



Environmental forcing on jellyfish communities in a small temperate estuary

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ABSTRACT

The impact of biological, hydrodynamic and large scale climatic variables on the jellyfish community of Mondego estuary was evaluated from 2003 to 2010. Plankton samples were collected at the downstream part of the estuary. Siphonophora *Muggiaea atlantica* and *Diphyes* spp. were the main jellyfish species. Jellyfish density was generally higher in summer and since 2005 densities had increased. Summer community analysis pointed out *Acartia clausi*, estuarine temperature and salinity as the main driven forces for the assemblage's structure. Also, Chl *a*, estuarine salinity, runoff and SST were identified as the major environmental factors influencing the siphonophores summer interannual variability. Temperature influenced directly and indirectly the community and fluctuation of jellyfish blooms in the Mondego estuary. This study represents a contribution to a better knowledge of the gelatinous plankton communities in small temperate estuaries.

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1. Introduction

The way that marine ecosystems respond to overexploitation and changing climate is of principal concern in sustainability science, and understanding how these factors interact to affect marine populations is a challenge for global ecology (Molinero et al., 2009). Changes in climatic condition may affect the dynamics of pelagic ecosystems and several studies have pointed out plankton as important indicators of these changes (e.g. Hays et al., 2005; Molinero et al., 2005).

In recent years, there has been growing evidence that gelatinous blooms are increasing in frequency and persisting longer than usual, and several studies have shown links between the abundance of gelatinous zooplankton and climatic fluctuations in marine ecosystems worldwide (e.g. Mills, 2001; Lynam et al., 2005; Purcell, 2005; Xian et al., 2005). Jellyfish show opportunistic life histories, responding quickly to environmental changes by enhancing their feeding, growth, and reproduction in optimal conditions, thereby reaching massive population size. These proliferations have a wide range of implications both ecological and economic interfering with fishing activities (Purcell and Arai, 2001;

Lynam et al., 2006), killing farmed fish (Doyle et al., 2008) or even acting as vectors of fish pathogens (Delanoy et al., 2011). Hence, identifying the factors shaping the population size of jellyfish is fundamental to achieve an ecosystem approach to fishery management (Lynam et al., 2005).

Recent studies have shown that the North Atlantic Oscillation (NAO) pattern is one of the main driving forces influencing north Atlantic marine systems (Hurrell et al., 2003) with several studies showing a relationship between the NAO and variability in gelatinous zooplankton (e.g. Lynam et al., 2004, 2005; Purcell, 2005; Attrill et al., 2007). The NAO Index alters the prevailing wind field over northern Europe and influences atmospheric variables (i.e. wind speed and direction, air temperatures, precipitation, etc.) leading to changes in sea temperature, salinity, river runoff, vertical mixing, and oceanic circulation (Lynam et al., 2005). According to Condon et al. (2012) the knowledge of historical ecosystem base-lines is essential to differentiate whether the number of gelatinous zooplankton blooms have increased or they are undergoing a longer-term (e.g., decadal) fluctuation driven by climate or other cycles.

Recent studies indicate that several nursery areas along the Iberian Coast have been exposed to climate-related hydrographic changes impacting both benthic (e.g. Cardoso et al., 2008; Grilo et al., 2011) and pelagic communities (e.g. Marques et al., 2007; Dolbeth et al., 2010; Primo et al., 2011) leading to the appearance of invasive species or to an increase in density of subtropical species (e.g. Chícharo et al., 2009; Martinho et al., 2010). Thus, this study

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aims to investigate jellyfish community of the Mondego estuary, by assessing the impact of biological, hydrodynamic and large scale climatic variables on species abundance. The impact of climate variability on jellyfish communities was evaluated by analysing eight years of historical data.

2. Material and methods

2.1. Study site

The Mondego River estuary is a mesotidal system, located in the western Atlantic coast of Portugal (40°08'N, 8°50'W) (Fig. 1). The hydrological basin of the Mondego has an area of 6670 km² and provides an average freshwater flow rate of 79 m³ s⁻¹ (Dolbeth et al., 2010). Mondego is a well-mixed estuary with two channels, northern and southern, separated by Murraceira Island. The north arm is deeper (5–10 m at the high tide), has a tidal range of 2–3 m and constitutes the main navigation channel. The south arm is shallower (2–4 m at high tide) and has a tidal range of 1–3 m and is characterised by large areas of exposed intertidal flats during low tide. Most of the freshwater discharge is throughout the northern channel since it is directly connected with the Mondego River. In the southern channel, water circulation is mostly due to tides and the freshwater input from a small tributary, the Pranto River which is small and artificially regulated by a sluice.

2.2. Sample collection

Jellyfish organisms were collected during plankton surveys performed monthly by subsurface (10 cm below surface) horizontal tows from January 2003 until December 2010, at three downstream sampling stations of the Mondego estuary (M – mouth, N1 – northern arm, S1 – southern arm) (Fig. 1). Samples were collected with a 335 µm mesh sized plankton net (diameter: 0.5 m) fitted with a Hydro-Bios flowmeter (average volume: 50 m³). After collection, samples were immediately preserved in 4% borax-buffered formalin seawater and transported to the laboratory. At each sampling site salinity and water temperature (°C) were recorded and subsurface water samples were collected for subsequent determination for chlorophyll *a* (mg m⁻³). In the laboratory, jellyfish were then sorted, identified to the species level whenever possible and densities expressed as number of individuals per cubic metre (ind. m⁻³). Densities of copepods *Acartia tonsa* and *Acartia clausi* (ind. m⁻³) and of fish larvae (ind. 100 m⁻³) present in each sample were also

recorded. Monthly freshwater discharge from the Mondego River was acquired from INAG (<http://snirh.pt/>) measured at Açude Ponte Coimbra 12G/01AE station. North Atlantic Oscillation (NAO) index (given by the pressure differences between Lisbon (Portugal) and Reykjavik (Iceland)) data were obtained from the Climatic Research Unit website (<http://www.cgd.ucar.edu>). Sea surface temperature (SST), wind data, both north–south and east–west components, were acquired from the International Comprehensive Ocean–Atmosphere Data Set (ICOADS) online database (<http://dss.ucar.edu/pub/coads>) concerning the 1°Lat × 1°Long square nearest to the Mondego estuary.

2.3. Data analysis

Only hydromedusae and siphonophorae jellyfish were considered for the analysis. Mean monthly estuary values were obtained by averaging non-zero values of the three sampling stations at each month.

Main species bloom duration was determined by calculating mean monthly density (across all years) and identifying the bloom beginning (the time at which density reached a level corresponding to 15% of the mean annual cumulative) and the bloom end (time at which density reached a level corresponding to 85% of the mean annual cumulative) (Schlüter et al., 2010).

Distance-based linear model (DISTLM) was carried out to perform permutational regression between jellyfish assemblages and environmental variables assessing the relative contributions of environmental variables structuring summer jellyfish communities. DISTLM allows for significance testing of explanatory variables for univariate or multivariate response variables in the form of a resemblance matrix performing simultaneously variation partitioning (Anderson et al., 2008).

Jellyfish species and environmental data were $\ln(x + 1)$ transformed (except for NAO and wind components) and a Bray–Curtis dissimilarity matrix was used. The best subsets model selection routine, with R^2 as the selection criterion based on 999 permutations, was used to choose a reduced number of environmental variables and the best model with 6 variables was selected. Only data corresponding to summer (June, July and August) was used and variables tested included biological (chlorophyll *a* concentration, *A. clausi*, *A. tonsa* and fish larvae mean densities), hydrological (water temperature, salinity and runoff) and large scale climate (NAO Index, Sea Surface Temperature (SST), N–S wind, E–W wind) variables. Difference between estuarine and sea surface temperature was also included (ΔT).

Interannual summer bloom period variability of the main species present in the community was also studied by analysing its relationships with the environmental variables using a univariate DISTLM for each of the species separately. Analysis was performed in summer $\ln(x + 1)$ transformed data based on Euclidean distance matrix and with the best 3 subset model with R^2 was used as the selection criterion. DISTLM routines were performed with PERMANOVA+ v1 for PRIMER® 6.1 package.

3. Results

3.1. Environmental characterization

Estuarine and sea surface temperature ranged between 8 and 22 °C (Fig. 2A). SST presented higher values than estuarine temperature however, during spring the latter was generally higher (Fig. 2A). Highest estuarine temperature was recorded during summer of 2008 (19.0 °C) and the lowest during winter 2003 (11.5 °C), while sea surface temperature reached maximum values in summer 2010 (22.7 °C) and minimum in spring 2004 (12.1 °C)

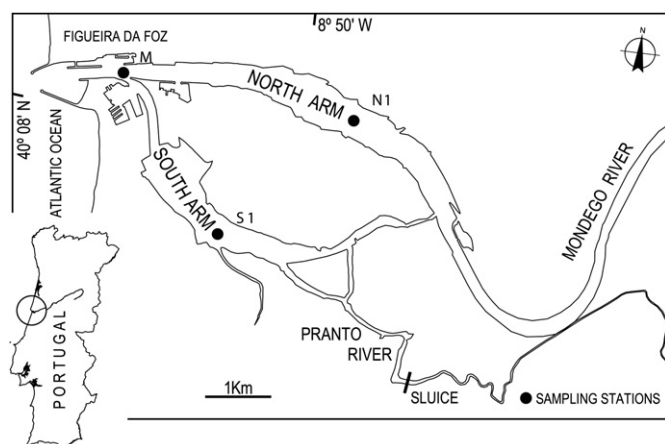


Fig. 1. Location of jellyfish sampling stations (M, Mouth, S1, southern arm, N1, northern arm) in the Mondego estuary.

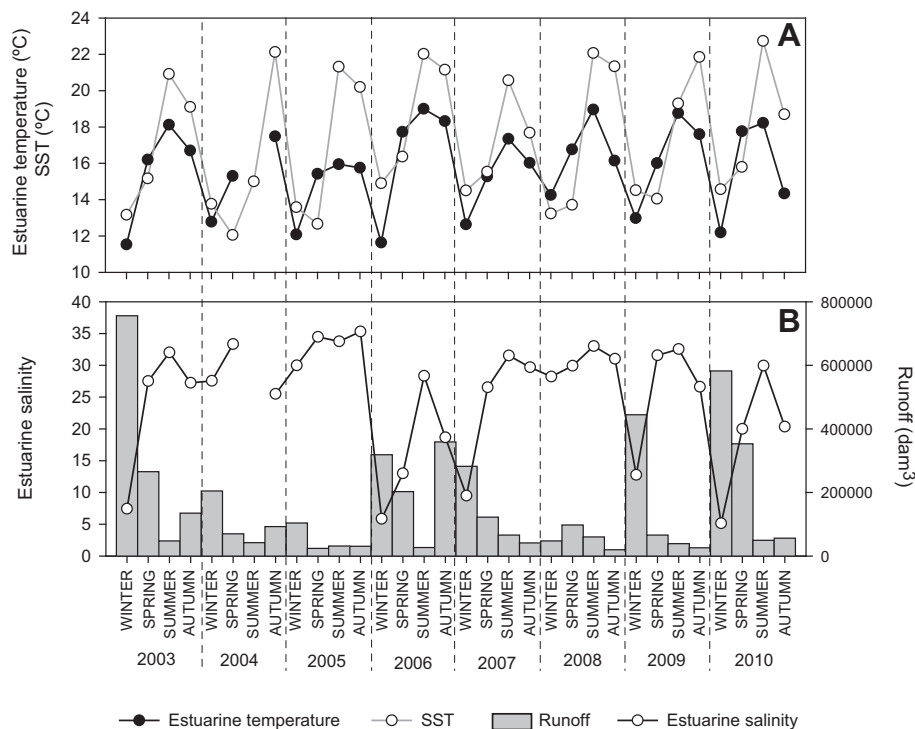


Fig. 2. Seasonal variability of estuarine and sea surface temperature (A), runoff and estuarine salinity (B) during the study period in the Mondego estuary.

(Fig. 2A). Both presented a clear seasonal pattern with higher temperatures during summer and lower during winter (Fig. 2A).

The Mondego estuary presented a typical seasonal pattern of runoff throughout the 8-year period with higher values during winter and lower during summer (Fig. 2B). However, 2004, 2005 and 2008 years showed a low runoff contrasting to 2006, 2007 and 2010 when the freshwater discharge was high, mainly during winter and spring (Fig. 2B). Estuarine salinity also presented higher values during summer, reaching maximum values during 2004–2005 period and in 2008. Lower values were recorded during winter of 2003, 2006, 2007 and 2010 (Fig. 2B).

3.2. Jellyfish abundance and composition

During the study, the mean density of jellyfish reached 273 ind. m^{-3} and densities were generally higher during summer (Fig. 3). Hydromedusae peak densities reached 30 ind. m^{-3} in 2003, lowered in 2005 and 2006 and maintained around 25 ind. m^{-3} in subsequent years (Fig. 3). Siphonophorae presented a similar pattern of total density since it was the main jellyfish group collected. This group presented high densities in summer and since 2005 peak densities have reached higher values (maximum in 2009) (Fig. 3). This pattern was not so evident for hydromedusae species (Fig. 3).

The Mondego estuary had 15 taxa of hydromedusae and 2 taxa of siphonophora (Table 1). *Leuckartiara octona* and *Hydractinia carnea* presented the highest mean density of hydromedusae but showed low frequency of occurrence representing punctual peaks of density. *Obelia* spp. and *Lizzia blondina* were the most frequent species which presented higher densities (Table 1). Unidentified hydromedusae represented 10% of the total hydromedusae catch and were generally damaged organisms. The two taxa of siphonophorae (*Muggiata atlantica* and *Diphyes* spp.) showed similar pattern of density and frequency of occurrence (Table 1).

M. atlantica and *Diphyes* spp. showed an extended period of occurrence since they can be found from January till November.

Comparatively, *M. atlantica* showed a longer bloom period (April–August) (Fig. 4). Concerning the hydromedusae species, *Obelia* spp. and *Hydractinia minima* were the species with higher persistence (January–November) (Fig. 4). The *Obelia* spp. bloom started in March while *L. blondina* only started in June. Furthermore *Clytia hemisphaerica* and *Solmaris corona* showed the largest bloom period (Fig. 4). *L. octona* and *H. carnea* presence occurred in summer 2008 (*L. octona*) and spring/autumn 2010 months (*H. carnea*) (Fig. 4).

Jellyfish assemblages were mainly constituted by *M. atlantica*, *Diphyes* spp. and *Obelia* spp. which were generally present in all seasons (Table 2). The majority of species presented higher densities during summer and lower in winter. However, in 2010 maximum densities occurred during spring (Table 2). *H. minima* was an important species in winter assemblages, mainly in 2008 and 2009 however, its higher density occurred during spring and summer periods (Table 2). *C. hemisphaerica* higher densities occurred mainly in spring, except during 2007 when its density reached maximum values during autumn (Table 2). In summer, *L. blondina* reach higher densities than *Obelia* spp., mainly in 2003 and 2007 (Table 2). The hydromedusae *Liriope tetraphylla* reach highest densities in autumn 2005 being also an important species on jellyfish assemblages in autumn 2009 and summer 2003 (Table 2).

Jellyfish mean density lowest values occurred in 2004. After that, density has increased until 2009, decreasing again in 2010 (Table 2). Similarly lower number of species occurred in 2004; however, 2010 presented the highest number of species and diversity (Table 2). Shannon Wiener diversity was also high during 2005 and 2007 while 2003 presented the lower diversity (Table 2).

Since the summer of 2004 was not sampled, this year was not considered in the subsequent analysis.

3.3. Jellyfish relationship with environmental factors

Marginal tests resulting from DISTLM analysis showed that summer jellyfish community presented a significant relationship

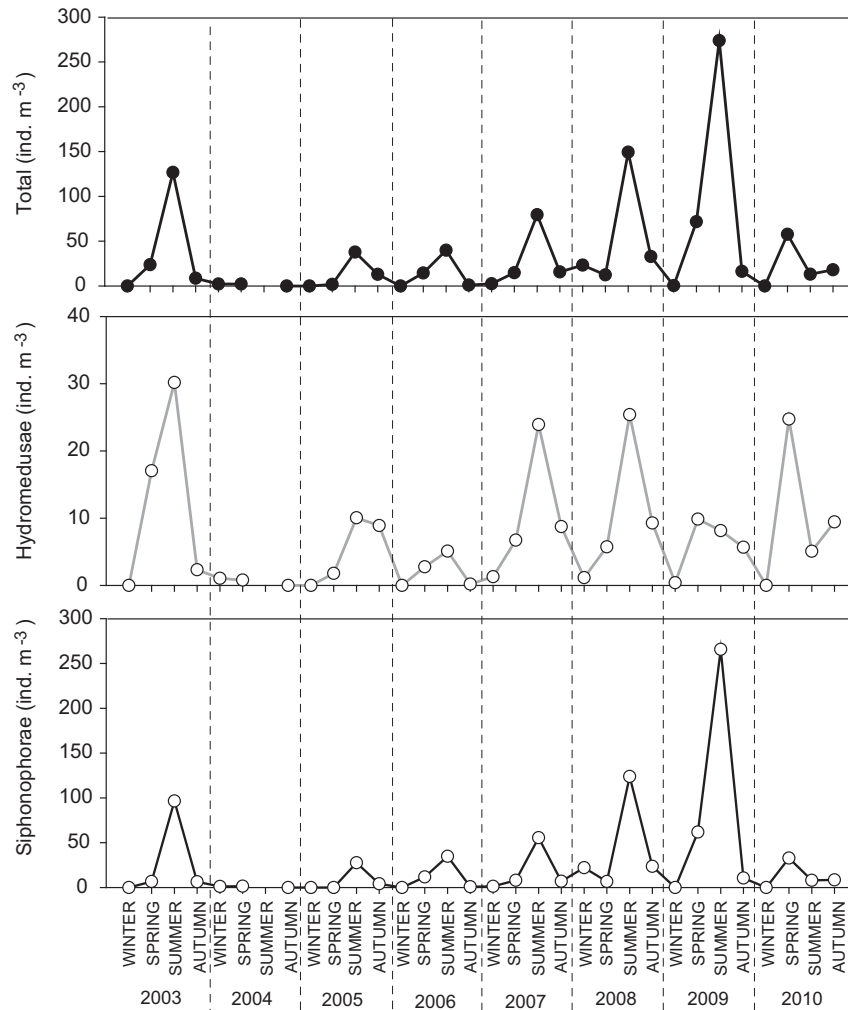


Fig. 3. Seasonal variability of jellyfish density (ind. m⁻³) during the study period in the Mondego estuary.

with *A. clausi*, temperature and salinity (Table 3). When considered alone, salinity explained 20% of the variability observed, *A. clausi* 17% and estuarine temperature 15% (Table 3). Despite not significant, sea surface temperature, deltaT and N–S wind component were also

Table 1

Mean density (ind. m⁻³ and %) and frequency of occurrence (%) of jellyfish in positive samples (i.e. samples with jellyfish) in the Mondego estuary.

		Mean	%	FO
Hydromedusae	<i>Leuckartiara octona</i>	10.4	19	4
	<i>Lizzia blondina</i>	7.9	14	27
	<i>Hydractinia carnea</i>	5.9	11	5
	Hydromedusae n.id.	5.7	10	4
	<i>Obelia</i> spp.	5.5	10	42
	<i>Amphinema dinema</i>	3.8	7	1
	<i>Liriope tetrphylla</i>	3.7	7	10
	<i>Sarsia gemmifera</i>	2.7	5	2
	<i>Clytia hemisphaerica</i>	2.6	5	18
	<i>Sarsia prolifera</i>	1.9	3	5
	<i>Hydractinia minima</i>	1.4	3	23
	<i>Solmaris corona</i>	1.4	2	13
	<i>Bougainvillia muscus</i>	1.0	2	2
	<i>Sarsia tubulosa</i>	0.9	2	2
	<i>Margelopsis haeckeli</i>	0.8	1	2
	<i>Eutima gracilis</i>	0.5	1	1
Siphonophorae	<i>Muggiaea atlantica</i>	27.7	52	55
	<i>Diphyes</i> spp.	25.2	48	42

included by the analysis in the best 6 subset model (Table 3). The selected model explained 58% of the variation observed in the jellyfish community during summer conditions (Table 3).

DISTLM analysis showed that *M. atlantica* summer interannual variability can be related with Chl *a* (Pseudo-*F* = 0.72, *p* = 0.412, prop. < 0.01), estuarine salinity (Pseudo-*F* = 9.08, *p* = 0.007, prop. = 0.34) and runoff (Pseudo-*F* = 0.33, *p* = 0.580, prop. = 0.02). The selected model explained 47% of the *M. atlantica* summer density variability observed. Model including Chl *a* (Pseudo-*F* = 0.25, *p* = 0.603, prop. = 0.01), estuarine salinity (Pseudo-*F* = 4.14, *p* = 0.058, prop. = 0.19) and sea surface temperature (Pseudo-*F* = 1.39, *p* = 0.263, prop. = 0.07) explained 50% of the *Diphyes* spp. summer interannual variability observed.

Generally, during the studied period, *M. atlantica* density increased with estuarine salinity and decreased with Chl *a* concentration. During 2003–2006 period increasing runoff lead to an increase of the siphonophorae density. After that, the relation seemed to change and *M. atlantica* density decreased with runoff (Fig. 5). Highest densities observed in 2003, 2008 and 2009 occurred with a combination of low runoff and Chl *a* concentration and high estuarine salinity (Fig. 5). *Diphyes* spp. density increased with increasing estuarine salinity, mainly during 2006–2009 period, and with sea surface temperature. On the contrary, *Diphyes* spp. summer density decreased with Chl *a* concentration (Fig. 5).

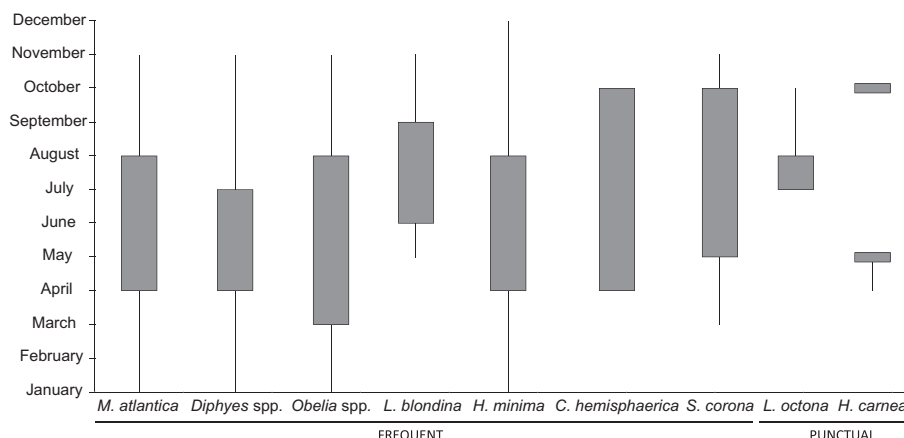


Fig. 4. Bloom periods of main jellyfish species present in the Mondego estuary. Lines indicate the species presence and grey boxes blooms periods.

4. Discussion

The Mondego estuary jellyfish assemblages presented higher hydromedusae than siphonophorae diversity. On the other hand, siphonophorae densities were superior. In contrast to hydromedusae, the siphonophore life-cycle is entirely pelagic (Bouillon et al., 2006), increasing its presence and density in plankton. Additionally, their higher vulnerability to currents and water mass movements may result in higher transport inside the estuary. Data on siphonophores are relatively scarce. They are widespread in the oceans and the majority of the species are mainly referred as truly oceanic (Pugh, 1999), however, its presence has already been detected also in coastal, bays and estuarine waters (e.g. Byrne, 1995; Molinero et al., 2005; Sanvicente-Añorve et al., 2009).

Hydromedusae diversity in the Mondego estuary (15 taxa) was higher than at the coastal areas of Northern Adriatic Sea (9 taxa; Benovic and Lucic, 1996) or NW Mediterranean Sea (8 taxa; Sabatés

et al., 2010) and similar to the reported at Southern Adriatic Sea (16 taxa; Benovic and Lucic, 1996). However, it was lower than the diversity reported for Bombay harbour, India (26 hydromedusae; Santhakumari et al., 1999) or Lough Hyne, Ireland (21 taxa; Ballard and Myers, 2000). Concerning siphonophorae diversity, the Mondego estuary (2 taxa) presented generally lower values than those reported at coastal areas of southern Gulf of Mexico (23 taxa; Sanvicente-Añorve et al., 2009) and NW Mediterranean Sea (13 taxa; Sabatés et al., 2010).

Siphonophores and hydromedusae presence close to the shelf/slope front was previously related to increased primary and secondary production in the frontal area (e.g. Sabatés et al., 2004). Also, coastal hydromedusae may be concentrated at the front as a result of advection since they cannot produce new medusae in open waters far from shore (Sabatés et al., 2010). Due to its proximity, eventually both organisms end up by being entrained to lower reaches of estuaries.

Table 2
Interannual and seasonal mean density (ind. m⁻³) and diversity of main jellyfish species present in the Mondego estuary.

		2003	2004	2005	2006	2007	2008	2009	2010	Mean
Winter	<i>Muggiaea atlantica</i>		1.19			0.77	14.61			2.07
	<i>Diphyes</i> spp.					1.08	7.46			1.07
	<i>Obelia</i> spp.		1.05			1.92	0.97			0.49
	<i>Hydractinia minima</i>						0.18	0.18		0.04
	<i>Liriope tetraphylla</i>							0.20		0.03
Spring	<i>Muggiaea atlantica</i>	6.70	1.37		4.40	4.26	3.61	40.64	17.40	9.80
	<i>Diphyes</i> spp.				7.29	3.69	2.99	21.18	15.43	6.32
	<i>Obelia</i> spp.	16.14			0.91	5.40	3.92	2.25	15.59	5.53
	<i>Clytia hemisphaerica</i>		0.45	1.78		0.58	0.54	1.75	3.95	1.13
	<i>Hydractinia minima</i>	0.51			0.94	0.48		2.45	0.67	0.63
Summer	<i>Lizzia blondina</i>				0.91		1.26	0.41		0.32
	<i>Muggiaea atlantica</i>	96.55	—	13.04	16.83	22.64	85.39	131.45	3.76	52.81
	<i>Diphyes</i> spp.		—	14.59	35.39	32.90	38.53	134.24	4.25	37.13
	<i>Lizzia blondina</i>	22.73	—	5.41	2.35	18.25	2.18	4.36	4.32	8.51
	<i>Obelia</i> spp.	4.33	—	1.69	4.35	5.27		2.63	0.35	2.66
Autumn	<i>Hydractinia minima</i>		—	2.46	0.48	0.40	0.43	0.22	0.19	0.60
	<i>Liriope tetraphylla</i>	2.93	—	0.23						0.45
	<i>Clytia hemisphaerica</i>	0.20	—					0.68	0.22	0.16
	<i>Diphyes</i> spp.			1.37	0.94	3.13	11.55	6.49	10.68	4.27
	<i>Muggiaea atlantica</i>	6.34		2.67	0.33	3.77	12.05	4.10	2.07	3.92
	<i>Obelia</i> spp.	0.56		1.84		3.37	0.77	1.04	2.32	1.24
	<i>Liriope tetraphylla</i>	0.48		5.65			0.17	2.71		1.13
	<i>Lizzia blondina</i>	1.11		0.94			5.17	0.25	0.33	0.97
	<i>Clytia hemisphaerica</i>					3.15	0.29	0.35	1.47	0.66
	<i>Hydractinia minima</i>	0.18			0.27		0.17	0.52		0.14
	Mean	6.35	0.23	2.07	3.02	4.44	7.69	14.32	3.32	
	Number of species	7	4	8	6	8	11	11	14	
	Shannon Diversity	0.41	0.45	0.75	0.49	0.67	0.53	0.44	0.79	

Table 3

Marginal tests for the six variables included in the DISTLM best 6 subset analysis. SST, Sea surface temperature; deltaT, difference between mean temperature at the estuary and mean Sea surface temperature; N–S, North–South wind component.

Variable	Pseudo-F	p	Prop.
<i>Acartia clausi</i>	3.78	0.025	0.17
Temperature	3.07	0.033	0.15
Salinity	4.42	0.014	0.20
SST	0.82	0.457	0.04
deltaT	1.37	0.224	0.07
N–S	0.78	0.471	0.04

Main hydromedusae species in Mondego estuary were *Obelia* spp. and *L. blondina*. Species of the genus *Obelia* were some of the most regularly encountered and abundant medusae in Lough Hyne being commonly found around Irish (Ballard and Myers, 2000), Danish (Hansson et al., 2005) and Mediterranean coastal waters (Sabatés et al., 2010). *L. blondina* was previous recorded in Iceland, North Sea, British Isles and Mediterranean Sea (Russell, 1953). The present study showed that hydromedusae assemblage at the Mondego estuary was mainly composed by a few common species (*Obelia* spp., *L. blondina*, *C. hemisphaerica* and *L. tetraphylla*, 80% of total density) and several occasional species. The presence of rare species may be related with specific environmental and advection patterns that entrain organisms into the estuary. Both siphonophores species presented similar densities and occurrence. Siphonophores species like *M. atlantica* may reach up to 30–50 ind. m⁻³ in very productive regions (e.g. Thibault-Botha et al., 2004) swarming up to 500 ind. m⁻³ during outbreak events (e.g. Greve, 1994).

Mondego estuary jellyfish showed a seasonal pattern with increased abundances mainly during summer months. Despite species presence throughout the year, summer was the main season of bloom occurrence in the estuary. Most gelatinous zooplankters have life-histories with asexual reproduction and extraordinary growth rates that allow them to undergo rapid population increases (Graham et al., 2001). According to Graham et al. (2001), rapid changes in jellyfish concentrations can be due either to rapid population growth (a true bloom) or to a re-distribution or re-dispersion of a stable population (an apparent bloom). True blooms are in part a consequence of seasonal life

cycles, and consequently, many jellyfish species have the potential to bloom, generally in spring and summer in temperate regions (Hamner and Dawson, 2009).

During the summer period, Mondego estuary salinity and temperature were higher which may promote jellyfish entrance and growth in the estuary. According to Arai (1992), seasonal distribution and abundance of planktonic cnidarians is primarily governed by factors controlling the release of the larvae and factors as temperature, food abundance, salinity or the ratio of light to dark are known to affect the liberation of medusae from hydroids. The seasonal jellyfish bloom is common in many marine environments, but there is also great interannual variability (Lynam et al., 2004; Purcell, 2005). Gibbons and Richardson (2009) found that at North Atlantic Ocean, seasonal and interannual variability on jellyfish peaks can be related with peaks in phyto, zooplankton and with temperature changes. In fact, salinity and runoff were also the environmental factors which presented higher interannual variability in the Mondego estuary. The years of 2004, 2005 and 2008 presented generally particularly low runoff and high salinity. Similar climatic conditions were already related with changes in Mondego estuarine pelagic and benthic communities (e.g. Marques et al., 2007; Martinho et al., 2007; Grilo et al., 2011; Primo et al., 2011). This high interannual variability also affected Mondego estuary jellyfish assemblages since they showed to be closely related with these environmental factors.

In the Mondego estuary, salinity was the main factor affecting jellyfish assemblages, explaining around 20% of the variability observed during summer, being particularly related with siphonophores abundance. Salinity was also the main environmental factor influencing the abundance of the dominant siphonophores in the Bay of Villefranche (Licandro et al., 2011). Abrupt changes in salinity may affect the buoyancy and reproduction rate of cnidarians (Mills, 1984; Ma and Purcell, 2005). The rate of osmotic acclimation of cnidarians is species-specific and varies according to their swimming behaviour (Mills, 1984). Additionally, the reduced turbulence and vertical mixing associated with high stability of the water column during thermal and halocline may favour the accumulation and maintenance of jellyfish swarms (Graham et al., 2001).

Foremost in estuaries, increased salinity indicate a higher predominance of oceanic water, enhancing the entrance of marine organisms and their presence in the estuary. In addition to salinity,

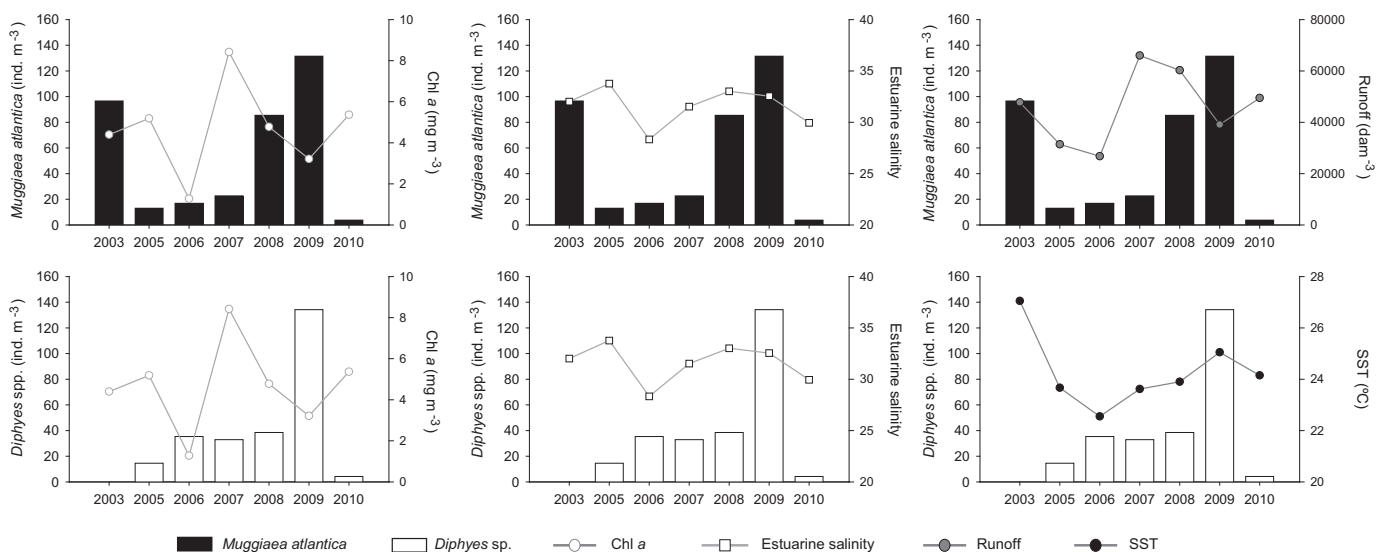


Fig. 5. Summer mean variability of *Muggiaea atlantica* and *Diphyes* spp. density and main environmental factors identified by best 3 subset DISTLM analysis for each species. Chl a, Chlorophyll a concentration; SST, sea surface temperature.

Chl *a* concentration and runoff were related with siphonophores interannual variability in the Mondego estuary. Chl *a* can be associated with turbidity which, as runoff, act as indicator of higher freshwater flux. In opposition to a salinity increase, an evidence of higher marine water intrusion in the estuary, an increased freshwater flow will prevent the entrance of marine organisms as siphonophores. Increased abundance of marine plankton during low runoff/high salinity periods was already recorded in the Mondego estuary (e.g. Marques et al., 2007; Primo et al., 2011).

Temperature was also an important factor structuring Mondego estuary summer jellyfish assemblages, either estuarine and sea surface temperature or the difference between both. According to Attrill and Power (2002) estuarine nursery grounds may act as thermal buffers against more severe open-sea conditions without being affected directly by marine conditions. Sea surface temperature was also the main environmental factor influencing the abundance of the siphonophores. A number of environmental cues have been linked to the release of medusae by benthic life-history stages of cnidarians however, temperature has the greatest support in the literature (e.g. Carré and Carré, 1990; Ballard and Myers, 2000; Sanvicente-Añorve et al., 2009). According to Brodeur et al. (1999), an increase in food or temperature could enable greater spring survival of young medusa, faster individual growth rates and overall jellyfish biomass. The role of temperature may be more complex since it can regulate directly or indirectly the food web through “bottom up” or “top down” alterations (Frank et al., 2005; Polovina et al., 2008). Also, direct effects of temperature can be positive (increased strobilation rates and hence the production of young medusoids) and negative (increased mortality of the benthic polyp) (Liu et al., 2009). Several studies had linked variations in jellyfish abundance with climate, particularly temperature and salinity (reviewed in Purcell, 2005, 2007) however the processes at play can differ by region. Purcell et al. (1999) concluded that the warm sea temperature in 1983 may have contributed to the extremely high medusa abundance by increasing the rate of strobilation and ephyrae production in Chesapeake Bay while Gibbons and Richardson (2009) found that SST correlated positively with gelatinous zooplankton abundance in the North Atlantic Ocean, but not in European shelf seas as a whole.

Sea surface temperature (SST) has been often related to the dominant signal of climatic variability NAO (e.g. Molinero et al., 2008, 2009; García-Comas et al., 2011; Lynam et al., 2011). However, in the Mondego estuary, increased jellyfish density was not directly related with the NAO index. This is probably due to the fact that, during summer, north Atlantic pressure dipole becomes much weaker and the immediate effect of the NAO becomes non-significant (Lynam et al., 2005). The NAO is primarily a winter phenomenon, so its connection with the wind, temperature and precipitation fields is strongest during winter. This suggests, in the first instance, that ecological mechanisms operating during winter are more likely to be affected by the NAO than those operating during summer (Ottersen et al., 2001). Also, the NAO appears to be a good proxy for winter SST and wind strength in the North Sea, but this is not the case on the western coast of the Iberian Peninsula (Ottersen et al., 2001).

Large climate events and their influence in winds and ocean currents seemed to influence directly and indirectly the community and the appearance of jellyfish blooms. In the Mondego estuary, temperature was a major factor influencing both jellyfish communities.

According to Condon et al. (2012), the major impediment to detecting trends in jellyfish populations is the lack of a defined baseline, due to a scarcity of long-term data on gelatinous zooplankton. This study, therefore, represents an important contribution to a better understanding of these communities and

environmental factors affecting their blooms. Also, with the increasing tendency of occurrence of extreme weather events, it is essential to determine in what extent these events affect plankton communities and the upper trophic levels and ecosystems functions and resilience.

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