High spatial heterogeneity of two planktonic cnidarian species related to the variability of a shelf-slope front at short time scales

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Summary: We investigated the variability in the mesoscale distribution of the siphonophore *Muggiaea atlantica* and the hydromedusa *Aglaura hemistoma* in relation to the rapid spatial oscillations of the shelf-slope front off the Catalan coast (NW Mediterranean). Three extensive surveys were carried out in spring at ten-day intervals. High variability in the position of the front resulted from the advection of low-salinity waters originating in the Gulf of Lions, mainly from the Rhône River runoff. High spatial variability in the distribution of the two species was closely related to the shifting positions of the front. Both species occurred on its inshore side in much higher abundances than on its offshore side, where they were scarce or absent. The front acts as a barrier limiting offshore displacement of these two cnidarians. Statistical analyses showed that bottom depth and salinity, as independent variables, were indicators of the signature and position of the front, explaining most of the variance in the distribution and abundance of the two species.

Keywords: Siphonophorae; Hydromedusae; *Muggiaea atlantica*; *Aglaura hemistoma*; mesoscale; NW Mediterranean.

Alta heterogeneidad espacial de dos especies de cnidarios planctónicos en relación a la variabilidad a corta escala temporal de un frente plataforma-talud

Resumen: La variabilidad en la distribución de meso-escala del sifonóforo *Muggiaea atlantica* y la hidromedusa *Aglaura hemistoma* se investigó en relación a las rápidas oscilaciones espaciales del frente plataforma-talud en la costa Catalana (Mediterráneo noroccidental). Durante la primavera, se realizaron tres campañas oceanográficas intensivas, distanciadas 10 días entre sí. La alta variabilidad en la posición del frente fue resultado de la advección de aguas de baja salinidad procedentes del Golfo de León, al norte del área de estudio, debido principalmente a los aportes del río Ródano. La alta variabilidad espacial observada en la distribución de las dos especies estuvo muy relacionada con la posición cambiante del frente. Ambas fueron mucho más abundantes en el lado costero que en el lado oceánico del frente, donde éstas fueron muy escasas o incluso ausentes. El frente actúa como una barrera limitando el desplazamiento hacia mar abierto de estos dos cnidarios. Los análisis estadísticos realizados mostraron que la profundidad y salinidad, como variables independientes, fueron indicadoras de la señal y la posición del frente, explicando la mayor parte de la varianza de la distribución y abundancia de ambas especies.

Palabras clave: Siphonophorae; Hydromedusae; *Muggiaea atlántica*; *Aglaura hemistoma*; meso-escala; Mediterráneo noroccidental.

INTRODUCTION

Shelf-slope fronts separating low-salinity coastal waters from high-salinity open-sea waters are common along continental shelves (Wang et al. 1988, Houghton 1997). Physical and biological coupling in these frontal zones shows strong spatio-temporal variability as a result of hydrographic complexity and the activity of the organisms (Mackas et al. 1985, Sournia 1994). In general, shelf-slope fronts are highly productive due

to the accumulation and active growth of microalgae and zooplankters (Sabatés et al. 1989, Fernández et al. 1993, Mann and Lazier 2006). These phenomena determine the distributions and abundance of many groups of zooplankton (e.g. Kahru et al. 1984, Nishikawa et al. 1995, Sabatés and Olivar 1996).

Gelatinous zooplankton are abundant in pelagic communities, playing an important role in food-web dynamics due to their great trophic impacts and rapid population growth, which sometimes results in seasonal blooms (Graham et al. 2001, Pagès et al. 2001). Appropriately classified as plankton, gelatinous organisms have limited horizontal mobility, so their abundance and distribution patterns depend on hydrodynamic features such as gyres, clines and fronts. However, explicit evidence for this bio-physical coupling is scarce (e.g. Pagès and Gili 1992, Graham et al. 2001, Pavez et al. 2010).

Off the Catalan coast (NW Mediterranean), the shelf-slope density front is a permanent structure defined by strong salinity gradients, separating low-salinity shelf waters from the more saline waters offshore (Font et al. 1988, Alvarez et al. 1996). It is present in the upper 300 to 400 m of the water column and usually intersects the surface over the 1000 m isobath. Associated with the front is the Northern Current flowing southwestward following the continental slope at 20 to 30 cm s^{-1} (Font et al. 1995). In spring, northern Catalan coastal waters experience strong spatial and temporal variability due to the large inputs of continental runoff, mainly from the Rhône River in the northern Gulf of Lions (Masó and Tintoré 1991, Sabatés et al. 2007). These relatively low-salinity waters, advected by the Northern Current along the shelf break, increase the mesoscale activity at the shelf-slope front, generating oscillations and eddies (Alvarez et al. 1996, Flexas et al. 2002). The continental shelf in the study area (Fig. 1) is relatively narrow, with a submarine canyon whose head is close to the coast.

Previous studies in the area have analysed the role of the front and the associated current in primary and secondary production (Estrada 1991, Estrada et al. 1999, Alcaraz et al. 2007), and in zooplankton and ichthyoplankton distribution (Sabatés et al. 1989, Sabatés and Olivar 1996, Sabatés et al. 2004). Recently, the importance of the front in the distributions of medusan species forming blooms, such as *Pelagia noctiluca* (Forsskål, 1775), has been reported (Sabatés et al. 2010). However, little is known about the influence of the shelf-slope front on the most abundant planktonic cnidarians, especially at short timescales.

The planktonic cnidarian community along the Catalan coast in spring is dominated by a few species. Siphonophorae constitute the bulk of the community, and the calycophoran *Muggiaea atlantica* Cunningham, 1892 is by far the most abundant and representative species. Among Hydromedusae, *Aglaura hemistoma* Péron and Lesueur, 1810, is the most abundant and widespread. Both species are neritic and epipelagic, accounting in the area for up to 95% of the planktonic cnidarian community in spring (Gili et al. 1987a, b, 1988). Although these two species are present in the Mediterranean all year around (Bouillon et al. 2004), the highest abundances of *M. atlantica* in the northwestern basin have been recorded from April to June (Gili et al. 1987b, 1988, Licandro et al. 2012), and peaks of *Aglaura hemistoma* occur between June and September (Gili et al. 1987b, 1988, Licandro and Ibañez 2000). Both species are particularly abundant in the first 50 m of the water column but can occur down to 200 m (Gili et al. 1987a, b, Batistić et al. 2004). The value of knowing the abundance and distribution patterns of planktonic cnidarians derives from their predation on most other zooplankton (e.g. Biggs 1977, Purcell 1997, Colin et al. 2005), affecting the structure and dynamics of the whole planktonic community.

Our goal was to investigate how the variability of hydrodynamic structures determines the mesoscale distributions of planktonic cnidarians. Our approach was to study the coupling between short-term variability in the location of the shelf-slope front and the distributions of *M. atlantica* and *A. hemistoma*. To achieve this aim, we analysed the changes in abundance and spatial distribution of both species during three cross-frontal surveys carried out at approximately 10-day intervals.

MATERIALS AND METHODS

The study area is located off the northern Catalan coast, NW Mediterranean (Fig. 1). Three oceanographic cruises were carried out from mid-May to late June 1992, at approximately 10-day intervals (13-21 May, 2-9 June and 18-25 June). On each survey, 43-44 stations were sampled for environmental and biological parameters. Stations were located approximately 8.5 km apart, and distributed along seven transects perpendicular to the shoreline, from near the coast to beyond the shelf-slope front. An additional transect in the northernmost part of the area (grey dots in Fig. 1) was conducted for environmental measurements only. Vertical profiles of basic hydrographic variables (temperature, salinity and fluorescence) were obtained at each station using a Mark-III Neil Brown CTD probe equipped with a Sea Tech fluorometer. Maps of the horizontal distribution of each environmental parameter (at 10 m depth) were generated by gvSIG (OADE-2010) and ArcGIS 10.2 software, applying the spline interpolations with a cell size of 200 m (see Fig. 2). The Catalano-Balearic Sea bathymetric chart (2005) was used to represent the bathymetry at 100 m intervals.

Zooplankton samples were collected using a bongo net of 60 cm mouth diameter and 300 μm mesh. Oblique hauls were performed, integrating the water column from a maximum depth of 200 m (or 5 m above the bottom in stations shallower than 200 m) to the surface. Samples were preserved immediately after collection in a 5% solution of formaldehyde in seawater buffered with borax. The volume of filtered water was estimated by means of a flowmeter placed in the centre of the net mouth.

In the laboratory, after the cruises took place, the siphonophore *M. atlantica* (polygastric stage) and the hydromedusa *A. hemistoma* were identified and counted under a stereomicroscope. Counts were standard-
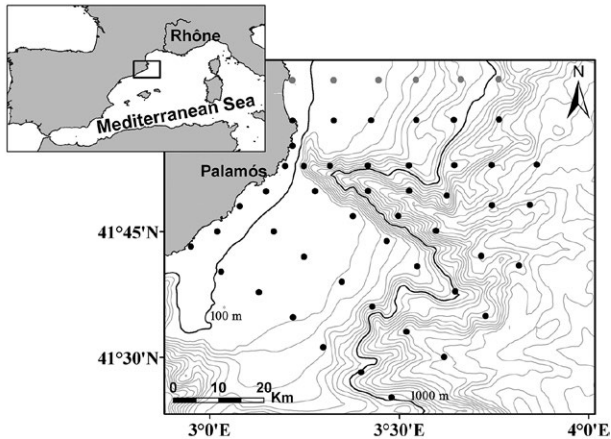
Fig. 1. – Geographical location of the study area off the northern Catalan coast (NW Mediterranean). Black dots represent the grid of sampled stations (hydrographic and biological). Grey dots are the additional northernmost transect of hydrographic stations. Grey lines indicate bathymetry (every 100 m).

ized to number of individuals per 1000 m^3. Recently, to complete the study with the rest of the cnidarian community, analysis of those same samples were carried out, however we found that the morphological conditions of the individuals had impoverished so much that the taxonomical identifications were not possible. The exceptional oceanographic conditions in which the cruises were performed and the ecological importance of these two species encouraged us to proceed with the study presented here.

Statistical analysis

The potential explanatory relationships between species abundance and the environmental variables: surface (10 m depth) salinity, fluorescence and temperature, and bottom depth were tested separately in each surveyed situation by fitting generalized additive models (GAMs), which account for non-linear changes in abundance with the environmental variables by applying other than Gaussian data distributions. The models were fitted with an error distribution from the negative binomial family and a log link function (Zuur et al. 2009), using the "mgcv" package (Wood 2014). To eliminate bias due to varying sampling units (volumes of seawater filtered by the net), we included the log of filtered volume as an offset inside the model (Penston et al. 2008, Zuur et al. 2009, Guerrero et al. 2013). Spatial autocorrelation of samples was checked by plotting the residual of the models in a variogram (Zuur et al. 2009); in all cases no spatial correlation was suggested and spatial independence was assumed.

GAM analyses were performed in two steps (Zarauz et al. 2007, Silva et al. 2014). First, GAMs were based on single explanatory variables to study the influence of each hydrographic parameter on the species abundance. Later, GAMs of increasing complexity were applied, combining multiple explanatory variables. In the first, we allowed information on collinear variables; in the second, a more realistic situation was modelled in which all the parameters interact as in the environment.

The amount of smoothing was minimized (k=3 to 5) to aid interpretation of the biological trends (Wood 2014). From among single variable-based GAMs, the best-fitting ones were selected based on the un-biased risk estimator (UBRE), the percentage of deviance explained, the smooth confidence region and the spread of the residual in the model validation step (Wood and Augustin 2002, Planque et al. 2007, Zuur et al. 2009, Silva et al. 2014). For multiple variable–based GAMs, collinearity between pairs of variables was evaluated by pairwise scatterplots, Pearson's correlation coefficients (cut-off value |0.5|) and corroboration by the variance inflation factor (Zuur et al. 2009). In early June, salinity and fluorescence were collinear. Since salinity was the variable best representing the front (see Fig. 2), and was also the strongest predictor among the single variable GAMs for that cruise, it was kept. The variables for multivariable GAMs were chosen by a backward-elimination process for the least significant predictor based on the chi-square statistic. Best-fitting combined GAMs where selected based on the UBRE score (the lowest the best), the percentage of deviance explained (the highest the best) and the spread of the residuals in the model validation step (Zuur et al. 2009, Silva et al. 2014).

Differences in species abundance between the two sides of the front, when detected at the surface (in mid-May and early June), were tested for significance in order to know whether the front per se had an influence on the species abundance distribution. To this end, an analysis of variance was performed using generalized linear models (GLM) with the "glm.nb" package (Venables and Ripley 2002), which fit a GLM with a negative binomial distribution. The model was applied with a log link function and an offset for the log of filtered volume in a way similar to that explained for GAMs. To identify the stations located on each side of the front, the geographical position of the front was defined from the maximum difference in salinity between adjacent stations on the same transect and between transects.

All analyses were performed using the free statistical software R, version 3.0.2 (R Development Core Team 2013).

RESULTS

Hydrographic conditions

In the first survey in mid-May, the salinity front was over the slope approximately 50 km offshore, running in a northeast to southwest direction. Maximum salinity values (~38.2) were recorded at the most offshore stations. A band of relatively low salinity (37.6-37.7) was observed between the shelf and the open sea, intensifying the salinity and density gradients over the slope. The highest fluorescence values (from 5 to 7 units) were mainly detected offshore in the northeastern area. The lowest temperatures (~14°C) were recorded in the northwestern corner of the grid, and the highest (17°C) were in the south (Fig. 2: A1-C1; Table 1).

In the second survey, ten days later in early June, a completely different spatial layout was found. The
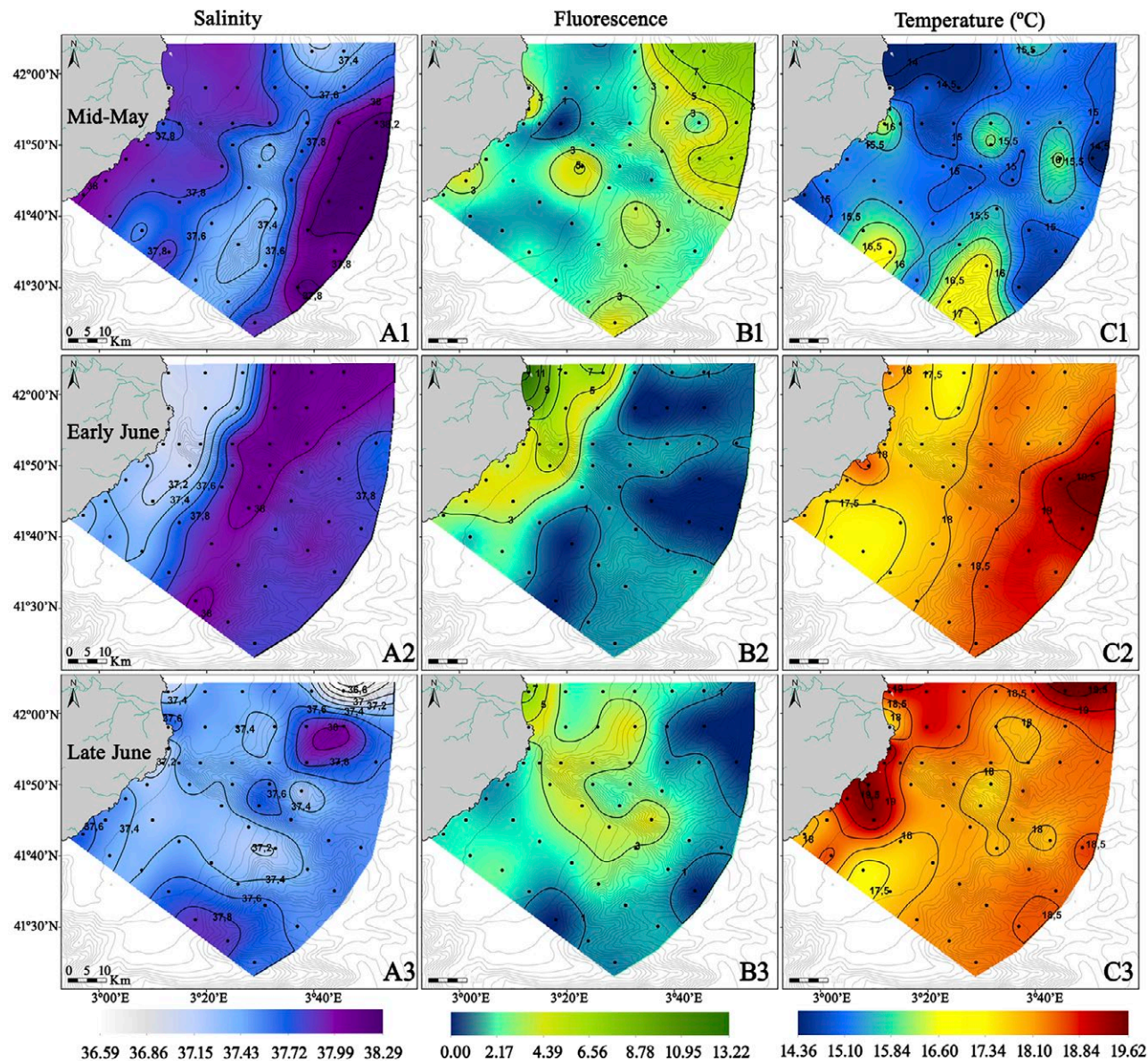
Fig. 2. – Surface (10 m) salinity, fluorescence and temperature distributions in the mid-May (A1-C1), early June (A2-C2) and late June (A3-C3) cruises off the northern coast of Catalonia (note the additional northernmost transect of hydrographic stations). Grey lines represent the bathymetry (every 100 m).

front, running parallel to the coast, was over the shelf at about 20 km from the coast, confining waters of low salinity (37.2) inshore and thus causing an intense salinity gradient. The highest fluorescence values (up to 13 units) were restricted to the inshore side of the front, associated with the low-salinity waters, while very low fluorescence values (<2) were measured on the offshore side. Temperature was higher than on the May

cruise, showing a gradient from near the coast (17.5°C) towards the open sea (~19°C) (Fig. 2: A2-C2; Table 1).

In the third survey, in late June, no frontal structure was detected in the upper layers, and the salinity distribution was complex, with patches of low values covering the whole area (Fig. 2: A3). Fluorescence decreased offshore, and the highest values (from 3 to 7 units) appeared to be associated with areas of low

Table 1. – Values of the environmental parameters measured off the northern Catalan coast during the three research cruises. Values include those from the additional northernmost transect of hydrographic stations (see Figs 1 and 2). T, temperature; S, salinity; Fl, fluorescence; Depth, bottom depth; Min., minimum value, Max., maximum value; Mean±SD, mean and standard deviation.

	Mid-May			Early June			Late June		
	Min.	Max.	Mean±SD	Min.	Max.	Mean±SD	Min.	Max.	Mean±SD
T (°C)	14.36	17.07	15.32±0.64	17.25	19.37	18.10±0.51	17.25	19.63	18.35±0.51
S	37.24	38.29	37.79±0.28	37.02	38.10	37.67±0.37	36.59	37.99	37.49±0.24
Fl	0.001	7.44	2.88±1.71	0.001	13.22	2.41±2.66	0.001	7.78	2.22±1.34
Depth (m)	30	2107	803±732	28	2187	850±712	34	2000	785±673

Table 2. – Mean abundance (Ind. 1000 m^{-3}), range (minimum and maximum abundance values) and % Occurrence (percentage of samples in which the species occur) for *Muggiaea atlantica* and *Aglaura hemistoma* during the three research cruises.

| | *M. atlantica* | | | *A. hemistoma* | | |
	Mean±SD	Range	% Occurrence	Mean±SD	Range	% Occurrence
Mid-May	8640±11580	0 - 51809	98%	1759±3434	0 - 17480	82%
Early June	9378±18818	0 - 77607	86%	128±286	0 - 1381	52%
Late June	4008±3794	0 - 13870	98%	478±845	3 - 4013	100%
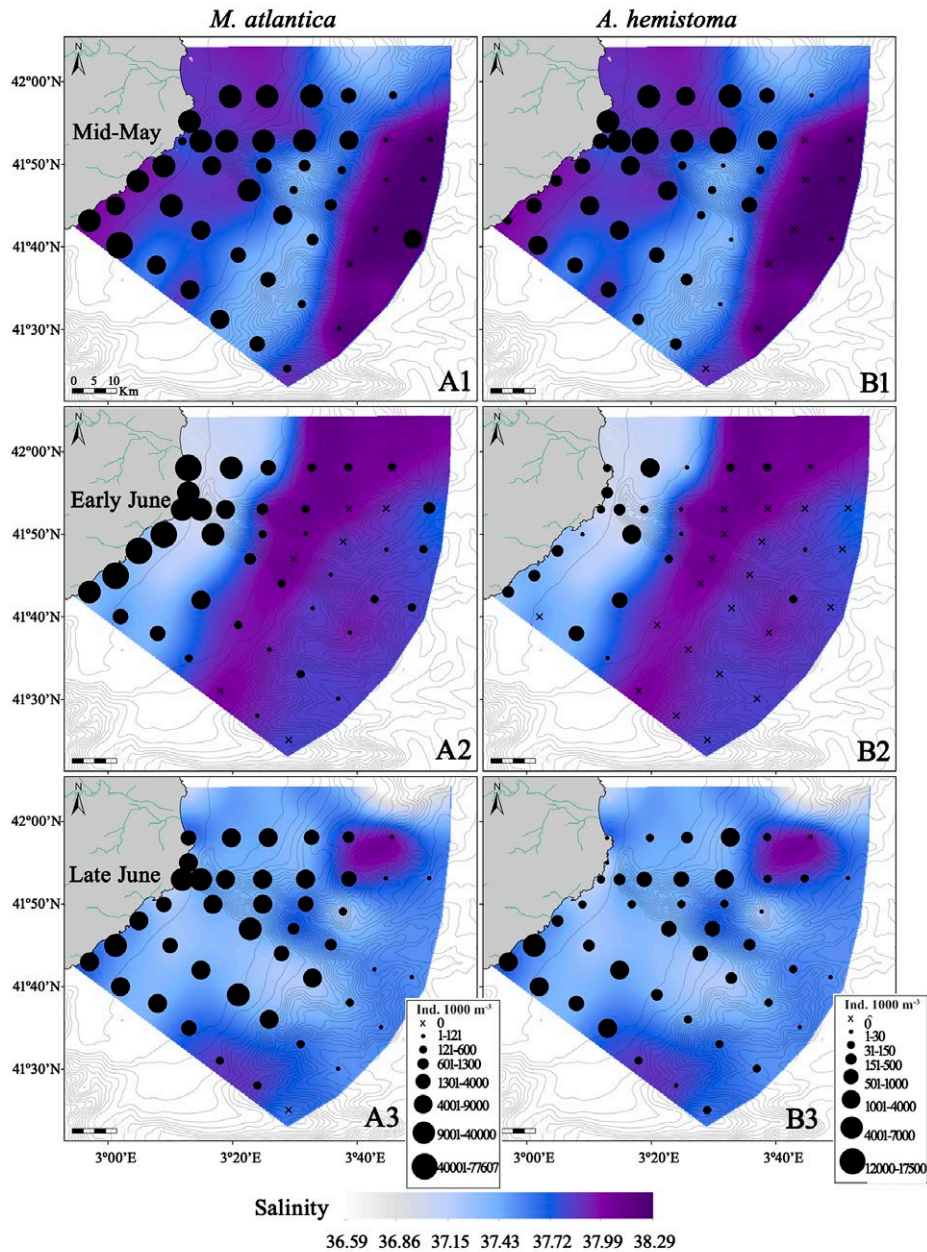
Fig. 3. – Distribution of *Muggiaea atlantica* and *Aglaura hemistoma* overlaid on surface (10 m) salinity in mid-May (A1-B1), early June (A2-B2) and late June (A3-B3). Grey lines represent the bathymetry (every 100 m).

salinity. During this survey, high temperatures were detected in coastal waters and offshore (~19.5°C) (Fig. 2: A3-C3, Table 1).

Spatio-temporal distribution of *Muggiaea atlantica* and *Aglaura hemistoma*

On all three cruises the mean abundance of *M. atlantica* was higher than that of *A. hemistoma* (Table 2). Abundance values for *M. atlantica* were high during the first two cruises (8640±11580 and 9378±18818 ind. 1000 m^{-3}, respectively) but lower during the last cruise (4008±3794 ind. 1000 m^{-3}). *Aglaura hemistoma* was relatively abundant on the first cruise (1759±343 ind. 1000 m^{-3}) but markedly lower on the two June cruises (128±286 and 478±845 ind. 1000 m^{-3}, respectively). For both species, the lowest frequency of occurrence was observed on the

Table 3. – Results of the single variable–based GAMs computed for *Muggiaea atlantica* and *Aglaura hemistoma* abundances and each environmental variable [bottom depth (Depth), salinity (S), fluorescence (Fl) and temperature (T)] for the three research cruises. For each single variable model, the degrees of freedom selected (k), the effective degrees of freedom (edf) generated by the model, the UBRE score, the percentage of deviance explained (% Dev.) and P-values, when significant, are given; n.s., not significant. The best predictor for each species on each cruise is in bold font.

				M. atlantica					*A. hemistoma*		
	Variables	k	edf	UBRE	% Dev.	P-value	k	edf	UBRE	% Dev.	P-value
Mid-May	s(Depth)	4	1.0	0.61	**47.1**	<0.001	4	2.9	2.15	36.1	<0.001
	s(S)	4	2.8	0.87	40.8	<0.001	4	2.8	1.15	**57.4**	<0.001
	s(Fl)	5	3.8	1.66	14.7	<0.001	4	2.9	2.85	21.2	<0.001
	s(T)	3	1.8	1.78	7.57	<0.01	3	1.9	3.55	5.3	<0.001
Early June	s(Depth)	4	1.6	3.71	25.9	<0.001	4	2.8	2.11	33.0	<0.001
	s(S)	4	2.9	1.15	**68.4**	<0.001	5	3.9	1.54	**47.1**	<0.001
	s(Fl)	4	2.4	1.91	55.6	<0.001	4	2.6	2.11	32.8	<0.001
	s(T)	5	3.9	3.84	25.6	<0.001	4	2.9	1.96	36.4	<0.001
Late June	s(Depth)	3	1.9	0.62	**37.4**	<0.001	4	1.0	0.74	**31.2**	<0.001
	s(S)	3	1.9	1.05	19.2	<0.001	3	1.9	1.07	19.3	<0.001
	s(Fl)	3	0.6	0.63	36.9	<0.001	4	2.4	0.99	23.4	<0.001
	s(T)	3	-	-	-	n.s.	4	1.0	1.25	10.0	<0.001

second cruise (86% and 52% for *M. atlantica* and *A. hemistoma*, respectively; Table 2).

High spatial variability in species abundance and distribution was observed over a short time scale (10 days), and in general both species displayed a similar onshore-offshore distribution pattern closely related to the variable location of the shelf-slope front (Fig. 3). In mid-May, *M. atlantica* and *A. hemistoma* were widely distributed over the whole study area, the location of the salinity front setting a clear limit for their distributions. Very low densities of *M. atlantica* were detected on the oceanic side of the front, and *A. hemistoma* was practically absent (Fig. 3: A1, B1). Higher densities of both species were observed at stations located over the edges of the submarine canyon than at those over the canyon axis (Fig. 3: A1, B1). Single variable-based GAMs revealed bottom depth as the strongest predictor for the spatial distribution of *M. atlantica*, explaining 47% of its variability, with a linear negative effect (Fig. 4: A1, Table 3). Depth was the second predictor for *A. hemistoma* (36%), with a negative effect from 500 m outwards (Fig. 5: A1, Table 3). Salinity was the second strongest predictor (41%) for *M. atlantica* and the first for *A. hemistoma* (57%, Table 3), and both species followed the same trend, positive up to ~37.9 (Fig. 4: B1) and ~37.8 (Fig. 5: B1), respectively, and decreasing above those values. Fluorescence was the third predictor for both species, whereas temperature was the least explanatory variable (Figs 4: C1-D1 and 5: C1-D1, Table 3).

In early June the spatial distribution of both species was restricted to a narrow belt over the shelf, limited offshore by the position of the front (Fig. 3: A2, B2). The abundance of *M. atlantica* was high close to the
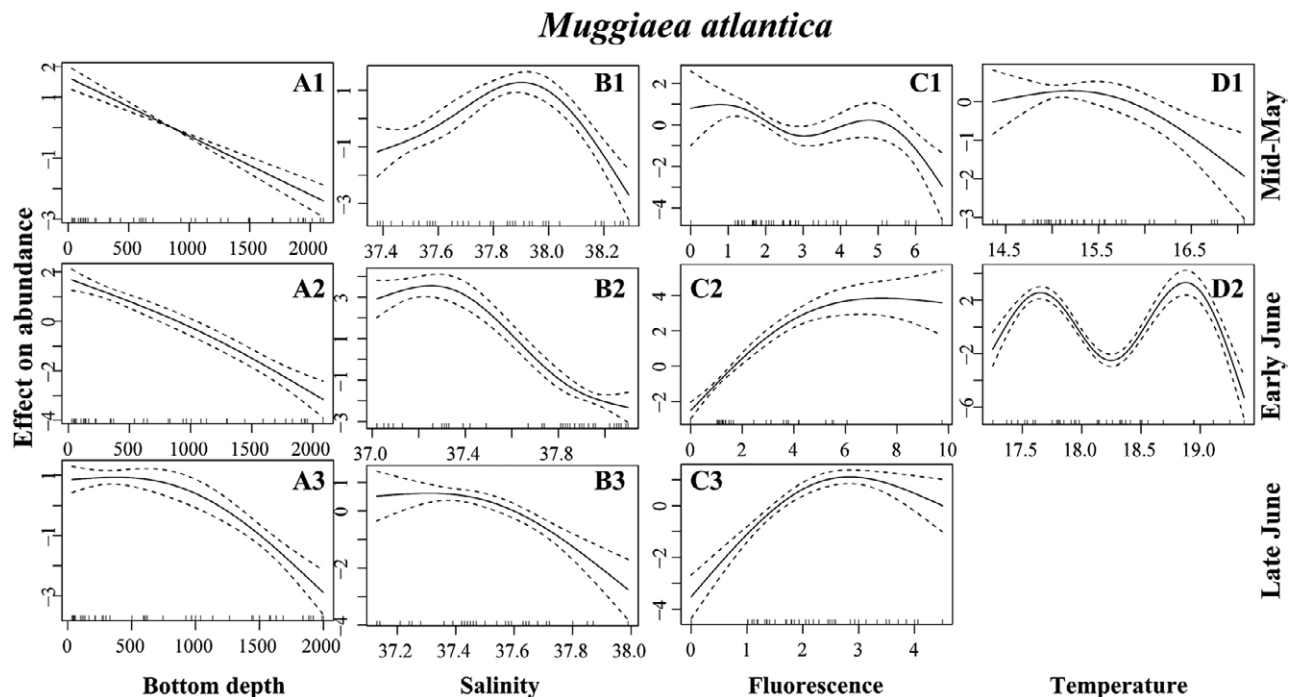
Muggiaea atlantica

Fig. 4. – Results of single variable–based GAMs for *Muggiaea atlantica*, showing the abundance trends of the siphonophore for each variable in each surveyed period (A1-D1, mid-May; A2-D2, early June; A3-D3, late June). Solid lines display the smoothing function according to the GAMs. The area between the dotted lines represents the 95% confidence interval. Short vertical lines on the x-axis indicate the values at which observations were made.
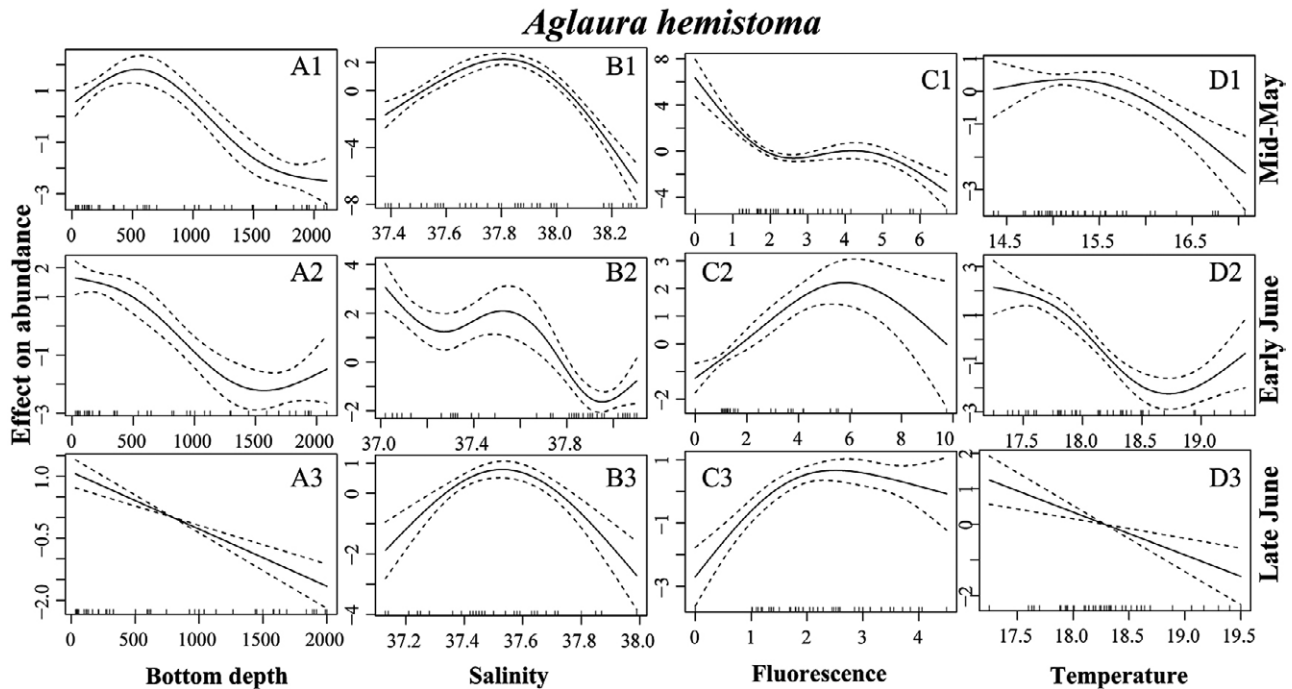
Aglaura hemistoma

Fig. 5. – Results of single variable–based GAMs for *Aglaura hemistoma* showing the abundance trends of the hydromedusa for each variable in each surveyed period (A1-D1, mid-May; A2-D2, early June; A3-D3, late June). Solid lines display the smoothing function according to the GAMs. The area between the dotted lines represents the 95% confidence interval. Short vertical lines on the x-axis indicate the values at which observations were made.

coast and very low on the open-ocean side of the front. *Aglaura hemistoma* showed the highest densities near to and inside the front, being almost absent on the offshore side of the front. Results of the single variable–based GAMs revealed salinity as the strongest explanatory variable for both the siphonophore (68%) and the hydromedusa (47%), with a marked decrease in abundance above ~37.3 for the former and a generally decreasing trend at higher salinity for the latter. As an exception, an increase was observed at ~37.6, corresponding to one of the isolines delimiting the salinity front (Figs 4: B2 and 5: B2; Table 3). Fluorescence was the second most important explanatory factor (56%) for *M. atlantica,* showing a positive effect up to ~7 with a plateau at higher values (Fig. 4: C2; Table 3). Temperature was the second most important variable for *A. hemistoma* (36%), with a negative trend in warmer waters (Fig. 5: D2; Table 3). The least significant variables during this period were bottom depth and temperature for *M. atlantica* (25.9% and 25.6%, respectively; Table 3) and bottom depth and fluorescence for *A. hemistoma* (33.0% and 32.8%, respectively; Table 3).

In late June, during the third cruise, as during the first cruise, the distributions of both species again covered a broad area, extending well beyond the shelf break, and higher densities of both species were recorded over the canyon flanks than at stations located over the canyon axis (Fig. 3: A3, B3). The GAMs showed bottom depth as the strongest explanatory variable for both species, explaining 37.4% for the siphonophore, with a negative effect from ~600 m outward (Fig. 4: A3, Table 3), and 31% for the hydromedusa with a linear negative effect (Fig. 5: A3, Table 3). Fluorescence was the second strongest predictor both for *M. atlan-*

tica (36.9%), showing a positive effect up to ~3 (Fig. 4: C3, Table 3) and slightly negative above that, and for *A. hemistoma* (23%), showing a positive effect up to ~2.5 and slightly negative one at higher values (Fig. 5: A3, Table 3). Salinity was the third factor for both species, while temperature was not significant for the siphonophore and the least explanatory factor for the hydromedusa (Figs 4: B3, C3 and 5: B3, C3, Table 3).

The analyses conducted with the multiple variable-based GAMs revealed an improvement of up to twice the variability explained in comparison with those based on a single variable. Results showed that not all variables included in the analyses significantly contributed to the overall combined models, and the relative importance of the different explanatory variables varied in comparison with the single variable–based analysis, although displaying the same trends. The most significant variable was always coincident with the strongest one obtained with single GAMs (Tables 3 and 4). In mid-May, the best fitting combined model for *M. atlantica* explained 53% of deviance and included two significant variables: bottom depth and temperature. The best fitting combined model for *A. hemistoma* explained 71% of the distribution and included three significant variables: salinity, bottom depth and fluorescence. In early June, both species shared the same best model: salinity and (marginally significant) bottom depth explaining 70% and 50% for *M. atlantica* and *A. hemistoma*, respectively. In late June, bottom depth and fluorescence explained 68% of deviance of *M. atlantica* and for *A. hemistoma* the best model included all variables: bottom depth, salinity, fluorescence and temperature explaining 63% of deviance (Table 4).

Table 4. – Results of the multiple variable–based GAMs computed for *Muggiaea atlantica* and *Aglaura hemistoma* abundances and the environmental variables [bottom depth (Depth), salinity (S), fluorescence (Fl) and temperature (T)] for the three studied cruises. For each combined model, effective degrees of freedom (edf) generated by the model for each variable, P-values, when significant, for each variable, the UBRE score and the percentage of deviance explained (% Dev.) are given; n.s., not significant; collinear, when that predictor was not taken into account for the model due to collinearity with another included predictor; asterisk (*) indicates a parameter that was marginally significant (p=0.06), but its inclusion considerably improved the model (Zuur et al. 2009).

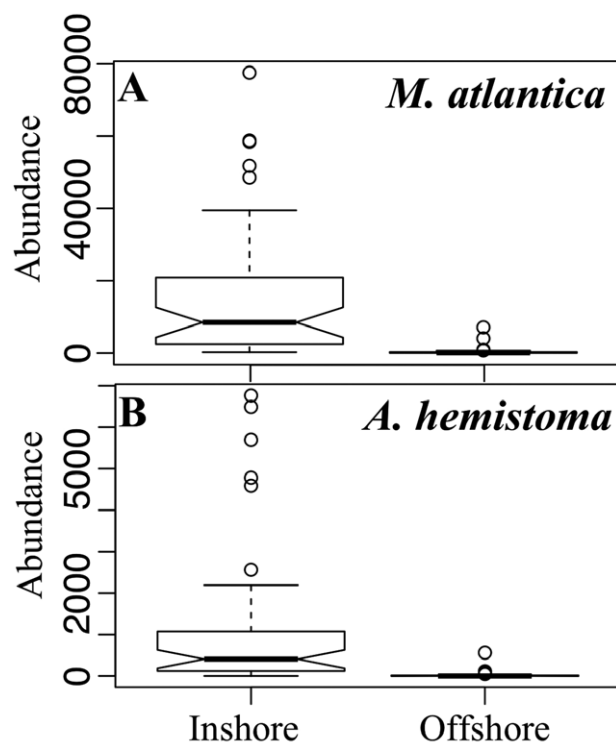|				*M. atlantica*				*A. hemistoma*		
	Variables	edf	P-value	UBRE	% Dev.		edf	P-value	UBRE	% Dev.
Mid-May	s(Depth)	1.0	<0.001				2.6	<0.001		
	s(S)	-	n.s.	0.51	53.2		2.9	<0.001	0.77	70.9
	s(Fl)	-	n.s.				2.9	<0.01		
	s(T)	1.8	<0.01				-	n.s.		
Early June	s(Depth)	1.0	0.06*				2.5	0.06*		
	s(S)	2.9	<0.001	1.11	69.7		3.6	<0.001	1.53	49.8
	s(Fl)	-	collinear				-	collinear		
	s(T)	-	n.s.				-	n.s.		
Late June	s(Depth)	1.7	<0.001				1.3	<0.001		
	s(S)	-	n.s.	-0.04	68.2		1.9	<0.01	0.18	62.7
	s(Fl)	1.9	<0.001				1.2	<0.05		
	s(T)	-	n.s.				1.0	<0.05		

Fig. 6. – Boxplot comparing abundances (Ind. /1000 m³) of *Muggiaea atlantica* (A) and *Aglaura hemistoma* (B) on the inshore and offshore sides of the shelf-slope front when it was observed in the upper layers of the water column (mid-May and early June). In graph B, the two highest values (17480 and 12079 Ind. /1000 m³) were extracted to obtain a better graphical display.

The GLM results showed significantly higher abundances for both *M. atlantica* and *A. hemistoma* on the inshore side of the front than on the offshore side (*M. atlantica*: z-value =–10.67, p<0.001, *A. hemistoma*: z-value =–9.410, p-value<0.001) (Fig. 6).

DISCUSSION

The temporal scale of the sampling allowed us to identify the short-term spatial variability of the shelf-slope density front and the responses of *M. atlantica* and *A. hemistoma* species to associated environmental changes. The shifting position of the front is characteristic of the spring period off the northern Catalan coast, and results from the advection of low-salinity waters by the Northern Current (Alvarez et al. 1996, Masó et al. 1998, Sabatés et al. 2007). The low-salinity waters originating in the Gulf of Lions, mainly due to the River Rhône outflow, help strengthen the gradient of the shelf-slope density front. The temporal scale at which the frontal system oscillates has been reported to exert a decisive influence on processes affecting the concentration and dispersal of zooplankton and fish larvae (Sabatés and Olivar 1996, Masó et al. 1998, Sabatés et al. 2004). The gelatinous zooplankton followed a similar trend, varying in their spatial distributions at short time scales. The two cnidarian species studied are epipelagic, mainly occurring in the surface layer between 0 and 50 m (Gili et al. 1987a, b), and holoplanktonic, making them particularly susceptible to surface-water dynamics (Mackie et al. 1987, Blackett et al. 2014).

The abundance values recorded for both species are in accordance with previous reports in the area during the same season (Gili 1986, Gili et al. 1987b, Sabatés et al. 2010). The higher mean abundance of *M. atlantica*, compared with *A. hemistoma*, is usual in the NW Mediterranean (Gili et al. 1988, Licandro and Ibañez 2000, Sabatés et al. 2010), and it has been observed since *M. atlantica* replaced the formerly dominant, congeneric species *Muggiaea kochii* (Will, 1844) (Kršinić and Njire 2001, Batistić et al. 2007, Licandro et al. 2012). However, the hydromedusa can display peaks of greater abundance at some periods of the year (Gili et al. 1987b, Licandro and Ibañez 2000). Both species varied considerably in their mean abundance between surveys. For *M. atlantica* the temporal abundance sequence agrees with the seasonal trend previously observed in the NW Mediterranean. The highest values are generally recorded from April to June, significantly decreasing at the end of June and in July (Gili et al. 1987b, 1988, Licandro and Ibañez 2000). The highest abundance of *A. hemistoma* was observed in May, and it decreased markedly in June. That pattern contrasts with previous observations of the highest seasonal densities for it in June and July, after much lower values

in May (Gili et al. 1987b, 1988, Licandro and Ibañez 2000). The inflow of low-salinity waters detected in early June inshore of the front could have negatively affected the abundance of *A. hemistoma* (Fig. 3: B2, Table 2). However, as this species has been observed inhabiting areas of similar and lower salinity (e.g.: Gili et al. 1988, Nagata et al. 2014), factors other than salinity per se probably affected its abundance.

Muggiaea atlantica and *A. hemistoma* displayed high spatio-temporal variability in the brief study period, apparently driven by the rapid onshore-offshore displacements of the shelf-slope front. Both species occurred predominantly inshore of the front, with significantly higher abundances there than on the offshore side (Figs 3 and 4). Previous studies in the region have also reported the highest concentration of *M. atlantica* and *A. hemistoma* on the inshore side of the front (Sabatés et al. 2010). The front acts as a natural barrier, limiting the distribution seaward of both species; this phenomenon has also been documented for larvae of coastal fish in the study area, with the front preventing their displacement to the open sea (Sabatés and Olivar 1996, Sabatés et al. 2004). In the case of the jellyfish, in addition to the barrier effect of the density front, we must consider that since they are mainly water with the same ionic concentration as the surrounding seawater, they tend to remain in waters of similar salinity (Graham et al. 2001). The accumulation over the shelf, very strong for *M. atlantica* when the front was close to the coast, could lead to high predation pressure on their planktonic prey; this species is known to be an effective predator, particularly on copepods (Purcell 1982), and when siphonophores are very abundant they can significantly affect planktonic populations (Purcell 1981, Purcell and Kremer 1983). Other dominant jellyfish species in the area, the siphonophores *Lensia subtilis* (Chun, 1886) and *Chelophyes appendiculata* (Eschscholtz, 1829) and the hydromedusae *Rhopalonema velatum* Gegenbaur, 1857 and *Solmundella bitentaculata* (Quoy and Gaimard, 1833), have also been reported to display similar patterns, with maximum abundances on the coastal side of the density front (Sabatés et al. 2010). However, oceanic species such as the siphonophore *Lensia conoidea* (Keferstein and Ehlers, 1860) and the scyphomedusa *Pelagia notiluca* were more abundant in the frontal area and offshore (Sabatés et al. 2010). Thus, the front seems to exert a barrier effect for both neritic and oceanic species, limiting their offshore and inshore displacement, respectively.

Studies conducted in other geographical areas have also shown the role of fronts shaping the distributions of gelatinous zooplankton. Analogies are found, for instance, in the salinity-driven mesoscale front in the Southern California Bight, where most gelatinous zooplankton organisms were located on the inshore side of the front (Luo et al. 2014). Pavez et al. (2010) also found the highest abundance of gelatinous zooplankton (hydromedusae, siphonophores and ctenophores) at the neritic inshore stations of a density front off central Chile. However, *M. atlantica*, evenly distributed over the shelf and slope, did not prove to be influenced by the position of the front. By contrast, the seasonal ther-

mohaline front in the southern Benguela Region delimited the distribution of most species to the offshore side of the front (Pagès and Gili 1992). High abundances of *A. hemistoma* and *M. atlantica* were detected over the edge of the continental shelf, offshore of the front, in relation to the intrusion of Agulhas water, whose input increases the gelatinous zooplankton density and diversity. In general, the different hydrodynamic variability associated with each frontal system is a key factor explaining the spatial heterogeneity of plankton distribution (Le Fèvre 1986).

The measured environmental parameters appeared to have important effects on the distributions and abundance of the two species. Bottom depth and salinity were the variables most closely related to the distribution patterns (Tables 3 and 4). When the front was located away from the coast, *M. atlantica* and *A. hemistoma* abundances gradually decreased with bottom depth. This trend has already been documented by other studies on the area (Gili et al. 1987a, b, 1988) and is in agreement with the neritic character of both species. Abundances also declined at the higher salinity values (see Figs 3, 4 and 5) characterizing waters on the seaward side of the front. In particular, when the front occurred over the shelf in early June, salinity was the variable most strongly related to the spatial distributions of both species (Tables 3 and 4). Salinity has previously been reported as a determinant factor for the distributions and abundance of gelatinous zooplankton at various locations in the NW Mediterranean (Gili et al. 1988, Licandro et al. 2012) and the North Atlantic (Blackett et al. 2014, Greer et al. 2015).

High fluorescence values were clearly associated with the presence of low-salinity waters. These waters come from the Rhône River runoff, advected by the Northern Current along the Catalan coast, and are highly productive at surface; the offshore location of these low-salinity waters is variable due to the horizontal oscillation of the shelf-slope front (Sabatés et al. 2007). Abundance of both species in relation to fluorescence showed different trends (almost opposite) in mid-May to those of the two June cruises (Figs 4 and 5). In mid-May high fluorescence values were located offshore, coinciding with low abundance values for *M. atlantica* and *A. hemistoma*. In June high fluorescence values were detected on the inshore side of the front at stations where the two species were particularly abundant (Figs 2 and 3). This suggests that productive waters per se had no direct effect on the abundance of either species, depth being in fact the responsible variable.

No clear trend in the distribution of the species was detected regarding temperature. Although both species showed lower abundance in warmer waters, the narrow temperature variability within each survey and the short seasonal period we covered prevent any temperature pattern or preference from being detected. Overall, our results show the key role of the position of the front, rather than values of the measured environmental parameters per se, as an explanation for the abundance and distributions of *M. atlantica* and *A. hemistoma*. In addition, the topography of the area, with the presence of a submarine canyon, seems to

have affected the observed distribution patterns. The presence of the Palamós submarine canyon has been reported to modify the circulation in the area, inducing a shelfward deflection on the upstream side of the canyon and an offshore flow on the downstream side (Alvarez et al. 1996, Jordi et al. 2005). In relation to these shelf-slope exchanges, high abundances of both species were observed on the canyon edges, particularly when the shelf-slope front intersected the canyon mouth (mid-May and late June surveys).

In summary, the shelf-slope front was the main factor controlling the abundance and distribution of the two most abundant and representative species of planktonic cnidarians in the NW Mediterranean, the siphonophore *M. atlantica* and the hydromedusa, *A. hemistoma*. A high degree of coupling was observed between the short timescale variability of the front's location and the spatio-temporal distributions of the species. The front seemed to act as a barrier preventing their offshore displacement, as was reflected by the fact that the bottom depth and salinity among the analysed variables best explained the distributions and abundances. The strong hydrographic variability associated with shelf-slope fronts largely determines the seasonal and interannual variability of gelatinous zooplankton and their predation impacts on the planktonic community in this region.

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