Variability of the planktonic cnidarian community at different spatio-temporal scales along the Catalan coast (Northwestern Mediterranean)

Elena Guerrero | Barcelona, 2017
Universitat Politècnica de Catalunya

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Variability of the planktonic cnidarian community at different spatio-temporal scales along the Catalan coast (Northwestern Mediterranean)

Variabilidad de la comunidad de cnidarios planctónicos a diferentes escalas espacio-temporales en la costa catalana (Mediterráneo noroccidental)

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“Variability of the planktonic cnidarian community at different spatio-temporal scales along the Catalan coast (Northwestern Mediterranean)”

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Graphic art: different species of siphonophores and hydromedusae (mixed painting techniques). Original work by A. Estefanía Sánchez-Guerrero Fuentes ©

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Barcelona, June 2017.

A mi abuela Lola,
que siempre quiso estudiar.

PREFACE

"When you feel connected to everything, you also feel responsible for everything. And you cannot turn away. Your destiny is bound with the destinies of others. You must either learn to carry the Universe or be crushed by it. You must grow strong enough to love the world, yet empty enough to sit down at the same table with its worst horrors."
Andrew Boyd

"The most unique feature of Earth is the existence of life, and the most extraordinary feature of life is its diversity."
Cardinale et al, 2012

"Biodiversity is ultimately essential to human survival in this planet"
Bilton, 2014

"There's so much magnificence near the Ocean"
Song by Miten and Deva Premal

"¿En qué medida la vida de otras criaturas de este planeta es menos sagrada que la vida humana?"
Ecología y la Bhagavad Gita

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ABSTRACT

ABSTRACT

Planktonic cnidarians are those species or their stages in the phylum Cnidaria that spent their life in the water column and, therefore, are tightly linked to oceanographic dynamics and water mass structures, such as fronts, and environmental gradients. The objective of this thesis is to understand the variability of the planktonic cnidarian community inhabiting the Catalan coast (NW Mediterranean) at different spatio-temporal scales, and their relationships with the hydrography and environmental parameters that characterized the study area. At short time scales (10 days), in spring, important changes in the abundance and spatial distribution of the two most abundant species were closely related to the shifting positions of a density front. The front acted as a barrier limiting offshore displacement of the species. At an interannual scale, changes in the abundance, structure and latitudinal distribution of the community were observed when comparing extreme warm (July 2003) and standard summer conditions (July 2004). The exceptional warm conditions in July 2003 due to a heat wave, lead to a reduction of the total abundance of the community and the latitudinal community ordination was reinforced. At an interdecadal scale, changes in species abundance, community composition and spatial distribution patterns were found during the month of June. Total cnidaria abundance increased and the latitudinal community distribution patterns were reinforced when comparing three representative years (1983, 2004 and 2011) of the climatic and anthropogenic changes occurred during the last three decades in the NW Mediterranean. Temperature was the main environmental factor explaining these changes, representative of the climatic trend from the colder 1980s to the warmer 2010s. Nevertheless, it is likely that others anthropogenic factors, such us overfishing, may have contributed to the observed changes over time. All these results are based in the study of a large and heterogeneous mesoscale area, characterized by different environmental gradients in bathymetry, temperature, salinity, primary production, and by different hydrodynamic structures as well as in the species level identification of the whole community. The planktonic cnidarian community along the Catalan coast presents a high variability both at temporal and spatial scales and is tightly related to hydrographic and environmental factors of the area, and influenced by climatic and anthropogenic changes occurred in the last three decades. These results show that it is extremely important to study and monitor planktonic cnidarians (included within gelatinous zooplankton) in mesoscale spatial areas, to robustly assess changes at temporal scales, and at species level, since species spatial changes are sensitive indicators of climate change.

RESUMEN

Los cnidarios planctónicos son aquellas especies o estadios de vida pertenecientes al fílum Cnidaria que habitan en la columna de agua y, por tanto, están fuertemente vinculados a la dinámica oceanográfica y estructuras hidrodinámicas como frentes y gradientes ambientales. El objetivo de esta tesis es entender la variabilidad de la comunidad de cnidarios planctónicos que habita la costa catalana (Mediterráneo noroccidental) a diferentes escalas espaciales y temporales y cómo ésta está asociada

a la hidrografía y a los parámetros ambientales del área. A corta escala temporal (10 días), durante la primavera, importantes cambios en la abundancia y distribución espacial de las dos especies más abundantes estuvieron fuertemente asociados a la variabilidad en la posición del frente de densidad. El frente actuó como barrera en la distribución de las especies hacia mar abierto. A escala interanual, se observaron cambios en la abundancia, estructura y distribución latitudinal de la comunidad de verano al comparar condiciones extremas de temperatura (julio 2003) y estándares (julio 2004). Las excepcionales temperaturas registradas en Julio 2003, debido a una ola de calor, comportaron una menor abundancia total de la comunidad y un patrón de distribución latitudinal reforzado. A escala interdecadal, se encontraron cambios en la abundancia, composición específica y patrones de distribución de la comunidad, durante el mes junio. La abundancia global de la comunidad aumentó y los patrones de distribución latitudinal se reforzaron al comparar tres años (1983, 2004 and 2011) representativos de cambios climáticos y antropogénicos ocurridos en las últimas tres décadas en el Mediterráneo noroccidental. El principal factor que explicó estos cambios fue la temperatura, representativa de la evolución climática desde los años 80, más frescos, a los años 2010, más cálidos. No obstante, es probable que otros factores antropogénicos como la sobrepesca también hayan podido influir. Todos estos resultados están basados en el estudio de mesoescala de un amplia y heterogénea área caracterizada por diferentes gradientes ambientales en batimetría, temperatura, salinidad, productividad primaria y distintas estructuras hidrodinámicas, así como en la identificación taxonómica a nivel de especie de la comunidad. La comunidad de cnidarios planctónicos en la costa catalana presenta una gran variabilidad, tanto a nivel temporal como espacial, fuertemente asociada a la hidrografía y a las características ambientales del área, e influenciada por los cambios climáticos y antropogénicos ocurridos en las últimas décadas. Los resultados de esta tesis muestran que es extremadamente importante el estudio y monitoreo de los cnidarios planctónicos (incluidos dentro del zooplancton gelatinoso) en áreas de mesoscala, para valorar de forma robusta cambios a escala temporal, y a nivel de identificación de especie, ya que cambios en la distribución espacial de las especies son sensibles indicadores del cambio climático.

GENERAL INTRODUCTION

Planktonic cnidarians and their spatio-temporal variability

Planktonic cnidarians are those species or their life stages in the phylum Cnidaria which live in the water column and drift or swim weakly in a body of water. Their life cycles can be either meroplanktonic, with a benthic phase (polyp) fixed to the bottom (or other substrate) and a planktonic phase (medusa) that swims in the water column, or holoplanktonic, with a free-swimming planktonic phase only (Fig. 1) (Bouillon *et al.*, 2004). Planktonic cnidarians are part of the gelatinous zooplankton, a non-taxonomic term that comprises organisms of diverse groups which share the following similarities among their body designs: high water content (> 95%), transparency, and high fragility. In this group are included medusae, siphonophores, ctenophores, planktonic tunicates (salps, pyrosomes and doliolids), radiolarians, planktonic molluscs, chaetognaths, appendicularians and planktonic worms (Haddock, 2004; Condon *et al.*, 2012). Gelatinous zooplankton is ubiquitous, abundant, and diverse; however it is still a poorly understood group of marine organisms (Pugh, 1989; Haddock, 2004; McClatchie *et al.*, 2012). In pelagic communities, gelatinous animals play an important role in food-web dynamics due to their considerable trophic impact and rapid population growth, which sometimes results in seasonal blooms (Graham *et al.*, 2001; Pagès *et al.*, 2001). These animals prey upon and compete with the co-existing plankton, including higher trophic levels such as fish (e.g.: Purcell and Arai, 2001). At the same time, gelatinous animals themselves are preyed upon by large fish, some of commercial importance, and other top predators such as tuna, sharks, swordfish and turtles (Carrassón and Cartes, 2002; Cardona *et al.*, 2012). Moreover, gelatinous organisms can have a large influence on the carbon, nitrogen, and phosphorus cycles in the ocean

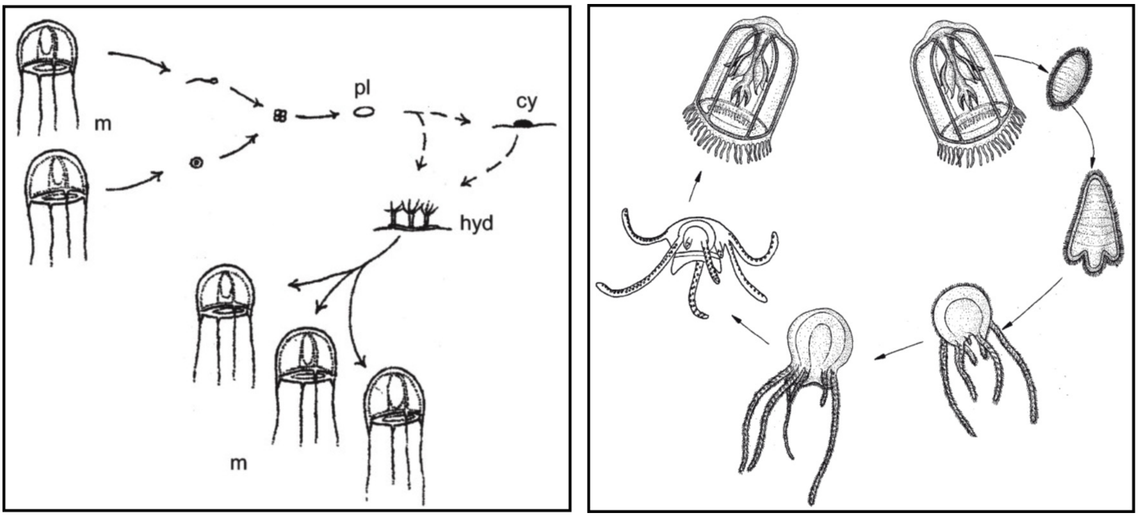

Fig. 1. Diagrams of the planktonic cnidarians life cycles: meroplanktonic type (left) and holoplanktonic type (right). Source: Bouillon et al. 2004.

and on the overall productivity of marine plankton (Pitt *et al.*, 2009). These organisms are also good indicators of water masses and recent mesoscale processes (Russell, 1934; Bigelow and Sears, 1937; Pagès and Gili, 1991). All these factors make the study and monitoring of gelatinous zooplankton an important subject for marine research, and a priority activity for the marine environment.

Planktonic cnidarians distribution and abundance may exhibit high spatial and temporal variability, at different spatio-temporal scales. The spatial distribution of species is determined by geographical latitude and by environmental factors, such as temperature and salinity, and hydrographical features such as currents and fronts (Pagès and Gili, 1991; Graham *et al.*, 2001; Macpherson, 2002). Temporal changes are influenced mainly by the annual temperature cycle (Gili *et al.*, 1987b; Batistić *et al.*, 2007; Licandro *et al.*, 2012), while climatic variability affects their distribution and abundance over longer time scales (Licandro *et al.*, 2012; Boero *et al.*, 2016).

The study of planktonic cnidarians

Nowadays, and for the past 100 years, the study of planktonic cnidarians and gelatinous zooplankton have been conducted using plankton nets. The advantages of this methodology are the following: large-scale areas can be covered, the vertical distributions of the taxa can be investigated and the animals can be quantified. However, due to the fragility of these organisms, nets often damage and break them up into pieces, making it difficult or impossible to identify them to species level, and also to quantify them in any way, especially since some species may not be represented in the samples (Pugh, 1989; Haddock, 2004). In the present century, the most sophisticated techniques for studying these beautiful and delicate animals are the manned or remotely operated submersibles that allow observe them in their natural habitat whilst barely disturbing them. In this way their interactions with the environment and with other organisms can be investigated, as well as their overall behaviour patterns (such as swimming and feeding). However, these methods can only cover a small area, capture few animals, and are also so expensive to employ that their use is usually beyond the reach of most researchers. An ideal method for sampling gelatinous zooplankton would be then to combine these different methods to give complimentary results and obtain a more complete picture of the reality and also help to understand their roles in the ecosystem (Pugh, 1989; Haddock, 2004). Analysis of planktonic cnidarians sampled with nets is made in the laboratory under a stereomicroscope. This is a time-consuming activity that requires considerable human expertise. Each specimen (and there may be thousands in a single sample) is taxonomically identified to species level, whenever its preservation condition permits, and quantified. Some taxonomically important structures, such as tentacles and statocysts, are typically lost during this type of sampling, as commented earlier, sometimes making their identification either difficult or impossible. In the case of siphonophores it is even worst since, in addition, they break up in the different pieces that comprise the colony, losing some of these parts and thus making their identification and quantification more difficult.

Relevance of species identification

Taxonomy is the science of identifying, naming, describing and classifying organisms. It is necessary to quantify the diversity or richness of life. Taxonomy is the first basic step in many other disciplines like medicine, forensic science, ecology, evolution, assessment of living resource stocks, protection and management of the environment and creation of nature reserves, amongst others (Noriega *et al.*, 2015). However in the last few decades, despite its necessity, taxonomy is in crisis. It has been excluded from university curricula in many countries, there are fewer and fewer experts worldwide and there is a lack of recognition within the scientific community and a lack of support by governments (Haddock, 2004; Bilton, 2014; Noriega *et al.*, 2015). The lack of taxonomy or deficient taxonomy seriously compromises the advance of many disciplines, and ecological studies thus generated have little validity beyond 'species X eats species Y' (Haddock, 2004; Noriega *et al.*, 2015). In this thesis taxonomical identification at species level of the whole planktonic cnidarian community has been the basic tool used in order to understand the structure of the community and how it responds to the changing environment. At species level covariance with climate is often stronger than at broader taxonomic levels because each species has its particular requirements depending on the niche it occupies and, if niche breadth is narrow slight climatic changes can critically alter its population dynamics (Thuiller *et al.*, 2005). Therefore, changes in the community are better-interpreted whit a species level approach and moreover, gives the possibility to identify intrusion of new species.

Area and periods of study

The study area covered in this work includes the continental shelf and slope of the Catalan coast, in the North-western Mediterranean Sea. This is a broad heterogeneous area with different environmental gradients including: bathymetry, temperature, salinity and primary production. The continental shelf is wide in the south, where the Ebro River flows into the sea, and narrow and abrupt in the mid-north region, where several submarine canyons occur close to the coast. The area is characterized by the presence of the Northern Current flowing south-westwards all along the continental slope (Font *et al.*, 1995). Associated to the current there is a permanent shelf-slope density front defined by strong salinity gradients, which separates low-salinity shelf waters from the more saline open sea waters (Font *et al.*, 1988; Alvarez *et al.*, 1996). In addition, there is a thermic front, perpendicular to the coast, in the northern part of the Blanes area, which separates the cold waters in the north from the warm waters in the south (Sabatés *et al.*, 2009). All these characteristics make the Catalan coast a highly heterogeneous and variable region.

The present study has been focused on the spring and summer months, when planktonic cnidarians show their highest abundance and biodiversity (Gili *et al.*, 1987b; Batistić *et al.*, 2007; Licandro *et al.*, 2012). Siphonophores constitute the bulk of this community, with the calycophoran *Muggiaea atlantica* Cunningham, 1892 being by far the most abundant and dominant species present. The hydromedusan *Aglaura hemistoma* Péron and Lesueur, 1810, is usually the second most abundant and widespread one. Both species are neritic and epipelagic, accounting for up to 95% of the planktonic cnidarian community in the area during spring (Gili *et al.*, 1987a, 1987b, 1988). Hydrographically, at this time of the year, the northern Catalan waters experience strong spatial and temporal variability due to 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 into the study area by the Northern Current, increase the mesoscale activity of the shelf-slope front and generate oscillations and eddies which increase the shelf-slope exchanges (Alvarez *et al.*, 1996; Flexas *et al.*, 2002).

Previous studies in the Catalan coast

Along the Catalan coast important and pioneering studies of planktonic cnidarians were carried out in the 1980s. These studies deal with diversity, abundance and spatial and seasonal distribution of these taxa in the region and the relationships between species abundance and environmental variables (Riera *et al.*, 1986; Gili *et al.*, 1987a, 1987b, 1988). The results of these studies showed that the main factors affecting the distribution, abundance and species richness of the community were distance from the coast (bathymetry) and latitude, the last related to temperature and salinity gradients detected in the area. In addition, they reported that the annual peaks of abundance and species richness take place mainly during the spring and summer months.

Climate change

The definition of climate change is a change in the weather patterns which last for an extended period of time (i.e., decades to millions of years). It may refer to a change in the average weather conditions and/or to the timed variation of weather around longer-term average conditions (i.e., more or fewer extreme weather events). Climate change is caused by factors such as biotic processes, variations in solar radiation received by the Earth, plate tectonics, and volcanic eruptions. Certain human activities have also been identified as significant causes of recent climate change, often referred to as global warming (America's Climate Choices, 2010). High ocean temperatures due to climate change have been documented at global and local scales, such as in the Mediterranean Sea, (Levitus *et al.*, 2005; IPCC, 2014), as well as an increase in the occurrence of extreme climatic events, like the exceptionally warm summer of 2003 which raised sea surface temperature by 2-3ºC in the whole Mediterranean (Grazzini and Viterbo, 2003; Schär *et al.*, 2004; Sparnocchia *et al.*, 2006). There is increasing evidence that these climatic variations significantly affect the geographic distribution, abundance and phenology of marine species (Stenseth *et al.*, 2002; Edwards and Richardson, 2004), including those of gelatinous zooplankton (Purcell, 2005; Brotz *et al.*, 2012; Boero *et al.*, 2016). In the NW Mediterranean, recent long time-series studies have investigated the effect of climate variability on planktonic cnidarians and other gelatinous zooplankton abundance and species composition (Molinero *et al.*, 2005, 2008; García-Comas *et al.*, 2011; Berline *et al.*, 2012; Licandro *et al.*, 2012). Some of these studies have found that an increase in gelatinous zooplankton is related to an increase in water temperature attributable to global warming (Molinero *et al.*, 2005, 2008). Others however, have found that high inter-annual variability occurs without an increasing abundance trend. Nevertheless, important changes in community composition has been observed in the last three decades (García-Comas *et al.*, 2011; Berline *et al.*, 2012; Licandro *et al.*, 2012).

THESIS AIM

The general aim of this thesis is to understand the variability of the planktonic cnidarian community along the Catalan coast, both at spatial and temporal scales, and to find out how environmental parameters affect that variability. Environmental parameters include both the gradient of different factors (as bathymetry, temperature, salinity and primary production) as well as the presence of hydrographic structures (such as currents, eddies and fronts), which characterize the area. Also, this thesis addresses how that variability is expressed in the community structure, by observing changes in the abundance, spatial distribution and specific composition of the community.

Chapter 1: "High spatial heterogeneity of two planktonic cnidarian species related to the variability of a shelf-slope front at short time scales".

This chapter is focused on investigating how the variability of hydrodynamic structures determines the mesoscale distribution 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*, the two most abundant and representative species in the community. 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 during the months of May and June.

Chapter 2: "Diversity and mesoscale changes in the planktonic cnidarian community under extreme warm summer conditions".

This chapter is focused on analysing how extremely warm conditions, such as those forecast for the future in climatic studies for this region, can affect the cnidarian community. To achieve this goal, we have investigated the abundance, spatial distribution and diversity of the planktonic cnidarian community along the Catalan coast during the extreme warm conditions of the summer 2003 and the standard 2004 summer. We assessed changes in the cnidarian community between both years and explored their relationships with the different environmental gradients (bathymetry, temperature, salinity and primary production) and hydrographic structures (currents and eddies) of the area. The study of both summers constitute a decisive opportunity to shed light on the potential effects of warmer ocean temperatures upon organisms such as gelatinous zooplankton, and their response to extreme temperature variations in the future.

Chapter 3: "Long-term changes of the planktonic cnidarian community in the NW Mediterranean"

This chapter is focused on studying the changes in the community over the last three decades off the Catalan coast. To achieve this aim we analysed abundance, distribution and species composition of the community during the month of June in the years 1983, 2004 and 2011. These three surveys were carried out in the same area, shared the same sampling methodology and have been analysed by the same group of experts, enabling direct comparison between them and the possibility of determining if long-term changes have indeed already occurred. The trends have been analysed and related to environmental and hydrographic variables. This is an uncommon opportunity to study long-term changes in the gelatinous zooplankton, including a mesoscale spatial dimension.

These studies will contribute to a better understanding of gelatinous zooplankton changes from a mesoscale spatial viewpoint, both at short and long temporal scales, a kind of study which is rarely carried out in recent times.

A beyond note

Plankton is essential for life in the oceans, for the survival of human beings and of our planet, as we know it today. It generates more than half (from 70 to 90% depending on the information source) of the atmospheric oxygen necessary for life. It is important to know, value, take care of and protect the Oceans. Marine ecosystems are of huge importance to the biology of the planet because they are among the largest of earth's aquatic ecosystems and play a major role in the overall health of both marine and terrestrial environments (Townsend *et al.*, 2003). Theories indicate that life started in the ocean, so if we care for life we need to care for the Oceans. Could this maybe be the reason why we feel so good near the sea?

This thesis aims to contribute with a grain of sand to the knowledge and value of these small animals inhabiting the ocean, and their biodiversity, which are of such huge importance for every person and life on the planet. Its preservation is fundamental to such daily activities as breathing, food, climate and enjoyment.

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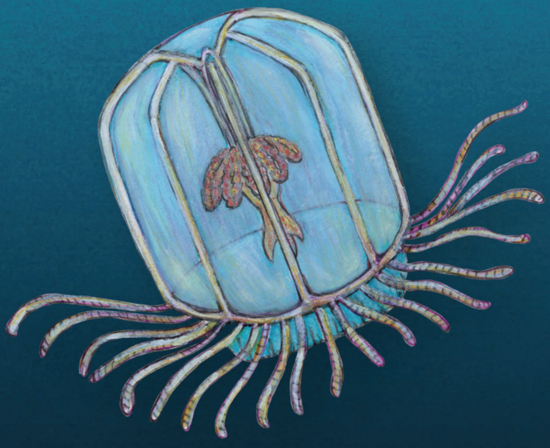
Chapter 1

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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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.

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–l (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 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

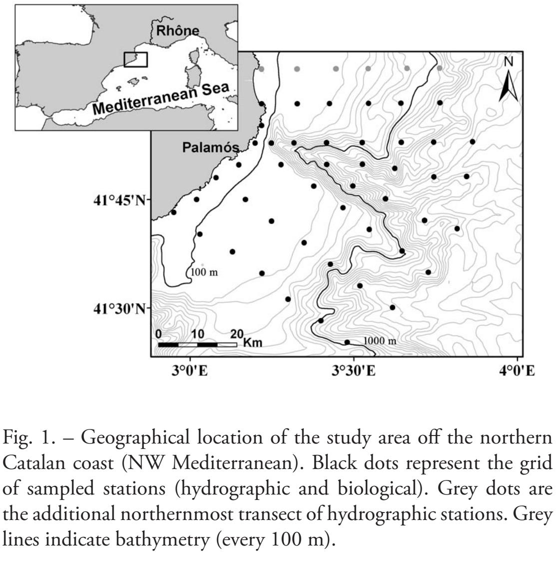

Fig. 1. – Geographical location of the study area off the northern Catalan coast (NW Mediterranean). Black dots represent the grid of sampled stations (hydrographic and biological). Grey dots are the additional northernmost transect of hydrographic stations. Grey lines indicate bathymetry (every 100 m).

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 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 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 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

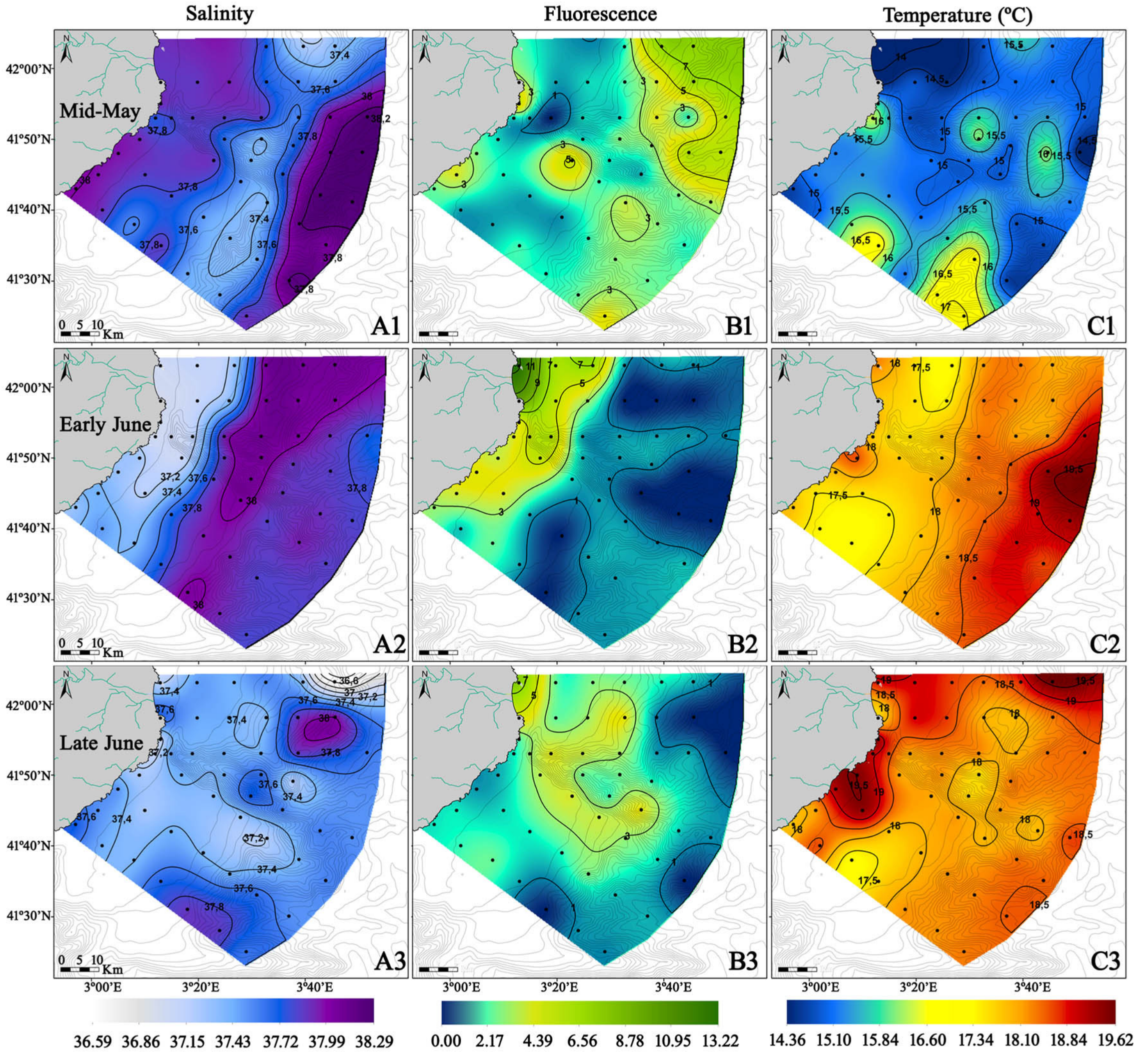

Fig. 2. – Surface (10 m) salinity, fluorescence and temperature distributions in the mid-May (A1-C1), early June (A2-C2) and late June (A3-C3) cruises off the northern coast of Catalonia (note the additional northernmost transect of hydrographic stations). Grey lines represent the bathymetry (every 100 m).

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 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

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

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. atlantica* (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 tempe-

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%

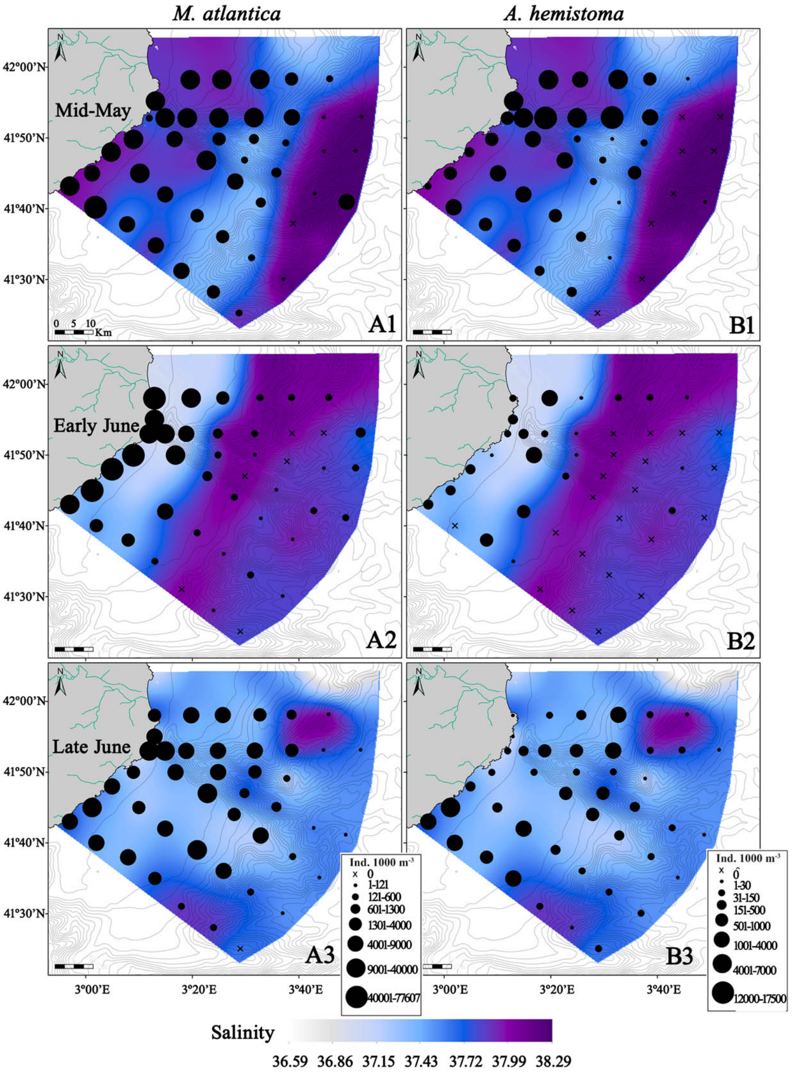

Fig. 3. – Distribution of *Muggiaea atlantica* and *Aglaura hemistoma* overlaid on surface (10 m) salinity in mid-May (A1-B1), early June (A2-B2) and late June (A3-B3). Grey lines represent the bathymetry (every 100 m).

rature explaining 63% of deviance (Table 4).

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

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

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

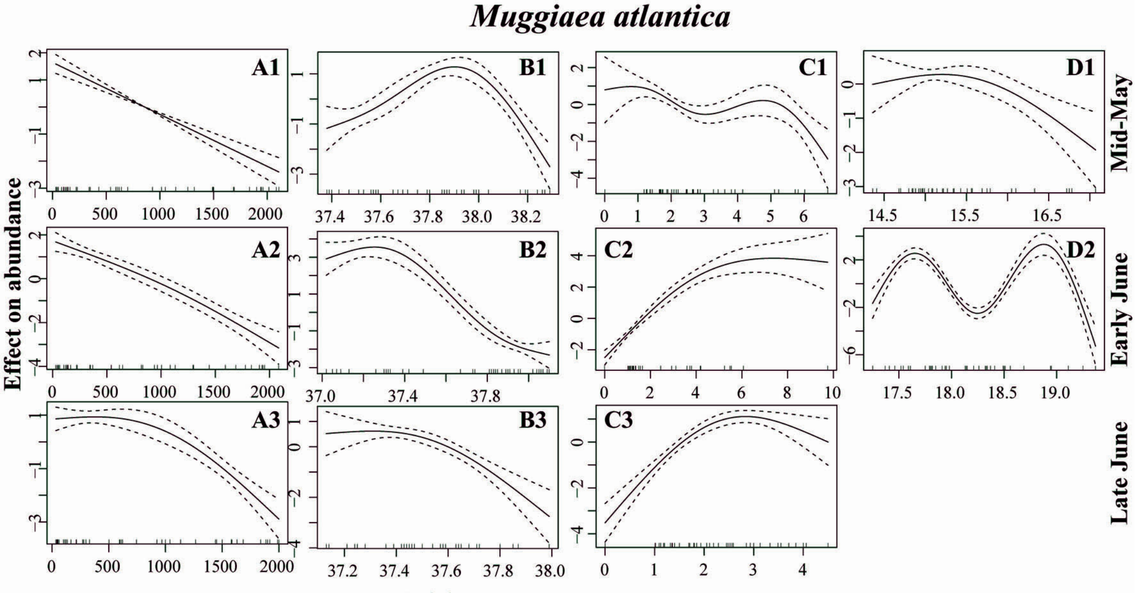

Fig. 4. – Results of single variable–based GAMs for *Muggiaea atlantica*, showing the abundance trends of the siphonophore for each variable in each surveyed period (A1-D1, mid-May; A2-D2, early June; A3-D3, late June). Solid lines display the smoothing function according to the GAMs. The area between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

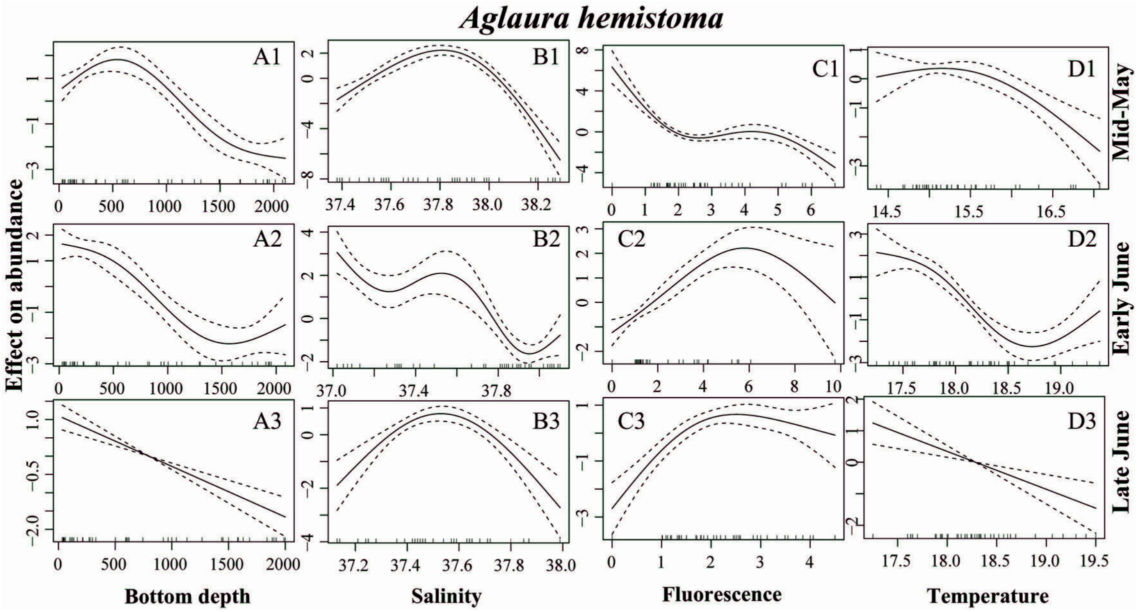

Fig. 5. – Results of single variable–based GAMs for *Aglaura hemistoma* showing the abundance trends of the hydromedusa for each variable in each surveyed period (A1-D1, mid-May; A2-D2, early June; A3-D3, late June). Solid lines display the smoothing function according to the GAMs. The area between the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

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

Table 4. – Results of the multiple variable–based GAMs computed for *Muggiaea atlantica* and *Aglaura hemistom*a 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	0.51	53.2	2.6	<0.001	0.77	70.9
	s(S)	-	n.s.			2.9	<0.001		
	s(Fl)	-	n.s.			2.9	<0.01		
	s(T)	1.8	<0.01			-	n.s.		
Early June	s(Depth)	1.0	0.06*	1.11	69.7	2.5	0.06*	1.53	49.8
	s(S)	2.9	<0.001			3.6	<0.001		
	s(Fl)	-	collinear			-	collinear		
	s(T)	-	n.s.			-	n.s.		
Late June	s(Depth)	1.7	<0.001	-0.04	68.2	1.3	<0.001	0.18	62.7
	s(S)	-	n.s.			1.9	<0.01		
	s(Fl)	1.9	<0.001			1.2	<0.05		
	s(T)	-	n.s.			1.0	<0.05		

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 thermohaline 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

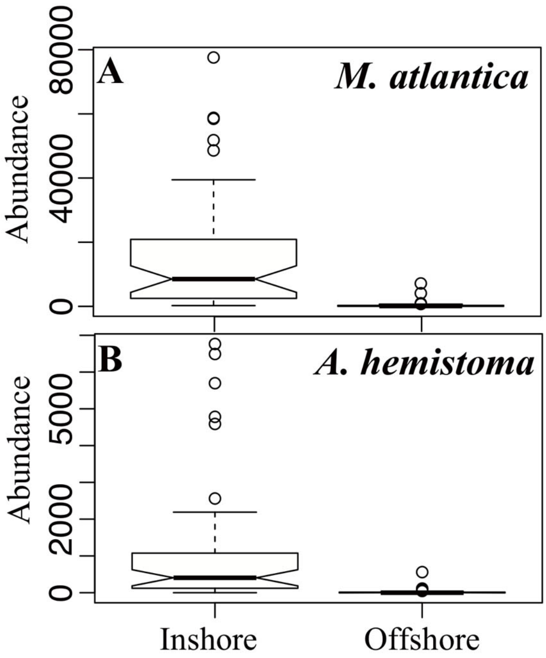

Fig. 6. – Boxplot comparing abundances (Ind. /1000 m^3) of Muggiaea atlantica (A) and Aglaura hemistoma (B) on the inshore and offshore sides of the shelf-slope front when it was observed in the upper layers of the water column (mid-May and early June). In graph B, the two highest values (17480 and 12079 Ind. /1000 m^3) were extracted to obtain a better graphical display.

(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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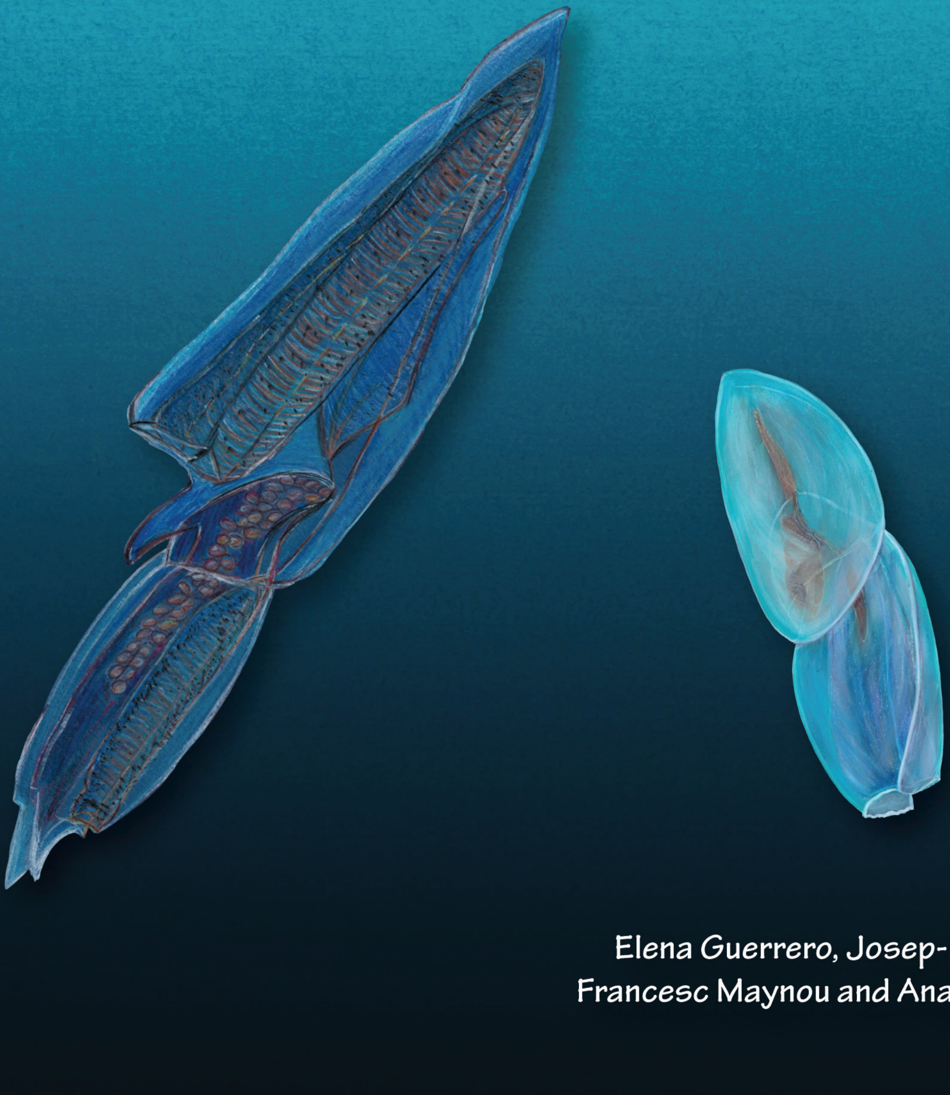
Chapter 2

Diversity and mesoscale spatial changes in the planktonic cnidarian community under extreme warm summer conditions



Elena Guerrero, Josep-Maria Gili,
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Diversity and mesoscale spatial changes in the planktonic cnidarian community under extreme warm summer conditions

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ABSTRACT

We have investigated the abundance, spatial distribution, species richness and community structure of the planktonic cnidarian community off the Catalan coast, NW Mediterranean, during the extreme warm summer conditions of 2003 with respect to the standard 2004 summer. The study covered a broad heterogeneous area with different environmental gradients (bathymetry, temperature, salinity and primary production). During the warm summer, the community was two fold less abundant than during the standard summer, whereas species richness remained nearly the same. The mesoscale spatial distribution of several species varied between both years and the structure of the community changed from a coastal-offshore to a north-south ordination, where the temperature gradient played the main role. Only hydromedusae, as a group, were more abundant during the warm summer. Siphonophores dominated in both years even though the dominant species, *M. atlantica,* showed one of the most important abundance decreases in the warm year. Our results pointed out that exceptional warm conditions during the summer season would lead a reduction of gelatinous zooplankton abundance as well as changes in their latitudinal distribution and community composition. We stress the importance of spatial mesoscale plankton surveys with detailed taxonomic identification as a critical tool for better understanding marine ecosystem responses to climatic variability.

Key words: Species richness, climate extreme event, Catalan coast, Shannon diversity index.

INTRODUCTION

Gelatinous zooplankton is a common component of the pelagic fauna with an important role within the trophic web (Pagès *et al.*, 2001; Robison, 2004). It is ubiquitous, diverse, and one of the most abundant component of the oceanic community (Pugh, 1989; Haddock, 2004; McClatchie *et al.*, 2012). In temperate seas, such as the Mediterranean, gelatinous zooplankton represents an important fraction of all zooplankton in terms of both abundance and species richness (Estrada *et al.*, 1985; Mills *et al.*, 1996; Saiz *et al.*, 2014). Its patterns of distribution, abundance and species richness, are tightly linked to oceanographic dynamics and water mass structures, as well as climate patterns (Graham *et al.*, 2001; García-Comas *et al.*, 2011; Brotz *et al.*, 2012; Licandro *et al.*, 2012). Thus, both mesoscale physical processes, such as currents, fronts and eddies, as well as climate variability, can shape and determine its distribution (Pagès and Gili, 1991; Graham *et al.*, 2001; Boero *et al.*, 2016; Guerrero *et al.*, 2016).

Changes in environmental and climatic conditions have been shown to affect the composition, abundance and distribution of several groups of zooplankton (Hays *et al.*, 2005; Piontkovski *et al.*, 2011; Saiz *et al.*, 2014), including gelatinous zooplankton (Lynam *et al.*, 2010; Licandro *et al.*, 2012). Climate change has been postulated as one of the global phenomena driving increased jellyfish abundance and blooms (Brotz and Pauly, 2012; Boero *et al.*, 2016), as well as changes in their richness (Batistić *et al.*, 2014; Boero *et al.*, 2016). In temperate regions, gelatinous zooplankton appears to be expanding its distribution and broadening its reproductive periods, thus resulting in larger populations with an attending significant negative socio-economical impact in maritime tourism in some areas (Boero *et al.*, 2016).

The Mediterranean is a highly seasonal sea (Estrada *et al.*, 1985; Bosc *et al.*, 2004) where the distribution and abundance of gelatinous zooplankton are regulated by the temperature annual cycle (Gili *et al.*, 1987b; Batistić *et al.*, 2007; Licandro *et al.*, 2012). The highest abundance and diversity occurring in spring and summer (Gili *et al.*, 1987b; Batistić *et al.*, 2007; Licandro *et al.*, 2012; Saiz *et al.*, 2014). In recent years, high ocean temperatures, due to climate change have been well documented at global and local scale, such as the Mediterranean Sea, (Levitus *et al.*, 2005; IPCC, 2014; Boero *et al.*, 2016), as well as an increase in the occurrence of extreme climatic events (Schär *et al.*, 2004). The 2003 summer was exceptionally warm in the European region, where a heat wave from early June to mid-August produced record air temperatures, 3 to 6ºC above the seasonal average (Schär *et al.*, 2004). This heat wave raised sea surface temperature by 2-3ºC in the whole Mediterranean (Grazzini and Viterbo, 2003; Sparnocchia *et al.*, 2006) an increase which is in line with values close to those foreseen in the future by the climatic trends for the region (Vargas-Yáñez *et al.*, 2010; Maynou *et al.*, 2014). During that same period, extensive mass mortality of rocky benthic macroinvertebrates (mainly gorgonians and sponges) in the entire NW Mediterranean (Garrabou *et al.*, 2009) and increased warm water planktonic species in the Adriatic Sea were documented (Piontkovski *et al.*, 2011). However, the consequences of such an anomaly for marine plankton communities are still poorly understood (Piontkovski *et al.*, 2011; Atienza *et al.*, 2016).

Studies of zooplankton time-series conducted in different areas of the Mediterranean Sea have shown long-term changes on gelatinous and non-gelatinous zooplankton in relation to climate variability (Benović *et al.*, 2000; Molinero *et al.*, 2005, 2008; García-Comas *et al.*, 2011; Berline *et al.*, 2012; Licandro *et al.*, 2012; Batistić *et al.*, 2014). Nevertheless, the observed effects show no strongly coherent response across sampling sites (Berline *et al.*, 2012; Saiz *et al.*, 2014). Most of these studies were conducted in few stations, over a geographic limited area, and examined some species or broad taxonomic groups. However, latitudinal changes in species distribution reflect the response of ecosystems to rising temperature (Hughes, 2000; Beaugrand *et al.*, 2002).

The present work aimed at providing a spatial dimension to the study of changes in marine zooplanktonic communities under extreme warm summer conditions, while dealing with the species level taxonomical identification of the whole planktonic cnidarian community. The study covered a broad heterogeneous area, the Catalan coast in the NW Mediterranean, with different environmental gradients (bathymetry, temperature, salinity and primary production). We have identified and quantified siphonophores, hydromedusae and scyphomedusae at the species level, both under the exceptionally warm summer conditions of the 2003, and the standard one of the 2004 (Sparnocchia *et al.*, 2006; Maynou *et al.*, 2014). The study of both summers constitute an opportunity to shed light on the potential effects of extreme high temperatures upon organisms, such as gelatinous zooplankton, and their response to strong and sudden temperature variations.

The lead hypothesis in this study was that the exceptional warm conditions of the 2003 summer would cause significant changes in the abundance, spatial distribution, species richness, and community structure of the planktonic cnidarian in the studied temperate area. The response of cnidarians community to this extreme event may provide new insights regarding the impact of climate change on marine ecosystems in future warming conditions.

MATERIAL AND METHODS

The study area was located in the Catalan coast, NW Mediterranean (Fig. 1). Two oceanographic cruises were conducted during the summer period of two consecutive years: 18–25 July 2003 and 21–29 July 2004. In each survey, 66 sampling stations were located on transects perpendicular to the shoreline, over the continental shelf and slope. On each transect, stations were placed 14 km apart while the distance between transects was 18.5 km. Vertical profiles of the basic hydrographic variables (temperature, salinity and fluorescence) were obtained with a Neil Brown Mark III-CTD (WOCE standard) equipped with a Sea Tech fluorometer. The vertical profiles were interpolated to 1 m depth intervals. Water samples for chlorophyll *a* determination were collected at each station with a rosette system at three depths down to 70 m, throughout day and night, in order to calibrate the *in situ* fluorometer

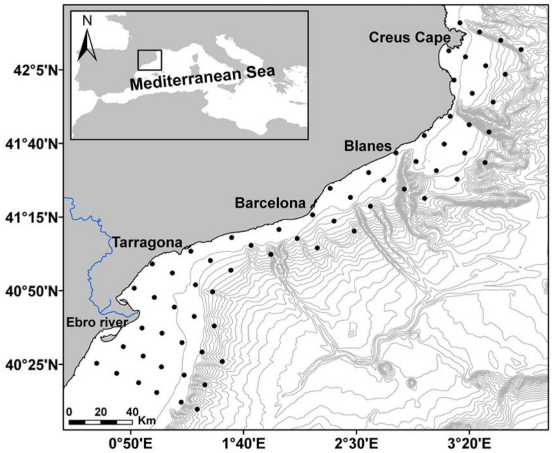

Figure 1. Geographical location of the study area off the Catalan coast (NW Mediterranean). Black dots represent the grid of sampled stations (n = 66). Grey lines indicate bathymetry (every 100 m).

(see Sabatés *et al.*, 2009 for the methodological description).

Circulation in the area was estimated from geostrophic fields obtained from dynamic heights at the stations. The reference level was 600 m and, where the depth of the station was lower, dynamic height was extrapolated using the continuity equation applied to the deepest level of three-station clusters (Hidaka, 1940). Along and across shore geostrophic velocity components at the stations were derived from the stream function obtained interpolating the dynamic heights over the whole area (Stewart, 2008). Given the general NE-SW orientation of the Catalan coast, the velocity components were rotated 45°, such as that U45 is the across shore component of the current velocity, with positive values directed offshore, and V45 is the alongshore component, with positive values towards the SW. Vorticity or curl of the water current velocity at each station was also obtained from the spatial derivative of the stream function (Stewart, 2008). Zooplankton was sampled with a Bongo net of 60 cm mouth diameter and 300 µm mesh size. Hauls were oblique from a maximum depth of 200 m to the surface (or from 5 m above the bottom to the surface at stations shallower than 200 m). The volume of filtered water was estimated by means of a flowmeter placed in the centre of the net mouth. Zooplankton samples were fixed immediately after collection in 5% formaldehyde buffered with sodium tetraborate.

In the laboratory, the whole planktonic cnidarian community (hydromedusae, siphonophores and scyphomedusae) was analysed at the species level under a stereomicroscope. Aliquots were taken only to quantify the most abundant species (usually *Muggiaea atlantica* and *Aglaura hemistoma*) where a minimum of 100 individuals were counted (Postel *et al.*, 2000). Calycophoran polygastric stages were counted as the number of complete colonies plus the highest number of either anterior or posterior nectophores. The eudoxid stage (sexual stage) of the species *Abylopsis tetragona*, *Chelophyes appendiculata* and *Eudoxoides spiralis* was identified and counted based on the number of detached bracts and intact eudoxids, this is a relevant piece of information since only their presence represents reproduction and continuity of the species in an area and its quantitative study is indispensable to estimate their importance in marine food webs (Gamulin and Kršinić, 1993; Grossmann *et al.*, 2014). Nectophores of physonect siphonophores and the calycophoran *Hippopodius hippopus* were counted and divided by 10, according to Pugh (1984), to estimate the number of sampled colonies. The number of hydromedusae individuals, siphonophore colonies and eudoxids stages were standardized to number of individuals per 1000 m^3 of filtered seawater.

Data analysis

For each species and survey the mean abundance values, frequency of occurrence (FO, percentage of stations where a taxon occurred) and the relative abundance (RA, percentage contribution of a taxon to the total mean abundance of individuals) were calculated. For each cruise, the species richness of the cnidarian community was estimated as the total number of species (S), and the diversity was calculated with the Shannon diversity index (H'), in natural logarithm base, for each station.

Significant differences in abundance between both years were tested for the total cnidarians and for the groups Siphonophorae, Hydromedusae and Scyphomedusae by means of an analysis of variance using Generalized Linear Models (GLM) in the free statistical software R, version 3.0.2 (R Development Core Team, 2013). The counts of total cnidarians and Siphonophorae, which followed a Poisson distribution, were analyzed with the function "glm" from the "stats" library (R Core Team). For Hydromedusae and Scyphomedusa, which followed a binomial negative distribution, the "glm.nb" package (Venables and Ripley, 2002) was used with a log link function (Zuur *et al.*, 2009). The log of filtered seawater by the net was included as an offset inside all models to eliminate bias due to varying sampling units (Penston *et al.*, 2008; Zuur *et al.*, 2009; Guerrero *et al.*, 2013).

To assess the existence of variations among different groups of stations based on species composition and their abundance, a cluster analysis was performed using the "vegan" package in the R software (Oksanen *et al.*, 2015). Species with five or less presences and/or FO < 3% in each survey were not included in the analyses. The abundance of species was log-transformed (log (x+1)). Clustering of stations was carried out using hierarchical clustering with Bray-Curtis distance and Ward's agglomeration method. The graphical display of the ordered community table was carried out with R routine "coldiss" given in Borcard *et al.* (2011). Afterwards, a Canonical Correlation Analysis (CCA) was performed for each survey with the "vegan" package in R software (Oksanen *et al.*, 2015), to explore the multivariate relationships between the same matrixes of species' abundance and the environmental variables. Collinearity between pairs of variables was evaluated by pairwise scatterplots, Pearson's correlation coefficients (cut-off value |0.6|) and corroborated by the variance inflation factor (Zuur *et al.*, 2009). The variables Chlorophyll *a* (at 5 m depth) and salinity (at 5 m depth) were collinear and salinity was kept for the analyses as this parameter has been previously recognized as important driver in the distribution of gelatinous zooplankton in the area (Gili *et al.*, 1988; Guerrero *et al.*, 2016). Initially, parameters at surface (5 m) and intermediate waters (60 m) were included in the analyses. However, since surface parameters resulted by far the determinant ones and the inclusion of the deeper variables implied to eliminate from the analyses the stations which depth was lower than 60 m (about 38% of the stations), the deeper parameters were not included in the final analyses. Thus, the environmental matrix used was composed by 8 explanatory variables: bathymetry (m, depth), time of the sampling (day and night), surface (5 m) temperature (ºC) and salinity, integrated chlorophyll *a* concentration (µg l^{-1}) (from a maximum depth of 100 m to the surface), across shore velocity (cm s^{-1}, U45), alongshore velocity (cm s^{-1}, V45) and vorticity (10^{-6} s^{-1}). Depth was log-transformed (log (x)). All statistical analyses were done using the free-statistical software R, version 3.0.2 (R Development Core Team, 2013). Maps of the horizontal distribution of the environmental parameters, spline interpolation, and species abundance were generated by ArcGIS 10.2 software.

RESULTS

Hydrographic conditions

Summer of 2003 was warmer than 2004, with sea surface temperatures 2 to 3°C higher in July 2003 than in July 2004. In both years, a substantial difference in temperature was detected between the northern and southern parts of the region, and a marked thermal front of nearly 2 °C, perpendicular to the coastline, was detected around 41° 30' N (Fig. 2). This front separated the coldest waters in the north, with minimum values of 23.13ºC in 2003 and 20.15ºC in 2004, from the warmer waters in the south, with maximum values of 27.62ºC in 2003 and 25.98ºC in 2004 (Table 1, Fig. 2).

The surface salinity distribution showed similar average values in both years and was characterized by the presence of low salinity patches on the Ebro River continental shelf in the southern part of the area (Table 1, Fig. 2). In both years, two salinity patches were detected: one close to the coast north of the Ebro delta, and the other near the shelf edge at the southern limit of the sampled area. In July 2004, a water mass of high salinity

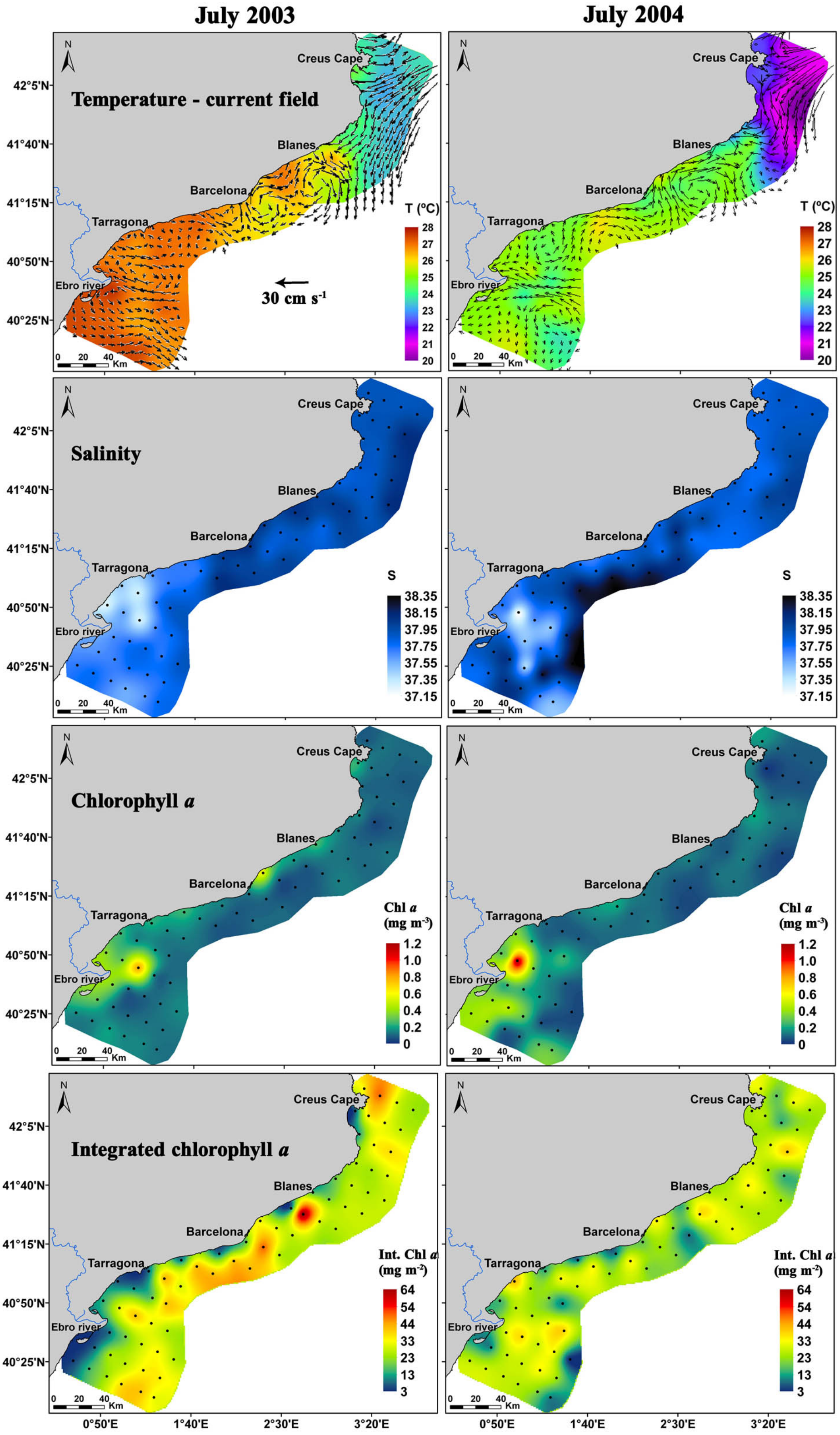

Figure 2. Geostrophic current fields at 21 m depth, relative to 600 m, overlaid on surface (5 m) temperature, salinity, chlorophyll a concentration and integrated (0-100 m) chlorophyll a concentration in July 2003 and 2004, off the Catalan coast.

Table 1. Values of the environmental parameters off the Catalan coast during July 2003 and July 2004.

	July 2003			July 2004		
	Mean ± SD	**Min.**	**Max.**	**Mean ± SD**	**Min.**	**Max.**
Depth (m)	289.53 ± 331.64	24.00	1331.00	291.45 ± 326.21	28.00	1322.00
T (ºC)	25.82 ± 1.47	23.13	27.62	24.05 ± 1.56	20.15	25.98
S	37.82 ± 0.19	37.26	38.09	37.86 ± 0.20	37.16	38.28
Chl *a* (mg m^{-3})	0.16 ± 0.12	0.05	0.79	0.17 ± 0.16	0.02	1.14
Int. Chl *a* (mg m^{-2})	27.16 ± 11.82	4.39	63.54	25.42 ± 8.18	3.86	41.24
U45 (cm s^{-1})	-2.01 ± 19.74	-74.19	32.7	-2.26 ± 20.9	-58.18	67.78
V45 (cm s^{-1})	-3.65 ± 10.63	-30.66	18.91	0.31 ± 13.44	-27.28	39.62
Vorticity (10^{-6} s^{-1})	-0.12 ± 0.89	-3.65	2.20	0.00 ± 0.93	-2.19	2.76

Depth = bottom depth, T = temperature, S = salinity; Chl a = chlorophyll a, Int. Chl a = 0 to 100 m integrated chlorophyll a, U45 = across shore component of the current velocity, V45 = alongshore component of the current velocity, SD = standard deviation, Min. = minimum value, Max. = maximum value.

(38.28) was located offshore in the southern half of the area.

Surface chlorophyll *a* showed very low values almost everywhere. There were, however, some patches of relatively high concentration near the Ebro delta (0.79 mg m^{-3} in 2003 and 1.14 mg m^{-3} in 2004, Table 1) whose position agreed with the low surface salinity patches described. Some other small patches were also observed close to the coast in the vicinity of Barcelona, a highly populated zone, and at secondary river mouths (Fig. 2). Integrated (0-100 m) chlorophyll *a* showed higher values in July 2003 than in 2004 (Table 1), with the lowest values located close to the coast, increasing over the shelf and slope (Fig. 2).

In both surveys, the southwest flowing Northern Current was very apparent in the NE of the study area, (>41°30' N), being more intense in July 2003 (Fig. 2). In the central part of the area, two anticyclonic eddies were located in 2003, and a large anticyclonic eddy was detected east of Barcelona in 2004. In both years, complex current patterns were detected in the vicinity of the Ebro delta over the continental shelf, dominated by negative (anticyclonic) vorticity, with well-defined eddies, particularly in 2003.

Abundance and species composition

A total of 56 species of planktonic cnidarians were found in the two studied periods, 17 siphonophores, 36 hydromedusae and 3 scyphomedusae. In both summers the number of species of planktonic cnidarians was quite similar, 46 in July 2003 and 44 in July 2004 (Table 2). Nevertheless, the abundance was over twofold higher in the standard summer (total cnidarians: z-value = 102.8, p-value <0.001; Siphonophorae: z-value = 108.0, p-value <0.001, Scyphomedusae: z-value = 4.6, p-value <0.001, Fig. 3, Table 2), except for hydromedusae that was higher in the warm summer (z-value = -3.2, p-value <0.01). The Shannon diversity index (H') was higher in the warm (1.38 ± 0.36) than in the standard summer (0.98 ± 0.57).

Siphonophores were the most abundant cnidarians in both summers, *M. atlantica* and *L. subtilis* polygastric stages being the most numerous and widespread species (Table 2). The species community composition was virtually the same in both years, although *Agalma elegans* was only found in 2004 and a free-swimming siphosome fragment of *Apolemia* sp. was collected in 2003 (Table 2). The dominant species, *M. atlantica,* showed one of the most important reduction in abundance in the warm summer, while *Muggiaea kochii* was more abundant in this warm year (Table 2). The quantified eudoxid stages constituted a relatively high percentage of the total cnidarian community (~10%) and showed a higher abundance in the standard year, being those of *C. appendiculata* the most abundant and widespread (Table 2).

Hydromedusae were the only cnidarian group that presented higher abundances in the warm summer, being *A. hemistoma* and *Rhopalonema velatum* the most common and widespread species. This group showed the most important changes in species composition between summers

Table 2: Mean (± SD) abundance values (Ind·1000 m-3), relative abundance (RA), frequency of occurrence (FO) and abundance range values for all species found during July 2003 and 2004 off the Catalan coast.

	July 2003				**July 2004**			
	Mean ± SD	RA	FO	Range	Mean ± SD	RA	FO	Range
Total Cnidaria	**1759.03 ± 1351.17**	**100**	**100**	**0 - 4155.9**	**3754.84 ± 3661.98**	**100**	**100**	**0 - 19013.5**
Siphonophorae	**1366.39 ± 1163.49**	**77.68**	**100**	**0 - 4155.9**	**3201.81 ± 2736.17**	**85.27**	**100**	**0 - 9513.6**
Abylopsis tetragona P	11.95 ± 20.67	0.68	60.6	0 - 94.1	25.37 ± 42.01	0.68	66.7	0 - 194.4
Abylopsis tetragona E	12.80 ± 15.66	0.73	68.2	0 - 73.6	15.44 ± 16.60	0.41	52.0	0 - 71.2
Chelophyes appendiculata P	53.17 ± 65.03	3.02	81.8	0 - 348.2	42.44 ± 30.65	1.13	97.0	0 - 155.0
Chelophyes appendiculata E	175.00 ± 266.28	9.95	83.3	0 - 1394.4	316.15 ± 361.36	8.42	98.5	0- 1973.9
Eudoxoides spiralis P	0.83 ± 2.57	0.05	13.6	0 - 13.6	0.05 ± 0.39*	0.001	1.5	0 - 3.2
Eudoxoides spiralis E	2.46 ± 8.51	0.14	15.2	0 - 42.5	-	-	-	-
Lensia conoidea	5.85 ± 8.68	0.33	54.5	0 - 42.3	6.70 ± 10.85	0.18	50.0	0 - 48.6
Lensia fowleri	0.12 ± 0.58	0.01	4.5	0 - 3.4	0.10 ± 0.56	0.003	3.0	0 - 3.3
Lensia meteori	3.87 ± 15.03	0.22	31.8	0 - 118.9	25.06 ± 64.15	0.67	39.4	0 - 307.3
Lensia subtilis	136.74 ± 135.98	7.77	95.4	0 - 611.3	122.05 ± 118.54	3.25	92.4	0 - 604.6
Lensia subtiloides	0.34 ± 2.74	0.02	1.5	0 - 22.2	0.21 ± 1.29	0.01	3.0	0 - 9.7
Muggiaea atlantica	865.51 ± 1002.11	49.20	95.5	0 - 4155.9	2610.93 ± 2709.88	69.54	100	4.7 - 9513.6
Muggiaea kochi	92.78 ± 209.30	5.27	89.4	0 - 1241.3	28.53 ± 30.98	0.76	84.8	0 - 138.4
Sulculeolaria chuni	0.08 ± 0.69*	0.005	1.5	0 - 5.6	0.04 ± 0.29*	0.001	1.5	0 - 2.4
Hippopodius hippopus	0.67 ± 2.12	0.04	12.1	0 - 10.5	0.05 ± 0.38*	0.001	1.5	0 - 3.1
Agalma elegans	-	-	-	-	0.21 ± 0.83	0.01	6.1	0 - 4.2
Halistemma rubrum	1.50 ± 2.47	0.09	34.9	0 - 10.3	2.84 ± 5.14	0.08	42.4	0 - 30.0
Nanomia bijuga	1.84 ± 1.89	0.10	56.1	0 - 7.4	5.67 ± 12.75	0.15	60.6	0 - 93.2
Apolemia sp.	0.04 ± 0.33*	0.002	1.5	0 - 2.6	-	-	-	-
Physophora hydrostatica	0.85 ± 1.87	0.05	24.2	0 - 9.8	0.14 ± 0.62	0.004	4.5	0 - 3.0
Hydromedusae	**388.22 ± 378.00**	**22.07**	**98.5**	**0 - 1786.7**	**221.98 ± 329.96**	**5.91**	**98.5**	**0 - 2173.8**
Order Anthoathecata	**7.47 ± 22.15**	**1.92°**	**59.1**	**0 - 169.1**	**15.70 ± 26.04**	**7.07°**	**83.3**	**0 - 166.5**
Thamnostoma dibalium	0.04 ± 0.32*	0.002	1.5	0 - 2.6	0.09 ± 0.38	0.002	6.1	0 - 2.0
Cystaeis sp.	0.03 ± 0.28*	0.002	1.5	0 - 2.3	-	-	-	-
Amphinema rubrum	0.17 ± 0.73	0.01	6.1	0 - 4.7	0.19 ± 1.19	0.01	3.0	0 - 9.1
Merga tergestina	-	-	-	-	0.39 ± 1.42	0.01	9.1	0 - 9.1
Merga tregoubovii	0.04 ± 0.29*	0.002	1.5	0 - 2.4	-	-	-	-
Leuckartiara octona	0.64 ± 1.61	0.04	19.7	0 - 9.0	0.86 ± 2.12	0.02	16.7	0 - 9.4
Neoturris pileata	-	-	-	-	0.05 ± 0.38*	0.001	1.5	0 - 3.2
Rhabdoon singulare	-	-	-	-	0.43 ± 1.73	0.01	9.1	0 - 12.5
Porpita porpita (col.)	-	-	-	-	0.28 ± 0.99	0.01	7.6	0 - 4.7
Velella velella (col.)	6.06 ± 21.79	0.34	42.4	0 - 169.1	12.40 ± 25.89	0.33	69.7	0 - 166.5
Zanclea sp.	-	-	-	-	0.10 ± 0.78	0.003	1.5	0 - 6.3
Zanclea sessilis	-	-	-	-	0.19 ± 1.20	0.01	3.0	0 - 9.2
Codonium proliferum	-	-	-	-	0.06 ± 0.50*	0.002	1.5	0 - 4.1
Corymorpha bigelowi	0.09 ± 0.75	0.01	1.5	0 - 6.1	-	-	-	-
Euphysa flammea	0.19 ± 1.24	0.01	3.0	0 - 9.8	-	-	-	-
Euphysa aurata	0.20 ± 0.96	0.01	6.1	0 - 6.9	0.11 ± 0.64	0.003	3.0	0 - 4.2
Order Leptothecata	**12.26 ± 17.49**	**3.16°**	**66.7**	**0 - 101.3**	**17.64 ± 95.60**	**7.95°**	**51.5**	**0 - 377.2**
Aequorea forskalea	0.06 ± 0.51*	0.004	1.5	0 - 4.2	-	-	-	-
Eirene viridula	0.03 ± 0.28*	0.002	1.5	0 - 2.3	-	-	-	-
Eutima gegenbauri	0.46 ± 2.70	0.03	4.5	0 - 20.8	0.25 ± 1.62	0.01	3.0	0 - 12.6
Eutima gracilis	-	-	-	-	5.76 ± 46.43	0.15	3.0	0 - 377.2
Eutonina scintillans	-	-	-	-	0.19 ± 1.55*	0.01	1.5	0 - 12.6
Helgicirrha schulzii	5.89 ± 7.81	0.34	56.1	0 - 29.2	4.68 ± 7.75	0.12	42.4	0 - 35.6
Laodicea undulata	0.12 ± 0.74	0.01	3.0	0 - 5.6	-	-	-	-
Staurostoma mertensii	0.04 ± 0.32*	0.002	1.5	0 - 2.6	-	-	-	-
Earleria araiae	0.07 ± 0.39	0.004	3.0	0 - 2.3	-	-	-	-
Clytia spp.	0.04 ± 0.32*	0.002	1.5	0 - 2.6	0.14 ± 1.17	0.004	1.5	0 - 9.5
Gastroblasta raffaelei	1.28 ± 4.56	0.07	10.6	0 - 23.4	-	-	-	-
Obelia spp.	4.27 ± 14.23	0.24	28.8	0 - 101.3	6.62 ± 46.42	0.18	13.6	0 - 377.2
Order Narcomedusae	**5.02 ± 10.88**	**1.29°**	**48.5**	**0 - 41.2**	**2.90 ± 5.83**	**1.31°**	**33.3**	**0 - 27.4**
Cunina octonaria	0.04 ± 0.31*	0.002	1.5	0 - 2.5	0.08 ± 0.68*	0.002	1.5	0 - 5.5
Solmissus albescens	1.17 ± 4.91	0.07	9.1	0 - 32.4	0.56 ± 2.35	0.01	6.1	0 - 12.8
Solmundella bitentaculata	3.81 ± 7.42	0.22	43.9	0 - 41.2	2.26 ± 5.11	0.06	27.3	0 - 27.4
Order Trachymedusae	**363.46 ± 369.00**	**93.62°**	**98.5**	**0 - 1786.7**	**185.74 ± 317.93**	**83.7°**	**97.0**	**0 - 2173.8**
Liriope tetraphylla	6.05 ± 8.36	0.34	63.6	0 - 33.4	0.81 ± 2.26	0.02	15.1	0 - 12.0
Aglaura hemistoma	234.37 ± 304.59	13.33	97.0	0 - 1786.7	117.55 ± 307.96	3.13	86.4	0 - 2173.8
Persa incolorata	25.14 ± 57.17	1.43	57.6	0 - 303.5	3.86 ± 26.15	0.10	12.1	0 - 212.1
Rhopalonema funerarium	0.09 ± 0.75	0.01	1.5	0 - 6.1	0.27 ± 1.68	0.01	3.0	0 - 12.6
Rhopalonema velatum	97.81 ± 104.15	5.56	89.4	0 - 413.7	63.24 ± 68.94	1.68	90.9	0 - 283.9
Scyphomedusae	**4.42 ± 7.36**	**0.25**	**47.0**	**0 - 33.3**	**331.06 ± 2340.13**	**8.82**	**72.7**	**0 - 19013.5**
Atolla sp.	3.06 ± 5.93	0.17	40.9	0 - 33.3	6.28 ± 10.52	0.17	53.0	0 - 63.4
Nausithoe punctata	0.02 ± 0.20*	0.001	1.5	0 - 1.6	-	-	-	-
Pelagia noctiluca	1.34 ± 4.60	0.08	16.7	0 - 31.2	324.77 ± 2340.99	8.65	27.3	0 - 19013.5

P = Polygastric stage (asexual), E = Eudoxid stage (sexual). *Only 1 individual found; °RA relative to Hydromedusae group.

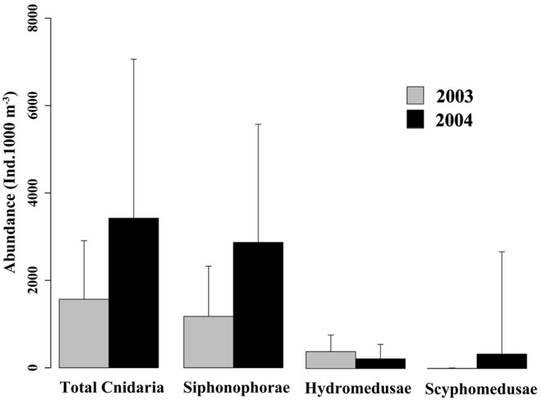

Figure 3. Mean abundance (± SD) differences between July 2003 and 2004 for the total cnidarian abundance, and the Siphonophorae, Hydromedusae and Scyphomedusae groups.

due to the more diverse orders Anthoathecata and Leptothecata, while the less diverse Narcomedusae and Thrachymedusae conserved the same species composition (Table 2). In both summers, holoplanktonic hydromedusae (Narco-, Trachymedusae and the neustonic colonies *P. porpita* and *V. velella*) were more abundant than the meroplanktonic species (Anthomedusae and Leptomedusae). The holoplanktonic species were more abundant in the warm summer (375 ± 371 respect to 201 ± 318 ind. 1000 m^{-3}) while meroplanktonics incremented its abundance in the standard summer (from 14±18 to 21±98 ind. 1000 m^{-3}).

Scyphomedusae was the second most abundant group in the standard summer due to the high abundance of *Pelagia noctiluca* ephyrae and juveniles. The abundance of this species was sensibly lower in the warm summer (Table 2). With regard to species composition, the only difference between years was the presence of *Nausithoe punctata* (only 1 specimen) in 2003.

Spatial distribution and relationships with environmental variables

In the warm summer (2003), station groups discriminated by cluster analysis showed a strong north–south separation (Fig. 5). Two groups were located in the northern part of the area (G3 and G5) and two groups in the south (G2 and G4), with a mixing zone between Blanes and Barcelona located south of the thermal front (Fig. 2 and 5). The two groups of the northern area were characterized by high abundances of *P. incolorata* and *C. appendiculata* (polygastric and eudoxids stages). G3 was located over the shelf and had the highest abundance of *M. kochii* and the exclusive occurrence of *E. aurata* and *E. gegenbauri* (Fig. 5), while G5 was located over the continental slope and presented the lowest abundances of *M. atlantica*, *A. hemistoma* and *R. velatum*. In the southern area, G4 was located close to the coast and presented the highest abundances of *Obelia* sp. and a low frequency of *C. appendiculata* (polygastric and eudoxids stages). Over the continental shelf and slope, G2 showed the highest abundance of *A. tetragona* (polygastric stage) and *P. noctiluca,* and the exclusive presence of *E. spiralis* and *G. raffaelei* (except for one station in G4). South of the Ebro Delta, one-station group (G1), showed the lowest number of species (Fig. 5).

In the standard summer (2004), however, a stronger coastal-offshore separation was evident (Fig. 5). The groups G1 and G4 extended all along the region, the first close to the coast and the second over the shelf-slope region. The other two groups were found near the coast and over the shelf, one in the north (G5) and the other in the south (G2) (Fig. 5). The coastal groups (G1 and G5) were characterized by the highest abundance of *Obelia* spp. and *M. kochii*, while the large group over the slope (G4) was defined by the highest abundance and frequency of occurrence of *L. conoidea*, and the exclusive presences of *L. meteori* (except one station in G5) and *S. albescens* (Fig. 5). Over the southern continental shelf, group G2 was characterized by the highest abundance and frequency of occurrence of *A. tetragona* and *P. noctiluca*. As in the warm summer, a group with few stations (G3) appeared south of the Ebro Delta, with the lowest number of species.

The relationships between planktonic cnidarians abundance and environmental variables derived

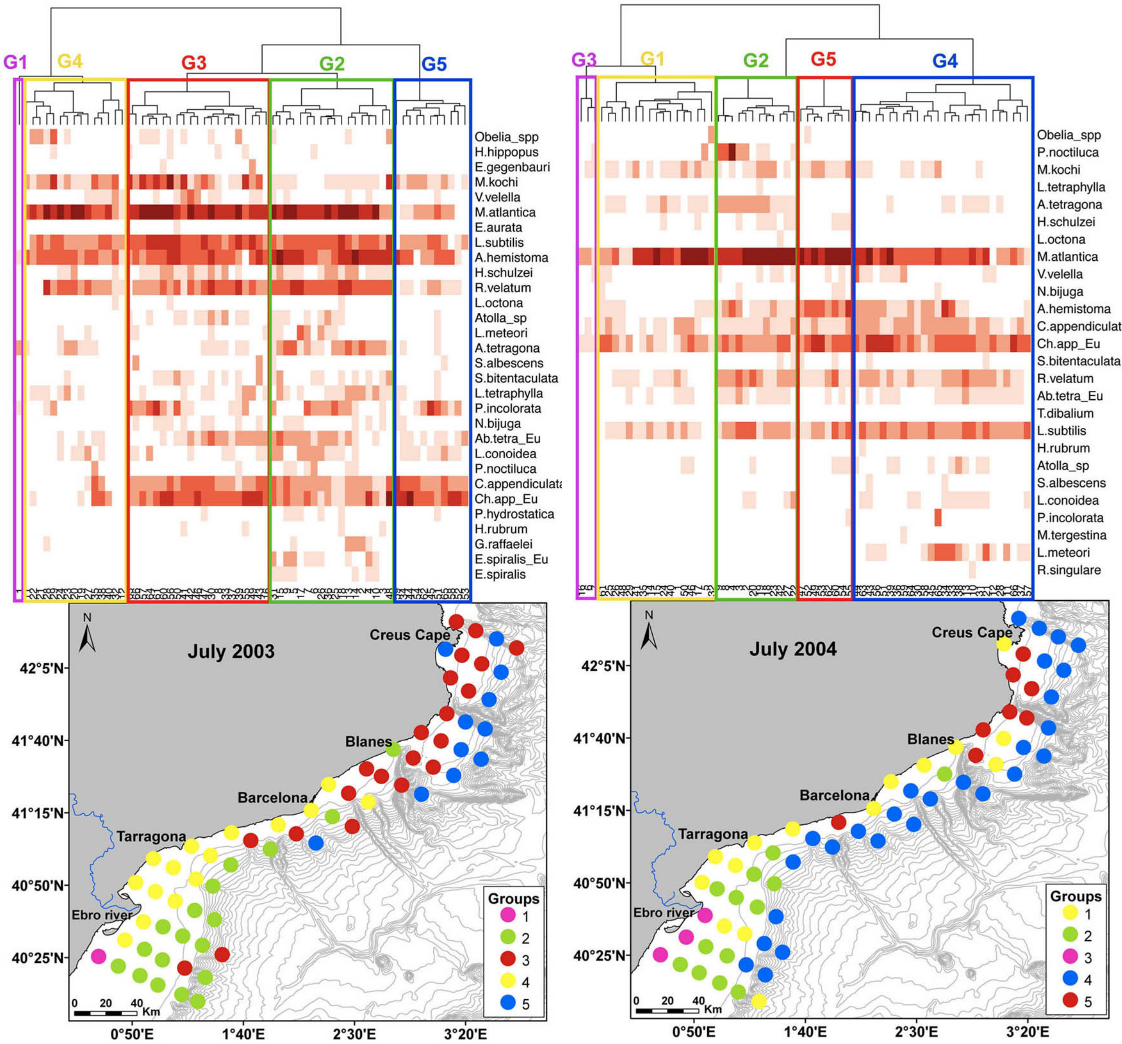

Figure 5. Upper: hierarchical clustering of stations in July 2003 (left panel) and July 2004 (right panel) and heatmap representing the abundance of the species (colour gradation from white to dark red represents from absence to the highest abundance), the five species-groups are indicated in different colour boxes. Lower: spatial distribution of the five species-groups in the study area; colours are in accordance with the hierarchical clustering group colours. Note that the same colour group indicates only a similar spatial distribution in both years, not the species composition or the number of the group.

from the CCA analyses explained 82% and 78% of the total variance in the warm and the standard summer, respectively. In the warm summer, the first ordination axis accounted for 37% of the constrained variance and was negatively correlated with temperature (-0.85) and positively with salinity (0.76) (Fig. 6 and Table 4). Species associated with this axis were *A. tetragona* (polygastric stage), *P. notiluca*, *E. spiralis* (polygastric and eudoxid stages) and *G. raffaelei* in the left side of the dispersion diagram, associated with increasing temperature and decreasing salinity (Fig. 6). These species were particularly abundant in the southern part of the study area, characterized by high temperature and low salinity, and very scarce north of the thermal front (Fig. 7). On the other side of the axis, *P. incolorata*, *M. kochii*, *E. aurata* and *E. gegenbauri* were related to decreasing temperature and increasing salinity (Fig. 6). These species were mainly distributed north of the thermal front and over the shelf break all along the area (Fig. 7). The second axis explained 28% of the constrained variance and was positively correlated with depth (0.72)

Table 3: Species richness (S) and Shannon diversity index (H') of the whole planktonic cnidarian community in July 2003 and 2004 off the Catalan coast.

	July 2003		**July 2004**	
	Total/Mean ± SD	Range	Total/Mean ± SD	Range
N. species (*S*)	46	3 - 22	44	1 - 17
Shannon index (H')	1.38 ± 0.36	0.52 - 2.19	0.98 ± 0.57	0.00 - 1.95

and integrated chlorophyll *a* (0.56). The species coupling with these environmental conditions were *L. conoidea*, *L. meteori* and *S. albescens*, in the upper-right side of the diagram, and associated with increasing depth and integrated chlorophyll *a* (Fig. 6). The spatial distribution of these species was limited to the most offshore stations, where the highest and intermediate values of integrated chlorophyll were found (Fig. 2). In the opposite side of the axis, the coastal hydromedusae *Obelia* spp. was related to shallower depths and decreasing integrated chlorophyll *a*, mainly in the central coastal area (Fig. 7).

In the standard summer, the first ordination axis explained 46% of the constrained variance and was positively correlated with depth (0.86) (Table 4; Fig. 6). As observed in the warm summer, the species associated with increasing depth were *L. conoidea*, *L. meteori* and *S. albescens*, while *Obelia* spp. was associated to shallower depths (Fig. 7). The second axis explained 19% of the constrained variance and was negatively correlated with temperature (-0.68). The species related to warmer waters were *A. tetragona* (polygastric stages), *P. noctiluca* and *L. tetraphylla* (Fig. 7) and, as observed in the previous summer, were mainly located in the warm southern part of the area. On the other side of the axis, species such as *P. incolorata* and *R. singulare* were associated with colder waters, appearing north of the thermal front (Fig. 7). Species with a weaker relationship with environmental parameters located close to axis origins in CCA plots, such as *M. atlantica, A. hemistoma, L. subtilis*, *C. appendiculata* and *R. velatum* showed a wide distribution all over the area (Fig. 8).

DISCUSSION

In summer 2003, the European region suffered an exceptional heat wave with air temperature records about 3–6°C above the seasonal average (Schär *et al.*, 2004). During that period, sea surface temperature values in the NW Mediterranean were close to those foreseen in the future by the climatic trends for the region (Vargas-Yáñez *et al.*, 2010), while water temperatures of summer 2004 were within the climatic average for the period 2000–2012 (Maynou *et al.*, 2014). In the Catalan coast, the effects of that extreme heat have been

Table 4: Summary of the results of the canonical correspondence analysis (CCA) performed with the planktonic cnidarians and the explanatory variables.

	July 2003		**July 2004**	
Total deviance explained (total inercia)	82 %		78 %	
Constrained variance explained by axis 1	37 %		46 %	
Constrained variance explained by axis 2	28 %		18 %	
Axis	1	2	1	2
Constrained eigenvalues	0.08	0.06	0.08	0.03
Correlation of environmental variables				
Depth	0.50	**0.71**	**0.86**	-0.36
Temperature (5 m)	**-0.85**	0.38	-0.54	**-0.68**
Salinity (5 m)	**0.76**	0.04	0.50	-0.14
Int. Chl *a*	0.18	**0.56**	0.02	-0.09
Day-Night	0.10	-0.25	-0.07	0.39
U45	-0.44	0.07	-0.21	-0.50
V45	-0.12	-0.14	0.01	0.09
Vorticity	-0.25	-0.23	-0.06	0.32

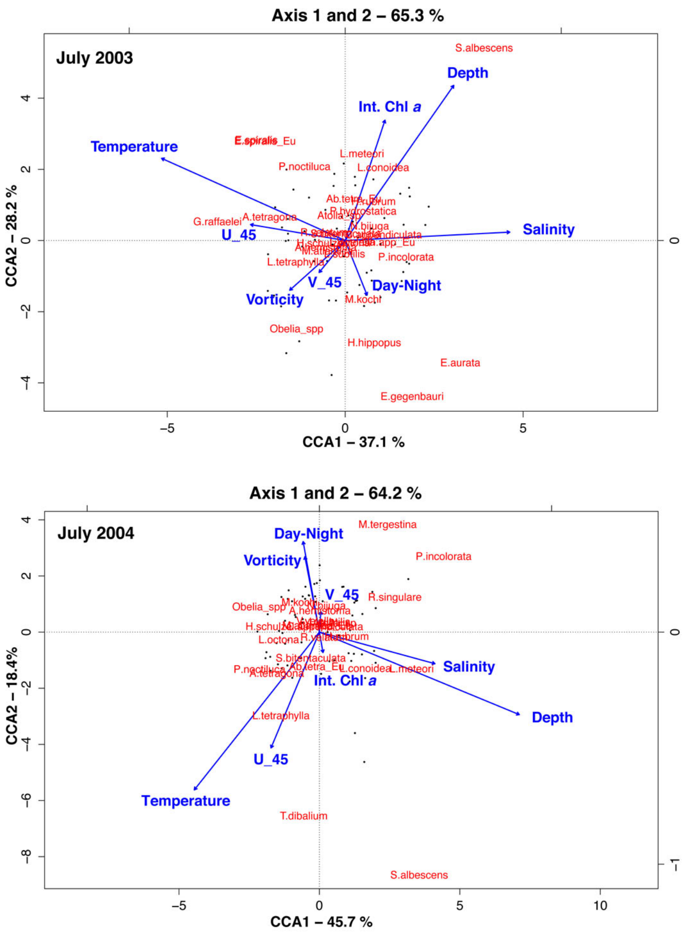

Figure 6. Ordination plots of the canonical correspondence analysis (CCA) showing the relationships between the species (in red) and the environmental variables (blue arrows) for July 2003 and 2004. Black dots represent the location of the sampling stations. Depth: bottom depth, Int. Chl a: integrated (0-100 m) chlorophyll a, U_45: across shore component of the current velocity, V_45: alongshore component of the current velocity.

described in planktonic (Maynou *et al.*, 2014; Atienza *et al.*, 2016) and benthic communities (Garrabou *et al.*, 2009). In the present study, the community structure of planktonic cnidarians was significantly impacted by the exceptionally warm summer conditions.

In both summers, siphonophores were the dominant group, as observed in previous studies conducted in the NW Mediterranean (Gili *et al.*, 1988; Sabatés *et al.*, 2010; Andersen *et al.*, 2001). *Muggiaea atlantica* was the most abundant species in both summers showing a marked decrease during the warm one. *Muggiaea atlantica* is the dominant species in the NW Mediterranean since it replaced the formerly dominant, congeneric species *Muggiaea kochii* in the 1980s (Cervigón, 1958; Riera *et al.*, 1986; Gili *et al.*, 1988; Licandro *et al.*, 2012). *Muggiaea atlantica* is a cold-temperate species, declining its abundance at temperatures higher than 24ºC (Marques *et al.*, 2008; Batistić *et al.*, 2013). *Muggiaea kochii* is a warm-temperate species displaying its seasonal peak of abundance in summer (Riera *et al.*, 1986; Gili *et al.*, 1988; Licandro *et al.*, 2012). The alternation of both species is a well known phenomenon in the English Channel and in other geographic regions (Russell, 1934; Mackie *et al.*, 1987; Blackett *et al.*, 2014). In the present study, this alternation seemed to take place in relation to water temperature changes. Probably, the high

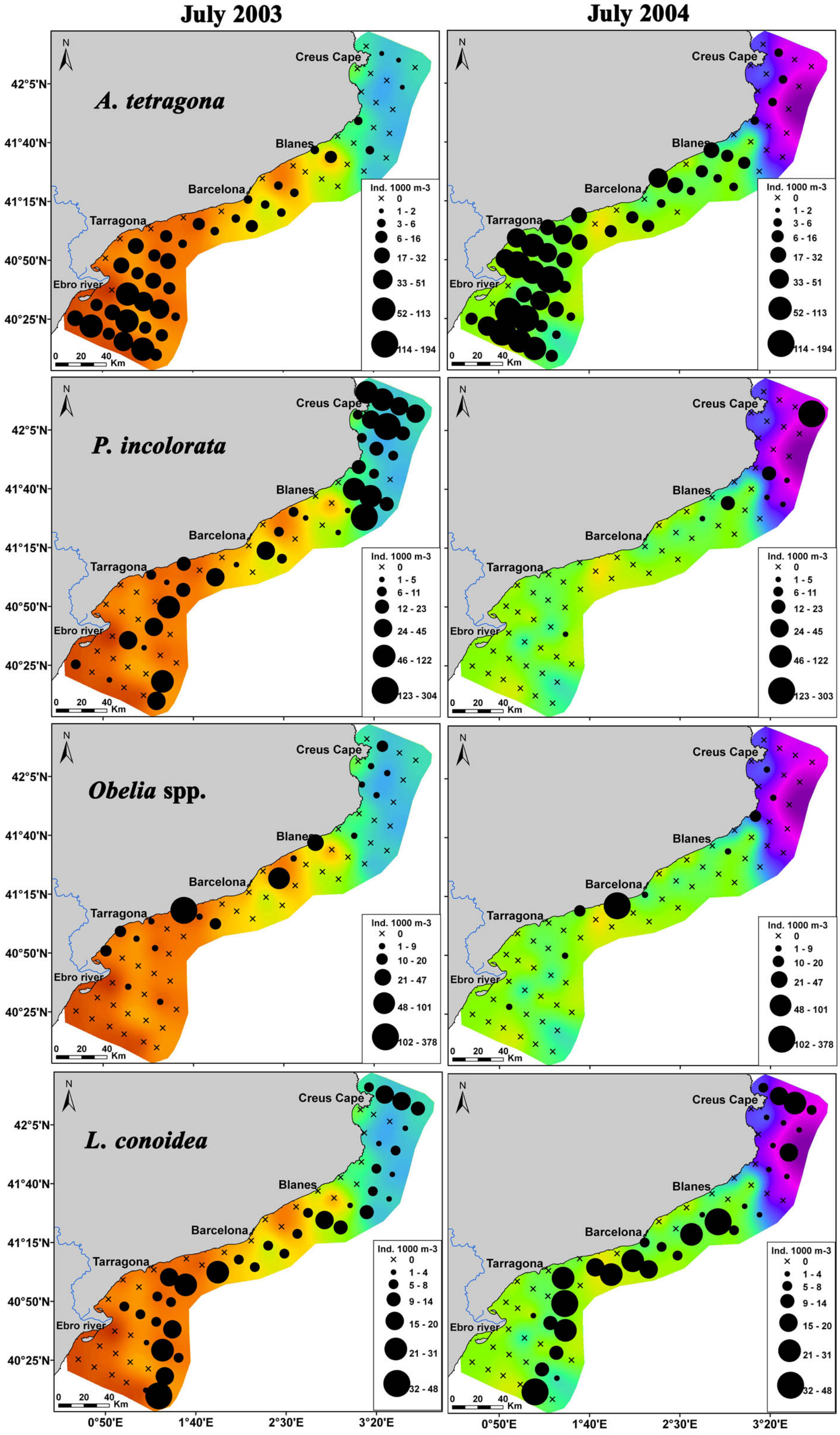

Figure 7. Spatial abundance distributions of the species *Abylopsis tetragona, Persa incolorata, Obelia spp.* and *Lensia conoidea* overlaid on surface (5 m) temperature in July 2003 and July 2004. For temperature scale see Fig. 2.

temperatures recorded in summer 2003 negatively affected *M. altantica* population, allowing other species to increase their abundance by taking advantage of the not-used trophic niche.

Among siphonophores, the eudoxid stages of several species were very well represented. Studies dealing with the distribution of the siphonophores eudoxid stages in the Western Mediterranean are very scarce (Cervigón, 1958; Dallot *et al.*, 1988; Sabatés *et al.*, 2010). In the present study, *C. appendiculata and A. tetragona* were the most abundant in agreement with the observations of Cervigón (1958) and Dallot *et al.* (1988), respectively. In the warm summer, when both eudoxid species showed lower abundance compared to the standard one, they were absent in the warmer southern area and their distributions were displaced northwards and oceanwards. This suggests that the higher temperatures of 2003 would be less favourable for the sexual reproduction of these species. In addition, during the warm summer low abundance of zooplankton was found in the southern area (Maynou *et al.*, 2014; Atienza *et al.*, 2016) and, according to Purcell (1982), the production of eudoxids decreases when food is scarce. In this line, Dallot *et al.* (1988) found a significantly higher abundance of eudoxids in areas of higher food availability.

Contrary to siphonophores, hydromedusae were more abundant in the warm summer, due to the high densities of holoplanktonic species, such as the trachymedusae *A. hemistoma* and *R. velatum*. They are warm-water species, very abundant in the western Mediterranean (Gili *et al.*, 1988; Licandro and Ibañez, 2000; Batistić *et al.*, 2007) and Atlantic Ocean (Pagès and Gili, 1991; Hosia *et al.*, 2008; Nogueira Júnior *et al.*, 2014), particularly in the summer months. The increased abundance of both species in the warm summer seems a natural consequence of the high temperatures favouring these warm-

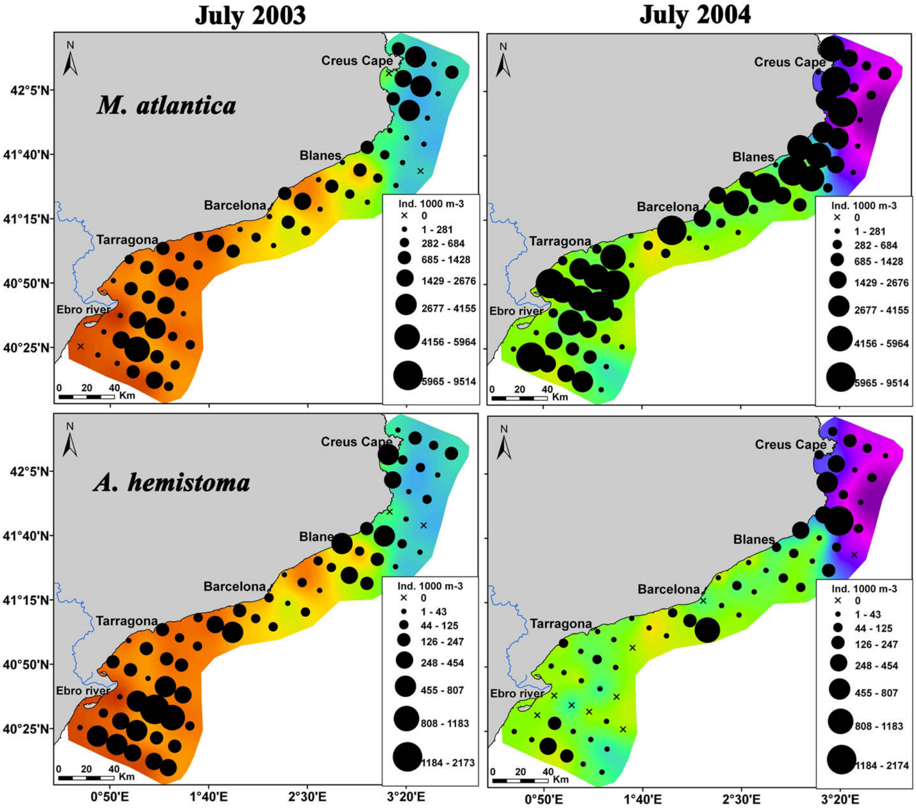

Figure 8. Spatial abundance distribution of the widespread species *Muggiaea atlantica* and *Aglaura hemistoma* overlaid on surface (5 m) temperature in July 2003 and July 2004. For temperature scale see Fig. 2.

water species. Moreover, holoplanktonic species could take advantage more efficiently than the meroplanktonic ones of the non-used trophic niche left by *M. atlantica* in the warm summer. The dominance of holoplanktonic hydromedusae with respect to meroplanktonic species relates to their different life cycles. Holoplanktonic hydromedusae are always present in the water column, while meroplanktonic hydromedusae have a seasonal presence in the plankton; when the environmental conditions are optimal for its benthic phase (polyp), it releases the free-swimming medusae for the sexual reproduction (Boero and Bouillon, 1993; Gili *et al.*, 1998). Thus, the different natural characteristics of both groups make holoplanktonic species tolerant to a wider range of temperatures. On the other hand, the lower abundance of meroplanktonic species in the warm summer, could be due to the earlier release of the medusae from the polyp (Boero *et al.*, 2016). It is known that higher temperatures promote faster lifecycles and higher reproductive rates in different jellyfish species (Purcell, 2005; Boero *et al.*, 2016). Moreover, the low abundance of zooplankton prey resource for the polyps found during the warm summer (Maynou *et al.*, 2014; Atienza *et al.*, 2016), could also have negatively affect the medusae release (Gili *et al.*, 1998). In this context, extreme warm conditions could especially and negatively affect the meroplanktonic species with a short-life medusa stage (Edwards and Richardson, 2004), since their survival depends on narrower temperature environments and sufficient food availability (Hays *et al.*, 2005).

The scyphomedusa *Pelagia noctiluca* ephyrae is one of the most abundant species of the planktonic cnidarians off the Catalan coast during the early summer months (Gili *et al.*, 1988; Sabatés *et al.*, 2010; Tilves *et al.*, 2016). Its abundance was remarkably lower during the warm summer (Table 2). As the sexual reproduction in this species takes place in late spring and early summer (Canepa *et al.*, 2014), the higher temperatures experienced during the 2003 summer could have triggered the earlier sexual reproduction and, thus, the lower abundance of ephyrae found during the sampling. On the other hand, the significantly lower abundance of siphonophores during the warm summer could affect the abundance of ephyrae, since it has recently reported that siphonophores are the most abundant and frequent prey of ephyrae in the area (Tilves *et al.*, 2016).

The species' composition and richness found in the two study summers were similar to those observed in previous studies of the area (Gili *et al.*, 1987b, 1988; Sabatés *et al.*, 2010). Although the total cnidarian abundance decreased in the warm summer, its diversity (H') was somewhat higher due to a higher number of meroplanktonic hydromedusae species per station and the much lower abundance of the dominant species, mainly *M. atlantica*, and also *P. noctiluca* in the southern area. The holoplanktonic community composition (siphonophores, trachyline medusae, *V. velella*, *P. porpita*, and *P. noctiluca*) remained practically constant in both summers since they are widely distributed and more eurytolerant than the meroplanktonic and thus being able to maintain viable populations in changeable environments (Gibbons *et al.*, 2010). However, the meroplanktonic community was more diverse and its composition largely changed between both summers in accordance to their life cycles (Arai, 1992; Boero and Bouillon, 1993; Gibbons *et al.*, 2010). There is few information regarding diversity indexes of planktonic cnidarian communities in extensive areas. Compared to other regions, our values during both summers are relatively lower than those found in the southern channels of Chile (Palma *et al.*, 2007a, 2007b) but similar to those reported in Redang Island, Malaysia (Nakajima *et al.*, 2013) and the upwelling zone off central Chile (Pavez *et al.*, 2010). Although the species richness (N. of species) found in the Catalan coast was quite higher than in the previous cited areas, the high abundance of *M. atlantica* (up to 70%) decreases diversity index values.

The spatial distribution patterns of the planktonic cnidarian community differed between cruises. In the standard summer, the community was primarily structured in a coastal-offshore axis defined by the bathymetry and, secondly, by the north-south temperature gradient, in accordance with previous studies of the area (Gili *et al.*, 1988; Sabatés *et al.*, 2010). A coastal-open sea gradient in the community composition has also been described in other geographic regions (e.g.: Palma *et al.*, 2007b; Nagata *et al.*, 2014). However, the conditions of the warm summer inverted the weight of the environmental factors, being the latitudinal temperature gradient the key factor structuring the community on a north-south axis, while the bathymetry played a secondary role.

During both summers the species characterizing the coastal and offshore communities remained the same. The coastal community was defined by *Obelia* spp. and *M. kochii*, both species very common in coastal areas (Gili *et al.*, 1988; Batistić *et al.*, 2013; Nagata *et al.*, 2014). *Obelia* spp are filter-feeding species able to feed even on bacteria (Boero *et al.*, 2007) taking advantage of high productive areas and seasons to rapidly increase their populations (Orejas *et al.*, 2000; Guerrero *et al.*, 2013), while *M. kochii* is one of the few siphonophores inhabiting coastal and estuarine waters (Nagata *et al.*, 2014; D'Ambrosio *et al.*, 2016). The offshore community, distributed all along the shelf-slope region, was defined by *L. conoidea*, *L. meteori* and *S. albescens*. These are mesopelagic species performing extensive diel vertical migrations (Pugh, 1974; Kirkpatrick and Pugh, 1984; Mills and Goy, 1988) and have been previously found over the slope area in the Catalan coast (Sabatés *et al.*, 2010). In contrast, the northern and southern communities showed important changes in species composition between both situations. In the standard summer, the northern community, related with the coldest and more saline waters, was defined by the presence of *R. singulare* while in the warm summer the species characterizing this group were *E. aurata, C. appendiculata* (poygastric and eudoxids stages) and *M. kochii*. In both situations, high abundances of *P. incolorata* were also found in that area. The hydromedusae *R. singulare, P. incolorata and E. aurata* are mesopelagic and have been previously related to cold and saline waters in the NW Mediterranean (Berhaut, 1969; Goy, 1991; Gili et al, 1988; Buecher and Gibbons, 1999). The siphonophores *C. appendiculata* and *M. kochii,* both warm-temperate species (Alvariño, 1971; Bouillon *et al.*, 2004), were mainly located in the north during the warm year probably because the high temperatures of the southern area affected negatively, direct or indirectly (low prey resources), their abundance. The southern community, related with warmer and less saline waters, was defined by *A. tetragona* and *P. noctiluca* in both years and only *E. spiralis* (poygastric and eudoxids stages) and *Gastroblasta raffaelei* were present in the warm summer. The two first are common and abundant species in the area, previously related with warm temperatures (Gili *et al.*, 1987a, 1988) The epipelagic *E. spiralis* has been also associated to high temperatures both in the Mediterranean and the Atlantic Ocean (Gamulin and Kršinić, 1993; Nogueira Júnior *et al.*, 2014). The hydromedusa, *G. raffaelei,* is an endemic species in the Mediterranean Sea found so far only in the Adriatic, Tyrrhenian and Ligurian Seas (Gravili *et al.*, 2007), being the present study the first report in the Catalan Sea. Only during the warm summer, the gradient of the integrated chlorophyll *a* contributed, to some extent, to the coastal-offshore axis ordination; however, since its distribution was correlated to the bathymetry (see Fig. 2), and not-significantly in the standard summer, we believe that this variable had no direct effect on the spatial distribution of cnidarians being bathymetry the main responsible factor. Even though hydrographic structures such as currents and vorticity has been reported to influence the spatial distribution of other zooplankters in the area, such as fish larvae (Sabatés *et al.*, 2013), in our study their effect on the planktonic cnidarians distribution could be masked by depth and temperature gradients.

In summary, bathymetry (coastal-offshore gradient) is the main factor determining the spatial distribution pattern of the planktonic cnidarian community under standard summer conditions. Anomalous high temperatures situation reinforced the latitudinal (N-S) community differentiation, with the appearance of some species characteristic of warmer waters (*E. spiralis* and *G. raffaelei*), and the northward displacement of certain species (*M. kochii* and *C. appendiculata*). These distribution changes were associated with an important reduction in the abundance of the dominant species (*M. atlantica* and *P. noctiluca*) and the sexual stages of siphonophores (*C. appendiculata*). Similar results, higher occurrence of warm-water species and a significant reduction of dominant ones, have been reported in the scarce works studying the footprints of the 2003 heat anomaly on marine plankton communities (Piontkovski *et al.*, 2011; Atienza *et al.*, 2016).

It is well known that climatic conditions, especially temperature variations, have a decisive influence on gelatinous zooplankton distribution and abundance (Brodeur *et al.*, 1999; Lynam *et al.*, 2010; Brotz *et al.*, 2012). In recent years, studies conducted in different regions have shown that frequent warmer conditions are accompanied by an increased abundance of gelatinous species (e.g. Purcell, 2005; Brodeur etal., 2002; Doyle et al., 2007). Long-term studies carried in the NW Mediterranean have reported an increase in the abundance of the jellyfish community (Molinero et al., 2005; 2008) while others did not show this increasing trend (García-Comas *et al.*, 2011; Berline *et al.*, 2012; Licandro *et al.*, 2012). Nevertheless, major changes in the community composition and high inter-annual abundance variability have been observed (García-Comas *et al.*, 2011; Berline *et al.*, 2012; Licandro *et al.*, 2012).

Our observations do not agree with the general increasing trend given the important decrease in planktonic cnidarian abundance during the anomalous warm summer. The effect of temperature changes on marine systems is far from being simple and depends on the temporal scale of variability, from sudden changes to trend over time, and the response capacity of the organisms. The summer heat conditions of 2003 constituted an extreme event (Schär *et al.*, 2004) that involved strong and sudden temperature changes, so that its effects on the planktonic community may not be comparable to those caused by the long-term warming trend. In addition, high temperatures may favour an earlier sexual and asexual reproduction of the species (Hays *et al.*, 2005; Boero *et al.*, 2016) thus advancing the timing of their seasonal abundance peak in that year, particularly in cool-temperate species. Finally, we must take into account the reduction of food availability, due to the general decrease of zooplankton during this extreme event (Piontkovski *et al.*, 2011; Maynou et al, 2014; Atienza *et al.*, 2016), that would negatively affected the planktonic cnidarians.

Our results pointed out that exceptionally warm conditions during the summer season lead to a reduction of gelatinous zooplankton abundance and changes in their latitudinal distribution and community composition. Distributional changes may increase the overlapping of trophic niches among species, thus affecting their survival and persistence. We wish to stress the importance of spatial mesoscale plankton surveys with detailed taxonomic identification (including their different life stages), as a critical tool for tracking changes in the community structure in high diversity regions, such as the Mediterranean, for better understanding marine ecosystem responses to climatic variability.

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Chapter 3

Long-term changes of the planktonic cnidarian community in the NW Mediterranean

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Long-term changes of the planktonic cnidarian community in the NW Mediterranean

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ABSTRACT

In the present work possible long-term changes in the planktonic cnidarian community have been investigated by analysing (1) species and community spatial distribution patterns, (2) variations in abundance and (3) changes in species richness during three mesoscale surveys representative of the climatic and anthropogenic changes occurred during the last three decades (1983, 2004 and 2011) in the NW Mediterranean. These surveys were conducted during summer (June), along the Catalan coast, covering the same area and using the same sampling methodology. An increase in abundance of total Cnidaria was found from 1983 to 2011. The siphonophore *M. atlantica* and the hydromedusae *A. hemistoma* were the most abundant species, and *M. kochii* presented the largest abundance increment over time. Temperature was the main environmental parameter that caused significant differences in community composition, abundance and spatial distribution patterns among surveys. However, it is likely that others anthropogenic factors such us overfishing may have contributed to the observed changes over time. Our results suggest that in the current climate change scenario warm-species abundance will be positively favoured and community latitudinal distribution patterns will be reinforced. We consider extremely important to study and monitor gelatinous zooplankton in mesoscale spatial areas to understand not only long-term gelatinous zooplankton abundance changes but also how these changes are revealed in their spatial distributions, since spatial changes are sensitive indicators to climate change.

INTRODUCTION

There is increasing evidence that ocean warming is driving changes in the abundance, composition and spatial distribution of gelatinous zooplankton worldwide (Brotz *et al.*, 2012; Boero *et al.*, 2016). Gelatinous zooplankton is a conspicuous component of planktonic communities but still relatively little is known about its role in the marine ecosystem (Pagès *et al.*, 2001; Haddock, 2004). These organisms are highly influenced by oceanographic dynamics, water mass structures, as well as climate variability (Graham *et al.*, 2001; Brotz *et al.*, 2012).

Increments in seawater temperature can lead to enhanced abundance of different gelatinous zooplankton groups, such us planktonic cnidarians (Purcell, 2005; Molinero *et al.*, 2008). Following the general global pattern (Levitus *et al.*, 2005), seawater temperature in the NW Mediterranean has shown an increasing trend over the last decades (Rixen *et al.*, 2005). This warming trend has been particularly evident in the 1980s and at the end of the 1990s (Rixen *et al.*, 2005; Vargas-Yáñez *et al.*, 2005). In the Mediterranean Sea, climate change is undoubtedly affecting the basic biology and ecology of organisms, as well as pelagic ecosystem functioning (e.g.: Conversi *et al.*, 2010; Calvo *et al.*, 2011).

Monitoring long-term changes in the plankton is of great importance as they act as sentinels to identify changes in marine ecosystems (Hays *et al.*, 2005). Luckily, in the Mediterranean several time series, based on one or few sampling stations, have been carried out since the late 1960s with a high temporal sampling frequency (weekly, monthly) (see Berline *et al.*, 2012), providing a rather extensive knowledge on gelatinous zooplankton population dynamics and trends compared to other areas (Brotz and Pauly, 2012). These time series allowed identifying long-term changes in the abundance and composition of different planktonic cnidarian species (Molinero *et al.*, 2005, 2008; García-Comas *et al.*, 2011; Licandro *et al.*, 2012). Since these series cover a restricted spatial area, in the present work we bring up the necessity of mesoscale spatial zooplankton studies in order to complement the knowledge of these long-term changes in planktonic cnidarians embracing a large spatial scale. Spatial changes can rely both on species-specific distribution changes or changes in the community distribution patterns. The study and monitoring of these spatial changes are of significant importance since they act as sensitive indicator to climate change (Hughes, 2000).

The study of mesoscale spatial areas, in the range of 100 to 1000 km, provide the opportunity to study population and community change rates in relation to changing physical conditions (Haury *et al.*, 1978). In this sense, studies covering a wide network of stations have revealed changes in patterns of distribution of planktonic communities coupled with the distribution of physical phenomena (Pagès and Gili, 1992; Graham *et al.*, 2001), providing valuable knowledge related to the ecological role of planktonic cnidarians (Pagès *et al.*, 2001). However, under the current climate change scenario changes in planktonic cnidarian distribution patterns have received little attention.

Gelatinous zooplankton may benefit from anthropogenic changes such as eutrophication, which can increase small-zooplankton abundance, turbidity and hypoxia, among other conditions that may favour jellyfish over fish (Purcell *et al.*, 2007). In this sense, overfishing has been pointed out as an important factor enhancing gelatinous zooplankton populations by reducing their predators and zooplanktivorous fish competitors (Purcell *et al.*, 2007; Lynam *et al.*, 2011).

This study aims to shed light on the long-term evolution of planktonic cnidarians from a mesoscale spatial point of view. For this purpose we have analysed (1) species and community spatial distribution patterns, (2) variations in abundance, (3) changes in species richness, during three surveys representative of the climatic and anthropogenic changes occurred during the last three decades (1983, 2004 and 2011) in the NW Mediterranean. The surveys were carried out during the summer season (June), when high annual abundances of this community are found (Gili *et al.*, 1987; Licandro *et al.*, 2012; Saiz *et al.*, 2014).

MATERIAL AND METHODS

Three mesoscale surveys were carried out in the Catalan Coast (NW Mediterranean) (Fig. 1) during June 1983, June 2004 and June 2011 (from now on referred to as 1983, 2004 and 2011). In all surveys the same area was covered and the same sampling methodology applied. Sampling stations were placed along 17 transects conducted perpendicular to the shoreline, from near the coast to the shelf break. On each transect, stations were placed between 14 and 16 km apart, and distance between transects was 18.5 km. The total number of sampled stations on each survey was: 39, 43 and 43, respectively.

Vertical profiles of the basic hydrographic variables (temperature and salinity) were obtained with a CTD, and water samples for chlorophyll a determination were collected at each station at different levels of the water column (see Masó and Duarte, 1989 and Sabatés *et al.*, 2009 for methodological descriptions).

Zooplankton was sampled with Bongo nets of 300 μm mesh size. Hauls were oblique from a maximum depth of 200 m to the surface (or from 5 m above the bottom to the surface at stations shallower than 200 m). The volume of filtered water was estimated by means of a flowmeter placed in the centre of the net mouth. Zooplankton samples were fixed immediately after collection in 5% formaldehyde buffered with sodium tetraborate. Planktonic

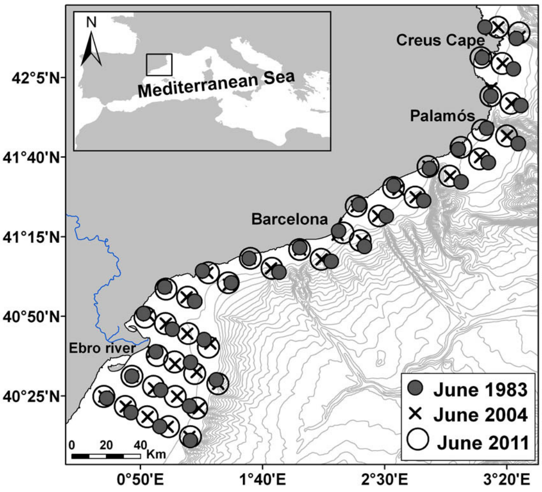


Figure 1. Geographical location of the study area along the Catalan coast, in the NW Mediterranean. Grey circles, crosses and open circles represent the sampled stations in June 1983, 2004 and 2011 surveys, respectively. Grey lines indicate bathymetry (every 100 m).

cnidarians (hydromedusae, siphonophores and scyphomedusae) were analysed to species level, under a stereomicroscope. Aliquots were taken only to quantify the most abundant species (e.g. *Muggiaea atlantica* and *Aglaura hemistoma*), For these species a minimum of 100 individuals were counted in order to calculate the actual number in the sample (Postel *et al.*, 2000). Following Pugh (1984) nectophores of physonectid siphonophores were counted and divided by 10 to estimate the actual number of sampled colonies. The number of hydromedusae individuals and siphonophore colonies were standardized to number of individuals per 1000 m^3 of filtered seawater.

In addition, data on monthly sea surface temperature for the period 1974–2011 were obtained from L'Estartit Meteorological Station, located at the north of the study area (42º 3'N, 3º13'15"E) over a bottom depth of 85 m, operated by Josep Pascual (http://www.meteoestartit.cat). These data were used to assess the evolution of temperature at annual scale and in the month of June. The mean annual values were plotted against the time-series mean and the June temperature anomalies were computed as deviations from the Junes time-series mean.

Data analysis

For each species and survey, the mean abundance values, frequency of occurrence (FO, percentage of stations where a taxon occurred) and the relative abundance (RA, percentage contribution of a taxon to the total mean abundance of individuals) were calculated. The species richness of the community was estimated as the total number of species (S) found in each year. Diversity of the whole cnidarian community was calculated with the Shannon diversity index (H'), in natural logarithm base, for each sampled station.

Significant differences in abundance between pairs of years were tested for the total Cnidaria abundance, and for the different groups, Siphonophorae, Hydromedusae and Scyphomedusae with an analysis of variance using Generalized Linear Models (GLM). The counts of total Cnidaria and Siphonophorae, following a Poisson distribution, were analyzed with the function "glm" and those of Hydromedusae and Scyphomedusa, following a binomial negative distribution, with the "glm.nb" package (Venables and Ripley, 2002) and a log link function (Zuur *et al.*, 2009). The log of filtered seawater by the net was included as an offset to eliminate bias due to varying sampling units (Penston *et al.*, 2008; Zuur *et al.*, 2009; Guerrero *et al.*, 2013).

To assess if planktonic cnidarian communities differed among cruises, a non-metric multidimensional scaling ordination (nMDS) of the sampling stations was performed with species abundances log (x+1) transformed, and ordination by a Bray-Curtis similarity matrix, using the r-language function metaMDS available in the "vegan" package (Oksanen *et al.*, 2015). Subsequently, an adonis permutation multivariate analysis of variance and pairwise tests were used to test for significant differences between each cruise's planktonic cnidarian communities. The adonis and pairwise test were performed with the r-language function adonis available in the "vegan" package (Oksanen *et al.*, 2015). To quantify the contribution of the species to the dissimilarity between pairs of cruises a similarity percentages routine (SIMPER) was performed.

A Canonical Correspondence Analysis (CCA) was performed in order to identify which environmental factors influenced most to the differences among each survey's planktonic cnidarian communities. The statistical significance of the axes of the CCA was evaluated using a permutation test with 999 permutations. Additionally, a CCA for each survey was performed to investigate which environmental factor contributed the most to the spatial distribution of the community. For both CCA analyses, the collinearity between pairs of environmental variables was evaluated by pairwise scatterplots and Pearson's correlation coefficients with a cut-off value of |0.5| (Zuur *et al.*, 2009). The variables chlorophyll a and salinity were collinear and salinity was kept for the analyses as this parameter has been previously observed to be more determinant in the distribution of planktonic cnidarians in the area (Gili *et al.*, 1988; Guerrero *et al.*, 2016). The species matrix used in all the statistical analyses was compound by those species with more than five presences (individuals) and/or present in more than 2 stations for the three years. GLMs and nMDS statistical analyses were carried out in the free statistical software R, version 3.0.2 (R Development Core Team, 2013), SIMPER and CCAs were performed in PAST free software (Hammer *et al.*, 2001). Maps of the horizontal distribution of the environmental parameters, using spline interpolation, species abundance and score values for the first axis from CCAs were generated by ArcGIS 10.2 software.

RESULTS

Environmental conditions

In the Catalan coast, the evolution of the annual mean temperature, from 1974 to 2011, showed that the 1980s were characterized by

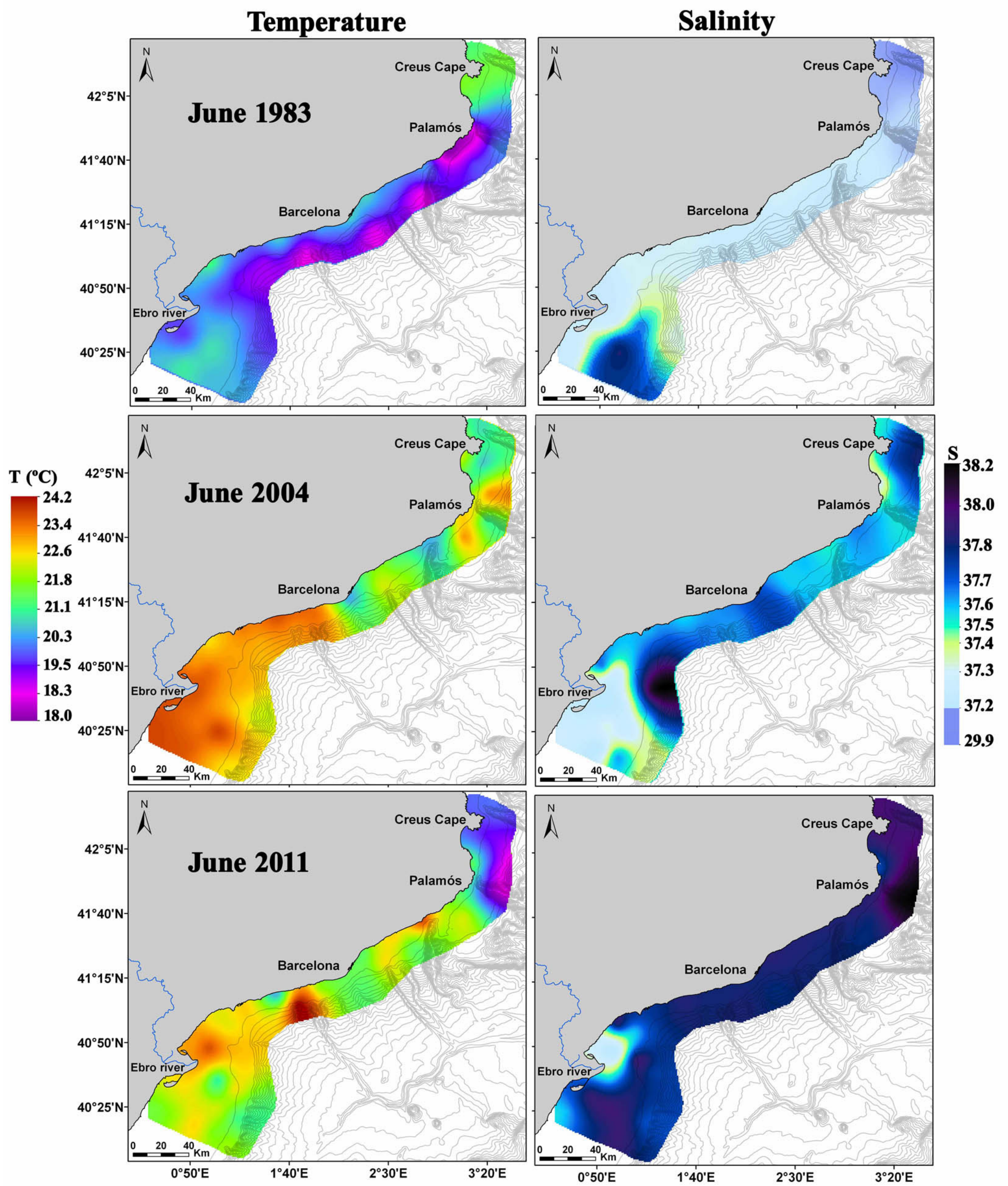


Figure 2. Surface temperature and salinity in June 1983, 2004 and 2011, along the Catalan coast.

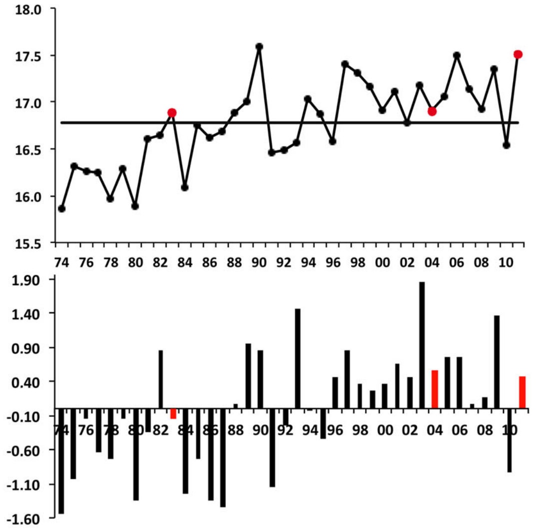


Figure 3. Upper panel: Annual mean sea surface temperature (SST), over 1974-2011. The mean value of the series is shown (black line). Lower panel: SST anomalies for the summer month of June, over 1974-2011. Data from the L'Estartit meteorological station.

values below the mean while from the end of 1990s values were higher than the mean (Fig. 3). As for June months, the tendency was similar and 1983 displayed a negative anomaly and 2004 and 2011 positive anomalies (Fig.3).

Among the three surveys, sea surface temperature showed the lowest values in 1983 and the highest in 2004, intermediate temperature values were found 2011 closer to those of 2004 (Table 1). In 1983, maximum temperatures were recorded close to the coast, in the northernmost part of area, and relatively high values were detected near shore all along the coast and in the southern continental shelf (Fig. 2). During 2004 and 2011 a marked thermal front was located in the northern half area, separating the cold waters in the north from the warmer in the south (Fig. 2). In 2004, the main thermal front was located around 42° 00'N, with a temperature difference of nearly 1 ºC, and a secondary surface temperature front was detected off Barcelona. In June 2011, the front was observed off Palamós with a temperature difference of 1 ºC (Fig. 2).

In the three cruises, the most notable feature of the horizontal surface salinity distributions was the presence of low salinity patches (<37.4) in the southern part of the area in the vicinity of the Ebro River mouth (Fig. 2). All along the area, and near the coast, salinity was generally lower than over the shelf break. In 1983, a surface plume of freshwater coming from the Rhone River was detected in the northernmost part of the area reaching values of 29.9 (Table 1; Fig. 2), while below 20 m salinity values were normal for the area, ranging between 37.1 and 38.0 (Masó and Tintoré, 1991).

Species composition and abundance

In the three surveys a total of 77 species of planktonic cnidarians were found, 19 siphonophores, 55 hydromedusae and 3 scyphomedusae. In the first two years, the number of species was similar, 35 and 38 respectively, while in 2011 the highest number of species, 59, was recorded (Table 2; Fig. 4). Nonetheless, the Shannon diversity index (H') remained constant over time (Table3; Fig 4).

An increase in abundance of total Cnidaria was found from 1983 to 2011 (Fig. 5; Table 4). This tendency was observed for siphonophores and hydromedusae groups, but not for scyphomedusae which abundance did not vary over time (Fig. 5; Table 4). The siphonophore *M. atlantica* and the hydromedusae *A. hemistoma* were the most abundant species in the three cruises (Table 2), which together accounted for 81% to 89% of the total cnidarian abundance (Table 2). The calycophoran siphonophore *M. kochii* presented the most important abundance increase over

Table 1. Values of the environmental parameters in the Catalan coast during the June surveys of 1983, 2004 and 2011.

	June 1983			June 2004			June 2011		
	Mean ± SD	**Min.**	**Max.**	**Mean ± SD**	**Min.**	**Max.**	**Mean ± SD**	**Min.**	**Max.**
Depth (m)	90 ± 77	15	300	107 ± 99	21	540	108 ± 112	27	685
T (ºC)	20.13 ± 0.84	18.06	21.77	22.50 ± 1.05	20.48	23.79	21.90 ± 1.09	19.51	24.14
S	36.49 ± 1.86	29.85	37.84	37.55 ± 0.20	37.17	38.14	37.78 ± 0.12	37.34	37.99
Chl *a* (μg l^{-1})	0.09 ± 0.09	0.01	0.34	0.23 ± 0.15	0.05	0.80	0.08 ± 0.04	0.03	0.25

Depth = bottom depth, T = temperature, S = salinity; Chl a = chlorophyll a, SD = standard deviation, Min. = minimum value, Max. = maximum value.

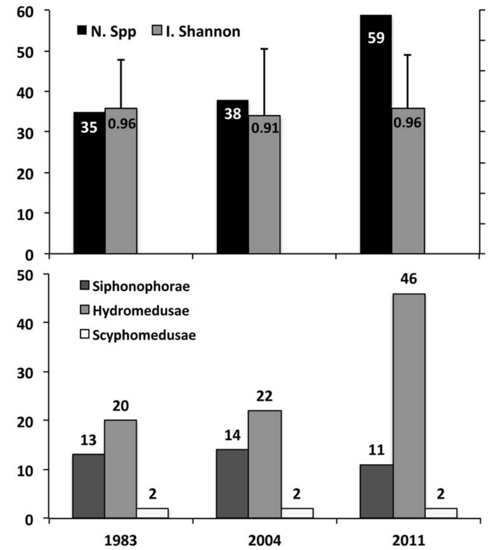


Figure 4. Upper panel: species richness (total number of species; N. Spp) and diversity (Shannon Index in the secondary axis; I. Shannon) for the total cnidarian community in each survey, June 1983, 2004 and 2011. Lower panel: Number of species for the different cnidarian groups, Siphonophorae, Hydromedusae and Scyphomedusa in each survey, June 1983, 2004 and 2011.

time; it was barely found in 1983, its abundance showed a fortyfold increase in 2004 and a following threefold increase in 2011, being widely distributed over the studied area in the last two surveys (Table 2; Fig. 7). The species composition for siphonophores and scyphomedusae remained similar over time however, hydromedusae showed major changes due to the orders Anthoathecata and Leptothecata. The lowest number of species of these two orders was found during 1983 and 2004. However, 1983 and 2011 shared more species of these orders than 1983 and 2004 (Table 2).

Differences among years

The nMDS analysis showed that samples from each survey were grouped separately. 1983 and 2011 stations were placed closer to each other, in the negative side of the first dimension, while 2004 stations were mostly located in the positive side (Fig. 6). Stations of 1983 were mainly characterized by *Lizzia blondina* and *Podocorynoides minuta*; 2004 stations by *Lensia subtilis*, *Rhopalonema velatum* and *Persa incolorata*; and 2011 stations by *Podocoryna carnea*, *Obelia* spp. and *Halistemma rubrum* (Fig. 6). Other species such as *Pelagia notiluca* were mainly found in 1983 and 2011 while *M. atlantica* and *A. hemistoma* were common in all the three surveys (Fig. 8). Adonis permutation multivariate analysis of variance and subsequent pairwise tests revealed that the communities identified in each cruise were significantly different ($p < 0.001$) among them.

The SIMPER analysis showed the highest average dissimilarity in species composition between 1983 and 2004 (Table 5). The number of species contributing up to 90% of the similarity ranged between 15 and 20 (Table 5). The three species that made the major difference between 1983 and 2004 were *L. subtilis, R. velatum* and *M. kochii*. Looking at their abundance and spatial distribution these three species were much more abundant and widely spread during 2004 than during 1983 (Table 2; Fig. 7). *Lensia subtilis* (Fig. 7) and *R. velatum* (not shown) followed a similar spatial distribution. The species that contributed the most to the dissimilarities between 2004 and 2011 were *L. subtilis* and *R. velatum*, and *P. noctiluca*. The two first were more abundant and widespread during 2004 than during 2011 while

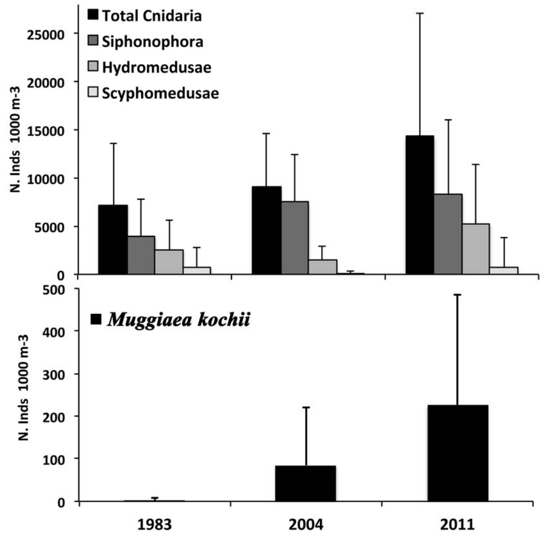
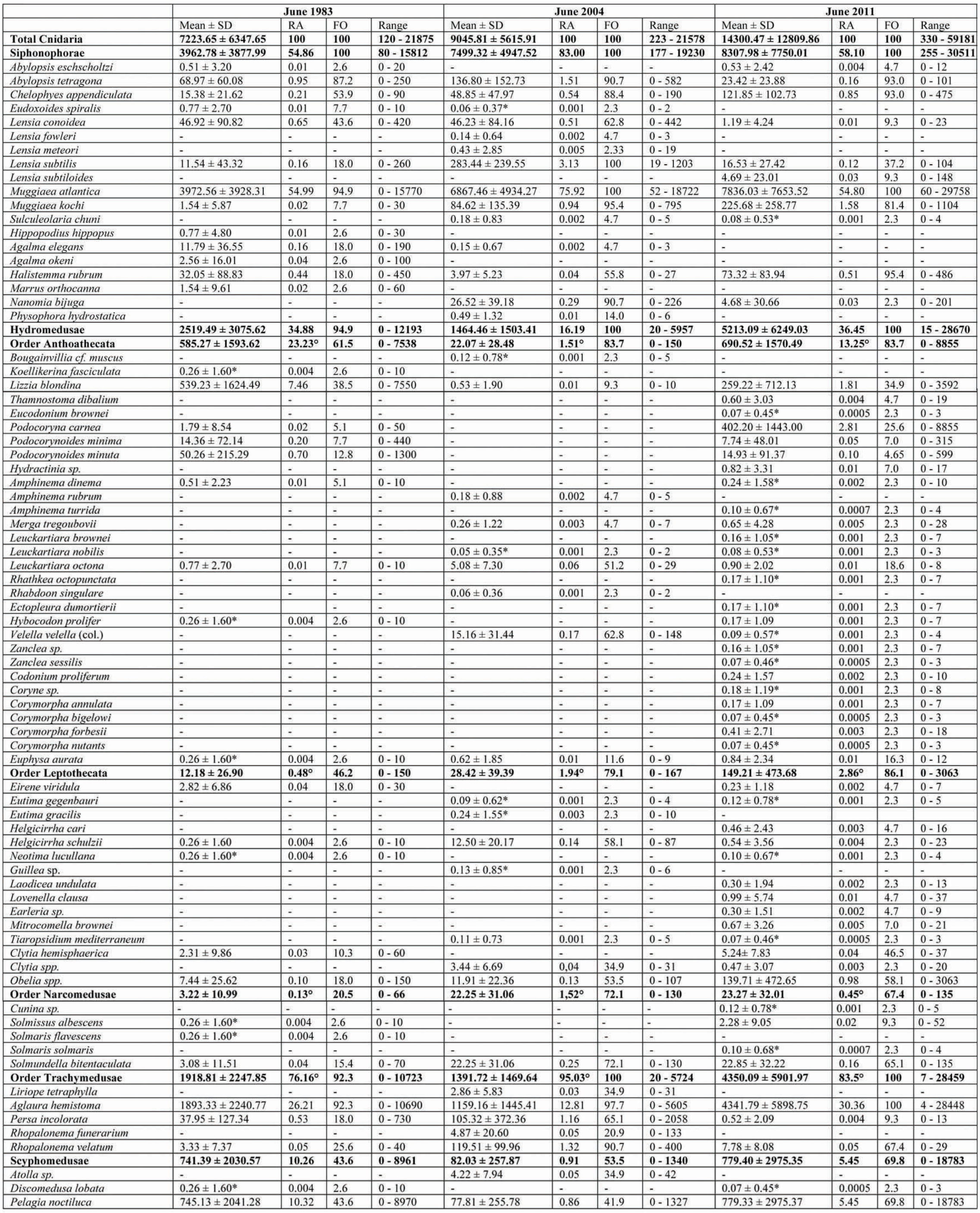


Figure 5. Upper panel: mean abundance (N. Inds 1000 m-3) (+ SD) for total Cnidaria, Siphonophorae, Hydromedusae and Scyphomedusae in each survey, June 1983, 2004 and 2011. Lower panel: mean abundance (N. Inds 1000 m-3) (+ SD) of the calycophoran siphonophore *M. kochii* in each survey, June 1983, 2004 and 2011.

Table 2: Mean ± SD abundance values (Ind·1000 m-3), relative abundance (RA), frequency of occurrence (FO) and range abundance values for all species found during the June surveys of 1983, 2004 and 2011 along the Catalan coast.



	June 1983				June 2004				June 2011			
	Mean ± SD	RA	FO	Range	Mean ± SD	RA	FO	Range	Mean ± SD	RA	FO	Range
Total Cnidaria	**7223.65 ± 6347.65**	**100**	**100**	**120 - 21875**	**9045.81 ± 5615.91**	**100**	**100**	**223 - 21578**	**14300.47 ± 12809.86**	**100**	**100**	**330 - 59181**
Siphonophorae	**3962.78 ± 3877.99**	**54.86**	**100**	**80 - 15812**	**7499.32 ± 4947.52**	**83.00**	**100**	**177 - 19230**	**8307.98 ± 7750.01**	**58.10**	**100**	**255 - 30511**
Abylopsis eschscholtzi	0.51 ± 3.20	0.01	2.6	0 - 20	-	-	-	-	0.53 ± 2.42	0.004	4.7	0 - 12
Abylopsis tetragona	68.97 ± 60.08	0.95	87.2	0 - 250	136.80 ± 152.73	1.51	90.7	0 - 582	23.42 ± 23.88	0.16	93.0	0 - 101
Chelophyes appendiculata	15.38 ± 21.62	0.21	53.9	0 - 90	48.85 ± 47.97	0.54	88.4	0 - 190	121.85 ± 102.73	0.85	93.0	0 - 475
Eudoxoides spiralis	0.77 ± 2.70	0.01	7.7	0 - 10	0.06 ± 0.37*	0.001	2.3	0 - 2	-	-	-	-
Lensia conoidea	46.92 ± 90.82	0.65	43.6	0 - 420	46.23 ± 84.16	0.51	62.8	0 - 442	1.19 ± 4.24	0.01	9.3	0 - 23
Lensia fowleri	-	-	-	-	0.14 ± 0.64	0.002	4.7	0 - 3	-	-	-	-
Lensia meteori	-	-	-	-	0.43 ± 2.85	0.005	2.33	0 - 19	-	-	-	-
Lensia subtilis	11.54 ± 43.32	0.16	18.0	0 - 260	283.44 ± 239.55	3.13	100	19 - 1203	16.53 ± 27.42	0.12	37.2	0 - 104
Lensia subtiloides	-	-	-	-	-	-	-	-	4.69 ± 23.01	0.03	9.3	0 - 148
Muggiaea atlantica	3972.56 ± 3928.31	54.99	94.9	0 - 15770	6867.46 ± 4934.27	75.92	100	52 - 18722	7836.03 ± 7653.52	54.80	100	60 - 29758
Muggiaea kochi	1.54 ± 5.87	0.02	7.7	0 - 30	84.62 ± 135.39	0.94	95.4	0 - 795	225.68 ± 258.77	1.58	81.4	0 - 1104
Sulculeolaria chuni	-	-	-	-	0.18 ± 0.83	0.002	4.7	0 - 5	0.08 ± 0.53*	0.001	2.3	0 - 4
Hippopodius hippopus	0.77 ± 4.80	0.01	2.6	0 - 30	-	-	-	-	-	-	-	-
Agalma elegans	11.79 ± 36.55	0.16	18.0	0 - 190	0.15 ± 0.67	0.002	4.7	0 - 3	-	-	-	-
Agalma okeni	2.56 ± 16.01	0.04	2.6	0 - 100	-	-	-	-	-	-	-	-
Halistemma rubrum	32.05 ± 88.83	0.44	18.0	0 - 450	3.97 ± 5.23	0.04	55.8	0 - 27	73.32 ± 83.94	0.51	95.4	0 - 486
Marrus orthocanna	1.54 ± 9.61	0.02	2.6	0 - 60	-	-	-	-	-	-	-	-
Nanomia bijuga	-	-	-	-	26.52 ± 39.18	0.29	90.7	0 - 226	4.68 ± 30.66	0.03	2.3	0 - 201
Physophora hydrostatica	-	-	-	-	0.49 ± 1.32	0.01	14.0	0 - 6	-	-	-	-
Hydromedusae	**2519.49 ± 3075.62**	**34.88**	**94.9**	**0 - 12193**	**1464.46 ± 1503.41**	**16.19**	**100**	**20 - 5957**	**5213.09 ± 6249.03**	**36.45**	**100**	**15 - 28670**
Order Anthoathecata	**585.27 ± 1593.62**	**23.23°**	**61.5**	**0 - 7538**	**22.07 ± 28.48**	**1.51°**	**83.7**	**0 - 150**	**690.52 ± 1570.49**	**13.25°**	**83.7**	**0 - 8855**
Bougainvillia cf. muscus	-	-	-	-	0.12 ± 0.78*	0.001	2.3	0 - 5	-	-	-	-
Koellikerina fasciculata	0.26 ± 1.60*	0.004	2.6	0 - 10	-	-	-	-	-	-	-	-
Lizzia blondina	539.23 ± 1624.49	7.46	38.5	0 - 7550	0.53 ± 1.90	0.01	9.3	0 - 10	259.22 ± 712.13	1.81	34.9	0 - 3592
Thamnostoma dibalium	-	-	-	-	-	-	-	-	0.60 ± 3.03	0.004	4.7	0 - 19
Eucodonium brownei	-	-	-	-	-	-	-	-	0.07 ± 0.45*	0.0005	2.3	0 - 3
Podocoryna carnea	1.79 ± 8.54	0.02	5.1	0 - 50	-	-	-	-	402.20 ± 1443.00	2.81	25.6	0 - 8855
Podocorynoides minima	14.36 ± 72.14	0.20	7.7	0 - 440	-	-	-	-	7.74 ± 48.01	0.05	7.0	0 - 315
Podocorynoides minuta	50.26 ± 215.29	0.70	12.8	0 - 1300	-	-	-	-	14.93 ± 91.37	0.10	4.65	0 - 599
Hydractinia sp.	-	-	-	-	-	-	-	-	0.82 ± 3.31	0.01	7.0	0 - 17
Amphinema dinema	0.51 ± 2.23	0.01	5.1	0 - 10	-	-	-	-	0.24 ± 1.58*	0.002	2.3	0 - 10
Amphinema rubrum	-	-	-	-	0.18 ± 0.88	0.002	4.7	0 - 5	-	-	-	-
Amphinema turrida	-	-	-	-	-	-	-	-	0.10 ± 0.67*	0.0007	2.3	0 - 4
Merga tregoubovii	-	-	-	-	0.26 ± 1.22	0.003	4.7	0 - 7	0.65 ± 4.28	0.005	2.3	0 - 28
Leuckartiara brownei	-	-	-	-	-	-	-	-	0.16 ± 1.05*	0.001	2.3	0 - 7
Leuckartiara nobilis	-	-	-	-	0.05 ± 0.35*	0.001	2.3	0 - 2	0.08 ± 0.53*	0.001	2.3	0 - 3
Leuckartiara octona	0.77 ± 2.70	0.01	7.7	0 - 10	5.08 ± 7.30	0.06	51.2	0 - 29	0.90 ± 2.02	0.01	18.6	0 - 8
Rhathkea octopunctata	-	-	-	-	-	-	-	-	0.17 ± 1.10*	0.001	2.3	0 - 7
Rhabdoon singulare	-	-	-	-	0.06 ± 0.36	0.001	2.3	0 - 2	-	-	-	-
Ectopleura dumortierii	-		-	-	-	-	-	-	0.17 ± 1.10*	0.001	2.3	0 - 7
Hybocodon prolifer	0.26 ± 1.60*	0.004	2.6	0 - 10	-	-	-	-	0.17 ± 1.09	0.001	2.3	0 - 7
Velella velella (col.)	-	-	-	-	15.16 ± 31.44	0.17	62.8	0 - 148	0.09 ± 0.57*	0.001	2.3	0 - 4
Zanclea sp.	-	-	-	-	-	-	-	-	0.16 ± 1.05*	0.001	2.3	0 - 7
Zanclea sessilis	-	-	-	-	-	-	-	-	0.07 ± 0.46*	0.0005	2.3	0 - 3
Codonium proliferum	-	-	-	-	-	-	-	-	0.24 ± 1.57	0.002	2.3	0 - 10
Coryne sp.	-	-	-	-	-	-	-	-	0.18 ± 1.19*	0.001	2.3	0 - 8
Corymorpha annulata	-	-	-	-	-	-	-	-	0.17 ± 1.09	0.001	2.3	0 - 7
Corymorpha bigelowi	-	-	-	-	-	-	-	-	0.07 ± 0.45*	0.0005	2.3	0 - 3
Corymorpha forbesii	-	-	-	-	-	-	-	-	0.41 ± 2.71	0.003	2.3	0 - 18
Corymorpha nutants	-	-	-	-	-	-	-	-	0.07 ± 0.45*	0.0005	2.3	0 - 3
Euphysa aurata	0.26 ± 1.60*	0.004	2.6	0 - 10	0.62 ± 1.85	0.01	11.6	0 - 9	0.84 ± 2.34	0.01	16.3	0 - 12
Order Leptothecata	**12.18 ± 26.90**	**0.48°**	**46.2**	**0 - 150**	**28.42 ± 39.39**	**1.94°**	**79.1**	**0 - 167**	**149.21 ± 473.68**	**2.86°**	**86.1**	**0 - 3063**
Eirene viridula	2.82 ± 6.86	0.04	18.0	0 - 30	-	-	-	-	0.23 ± 1.18	0.002	4.7	0 - 7
Eutima gegenbauri	-	-	-	-	0.09 ± 0.62*	0.001	2.3	0 - 4	0.12 ± 0.78*	0.001	2.3	0 - 5
Eutima gracilis	-	-	-	-	0.24 ± 1.55*	0.003	2.3	0 - 10	-			
Helgicirrha cari	-	-	-	-	-	-	-	-	0.46 ± 2.43	0.003	4.7	0 - 16
Helgicirrha schulzii	0.26 ± 1.60	0.004	2.6	0 - 10	12.50 ± 20.17	0.14	58.1	0 - 87	0.54 ± 3.56	0.004	2.3	0 - 23
Neotima lucullana	0.26 ± 1.60*	0.004	2.6	0 - 10	-	-	-	-	0.10 ± 0.67*	0.001	2.3	0 - 4
Guillea sp.	-	-	-	-	0.13 ± 0.85*	0.001	2.3	0 - 6	-	-	-	-
Laodicea undulata	-	-	-	-	-	-	-	-	0.30 ± 1.94	0.002	2.3	0 - 13
Lovenella clausa	-	-	-	-	-	-	-	-	0.99 ± 5.74	0.01	4.7	0 - 37
Earleria sp.	-	-	-	-	-	-	-	-	0.30 ± 1.51	0.002	4.7	0 - 9
Mitrocomella brownei	-	-	-	-	-	-	-	-	0.67 ± 3.26	0.005	7.0	0 - 21
Tiaropsidium mediterraneum	-	-	-	-	0.11 ± 0.73	0.001	2.3	0 - 5	0.07 ± 0.46*	0.0005	2.3	0 - 3
Clytia hemisphaerica	2.31 ± 9.86	0.03	10.3	0 - 60	-	-	-	-	5.24± 7.83	0.04	46.5	0 - 37
Clytia spp.	-	-	-	-	3.44 ± 6.69	0,04	34.9	0 - 31	0.47 ± 3.07	0.003	2.3	0 - 20
Obelia spp.	7.44 ± 25.62	0.10	18.0	0 - 150	11.91 ± 22.36	0.13	53.5	0 - 107	139.71 ± 472.65	0.98	58.1	0 - 3063
Order Narcomedusae	**3.22 ± 10.99**	**0.13°**	**20.5**	**0 - 66**	**22.25 ± 31.06**	**1,52°**	**72.1**	**0 - 130**	**23.27 ± 32.01**	**0.45°**	**67.4**	**0 - 135**
Cunina sp.	-	-	-	-	-	-	-	-	0.12 ± 0.78*	0.001	2.3	0 - 5
Solmissus albescens	0.26 ± 1.60*	0.004	2.6	0 - 10	-	-	-	-	2.28 ± 9.05	0.02	9.3	0 - 52
Solmaris flavescens	0.26 ± 1.60*	0.004	2.6	0 - 10	-	-	-	-	-	-	-	-
Solmaris solmaris	-	-	-	-	-	-	-	-	0.10 ± 0.68*	0.0007	2.3	0 - 4
Solmundella bitentaculata	3.08 ± 11.51	0.04	15.4	0 - 70	22.25 ± 31.06	0.25	72.1	0 - 130	22.85 ± 32.22	0.16	65.1	0 - 135
Order Trachymedusae	**1918.81 ± 2247.85**	**76.16°**	**92.3**	**0 - 10723**	**1391.72 ± 1469.64**	**95.03°**	**100**	**20 - 5724**	**4350.09 ± 5901.97**	**83.5°**	**100**	**7 - 28459**
Liriope tetraphylla	-	-	-	-	2.86 ± 5.83	0.03	34.9	0 - 31	-	-	-	-
Aglaura hemistoma	1893.33 ± 2240.77	26.21	92.3	0 - 10690	1159.16 ± 1445.41	12.81	97.7	0 - 5605	4341.79 ± 5898.75	30.36	100	4 - 28448
Persa incolorata	37.95 ± 127.34	0.53	18.0	0 - 730	105.32 ± 372.36	1.16	65.1	0 - 2058	0.52 ± 2.09	0.004	9.3	0 - 13
Rhopalonema funerarium	-	-	-	-	4.87 ± 20.60	0.05	20.9	0 - 133	-	-	-	-
Rhopalonema velatum	3.33 ± 7.37	0.05	25.6	0 - 40	119.51 ± 99.96	1.32	90.7	0 - 400	7.78 ± 8.08	0.05	67.4	0 - 29
Scyphomedusae	**741.39 ± 2030.57**	**10.26**	**43.6**	**0 - 8961**	**82.03 ± 257.87**	**0.91**	**53.5**	**0 - 1340**	**779.40 ± 2975.35**	**5.45**	**69.8**	**0 - 18783**
Atolla sp.	-	-	-	-	4.22 ± 7.94	0.05	34.9	0 - 42	-	-	-	-
Discomedusa lobata	0.26 ± 1.60*	0.004	2.6	0 - 10	-	-	-	-	0.07 ± 0.45*	0.0005	2.3	0 - 3
Pelagia noctiluca	745.13 ± 2041.28	10.32	43.6	0 - 8970	77.81 ± 255.78	0.86	41.9	0 - 1327	779.33 ± 2975.37	5.45	69.8	0 - 18783

*Only 1 individual found; °RA relative to Hydromedusae group.

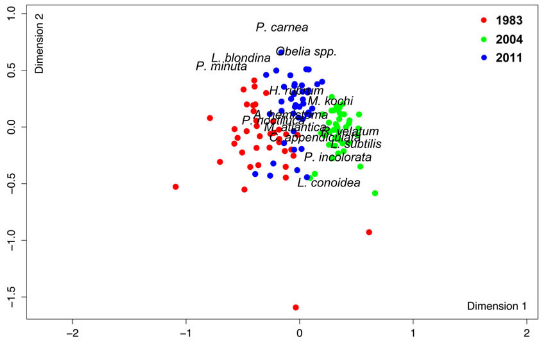


Figure 6. Non-metric multidimensional scaling (nMDS) ordination plot. Species abundance was log (x+1) transformed and analysis performed on Bray-Curtis dissimilarity matrix. Red, green and blue dots symbolize sample stations of June 1983, 2004 and 2011 respectively. A stress estimate of 0.21 was obtained. The most abundant and representative species of each survey are indicated in the plot.

P. noctiluca was much more abundant during 2011 (Table 2; Fig. 7). Dissimilarities between the first and the last cruise mainly derived from *M. kochii*, the physonectid *H. rubrum* and *P. noctiluca*. The two first were found more abundantly and frequently in 2011 (Table 2; Fig. 7, only *M. kochii* shown). The scyphomedusa *P. noctiluca* presented similar abundance values in both years (Table 2) however it was more widespread in 2011 and presented its highest densities related to the shelf and shelf edge areas in comparison to 1983 when were observed related to the coast.

Relationships between the community and the environmental factors

In the CCA analysis combining all years the first ordination axis was strongly and negatively correlated with temperature (-0.70) and accounted for the 63% of the constrained variance (Table 6). Stations of 2004 were grouped in the negative side of the axis, showing their relation with higher temperatures. 1983 and 2011 stations were in the positive side of the axis, with those of 1983 especially related with cooler temperatures (Fig. 9). The second ordination axis was positively correlated with depth (0.42) accounting for the 37% of the constrained variance (Table 6). Samples of 1983 and 2011 were spread at both sides of the axis while those of 2004 were grouped mostly in the positive side (Fig. 9). This distribution shows that the communities found in the different stations of 1983, especially, and 2011 were related to certain depth ranges while that of 2004 were distributed more independently of the bathymetry. Salinity was barely related to the first axis (-0.22) (Table 6). The permutation test indicated high significance ($p < 0.001$) of the two first ordination axes. These results show that temperature was the main environmental factor influencing the differences among years.

Results of the CCAs performed for each year demonstrated that the weight of the environmental factors affecting the distribution of the community differed amongst years. In 1983, depth was the main factor, while in 2004 and 2011 it was temperature (Table 6). In addition, a lower influence of the depth factor was observed over time. In all cases, axis 1 was revealed significant by the permutation test. The spatial distribution of the score values of each sampled station for the first axis clearly showed how the community in 1983 was ordinated in relation to the coast-offshore axis, while during 2004 and 2011 this pattern was not so clear and a north-south ordination was noticeable, especially in 2004 (Fig. 10).

DISCUSSION

In the present study the spatio-temporal variability in the planktonic cnidarian community were investigated in three different summer (June) surveys conducted in the last three decades (1983, 2004 and 2011) over a mesoscale spatial area along the Catalan coast. The results show changes in the community composition as well as an increment in their abundance over time. Among the different environmental variables considered in this study, water temperature was the variable that contributed the most to these differences (Fig. 9). Temperature has been suggested to be a key factor driving long-term changes in zooplankton communities in several areas (Richardson, 2008; Suikkanen *et al.*, 2013). Over the last decades, seawater temperature in the NW Mediterranean has shown an increasing trend (Rixen *et al.*, 2005), following the general global pattern (Levitus *et al.*, 2005). This warming trend has been particularly evident since the 1980s and at the end of the 1990s (Rixen *et al.*, 2005; Vargas-Yáñez *et al.*, 2005). The temperature increase in the Catalan coast over the last two decades is well documented (Calvo *et al.*, 2011). As observed in the present study, Sabatés *et al.*, 2012 identified two marked temperature shifts, the first one in the early 1980s and the second around 1997.

The planktonic cnidarian communities identified during each survey significantly differed from one another and were clearly segregated by temperature (Fig. 6 and 9; Table 6). The siphonophore *L. subtilis* and the hydromedusae *R. velatum*, both considered warm water species (Mayer, 1910; Alvariño, 1971), characterized the community of 2004 (Fig. 5). This would agree with the fact that 2004 presented the warmest

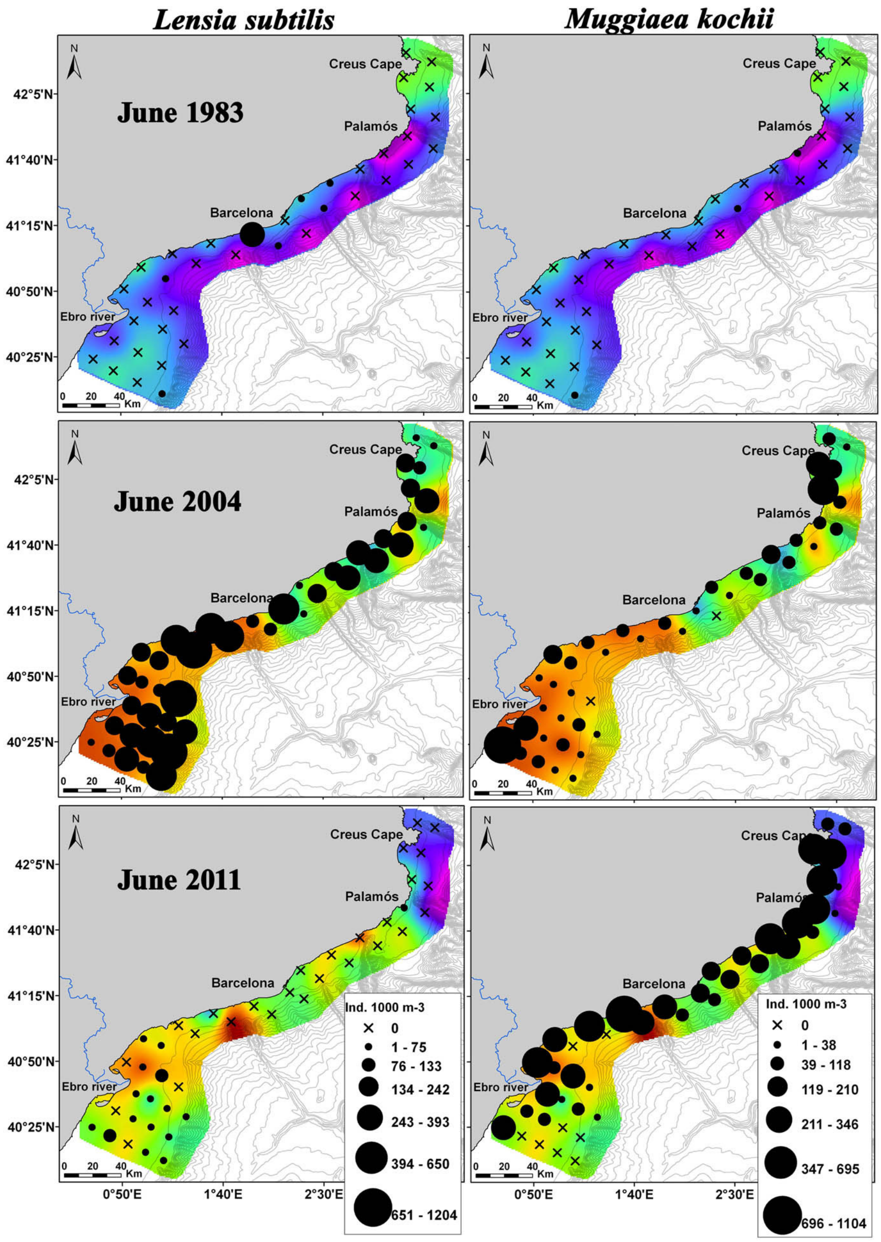


Figure 7. Spatial distribution of the species *L. subtilis* and *M. kochii* overlaid on surface temperature for each survey, from top to down: June 1983, 2004 and 2011. For temperature scale see Fig. 2.

Table 3: Species richness (S) and Shannon diversity index (H') of the planktonic cnidarian community in the June surveys of 1983, 2004 and 2011 along the Catalan coast.

	June 1983		June 2004		June 2011	
	Total/Mean ± SD	Range	Total/Mean ± SD	Range	Total/Mean ± SD	Range
N. species (*S*)	35	2 - 12	38	5 - 21	59	6 - 16
Shannon index (H')	0.96 ± 0.31	0.2 - 1.6	0.91 ± 0.44	0.11 - 1.82	0.96 ± 0.35	0.12 - 1.64

temperatures (Fig. 2) and the highest positive anomalies, of the three studied periods (Fig. 11). The community in 1983 was influenced by the coldest temperatures, in 2011 by intermediate temperatures, and both were segregated by depth (Fig. 9). The small and coastal hydromedusa species *L. blondina* and *P. minuta* (Schuchert, 2007) characterized the community in 1983 (Fig. 5). The community in 2011 was defined by other small and coastal hydromedusae species, *P. carnea* and *Obelia* spp. (Schuchert, 2008). Although the aforementioned species were among the most abundant during each corresponding survey (Table 2), the sipohonophore *M. atlantica* and the hydromedusae *A. hemistoma*, were the dominant species during all surveys (Table 2). The dominance of these two species in the NW Mediterranean is a phenomenon observed since early 1980s, when both species outcompeted the previous dominant species, *M. kochii* and *L. blondina* (Riera *et al.*, 1986; Gili *et al.*, 1988; Licandro *et al.*, 2012) and their dominance over time suggest that they can tolerate wide environmental ranges.

During early 1980s the calycophoran siphonophore *M. kochii* showed an abrupt abundance decline in the NW Mediterranean (Riera *et al.*, 1986; Licandro *et al.*, 2012). However, we have observed a marked and progressive increase in the abundance of this species, being widely distributed over the studied area in the last two surveys (Table 2; Fig. 8). This siphonophore is considered a warm-temperate species (Alvariño, 1971) and therefore it could benefit from the observed increase in water temperature (Fig. 11). In different areas of the world an alternation pattern in the abundance of *M. kochii* and its congeneric *M. atlantica* has been observed (Russell, 1934; Mackie *et al.*, 1987; Blackett *et al.*, 2014). Surprisingly in the present study both species abundances simultaneously increased along the study period (Table 2; Fig. 7 and 8).

On the Western Mediterranean, long-term series conducted in historic stations (e.g. Villefranche and Naples) over the last three decades, showed that rises in water temperature were associated to changes in the abundance of planktonic cnidarians (Molinero *et al.*, 2005, 2008; García-Comas *et al.*, 2011; Berline *et al.*, 2012; Licandro *et al.*, 2012). Molinero *et al.* (2005, 2008) (studied period: 1966-1993), studying some target species (2 siphonophores and 3 hydromedusae), showed a rise of jellyfish abundance related to water temperature increments during the 1980s and early 1990s. Nevertheless, Licandro *et al.* (2012) and García-Comas *et al.* (2011) García-Comas *et al* (2011) (studied periods; 1974-1999 and 1974-2003, respectively) found that the siphonophore and medusae community stock did not increased from the late 1980s despite sea warming increase. In our study, considering a mesoscale spatial area, the total abundance of planktonic cnidarians significantly and progressively increased over time (Fig. 3 and Table 4) being water temperature, among the studied parameters, the main environmental factor driving these changes (Fig. 5 and Table 6). Salinity gradients have been associated with changes in planktonic cnidarian abundance and community composition (Purcell

Table 4. Results of the analyses of variance using Generalized Linear Models (GLM) for the total Cnidaria abundance and the different groups Siphonophorae, Hydromedusae and Scyphomedusae between pairs of years.

	1983 - 2004		2004 - 2011		1983 - 2011	
	z-value	p-value	z-value	p-value	z-value	p-value
Total Cnidaria	47.8	<0.001	87.6	<0.001	106.6	<0.001
Siphonophorae	72.5	<0.001	22.5	<0.001	86.6	<0.001
Hydromedusae	-2.1	<0.05	4.9	<0.001	2.5	= 0.01
Scyphomedusae	-3.3	<0.001	3.9	<0.001	0.08	n.s.

et al., 2007; Licandro *et al.*, 2012). However, this does not seem to be the case for our study since this factor barely affected the abundance and community composition (Fig. 9 and Table 6) despite the observed salinity differences among the surveys (Fig. 2 and Table 1).

Although no significant differences in species diversity (H') were found among the three surveys, in 2011 species richness considerably increased (Table 3 and Figure 4). This increment derived from a higher number of Anthoathecata and Leptothecata hydromedusae, species that are characterized by having a benthic stage (polyp) in their life cycle. It is known that higher water temperatures promote faster lifecycles and higher reproductive rates (Purcell *et al.*, 2007; Boero *et al.*, 2016). The sea warming trend along the studied period (Fig. 11) could help to explain

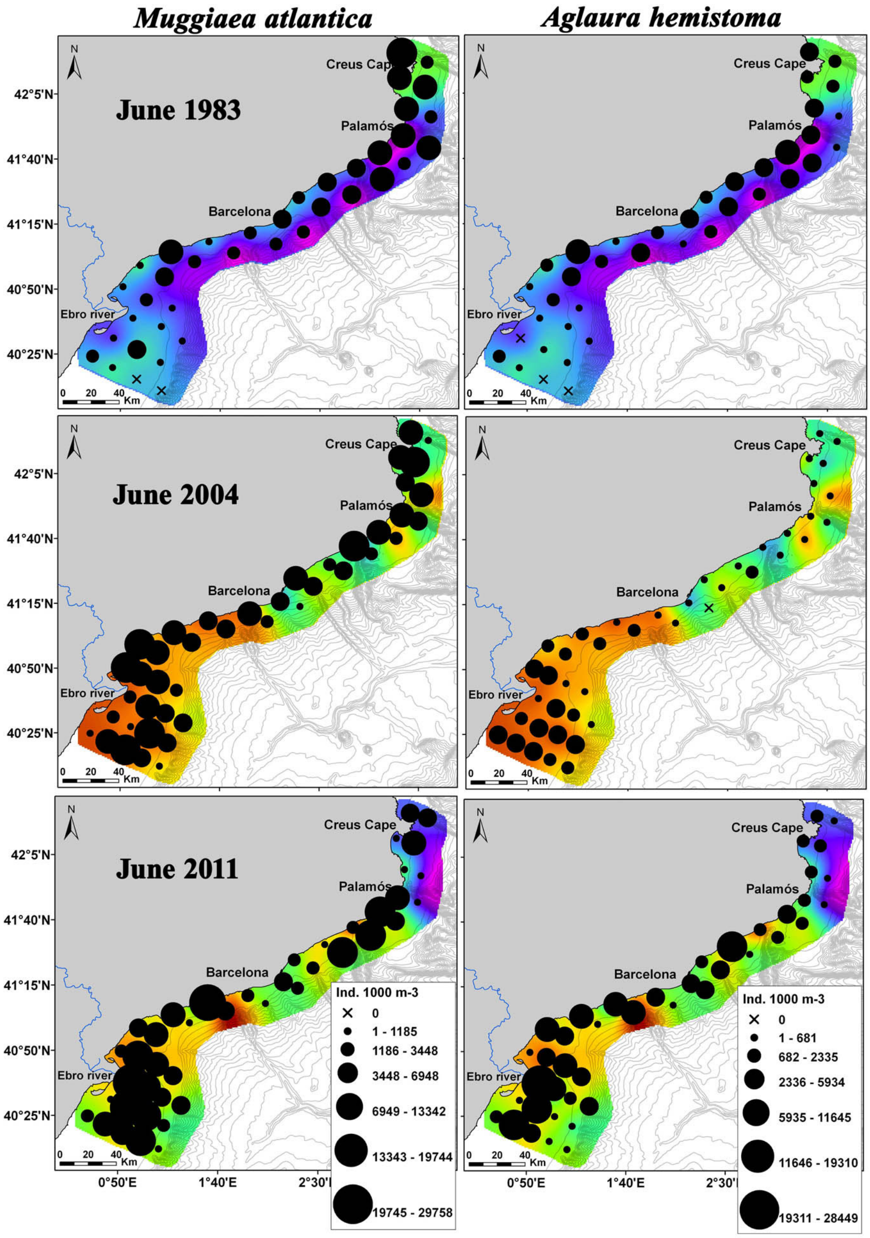


Figure 8. Spatial distribution of the dominant species *Muggiaea atlantica* and *Aglaura hemistoma* overlaid on surface temperature for each survey, from top to down: June 1983, 2004 and 2011. For temperature scale see Fig. 2.

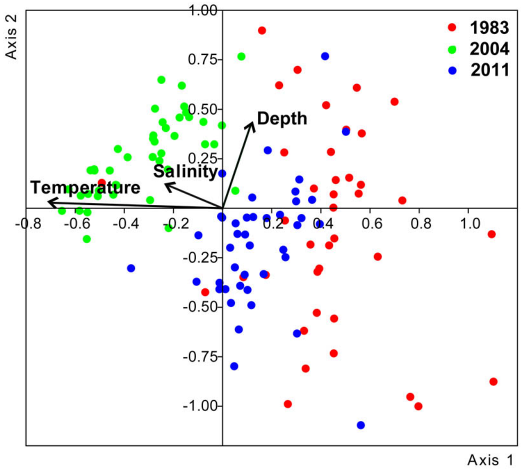


Figure 9. Ordination plot of the canonical correspondence analysis (CCA) showing the relationships between the sampling stations (red for 1983, green for 2004 and blue for 2011) and the environmental variables (arrows).

this result; higher temperatures would trigger the release of high number of medusae individuals from the polyp probably favouring earlier asexual reproduction (Boero and Bouillon, 1993), although it was not observed in 2004 .

Changes in the spatial distribution pattern of the community among surveys were observed based on the weight of environmental factors (Table 6). In the coldest 1983 the community showed a clear coast-offshore ordination pattern while in the warmer 2004 and 2011 a north-south pattern was noticeable (Fig. 10). This north-south pattern has also been observed in the area during exceptional warm summer conditions (Guerrero *et al*, in prep), which could indicate that under increasing temperature scenarios a latitudinal ordination pattern will become more evident.

The changes in the cnidarian community along the Catalan coast observed in the present study could also derive from the decrease in abundance of predators. It is well known that many species of fish consume gelatinous zooplankton (Arai, 1988; Purcell and Arai, 2001). In the NW Mediterranean large deep-sea fish have been showed to positively select siphonophores as prey (Carrassón and Cartes, 2002), while other species of commercial interest, such as bluefin tuna or swordfish, are gelatinous plankton consumers (Cardona *et al.*, 2012). In the Catalan coast an important decrease on fisheries catch from late 1900s on has been documented as a possible consequence of the pelagic stocks decrease (Lleonart and Bas, 2012). Therefore, the decreasing of fish populations may lead to a lower predation pressure on gelatinous zooplankton and lower competition for food resources (Bakun and Weeks, 2006; Tilves *et al.*, 2016), favouring the increase of gelatinous zooplankters. Besides, gelatinous zooplankton and fish interact as competitors of each other (Brodeur *et al.*, 1999; Purcell *et al.*, 2007), as both are consumers of zooplankton. Studies related with long-term variation of zooplankton in the Western Mediterranean (Ribera d'Alcalà *et al.*, 2004; Fernández De Puelles and Molinero, 2008) suggest that the total biomass have not decreased in the last decades, fact that could also be favouring the increase of carnivorous gelatinous zooplankton due to the unvarying food availability.

The observed increase of planktonic cnidarians might be a response to the climate and the anthropogenic changes occurred during the last decades in the NW Mediterranean. This could imply a great difficulty for the recovery of certain pelagic fish stocks competing for the same food (Purcell and Arai, 2001; Brodeur *et al.*, 2008), but also a higher availability of gelatinous prey for other fish and vertebrates (Carrassón and Cartes,

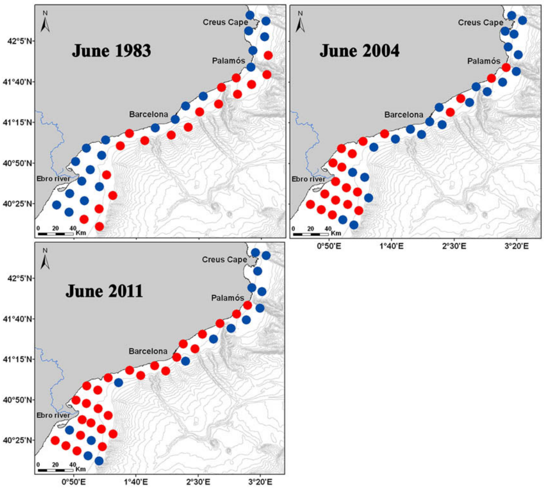


Figure 10. Spatial distributions of the score values of each sampled station for the first axis resulted from the CCA analyses for each survey. Blue dots represent negative score values,red dots positive.

Table 5: Species contribution as average dissimilarities (Av. Dis.) to the overall average dissimilarity between each pair of years indicated by the SIMPER analysis. Species accounting to the first 90% of the dissimilarity are shown in decreasing order of percentage contribution. The three higher average dissimilarities (one year vs other) for each species are in bold.

1983 - 2004				**2004 - 2011**				**1983 - 2011**			
Overall average dissimilarity: 54 %					**46%**				**49%**		
Taxon	**Av. Dis.**	**Contrib. %**	**Cum. %**	**Taxon**	**Av. Dis.**	**Contrib. %**	**Cum. %**	**Taxon**	**Av. Dis.**	**Contrib. %**	**Cum %**
L. subtilis	5.591	**10.34**	10.34	***L. subtilis***	3.995	**8.681**	8.681	***M kochi***	5.029	**10.24**	10.24
R. velatum	4.178	**7.727**	18.07	***R. velatum***	2.852	**6.199**	14.88	***H. rubrum***	4.335	**8.829**	19.07
M. kochi	4.157	**7.689**	25.76	***P. noctiluca***	2.82	**6.129**	21.01	***P. noctiluca***	4.236	**8.628**	27.7
P. noctiluca	3.078	5.693	31.45	*H. rubrum*	2.695	5.857	26.87	*C. appendiculata*	3.671	7.477	35.18
N. bijuga	3.011	5.569	37.02	*A. hemistoma*	2.564	5.572	32.44	*L. blondina*	3.505	7.139	42.32
A. hemistoma	2.926	5.411	42.43	*N. bijuga*	2.558	5.56	38	*A. hemistoma*	3.299	6.72	49.04
P. incolorata	2.771	5.124	47.55	*Obelia spp.*	2.234	4.855	42.85	*Obelia spp.*	2.885	5.876	54.91
L. conoidea	2.752	5.09	52.64	*L. conoidea*	2.214	4.812	47.67	*M. atlantica*	2.703	5.505	60.42
C. appendiculata	2.564	4.742	57.38	*M. kochi*	2.197	4.774	52.44	*S. bitentaculata*	2.471	5.033	65.45
L. blondina	2.397	4.434	61.82	*P. incolorata*	2.166	4.707	57.15	*L. conoidea*	2.36	4.807	70.26
A. tetragona	2.378	4.399	66.22	*A. tetragona*	2.022	4.395	61.54	*A. tetragona*	2.321	4.727	74.98
S. bitentaculata	2.278	4.212	70.43	*S. bitentaculata*	1.858	4.037	65.58	*L. subtilis*	2.032	4.138	79.12
M. atlantica	2.226	4.118	74.55	*C. appendiculata*	1.742	3.786	69.37	*R. velatum*	1.918	3.907	83.03
V. velella	1.881	3.479	78.03	*L. blondina*	1.738	3.777	73.14	*P. carnea*	1.718	3.5	86.53
H. rubrum	1.779	3.29	81.32	*V. velella*	1.59	3.456	76.6	*C. hemisphaerica*	1.527	3.11	89.64
Obelia spp.	1.742	3.221	84.54	*M. atlantica*	1.573	3.42	80.02				
H. schulzei	1.704	3.152	87.69	*H. schulzei*	1.464	3.181	83.2				
L. octona	1.342	2.482	90.17	*P. carnea*	1.236	2.686	85.89				
				L. octona	1.118	2.429	88.32				
				C. hemisphaerica	1.094	2.377	90.69				

2002; Cardona *et al*., 2012). Based on the results of the present study, it would appear that in the current climate change scenario warm-species abundance and distribution will be positively favoured and community latitudinal distribution patterns will be reinforced. For all these, we deeply recommend the study and monitoring of mesoscale spatial areas to understand not only long-term gelatinous zooplankton abundance changes but also how these changes are revealed in their spatial distributions.

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Table 6. Summary of the relationships between the environmental variables and axis 1 resulted from the Canonical Correspondence Analyses (CCA) performed for all surveys combined and for each June survey (1983, 2004 and 2011). The most significant factor in each case is in bold. Cons. var. explained = constrained variance explained.

	Axis 1			
	CCA combined	CCA 1983	CCA 2004	CCA 2011
Cons. var. explained	63 %	63%	76%	78%
Depth	0.11	**-0.61**	0.56	0.46
Temperature	**-0.70**	0.49	**-0.67**	**-0.55**
Salinity	-0.22	-0.34	0.55	0.29

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GENERAL DISCUSSION

The study of a mesoscalespatial area

Plankton is patchy on a wide variety of space and time of scales. As it is difficult to observe the pelagic realm, simply because we cannot see into the ocean, we must depend on sampling to obtain an impression of these scales of pattern in this habitat (Haury *et al.*, 1978). In the range of 100 to 1000 km, the mesoscale provides the opportunity to study change rates in populations and communities related to environmental conditions (Haury *et al.*, 1978).

In this sense, studies covering a wide network of stations have revealed changes in patterns of distribution of planktonic communities coupled with the distribution of physical processes and structures (Pagès and Gili, 1992; Graham *et al.*, 2001), and have provided valuable knowledge related to the ecological role of planktonic cnidarians at regions such as the Humboldt current system or the Benguela upwelling system, some of the most productive marine regions in the world's ocean (Pagès and Gili, 1991; Pagès *et al.*, 2001).

The Catalan coast, in the NW Mediterranean, is a large (ca. 350 km long) and highly heterogeneous area characterized by different hydrodynamic structures, such as fronts, and different environmental gradients: bathymetry, temperature, salinity and primary production. Therefore, to understand the spatio-temporal variability of planktonic cnidarians and their bio-physical coupling spatial mesoscale approaches are desirable.

Relevant species

The three studies encompassing the present thesis were carried out during spring and summer months, when planktonic cnidarians show their highest annual abundance and species richness (Gili *et al.*, 1987b; 1988; Licandro *et al.*, 2012) and the Catalan coast experiences strong spatial and temporal hydrodynamic variability (Masó and Tintoré, 1991).

In all the analysed surveys, the most abundant species were the siphonophore *Muggiaea atlantica* and the hydromedusae *Aglaura hemistoma*. They constituted up to 90 % of the total community abundance and were widely distributed all over the area. The dominance of these two species, at least in summer months, occurred also under extreme warm conditions (Chapter 2) and over the last three decades (Chapter 3), which suggests that they may be tolerant to wide environmental ranges and able to exploit resources more efficiently than other species. Although different species show different spatial distributions and relationships with the environmental conditions (Chapter 2), these two dominant species constitute the bulk of the spring and summer community and thus can be considered as representative of the whole planktonic cnidarian community abundance and spatio-temporal variability (Chapter 1).

Other abundant species integrating the community were the warm-water species *Lensia subtilis* and *Rhopalonema velatum*. The siphonophore *L. subtilis* was the third most abundant species during July months (Chapter 2) and in the relatively warm June of 2004 (Chapter 3). The thrachymedusae *R. velatum*, was also among the most abundant species in July months (Chapter 2) and in the warm June of 2004 (Chapter 3). During these mentioned warm months, both species were widely distributed over the area, however, in the coldest June 1983 and temperate 2011 their abundances were much lower and their distribution more restricted (Chapter 3). The results suggest that these warm-water species could be utilized as a good indicator of seawater temperature increase.

The siphonophore *Muggiaea kochii* seems to have experienced an increasing trend from 1983 to 2011 (Chapter 3). This is particularly relevant given the decreasing appearance of this species in NW Mediterranean since the middle 1980s, when it was replaced by its congeneric *M. atlantica* (Riera *et al.*, 1986; Licandro *et al.*, 2012). Recently, a10-years time series study in an Atlantic estuarine ecosystem also reported an abundance increase of *M. kochii* in the last years (D'Ambrosio *et al.*, 2016). However, in the English Channel decreasing abundances have been recorded in recent years (Blackett *et al.*, 2015). Despite this species seem to show different trends in different areas, it would be of great interest to study and follow this increasing tendency of *M. kochii* in the NW Mediterranean and other temperate regions. Another interesting evidence is the simultaneous increasing trend of both congeneric species, *M. kochii* and *M. atlantica,* despite their usual abundance alternation pattern (Russell, 1934; Blackett *et al.*, 2014). If we calculate an abundance *M. atlantica*/*M. kochii* ratio, it is possible to see a decreasing ratio in favour of *M. kochii* over time. These ratio values were: 2000 for June 1983, 80 for June 2004 and 35 for June 2011. This result indicate that even though the summer abundance of both species increased over time, *M. kochii* is experiencing a higher increasing rate than *M. atlantica*, suggesting that the warm-temperate species *M. kochii* may be favoured by the sea warming conditions in front of the cold-temperate *M. altantica* under the current climate change scenario. Attention should be paid in the abundance trends and rates between both congeneric species in different temperate places worldwide as indicator of warming oceans. The abundance ratio between the two species could be suggested as a good index of zooplankton response to temperature changes in a particular area.

It is worth mentioning that sexual stages (eudoxids) of siphonophores (mainly *C. appendiculata* and *A. tetragona*) represented an important fraction of the total community abundance (up to 11%) and were widely distributed over the area (Chapter 2). This data indicates that the Catalan coast is a favourable breeding area for temperate siphonophore species and could represent a population source for other Mediterranean areas.

Spatio-temporal variability of the community

The spatial variability of the planktonic cnidarian community in the Catalan coast has been studied at different temporal scales; at 10 days intervals (Chapter 1), between two consecutive years (Chapter 2), and in three years during the last three decades (Chaper 3). In this section spatial and temporal variability of the community is commented separately to understand the importance of each approach and lately their coupling with environmental factors.

A. Spatial variability

The spatial variability of the studied species was determined and shaped by physical factors such as bathymetry and salinity and thermal fronts.

A1. Bathymetry

The bathymetry was revealed as a key factor determining the spatial distribution of many species and of the community. It is, probably, the main factor which on occasions can be masked by other

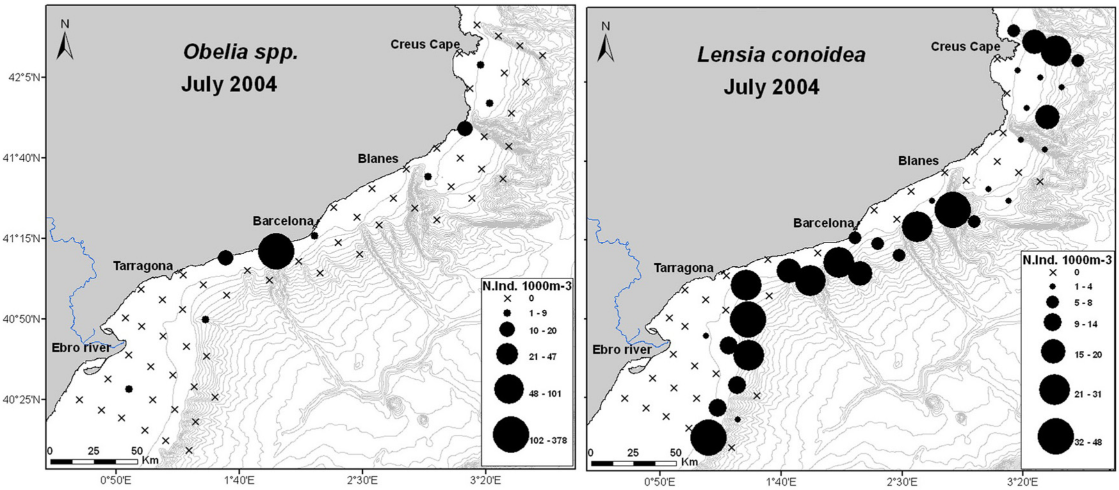

Fig. 1. Spatial distribution of *Obelia* spp. and *L. Conoidea* along the Catalan coast in relation to the bathymetry, in July 2004. Different size dots represent the abundance, grey lines the bathymetry (every 100 m).

processes, such the inshore displacement of the shelf-slope front (Chapter 1) or extreme warm conditions (Chapter 2), when salinity and temperature, respectively, had the relevant role. Some species were particularly influenced by shallower depths and their distribution was mainly restricted to the coast, like the hydromedusae *Obelia* spp. Others were influenced by greater depths and distributed over the shelf edge and slope, and over the submarine canyons, like the siphonophore *L. conoidea* (Fig. 1). The life cycle of species is associated to bathymetry. Many of the species found near the coast have meroplanktonic life cycles while offshore species have mainly holoplanktonic life cycles (Boero and Bouillon, 1993).

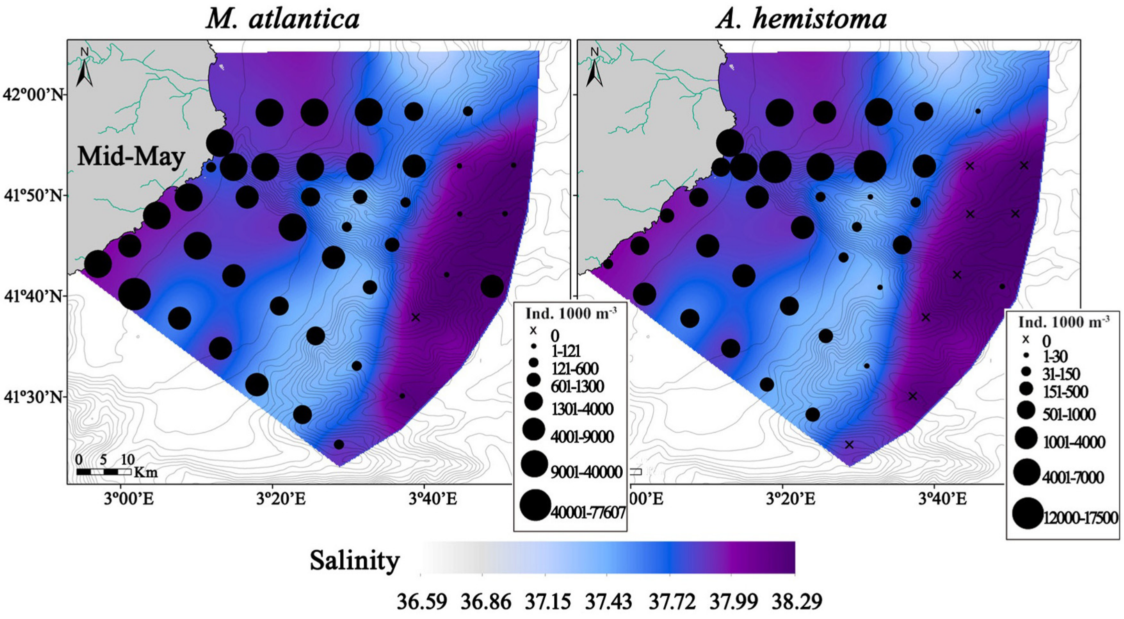

Fig. 2. Spatial distribution of *M. atlantica* and *A. hemistoma* in relation to the shelf-slope front in the northern Catalan coast in mid-May 1992. Different size dots represent the abundance, colour gradient represents the surface salinity distribution and grey lines the bathymetry (every 100 m).

A2. Hydrographic structures: fronts

A2.1. The salinity shelf-slope front. During spring large inputs of continental waters coming mainly from the Rhône River, in the northern Gulf of Lions, appear in the north part of the study area causing high mesoscale activity of the shelf-slope density front (Masó and Tintoré, 1991; Sabatés *et al.*, 2004). In this context the two most abundant and representative species of the cnidarian community presented a marked spatial variability delimited by the position of the shelf-slope front (Chapter 1). The species occurred on its inshore side of the front in significantly higher abundances than on its offshore side, where they were scarce or absent (Fig. 2). In addition, this front has been reported as a concentration area of shelf and offshore species in relation to the productivity of the area (Gili *et al.*, 1988; Sabatés *et al.*, 2010).

A2.2. The thermal front. During spring and summer a seasonal thermal front is formed across the shelf between 41 and 42°N, which separates cold waters in the north from warm waters in the south (López-García *et al.*, 1994). This latitudinal temperature gradient influenced the latitudinal distribution of certain species such *Abylopsis tetragona*, with its highest abundances south of the front in warm waters, and *Persa incolorata*, with its highest abundances concentrated north of the front in cold waters (Fig. 3).

B. Temporal variability.

B1. Short-term scale: 10 days.

High variability in the spatial distribution of the two most abundant species were observed at ten days interval associated to high variability in the location of the shelf-slope density front (Chapter 1). Their distributions were strongly modified by the changing position of the density front; from a widely distribution (mid-May) to one restricted in a narrow belt over the shelf (early June). The front moved from a position over the slope, at approximately 50 km offshore, to over the shelf, at about 20 km from the coast (Fig. 4; *M. atlantica* as example).

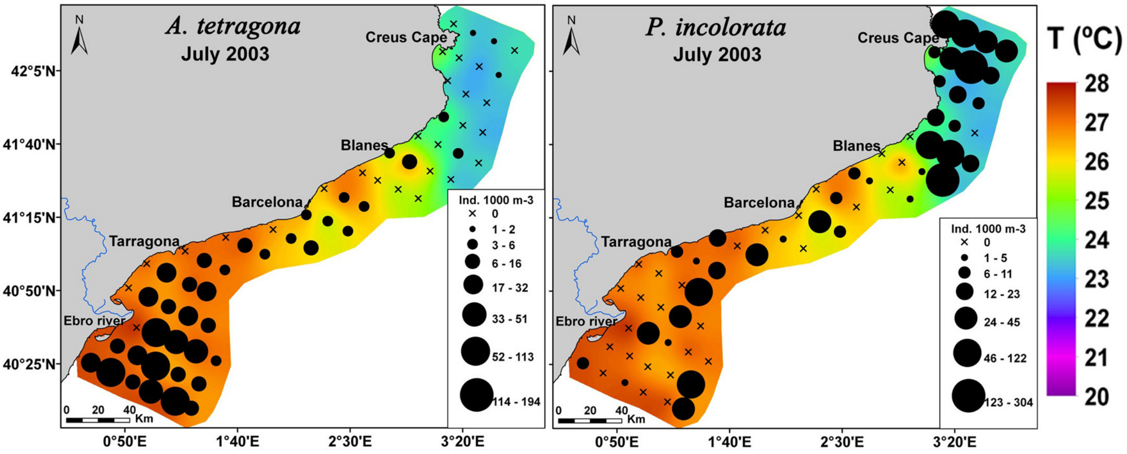

Fig. 3. Spatial distribution of *A. tetragona* and *P. incolorata* in relation to the latitudinal temperature gradient and the thermal front, in July 2003. Different size dots represent the abundance and colour gradient represents the surface temperature distribution.

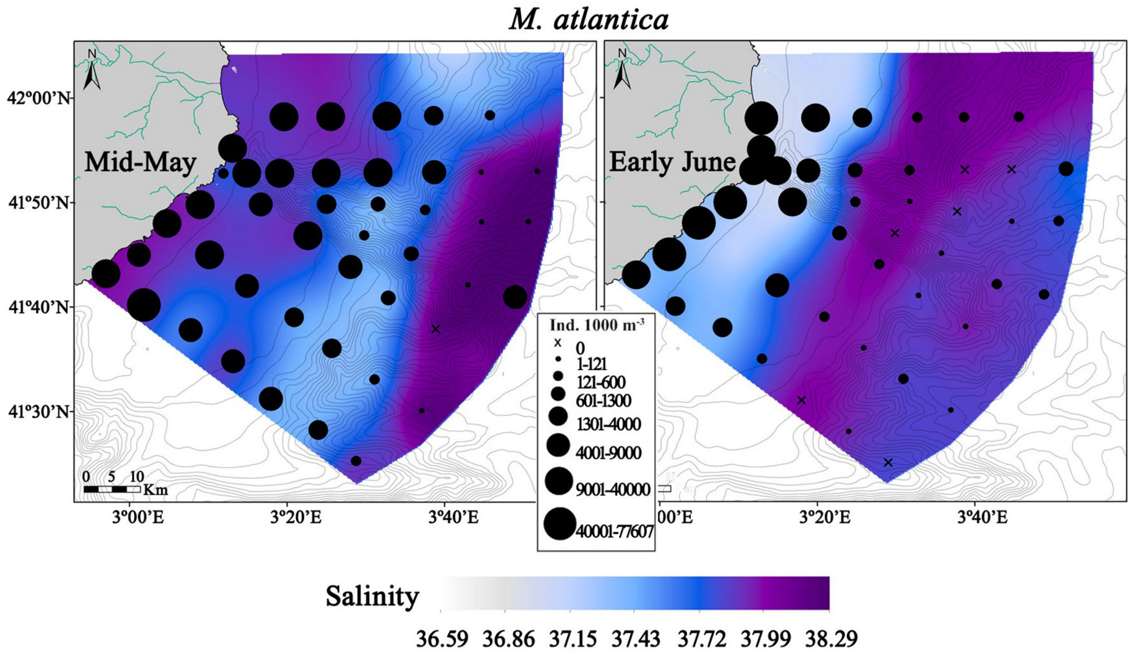

Fig. 4. Changing spatial distribution of *M. atlantica* in relation to the shelf-slope front in the northern Catalan coast in mid-May and early June 1992. Different size dots represent the abundance, colour gradient represents the surface salinity distribution and grey lines the bathymetry (every 100 m).

B2. Interannual scale: 1 year.

High interannual variability between two consecutive years was observed in some species distribution such as *C. appendiculata* and *M. kochii* (Chapter 2). They were homogenously distributed along the area under standard summer conditions (July 2004) while under extreme warm summer conditions (July 2003), their distributions were displaced northwards. They were absent or very low abundant in the southern shelf area while high abundances were detected towards the north (Fig. 5; *C. appendiculata* as example).

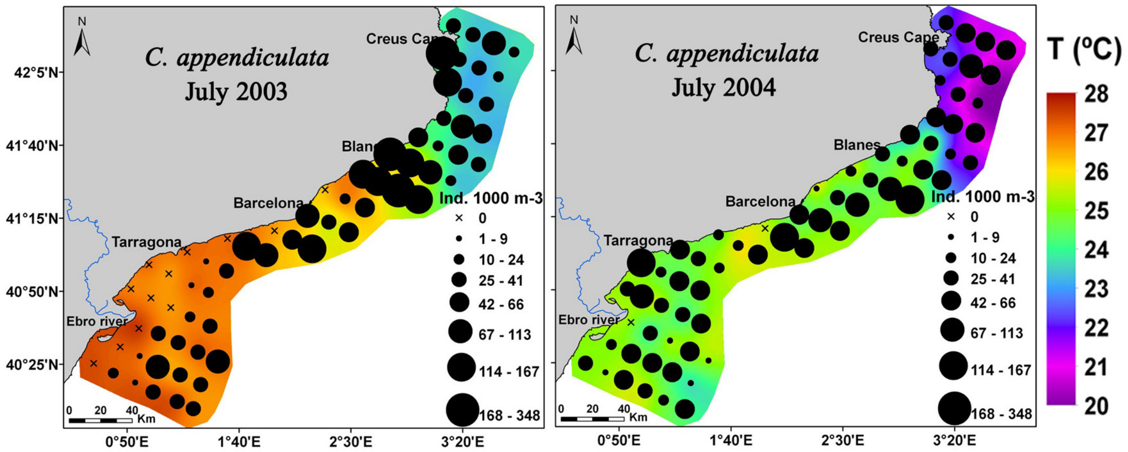

Fig. 5. Spatial distribution of *C. appendiculta* in relation to the latitudinal temperature gradient and the thermal front, in July 2003 and 2004. Different size dots represents the abundance and colour gradient represents the surface temperature distribution.

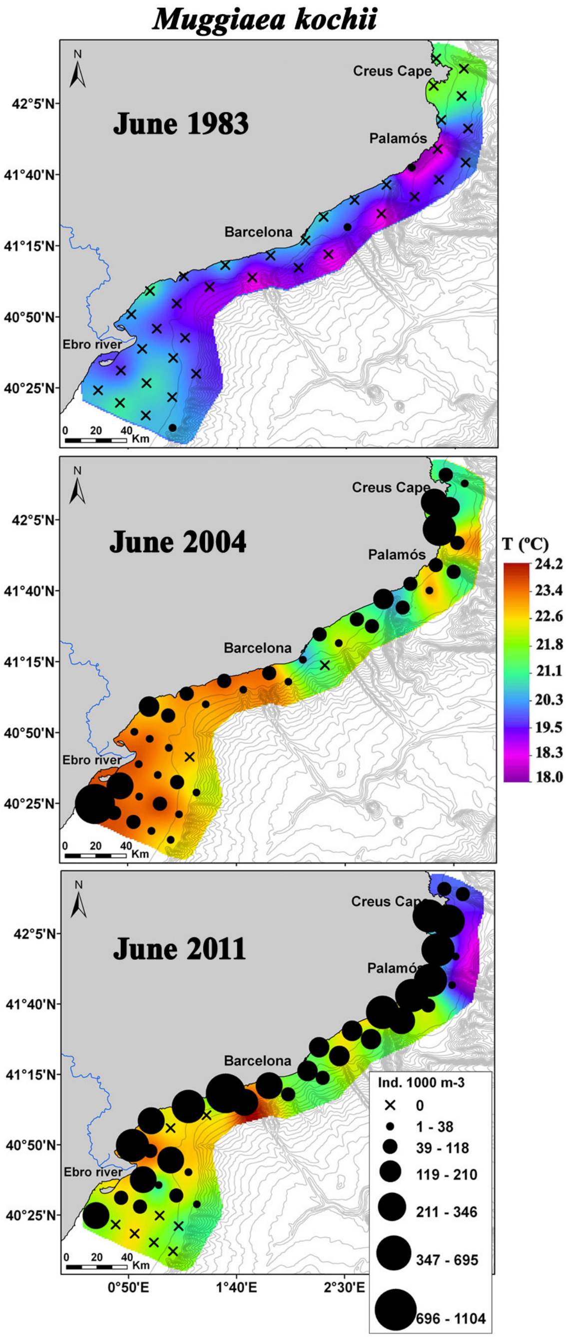

Fig. 6. Changes in the spatial distribution of *M. kochii* along the Catalan coast in June 1983, 2004 and 2011. Different size dots represent the abundance, colour gradient represents the surface temperature distribution and grey lines the bathymetry (every 100 m).

B3. Interdecadal scale: 3 decades

Interdecadal spatial variability was also observed in species like *M. kochii* (Chapter 3). This species was very scarce and localized in a few stations in June 1983, widely distributed all along the coast in June 2004, and highly abundant all along the area in June 2011. As commented previously, increasing temperatures in the last decades is probably favouring the abundance of this warm-temperate species occupying a wider area in last years compared to the colder 1980s (Fig. 6).

All these results and examples demonstrated the high degree of bio-physical coupling between planktonic cnidarians and mesoscale hydrographic structures and environmental gradients. In addition, it is shown the high spatial variability in very short distances (two adjacent stations) and in short time intervals (10 days). Therefore, in order to study long-term abundance trends and change rates of planktonic cnidarians in highly heterogeneous areas, large areas should be covered. Our studies contribute to confirm the relevance of the mesoscale scale approach for more robust comparisons on long-term studies in gelatinous zooplankton.

Temperature as important factor driving interannual and long-term changes

Water temperature has been described as one of the most important factors determining abundance and distribution of gelatinous zooplankton, at seasonal and long-term scales (Buecher and Gibbons, 2000; Purcell *et al.*, 2007; Boero *et al.*, 2016). The results obtained in this thesis agree with this fact and show the importance of temperature as a key factor driving interannual (Chapter 2) and long-term (Chapter 3) changes in the planktonic cnidarian community in the Catalan coast. During the extreme warm event of July 2003 (Chapter 2), temperatures were close to those foreseen in the future by the climatic trends for the Western Mediterranean (Vargas-Yáñez *et al.*, 2010; Maynou *et al.*, 2014). Exceptionally high temperatures negatively affected the community and low abundance of planktonic cnidarians was found compared to the standard summer conditions of 2004. On the other hand, at interdecadal scale (Chapter 3) the total summer abundance of cnidarians increased over time in relation to increasing seawater temperature. The difference between these two situations lay on the temporal scale of the environmental process in the frame of our studies. In the interanual comparison, the summer heat conditions of 2003 constituted an extreme event (Schär *et al.*, 2004) that involved strong and sudden temperature changes, while the interdecadal study considers a long-term temperature increasing trend. Sudden changes in temperature can lead to dramatic consequences for the survival of certain species (Garrabou *et al.*, 2009; Sabatés *et al.*, 2013) however, long-term temperature changes may allow the adaptation of the species or their spatial relocation. The lower abundance found during the extreme warm summer conditions of July 2003 may be caused by several reasons: 1) a direct negative effect of high temperatures on the organisms survival; 2) earlier sexual and asexual reproduction of the species, thus advancing the timing of their seasonal abundance peak; and 3) the reduction of food availability due to the general decrease of zooplankton during this extreme event (Maynou *et al.*, 2014; Atienza *et al.*, 2016). However, the increasing abundances observed at the interdecadal scale comparison may be due to: 1) major abundances of warm-water species; 2) reduction of predators and zooplanktivorous competitors such as fish (Purcell and Arai, 2001; Lleonart and Bas, 2012) and 3) food availability maintenance over time (Fernández De Puelles and Molinero, 2008; García-Comas *et al.*, 2011). Therefore, the effect of extreme warm conditions on cnidarian planktonic communities should be interpreted with caution. Taking the risk of forecasting, it could represent an extreme future situation of a long-term trend, and the effects of extreme warm conditions have a drastic impact on planktonic communities that could change the current general trends in the future.

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CONCLUSIONS

GENERAL CONCLUSIONS

The main conclusions derived from the studies encompassing the present PhD thesis are the following:

Chapter 1:

1. Short-term spatial variability in the distribution of planktonic cnidarians was closely related to the spatio-temporal variability in the location of a shelf-slope density front.
2. The front acted as a barrier limiting offshore displacement of the studied species.
3. The main environmental factors explaining the distribution of the species were bathymetry and salinity as indicators of the signature and position of the shelf-slope front.

Chapter 2:

4. Extreme warm summer conditions affected the abundance, composition and distribution of the planktonic cnidarian community.
5. Under the extreme warm summer conditions the total cnidaria abundance was lower than in the standard summer conditions, some species characteristic of warm waters appeared, and the spatial distribution of several species showed a northward displacement.
6. Under the extreme warm summer conditions the structure of the community changed from a coastal-offshore to a north-south ordination, where the temperature gradient, instead of bathymetry, played the main role.
7. The reduction of gelatinous zooplankton under extreme warm summer conditions would not be comparable to those caused by the long-term warming trend and could be explained by an earlier development of annual abundance peaks and low food availability.

Chapter 3:

8. Taking into account a mesoscale spatial coverage, long-term changes in the abundance, composition and distribution patterns of the planktonic cnidarian community have been detected in relation to temperature increase.
9. Total cnidaria abundance showed a significant increase over time, warmer conditions favoured warm-water species abundance and the spatial distribution of the community changed from a coastal-offshore pattern to a north-south one.
10. The study and monitoring of mesoscale spatial areas is essential to understand long-term changes in gelatinous zooplankton abundance and spatial distribution in the current climate change scenario.

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