnidarian, scyphozoa) on the standing stock and community composition of mesozooplankton in the Kiel Bight (western Baltic Sea). *Marine Ecology Progress Series*, **127**, 39–45.

Benovic A., Lucic D. (1996) Comparison of hydromedusae findings in the northern and southern Adriatic Sea. *Scientia Marina*, **60**, 129–135.

Benovic A., Justic D., Bender A. (1987) Enigmatic changes in the hydromedusan fauna of the northern Adriatic Sea. *Nature*, **326**, 597–600.

Berhaut J. (1969) Etude qualitative, quantitative et écologique des hydroméduses du Golfe de Marseille. *Tethys*, **1**, 667–708.

Boero F., Mills C.E. (1997) Agricultural *versus* ethological oceanography. *Trends Ecology Evolution*, **12**, 208–209.

Boero F., Bouillon J., Gravili C., Miglietta M.P., Parson T., Piraino S. (2008) Gelatinous plankton: irregularities rule the world (sometimes). *Marine Ecology Progress Series*, **356**, 299–310.

Bone Q. (1998) *The Biology of Pelagic Tunicates*. Oxford University Press, Oxford: 340 pp.

Brodeur R.D., Sugiasaki H., Hunt G.L. (2002) Increase in the jellyfish biomass in the Bering Sea: implications for the ecosystem. *Marine Ecology Progress Series*, **233**, 89–103.

Burnett J.W. (2001) Medical Aspects of jellyfish envenomation: pathogenesis, case reporting and therapy. *Hydrobiologia*, **451**, 1–9.

Daly Yahia M.N., Goy J., Daly Yahia-kefi O. (2003) Distribution et écologie des méduses (Cnidaria) du golfe de Tunis (Méditerranée sud occidentale). *Oceanologica Acta*, **26**, 645–655.

Daly Yahia M.N., Daly Yahia-Kefi O., Souissi S. (2004) Distribution verticale du plancton gélatineux dans le golfe de Tunis (Automne 1995). *Rapport de la Commission Internationale pour l'Exploration Scientifique de la Mer Méditerranée*, **37**, 339.

Deason E.E., Smayda T.J. (1982) Ctenophore-zooplankton-phytoplankton interactions in Narragansett Bay, Rhode Island, USA, during 1972–1977. *Journal Plankton Research*, **4**, 203–216.

Deibel D. (1998) Feeding and metabolism of appendicularia. In: Bone Q. (Ed.), *The Biology of Pelagic Tunicates*. Oxford University Press, Oxford: pp. 139–149.

Doyle T.K., De Haas H., Cotton D., Dorshell B., Cummins V., Houghton J.D.R., Davenport J., Hays G.C. (2008) Widespread occurrence of the jellyfish *Pelagia noctiluca* in Irish coastal and shelf waters. *Journal of Plankton Research*, **30**, 963–968.

Fernandez de Puelles M.L., Molinero J.C. (2007) North Atlantic climate control on plankton variability in the Balearic Sea (Western Mediterranean). *Geophysical Research Letters*, **34**, L04608 5.

Fernandez de Puelles M.L., Gras D., 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*, **24**, 123–139.

Flood P.R., Deibel D., Morris C. (1992) Filtration of colloidal melanin from sea water by planktonic tunicates. *Nature*, **355**, 630–632.

Fromentin J.M., Planque B. (1996) *Calanus* and environment in the eastern north Atlantic. II. Influence of the north Atlantic oscillation on *C. finmarchicus* and *C. helgolandicus*. *Marine Ecology Progress Series*, **134**, 101–109.

Gamulin T., Krsinie F. (1993) Distribution and abundance of Calycophores in the Mediterranean and Adriatic Sea. *Marine Ecology*, **14**, 97–111.

Giorgi R., Avian M., De Olazabel S., Rottini-Sandrini L. (1991) Feeding of *Pelagia noctiluca* in open sea. Jellyfish blooms in the Mediterranean. In: *Proceeding of the II Workshop on Jellyfish in the Mediterranean Sea, Trieste*, **47**, 102–111.

Gorsky G., Fenaux R. (1998) The role of appendicularia in marine food webs. In: Bone Q. (Ed), *The Biology of Pelagic Tunicates*. Oxford University Press, Oxford: pp. 161–169.

Goy J. (1972) Les Hydroméduses de la mer Ligure. *Bulletin du Museum National d'Histoires Naturelles*, **62**, 965–1009.

Goy J. (1991) Hydromedusae of the Mediterranean Sea. *Hydrobiologia*, **216/217**, 351–354.

Goy J., Morand P., Etienne M. (1989) Long-term fluctuations of *Pelagia noctiluca* (Cnidaria, Scyphomedusa) in the western Mediterranean Sea: prediction by climatic variables. *Deep-Sea Research*, **36**, 269–279.

Goy J., Lakkis S., Zeidane R. (1991) Les Méduses (Cnidaria) des eaux libanaises. *Annales de l'Institut Océanographique de Paris*, **67**, 99–128.

Graham W.M., Pagès F., Hamner W.H. (2001) A physical context for gelatinous zooplankton aggregations: a review. *Hydrobiologia*, **451**, 199–212.

Greve W. (1994) The 1889 German Bight invasion of *Muggiaea atlantica*. *ICES Journal of Marine Sciences*, **51**, 355–358.

Harzallah A. (2003) Transport de polluants dans la lagune de Bizerte simulé par un modèle de circulation de l'eau. *Bulletin de l'Institut National des Sciences de la Mer Salammbô*, **30**, 121–133.

Hopcroft R.R., Roff J.C. (1998) Production of tropical larvaceans in Kingston Harbour, Jamaica: are we ignoring important secondary producer? *Journal of Plankton Research*, **20**, 557–569.

Hopcroft R.R., Roff J.C., Boumon H.A. (1998) Zooplankton growth rates: the larvaceans Appendicularia, Fritillaria and Oikopleura in tropical waters. *Journal of Plankton Research*, **20**, 539–555.

Licandro P., Ibanez F. (2000) Changes of zooplankton communities in the gulf of Tigullio (Ligurian Sea, Western Mediterranean) from 1985 to 1995. Influence of hydroclimatic factors. Journal of Plankton Research, **22**, 2225–2253.

Licandro P., Batistic M., Daly Yahia M.N., Daly Yahia O., Malej A., Molinero J.C., Souissi S., Touzri C., Carré C. (2008) *Muggiaea atlantica*: an Atlantic indicator of hydroclimatic changes in the Mediterranean. Joint ICES/CIESM Workshop to Compare Zooplankton Ecology and Methodologies between the Mediterranean and the North Atlantic.

Malacic V., Petelin B., Malej A. (2007) Advection of the jellyfish *Pelagia noctiluca* (Schyphozoa) studied by the Lagrangian tracking of water mass in the climatic circulation of the Adriatic Sea. *Geophysical Research Abstract*, **9**, 02802.

Matsakis S., Conover R.J. (1991) Abundance and feeding of medusa and their potential predators on other zooplankton in Bedford basin (Nova Scotia, Canada) during spring. *Canadian Journal of Fisheries and Aquatic Sciences*, **48**, 1419–1430.

Millot C. (1987) Circulation in the Western Mediterranean Sea. *Oceanologica Acta*, **10**, 143–149.

Mills C.E. (2001) Jellyfish blooms: are populations increasing globally in response to changing ocean conditions? *Hydrobiologia*, **451**, 55–68.

Mills C.E., Pugh P.R., Harbison G.R., Haddock S.H.D. (1996) Medusae, Siphonophores and ctenophores of the Alboran Sea, south western Mediterranean. *Scientia Marina*, **60**, 145–163.

Molinero J.C., Ibanez F., Nival P., Buecher E., Souissi S. (2005) North Atlantic climate and north western Mediterranean plankton variability. *Limnology Oceanography*, **50**, 1213–1220.

Nicholas K.R., Frid C.L.J. (1999) Occurrence of hydromedusae in the plankton off Northumberland (western central North Sea) and the role of planktonic predators. *Journal of the Marine Biological Association of the United Kingdom*, **79**, 979–992.

Nomura H., Murano M. (1992) Seasonal variation of meso- and macrozooplankton in Tokyo Bay, central Japan. *La Mer*, **30**, 49–56.

Pagès F., Gonzalez H.E., Roman M., Sobarzo M., Gili J.M. (2001) Gelatinous zooplankton assemblages associated with water masses in the Humboldt current system, and potential predatory impact by *Bassia bassensis* (Siphonophora, Calycophorae). *Marine Ecology Progress Series*, **210**, 13–24.

Pugh P.R. (1975) The distribution of siphonophores in a transect across the North Atlantic Ocean at 32°N. *Journal of Experimental Marine Biology and Ecology*, **20**, 77–97.

Purcell J.E. (1997) Pelagic cnidarians and ctenophores as predators: selective predation, feeding rates and effects on prey populations. *Annales de l'Institut Océanographique de Paris*, **73**, 125–137.

Purcell J.E., Arai M.N. (2001) Interactions of pelagic Cnidarians and Ctenophores with fish: a review. Series developments in hydrobiology 155. *Hydrobiologia*, **451**, 27–44.

Purcell J.E., Uye S.I., Lo W.T. (2007) Anthropogenic causes of jellyfish blooms and their direct consequences for humans: a review. *Marine Ecology Progress Series*, **350**, 153–174.

Purcell J.E., Hoover R.A., Schwarck N.T. (2009) Interannual variation of strobilation by the Scyphozoan *Aurelia labiata* in relation to polyp density, temperature, salinity and light conditions *in situ*. *Marine Ecology Progress Series*, **375**, 139–149.

Richardson A.J., Bakun A., Hays G.C., Gibbons M.J. (2009) The jellyfish joyride: causes, consequences and management responses to a more gelatinous future. *Trends in Ecology and Evolution*, **24**, 312–322.

Sabates A., Pagès F., Antienza D., Fuentes V., Purcell J.E., Gili J.M. (2010) Planktonic cnidarian distribution and feeding of *Pelagia noctiluca* in the NW Mediterranean Sea. *Hydrobiologia*, **645**, 153–165.

Suchman C.L., Daly E.A., Keister J.E., Peterson W.T., Brodeur R.D. (2008) Feeding patterns and predation potential of Scyphomedusae in a highly productive upwelling region. *Marine Ecology Progress Series*, **358**, 161–172.

Tomita M., Shiga N., Ikeda T. (2003) Seasonal occurrence and vertical distribution of appendicularians in Toyama Bay, Southern Japan Sea. *Journal of Plankton Research*, **25**, 579–589.

Touzri C., Daly Yahia M.N., Goy J. (2004) Le plancton gélatineux de la baie de Sousse (Méditerranée Méridionale): Systematique et Ecologie. *Bulletin de la Société Zoologique de France*, **129**, 379–392.

Touzri C., Daly Yahia-Kefi O., Hamdi H., Goy J., Daly Yahia M.N. (2010) Spatio-temporal distribution of medusa (Cnidaria) in the Bay of Bizerte (South Western Mediterranean Sea). *Cahiers de Biologie Marine*, **51**, 167–176.

UNEP. (1991) Jellyfish blooms in the Mediterranean Sea. UNEP. MAP Technical Report Series, 47.

Uye S., Ichino S. (1995) Seasonal variation in abundance, size composition, biomass and production rate of *Oikopleura dioica* (Fol) (Tunicata; Appendicularia) in a temperate eutrophic inlet. *Journal of Experimental Marine Biology and Ecology*, **189**, 1–11.

Verity P.G., Smetacek V. (1996) Organism life cycles, predation and the structure of marine pelagic ecosystems. *Marine Ecology Progress Series*, **130**, 277–293.

Vignudelly S., Gasparini G.P., Astraldi M., Schiano M.E. (1999) A possible influence of the North Atlantic Oscillation on the circulation of the Western Mediterranean. *Geophysical Research Letters*, **26**, 623–626.

Zakaria H.Y. (2004) Pelagic coelenterates in the waters of the western part of the Egyptian Mediterranean coast during summer and winter. *Oceanologia*, **46**, 253–268.