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Species composition and distribution of medusae (Cnidaria: Medusozoa) along the Algerian coast between 2°E and 7°E (SW Mediterranean Sea)

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Abstract

The species composition, abundance and distribution of the medusa community along the Algerian coast (between 2°E and 7°E) were investigated during the autumn of 2014. Zooplankton sampling was performed in the upper layer (0-100 m) at 14 stations. Fourteen species of hydromedusae and scyphomedusae were identified. The hydromedusae populations were represented by Leptomedusae (5 species), Narcomedusae (3 species), Trachymedusae (3 species) and Anthomedusae (2 species). Some species, such as *Cirrhovenia tetranema* and *Cunina globosa*, were new species records for the sampling areas. The total abundance of medusae was less than 10 individuals.m⁻³. The areas with the highest concentrations (> 4 ind.m⁻³) were located along the central coast between the Bou Ismail (2.6° E) and Algiers (3.2° E) Bays. Here, the populations of *Aglaura hemistoma* and *Liriope tetraphylla* were dominant (≈ 40%). A quantitative variability was recorded for three species, *Liriope tetraphylla*, *Pelagia noctiluca* and *Rhopalonema velatum*, of which the first two species were particularly abundant in the central region and the latter species was particularly abundant in the eastern region. The distributions of these species were analysed in relation to the environmental parameters (temperature, salinity and chlorophyll *a*) and their interaction with copepod prey.

Keywords: Medusae; Algerian coast; biodiversity; distribution.

Introduction

“Medusae” is a generic term referring to free-floating gelatinous carnivorous zooplankton belonging to the phylum Cnidaria. Medusae are the most well-known group of gelatinous zooplankton and include three classes: hydromedusae, which is the most diverse gelatinous group, and scyphomedusae and cubomedusae (Bouillon & Boero, 2000). The group is widely distributed in all of the world's oceans and its members are recognized as efficient pelagic predators that can exert significant predation pressure on the other zooplanktonic groups (Purcell, 1997; Richardson *et al.*, 2009). Highest abundances of medusae have a significant impact on the pelagic food web and on the structure and dynamics of pelagic communities, particularly on ichthyologic fauna (Purcell *et al.*, 2007). During the past three decades, jellyfish populations have shown increases in diverse marine areas (Purcell, 2012; Condon *et al.*, 2014), causing detrimental effects on fisheries, aquaculture and tourism (Purcell *et al.*, 2007). The spatiotemporal distribution of jellyfish

can be explained by environmental and trophic factors. High phytoplanktonic densities can cause an increase in mesozooplankton, which can induce an increase in medusan fauna (Mills, 2001). However, climate change, pollution, over-fishing and habitat modifications may lead to changes in population production (Purcell *et al.*, 2007; Richardson *et al.*, 2009; Purcell, 2012).

In the Mediterranean Sea, jellyfish have been most closely studied in the northwestern basin (Goy, 1997; Buecher & Gibbons, 1999; Sabatés *et al.*, 2010; Goy *et al.*, 2016) and the eastern basin (Batistic *et al.*, 2007; Lučić *et al.*, 2009; Pestorić *et al.*, 2012). In the southwestern Mediterranean Sea, there have been few studies and investigations. Some investigations have been performed along the Tunisian coast (Daly Yahia *et al.*, 2003; Touzri *et al.*, 2010, 2012). These studies have mainly described the biodiversity and quantitative distribution of jellyfish in relation to the seasonal variation associated with hydrological parameters.

Along the Algerian coast, the majority of zooplankton studies have focused on mesozooplanktonic groups

(Seridji & Hafferssas, 2000, Hafferssas & Seridji, 2010, Ounissi *et al.*, 2016; Chaouadi & Hafferssas, 2018), and a few observations of diversities and abundances have been reported for gelatinous plankton (Khames & Hafferssas, 2018; 2019).

The aim of this study was to provide complementary information about gelatinous zooplankton on the Algerian coast by describing the main patterns of medusan biodiversity and their quantitative distributions in relation to environmental parameters.

Material and Methods

Sampling areas

The oceanographic cruise was carried out during September 2014 on board the oceanographic vessel *Grine Belkacem* of the National Center of the Research and Fisheries and Aquaculture Development (CNRDPA). This study was conducted between 2°E and 7°E; the study area included 14 stations, with 7 in central areas and 7 in eastern areas (Fig. 1 and Table 1).

Environmental parameters measurement and zooplankton collection

Zooplankton samples were collected with vertical hauls during the day between depths of 0 and 100 m using a Working Party II net (200 µm mesh size).

The zooplankton samples were fixed by adding formaldehyde to reach a final concentration of 4%. Species identifications were performed under a stereomicroscope (Zeiss Stemi SV 6/ Germany) and completed according to appropriate taxonomic references (e.g., Tregouboff & Rose, 1957; Bouillon, 1999; Bouillon *et al.*, 2006). The medusan abundances were calculated as the number of individuals per cubic metre of filtered sea water. For the scyphomedusae *Pelagia noctiluca*, only ephyrae were counted. The larger individuals that were occasionally collected were not included in the abundance data because the net used in this study was inappropriate for large medusa (Sabatés *et al.*, 2010). The biogeographical affinity was defined for each collected species (Boero & Bouillon, 1993). The species were classified according

to their occurrence frequency (Fr), which was the ratio between the number of samples that contained an individual of species *i* and the total number of samples. Three groups were formed: frequent (Fr > 50%), common (25% < Fr < 50%) and rare species (Fr < 25%) (Dajoz, 2006).

Biological sampling was followed by temperature (T) and salinity (S) measurements with a multiparameter (HI 9828-12202/ Romania) and chlorophyll *a* (Chl *a*) measurement using the spectrophotometric method.

Data analysis

To compare the differences in medusan abundance between the two regions (central and eastern), a non-parametric Mann – Whitney test (χ) was used (Pestorić *et al.*, 2012). This test was also used to compare the variability of environmental parameters.

To identify the species that contributed most to the total abundance, correspondence analysis (CA) was performed. The populations that showed occurrence frequencies above 25% were used in the analysis (Hafferssas & Seridji, 2010).

The spatial segregation between the species compositions was analysed as follows: the *D index* = $1/2 \sum |(N_{1i}/N_1) - (N_{2i}/N_2)|$ (Fenaux, 1963, Flores-Coto *et al.*, 2016), where N_{1i} and N_{2i} represent the number of individuals of species 1 and species 2, respectively, at station *i* and N_1 and N_2 are the total numbers of individuals of species 1 and species 2, respectively.

Spearman's rank correlation coefficient (ρ) was used to analyse the relationships among total medusan abundance, copepod abundance and environmental variables. However, to describe the relationships between the latter factors and the medusa species, principal component analysis (PCA) was used. All data were log (x+1) transformed to avoid strong influences from the most abundant populations and to test for a normal distribution (Hafferssas & Seridji, 2010). All analyses were performed with the *STATISTICA 10* software.

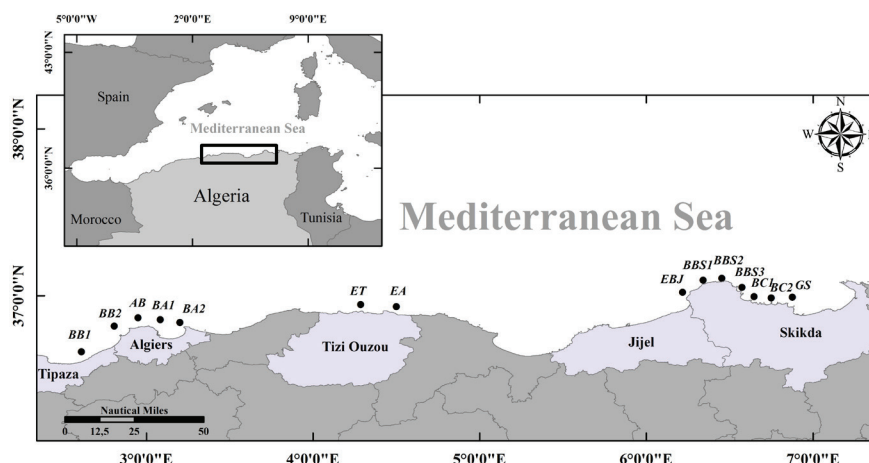


Fig. 1: Sampling area along the Algerian coast.

Table 1. Locations and hydrological characteristics of the sampling stations along the Algerian coast.

Stations	Longitude (°E)	Latitude (°N)	Date	T (°C)	S	Chl <i>a</i> (mg.m ⁻³)
Central coast of Bou Ismail Bay (BB1)	2,610	36,665	26/09/2014	26.00	36.70	0.210
Eastern coast of Bou Ismail Bay (BB2)	2,807	36,818	26/09/2014	25.30	37.10	0.116
Ain Benian offshore coasts (AB)	2,950	36,868	25/09/2014	24.50	37.5	0.021
Western coast of Algiers Bay (BA1)	3,084	36,857	25/09/2014	25.20	37.0	0.244
Eastern coast of Algiers Bay (BA2)	3,201	36,840	25/09/2014	25.10	36.9	0.265
Eastern coast of Tizirt (ET)	4,286	36,948	23/09/2014	25.4	36.4	0.137
Eastern coast of Azzefoun (EA)	4,500	36,935	23/09/2014	25.4	37.0	0.146
Eastern coast of Jijel Bay (EBJ)	6,218	37,021	21/09/2014	26.4	36.4	0.037
Western coast of Beni Said Bay (BBS1)	6,341	37,094	21/09/2014	26.4	37.4	0.035
Western coast of Beni Said Bay (BBS2)	6,453	37,106	21/09/2014	26.4	37.4	0.033
Offshore coast of Beni Said Bay (BBS3)	6,574	37,051	21/09/2014	26.4	37.5	0.031
Offshore coast of Collo Bay (BC1)	6,647	36,995	21/09/2014	26.5	37.4	0.029
Offshore coast of Collo Bay (BC2)	6,750	36,988	21/09/2014	26.5	37.5	0.027
Gulf of Stora (GS)	6,877	36,992	21/09/2014	26.5	37.4	0.025

Results

Environmental data

The sea surface temperature ranged between 24.50°C (Station AB) and 26.50°C (EBJ, BBS1, BBS2, BBS3, BC1, BC2 and GS). Indeed, from station AB, an increasing gradient was observed from the central region to the eastern region (Table 1 and Fig. 2a). A significant difference ($\chi = -3.12$, $p = 0.002$) was found between these two regions.

The sea surface salinity fluctuated between 36.40 (stations ET and EBJ) and 37.50 (BBS3) (Table 1 and Fig. 2b). The chlorophyll *a* concentrations ranged between 0.021 mg.m⁻³ and 0.265 mg.m⁻³ (Table 1 and Fig. 2c). Chlorophyll *a* concentrations greater than 0.10 mg.m⁻³ were generally observed in the central region in the Bay of Bou Ismail (BB1), Bay of Algiers (BA1, BA2) and Tizi Ouzou coast (ET, EA). In the eastern region (EBJ, BBS1, BBS2, BBS3, BC1, BC2 and GS), the Chl *a* concentrations were low (less than 0.05 mg.m⁻³). Overall, the Chl *a* values were significantly different ($\chi = 2.17$, $p = 0.03$) between the two regions.

Biodiversity composition

A total of 14 species of medusa were identified during the cruise (Table 2). These species were distributed in two classes (hydromedusae and scyphomedusae) and five orders (Anthomedusae, Leptomedusae, Narcomedusae, Trachymedusae and Semaostomeae).

Among the hydromedusae group, the Leptomedusae order was composed of *C. hemisphaerica*, *Clytia* spp., *Obelia* spp., *C. tetranema* and *E. paradoxica*. These populations were widely distributed in the central region of the Algerian coast. Anthomedusae were characterized by

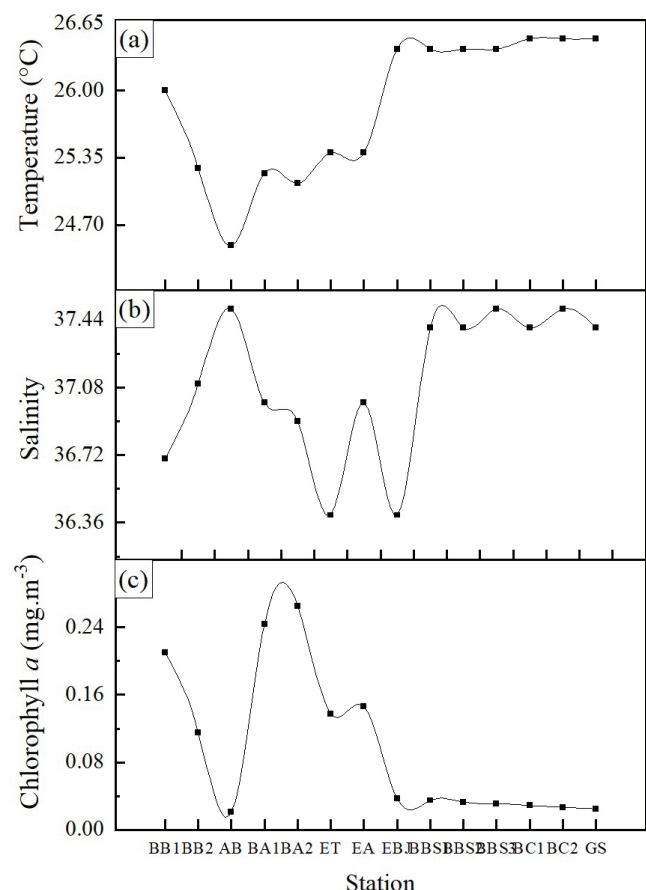


Fig. 2: Fluctuation of the environmental parameters at the sampling stations along the Algerian coast (a: temperature; b: salinity; c: chlorophyll *a*).

low diversity, with only two species (*L. blondina* and *P. minima*) reported. Narcomedusae and Trachymedusae were each represented by 3 species: *S. bitentaculata*, *C. globosa* and *Solmaris* sp. and *R. velatum*, *A. hemistoma*

Table 2. Biodiversity of the medusae populations along the Algerian coast (2° E and 7° E) in relation to their frequencies of occurrence (F = frequent, C = common, R = rare) and biogeographical affinities.

Species	Biogeographical Affinity	Occurrence frequencies (%)													
		BB1	BB2	AB	BA1	BA2	ET	EA	EBJ	BBS1	BBS2	BBS3	BC1	BC2	GS
Anthomedusae															
<i>Lizzia blondina</i>	Boreal ^[1]					+									R
<i>Podocorynoides minima</i>	Mediterranean Atlantic ^[1]				+										R
Leptomedusae															
<i>Clytia hemisphaerica</i>	Cosmopolitan ^[1]	+		+		+		+							C
<i>Clytia</i> spp.	-					+	+	+	+		+		+	+	C
<i>Obelia</i> spp.	-	+	+	+	+	+									C
<i>Cirrholovenia tetranema</i>	Indo-Pacific ^[1]		+		+										R
<i>Eucheilota paradoxa</i>	?	+	+	+	+	+		+							C
Tachymedusae															
<i>Rhopalonema velatum</i>	Circumtropical ^{[1]; [3]}			+	+	+	+		+	+	+	+	+	+	F
<i>Aglaura hemistoma</i>	Circumtropical ^{[1]; [3]}	+	+	+	+	+	+	+	+	+	+	+	+	+	F
<i>Liriope tetraphylla</i>	Circumtropical ^{[1]; [3]}	+	+	+	+	+	+	+		+				+	F
Narcomedusae															
<i>Solmundella bitentaculata</i>	Circumtropical ^{[1]; [3]}	+	+	+	+	+	+						+	+	F
<i>Solmaris</i> sp.		+						+							R
<i>Cunina globosa</i>	Circumtropical ^[1]											+	+		R
Semaeostomeae															
<i>Pelagia noctiluca</i>	Cosmopolitan ^[2]		+				+			+			+	+	C
Number of species		7	7	7	8	9	6	6	3	4	2	4	5	5	6

[1] Boero & Bouillon, 1993; [2] Purcell, 2005; [3] Pestorić *et al.*, 2010.

and *L. tetraphylla*, respectively. Scyphomedusae were only represented by the species *P. noctiluca* in the order Semaeostomeae in the two regions (Table 2).

More species (*R. velatum*, *A. hemistoma*, *L. tetraphylla*, *S. bitentaculata*, *Solmaris* sp., *C. hemisphaericum*, *Clytia* spp., *Obelia* spp. *C. tetranema*, *E. paradoxa*, *L. blondina*, *P. minima* and *P. noctiluca*) were found in the central region. In the eastern region, 8 species (*S. bitentaculata*, *C. globosa*, *Solmaris* sp., *R. velatum*, *A. hemistoma*, *L. tetraphylla*, *Clytia* spp. and *P. noctiluca*) were sampled (Table 2).

The most frequent species (Fr > 50%) were *A. hemistoma*, *R. velatum*, *S. bitentaculata* and *L. tetraphylla*. The populations of *Clytia* spp., *P. noctiluca*, *E. paradoxa*, *Obelia* spp. and *P. hemisphaericum* were common, with occurrences of less than 50%. On the other hand, six species were considered rare (F < 25%). Generally, these populations were found in the central region (EA, BA1, BA2, BB2 and BB1).

Fauna were classified as having several biogeographical origins: (i) cosmopolitan species (*P. hemisphaericum*), which were widely distributed throughout world

ocean; (ii) circumtropical species (*A. hemistoma*, *R. velatum*, *S. bitentaculata*, *L. tetraphylla* and *C. globosa*); (iii) Mediterranean-Atlantic species (*P. minima*); (iv) Indo-Pacific species (*C. tetranema*); and (v) boreal species (*L. blondina*).

Total abundances

In both regions (central and eastern), the abundances varied from 0.5 ind.m⁻³ to 8 ind.m⁻³ (Fig. 3). The lowest abundances (less than 1 ind.m⁻³) were found in the majority of the eastern region (EBJ; BBS2, BBS3, BC1). The highest values (more than 4 ind.m⁻³) were recorded in Collo Bay (BC2), Bou Ismail Bay (BB1), Algiers Bay (BA1) and Azzefoun Bay (EA).

Intermediate values (1 ind.m⁻³ and 3 ind.m⁻³) were recorded in the eastern region at the Stora Gulf (GS) and Beni Said Bay (BC2) and in the central region (stations BB2, BA2, AB and ET).

Between the eastern and central regions of the Algerian coast, a quantitative significant difference was found

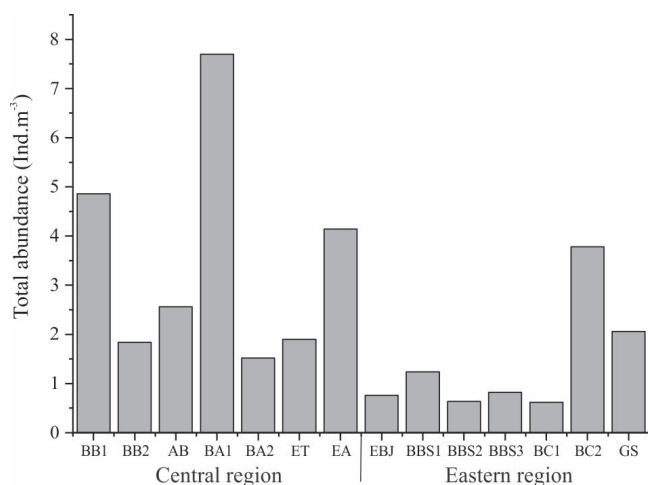


Fig. 3: Distribution of the total abundance of medusae along the Algerian coast (2°E -7°E).

($\chi = 2.17$, $p = 0.03$).

With the use of Spearman correlation, a strong relationship was found between the abundances of medusa and copepods ($\rho = 0.56$, $p < 0.05$).

Species composition

Based on the multivariate analysis (correspondence analysis) results, different species were selected as the predominant species (Fig. 4). Correspondence analysis allowed comparison and separation of the faunal groups in relation to their geographical distributions. The contribution to the total inertia of the first and second axis was 72.30% (Fig. 4). CA revealed two groups of variables.

The negative part of the first axis (44.91% of total inertia) was linked to *L. tetraphylla* (relative contribution of 46.32%). The populations of *R. velatum* (relative contribution of 20.60%) and *P. noctiluca* (relative contribution of 9.10%) were found in the positive part. This axis represented a gradient of dominance in these populations. In fact, we found that the stations in the central region, BA1 (34.78%), BB1 (6.91%) and EA (2.79%), had high numbers of *L. tetraphylla* (negative side of axis 1). The stations in the eastern region, BBS 3 (17.64%), BC2 (14.99%), GS (7.53%) and EBJ (6.95%), showed high abundances of *R. velatum* and *P. noctiluca* (positive side of the axis).

The second axis (27.39% of total inertia) showed the opposite trend for the populations belonging to the same geographical area (eastern coasts). The second axis separated *R. velatum* (51.82%) (negative side) from *P. noctiluca* (23.59%) (positive side).

All these populations, which were identified by correspondence analysis, were considered main species as a result of their abundances and their frequencies.

In fact, Trachymedusae (*A. hemistoma*, *L. tetraphylla* and *R. velatum*) and the Semaestomeae (*P. noctiluca*) were the most common groups, making up more than 70% of the total abundance at all stations. Leptomedusae were essentially represented by *E. paradoxica* (0.02

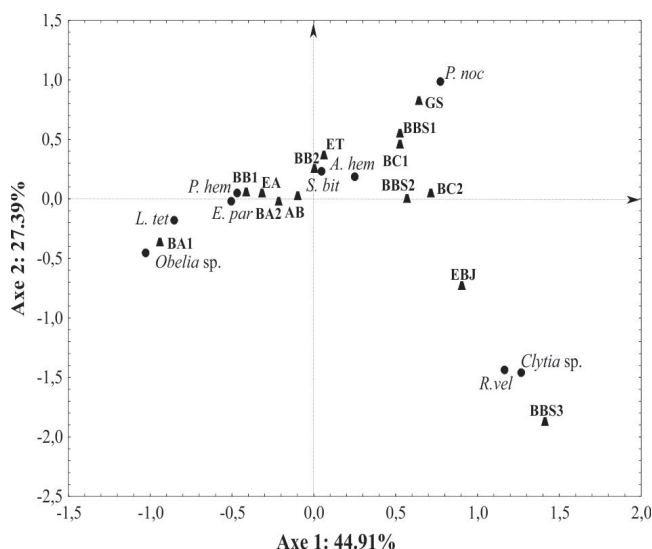


Fig. 4: Correspondence analysis (CA) showing the repartitions of the medusa species between the central and eastern regions.

ind.m⁻³- 0.54 ind.m⁻³) and *Obelia* spp. (0.02 ind.m⁻³- 0.28 ind.m⁻³) in the central coast. In the eastern region, this group was rare and only included *Clytia* spp. (0.02 ind.m⁻³- 0.08 ind.m⁻³). Narcomedusae were less abundant and were essentially represented by *S. bitentaculata* (0.02 ind.m⁻³- 0.18 ind.m⁻³). However, the lowest abundances were found for the order Anthomedusae (0.02 ind.m⁻³).

Distribution of the main species

A. hemistoma was considered a cosmopolitan form and was widely distributed. In the present study, *A. hemistoma* was the most abundant medusa found at all stations (Fig. 5a), which justified its position in the factorial plan (Fig. 4). The values of *A. hemistoma* fluctuated between 0.26 ind.m⁻³ (BBS3) and 3.68 ind.m⁻³ (BC2).

L. tetraphylla was the second most abundant species (Fig. 5b). *L. tetraphylla* showed a variable distribution in both regions and tended to be most numerous (10% to 89% of total) in the central region, with a maximum abundance of 6.28 ind.m⁻³ (BA2). However, in the eastern region, the contribution of this population was less than 2%, with a significantly lower maximum abundance of 0.02 ind.m⁻³ (BBS1 and GS).

R. velatum appeared at the majority of stations. The concentrations of *R. velatum* varied from 0.02 ind.m⁻³ to 0.44 ind.m⁻³ (Fig. 5c).

In this study, the most common Semaestomeae species (*P. noctiluca*) in the Mediterranean was the only scyphomedusae inventoried in the central region (BB2, ET) and in the eastern region (BBS1, BC1, BC2 and GS). The abundances of *P. noctiluca* fluctuated between 0.04 ind.m⁻³ (BB2) and 0.48 ind.m⁻³ (GS) (Fig. 5d).

To confirm the spatial pattern association among the dominant species, the segregation index (D) seemed to indicate a high separation between the main populations (Table 3):

L. tetraphylla (central coast) and *P. noctiluca* (eastern

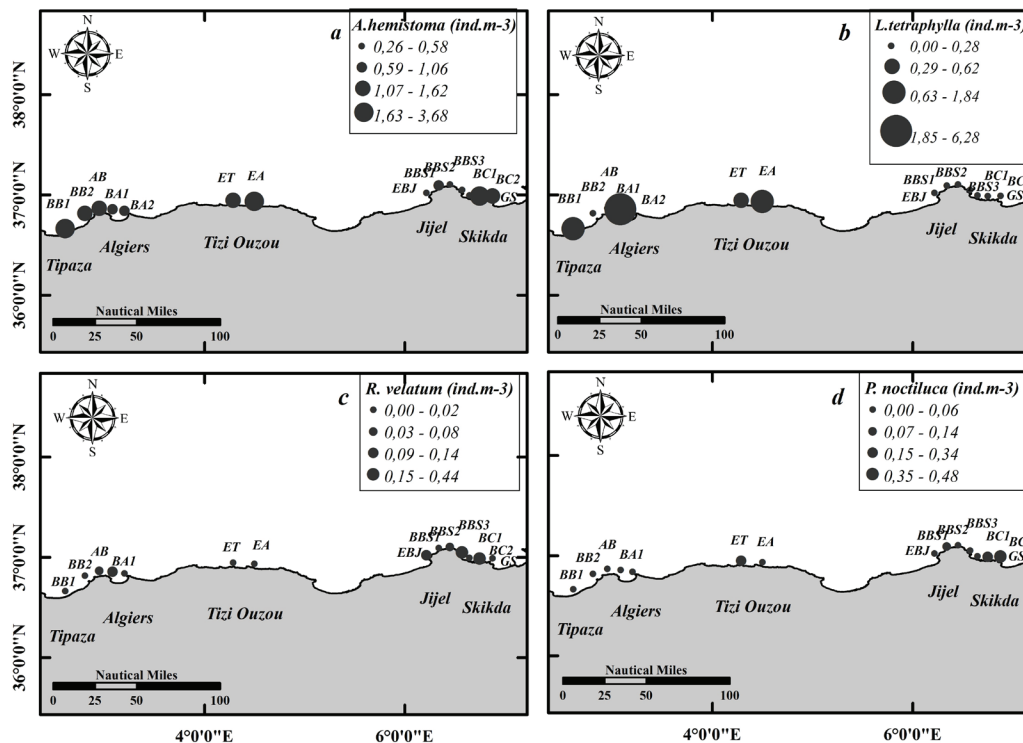


Fig. 5: Spatial distribution of the main species: a. *A. hemistoma*; b. *L. tetraphylla*; c. *R. velatum*; and d. *P. noctiluca* along the Algerian coast (2°E - 7°E) during the surveyed period.

Table 3. Segregation values (*D* index) recorded between pairs of dominant species along the Algerian coast.

Species	Segregation Index
<i>P. noctiluca</i> - <i>L. tetraphylla</i>	0,92
<i>R. velatum</i> - <i>L. tetraphylla</i>	0,86
<i>R. velatum</i> - <i>P. noctiluca</i>	0,76
<i>A. hemistoma</i> - <i>P. noctiluca</i>	0,55
<i>A. hemistoma</i> - <i>R. velatum</i>	0,50

coast), with $D = 0.92$;

L. tetraphylla (central coast) and *R. velatum* (eastern coast), with $D = 0.86$

R. velatum (eastern coast) and *P. noctiluca* (eastern coast), with $D = 0.76$.

Relationship between the species and environment factors

To identify the relationships between the medusae and environmental parameters, principal component analysis was used (Fig. 6). This analysis revealed the following three groups of variables:

Group 1 was composed of *P. noctiluca* and *R. velatum*, and they seemed to be associated with high temperature and high salinity.

Group 2 was composed of *A. hemistoma*, *S. bitentaculata*, *Clytia* spp. and *P. hemisphaericum*, and they seemed to be negatively correlated with temperature and salinity.

Group 3 was composed of the characteristic species of the central region, *L. tetraphylla* and the *E. paradoxica*

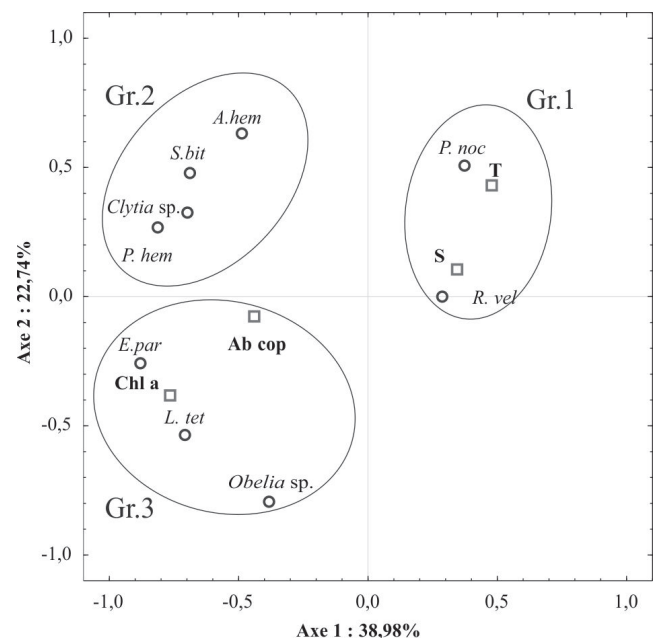


Fig. 6: Principal component analysis (PCA) showing the relationships between the medusae species and the environmental variables.

and *Obelia* spp., and the distribution of these species was positively correlated with the chlorophyll *a* concentrations and mesozooplankton prey abundance (copepods) (Fig. 6).

Table 4. Medusea found along the Algerian coast and in the Mediterranean Sea.

[1]: Dallot *et al.*, 1988 ; [2]: Goy *et al.*, 1991; [3]: Boero & Bouillon, 1993; [4]: Buecher & Gibbons, 1999; [5]:Daly Yahia *et al.*, 2003;[6]: Benović *et al.*, 2004; [7]: Sabatés *et al.*, 2010; [8]: Touzri *et al.*, 2010, 2012; [9]: Pestorić *et al.*, 2012; [10]: Ounissi *et al.*, 2016; [11]: Goy *et al.*, 2016.

Species	[1]	[2]	[3]	[4]	[5]	[6]	[7]	[8]	[9]	[10]	[11]
<i>L. blondina</i>	+	+	+	+	+	+		+			
<i>P. minima</i>	+	+	+	+				+	+		
<i>Clytia</i> spp.	+		+		+		+	+	+		
<i>C. hemisphaericum</i> (<i>C. hem</i>)		+	+			+		+			
<i>C. tetranema</i>			+								+
<i>E. paradoxica</i> (<i>E. par</i>)	+	+	+	+	+			+			
<i>Obelia</i> spp.	+	+	+	+	+	+	+	+	+	+	
<i>A. hemistoma</i> (<i>A. hem</i>)	+	+	+	+	+	+	+	+	+	+	
<i>L. tetraphylla</i> (<i>L. tet</i>)	+	+	+	+	+		+	+	+		
<i>R. velatum</i> (<i>R. vel</i>)	+	+	+	+	+	+	+	+	+		
<i>C. globosa</i>			+			+					
<i>Solmaris</i> sp.	+		+	+					+		
<i>S. bitentaculata</i> (<i>S. bit</i>)	+	+	+	+	+	+	+	+			
<i>P. noctiluca</i> (<i>P. noc</i>)			+	+	+		+	+		+	

Discussion

Biodiversity composition

Altogether, 14 species were sampled and identified that belonged to hydromedusae (13 species) and scyphomedusae (one species was *P. noctiluca*). The recorded species have previously been found in the Mediterranean Sea (Table 4). However, in the present study, in comparison with other investigations (Dallot *et al.*, 1988; Daly Yahia *et al.*, 2003; Touzri *et al.*, 2010, 2012), two species (*Cirrholovenia tetranema* and *Cunina globosa*) were recorded for the first time in the southwestern Mediterranean Sea.

Comparisons with the other studies from the adjacent areas of the Mediterranean were very delicate due to the different efforts and sampling periods. However, in the southwestern Mediterranean Sea (Alboran Sea), 27 species (Dallot *et al.*, 1988) and 18 species (Mills *et al.*, 1996) were counted. Along the Algerian coast, a lower biodiversity (6 species) was found in Algiers Bay (Seguin, 1973) and Annaba Bay (Ounissi *et al.*, 2016). Along the Tunisian coast, the biodiversity was composed of more than 20 species (Daly Yahia *et al.*, 2003; Touzri *et al.*, 2010). In the northern region (Ligurian Sea), more than 30 species were identified within the community (Berhaut, 1969; Goy, 1972; Buecher & Gibbons, 1999; Goy *et al.*, 2016). In the eastern Mediterranean Sea, more than 25 species were inventoried in the Adriatic Sea (Benović *et al.*, 2004; Lučić *et al.*, 2009) and 71 species were identified along the Lebanese coast (Goy *et al.*, 1991).

Medusa were mainly represented by holoplanktonic species. Certain species, such as *A. hemistoma* and *R. velatum*, were frequent and others were common (*S. bitentaculata*, *L. tetraphylla* and *P. noctiluca*). This trend

was also reported for the same populations in the western Mediterranean Sea (Buecher *et al.*, 1997; Daly Yahia *et al.*, 2003; Colin *et al.*, 2005; Benović *et al.*, 2004; Touzri *et al.*, 2010). On the other hand, except the populations of *Clytia* spp., *E. paradoxica*, and *Obelia* spp., meroplanktonic medusae, such as *C. tetranema*, *C. globosa*, *L. blondina*, and *P. minima*, were rarely sampled.

The most important forms identified in the present study were circumtropical species (*A. hemistoma*, *R. velatum*, *S. bitentaculata*, *L. tetraphylla* and *C. globosa*). In the Mediterranean Sea, medusa communities are strongly represented by species of this biogeographical origin (Boero & Bouillon, 1993) and are frequently dominated by a small number of highly adaptable species (Gili *et al.*, 1988).

Dominant populations and their variability

The total medusa abundances were less than 10 individuals.m⁻³. Multivariate analysis showed two different clusters: the central area (Bou Ismail and Algiers Bays; Tizi Ouzou coast), with up to 2 individuals.m⁻³, and the eastern area (Jijel coast; Beni Said and Collo Bays), which was characterized by low abundances (less than 2 ind.m⁻³). This quantitative difference was related to the higher contributing holoplanktonic species (*A. hemistoma*, *R. velatum*, *L. tetraphylla*, *P. noctiluca*). A similar result was reported in the other Mediterranean regions, including in Marseille (Berhaut, 1969), the Ligurian Sea (Goy, 1972), the Catalan Sea (Gili *et al.*, 1987), the Adriatic Sea (Benović & Bender, 1987; Lučić *et al.*, 2009) and the Tunisian coast (Touzri *et al.*, 2010).

The narrowness of the continental shelf could explain the dominance of these populations along the central part

of the Algerian coast. Holoplanktonic species are known to be most abundant in open waters (Trachymedusae and Narcomedusae). The same pattern has been reported in the South Adriatic (Pestorić *et al.*, 2012), the southern Benguela waters (Pagès & Gili, 1992) and the shelf area off the Mexican coasts (Seguar-puerta *et al.*, 2010).

Within the epipelagic layer (0-50 m), except during spring, Trachymedusae populations were the most represented (more than 50%). Holoplanktonic forms (Trachymedusae and Narcomedusae) appeared dominant during the oligotrophic period of the year. However, meroplanktonic species (Anthomedusae and Leptomedusae) were dominant during spring. The life cycles of meroplanktonic species are dependent on benthic food sources (Goy, 1997; Goy *et al.*, 2016).

The typical open-water species *A. hemistoma* (Touzri *et al.*, 2010) was the most abundant and widely distributed species in the two studied areas. Among hydromedusae, this species is the most abundant and is present year-round (Bouillon *et al.*, 2004; Sabatès *et al.*, 2010). Unlike most other medusae, *A. hemistoma* occupies a large trophic niche as an omnivore that feeds on microphytoplankton and protists (Colin *et al.*, 2005).

In contrast to the previous species, the population of *L. tetraphylla*, which is an oceanic and epipelagic species (Kramp, 1961), was mainly found in the central region, where it occurred in the highest numbers (0.74 ind.m⁻³ to 6.28 ind.m⁻³). *L. tetraphylla* represented up to 89% of the total abundance in the central region. In the eastern region, the contribution of this population was less than 2%. In the Mediterranean Sea, this medusa is among the most common epipelagic species and shows large interannual variations in both abundance and seasonality in relation to hydroclimatic conditions (Buecher *et al.*, 1997).

Furthermore, populations of warm-water oceanic species, such as *R. velatum* and *P. noctiluca*, (Russell, 1953; Goy *et al.*, 1989a), were common in the eastern region and represented up to 20% of the medusan abundance. The mauve stinger *P. noctiluca* is the most well-known medusae in the Mediterranean Sea. *P. noctiluca* has been reported to be the most abundant gelatinous predator characterized by undecennial blooming periods (Morand *et al.*, 1992; Buecher *et al.*, 1997).

The segregation index *D* among *L. tetraphylla* - *P. noctiluca* (0.92) and among *L. tetraphylla* - *R. velatum* (0.85) reflected the trend in their geographical distributions between the central and eastern regions. This species separation, which was especially recorded for more abundant and frequent species, is not specific to these pairs. This trend has also been observed between other medusa species, such as *L. tetraphylla* - *Nausisthoe punctata* and *A. hemistoma* - *Nausisthoe punctata* (Flores-Coto *et al.*, 2016).

In the Ligurian Sea, this phenomenon was documented for *P. noctiluca* in particular (Goy *et al.*, 1989b). The pullulation of this scyphomedusa is more pronounced in summer and autumn and is accompanied by low *Geryonia proboscoidalis* (Trachymedusae) and *Hippopodius hippopus* (Siphonophore) populations.

Relationships with hydrological parameters and food availability

Multivariate analysis indicated that temperature, salinity, chlorophyll *a* and copepod abundance were affected by the quantitative distributions (Fig. 6). Many investigations have found relationships between biological and hydrological parameters (Benović & Bender, 1987; Buecher *et al.*, 1997; Daly Yahia *et al.*, 2003; Purcell *et al.*, 2007).

The quantitative distributions of the medusae were positively correlated with the copepod community (Spearman rho $\rho = 0.56$). This result has been previously found in the Mediterranean (Gili *et al.*, 1988; Batistic *et al.*, 2004; Benović *et al.*, 2004). This mesozooplanktonic group has been recognized as important prey for medusan fauna (Colin *et al.*, 2005). In the central region (2.61° to 4.50° E), the greatest abundances of medusae (up to 2 individuals.m⁻³) were linked to the highest levels of mesozooplankton (up to 50 individuals.m⁻³). The lowest values (less than 2 individuals.m⁻³) reported in the eastern region (6.61° to 6.65° E) were associated with the lowest levels of mesozooplankton (< 50 individuals.m⁻³). These results explain the statistical differences between the two sampling regions ($p = 0.029$).

The greatest abundances of the most common species, such as *L. tetraphylla*, were linked to the chlorophyll *a* concentrations and copepods abundance. These populations are known to be associated with enriched waters with enhanced zooplanktonic production (Buecher *et al.*, 1997). Other populations (*Obelia* spp.) were associated with the chlorophyll *a* concentrations. This genus omnivorously feeds on planktonic and bacterial prey (Boero *et al.*, 2008). This relationship could explain the predominance of these populations in the central region, where the highest chlorophyll *a* concentrations, probably due to anthropogenic eutrophication, were recorded.

In addition, the low abundance (< 10 ind.m⁻³) of medusae was a response to a decrease in the abundance of mesozooplankton prey (< 50 ind.m⁻³). This decrease was linked to the low chlorophyll *a* values (Mills, 2001). In the Algerian basin, except in the inshore cyclonic eddy and frontal area (1°E – 4°E), the concentration of chlorophyll *a* (< 1 mg.m⁻³) was representative of an oligotrophic ecosystem (Taupier-Letage *et al.*, 1988; Raimbault *et al.*, 1993).

The abundance of *P. noctiluca* was associated with warm water (> 26°C). The same results were reported in the northern Mediterranean Sea (Goy *et al.*, 1989a). The evolution of their biological cycle from eggs to the adult stages was faster as the temperature increased (Morand *et al.*, 1992). This parameter was most important because it controlled the temporal and spatial distributions of the populations (Buecher *et al.*, 1997; Purcell *et al.*, 2007).

On the other hand, concerning the segregation observed between the populations of *L. tetraphylla* and *P. noctiluca* that was previously reported in the Mediterranean Sea (Buecher *et al.*, 1997), food availability, either through competitors or predators, could explain the distributions of these species (Legovic, 1987; Buecher *et al.*, 1997). *L.*

tetraphylla and *P. noctiluca*, at the same size, they have similar trophic regimes. Nevertheless, during different biological activities (reproduction or growth), the trophic behaviours of the two jellyfish populations are different. *L. tetraphylla* mostly feeds on copepods, but *P. noctiluca* can catch a large prey, including medusae (e.g., *L. tetraphylla*) and meso-macrozooplankton (Buecher *et al.*, 1997).

The present study provides the first report on the composition and quantitative repartition of the medusa community along the Algerian coast. The biodiversity of this fauna in the autumn of 2014 included fourteen species. The results obtained in this study indicate that the distribution pattern of this gelatinous group can be linked to environmental conditions. The dominant and most common species were abundant due to their life cycle characteristics, environmental conditions and food availability.

This knowledge should be considered as complementary to anterior zooplankton studies along the Algerian coast and the southwestern Mediterranean Sea. However, the accumulation of sampling series across different regions and seasons remains necessary to better understand the distribution pattern in relation to environmental and climatological factors and to allow the understanding of the role and the impact of these zooplankton on the pelagic ecosystem.

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