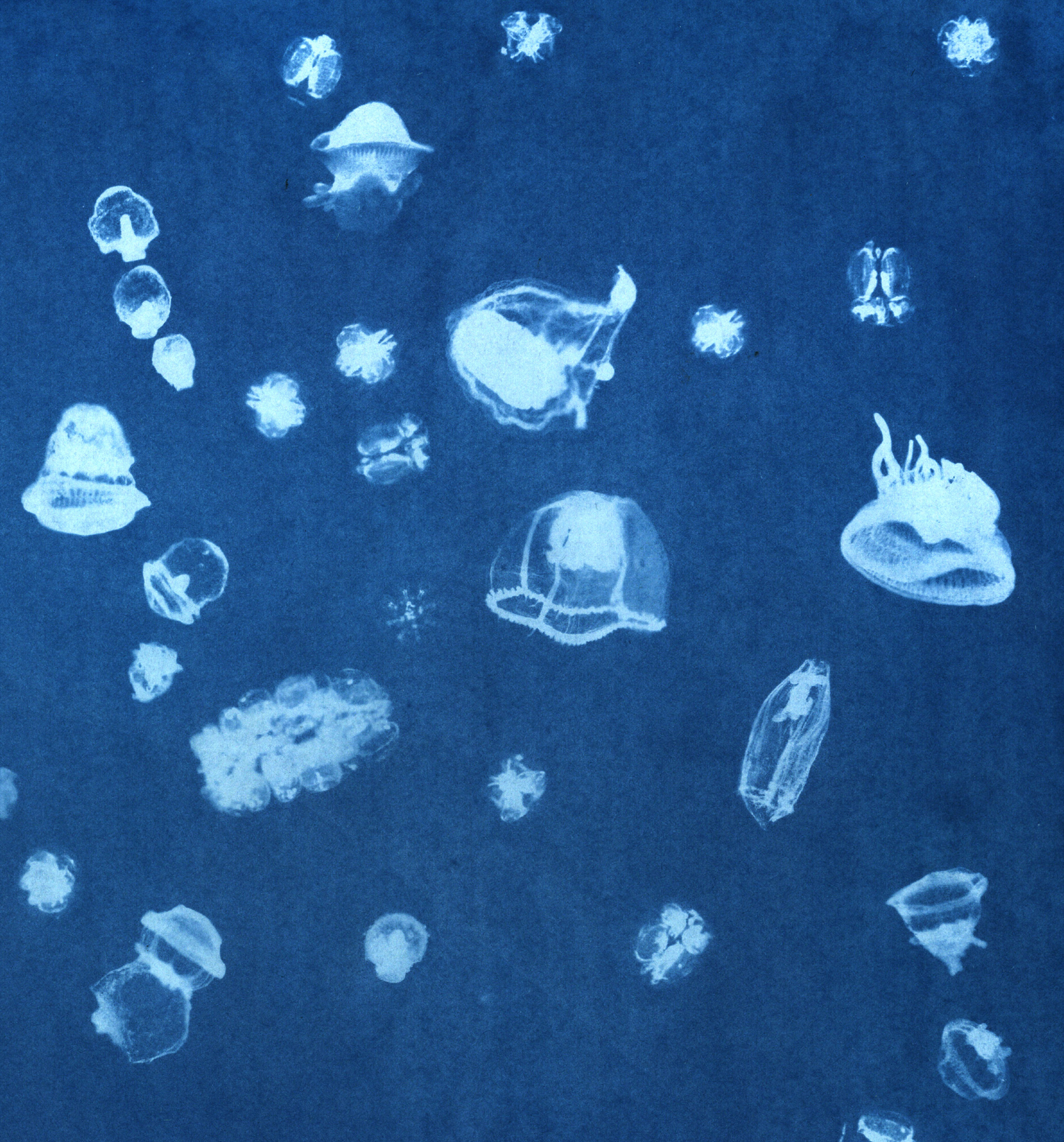
New contributions to the ecology of gelatinous zooplankton in the Western Mediterranean: abundance, distribution and diversity

Marina Pastor Prieto



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Marina Pastor Prieto | 2022

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Ph.D. thesis
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New contributions to the ecology of gelatinous zooplankton in the Western Mediterranean: abundance, distribution and diversity

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Memòria presentada per Marina Pastor Prieto per optar
al Grau de Doctora per la Universitat de Barcelona

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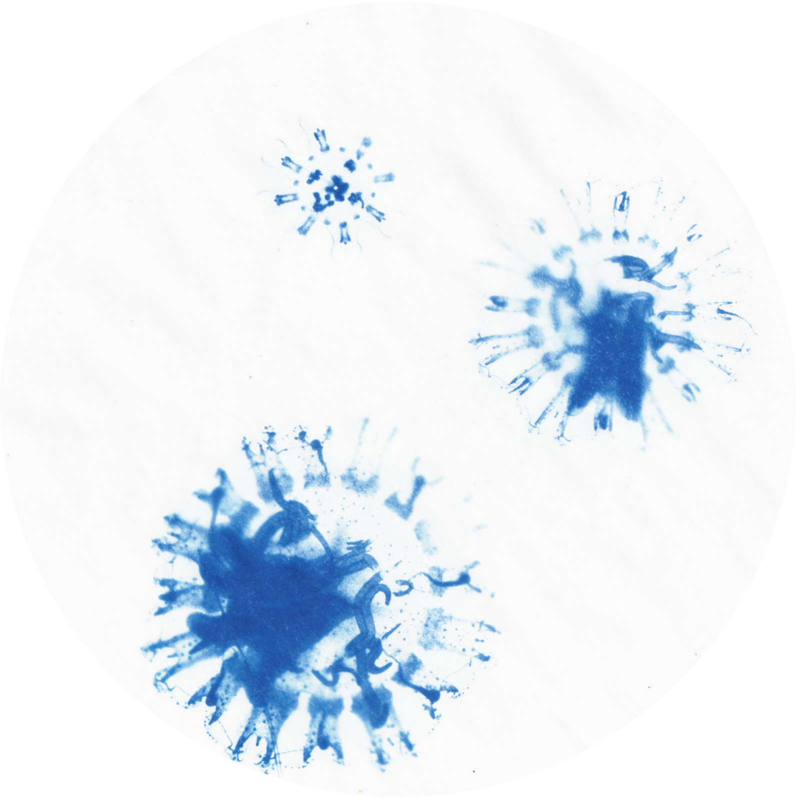

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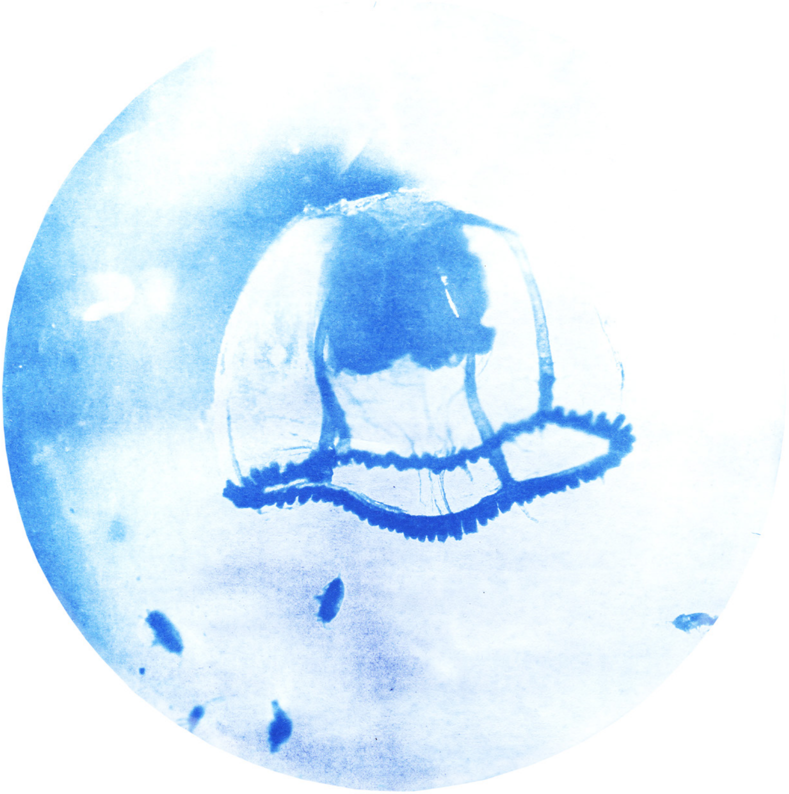


Abstract

Gelatinous zooplankton has been studied in the Western Mediterranean for a long time, however, its spatial structure has been mainly addressed in coastal areas, during spring and summer periods. Hence, information regarding its large-scale distribution in the open sea, the role of hydrodynamic factors on the distribution of poorly known taxa and the characterization of gelatinous communities in the winter season remain unknown. In this context, the present Ph.D. thesis aims to improve the knowledge on the ecology of gelatinous zooplankton in the Western Mediterranean, focusing on the study of less known areas, species and seasonal periods. The first chapter addresses the spatial heterogeneity of *Pelagia noctiluca* ephyrae along a wide latitudinal gradient in the Western Mediterranean. The second chapter examines the oceanographic conditions and colony size shaping the mesoscale distribution of *Pyrosoma atlanticum* in the NW Mediterranean. Finally, the third chapter analyses the whole planktonic cnidarian community during winter in the NW Mediterranean.

Ephyrae of *P. noctiluca* showed a heterogeneous spatial distribution in open waters of the Western Mediterranean linked to different water masses and the resulting mesoscale hydrographic features. Their horizontal distribution showed a clear latitudinal gradient with high abundances in the south, associated with the recent Atlantic Water, and low abundances or even absence in the north, in coincidence with the old Atlantic Water transported by the Northern Current. These results suggested the occurrence of *P. noctiluca* population connectivity between the Atlantic and the Mediterranean. Ephyrae were present in the upper 50 m of the water column, where they performed short-extent diel vertical migrations. During the day, ephyrae presented a wide distribution well above and within the thermocline, far from the Deep Chlorophyll Maximum, while during the night they were concentrated near the surface, in coincidence with their potential prey.

The mesoscale and vertical distribution of *P. atlanticum*, a species scarcely studied so far in the Mediterranean, were shaped by oceanographic and biological features, as well as by the ontogenetic stage of the colonies. Large colonies (≥ 7 mm long) were found on the slope, all along the shelf-slope density front, which probably aggregates them and prevents their dispersion towards the open sea. Small (< 4 mm) and medium colonies (4–6.9 mm) extended their distribution over the shelf because of front instabilities, being practically absent in the cold, low salinity coastal waters. The fine-scale analysis of their vertical distribution allowed to detect the onset of a migratory behaviour when colonies were 4–6.9 mm long. At night, colonies of all sizes remained close to the surface, where chlorophyll-*a* levels were high, whereas during the day medium and large colonies migrated to deeper layers, with larger colonies reaching greater depths. This migratory behaviour might contribute to the transport of carbon to deeper layers of the water column.

The species assemblages and the spatial characterization of the whole cnidarian community (Siphonophorae, Hydromedusae and Scyphomedusae) were studied in winter 2017 and 2018. High species richness was found in 2017 in relation to an advancement of the spring conditions and the subsequent phytoplankton bloom, favouring a mixture of winter and spring species. The "typical" winter oceanographic conditions in 2018 might have allowed the development of the winter species populations resulting in a lower number of species but a higher abundance of cnidarians. The most abundant species were *Lensia subtilis*, *Muggiaea kochii*, *Chelophyes appendiculata*, *Abylopsis tetragona* (eudoxid stage), *Aglaura hemistoma* and *Velella velella* larvae. In both winters, the species assemblages presented a coastal-offshore ordination resulting from the combined effect of environmental variables, particularly bathymetry, and oceanographic features, such as water masses and the shelf-slope density front. This ordination was only disrupted over the submarine canyons where coastal and offshore cnidarian communities coexisted.

Overall, this Ph.D. thesis provides novel information on the ecology of gelatinous zooplankton in the Western Mediterranean, but at the same time points to other lines of research that still need to be investigated in order to obtain a global knowledge of these organisms in this temperate sea.

Resum

El zooplàncton gelatinós s'ha estudiat al Mediterrani Occidental durant molt de temps, no obstant, la seva estructura espacial s'ha abordat principalment en àrees costaneres i durant la primavera i l'estiu. Actualment, encara es desconeixen aspectes com la seva distribució a gran escala i a mar obert, el paper dels factors hidrodinàmics en la distribució de taxons poc estudiats i la caracterització de les comunitats gelatinoses durant l'hivern. En aquest context, aquesta tesi doctoral té com a objectiu incrementar el coneixement de l'ecologia del zooplàncton gelatinós al Mediterrani Occidental, a partir de l'estudi d'aquelles àrees, espècies i períodes de l'any menys coneguts. El primer capítol aborda l'heterogeneïtat espacial de les èfires de *Pelagia noctiluca* al llarg d'un ampli gradient latitudinal al Mediterrani Occidental. El segon capítol examina el paper de les condicions oceanogràfiques i la mida de la colònia en la distribució de mesoescala de *Pyrosoma atlanticum* al Mediterrani nord-occidental. Finalment, el tercer capítol analitza tota la comunitat de cnidaris planctònics durant l'hivern al Mediterrani nord-occidental.

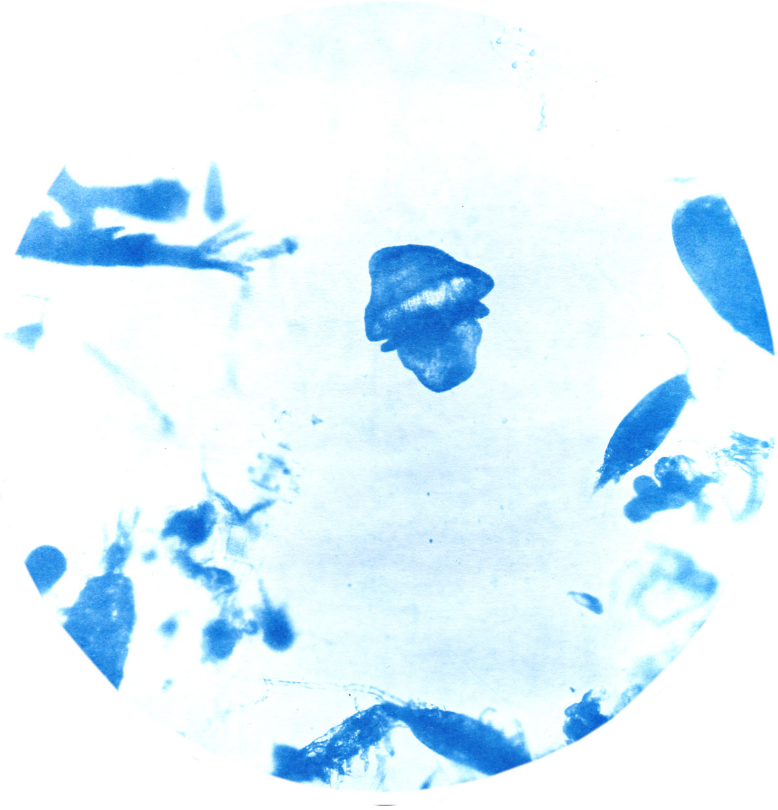
A les aigües obertes del Mediterrani Occidental les èfires de *P. noctiluca* van mostrar una distribució espacial heterogènia, lligada a diferents masses d'aigua i les característiques hidrogràfiques que se'n deriven. La seva distribució horitzontal va presentar un gradient latitudinal clar amb altes abundàncies al sud, associades a l'Aigua Atlàntica recent, i baixes abundàncies o fins i tot absència d'èfires al nord, coincidint amb l'Aigua Atlàntica antiga que és transportada pel Corrent del Nord. Els resultats suggereixen la connectivitat entre les poblacions de *P. noctiluca* de l'Atlàntic i el Mediterrani. Les èfires es van trobar als 50 primers metres de la columna d'aigua, on realitzaven migracions nictemerals. Durant el dia, les èfires van presentar una àmplia distribució per sobre de la termoclina o al voltant d'aquesta, lluny del Màxim Profund de Clorofil·la, en canvi, durant la nit es van concentrar a la superfície, coincidint amb les seves preses potencials.

Pyrosoma atlanticum, una espècie poc estudiada fins ara al Mediterrani, va presentar una distribució vertical i de mesoescala determinada per les estructures oceanogràfiques i biològiques, així com per l'estadi ontogenètic de les colònies. Les colònies grans (≥ 7 mm de llarg) estaven presents sobre el talús, al llarg del front de densitat plataforma-talús, que agregaria les colònies evitant la seva dispersió cap a

mar obert. Les colònies petites (< 4 mm) i mitjanes (4–6.9 mm) van presentar una distribució més extensa sobre la plataforma, degut a les inestabilitats del front, però van ser pràcticament absents a les aigües costaneres, fredes i poc salines. L'anàlisi detallat de la distribució vertical va permetre detectar l'inici del comportament migratori en colònies de 4-6.9 mm de llarg. A la nit les colònies de totes les mides es trobaven a prop de la superfície, on els nivells de clorofil·la-*a* eren més elevats, mentre que durant el dia les colònies mitjanes i grans migraven cap a aigües més profundes, arribant a majors profunditats a mesura que augmentava la mida de la colònia. Aquest comportament migratori contribuiria al transport de carboni cap a aigües profundes.

La caracterització espacial i les associacions d'espècies de tota la comunitat de cnidaris (Siphonophorae, Hydromedusae i Scyphomedusae) es va estudiar durant els hiverns de 2017 i 2018. Es va observar una elevada riquesa especifica al 2017 relacionada amb l'avançament de les condicions de primavera i el posterior *bloom* de fitoplàncton, que afavoriria la presència conjunta d'espècies d'hivern i de primavera. Les condicions oceanogràfiques del 2018, "típiques" d'hivern, haurien permès el desenvolupament de les poblacions d'espècies d'hivern, donant lloc a un menor nombre d'espècies, però a una major abundància de cnidaris. Les espècies més abundants van ser *Lensia subtilis*, *Muggiaea kochii*, *Chelophyes appendiculata*, *Abylopsis tetragona* (estadi eudòxia), *Aglaura hemistoma* i *Velella velella* (estadi larvari). En ambdós hiverns, les associacions d'espècies van presentar una ordenació costa-mar obert, resultat de l'efecte de les variables ambientals, particularment la batimetria, i les estructures oceanogràfiques, com masses d'aigua i el front de densitat plataforma-talús. Aquesta ordenació es va alterar sobre els canyons submarins, on coexistien les comunitats de cnidaris costaners i de mar obert.

Aquesta tesi doctoral proporciona nova informació sobre l'ecologia del zooplàncton gelatinós al Mediterrani Occidental i, al mateix temps, apunta altres línies de recerca que encara cal investigar per tal d'obtenir un coneixement global d'aquests organismes en aquest mar temperat.



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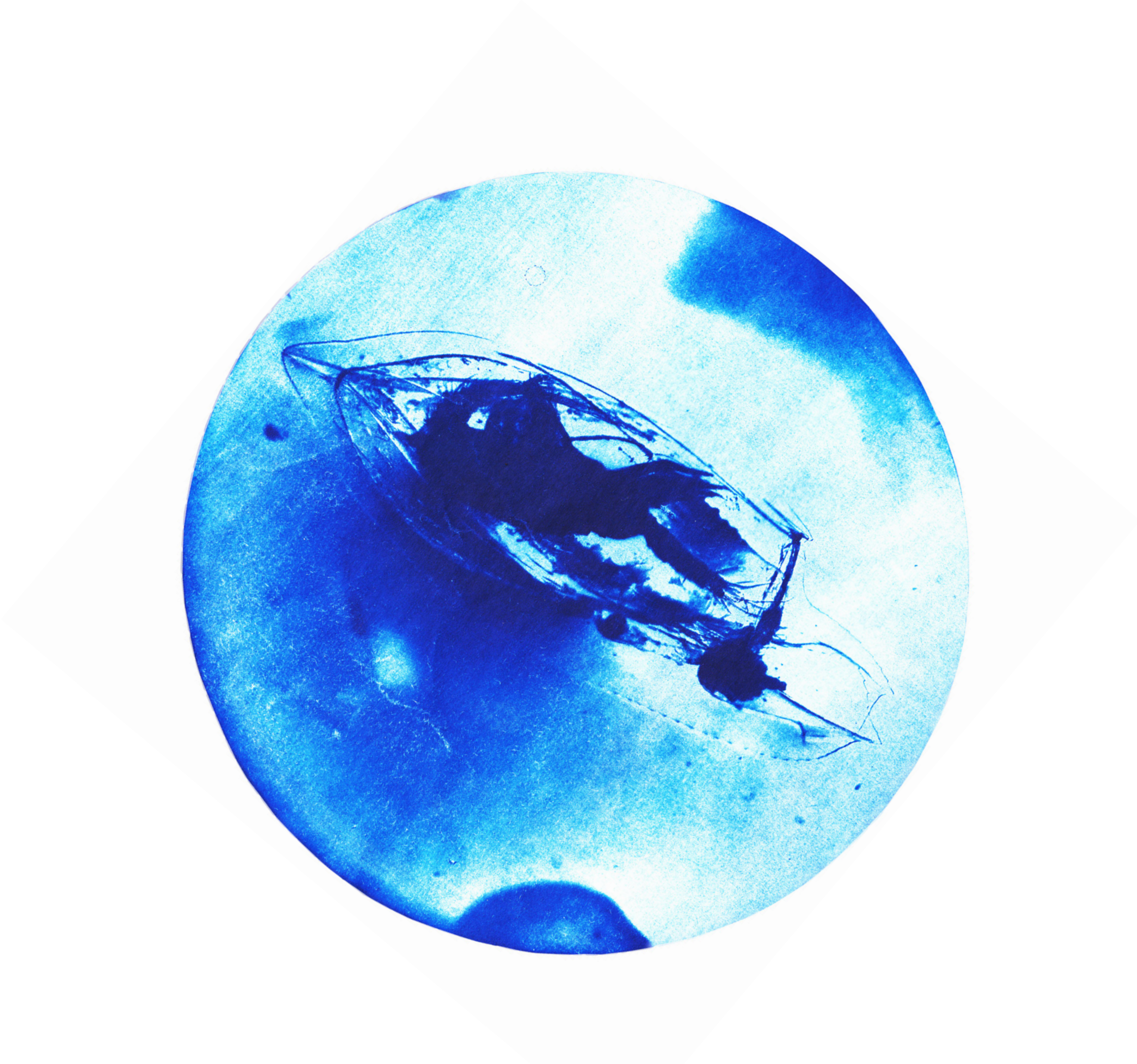


General introduction

Gelatinous zooplankton

The gelatinous zooplankton comprises distinct groups of marine pelagic invertebrates without taxonomic association, including ctenophores, cnidarians (siphonophorans, hydromedusans, scyphomedusans), planktonic tunicates (salps, doliolids, pyrosomes, appendicularians), chaetognaths, planktonic molluscs (heteropods, pteropods, a few nudibranchs), and some taxa within echinoderms, annelids and nemerteans (Fig. 1) (Pugh, 1989; Miller and Pawson, 1990; Haddock, 2004; Lucas and Dawson, 2014). These organisms, or their planktonic phase, live in the water column, drifting or with limited swimming capacity unable to cope with the currents (Richardson et al., 2009). Despite being a polyphyletic group their distinct evolutionary histories have led them to share some characteristics such as fragility; transparency that helps to avoid predation; high water content (>95%) conferring them neutral buoyancy; low-carbon growth strategies and being weak swimmers at the mercy of currents (Hamner et al., 1975; Pugh, 1989; Arai, 1997; Bone, 2005). Gelatinous zooplankton presents a widespread distribution in all oceans and constitutes a large component of the zooplankton biomass (Pugh, 1989; Siokou-Frangou et al., 2010; Lucas and Dawson, 2014), being considered as key member of ocean ecosystems (Hamner et al., 1975; Purcell et al., 2007; Condon et al., 2012).

Gelatinous zooplankton exhibits a wide variety of trophic strategies covering different trophic levels, from herbivory to secondary carnivory (Pugh, 1989). These organisms play an important role in the structure and dynamics of planktonic food webs, that can decimate their prey populations and cause cascading trophic effects when they are extremely abundant (Alldredge, 1984; Verity and Smetacek, 1996). Filter feeders, such as pyrosomes and salps, present high clearance rates over small phytoplankton particles that can result in a high energy transfer to deep waters due to their large production of faecal pellets (Drits et al., 1992; Madin and Deibel, 1998; Sutherland et al., 2010; Henschke et al., 2019). On the other hand, gelatinous zooplankton comprises nonvisual generalist predators, such as ctenophores and siphonophores, and also visual predators as heteropods (Mills, 1995; Lischka and Ossenbrügger, 2017). These predatory species can affect zooplankton populations, including other gelatinous organisms as well as ichthyoplankton, through predation and food competition, since they have high consumption rates when food abundance is high (Alldredge, 1984; Purcell, 1997; Tilves et al., 2016; Brodeur et al., 2021). Gelatinous zooplankton species have historically been considered as trophic "dead-end" due to their high water and low carbon content (up to 2.9%) that together with the inability to detect them in gut contents analysis, as they are digested very rapidly, has raised the assumption that they are a poor food option (Arai, 2005; Lucas et al., 2011). However, recent studies and the use of other techniques (e.g. cnidarian-specific mtDNA primers, predator-borne videos) have shown that they are consumed by a substantial number of marine predators, such as turtles, fish, squids, seabirds and sea lions (Childerhouse et al., 2001; Lamb et al., 2017; Thiebot et al., 2017; Brodeur et al., 2021). In addition, after a bloom situation a large amount of gelatinous biomass can reach the seafloor, providing nutrients to benthic consumers (Ates, 2017; Archer et al., 2018).

Some cnidarian and pelagic tunicates have the ability to occur in large numbers (i.e. bloom) and, therefore, have the potential to cause large direct and indirect impacts on marine food webs due to their role as filter feeders, predators and competitors (Brotz et al., 2012). These blooms are mainly known for their negative effects on human activities, such as fishing by clogging of nets, tourism due to stinging swimmers, desalination and power production plants due to clogged water intakes, and aquaculture due to fish kills (Purcell et al., 2007; Bosch-Belmar et al., 2017). These negative impacts have attracted public attention and resulted in an increased study of bloom-forming species to understand the ecological processes and environmental factors that lead to bloom formation, while non-bloom-forming species (e.g. molluscs, annelids) have remained less studied (Condon et al., 2012).

Their capacity to form blooms is closely related to having sexual and asexual reproduction, short generation times and high fecundity (Alldredge, 1984; Purcell et al., 2007). Gelatinous zooplankton has complex life cycles, which vary from taxon to taxon. Cnidarians exhibit a wide variety of reproductive strategies that can be simplified into a meroplanktonic life cycle, with an asexual benthic phase (polyp) and a sexual planktonic phase (medusa), or a holoplanktonic life cycle with only a planktonic phase (Bouillon et al., 2004; Boero et al., 2008). By contrast, ctenophores and tunicates lack a benthic stage in the life cycle (i.e. they are holoplanktonic) (Godeaux et al., 1998; Purcell et al., 2007). Most ctenophores are hermaphroditic and have direct development and great fecundity (Purcell, 2005; Purcell et al., 2007). Planktonic tunicates, such as salps and

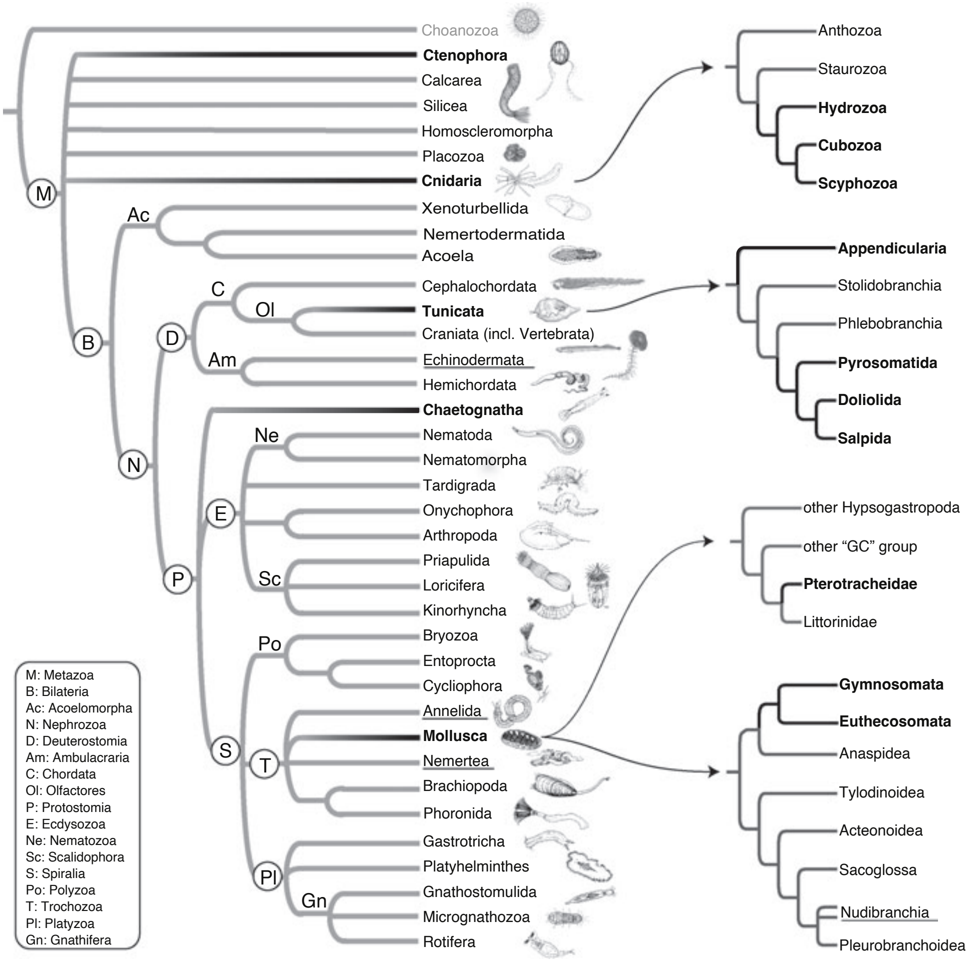


Fig. 1: Phylogeny of metazoan indicating the principal gelatinous phyla (black branches) and also other phyla in which there are occasional gelatinous zooplanktonic taxa (underlined). Modified from Lucas and Dawson (2014).

pyrosomes, have high fecundity and are viviparous, which reduces the predation on the new generation (Alldredge and Madin, 1982; Godeaux et al., 1998). All these characteristics allow populations to respond quickly to environmental variability and increase exponentially under suitable environmental conditions, resulting in the sudden appearance of these organisms (Alldredge and Madin, 1982; Purcell et al., 2007; Lucas and Dawson, 2014).

Apart from the biomass fluctuations linked to the life history of these organisms that result in high temporal variability in their abundance, their spatial distribution and abundance are also strongly influenced by hydrodynamic structures such as fronts, eddies and currents, that may confine or transport gelatinous plankton, contributing to shape their mesoscale distribution (Greer et al., 2015; Guerrero et al., 2016). In addition, fronts are areas of high primary production and intense trophic activity, offering favourable feeding conditions for the survival, growth and reproduction of gelatinous organisms, enhancing their biomass in those areas (Estrada and Margalef, 1988; Graham et al., 2001; Luo et al., 2014). On the other hand, these organisms are iono- and osmo-conformers, adjusting slowly to small salinity gradients and thus, physical discontinuities such as thermocline, pycnocline or halocline can act as barriers, where they tend to aggregate (Mills, 1984; Graham et al., 2001; McManus et al., 2003).

Gelatinous organisms are often underestimated because their fragile bodies are frequently destroyed or broken by sampling nets, and when sampled, some taxonomically important structures, or even the whole body (e.g. ctenophores), may dissolve in the preservation liquid, hindering their identification and enumeration (Pugh, 1989; Purcell, 2005; Siokou-Frangou et al., 2010). These limitations of conventional sampling methods mean that fundamental aspects of the life cycle and ecology of most gelatinous species remain unstudied (Purcell, 2005; Condon et al., 2012). Fortunately, *in situ* modern techniques, such as towed camera systems and manned submersibles, allow to study these organisms in their natural environment, observe their interactions with other organisms and even capture them alive. However, their high economic cost can be a limitation (Lindsay et al., 2001; Haddock, 2004; Luo et al., 2014). In any case, most of the attention has focused on large scyphomedusans and bloom-forming species (e.g., *Nemopilema nomurai*, *Mnemiopsis leidyi*, *Aurelia aurita*) (Mills, 2001; Uye, 2008; Shiganova et al., 2019), disregarding other non-bloom-forming species.

The Mediterranean Sea

The Mediterranean Sea is a relatively small, semi-enclosed sea, located in the temperate zone of the Northern Hemisphere in a relatively narrow band of latitudes (30º - 45º N). It presents two basins (western and eastern) and is connected to the Atlantic Ocean through the Strait of Gibraltar, to the Black Sea by the Dardanelles and Bosphorous straits, and to the Red Sea *via* the Suez Canal. Similarly to the global ocean, the Mediterranean displays a thermohaline circulation driven by the inflow of Atlantic Water through the Strait of Gibraltar and by the deep-water formation that occurs in both sub-basins (Millot, 1999). Because of the presence of these major oceanic processes, though at a smaller scale than those occurring in the world ocean, the Mediterranean is often referred to as a 'miniature ocean'.

The heterogeneity of habitats in the Mediterranean and the succession of colonization events have resulted in a remarkable species diversity, exhibiting a singular mixture of temperate and subtropical species with a high level of endemism (Sarà, 1985). Despite its small area (0.82% of the world's ocean surface), the Mediterranean Sea hosts around 4-18% of all known marine species (Bianchi and Morri, 2000). These characteristics lead this sea to be considered a hotspot of biodiversity (Coll et al., 2010).

The dimensions and location of the Mediterranean Sea result in a marked seasonal cycle with alternating periods of stratification and mixing of the upper layer containing the photic zone, which confers strong seasonality to primary production (Estrada et al., 1985). In spring, the increase in sea surface temperature due to solar heating, allows the thermocline to start to develop, gaining depth during the summer, which restricts vertical water motion preventing surface nutrient renewal. Consequently, in summer almost all the surface nutrients become depleted and primary production is restricted to the Deep Chlorophyll Maximum, a thin layer at the deepest levels of the photic zone (Estrada et al., 1993). In late summer, night cooling, breezes and occasional wind storms result in convective processes and the formation of the surface mixed layer, which becomes thicker in autumn. Winter cooling leads to a breakdown of the thermocline and vertical mixing brings nutrients from the deep waters to the photic zone (Salat et al., 2010). This cycle is common in all mid-latitudes, but in the NW Mediterranean the stratification period is rather long and the winter convection may reach the deepest layers (Lacombe et al., 1981). Winter convection involves nutrient supply to the photic zone from deeper areas, allowing the increase of primary productivity (Saiz et al., 2014) and, by the late winter-early spring, when surface waters begin to stabilize, a phytoplankton bloom takes place, generally followed one month later by a zooplankton peak (Nival et al., 1975; Ribera d'Alcalà et al., 2004; D'Ortenzio and Ribera D'Alcalà, 2009; Bozzano et al., 2014). Nevertheless, high interannual variability can be found in the timing and extent of the mixed layer depth formation and in the seasonal primary production peaks (Marty and Chiavérini, 2002; Ribera d'Alcalà et al., 2004). The alternation of stratified and mixed periods confers a strong seasonality to the primary production, that can be transferred to upper trophic levels (Estrada et al., 1985; Saiz et al., 2014). Overall, primary production values reveal an increasing west-east oligotrophy gradient across the Mediterranean (Siokou-Frangou et al., 2010). Primary productivity is also enhanced by other mechanisms such as riverine run-off and the interaction of topographic features (e.g. submarine canyons, relatively shallow seamounts) and currents creating upward vertical movements that can provide nutrients to the photic zone from dark layers (Font et al., 1990; Masó et al., 1990; Sabatés et al., 2007).

The Western Mediterranean basin

The Western Mediterranean basin is characterized by narrow continental shelves except in the Gulf of Lions and the Ebro shelf, near the main mouths of the Rhone and Ebro rivers, respectively. Along the continental slope several submarine canyons of variable width and depth are present, with the most conspicuous ones occurring from Toulon to Blanes (Salat, 1996).

The basin presents a thermohaline cyclonic circulation driven by the inflow of surface and less saline Atlantic Water through the Strait of Gibraltar (Fig. 2), its signature being modified as it travels eastward (Millot, 1999, 2005). The flow of Atlantic Water from the ocean follows the north African coast creating anticyclonic eddies, which can be trapped by the topography of the Alboran Sea or freely displaced around the Algerian basin and reach the Balearic Islands

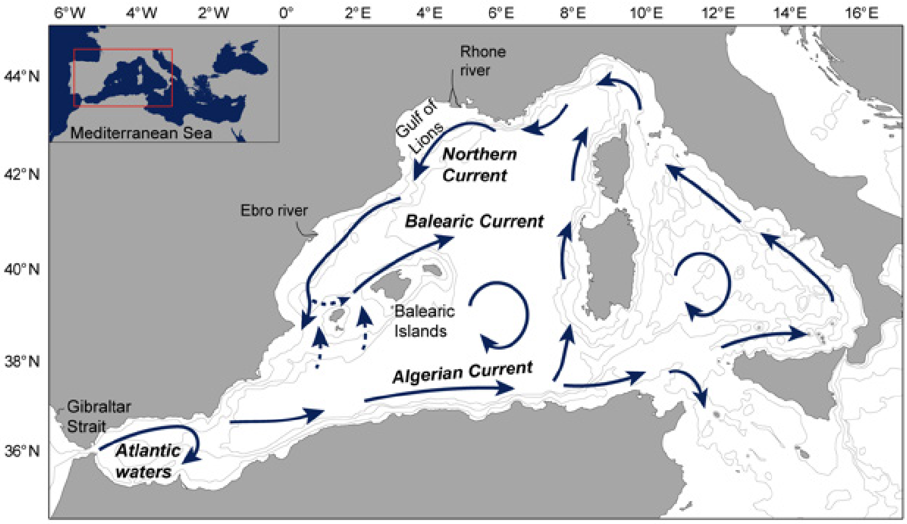


Fig. 2: Surface circulation of the Western Mediterranean. Redrawn from Heslop et al. (2012), Balbín et al. (2014) and Saiz et al. (2014).

(Millot, 1985, 2005). The Balearic Islands can be considered the transitional region between the two main Western Mediterranean sub-basins: the Liguro-Provençal and the Algerian basins. Part of the Atlantic Water flows through the Balearic channels and forms the Balearic Current, which follows the northern side of the Balearic Islands towards the west of Corsica (Hopkins, 1985; García-Ladona et al., 1994; Pinot et al., 2002; Heslop et al., 2012). Associated with the Balearic Current, a surface front (not deeper than 200 m) separates the recent Atlantic Water, brought by the current, from the resident waters of the centre of the northern basin, that typically are 1 unit more saline than the recent Atlantic Water (Font et al., 1988; Salat, 1995).

On the eastern side of the Liguro-Provençal basin, the recent Atlantic Water from the Balearic Current joins the old Atlantic Water from the Tyrrhenian sea, forming the Northern Current which flows to the south-west along the continental slope, adapted to the bathymetry and contouring the northwestern basin cyclonically (Allain, 1960; Béthoux et al., 1988; Font et al., 1988; Astraldi and Gasparini, 1992). Associated to the Northern Current, there is a marked shelf-slope density front (reaching up to 400 depth) that separates the coastal low-salinity waters from the open sea high-salinity waters (Font et al., 1988). This front is strengthened by the local riverine run-off (e.g. Rhone and Ebro rivers) on its coastal side and by the strong evaporation due to the northern winds on the open sea (Salat and Font, 1987). The Northern Current displays a significant mesoscale activity such as meanders and eddies that can develop and propagate along its path (Millot, 1990; Flexas et al., 2002). This current may also interact with the canyons, strongly modifying the local circulation and generating shelf-slope water exchanges (Flexas et al., 2008).

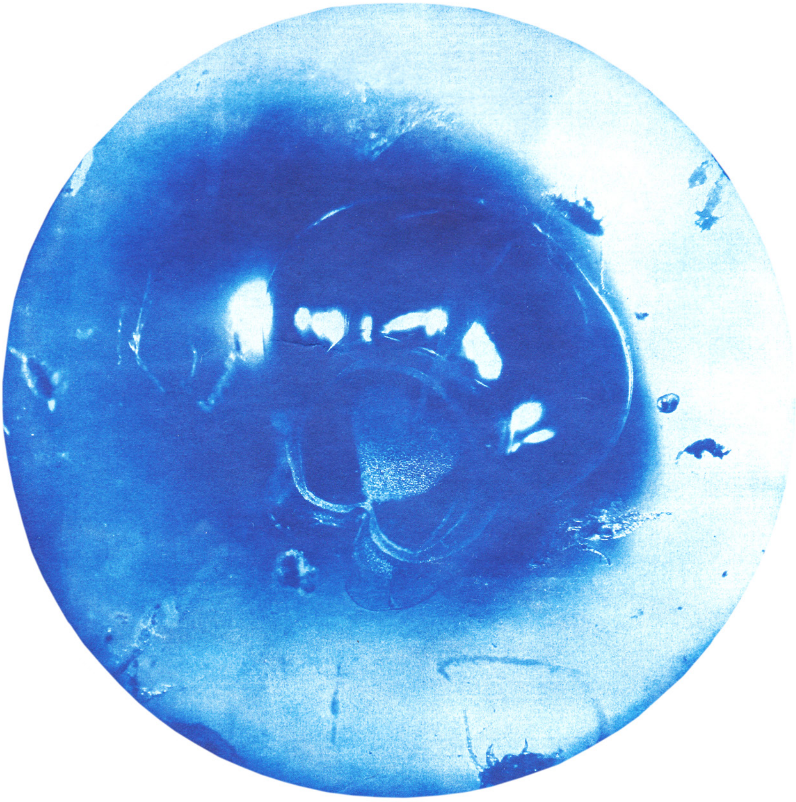
Gelatinous zooplankton in the Western Mediterranean: state of the art

In the Western Mediterranean, long zooplankton and hydrographic time series have been conducted at several coastal stations (Villefranche, Balearic Islands, Gulf of Naples and Trieste) allowing to investigate the variability in abundance and phenology of some gelatinous taxa at broad taxonomic levels (e.g. chaetognats, thaliaceans, appendicularians, molluscs) (Fernández De Puelles et al., 2003; Berline et al., 2012; Mackas et al., 2012; Fullgrabe et al., 2020). The oscillations in the abundance of the different taxa throughout the year show peaks at different times, although the highest abundances occur in spring, after the late winter-early spring phytoplankton bloom (Gili et al., 1987b; Saiz et al., 2014; Fullgrabe et al., 2020). These long-term studies have also addressed the interannual variability of these gelatinous organisms in relation to climatic variability, pointing out the importance of the winter North Atlantic Oscillation, since it is correlated with the winter environmental conditions of the northwestern Mediterranean, driving the productivity of the pelagic ecosystem (Molinero et al., 2005; García-Comas et al., 2011; Fullgrabe et al., 2020).

Several studies have also investigated the vertical distribution and migration patterns of these gelatinous taxa (Andersen et al., 1992, 1998; Batistic et al., 2004; Granata et al., 2020). As a general pattern, most of them remain at the upper levels of the water column during the night and reach higher depths during the day. However, these studies have been performed repeatedly at the same stations and do not consider the horizontal spatial dimension. The mesoscale distribution of gelatinous zooplankton have been mainly studied in the NW Mediterranean through grids of sampling stations to incorporate the high spatial environmental heterogeneity of the region in the distribution of these organisms. These studies have been carried out mainly in spring and summer, when these organisms show the highest abundances (Gili et al., 1988; Duró and Saiz, 2000; Guerrero et al., 2018a; Ottmann et al., 2021). However, the information available for the winter period is very limited. Furthermore, while these studies have provided valuable information on the relationships between environment and the distribution of these organisms, new approaches covering larger areas would allow to obtain a broad vision of the main oceanographic structures taking place in the Western Mediterranean that may determine their mesoscale distribution. Considering that the distribution of gelatinous zooplankton is highly influenced by temperature and salinity gradients, hydrographic structures and food availability (Riandey et al., 2005; Graham et al., 2001; Guerrero et al., 2018b; Sabatés et al., 2018) which, in turn, show a marked seasonality in the Mediterranean, the study of the mesoscale distribution of gelatinous communities would contribute, to a great extent, to the global understanding of these organisms.

In addition to vertical and mesoscale distribution, several studies have addressed other aspects of the ecology of gelatinous zooplankton such as trophic relationships (Duró and Saiz, 2000; Tilves et al., 2016), life cycles (Carré and Carré, 1991; Kienberger et al., 2018) and population dynamics (Pascual et al., 2016). However, not all taxa have received the same attention, since most studies have focused on the most abundant species or those that exert negative impacts on socioeconomic activities of humans.

Despite gelatinous zooplankton has been studied in the Western Mediterranean for a long time, some relevant aspects of its ecology remained uncovered, such as large-scale spatial distribution, the role of hydrodynamic factors on the distribution of poorly known groups and the characterization of gelatinous communities in the winter season. *Pelagia noctiluca* is the most common jellyfish in the Mediterranean and its spatial distribution in relation to hydrodynamic structures have been mainly studied in the northwestern region (Morand et al., 1992; Canepa et al., 2014; Sabatés et al., 2018). However, the lack of knowledge on its distribution further south limits our understanding of the large-scale spreading patterns of this species in the Western Mediterranean. In contrast to adult jellyfish, the ephyrae stage can be efficiently collected with plankton nets, thus the study of its large-scale distribution can be a good proxy of the global abundance and distribution of the species. On the other hand, *Pyrosoma atlanticum*, that can have a role in energy transfer to deep waters (Henschke et al., 2019), is a poorly studied species in the Mediterranean. Some studies, mainly conducted in fixed stations or single transects during spring, have addressed its vertical distribution (Palma, 1985; Andersen and Sardou, 1994; Sardou et al., 1996), population dynamics and seasonality (Franqueville, 1971; Braconnot, 1974), with the mesoscale distribution of the species remaining unaddressed. Therefore, studies dealing with the role of hydrodynamic factors on its spatial distribution or performed in other seasons, such as winter, would provide valuable knowledge of this little studied species in the Mediterranean. Indeed, winter is the least studied season in the ecology of gelatinous zooplankton in this sea and its environmental conditions drive the productivity of the pelagic ecosystem (Saiz et al., 2014). The cnidarians, one of the most abundant taxa within gelatinous organisms, have their maximum peak in spring and beginning of summer, after the seasonal phytoplankton bloom in the Western Mediterranean (Gili et al., 1987a; Alan R. Longhurst, 2006; Licandro et al., 2012; Touzri et al., 2012). Thus, the study of cnidarian communities and their spatial distribution during winter conditions, with a homogeneous water column, high nutrient concentrations, and moderate phytoplankton levels (Latasa et al., 2022), is of special interest. Bearing this in mind, further knowledge of these aspects will help to enhance our understanding of the role of the gelatinous zooplankton in the Mediterranean planktonic ecosystem.



Objectives

The general objective of the present Ph.D. thesis is to improve the knowledge on the ecology of the gelatinous zooplankton in the Western Mediterranean Sea, focusing on the study of less known areas, species and seasonal periods. The overall objective of the thesis is divided into the following specific ones:

Objective 1

To identify how the mesoscale water dynamics shapes the spatial structure of *Pelagia noctiluca* ephyrae along the continental slope of the Western Mediterranean.

This specific objective is addressed in chapter one.

Objective 2

To explore the spatial structure of the poorly known species *Pyrosoma atlanticum* in the NW Mediterranean during winter oceanographic conditions.

- To analyse how the mesoscale water dynamics shape the horizontal distribution of *P. atlanticum* at different ontogenetic stages.

- To determine the diel and ontogenetic changes in vertical distributions of *P. atlanticum* in relation to the structure of the water column.

This specific objective is addressed in chapter two.

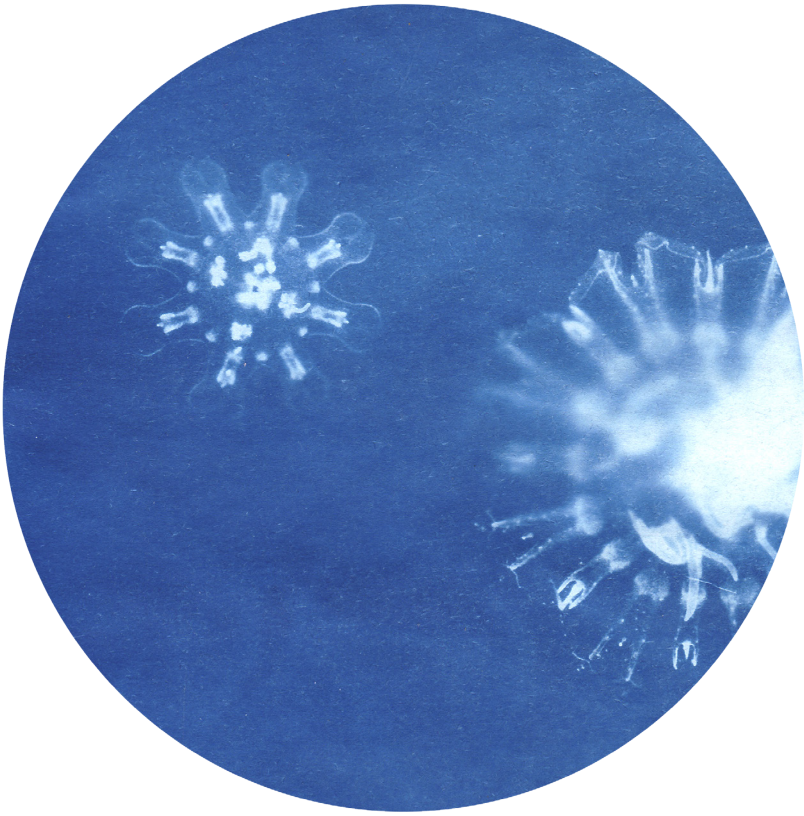
Objective 3

To address the spatial characterization and species assemblages of the whole planktonic cnidarian community (Siphonophorae, Hydromedusae and

Scyphomedusae) during two consecutive winters.

- To describe the species composition, abundance and diversity of the cnidarian community.
- To determine the spatial distribution of species assemblages.
- To explore the influence of environmental conditions on the spatial structure of cnidarian species.

This specific objective is addressed in chapter three.



Advisors' report

Dr. Josep-Maria Gili Sardà, Profesor de Investigación del CSIC at the Institut de Ciències del Mar (ICM-CSIC) and Dra. Ana Maria Sabatés Freijo, Investigadora Científica del CSIC at the Institut de Ciències del Mar, advisors of the Ph.D. thesis entitled "New contributions to the ecology of gelatinous zooplankton in the Western Mediterranean: abundance, distribution and diversity".

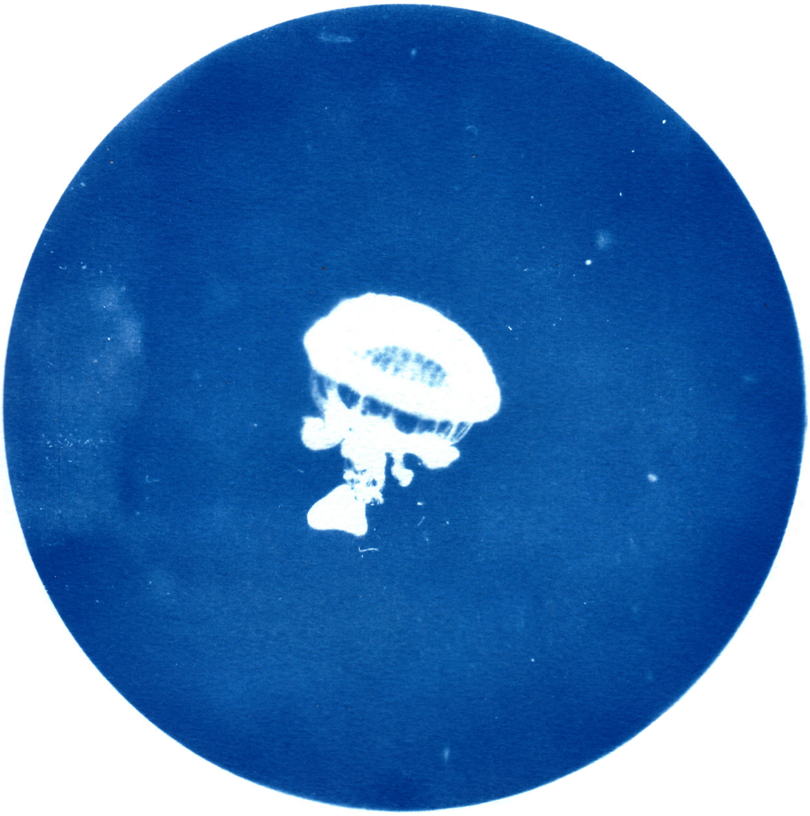
INFORM, that the research studies developed by Marina Pastor Prieto for her Ph.D. thesis have been organized in three chapters, which correspond to three scientific papers listed below: two of them are already published, and the last one will be submitted in the next few weeks;

and CERTIFY, that the work has been carried out by Marina Pastor Prieto, participating actively in all the tasks of the three chapters: conceiving and setting the objectives, conceiving and performing the analyses, participating actively in the field work, analyzing the samples and writing the manuscripts.

Finally, we certify that the co-authors of the publications listed below and that conform this doctoral thesis, will not use these manuscripts in another Ph.D. thesis.

Barcelona, 12th December 2022

Advisor Dr. Josep-Maria Gili Sardà ICM – CSIC	Advisor Dra. Ana Maria Sabatés Freijo ICM – CSIC



List and publication status of the chapters of this thesis

Chapter I

Pastor-Prieto M[1], Bahamon N[1], Sabatés A[1], Canepa A[2], Gili J-M[1], Carreton M[1], Company JB[1] (2021) Spatial heterogeneity of *Pelagia noctiluca* ephyrae linked to water masses in the Western Mediterranean. PLoS ONE, 16, e0249756. https://doi.org/10.1371/journal.pone.0249756. 5-year impact factor: 3.75; quartile: Q1; relative position: 28/135.

Chapter II

Pastor-Prieto M[1], Sabatés A[1], Raya V[1], Canepa A[2], Parraguez TI[1], Gili J-M [1] (2022) The role of oceanographic conditions and colony size in shaping the spatial structure of *Pyrosoma atlanticum* in the NW Mediterranean Sea. Journal of Plankton Research, 44, 984–999. https://doi.org/10.1093/plankt/fbac056. 5-year impact factor: 2.93; quartile: Q1; relative position: 43/113.

Chapter III

Pastor-Prieto M[1], Raya V[1], Sabatés A[1], Guerrero E[1], Mir-Arguimbau J[1], Gili J-M[1] (to be submitted). Assemblages of planktonic cnidarians in winter and their relationship to environmental conditions in the NW Mediterranean Sea. Marine Ecology Progress Series. 5-year impact factor: 3.084; quartile: Q1; relative position: 24/121.

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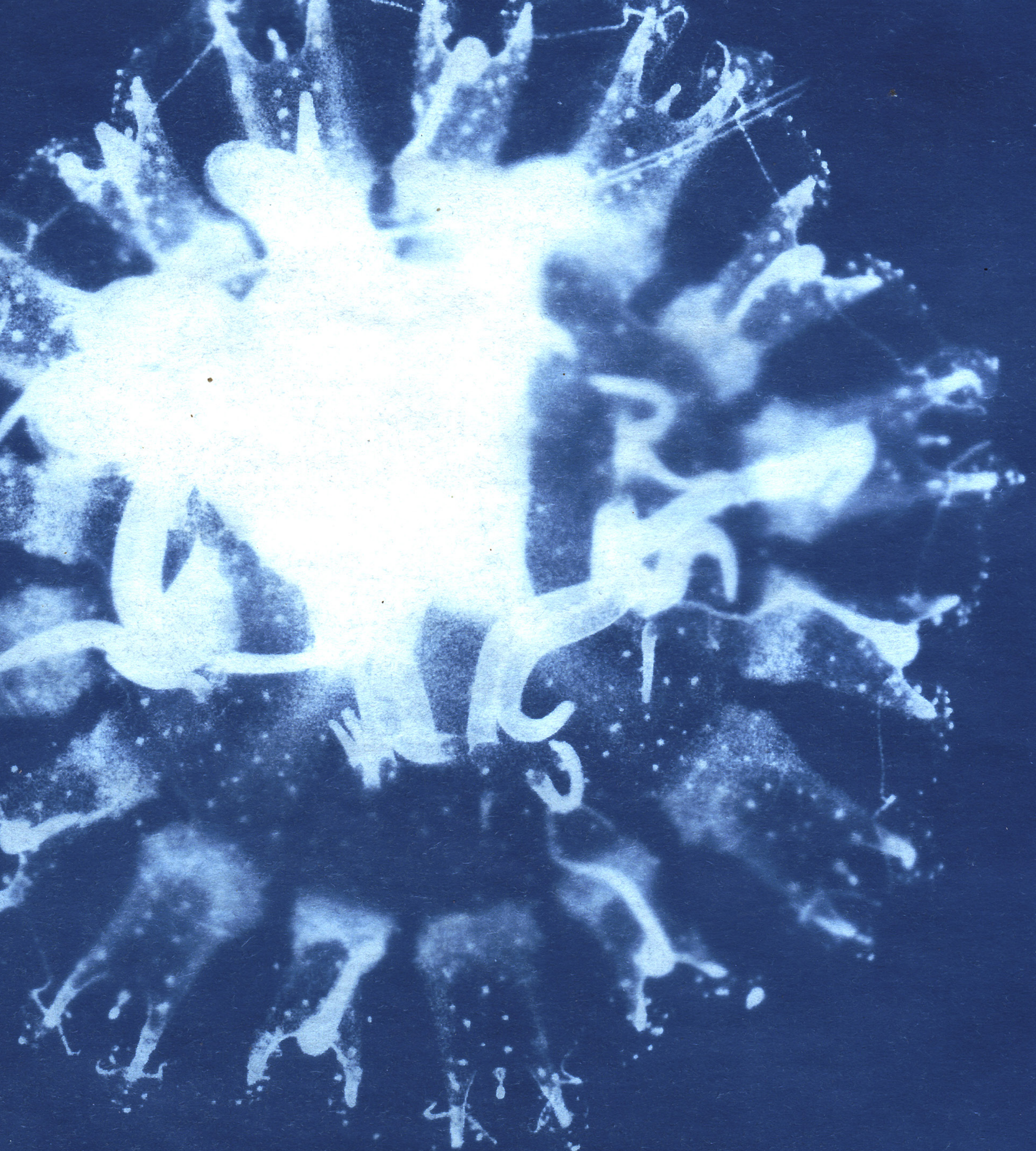

Chapter I

Spatial heterogeneity of *Pelagia noctiluca* ephyrae linked to water masses in the Western Mediterranean

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Antonio Canepa[2], Josep-Maria Gili[1], Marta Carreton[1],
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Abstract

Pelagia noctiluca is the most common jellyfish in the Western Mediterranean Sea, living in oceanic waters with a holoplanktonic lifecycle. Frequent outbreaks have been well documented in coastal areas, yet little is known about their offshore distribution. In this study we address the relationship between oceanographic structures and the distribution of *P. noctiluca* ephyrae along the central continental slope of the Western Mediterranean, covering a wide latitudinal gradient, during July-August 2016. The region is characterized by a rich and complex mesoscale surface circulation driven by the inflow of Atlantic Water into the Western Mediterranean through the Strait of Gibraltar. The results revealed a high variability in the ephyrae spatial paterns related to different water masses and the resulting mesoscale hydrographic features. Their horizontal distribution showed a clear latitudinal gradient with high abundances in the south, associated with recent Atlantic Water, and low abundances or absence in the north, in coincidence with the old Atlantic Water transported by the Northern Current. Ephyrae showed diel vertical migrations of short-extent in the first 50 m, with a wide distribution above the thermocline and the Deep Chlorophyll Maximum during daytime, being more concentrated towards the surface at night. The results suggest the population connectivity of *P. noctiluca* between the Atlantic and the Mediterranean. In that case, the abundance variability of the species in the Mediterranean could be modulated by its entrance associated with the inflow of Atlantic Water through the Strait of Gibraltar.

Introduction

Jellyfish are conspicuous components of pelagic communities that show increases in population size often resulting in mass occurrences, or blooms, worldwide (Purcell, 2012; Condon et al., 2013). While there is a lack of scientific consensus in identifying global trends in jellyfish blooms (Condon et al., 2012), their negative impacts on human activities in coastal waters are remarkably increasing in frequency and severity (Purcell et al., 2007; Brotz et al., 2012). These increases in jellyfish abundance have the potential to alter the balance of trophic pathways between smaller zooplankton and their predators in marine ecosystems (Mills, 1995). Jellyfish distribution and aggregation are determined by the combination of environmental conditions and life history events resulting in a rapid increase in population numbers (Graham et al., 2001). Hydrodynamic structures such as currents, fronts and eddies may act as mechanisms for their transport or confinement (Greer et al., 2015; Guerrero et al., 2016) thereby contributing to an increase in mesoscale spatial heterogeneity. These structures support high levels of biological activity e.g. (Pingree et al., 1977; Yamamoto and Nishizawa, 1986) controlling the interactions among organisms with limited horizontal mobility (Mackas et al., 1985) such as jellyfish. Differently, they have the ability to actively swim vertically through sharp clines (Mills and Vogt, 1984).

The Western Mediterranean Sea (WM) is characterized by a complex physical dynamics with distinctive traits, especially in regard to the thermohaline circulation. The surface circulation is mainly driven by the inflow of Atlantic Water (AW) through the Strait of Gibraltar, its signature being modified as it travels eastward (Millot, 1985). The input flow of AW in the WM follows the north African coast creating anticyclonic eddies (Millot, 1985, 2005) which can be trapped by the bottom topography of the Alboran Sea or freely displaced around the Algerian basin and reach the Balearic Islands. The Balearic Islands can be considered a transitional region between the two main WM sub-basins: the Liguro-Provençal and the Algerian basins. Part of the AW flows across the Balearic channels forming the Balearic Current (Pinot et al., 2002; Heslop et al., 2012) that follows the northern side of the Balearic Islands to the west coast of Corsica (Hopkins, 1985; García-Ladona et al., 1994). A surface front, which is not deeper than 200 m, associated with the Balearic Current, separates recent AW brought by the current from the resident waters of the centre of the northern part of the basin (Salat, 1995). Typically, the salinity of recent AW is nearly 1 unit lower than the older resident AW waters (Font et al., 1988). On the eastern side of the Liguro-Provençal basin, the recent AW flow from the Balearic basin joins the old AW from the Tyrrhenian Sea (Astraldi and Gasparini, 1992), forming the Northern Current which flows southwestwards along the continental slope, adapted to the bathymetry and contouring the northwestern basin cyclonically (Allain, 1960; Béthoux et al., 1988).

Pelagia noctiluca is the most common jellyfish in the Mediterranean Sea, living in oceanic waters (Mariottini et al., 2008; Canepa et al., 2014). It is a holoplanktonic species with a variable reproductive period depending on the region, and the presence of ephyrae has been reported throughout the year (Malej and Malej, 1992; Morand et al., 1992; Milisenda et al., 2018). In the WM, the highest abundance of *P. noctiluca* occurs during spring and summer (Morand et al., 1992; Gili and Pagès, 2005; Licandro et al., 2010) and their blooms appear to be increasing in frequency and duration (Daly Yahia et al., 2010; Bernard et al., 2011; Canepa et al., 2014). The studies on the spatial distribution of *P. noctiluca* in relation to hydrodynamic structures in open sea waters of the basin are scarce and restricted to some areas of the northwestern region. These studies have shown that the species is particularly abundant in the vicinity of the shelf-slope front associated with the Northern Current (Morand et al., 1992; Ferraris et al., 2012; Sabatés et al., 2018). The particular hydrodynamic conditions of that region enhance and maintain high levels of biological production (Ibanez and Boucher, 1987; Estrada and Margalef, 1988; Sabatés et al., 2004) providing ideal conditions for feeding, growth and reproduction of the zooplanktonic organisms. However, the lack of knowledge on the distribution of *P. noctiluca* in open waters further south limits our understanding of a large-scale picture of its spreading patterns in the WM.

Jellyfish are difficult to sample quantitatively (Pierce, 2009; Smith et al., 2016) and the mechanisms of jellyfish transport and aggregation cannot be understood without a large scale sampling of their abundances combined with synoptic environmental measurements. In contrast, ephyrae can be efficiently collected with plankton nets and its distribution can be a good proxy of the global abundance and distribution of the species (Sabatés et al., 2018). Considering this approach, the objective of the present study was to identify how the mesoscale water dynamics shapes the spatial structure of *P. noctiluca* ephyrae along the continental slope of the WM. To this aim, we performed an extensive plankton and hydrographic sampling, with a wide latitudinal and vertical coverage, that will result in a general view of the distribution of the species driven by hydrodynamic processes in open waters of the WM, and provide new insights on its potential populations increase.

Methods

Field sampling

The study was conducted on the central continental slope of the WM along a wide latitudinal gradient (37.4 °N - 42.3 °N) in a south north direction, between 22nd July and 28th August 2016 on board the R/V García del Cid (Fig. 1). A total of 170 hydrographic stations, with plankton sampling at 75 stations (29 at night and 46 during the day) were completed. At each hydrographic station, vertical profiles of basic hydrographic variables (salinity, temperature and fluorescence), from surface to 200 m depth, were obtained by means of conductivity-temperature-depth profilers (CTD) (SBE25 and SBE911), equipped with a fluorometer. At the plankton stations, hydrographic parameters were measured with a CTD (SBE3F) integrated in the plankton net. CTD data were inter-calibrated to make them readily comparable. Afterwards, data were bin averaged at 1 m depth intervals.

Zooplankton was sampled with a Multiple Opening/Closing Net Environmental Sensing System (MOCNESS net) of 1 m^2 opening mouth and a 300 µm mesh. Hauls were oblique from deep to shallow waters, at a vessel speed of 1.2 ± 0.4

knots. The depth strata examined were: 200 - 100, 100 - 50, 50 - 25, 25 - 0 m, and the volume of filtered water was recorded by a flowmeter attached to the mouth of the net. Immediately after collection, zooplankton samples were fixed in 5% formaldehyde buffered with sodium tetraborate.

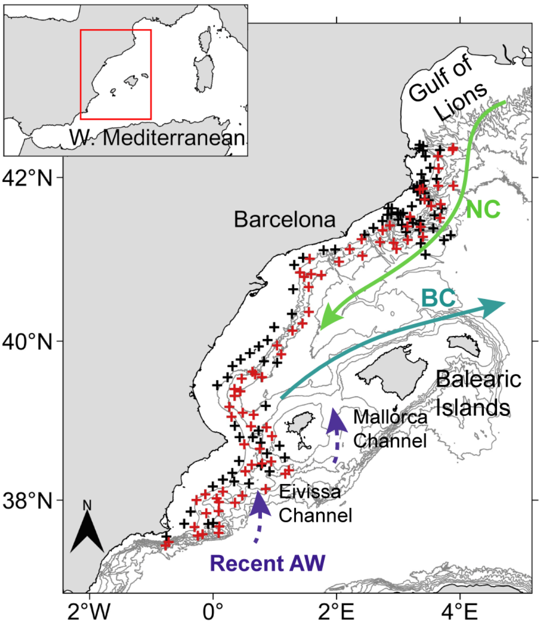


Fig. 1: Study area in the Western Mediterranean. Hydrographic (black and red crosses) and plankton (red crosses) stations during the survey. The schematic lines indicate the main currents, Northern Current (NC) and Balearic Current (BC), and recent AW inflow through the Eivissa and Mallorca Channels. Coastline is from Natural Earth (2021) and Instituto Hidrográfico de la Marina (2021), and isobaths (every 400 m depth) are from European Marine Observation and Data Network (EMODnet, 2018).

Data analyses and sample processing

2D maps showing the latitudinal variation of surface salinity and temperature data were produced by applying Data-Interpolating Variational Analysis (DIVA) gridding to 10 m depth CTD data, using the Ocean Data View (ODV) software (Schlitzer, 2020). DIVA gridding was also applied using ODV, for creating sections of the depth variation with latitude of the upper 100 m depth from environmental data collected at all the stations. In addition, daily salinity and temperature at 10 m depth reanalysis products from Copernicus Marine Environment Monitoring Service (CMEMS, Simoncelli et al., 2019) were used to estimate mean salinity and temperature values for the surrounding areas during the study period, and were represented with QGIS v3.4.11 (2019). Mean currents data for August 2016, at 10 m depth, from CMEMS were represented through QGIS v2.18.28 (2016).

In the laboratory, the zooplankton samples were examined using a stereomicroscope in order to identify and count the ephyrae of *P. noctiluca* (total body diameter: 0.55 – 3.55 mm, Fig. S1). The number of individuals within each depth strata was standardized to number per 100 m^3 of filtered water.

A preliminary exploration of the ephyrae vertical distribution, from surface to 200 m depth, was carried out for 12 of the 75 sampled stations, randomly selected and distributed along the sampling area. Considering these stations, 99.9 % of ephyrae were found between 0 - 50 m depth. Based on these results, only 0 - 25 m and 25 - 50 m depth levels were considered for the vertical distribution analysis. For the mesoscale horizontal distribution, the two depth levels were grouped together (0 - 50 m). The effect of light (day/night) and depth on the ephyrae vertical distribution was analysed through a Generalized Linear Mixed Model (GLMM) (see Equation S1 in supporting information). A GLMM was also fitted to assess the effects of independent (Pearson's cross-correlation coefficient < 0.5) oceanographic variables (mean surface, 5-10 m depth, salinity and temperature) from CTD data on the horizontal distribution of the ephyrae (see Equation S2 in supporting information). In order to avoid any spatial lack of independence among close sampling stations, the geographical position of each station was included as a random effect in both GLMMs. In addition, in both analyses the error family distribution used was a negative binomial, due to the patchy distribution of ephyrae (a normal condition in plankton ecology (Omori and Hammer, 1982)), and with a log-link to avoid predicting negative numbers of ephyrae, using the "glmer.nb" function from the "MASS" package (Venables and Ripley, 2002). To reduce the bias due to different filtered volumes by the nets (mean 471 m^3 ± 124 standard deviation) the (log-transformed) volume of filtered seawater was included as an offset inside GLMMs (Zuur et al., 2009). The GLMMs were carried out using the statistical programming language R v3.5.3 (R Core Team, 2020).

Results

Hydrographic conditions

The TS diagram of the upper 100 m showed the more recent AW, characterized by relatively low salinity, and the old and more saline AW transported by the Northern Current, that stayed longer time in the basin (Fig. 2).

The spatial distribution of sea surface salinity (10 m) contrasted between the south (≈ 37.1) and the north (≈ 38.1) with a marked gradient between 39.5 °N and 40.0 °N, clearly separating the recent AW to the south and the old AW to the north (Fig. 3a). Temperature (10 m) showed values around 24.0 °C (23rd July – 26th July) in the southern part of the area, south of 38.3 °N. Warm waters (≈ 25.2 °C, 27th July - 23rd August) were detected in the central zone, while the northernmost part of the area presented the lowest temperatures (≈ 22.0 °C, 24th August – 28th August) (Fig. 3b).

The vertical section of salinity (Fig. 4a) suggested the presence of a saline front between 39.5 °N and 40.0 °N, delimiting the presence of recent AW in the south and the old AW in the north. The recent AW was detected in the upper 60 m depth

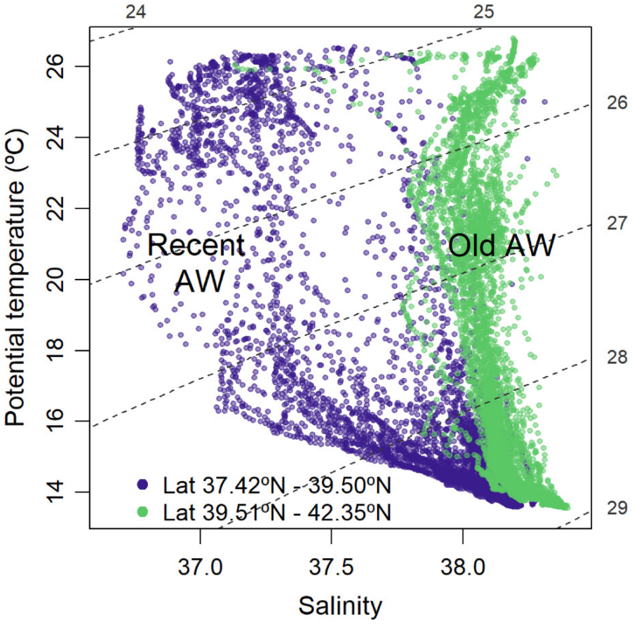


Fig. 2: TS diagram of the water layer from 0 to 100 m depth. Recent Atlantic Water (blue dots), south of 39.5 °N; old Atlantic Water (green dots), north of 39.5 °N.

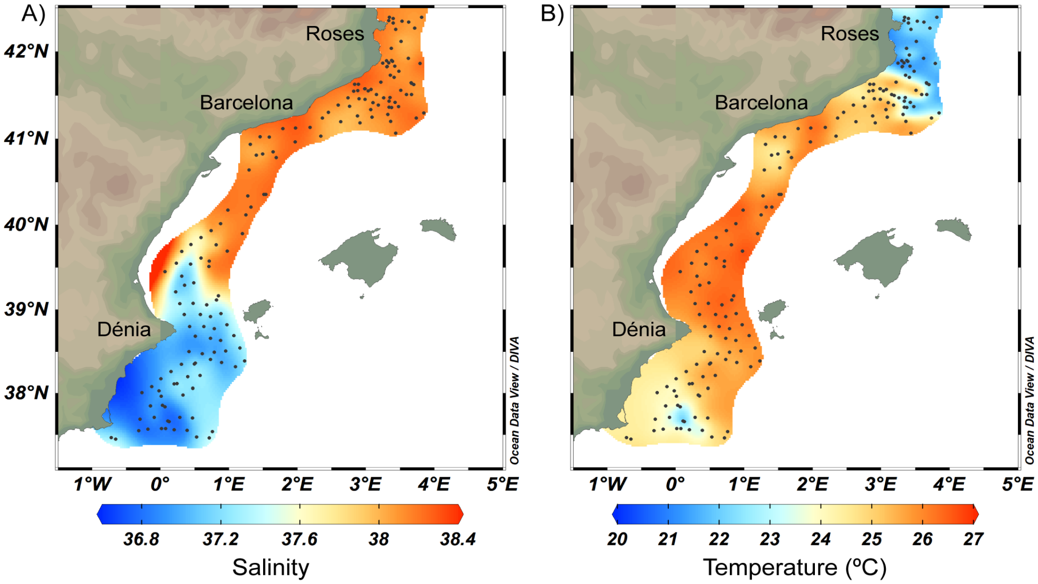
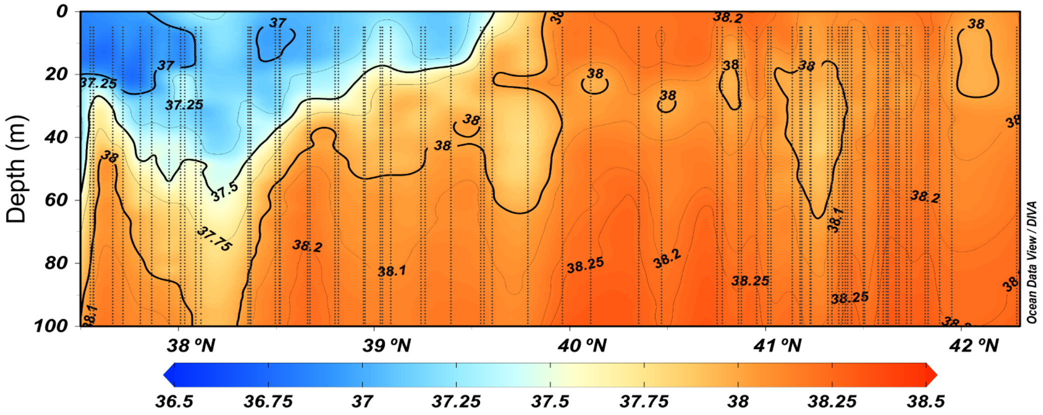


Fig. 3: Horizontal distribution of a) salinity and b) temperature at 10 m depth from CTD data. Dots show the sampling stations. Images were created using ODV (Schlitzer, 2020).

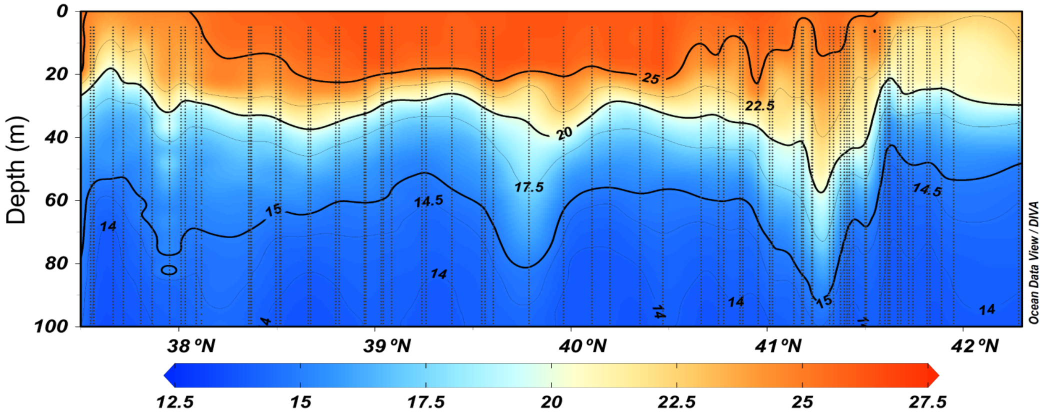
in the south and became shallower until 39.5 °N (Fig. 4a). The vertical section of temperature along the continental slope showed a surface mixed layer of about 20 m thickness, with temperature values above 25.0 °C between 38.0 °N and 41.0 °N (Fig. 4b). This central zone also showed the strongest thermocline gradient below the mixed layer, between 20 and 30 m depth. The thermocline becomes weaker south of 38.0 °N and north of 41.0 °N, with slightly lower surface temperature (Fig. 4b). The vertical section of fluorescence was typical of the season with a clear Deep Chlorophyll Maximum (DCM) below the thermocline, between 50 and 90 m (Fig. 4c).

The surface currents were characterised by the strong jet of the Balearic Current flowing to the northeast along the northern coast of the Balearic Islands (Fig. 5). This current displayed a deflection towards the northwest, at around 4.0 °E, joining the Northern Current path. The presence of the Northern Current was evident in the northern part of the area flowing to the southwest along the continental slope (Fig. 5).

A) Salinity



B) Temperature (ºC)



C) Fluorescence

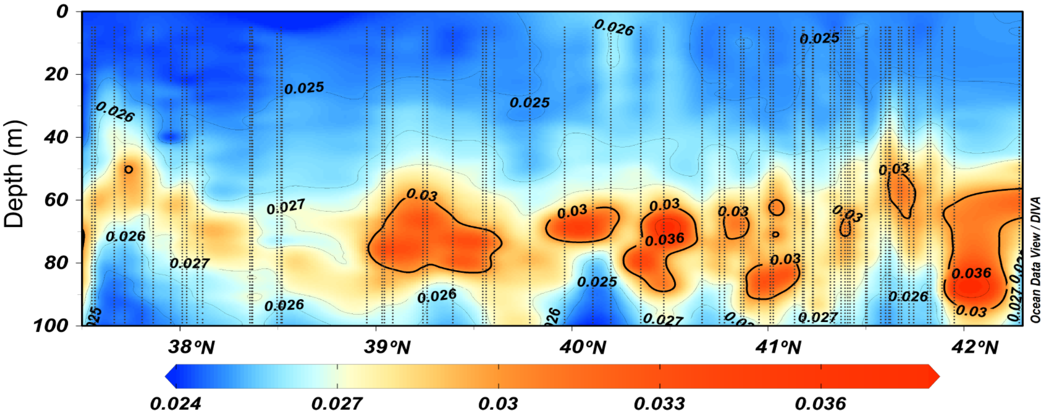


Fig. 4: Vertical distribution of a) salinity, b) temperature and c) fluorescence in the upper 100 m depth from CTD data, along the continental slope. Horizontal axis indicates latitude range. Vertical dotted lines represent 1 m binned CTD profiles data.

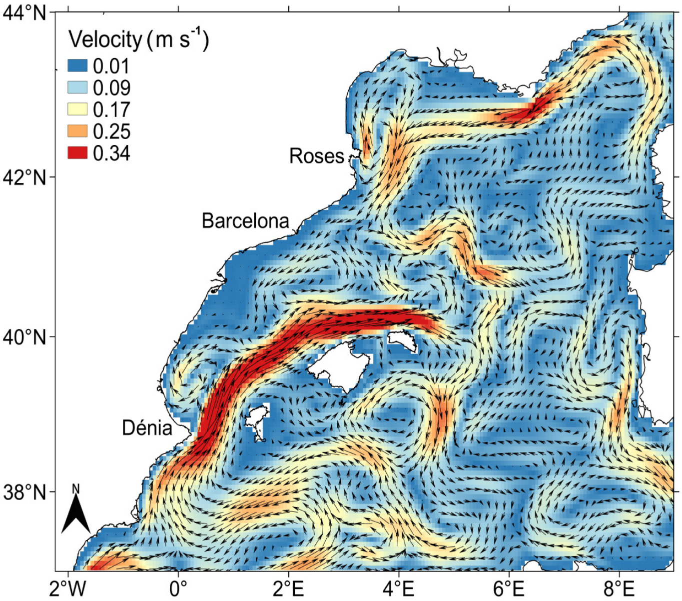


Fig. 5: Mean velocity field for August 2016 at 10 m depth from CMEMS reanalysis (Simoncelli et al., 2019). The current velocity is depicted through the colour scale and arrows show the current direction. Coastline is from Natural Earth (2021) and Instituto Hidrográfico de la Marina (2021).

Vertical distribution of *P. noctiluca* ephyrae

The preliminary analysis of the vertical distribution of *P. noctiluca* ephyrae revealed that practically all individuals (99.9 %) were located in the upper 50 m of the water column (63.3 % at 0 - 25 m and 36.6 % at 25 - 50 m). The remaining 0.1 % of ephyrae was found between 50 and 100 m, being absent below 100 m depth. Thus, the subsequent analyses, considering all the sampled stations, were focused on the first 50 metres. The GLMM analysis indicated that the light level (day/night) effect on ephyrae vertical distribution was significant ($z = -3.85$, p-value < 0.001) and that this effect of the light depended on depth ($z = 3.09$, p-value $= 0.002$; see Table S1 and Fig. S2). During the night, the ephyrae were mainly found in the upper 25 m, with low abundances at 25 - 50 m, whereas during the day they showed a more homogeneous distribution between surface and 50 m (Table 1; Fig. 6). The vertical displacement of ephyrae during the day toward deeper water layers never crossed the lower limit of the thermocline and therefore, did not reach the DCM level (Fig. 6).

Horizontal distribution of *P. noctiluca* ephyrae

P. noctiluca ephyrae were particularly abundant south of 40.0 °N, in coincidence with the presence of less saline surface water (Fig. 7a). These high abundances also fit well with the path of the Balearic Current (Fig. 5). In that area, ephyrae were present in almost all stations reaching the maximum abundance value (78

Ephyrae 100m^{-3}	Night	Day
0 – 25 m	4.7 ± 2.90	7.6 ± 2.91
25 – 50 m	1.1 ± 0.91	6.7 ± 3.81

Table 1: Ephyrae abundance (mean ± standard error) by day/night and depth stratum.

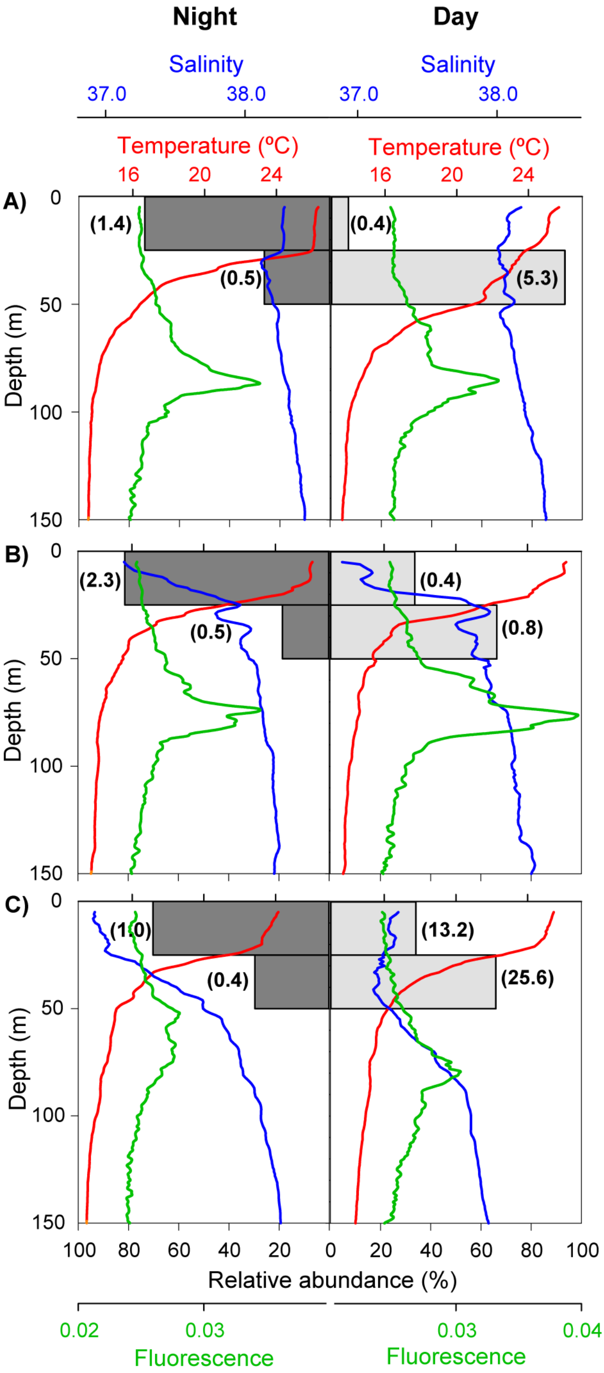


Fig. 6: Vertical distributions of ephyrae in night time (dark grey bars) and daytime (light grey bars) and temperature (red), salinity (blue), and fluorescence (green). Data of six stations representative of the hydrographic conditions at the a) north (41.0 ºN, 2.0 ºE), b) centre (39.5 ºN, 0.5 ºE) and c) south (38.0 ºN, 0.2 ºE) of the sampling area. Ephyrae relative abundance by station. Values in parenthesis indicate ephyrae abundance 100 m^{-3}.

ephyrae 100 m^{-3} per station) slightly south of the Eivissa Channel (around 38.5 °N; Fig. 7). However, in the northern half of the area, occupied by the more saline waters, the abundance of ephyrae along the Northern Current path was much lower, being practically absent in the northernmost part characterized by the coldest temperatures (Fig. 7b). This low abundance, between 40.0 °N and 41.3 °N, coincided with the mixture of waters from the Northern and Balearic Currents after the deflection of the Balearic Current at 4.0 °E (Fig. 5). The GLMM results showed that ephyrae abundance presented a negative association with salinity ($z = -5.45$, $p\text{-value} < 0.001$) and positive with temperature ($z = 4.82$, $p\text{-value} < 0.001$; see Table S2 and Fig. S3), with the highest values in the warm and low saline waters, between slightly south of the Eivissa Channel and 40.0 °N (Fig. 7).

Ephyrae abundance by station superimposed to surface salinity and temperature clearly defines three groups of stations (Fig. 8). The highest abundance values were associated with recent AW, characterized by salinities lower than 37.5 and temperatures between 22.5 °C and 26.5 °C. Lower abundances were found associated to old AW (salinity >37.5) at temperatures between 24.0 °C and 26.6 °C, while ephyrae were practically absent in old AW with temperatures lower than 24.0 °C (Fig. 8). It is worth noting the high ephyrae abundance in a station not included in any of the three stations groups, located on the boundary between the low and high salinity waters, around 40.0 °N (Fig. 7a).

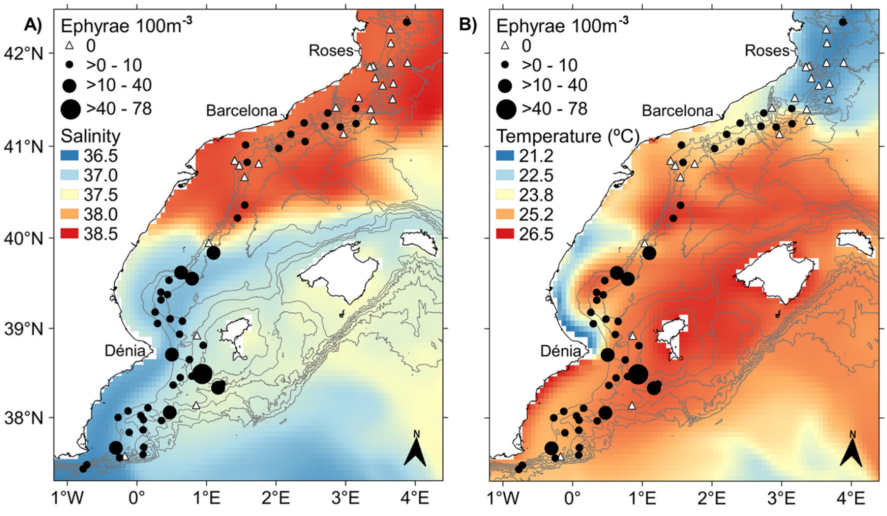


Fig. 7: Horizontal distribution of *P. noctiluca* ephyrae overlaid on the mean a) salinity and b) temperature at 10 m depth for the sampling period from CMEMS reanalysis (Simoncelli et al., 2019). Coastline is from Instituto Hidrográfico de la Marina (2021) and isobaths (every 400 m) are from EMODnet (2018).

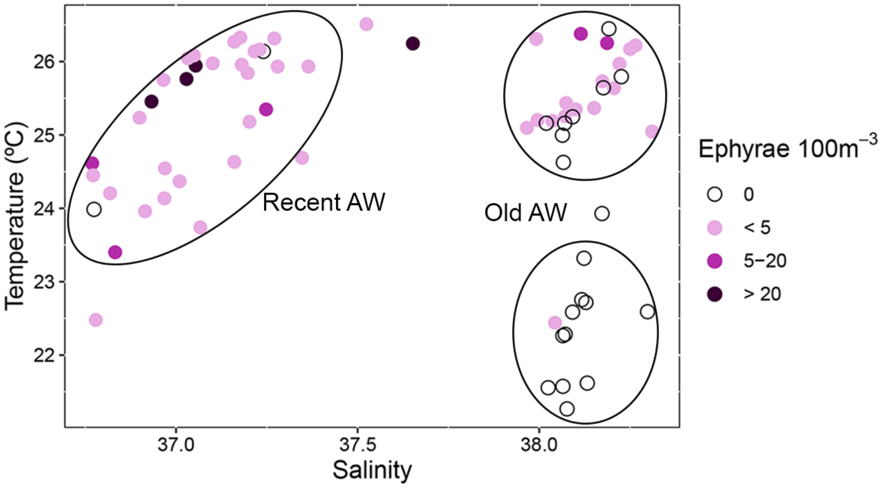


Fig. 8: Depth-integrated ephyrae abundances in relation to mean surface (5 - 10 m depth) salinity and temperature at plankton stations.

Discussion

The results of the present study revealed a high variability in the spatial structure of *P. noctiluca* ephyrae in surface waters linked to the recent and old AW masses. The presence of *P. noctiluca* ephyrae in the upper water layer is in agreement with previous observations (Morand et al., 1992; Buecher and Gibbons, 1999; Ottmann et al., 2021). In the present study, however, we detected short-extent diel vertical migrations of ephyrae in these surface levels, with a wide distribution well above and within the thermocline during daytime, being more concentrated towards the surface at night. In any case, their vertical distribution was found far from the characteristic DCM that develops in the Mediterranean during the summer stratification period (Estrada, 1985). This vertical distribution contrasts with that described for the epipelagic zooplankton, characterized by the presence of a zooplankton maximum at approximately the same depths than the DCM during the daytime, whereas at night zooplankton ascends to upper layers (Alcaraz, 1985; Saiz et al., 2014; Pascual et al., 2017). This behaviour allows for feeding during the day at the DCM, avoiding the predation at the surface (Bollens and Frost, 1989). Taking into account that *P. noctiluca* ephyrae feed on a variety of zooplanktonic prey, such as copepods, siphonophorans, salps or fish larvae (Purcell et al., 2014; Tilves et al., 2018), the migratory behaviour of the zooplankton would allow the overlap between *P. noctiluca* ephyrae and their prey during the night in surface waters. This would be supported by the high variety of prey detected in the gastric pouches of ephyrae during the night with respect to the day (Tilves et al., 2016). Moreover, we cannot discard the possibility that ephyrae might feed on microzooplankton, such as ciliates and flagellates, as observed in ephyrae of *Aurelia coerulea* (Kamiyama, 2018). These microzooplanktonic organisms are very abundant in the upper layers of stratified waters (Almeda et al., 2011) and have been reported to be an important food source for other planktonic organisms, such as cladocerans and fish larvae, living in surface waters (Atienza et al., 2006, 2016; Rossi et al., 2006). We can also consider that the vertical migration to slightly deeper and colder layers during the day would allow ephyrae to save energy, decreasing their metabolic rates and prey requirements (Morand et al., 1987; Lilley et al., 2014). The location of ephyrae in the illuminated levels of the water column could make them particularly vulnerable to visual predators such as crustaceans and fish (Avian, 1986; Lamb et al., 2017). However, the morphology and transparency of their bodies would make them barely visible to their predators (Hamner, 1995). All these strategies would allow *P. noctiluca* ephyrae to survive in this oligotrophic environment, avoiding the energy expense to cross the thermocline and reach the DCM zone where, furthermore, they would have to compete with other zooplankton species. The observed vertical migration of ephyrae would probably be constrained by the conditions of water column stratification. As vertical migration in jellyfish is accomplished by swimming (Mills and Vogt, 1984), the weak swimming capability of ephyrae, in comparison with adult stages (Higgins et al., 2008), may hinder large amplitude migration across the thermocline. *Pelagia noctiluca* adults are strong swimmers that perform extensive vertical migrations from deep waters, below 300 m, during the day to the surface at night (Franqueville, 1971; Ferraris et al., 2012). Although this migration can be attributed to feeding, following its zooplankton prey, other factors, such as the reproductive behaviour, could determine this migration pattern (Ferraris et al., 2012).

The horizontal distribution of *P. noctiluca* ephyrae showed a clear latitudinal gradient with high abundances in the southern part of the area, associated with the low saline recent AW. In summer, the surface AW which enters the Mediterranean may reach the Balearic Islands progressing northward across the Eivissa and Mallorca Channels (Pinot et al., 2002; Heslop et al., 2012) forming the warm fresh core of the Balearic Current. The ephyrae found in the recent AW along the Balearic Current path would have been generated by adults of *P. noctiluca* associated with the entrance of waters from the Atlantic into the Mediterranean, or trapped by the AW flow along its path. The maximum total body diameter of the collected ephyrae was 3.55 mm. According to Ramondenc et al. (2019) their estimated age would be around 18 days, enough time to come from distant areas. However, we must consider that the instabilities of the current along the continental slope, that generate meanders and eddies (Rubio et al., 2005), will ultimately determine the transport of ephyrae. Further modeling studies implementing individual-based models with a Lagrangian particle-tracking framework using hydrodynamic model outputs, will help to understand the trajectories and potential origin of these ephyrae. The highest abundance of ephyrae was detected in the warm recent AW at the Eivissa Channel, where the currents could have caused a funnel effect. As the recent AW inflow through Eivissa or Mallorca Channel presents not only seasonal (Heslop et al., 2012) but also interannual variability (Pinot et al., 2002), changes in the abundance of the species over time in the study area could be related to the interannual variability of this mechanism. We should consider that other hydrodynamic structures eastwards of the continental slope could also influence the ephyrae observed pattern, but the sampling strategy does not allow to test the possible effect of these processes. The transport of gelatinous organisms through the Strait of Gibraltar linked to the inflow of the AW into the Mediterranean has been previously reported for other species, such as *Rhizostoma luteum* (Prieto et al., 2013). The inflowing Atlantic jet involves high mesoscale activity (Tintoré et al., 1991), generating structures such as fronts and eddies that support high biological productivity (Reul et al., 2005; Vargas-Yáñez and Sabatés, 2007; Macías et al., 2008). These physical structures would favour gelatinous zooplankton advection and aggregation since, as osmoconformers that adjust to small salinity gradients, they tend to aggregate at density discontinuities (Mills, 1984; Graham et al., 2001; Greer et al., 2015; Guerrero et al., 2016).

In the northern half of the area, occupied by the old AW, the abundance of *P. noctiluca* ephyrae along the Northern Current path was much lower, being absent in the northernmost part. The low abundance of ephyrae contrasts with previous observations where high concentrations of *P. noctiluca*, adults and ephyrae, and other gelatinous organisms have been found associated to the Northern Current (Morand et al., 1992; Sabatés et al., 2010, 2018; Ferraris et al., 2012; Guerrero et al., 2016) in relation with the high levels of biological production in that area (Ibanez and Boucher, 1987; Estrada and Margalef, 1988; Sabatés et al., 2004). This scarcity of ephyrae together with their absence at the northern end of the area would suggest that the ephyrae found in the Northern Current would not come from areas further north but their presence would be related to the influx of the Balearic Current. The Balearic Current flowing to the northeast, carrying ephyrae, showed a deflection to the west around 4.0 ºE and joined the Northern Current probably supplying ephyrae to this current, where the mixture of waters would dilute their abundance. The absence of ephyrae in the northernmost part, characterized by the lowest temperature and more homogeneous upper layer, could suggest that temperatures in that area might have been too low for the development of the species. Nevertheless, taking into account the wide range of temperatures *P. noctiluca* tolerates (Mariottini et al., 2008; Canepa et al., 2014) the temperature "per se" would not explain the absence of ephyrae. Previous works already reported the absence of ephyrae in that area in coincidence with high concentrations of anchovy larvae (Guerrero et al., 2018; Sabatés et al., 2018). Sabatés et al. (2018) argued that these colder waters come from further north, advected by the Northern Current, and involved a significant amount of waters from the shelf of the Gulf of Lions, an important spawning anchovy area (Palomera et al., 2007). Thus given the oceanic habitat of *P. noctiluca* (Canepa et al., 2014), the origin of these waters would be the most likely explanation for the absence of ephyrae in that area.

Licandro et al. (2010) already suggested that the seasonal occurrence of high densities of *P. noctiluca* adult swarms in the WM followed the progression of the AW surface stream, through the Strait of Gibraltar, along the North African coast before circulating anticlockwise around the WM basin (Pinardi and Masetti, 2000). In the present study, the possible flux of *P. noctiluca* ephyrae towards the north would depend on the seasonality of the currents pattern and on the high mesoscale variability of hydrodynamic processes (Millot, 1985; Heslop et al., 2012). The entrance of individuals through the Strait of Gibraltar would be supported by the similar genetic structure between *P. noctiluca* from the North Atlantic and the Mediterranean, resulting from an extensive gene flow and a high degree of connectivity between both populations (Stopar et al., 2010; Glynn et al., 2016). Following the main currents in the WM, and considering the lifespan of this species, between 9 months and 1 year (Malej and Malej, 1992; Morand et al., 1992), individuals entering through the Strait of Gibraltar, or their offsprings, could act as sink populations at different Mediterranean regions (e.g. northern Adriatic, Naples Bay, Tunis Bay and Villefranche Bay (Kogovsek et al., 2010)).

The frequency of *P. noctiluca* adult blooms in the Mediterranean has increased significantly since the 1990s, particularly in the western basin (Daly Yahia et al., 2010; Bernard et al., 2011; Canepa et al., 2014). This increase has been related with climatic (mild winters, high temperature, low rainfall and high atmospheric pressure) and anthropogenic factors (lack of predators and decrease of pelagic fish populations, their competitors for food) (Purcell, 2012; Canepa et al., 2014; Gravili, 2020). However, we cannot rule out that these population increases could benefit from the contribution of individuals from the Atlantic across the Strait of Gibraltar. The results of the present study suggest the population connectivity of *P. noctiluca* between the Atlantic and the Mediterranean, a key issue for the understanding of the species population dynamics and its increasing abundance in the Mediterranean. Further observational and numerical simulation studies may contribute to better understand this potential connectivity and its seasonal and interannual variability.

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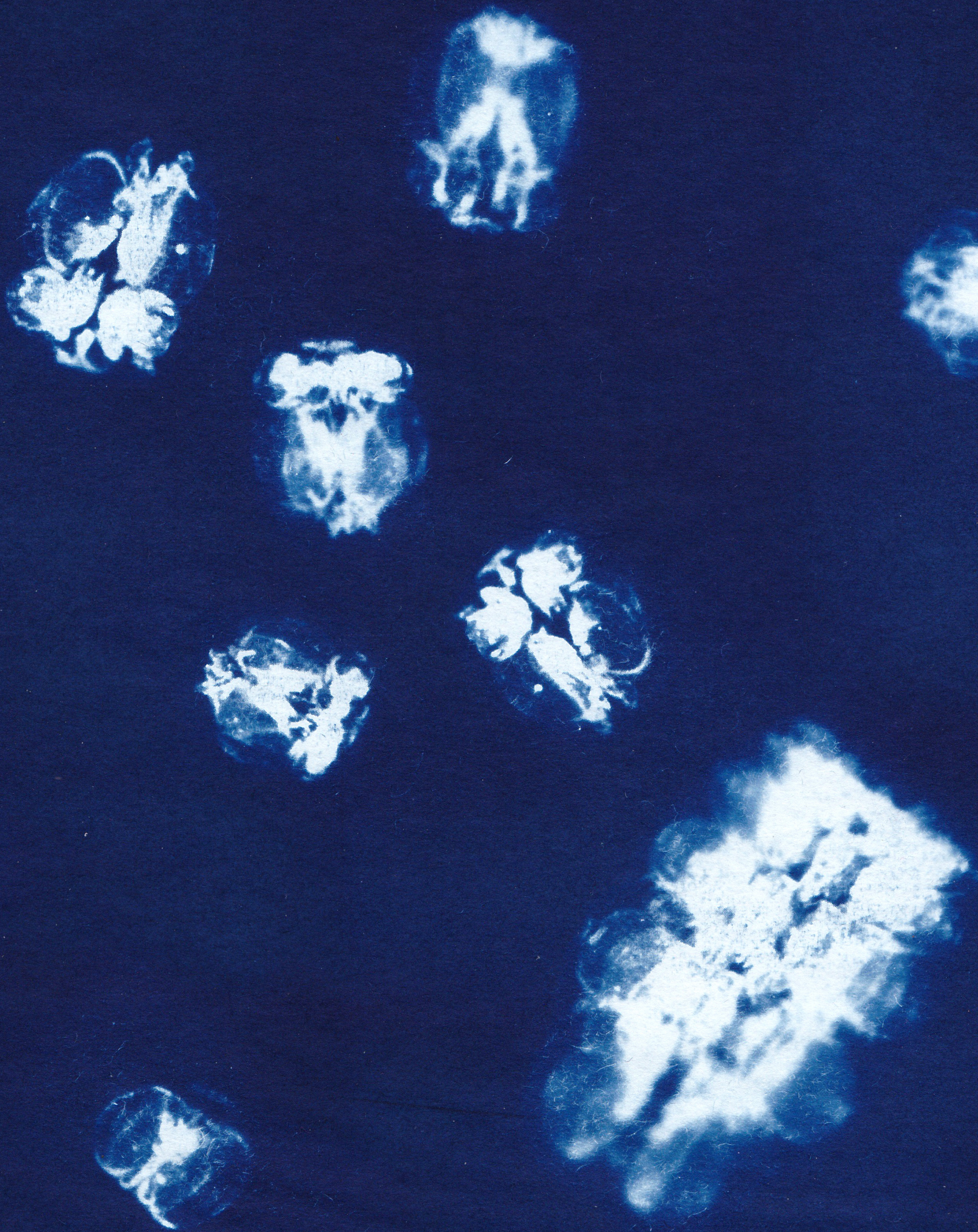

Chapter II

The role of oceanographic conditions and colony size in shaping the spatial structure of *Pyrosoma atlanticum* in the NW Mediterranean Sea

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Abstract

This study investigates the role of winter oceanographic conditions on the horizontal and vertical spatial structure of *Pyrosoma atlanticum* at different ontogenetic stages. Data were obtained on two oceanographic cruises (February 2017 and 2018) in the NW Mediterranean. Small colonies were exceptionally abundant in 2017, linked to an earlier development of spring conditions and the subsequent seasonal phytoplankton bloom. The mesoscale distribution of *P. atlanticum* differed depending on the colony size. Large colonies (≥ 7 mm) were found on the slope all along the density front, whereas small (< 4 mm) and medium colonies (4–6.9 mm) extended their distribution over the shelf because of instabilities of the front, and were mostly absent in the cold, low salinity coastal waters. The analysis of their vertical distribution showed that at night colonies of all sizes remained close to the surface, where chlorophyll-*a* levels were high, while during the day they migrated to deeper layers, reaching greater depths as the colony size increased. The migratory behaviour started when colonies were 4–6.9 mm long. The relative importance of the species in the downward carbon transport is discussed. Our results highlight the need to further study the ecology of this efficient filter feeder in the Mediterranean.

Introduction

Pyrosomes (greek for “fire bodies” because of their bioluminiscence) are colonial pelagic tunicates made up of tens to thousands of zooids encased in a common gelatinous tunic (Godeaux et al., 1998; Madin and Deibel, 1998) ranging from <1 cm to a maximum recorded length of 20 m, depending on the species (Van Soest, 1981). These colonies are holoplanktonic grazers, feeding mainly on phytoplankton of a wide range of types and sizes (Drits et al., 1992; Perissinotto et al., 2007; Décima et al., 2019). As with other pelagic tunicates, pyrosomes have high clearance rates that result in a substantial energy transfer to deep waters (Henschke et al., 2019) through their large production of faecal pellets (Drits et al., 1992) and carcass depositions (Lebrato and Jones, 2009). Pyrosomes are preyed by sea lions, fish, turtles and seabirds in the water column (Harbison, 1998; Childerhouse et al., 2001; Hedd and Gales, 2001), and by arthropods, cnidarians, fish and sharks on the seafloor (Carrassón and Cartes, 2002; Lebrato and Jones, 2009; Archer et al., 2018; Brodeur et al., 2021). These biological traits and trophic interactions give pyrosomes an important role in the marine trophic web and carbon transport (Lebrato and Jones 2009; Henschke et al., 2019).

Pyrosoma atlanticum is the most widespread and common species. Historically it has been found in open waters of all oceans between 50ºN and 50ºS (Van Soest, 1981), but it has recently been reported further north in the Pacific linked to a large marine heat wave (Brodeur et al., 2018; Miller et al., 2019). As found in other gelatinous zooplankton, hydrodynamic structures such as currents, gyres and fronts drive their transport and concentration, ultimately shaping their areas of distribution and abundance (Graham et al., 2001; Guerrero et al., 2016; Bellido et al., 2020). Physical and biological gradients in the water column (e.g. thermoclines and subsurface chlorophyll maxima) determine the vertical distribution of these organisms, limiting their movement or leading to an increase in abundance that results in a patchy distribution (Gibbons et al., 1999; McManus et al., 2003; Nogueira Júnior et al., 2015). *P. atlanticum* is known as a strong migrator that can reach up to 2500 m depth during the day and migrates towards the surface at night (Roe et al., 1987; Angel, 1989). Its short generation time and rapid growth, together with its high filtration rates, allow an exponential population increase of *P. atlanticum* under favourable environmental conditions (Alldredge and Madin, 1982), in some cases leading to large swarms (Angel, 1989; Drits et al., 1992). Unprecedented high densities of large colonies of *P. atlanticum* were reported in the northeast Pacific associated with a warm water mass and a strong El Niño (Brodeur et al., 2018; Sutherland et al., 2018). Despite observations of aggregations in the Tasman Sea (Henschke et al., 2019), southeast Atlantic (Drits et al., 1992), Gulf of Mexico (Archer et al., 2018) and Mediterranean Sea (Braconnot and Goy, 1981), the environmental drivers of these blooms remain unclear.

The Mediterranean Sea has a marked seasonal cycle, with the alternation of stratified (summer) and mixed (winter) periods that confers strong seasonality to primary production (Estrada et al., 1985). Recurrent late winter–early spring blooms are only observed regularly in the northwestern region and intermittently in a few other areas (D'Ortenzio and Ribera d'Alcalà, 2009). The seasonal bloom in the NW Mediterranean is triggered by deep water formation episodes that take place in the Gulf of Lions, driven by evaporation caused by strong, cold and dry northerly winds (MEDOC group, 1970; Schott et al., 1996). Interannual variability in primary production is highly dependent on the extent, intensity and duration of the deep water formation episodes, which increase in colder and drier years (Marty and Chiavérini, 2010; Herrmann et al., 2013). The dynamics of the NW Mediterranean is characterized by the presence of a permanent shelf-slope density front along the slope separating open sea high-salinity waters from coastal low-salinity waters (Font et al., 1988). A geostrophic current (the Northern Current) associated with the front flows from NE to SW, roughly parallel to the coast (Millot, 1999). The front and the associated current are subject to high mesoscale variability that causes oscillations, meandering and eddy generation (Sabatés et al., 2004; Rubio et al., 2005), playing a key role in the distribution and abundance of planktonic organisms (e.g. Sabatés et al., 2004; Guerrero et al., 2016).

Previous studies carried out on gelatinous zooplankton in the NW Mediterranean have shown high spatial variability closely linked to oceanographic dynamics and water mass structure (Guerrero et al., 2016; Sabatés et al., 2018). At a temporal scale, high interannual variability has been reported in abundance and species composition (Licandro and Ibanez, 2000; Guerrero et al., 2018b; Feuilloley et al., 2021), but there is no clear consensus on long-term trends (Molinero et al., 2005; García-Comas et al., 2011; Licandro et al., 2012; Guerrero et al., 2018a;). Studies on *P. atlanticum* in the Mediterranean are scarce. While some sporadic records of the species have been reported in the eastern basin (Galil and Goren, 1994), most of the studies have been conducted in the western basin. These studies have addressed the vertical distribution (Palma, 1985; Andersen and Sardou, 1994; Sardou et al., 1996), seasonality and population dynamics (Franqueville, 1971; Braconnot, 1974) of *P. atlanticum* mainly from fixed stations or single transects in which sampling was performed in spring. In the present study, we addressed the spatial structure of *P. atlanticum* in the NW Mediterranean during winter oceanographic conditions. The specific objectives were i) to analyse how the mesoscale water dynamics shape the horizontal distribution of *P. atlanticum* at different ontogenetic stages; and ii) to determine diel and ontogenetic changes in vertical distributions of *P. atlanticum* in relation to the structure of the water column.

Methods

Field sampling

Two oceanographic cruises were conducted in the NW Mediterranean (41.3–42.5ºN and 2.8–3.8ºE) during two consecutive winters (18 February–20 March 2017 and 18–28 February 2018) on board the R/V García del Cid. Sampling stations were placed along transects perpendicular to the coast located 7–14 km apart and covering the shelf and slope regions (Fig. 1). At each station, vertical profiles of basic hydrographic variables (salinity, temperature and fluorescence) were obtained by means of a conductivity-temperature-depth profiler (CTD) equipped with a fluorometer, and data were interpolated to 1 m depth intervals.

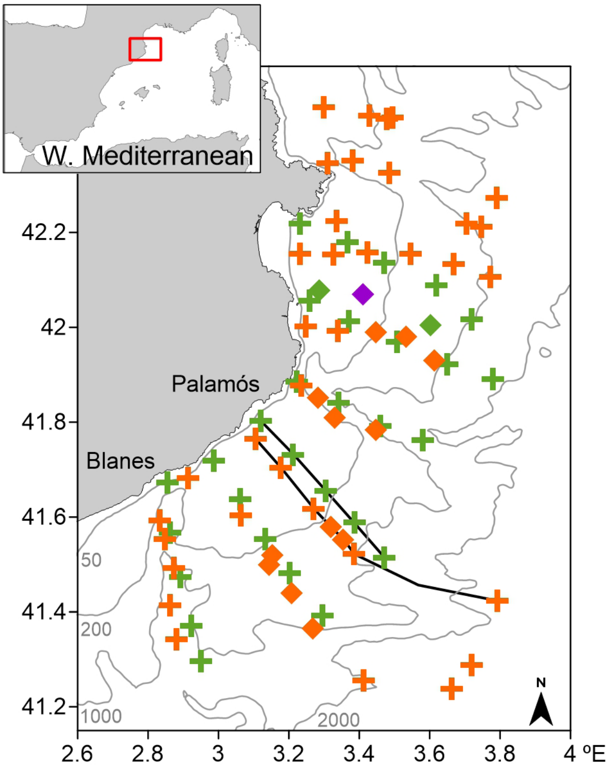


Fig. 1: Study area in the NW Mediterranean. Sampling stations during 2017 (orange) and 2018 (green) surveys. Lines indicate the location of the vertical sections in Fig. 3. Diamonds represent depth-stratified samplings, the purple one corresponds to a fixed station sampled for 48 h in the 2017 survey. Thin grey lines show isobaths (50, 200, 1000 and 2000 m).

Dynamic heights at the stations were calculated with a reference depth level of 500 m. Where station depth was lower, dynamic height was extrapolated using the continuity equation applied to the deepest level of three-station clusters (cf. Hidaka, 1940). Water samples for chlorophyll-*a* (chl-*a*) determination were collected at some stations using a rosette system at three depths down to 80 m throughout the day and night in order to calibrate the fluorometer. The chl-*a* concentration (µg/L) was determined fluorometrically (Yentsch and Menzel, 1963). Water samples of 150 mL were filtered through Whatman GF/F filters. Chl-*a* was extracted from filters immersed in 6 mL of 90% acetone (24 hours at 4°C in darkness). The extract was analysed with a Turner Designs fluorometer calibrated with pure chl-*a*. The relationship between chl-*a* concentration and fluorescence obtained in each survey was used to convert the continuous CTD fluorescence register into the chl-*a* concentration.

Zooplankton mesoscale sampling was conducted at 35 stations in 2017 and at 29 stations in 2018, using a Bongo net (60 cm diameter and 300 µm mesh size) towed obliquely from a maximum depth of 500 m, or 5 m above the seafloor at shallower stations, to the surface and at a vessel speed of 3.7 km/h (Fig. 1). In addition, depth-stratified samplings were performed at selected stations from a maximum depth of 550 m on the shelf and slope during the day (8:30–18:00 h UTC) and night (20:00–06:00 h UTC), avoiding sunset and sunrise. In 2017, these samplings were performed at 13 stations, three of which were fixed stations sampled for 24 or 48 h, and in 2018 two fixed stations were sampled for 24 h (Fig. 1). Depth-stratified samplings were carried out using a Multiple Opening/Closing Net Environmental Sensing System (a MOCNESS net with a 1 m^2 mouth opening consisting of eight nets with a 300 µm mesh size) towed obliquely at a ship speed of 3.7–4.6 km/h. Depth strata were defined according to the maximum depth at each station (shallow stations 120, 100, 80, 60, 40, 30, 20 and 10 m; deep stations 550, 400, 300, 200, 150, 100, 50 and 25 m). The volume of filtered water was recorded by a flowmeter placed in each net mouth. Immediately after collection, the zooplankton samples were fixed in 5% formaldehyde buffered with sodium tetraborate.

Sampling processing and data analysis

In the laboratory, colonies of *P. atlanticum* were sorted from zooplankton samples using a stereomicroscope. All *P. atlanticum* colonies were counted, but when samples were estimated to contain >200 colonies, aliquots were taken to obtain at least 100 colonies and extrapolate the count to the whole sample. In order to determine colony size, all *P. atlanticum* colonies were scanned using a ZooScan (Hydroptic III) (Grosjean et al., 2004) and measured from the diaphragm to the opposite end to the nearest 0.1 mm using the ImageJ software v.1.51j8 (Rasband, 2018). A preliminary exploration of the vertical distribution of *P. atlanticum* colonies (grouped in 1 mm length intervals) revealed that the diel vertical migration did not always initiate at the same colony size but instead was observed in some colonies of 4 mm, some of 5 mm and some of 6 mm (Fig. S1). In addition, colonies of these sizes showed a similar vertical distribution pattern (Fig. S1) and were grouped for the analysis of the vertical distribution. For this analysis, three colony size classes were considered: < 4 mm (including tetrazoids), 4–6.9 mm and ≥ 7 mm (hereinafter referred to as small, medium and large, respectively). Data from all MOCNESS stations were considered and the number of colonies per size class collected at each depth stratum was standardized to a number per 1000 m^3

of filtered water at each depth stratum. The horizontal distribution of small and medium colonies was similar and quite different from that of the large colonies, so for the analysis of the mesoscale distribution two size classes were considered (≤ 6.9 and ≥ 7 mm; hereinafter referred to as small-medium and large, respectively). This analysis was conducted from data obtained with the Bongo and MOCNESS nets (except at the fixed stations) (See Fig. 1). The number of colonies of each size class collected by the Bongo was standardized to a number per 1000 m^3 of filtered water. The number of colonies of each size class collected by the MOCNESS at each depth stratum was pooled and divided by the sum of the filtered water at each depth stratum and standardized to a number per 1000 m^3 of filtered water.

To investigate the effect of environmental variables on the mesoscale horizontal distribution of *P. atlanticum*, the explanatory variables considered were temperature, salinity, density and chl-*a* at 10, 30 and 50 m depth, and bathymetry. Temperature and chl-*a* at 10 m, density at 30 m and bathymetry were selected as independent variables after evaluating collinearity through the Pearson cross-correlation (coefficient < |0.6|). A Generalized Linear Model (GLM) was fitted to assess the effect of the independent oceanographic variables on the mesoscale horizontal distribution of small-medium and large *P. atlanticum* colonies. For large colonies, the best model, based on the Akaike information criterion (AIC) (Akaike, 1974) and residual inspection, showed a structure that was included in a Generalized Linear Mixed Model (GLMM), considering the region of the sampling stations ("shelf" when < 200 m depth; and "slope" when > 200 m depth) as a random effect. In addition, standardized environmental variables [(value-mean) / standard deviation (sd)] were required for the convergence of the GLMM. The number of *P. atlanticum* colonies (counts) of both size classes, which followed a negative binomial distribution, was analysed using the "glm.nb" (for GLM) and "glmer.nb" function (for GLMM) from the "MASS" package and with a log-link to avoid predicting negative numbers of colonies (Venables and Ripley, 2002). The (log-transformed) volume of filtered seawater was included as an offset inside GLM and GLMM to reduce the bias owing to different volumes filtered by the nets (826 m^3 mean ± 857 sd) (Zuur et al., 2009; Canepa et al., 2017). In both cases, the optimal model was obtained through a backwards selection criterion based on the significance of each explanatory variable ($\alpha = 0.05$), using the AIC comparison and through the inspection of the residuals. Models were carried out using the R statistical programming language v3.5.3 (R Core Team, 2020). Maps of temperature, salinity and chl-*a* at 10 m and density at 30 m for 2017 and 2018 were generated by means of the minimum curvature interpolation method. Vertical sections of temperature, salinity and chl-*a* for both years were obtained using kriging, considering the anisotropy of the water column. All were performed using Surfer® v13.4 (Golden Software, LLC).

To analyse the vertical distribution of *P. atlanticum* at each size class during day and night, the weighted mean depth (WMD) was calculated for each sampling station (MOCNESS net) by size class and light (day/night) as follows:

$$WMD = \sum_{i=1}^{n} P_i Z_i$$

where Pi is the proportion of colonies in the *i*th depth stratum:

$$P_i = \frac{C_i H_i}{\sum_{i=1}^{n} C_i H_i}$$

Zi is the mean sampling depth of the ith depth stratum; Ci is the concentration of colonies in the ith depth stratum; and Hi is the width of the ith depth stratum.

The effect of size class (< 4 mm, 4–6.9 mm, ≥ 7 mm), light (day/night) and different oceanographic variables on the vertical distribution of *P. atlanticum* was tested through a GLM. Mean temperature, salinity, density and chl-*a* concentration were calculated for each depth stratum and MOCNESS haul. After evaluating collinearity through the Pearson cross-correlation test, temperature and chl-*a* were selected as independent variables (coefficient < |0.6|). The vertical counts of *P. atlanticum*, following a negative binomial distribution, were analysed using the "glm.nb" function from the "MASS" package and with a log-link function (Venables and Ripley, 2002; Zuur et al., 2009). The (log-transformed) volume of filtered seawater at each depth stratum was included as an offset inside GLM in order to reduce the bias arising from different volumes filtered by the nets (216 m^3 mean ± 276 sd) (Zuur et al., 2009; Canepa et al., 2017), and the oceanographic variables were standardized. The GLM was carried out using the R statistical programming language v3.5.3 (R Core Team, 2020).

Results

Hydrographic conditions

In both years, surface temperature and salinity increased towards the open sea (Fig. 2a, b, c, d). In 2017, the coastal zone showed low temperature (≈ 12.5°C) and salinity (≈ 37.2), while on the shelf edge and slope the temperature reached 13.6°C and salinity 38.4. In 2018, coastal waters also showed low temperature (≈ 12.9°C) and relatively low salinity (≈ 38.3); on the shelf edge and in the open sea salinity was similar to that detected in the previous year and temperature was slightly lower, around 13.2°C. Surface chl-*a* did not show a consistent pattern (Fig. 2e, f). In 2017, relatively high values were detected on the shelf, but also in the open sea (≈ 1.2 µg/L), while in 2018 high chl-*a* concentrations (≈ 1.9 µg/L) were found in the southwest part of the area. On both cruises, the distribution of density at 30 m increased from near the coast towards the open sea, following a similar pattern to that of salinity. The dynamic height overlaid on the density at 30 m showed the signature of the shelf-slope front associated with the Northern Current (Font et al., 1988) along the continental slope (Fig. 2g, h). Some detected intrusions onto the shelf were related to the instabilities of the current (Fig. 2g, h). The vertical section of temperature and salinity showed the presence of colder and less saline waters close to the coast, which reached the seafloor up to around 100 m depth in both years and were more evident in 2017 (Fig. 3a, b, c, d). Chl-*a* was detected in the first 80 m of the water column, with the highest values in the upper ≈ 25 m (≈ 1.15 µg/L in 2017 and ≈ 0.80 µg/L in 2018) (Fig. 3e, f).

Horizontal distribution of *P. atlanctium*

P. atlanticum colonies were much more abundant in 2017 than in 2018 (mean abundance 228.70 col./1000 m^3 ± 394.77 sd and 5.12 col./1000 m^3 ± 6.08 sd, respectively), owing to the massive concentration of small size colonies in 2017. However, small colonies (< 4 mm) dominated in both years, 2–3 mm (range: 0.9–82.0 mm) in 2017 and 1–2 mm (range: 1.2–59.0 mm) in 2018 (Fig. S2). The distribution pattern of colonies within the small-medium (≤ 6.9 mm) and large (≥ 7 mm) size classes was quite similar in both years. The small-medium colonies were present all over the area, with low abundances or even absence at stations close to the coast and high abundances on the shelf edge (Fig. 4a, b). The GLM identified surface temperature and density (30 m) as significant variables (p <

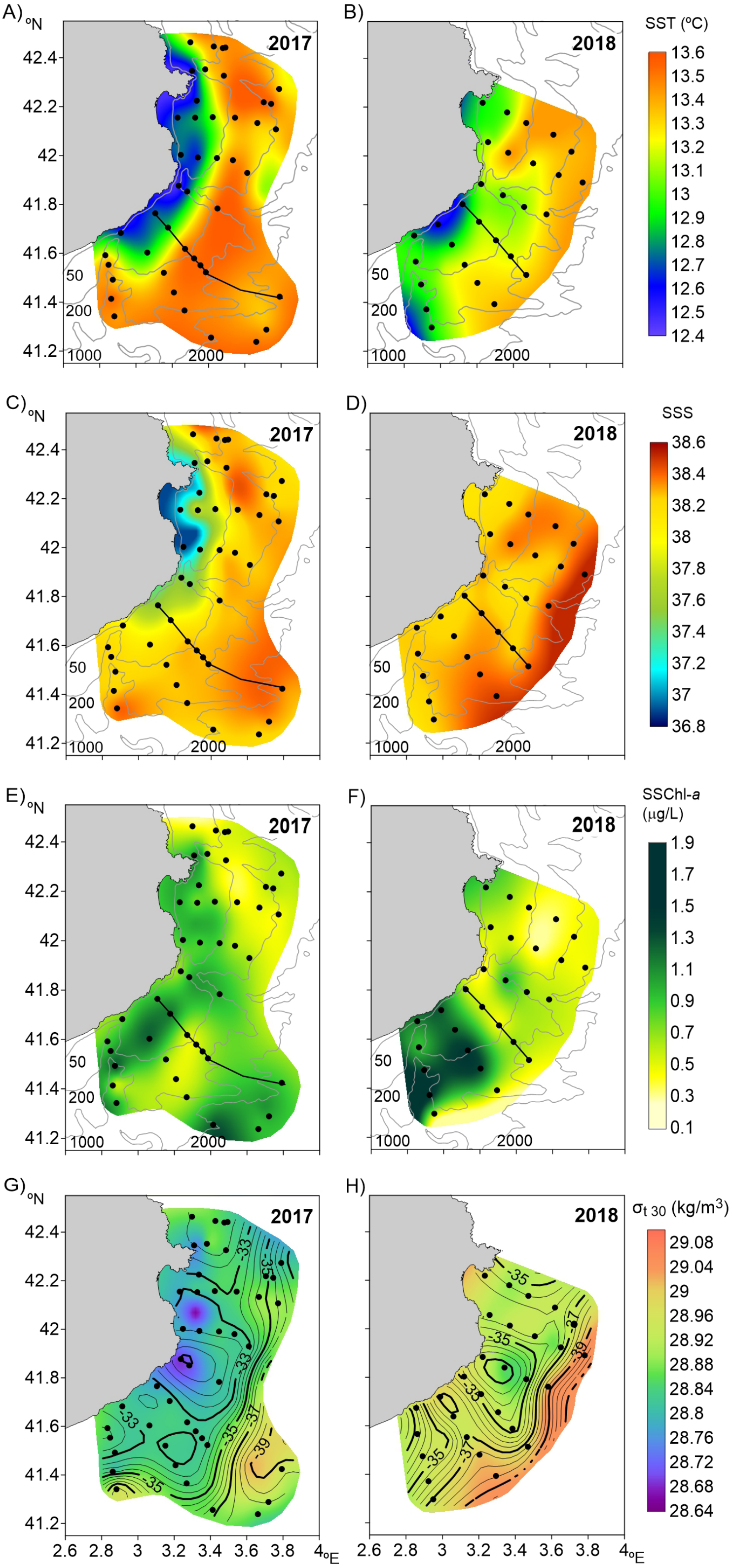


Fig. 2: Maps of surface (10 m) temperature (SST; a, b), salinity (SSS; c, d) and chlorophyll-*a* (SSChl-*a*; e, f) and dynamic height (contour lines, dynamic cm) at 30 m relative to 500 m overlaid on density at 30 m (σt 30; g, h) in winter 2017 (left panels) and 2018 (right panels). Thin grey lines show isobaths (50, 200, 1000 and 2000 m).

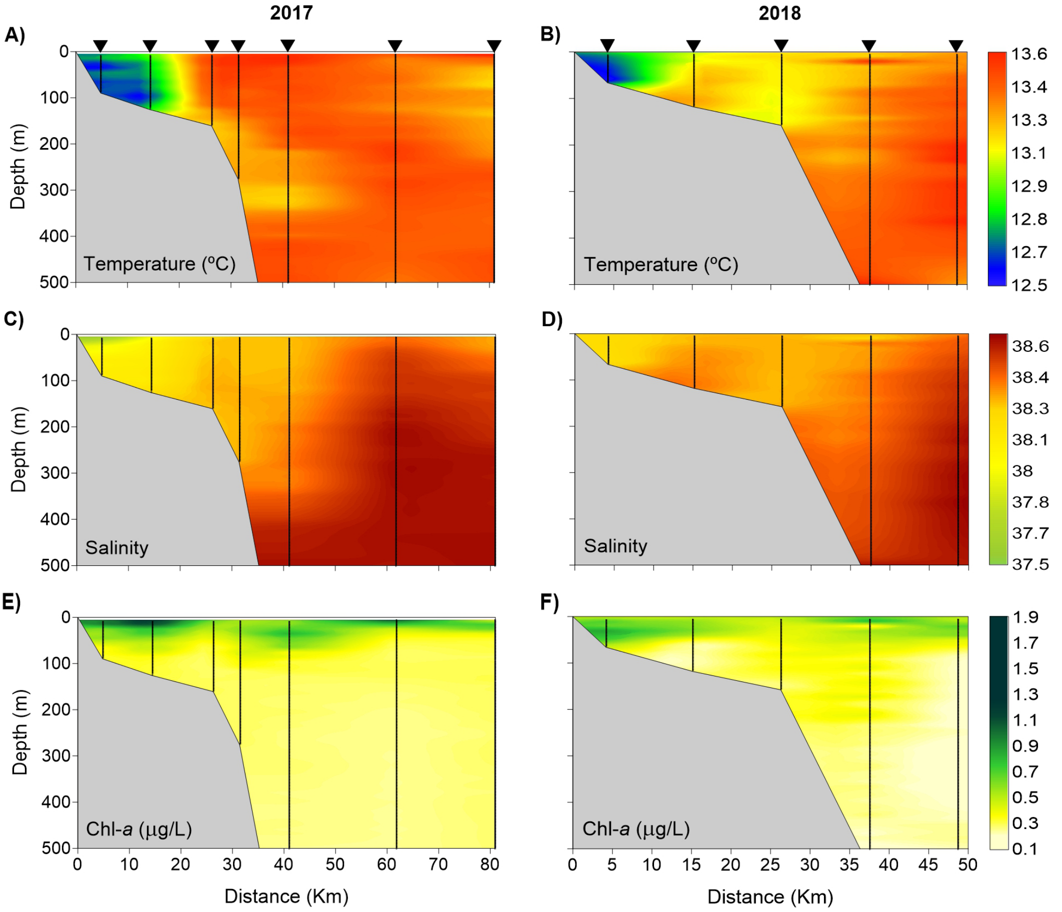


Fig. 3: Vertical distribution of temperature (a, b), salinity (c, d) and chlorophyll-*a* (e, f) in the upper 500 m depth in winter 2017 (left panels) and 2018 (right panels) in the sections marked in Fig. 1. Horizontal axis indicates distance from the coast. Vertical lines represent 1 m binned CTD profile data.

0.05) related to *P. atlanticum* distribution (Table I, Fig. S3). High abundances were found in warm waters (13.1–13.6ºC) and of moderate density (28.7–28.9 kg/m^3) (Fig. 5a, b). Large colonies were mainly found on the slope at depths greater than 400 m and in relatively low chl-*a* surface waters (0.5–1.0 µg/L) (Fig. 2e, f, 6a, b) in the vicinity of the front throughout the area, but were practically absent in shelf waters. The GLMM identified bathymetry as a significant variable ($p < 0.05$) related to this size class distribution (Table I, Fig. 7, S4). Although surface chl-*a* was not a significant variable for the distribution of large colonies (negative relationship, Table I, Fig. S5), it was kept in the GLMM because its inclusion improved the explanatory capacity of the model, providing a lower AIC value (Fig. S4) (Zuur et al., 2009).

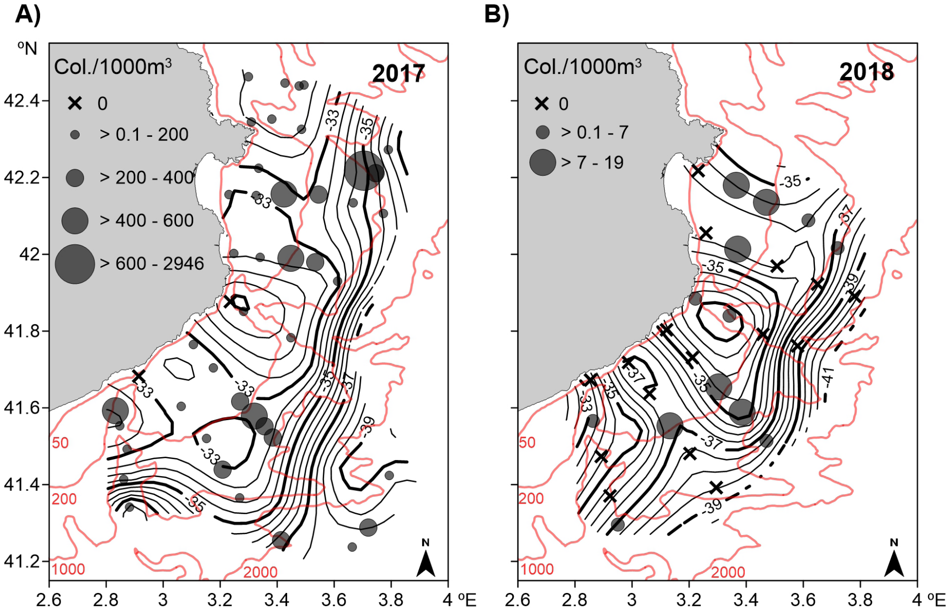


Fig. 4: Horizontal distribution of small-medium (≤ 6.9 mm) *Pyrosoma atlanticum* colonies overlaid on dynamic height (contour lines; dynamic cm) at 30 m relative to 500 m and bathymetry (in red; 50, 200, 1000 and 2000 m) in 2017 (a) and 2018 (b).

Table I: Model results for horizontal distribution of small-medium colonies (≤ 6.9 mm; GLM) and large colonies (≥ 7 mm; GLMM) of *Pyrosoma atlanticum*. * α = 0.05; std = standardized variables; n.s. = non-significant; + variable still included in the model following AIC criteria.

Model	Parameter	Estimate	z-value	p-value
GLM	Intercept	$-1.50e^{5}$	-4.95	< 0.01*
	Temperature (10 m)	2.41	3.95	< 0.01*
	Density (30 m)	$1.04e^{4}$	4.96	< 0.01*
	Density (30 m)^{2}	$-1.81e^{2}$	-4.97	< 0.01*
GLMM	Intercept	-6.85	-22.22	< 0.01*
	Bathymetry (std)	2.12	4.22	< 0.01*
	Bathymetry (std)^{2}	-0.76	-3.01	< 0.01*
	Chlorophyll-*a* (10 m) (std)	-0.54	-1.64	0.101 n.s.+

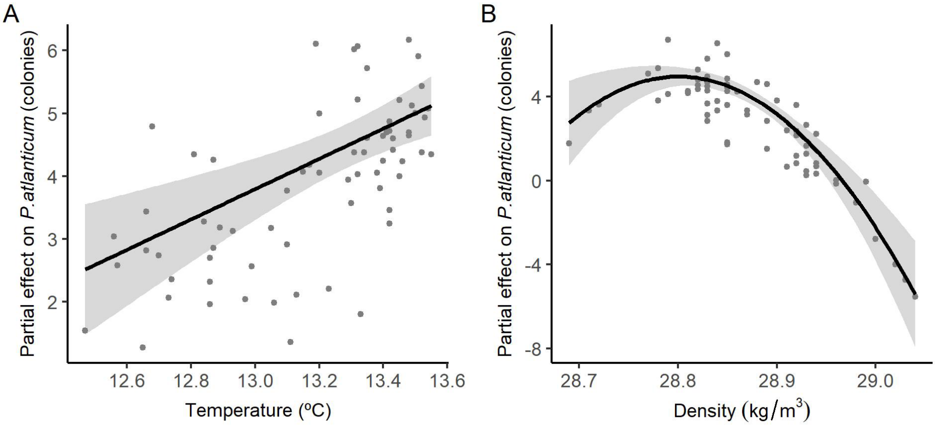


Fig. 5: Partial effect of temperature (10 m; a) and density (30 m; b) on small-medium (≤ 6.9 mm) *Pyrosoma atlanticum* colonies (number). Partial effect shows the change in response variable for each value of the variable on the x-axis, holding all other variables constant (median). Central (bold) lines show the best fit, the shaded areas show the 95% confidence intervals of the GLM model and dots correspond to observations.

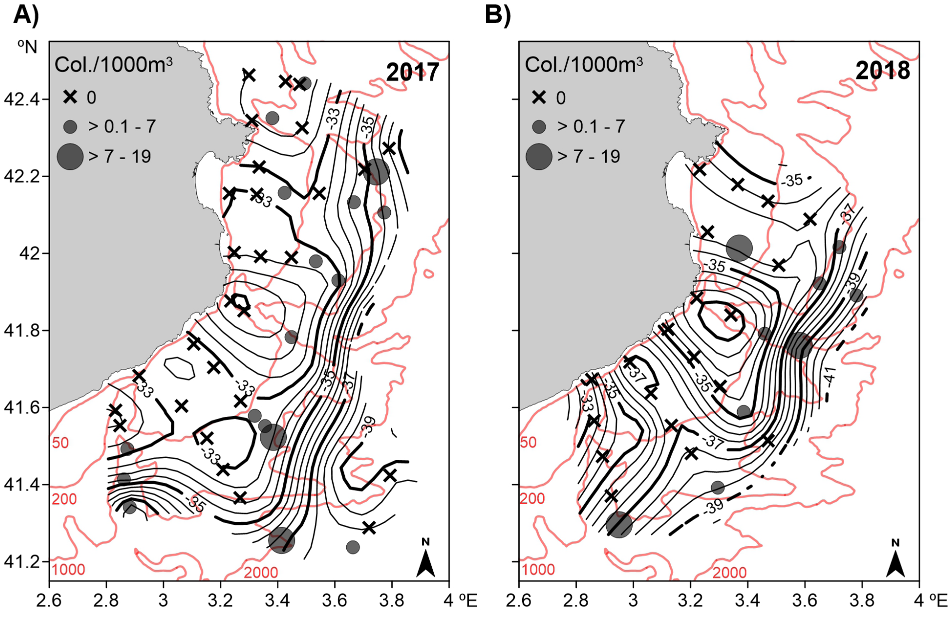
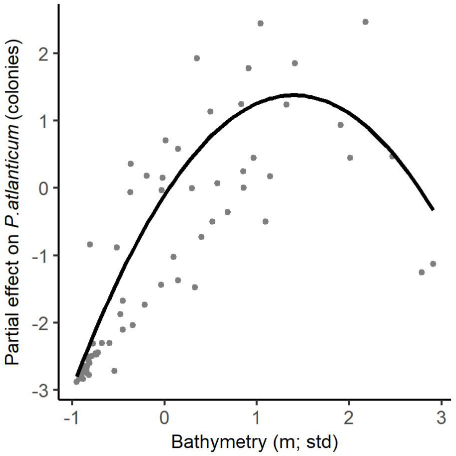


Fig. 6: Horizontal distribution of large (≥ 7 mm) *Pyrosoma atlanticum* colonies overlaid on dynamic height (contour lines; dynamic cm) at 30 m relative to 500 m and bathymetry (in red; 50, 200, 1000 and 2000 m) in 2017 (a) and 2018 (b).

Fig. 7: Partial effect of bathymetry (standardized) on large (≥ 7 mm) *Pyrosoma atlanticum* colonies (number). Partial effect shows the change in response variable for each value of the variable on the x-axis, holding all other variables constant (median). Bold line show the best fit of the GLMM model and dots correspond to observations.



Vertical distribution of *P. atlanticum*

The GLM analysis indicated a significant effect ($p < 0.01$) of the colony size class (< 4 mm, 4–6.9 mm, ≥ 7 mm), light level (day/night), and mean chl-*a* concentration by sampling strata on *P. atlanticum* vertical distribution (Table II). During the night, colonies of all size classes were located in the upper part of the water column (WMD was 36 m, 39 m and 67 m for the small, medium and large colonies, respectively; Table III), while during the day their distribution varied significantly depending on the colony size. Thus, during daylight hours, small colonies remained in the upper part of the water column (WMD = 69 m), medium size colonies showed a slightly deeper distribution (WMD = 110 m) with a migration amplitude of 71 m, and large colonies were located deeper (WMD = 304 m), with a migration amplitude of 237 m (Fig. 8, Table III), reaching a maximum depth of 550 m. The fine-scale vertical distribution obtained at the fixed station performed in 2017 (see Fig. 1) followed the pattern described above and allowed us to visualize its relation to the chl-*a* concentration in the water column (Fig. 9). Small colonies remained, day and night, in the upper part of the water column (mainly between 10 and 40 m), coinciding with a high chl-*a* concentration in these waters. Medium colonies were also located between 10 and 40 m at night, while during the day they showed a wider distribution (between 10 and 120 m), around 52% of the colonies migrating downwards and the rest remaining in the upper layers (Fig. 9). This distribution pattern was followed by colonies of each millimetre (4, 5 and 6 mm) within this medium size class (Fig.

Table II: GLM results for chlorophyll-*a*, colony size class [< 4 mm (small), 4–6.9 mm (medium) and ≥ 7 mm (large)] and light (day-time/night-time) effects on *Pyrosoma atlanticum* vertical distribution. *α = 0.05; std = standardized variable.

Parameter	Deviance	Pr (>Chi)
Mean chl-*a* (std)	102.52	< 0.01*
Colony size	59.60	< 0.01*
Light (day/night)	8.92	< 0.01*
Colony size : light (day/night)	16.16	< 0.01*

Table III: Average weighted mean depth (WMD) and standard deviation (sd) during day-time and night-time and migration amplitude of *Pyrosoma atlanticum* by colony size class.

	WMD (m)				
	Day		Night		Migration amplitude (m)
Size class	mean	sd	mean	sd	
< 4 mm (small)	69	35	36	19	33
4 – 6.9 mm (medium)	110	55	39	34	71
≥ 7 mm (large)	304	146	67	64	237

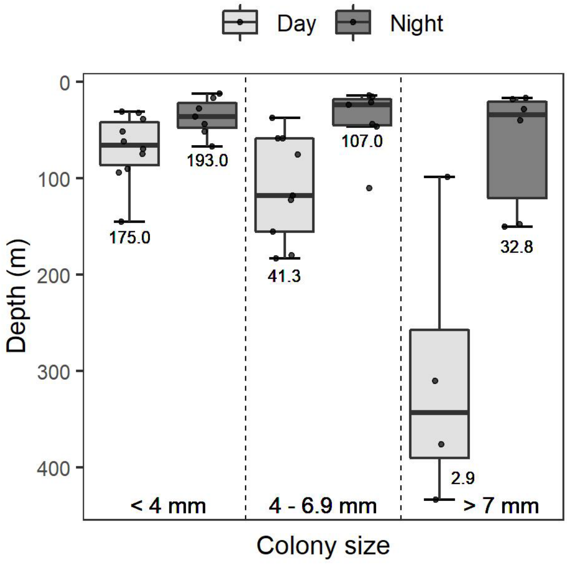


Fig. 8: Weighted mean depth (WMD) of *Pyrosoma atlanticum* by colony size class [< 4 mm (small), 4–6.9 mm (medium) and ≥ 7 mm (large)] during day-time (light grey) and night-time (dark grey). The central marks of each box represent the median of the WMD, the boxes show the interquartile ranges and the whiskers correspond to the ranges of observations. Mean abundance of colonies is indicated below each box (col./1000m^3).

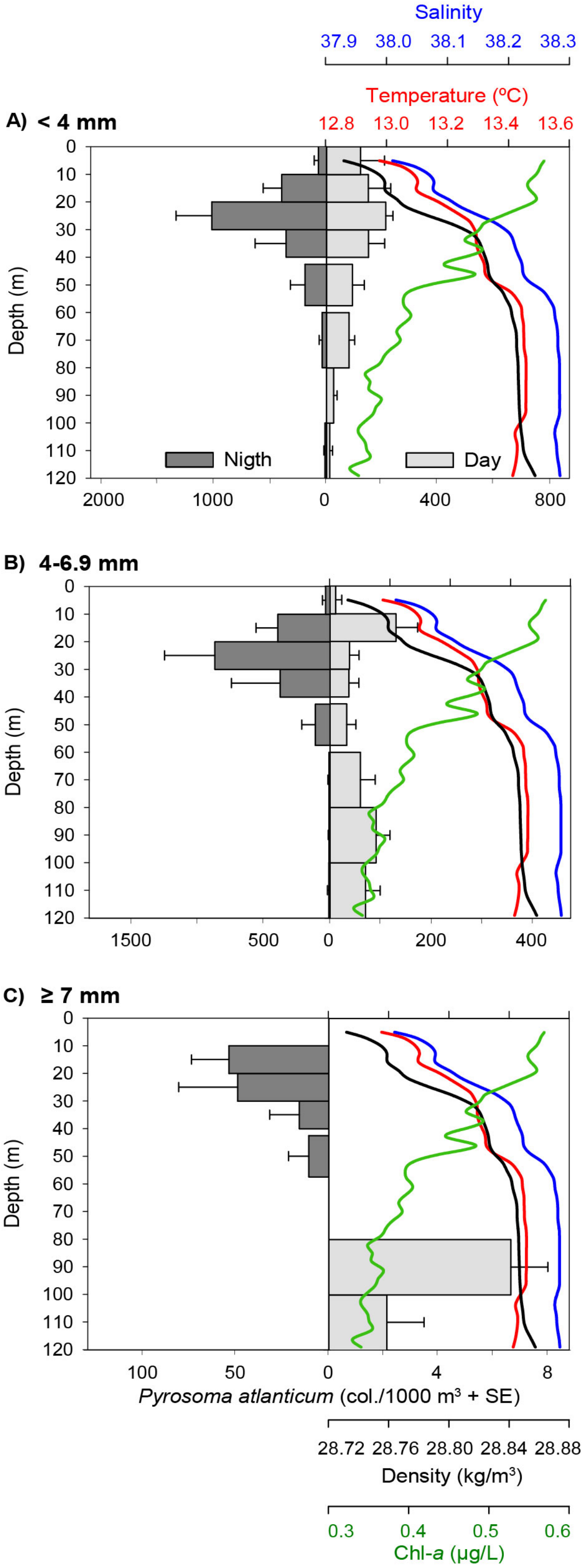


Fig. 9: Mean vertical distribution (+ standard error) of *Pyrosoma atlanticum* by colony size class [< 4 mm (small), a; 4–6.9 mm (medium), b; ≥ 7 mm (large), c] in night-time (dark grey bars) and day-time (light grey bars), overlaid on vertical profiles of temperature (red), salinity (blue), density (black) and chlorophyll-*a* (green). Note that the colony abundance scales are different for each size class. Data correspond to the 48 h fixed station sampled in 2017 (see Fig. 1).

S1). Large colonies showed a clearly different distribution between day and night, being located in shallow (10–30 m) productive waters during the night and in deeper waters (below 80 m) during the day (Fig. 9). Overall, the abundance of colonies was higher during the night than during the day, and this pattern was more marked in the largest size class (Fig. 8, 9).

Discussion

Our study evidenced that the spatial distribution (horizontal and vertical) of *P. atlanticum* in the Mediterranean Sea depends on the colony size and is ultimately determined by oceanographic and biological structures. The abundance and size range of *P. atlanticum* colonies found in our study were similar to those recorded previously in the NW Mediterranean: maximum abundance of 7 col./1000m^3, 8–88 mm long (Andersen et al., 1992); max. 187 col./1000m^3, 3–51 mm (Andersen and Sardou, 1994); max. 2000 col./1000m^3, 20 mm (Braconnot and Goy, 1981); max. 900 col./1000m^3, 4–6 mm and max. 213 col./1000m^3, 50 mm long (Granata et al., 2020). In the Atlantic and Pacific oceans the abundances reported using a similar sampling methodology were much higher and colonies were generally larger, reaching 41000 col./1000m^3 for colonies between 50 and 65 mm long (Drits et al., 1992) and 5000 col./1000m^3 for colonies between 60 and 780 mm long (Schram et al., 2020). In both years studied, the small size classes were dominant (Fig. S2), suggesting that sexual reproduction occurs in winter (Franqueville, 1971; Braconnot, 1974). Several studies carried out in the Mediterranean and northeast Pacific also reported a high abundance of small colonies in late winter and spring (Franqueville, 1971; O'Loughlin et al., 2020; Lyle et al., 2022). Although in both years the sampling was conducted in February, in 2017 the abundance of small-medium (≤ 6.9 mm) colonies was very high, the largest registered in the Mediterranean (Andersen and Sardou, 1994; Granata et al., 2020). This exceptional abundance might be related to an earlier development of spring conditions and the subsequent seasonal phytoplankton bloom in 2017 in comparison with 2018 (Mir-Arguimbau et al., 2022). The life history traits of *P. atlanticum*, with short generation times and rapid growth, could allow for a rapid population increase during suitable trophic conditions associated with the seasonal production bloom (Alldredge and Madin, 1982).

Horizontal distribution of *P. atlanticum*

The mesoscale distribution of *P. atlanticum* showed that large (≥ 7 mm) colonies were found on the slope (around 400 m depth), coinciding with the presence of the front all along the area (Fig. 6). This suggests that the species inhabits waters over the slope, and the front could aggregate and prevent its dispersion towards the open sea, as reported in other zooplanktonic organisms in the area (Masó et al., 1998; Guerrero et al., 2016). However, the lack of sampling beyond the front precludes any knowledge of the abundance and distribution of *P. atlanticum* in open sea waters, where the species has also been found in the Mediterranean (Bo et al., 2020; Granata et al., 2020). Though it is a filter feeder, a negative but non-significant relationship was found between colony abundance and chl-*a* concentration (Fig. 2e, f, 6, S5). It has been reported that high abundances of phytoplankton prey, usually found in coastal waters, may become harmful because the mucous filters of *P. atlanticum* can become clogged (Harbison et al., 1986; Lyle et al., 2022). Also, it has been suggested that food quality rather than its availability is a determining factor in the species distribution (Schram et al., 2020). However, Henschke et al. (2019) reported that chl-*a* concentration was a significant driver of *P. atlanticum* biomass.

In both years studied, small-medium colonies were present throughout the area, with the highest abundances along the edge of the shelf, being very low close to the coast, where the waters were colder and less saline (Fig. 2a, b, c, d, 4). However, the presence of *P. atlanticum* in colder (7-10°C) (Thompson, 1948; Sutherland et al., 2018) and less saline (31-33) waters than the Mediterranean (Schram et al., 2020) suggests that the temperature and salinity values detected near the coast do not represent a limitation to its distribution, and the low abundance of *P. atlanticum* in the coastal area is probably associated with the intrusion of a coastal water mass. A high abundance of small-medium colonies was found at the moderate water density values that were found at the shelf edge, close to the highest abundance of large colonies on the slope (Fig. 2g, h, 4, 6). This distribution would support the idea that the young colonies would be offspring of the large ones, taking into account that sexually mature zooids appear in colonies of 40 mm onwards (Van Soest, 1981) and that young colonies grow rapidly (coefficients of exponential growth of 0.24–0.75 per day on a length basis (Andersen and Sardou, 1994)). Overall, the observed distributions suggest that large *P. atlanticum* inhabit waters over the slope, where reproduction might take place, in association with the front, and the presence of young colonies on the shelf could be related to the offshore water intrusions associated with instabilities of the front (Sabatés et al., 2004). Similar observations have been made in this area for other gelatinous organisms. Sabatés et al. (2018) reported that adult stages of the Scyphozoan *Pelagia noctiluca* were found along the slope in association with the front. Ephyrae (young stages), which inhabit surface waters (Ottmann et al., 2021; Pastor-Prieto et al., 2021), showed a wider distribution extending over the shelf and their occurrence was associated with offshore water intrusions generated by the oscillatory behaviour of the front. The frontal area is a transitional zone with enhanced primary and secondary production (Ibanez and Boucher, 1987; Estrada and Margalef, 1988; Sabatés et al., 2004) that offers favourable feeding conditions for the reproduction, growth and survival of gelatinous organisms. Nevertheless, it is possible that *P. atlanticum* colonies, as planktonic organisms with limited horizontal mobility, were passively accumulated in that area by physical discontinuities of the ocean, such as fronts and pycnoclines (Graham et al., 2001; Greer et al., 2015, 2018). Studies conducted in the Atlantic and Pacific oceans have suggested that *P. atlanticum* colonies were located in open sea waters (Angel, 1989; Brodeur et al., 2018) and that they may have been transported by advection to the shelf, where they were less abundant (Miller et al., 2019; Schram et al., 2020; Lyle et al., 2022).

Vertical distribution of *P. atlanticum*

The analysis of the vertical distribution of *P. atlanticum* allowed us to detect different migration amplitudes as a function of colony size (Fig. 8). Small colonies showed no diel vertical migration, being mainly located in the upper 40 m of the water column during both day and night, as previously observed by Palma (1985) in the Mediterranean (Fig. 9). The migratory behaviour of remaining in the surface layers during the night and going to deeper layers during the day started in some colonies of 4 mm, 5 mm, and 6 mm (the medium size class), but not all colonies of these sizes exhibited this behaviour (Fig. S1). This would suggest that migration, as an individual response, can start at any of these sizes. The migration amplitude increased from 71 m in medium colonies to 237 m in the large ones. A similar migration amplitude (210 m) for the same size colonies was reported by Sardou et al. (1996) in the Mediterranean, while other studies described more extensive migrations in that area (515 m) (Andersen et al., 1992) and in the Atlantic Ocean

(650 m) (Roe et al., 1987; Angel, 1989; Andersen et al., 1992). Considering that *P. atlanticum* is a strong vertical migrator, being able to reach depths of up to 900 m in the Mediterranean (Sardou et al., 1996) and 2500 m in the Atlantic (Roe et al., 1987), the limited maximum depth reached in our study (550 m) might be related to the lower depth of our samplings (maximum 550 m). The lower abundance of colonies during the day than during the night, particularly in the largest size class, could be due to the location of colonies below the sampling depth (Fig. 8).

In the present study, the lack of stratification typical of winter conditions allowed us to observe the migratory behaviour of the species without the presence of clines that could influence their vertical movement (Graham et al., 2001). Peak densities of colonies had been associated with vertical gradients of environmental parameters such as density and fluorescence (Lyle et al., 2022). The shallow levels reached by medium and large colonies during the night correspond to the highest values of chl-*a* in the water column (Fig. 9), a proxy of photosynthetic taxa, the main prey of the species (Drits et al., 1992; Perissinotto et al., 2007). *P. atlanticum* mainly feeds on a wide variety of phytoplankton (e.g. diatoms, dinoflagellates, prymnesiophytes and coccolithophores (Drits et al., 1992; Perissinotto et al., 2007)) by continuous filtration of seawater (Alldredge and Madin, 1982). Thus, colonies would be expected to find higher food availability in surface waters than in deeper ones. On the other hand, pelagic tunicates also exhibit high filtration rates of microbial prey, including heterotrophic bacteria (Sutherland et al., 2010; Sutherland and Thompson, 2021; Thompson et al., 2021), which probably allow them to feed at depth and supplement the food acquired in surface waters. The vertical migration pattern observed in *P. atlanticum* is that followed by most zooplankton, which ascend to upper layers during the night to take advantage of the high phytoplankton abundance at the surface before returning to deeper layers during the day (Lampert, 1989; Saiz et al., 2014) to avoid predation in the illuminated layers (Bollens and Frost, 1989). However, other factors such as reproductive behaviour may also play a role, with adults migrating towards the surface to provide a suitable environment for the development of their offspring (Lampert, 1989; Ferraris et al., 2012). The location of small colonies both day and night in the upper layers, where chl-*a* levels are highest, suggests a strategy of maximizing the colony growth to reduce the high predation rates of small size organisms (Miller et al., 1988). Ontogenetic variations in the vertical distribution are a common trait of other zooplanktonic taxa, such as copepods (Andersen et al., 2001) and euphausiids (Pillar et al., 1989), with younger stages inhabiting shallower waters and adults performing the typical diel vertical migration pattern. It should also be considered that the permanency of small colonies in surface waters may be related to their limited migratory capacity, since their propulsive capacity—and hence migratory amplitude—increase with colony size. The growth of the colony would not only increase its propulsive capacity, but also enhance its visibility, forcing the colony to migrate deeper to avoid visual predators (Angel, 1979). It is unclear whether the increase in migration amplitude with colony size is due to higher visibility, increased propulsive capacity, or a combination of the two.

Ecological implications

The vertical migration performed by *P. atlanticum* might enhance the vertical transport of carbon to deeper waters. The species shows one of the highest clearance rates of any zooplankton grazer (Perissinotto et al., 2007), rapidly producing a high amount of faecal pellets (Drits et al., 1992) that are transported to deep waters through diel vertical migration (Henschke et al., 2019). It has been reported that mass deposition of *P. atlanticum* may provide an extra input of carbon to benthic consumers (Carrassón and Cartes, 2002; Lebrato and Jones, 2009; Lebrato et al., 2013), which rely on the contribution of nutrients from the surface (Smetacek, 1984). In bloom conditions, *P. atlanticum* can exert considerable control over phytoplankton standing stocks (Drits et al., 1992; O'Loughlin et al., 2020) through competition or direct grazing, playing an important role in the marine food web dynamics (Andersen, 1998; Lavaniegos and Ohman, 2003). Although several *P. atlanticum* bloom events have been reported worldwide, the most impressive was detected in the northeast Pacific, with high abundances of large colonies lasting several years, disrupting marine activities and altering the ecosystem (Brodeur et al., 2018, 2019; Schram et al., 2020). In the NW Mediterranean, the smaller colonies (Andersen et al., 1992; Andersen and Sardou, 1994; this study) and weaker blooms of *P. atlanticum* and other filter-feeding gelatinous taxa than in other regions (Andersen, 1998; Granata et al., 2020; O'Loughlin et al., 2020) could be related to the oligotrophic nature of this sea. Following Henschke et al. (2019), we have estimated that downward carbon transport in our study area would be around 5.26 µg $C/m^3 \cdot d$ (0.56 mg $C/m^2 \cdot d$) in 2017 and 0.54 µg $C/m^3 \cdot d$ (0.05

mg C/m^2·d) in 2018 (defecation contributing to ≈ 17% and ≈ 14%, respectively; see supporting information). These values would be at the lower limit of the estimated ranges of downward carbon transport (0.42 to 59.57 mg C/m^2·d) by mesozooplankton and macrozooplankton communities in the Mediterranean (Frangoulis et al., 2011; Isla et al., 2015; Yebra et al., 2018). Compared to previous estimates for *P. atlanticum*, our obtained values were two and three orders of magnitude lower than the 363 µg C/m^3·d reported in the Tasman Sea (Henschke et al., 2019). However, considering the chl-*a* (i.e. carbon) concentration in the upper water layers observed in both regions (1.33 µg chl-*a*/L in the Tasman Sea, 0.65 µg chl-*a*/L in 2017 and 0.86 µg chl-*a* /L in 2018 in our study area), these differences decrease by one order of magnitude each year (see supporting information). However, the lower values estimated in the present study are probably related to the smaller size of colonies than those observed in the Tasman Sea (range: 11-318 mm) (Henschke et al., 2019).

Although our results show a strong difference in the abundance of *P. atlanticum* in the two years studied, longer time series would be necessary to confirm the high interannual variability that has been described for gelatinous zooplankton in the Mediterranean (García-Comas et al., 2011; Fullgrabe et al., 2020; Feuilloley et al., 2021). This high variability has been related to the winter environmental conditions, which cause mixing of the water column and the input of nutrients to the surface waters, ultimately modulating the phytoplankton bloom (García-Comas et al., 2011; Fullgrabe et al., 2020). The recently observed climatic trends for the Mediterranean, showing an increase in sea water temperature, a lower wind speed and a lengthening of the seasonal stratification period (Rixen et al., 2005; Calvo et al., 2011; Vargas-Yáñez et al., 2017), could modify the intensity and regularity of phytoplankton blooms, altering the abundance, distribution, and species composition of gelatinous zooplankton (Guerrero et al., 2018a). Future studies should address the long-term interannual variability of *P. atlanticum*, as well as relevant aspects of its biology (e.g. feeding and propulsive capacity) to understand its ecological role in the current context of climate change in the Mediterranean.

Conclusions

The mesoscale and vertical distribution of *P. atlanticum* in the NW Mediterranean were shaped by the oceanographic and biological structures, as well as by the ontogenetic stage of the colonies. The higher abundance of colonies in 2017 than in 2018 was likely related to an earlier onset of the phytoplankton bloom. Large colonies (≥ 7 mm) were found on the slope, in association with the shelf-slope front, which would aggregate them, preventing their dispersion towards the open sea. Small (< 4 mm) and medium (4–6.9 mm) colonies extended their distribution over the shelf owing to instabilities of the front, and were practically absent in the cold, low salinity coastal waters. The vertical migration amplitude increased with colony size. At night colonies of all sizes remained close to the surface, where chl-*a* levels were high, while during the day they migrated to deeper layers, reaching greater depths as colony size increased. The migratory behaviour started when colonies were 4–6.9 mm long, though not all colonies of these sizes exhibited this behaviour, suggesting that migration can start at any of these sizes. This vertical migration might contribute to carbon transport to depth. Our observations shed light on these gelatinous organisms, scarcely studied in the Mediterranean, which may play a relevant role in the marine trophic web.

Acknowledgements

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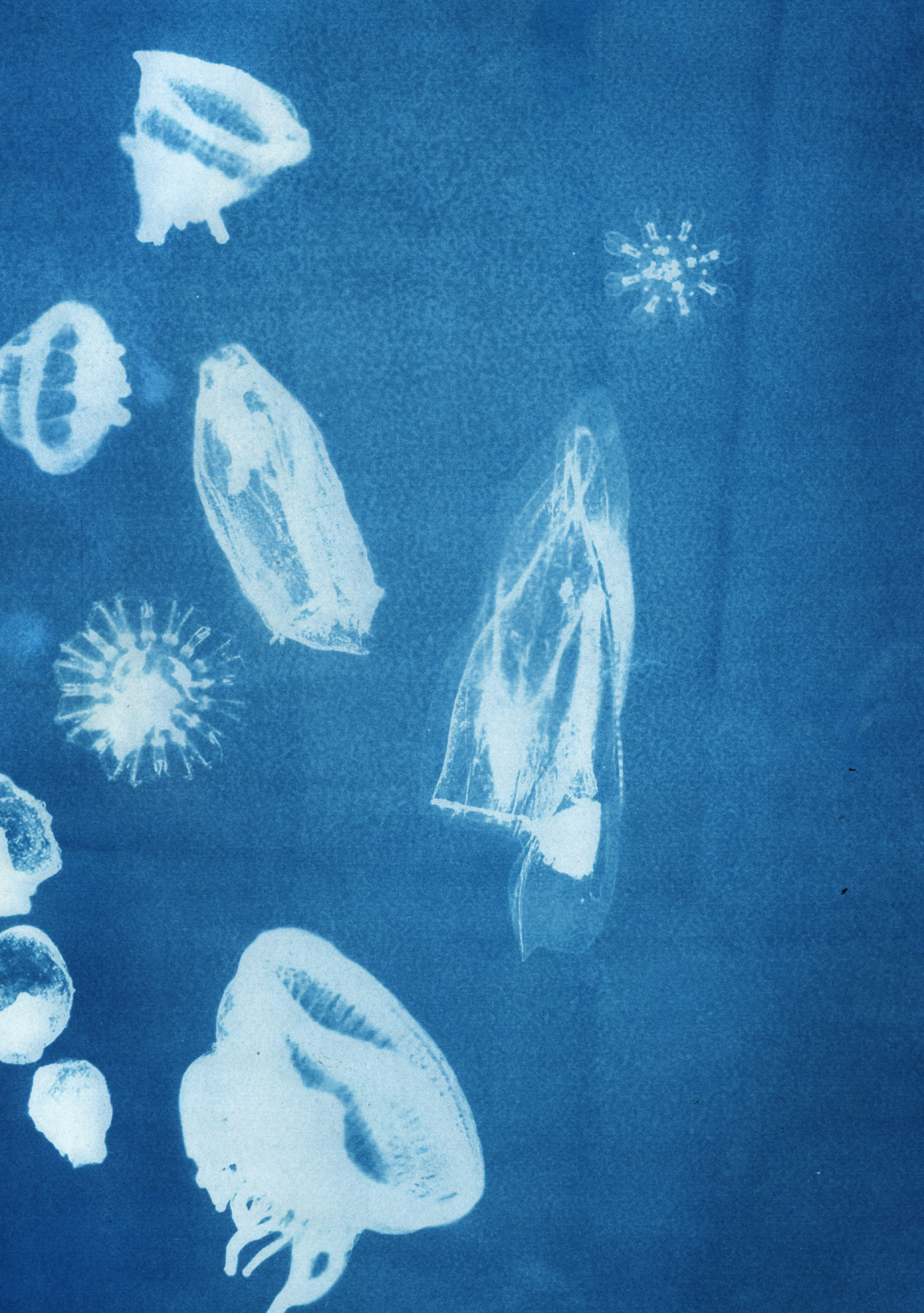

Chapter III

Assemblages of planktonic cnidarians in winter and their relationship to environmental conditions in the NW Mediterranean Sea

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Abstract

In the present study we addressed the spatial characterization and species assemblages of the planktonic cnidarian community (Siphonophorae, Hydromedusae and Scyphomedusae) in winter, a scarcely studied period in the NW Mediterranean. Data were obtained on two oceanographic cruises (February 2017 and 2018). Our results revealed a higher species richness in 2017 in relation to an advancement of the spring conditions and the subsequent phytoplankton bloom, favouring a mixture of winter and spring species. The "typical" winter oceanographic conditions in 2018 might have allowed the development of the winter species populations resulting in higher abundances of cnidarians. The most abundant species in both winters were *Lensia subtilis*, *Muggiaea kochii, Chelophyes appendiculata*, *Abylopsis tetragona* (eudoxid), *Aglaura hemistoma* and *Velella velella* larvae, while *Obelia* spp. was particularly numerous in 2017. In both years, the species assemblages presented a coastal-offshore ordination resulting from the combined effect of environmental variables, particularly bathymetry, and oceanographic structures, as water masses and the shelf-slope density front. This ordination was only disrupted over the submarine canyons where coastal and offshore cnidarian communities were found together. Our results highlight the relevance of studying the planktonic cnidarians in winter and during the transition periods to gain a comprehensive knowledge of its spatial and temporal variability throughout the annual cycle.

Introduction

Gelatinous zooplankton constitutes a large component of the zooplankton biomass, with a widespread distribution in all oceans (Pugh, 1989; Brotz et al., 2012; Lucas and Dawson, 2014). Within gelatinous zooplankton, cnidarians (Siphonophorae, Hydromedusae and Scyphomedusae) are one of the most representative groups, both in terms of abundance and species richness (Alldredge, 1984; Alan R. Longhurst, 2006) and exhibit a wide variety of life cycle strategies (Fautin, 2002). Those taxa with a planktonic phase can be classified as holoplanktonic (lack of benthic stage, such as in Siphonophorae and certain Hydromedusae and Scyphomedusae) or as meroplanktonic (presence of benthic stage, such as some Hydromedusae and Scyphomedusae) (Bouillon et al., 2004; Boero et al., 2008). The particular life-cycles of cnidarians, with the ability to rapidly produce new individuals, allow them to reach high abundances when environmental conditions are favourable (Boero et al., 2008). In these situations, they can exert severe effects on the planktonic community through direct predation or competition for food (Alldredge, 1984; Behrends and Schneider, 1995; Nicholas and Frid, 1999). In temperate seas, like the Mediterranean, the species composition and abundance of planktonic cnidarians is highly seasonal and is ultimately determined by climatic and oceanographic conditions (through changes in salinity, temperature and water stratification) (Batistic et al., 2004; García-Comas et al., 2011; Saiz et al., 2014). As part of the plankton, the distribution and abundance of cnidarians are influenced by oceanographic structures, such as currents, eddies and fronts (Graham et al., 2001; Guerrero et al., 2016; Pastor-Prieto et al., 2021). These structures can drive the aggregation and spreading of organisms, determining the species assemblages of an area.

The Mediterranean Sea is considered a complex marine environment because of the variety of physical processes operating in it, including deep water formation, thermohaline circulation, and mesoscale activity (Pinardi and Masetti, 2000). The plankton productivity in the Mediterranean is influenced by a variety of physical factors, acting at both local and regional scales, whose effect in most cases depends on the seasonal cycle. During the year, the upper layer of the water column containing the photic zone shifts from a period of well-mixed water (winter) to a strongly stratified one (summer) that confers a marked seasonality to primary production (Estrada et al., 1985). Recurrent late winter-early spring blooms are only observed regularly in the northwestern region (D'Ortenzio and Ribera D'Alcalà, 2009) triggered by deep water formation episodes that take place in the Gulf of Lions (MEDOC Group, 1970; Schott et al., 1996). Interannual variability in primary production is highly dependent on the intensity of these episodes, which increase in colder and drier years (Marty and Chiavérini, 2010; Herrmann et al., 2013). The late winter-early spring bloom is generally followed one month later by a zooplankton peak (Nival et al., 1975; Bozzano et al., 2014), with the maximum cnidarian abundance taking place in spring and beginning of summer (Gili et al., 1987b; Saiz et al., 2014).

The Catalan coast, located in the NW Mediterranean, has a narrow continental shelf and is furrowed by the Blanes and Palamós canyons. The oceanographic dynamics is characterized by the presence of a permanent shelf-slope density front along the slope, that separates coastal low-salinity waters from open sea high-salinity waters (Font et al., 1988). A geostrophic current, the Northern Current, associated with the front flows from NE to SW (Millot, 1999) and may interact with the canyons, strongly modifying the local circulation and generating shelf-slope water exchanges (Flexas et al., 2008). The mesoscale variability of the front and the associated current have been described to play a key role in the distribution and aggregation of planktonic organisms (e.g. Ibanez and Boucher, 1987; Guerrero et al., 2016; Pastor-Prieto et al., 2022). The coastal area is under the influence of continental runoff waters that contributes to surface productivity in these areas (Salat and Pascual, 2006). All these regional features result in a high physical heterogeneity that has a major role in the organization of zooplanktonic communities (Alcaraz et al., 2007; Sabatés et al., 2007; Olivar et al., 2010).

In the NW Mediterranean, the study of planktonic cnidarians, at a broad taxonomic level, has been addressed through the analysis of zooplankton time series, allowing to identify their seasonal variability, with maximum abundances in spring and beginning of summer, as well as their interannual variability in relation to environmental changes (García-Comas et al., 2011; Licandro et al., 2012; Fullgrabe et al., 2020). In addition, several studies have also addressed the analysis of the vertical distribution of the most abundant cnidarian species, e.g. *Abylopsis tetragona*, *Chelophyes appendiculata* and *Aglaura hemistoma* showing different nictemeral migration patterns (Sardou et al., 1996; Buecher and Gibbons, 1999). However, all these studies were carried out at few stations and over limited geographical areas. The mesoscale distribution of cnidarians and species assemblages in relation to oceanographic structures have been mainly studied in spring and summer (Gili et al., 1988; Licandro and Ibanez, 2000; Guerrero et al., 2018a) and no information is available for the winter season. Although the maximum abundance of cnidarians occurs in spring and beginning of summer, after the seasonal phytoplankton bloom, the winter conditions, with an homogeneous water column, high nutrient concentrations, and moderate phytoplankton levels (Latasa et al., 2022), make the study of the cnidarian community of special interest in this period.

In the present study we addressed the spatial characterization and species assemblages of the whole planktonic cnidarian community (Siphonophorae, Hydromedusae and Scyphomedusae) during two consecutive winters. The specific objectives were to (1) provide a comprehensive description of the species composition, abundance and diversity of the cnidarian community; (2) determine the spatial distribution of species assemblages; and (3) explore the influence of environmental conditions on the spatial structure of cnidarian species.

Methods

Field sampling

Two oceanographic cruises were conducted in the NW Mediterranean (41.3–42.5ºN and 2.8–3.8ºE) during two consecutive winters (18 February–20 March 2017 and 18–28 February 2018) on board the R/V García del Cid. Sampling stations, 44 in 2017 and 29 in 2018, were placed along transects perpendicular to the coast and located 7–14 km apart (Fig. 1). At each station, vertical profiles of basic hydrographic variables (temperature and salinity) were obtained by means of a conductivity-temperature-depth profiler (CTD) equipped with a fluorometer, and data were interpolated to 1 m depth intervals. Dynamic heights at the stations were calculated with a reference depth level of 500 m. Where station depth was lower, dynamic height was extrapolated using the continuity equation applied to the deepest level of three-station clusters (cf. Hidaka, 1940).Water samples for chlorophyll-*a* (chl-*a*) determination were collected at some stations using a rosette system at three depths down to 80 m throughout the day and night in order to calibrate the fluorometer. The chl-*a* concentration (µg/L) was determined fluorometrically (Yentsch and Menzel, 1963). Water samples of 150 mL were filtered through Whatman GF/F filters. Chl-*a* was extracted from filters immersed in 6 mL of 90% acetone (24 hours at 4°C in darkness) and the extract was analysed with a Turner Designs fluorometer calibrated with pure chl-*a*. The relationship between chl-*a* concentration and fluorescence obtained in each survey was used to convert the continuous CTD fluorescence register into the chl-*a* concentration.

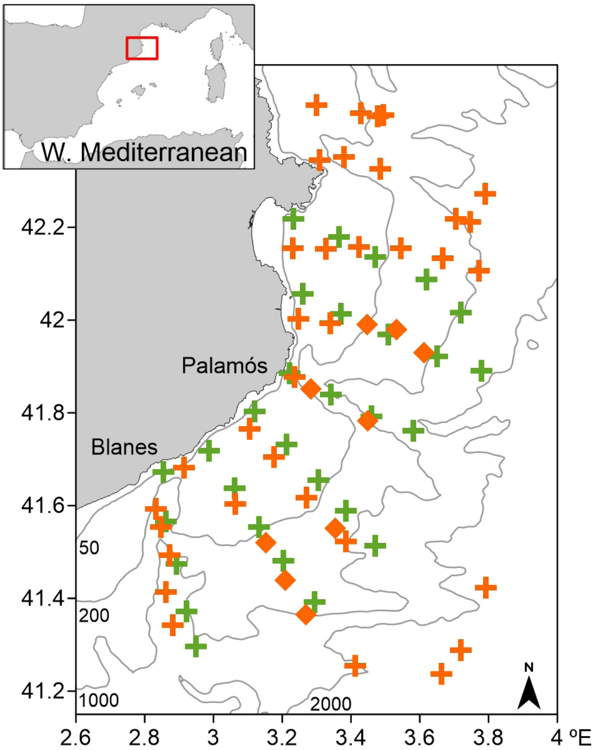

Fig. 1: Study area in the NW Mediterranean. Sampling stations during 2017 (orange) and 2018 (green) surveys. Crosses indicate stations sampled using Bongo net, diamonds stations sampled using MOCNESS net. Thin grey lines show isobaths (50, 200, 1000 and 2000 m).

Zooplankton sampling was performed using a Bongo net of 60 cm diameter and 300 µm mesh size. The net was towed obliquely from a maximum depth of 500 m, or 5 m above the seafloor at shallower stations, to the surface at a vessel speed of 3.7 km/h (Fig. 1). At 9 stations in 2017, sampling was performed using a MOCNESS net (1 m^2 mouth opening and 300 µm mesh size) towed obliquely from a maximum depth of 500 m, or 5 m above the seafloor, at a ship speed of 3.7–4.6 km/h. The volume of filtered water was recorded by a flowmeter placed in each net mouth. Immediately after collection, the zooplankton samples were fixed in 5% formaldehyde buffered with sodium tetraborate.

Sample processing and data analysis

In the laboratory, the planktonic cnidarian community (Siphonophorae, Hydromedusae and Scyphomedusae) was analysed to the species level or to the lowest taxonomic level possible using a stereomicroscope. In most samples all organisms were counted, but when the abundance was high (26 % of stations), 1/3 or 1/2 aliquots were taken and all individuals from each taxon were counted. Calycophoran polygastric stages were counted as the number of complete colonies, plus the highest number of either anterior or posterior nectophores (Guerrero et al., 2018b). The number of eudoxid sexual stages of *Abylopsis eschscholtzii*, *A. tetragona*, *Enneagonum hyalinum* and *Eudoxoides spiralis* was obtained from counts of intact eudoxid and detached bracts. Colony numbers of *Hippopodius hippopus* and physonect siphonophores were obtained from nectophore counts divided by 10 (Pugh, 1984) or from pneumatophore counts (when present in physonect) if the latter were higher. The number of medusae, siphonophore colonies and eudoxid stages collected by the Bongo net was standardized to a number per 1000 m^3 of filtered water. The number of these taxa collected by the MOCNESS net at each depth stratum were pooled and divided by the sum of the filtered water at each stratum and standardized to a number per 1000 m^3 of filtered water to be comparable with the Bongo data.

For each species and cruise the mean abundance, the relative abundance (RA, percentage of contribution of a species to the total abundance of the cnidarian community) and the frequency of occurrence (FO, percentage of stations where a species was present) were calculated. For each station and cruise, the species richness (S, total number of species) and diversity (H', Shannon-Weaver diversity index; using natural logarithm) of the cnidarian community were calculated considering only the polygastric stage when polygastric and eudoxid stages were present.

To determine the structure of the winter cnidarian community, a cluster analysis was performed using the species composition and abundance from each cruise and station. Rare taxa (<4 % FO) were discarded from the analysis and cnidarian abundances were ln(x+1) transformed. Clustering of stations was carried out using Bray–Curtis index and Ward's hierarchical agglomeration method. To discern patterns in cnidarian assemblages, a non-metric multidimensional scaling analysis (nMDS; see Fig. S1.) was performed (Clarke, 1993). An adonis permutation multivariate analysis of variance and pairwise tests were used to test for significant differences in the cnidarian abundance and composition between clusters. All the analyses were performed using the "vegan" package (Oksanen et al., 2019).

To test the relationship between cnidarian species distribution and winter environmental conditions, a Redundancy Analysis (RDA) was performed on the matrices containing the cnidarian abundances and environmental variables measured during the cruises. The environmental variables initially considered were: surface (10 m depth) temperature (SST), salinity (SSS), density (SSSig) and chl-*a* (SSChla); mean chl-*a* from surface to 50 m depth (MChla_50), log transformed bathymetry (BAT) and distance from a sampling station to the coast (Dist_Coast). After evaluating collinearity between pairs of variables through the Pearson's correlation coefficients (cut-off value |0.6|), the independent environmental variables included in the RDA were: surface temperature, density and chl-*a*, and bathymetry. RDA was performed using the "vegan" package (Oksanen et al., 2019) and all the analyses were carried out using the R statistical programming language v3.5.3 (R Core Team, 2020). Maps of surface temperature, salinity, density and chl-*a* for 2017 and 2018 were generated by means of the minimum curvature interpolation method using Surfer® v13.4 (Golden software LCC, 2016).

Results

Hydrographic conditions

In both years, surface temperature and salinity increased towards the open sea (Fig. 2a, b, c, d). In 2017, the coastal zone showed low temperature (≈ 12.5ºC) and salinity, mainly in the northern part (≈ 37.2), while in the open sea the temperature reached 13.6ºC and salinity 38.4. In 2018, coastal waters also showed low temperature (≈ 12.9ºC) and relatively low salinity (≈ 38.3), and in the open sea salinity values were similar to those detected in the previous year and temperature was slightly lower, around 13.2ºC. On both cruises, the distribution of density increased from near the coast towards the open sea, following a similar pattern to that of salinity (Fig. 2e, f). In 2017 the coastal zone showed low density, particularly in the northern part of the area (≈ 28.1 kg/m^3) with values around 28.9 kg/m^3 in the open sea. In 2018, density was more homogeneous increasing towards the open sea (≈ 29.0 kg/m^3). In both years, the dynamic height overlaid on the surface density showed the signature of the shelf-slope front along the continental slope (Fig. 2e, f). Surface chl-*a* did not show a consistent pattern (Fig. 2g, h). In 2017, relatively high values were detected on the shelf, but also in the open sea (≈ 1.2 µg/L), while in 2018 high chl-*a* concentrations (≈ 1.9 µg/L) were found in the southwest part of the area.

Species composition and abundance

A total of 70 species of planktonic cnidarians were found in the two winters, 28 Siphonophorae, 38 Hydromedusae and 4 Scyphomedusae (Table I). In 2017, the species richness (56 species; range: 5 - 22) was higher than in 2018 (41 species; range: 9 - 21) (Table I). The abundance in 2018 (mean 878 ind/1000m^3 ± 920 standard deviation (sd)) was twice as high as in 2017 (400 ind/1000m^3 ± 629) and the three main groups (Siphonophorae, Hydromedusae, Scyphomedusae) showed this increase in abundance (Fig. 3, Table I). The Shannon-Weaver diversity index (H') was similar in both years (1.68 ± 0.39 in 2017 and 1.84 ± 0.22 in 2018).

Siphonophorae was the most abundant group in both winters, being *Lensia subtilis*, *Muggiaea kochii*, *C. appendiculata* and *A. tetragona* (eudoxid) the most numerous species (Fig. 3, Table I). Hydromedusae showed the highest species richness in both winters (Fig. 3) and the most abundant species were *A. hemistoma*

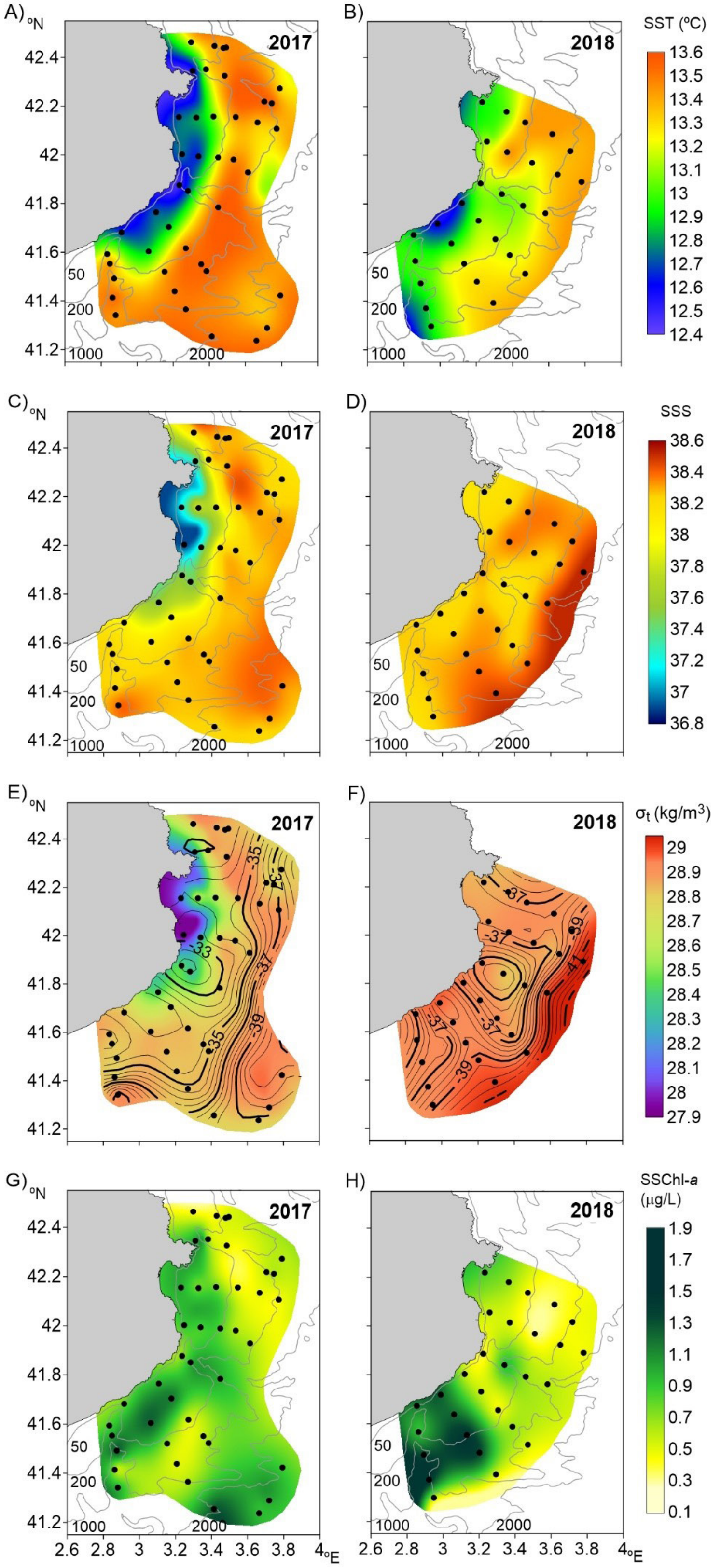

Fig. 2: Maps of surface temperature (SST; a, b), salinity (SSS; c, d), dynamic height (contour lines, dynamic cm) at 10 m relative to 500 m, overlaid on surface density (SSSig; e, f) and chlorophyll-*a* (SSChl-*a*; g, h) in winter 2017 (left panels) and 2018 (right panels). Thin grey lines show isobaths (50, 200, 1000 and 2000 m).

Table I: Mean abundance (± SD) and range values (ind/1000m^3), relative abundance (RA; %) and frequency of occurrence (FO; %) for all species found during winter (2017 and 2018) in the NW Mediterranean. E = eudoxid stage (sexual); P = polygastric stage (asexual); in Calycolphorae taxa, when not specified, refers to the polygastric stage.

	2017				**2018**			
	Mean ± SD	**Range**	**RA**	**FO**	**Mean ± SD**	**Range**	**RA**	**FO**
Total Cnidaria	**400.2 ± 628.65**	**30.52 - 2957.91**	**100**	**100**	**877.99 ± 919.69**	**147.1 - 4164.02**	**100**	**100**
Siphonophorae	**240.88 ± 378.91**	**18.5 - 1693.76**	**60.19**	**100**	**539.06 ± 593.4**	**81.1 - 2956.7**	**61.40**	**100**
Calycophorae								
Abylopsis eschscholtzii E	0.41 ± 1.17	0 - 5.25	0.10	13.95	-	-	-	-
Abylopsis eschscholtzii P	0.23 ± 1.12	0 - 7	0.06	6.98	-	-	-	-
Abylopsis tetragona E	18.1 ± 21.04	0 - 102	4.52	90.70	45.19 ± 30.64	0 - 122.07	5.15	96.55
Abylopsis tetragona P	6.03 ± 10.35	0 - 63.21	1.51	72.09	8.45 ± 9.58	0 - 40.36	0.96	86.21
Chelophyes appendiculata	17.85 ± 13.26	0 - 49.5	4.46	88.37	46.99 ± 22.01	0 - 88.62	5.35	96.55
Chelophyes contorta	0.12 ± 0.67	0 - 4.3	0.03	4.65	-	-	-	-
Enneagonum hyalinum E	-	-	-	-	1.36 ± 3.29	0 - 13.18	0.15	17.24
Eudoxoides spiralis E	0.17 ± 0.72	0 - 3.95	0.04	6.98	0.69 ± 2.64	0 - 11.93	0.08	6.90
Eudoxoides spiralis P	0.24 ± 0.83	0 - 4.53	0.06	11.63	2.79 ± 4.13	0 - 16.01	0.32	48.28
Hippopodius hippopus	0.34 ± 0.73	0 - 2.87	0.09	23.26	1.03 ± 2.15	0 - 9.59	0.12	34.48
Lensia campanella	0.51 ± 2.26	0 - 11.46	0.13	6.98	0.24 ± 1.3	0 - 7.02	0.03	3.45
Lensia conoidea	2.14 ± 3.58	0 - 19.92	0.54	46.51	8.35 ± 7.54	0 - 23.84	0.95	68.97
Lensia fowleri	0.16 ± 0.67	0 - 3.73	0.04	6.98	-	-	-	-
Lensia meteori	2.74 ± 4.92	0 - 24.87	0.68	44.19	23.39 ± 22.7	0 - 88.77	2.66	79.31
Lensia multicristata	1.13 ± 3.52	0 - 22.14	0.28	23.26	7.98 ± 7.32	0 - 26.36	0.91	79.31
Lensia spp.	0.84 ± 3.72	0 - 23.74	0.21	11.63	-	-	-	-
Lensia subtilis	128.84 ± 286.44	0 - 1529.61	32.19	90.70	164.11 ± 183.66	2.74 - 788.45	18.69	100
Lensia subtiloides	0.05 ± 0.35	0 - 2.28	0.01	2.33	2.36 ± 12.69	0 - 68.36	0.27	3.45
Muggiaea atlantica	0.18 ± 1.15	0 - 7.55	0.04	2.33	-	-	-	-

Muggiaea kochii	45.47 ± 137.84	0 - 818.04	11.36	53.49	212.35 ± 415.02	0 - 1962.92	24.19	86.21
Rosacea plicata	-	-	-	-	0.04 ± 0.21	0 - 1.15	0.00	3.45
Sulculeolaria chuni	0.08 ± 0.29	0 - 1.43	0.02	6.98	-	-	-	-
Vogtia glabra	0.05 ± 0.22	0 - 1.16	0.01	4.65	-	-	-	-
Vogtia spp.	0.07 ± 0.2	0 - 0.61	0.00	11.11	-	-	-	-
Cystonectae								
Bathyphysa conifera	0.03 ± 0.22	0 - 1.43	0.01	2.33	-	-	-	-
Cystonectae ni.	-	-	-	-	0.07 ± 0.36	0 - 1.94	0.01	3.45
Rhizophysa filiformis	0.06 ± 0.32	0 - 1.89	0.01	2.94	-	-	-	-
Rhizophysa spp.	0.4 ± 1.67	0 - 9.43	0.08	8.82	0.42 ± 2.28	0 - 12.26	0.05	3.45
Phystonectae								
Agalma elegans	0.42 ± 1.12	0 - 4.74	0.10	16.28	-	-	-	-
Agalma spp.	0.85 ± 2.71	0 - 13.5	0.21	18.60	-	-	-	-
Apolemia uvaria	1.48 ± 4.07	0 - 20.12	0.37	18.60	-	-	-	-
Forskalia edwardsii	0.27 ± 1	0 - 5.25	0.07	9.30	2.16 ± 4.57	0 - 18.64	0.25	31.03
Halistemma rubrum	2.65 ± 5.16	0 - 25.5	0.66	41.86	10.44 ± 14.32	0 - 57.49	1.19	89.66
Nanomia bijuga	1.03 ± 5.25	0 - 30.37	0.20	5.88	-	-	-	-
Nanomia cara	-	-	-	-	0.62 ± 3.33	0 - 17.95	0.07	3.45
Physonectae ni.	8.24 ± 18.07	0 - 93.23	2.06	51.16	-	-	-	-
Physophora hydrostatica	0.05 ± 0.2	0 - 0.89	0.01	6.98	-	-	-	-
Hydromedusae	**157.76 ± 326.89**	**3.04 - 1971.94**	**39.42**	**100**	**310.11 ± 305.18**	**66 - 1437.32**	**35.32**	**100**
Anthoathecata	**25.45 ± 43.05**	**0 - 223.77**	**6.36**	**90.70**	**116.59 ± 135.46**	**24.86 - 769.35**	**13.28**	**100**
Amphinema rubrum	-	-	-	-	0.23 ± 0.64	0 - 2.76	0.03	13.79
Anthoathecata ni.	-	-	-	-	0.04 ± 0.21	0 - 1.15	0.00	3.45
Corymorpha annulata	0.09 ± 0.57	0 - 3.73	0.02	2.33	-	-	-	-
Corymorpha nutans	-	-	-	-	0.11 ± 0.57	0 - 3.06	0.01	3.45
Coryne sp.	0.37 ± 2.13	0 - 12.44	0.07	2.94	-	-	-	-
Cytaeis sp.	-	-	-	-	0.07 ± 0.36	0 - 1.94	0.01	3.45
Euphysa aurata	2.14 ± 7.42	0 - 45.86	0.53	20.93	2.05 ± 6.54	0 - 32.85	0.23	24.14
Euphysa flammea	-	-	-	-	0.57 ± 3.05	0 - 16.43	0.06	3.45

Kantiella enigmatica	-	-	-	-	0.15 ± 0.79	0 - 4.24	0.02	3.45
Koellikerina fasciculata	-	-	-	-	0.14 ± 0.74	0 - 4	0.02	3.45
Leuckartiara nobilis	-	-	-	-	0.61 ± 3.05	0 - 16.43	0.07	6.90
Leuckartiara octona	-	-	-	-	0.25 ± 1.17	0 - 6.21	0.03	6.90
Lizzia blondina	-	-	-	-	0.57 ± 3.05	0 - 16.43	0.06	3.45
Lizzia octostyla	0.06 ± 0.19	0 - 0.58	0.00	11.11	-	-	-	-
Neoturris pileata	-	-	-	-	0.04 ± 0.21	0 - 1.15	0.00	3.45
Nubiella mitra	-	-	-	-	0.14 ± 0.74	0 - 4	0.02	3.45
Oceania armata	0.25 ± 1.04	0 - 6.64	0.06	13.95	-	-	-	-
Podocorynoides minima	0.11 ± 0.6	0 - 3.89	0.03	4.65	-	-	-	-
Sarsia tubulosa	0.06 ± 0.19	0 - 0.58	0.00	11.11	-	-	-	-
Stauridiosarsia gemmifera	0.37 ± 2.13	0 - 12.44	0.07	2.94	0.33 ± 1.78	0 - 9.59	0.04	3.45
Velella velella (rataria larva)	22.05 ± 43.39	0 - 223.77	5.51	81.40	111.07 ± 134.56	18.64 - 757.42	12.65	100
Zanclea sp.	0.28 ± 1.62	0 - 9.43	0.05	2.94	0.24 ± 0.92	0 - 4.24	0.03	6.9
Leptothecata	**56.77 ± 233.52**	**0 - 1478.96**	**14.19**	**53.49**	**7.33 ± 13.11**	**0 - 59.74**	**0.84**	**44.83**
Clytia gracilis	0.2 ± 0.61	0 - 1.82	0.01	11.11	-	-	-	-
Clytia hemisphaerica	0.93 ± 2.6	0 - 11.46	0.23	23.26	3.17 ± 8.84	0 - 43.44	0.36	27.59
Clytia spp.	0.4 ± 1.21	0 - 3.64	0.02	11.11	-	-	-	-
Eirene viridula	0.39 ± 2.28	0 - 13.28	0.08	2.94	0.28 ± 1.53	0 - 8.21	0.03	3.45
Eutima gegenbauri	0.02 ± 0.11	0 - 0.72	0.00	2.33	-	-	-	-
Laodicea cf. *fijiana*	0.11 ± 0.64	0 - 3.73	0.02	2.94	-	-	-	-
Leptothecata ni.	0.03 ± 0.18	0 - 1.16	0.01	4.65	-	-	-	-
Obelia spp.	54.98 ± 231.67	0 - 1467.49	13.74	44.19	3.88 ± 7.04	0 - 27.82	0.44	37.93
Octophialucium funerarium	0.37 ± 2.13	0 - 12.44	0.07	2.94	-	-	-	-
Limnomedusae	**0.46 ± 3.04**	**0 - 19.92**	**0.12**	**2.33**	**0.5 ± 1.5**	**0 - 5.96**	**0.06**	**13.79**
Liriope tetraphylla	0.59 ± 3.42	0 - 19.92	0.12	2.94	0.5 ± 1.5	0 - 5.96	0.06	13.79
Narcomedusae	**4.68 ± 8.88**	**0 - 38.3**	**1.17**	**44.19**	**2.76 ± 5.94**	**0 - 28.86**	**0.31**	**34.48**
Cunina globosa	0.01 ± 0.06	0 - 0.38	0.00	2.33	-	-	-	-
Cunina octonaria	0.1 ± 0.31	0 - 0.93	0.01	11.11	-	-	-	-
Solmaris flavescens	0.58 ± 2.02	0 - 10.28	0.15	11.63	-	-	-	-

Solmaris leucostyla	0.14 ± 0.56	0 - 2.67	0.03	5.88	-	-	-	-
Solmissus albescens	3.85 ± 7.89	0 - 37.92	0.96	39.53	2.76 ± 5.94	0 - 28.86	0.31	34.48
Solmissus cf. *incisa*	0.11 ± 0.58	0 - 3.64	0.03	4.65	-	-	-	-
Trachymedusae	**70.4 ± 137.08**	**0 - 489.77**	**17.59**	**93.02**	**182.92 ± 214**	**5.64 - 859.83**	**20.83**	**100**
Aglaura hemistoma	65.54 ± 135.18	0 - 489.77	16.37	79.07	165.36 ± 199.66	3.76 - 804.18	18.83	100
Persa incolorata	0.21 ± 0.7	0 - 3.73	0.05	11.63	3.47 ± 7.8	0 - 38.81	0.40	41.38
Rhopalonema velatum	4.65 ± 8.39	0 - 49.74	1.16	65.12	14.09 ± 16.53	0 - 65.7	1.61	89.66
Scyphomedusae	**1.56 ± 3.18**	**0 - 15.98**	**0.39**	**41.86**	**28.83 ± 100.85**	**0 - 468.14**	**3.28**	**34.48**
Coronatae	**0.67 ± 2.02**	**0 - 10.8**	**0.17**	**20.93**	**0.29 ± 1.13**	**0 - 5.96**	**0.03**	**10.34**
Nausithoe punctata	0.6 ± 2.02	0 - 10.8	0.15	13.95	0.29 ± 1.13	0 - 5.96	0.03	10.34
Paraphyllina intermedia	0.13 ± 0.38	0 - 1.14	0.01	11.11	-	-	-	-
Periphylla periphylla	0.05 ± 0.23	0 - 1.4	0.01	4.65	-	-	-	-
Semaeostomeae	**0.89 ± 2.68**	**0 - 15.98**	**0.22**	**23.26**	**28.54 ± 100.31**	**0 - 468.14**	**3.25**	**31.03**
Pelagia noctiluca (ephyra)	0.89 ± 2.68	0 - 15.98	0.22	23.26	28.54 ± 100.31	0 - 468.14	3.25	31.03

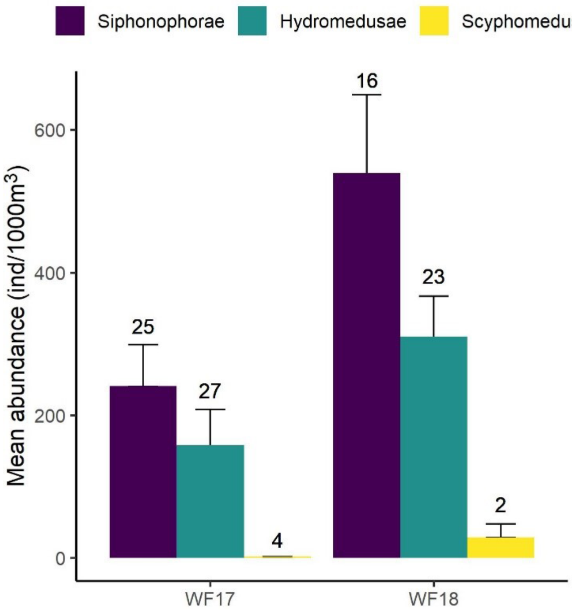

Fig. 3: Mean abundance (+ standard error) of Siphonophorae, Hydromedusae and Scyphomedusae in 2017 and 2018. Species richness is indicated for each taxon and year.

and *Velella velella* rataria larvae in both years and *Obelia* spp. in 2017 (Table I). Scyphomedusae abundance and species richness was low both winters, and the only noteworthy data was the higher abundance of *Pelagia noctiluca* ephyrae in 2018 compared to 2017 (Table I). The mean abundance of holoplanktonic and meroplanktonic species (only considering Hydromedusae and Scyphomedusae) was similar in 2017 (98 ind/1000m^3 ± 134 of holoplanktonic and 61 ind/1000m^3 ± 241 of meroplanktonic). However, in 2018 the abundance of holoplanktonic species markedly increased (326 ind/1000m^3 ± 362) while that of meroplanktonic species decreased (13 ind/1000m^3 ± 22) (Fig. 4).

Spatial distribution

The spatial distribution of cnidarians showed differences between the two studied years. In 2017 the highest species richness was located along the upper slope, whereas the highest abundances were found in the coastal zone, particularly in the southern part (Fig. 5). Considering these trends, the highest diversity values were detected along the upper slope. In 2018, the species richness, abundance and diversity were quite homogeneous throughout the area (Fig. 5).

Cluster analysis discriminated stations according to coastal and offshore zones and by sampling year, although stations from 2017 were present in all clusters. Five clusters were obtained, and the adonis analysis and subsequent pairwise

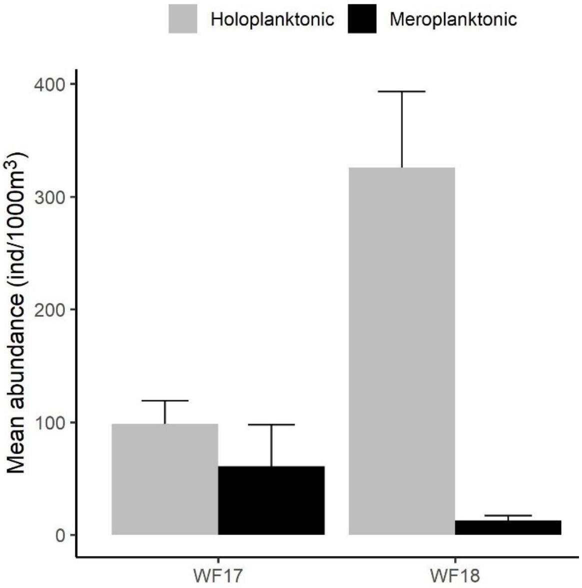

Fig. 4: Mean abundance (+ standard error) of holoplanktonic and meroplanktonic medusae (Hydromedusae and Scyphomedusae together) in 2017 and 2018.

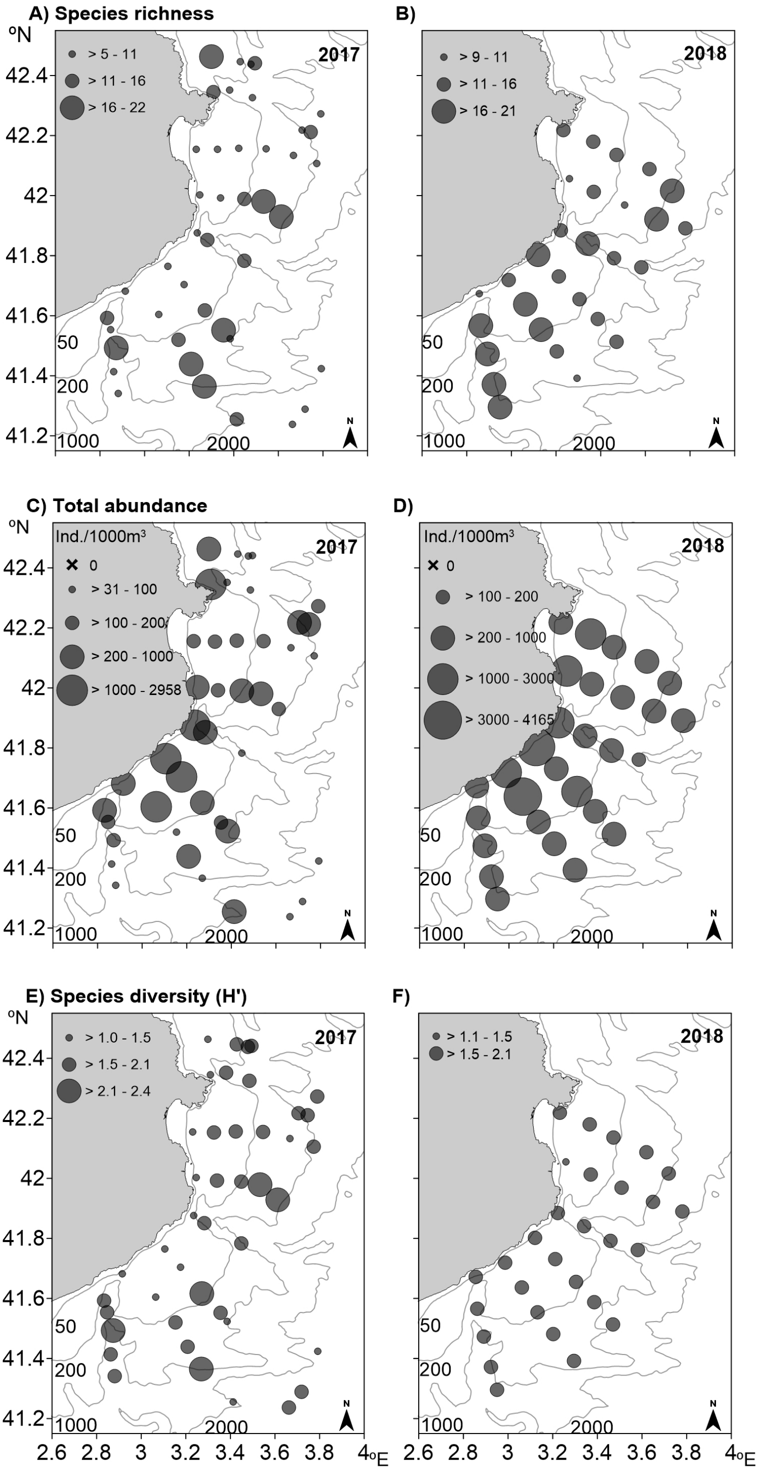

Fig. 5: Spatial distribution of species richness (a, b), total abundance (ind/1000m^3; c, d) and species diversity (Shannon-Weaver index; e, f) for 2017 and 2018, overlaid on bathymetry (50, 200, 1000 and 2000 m).

tests revealed that they were significantly different from each other ($p < 0.01$; nº permutations = 9999). Three clusters of stations (A, B and D) were identified at the coastal zone, although one station belonging to cluster B was located offshore, northeast of the sampling area (Fig. 6). Clusters A and B only included stations from 2017, differentiating the coastal zone north of the Palamós canyon (lower cnidarian abundance) from the southern coastal zone (higher abundance). Cluster A was characterized by a high abundance of *M. kochii*, *L. subtilis*, *A. hemistoma* and *Obelia* spp. (Fig. 7a, 8), whereas cluster B was characterized by a lower abundance of these species (although they were still the most abundant of the cluster) and the practically absence of *Obelia* spp. (Fig. 7b, 8); both clusters presented low abundances of *V. velella* larvae and *C. appendiculata* (Fig. 8). Cluster D included mainly stations sampled in 2018 on the shelf (Fig. 6) and was characterised by the highest abundances of *V. velella* larvae, *A. tetragona* (eudoxid) (Fig. 7c) and *Rhopalonema velatum*, that were more abundant in the coastal zone, in addition to *M. kochii*, *L. subtilis* and *A. hemistoma* (Fig. 8). Clusters C and E were located offshore (Fig. 6). The first one mainly contained stations sampled in 2018 and was characterized by *Lensia conoidea* (Fig. 7d), *Lensia meteori* and *Lensia multicristata* (Fig. 8). Cluster E only included stations sampled in 2017 and, although the cnidarian abundance was generally low, *C. appendiculata*, *V. velella*

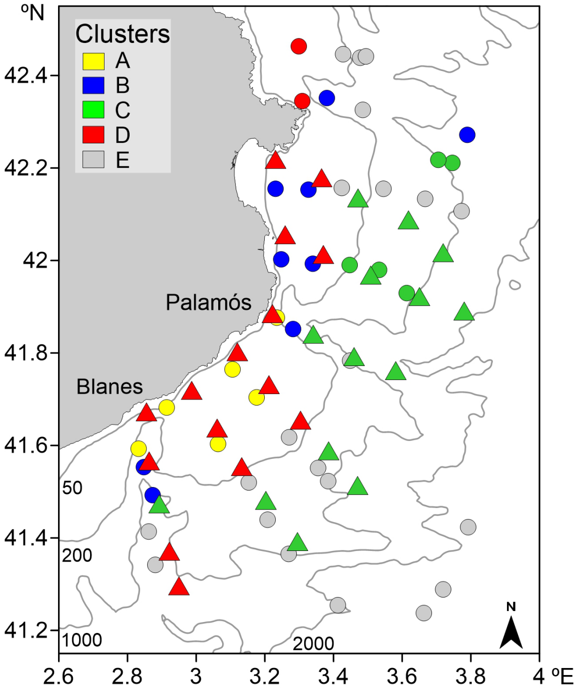

Fig. 6: Spatial distribution of sampling stations according to cluster results. Note that the same colour symbols indicate similar species composition. Circles correspond to the stations sampled in 2017 and triangles to those sampled in 2018. Thin grey lines show isobaths (50, 200, 1000 and 2000 m).

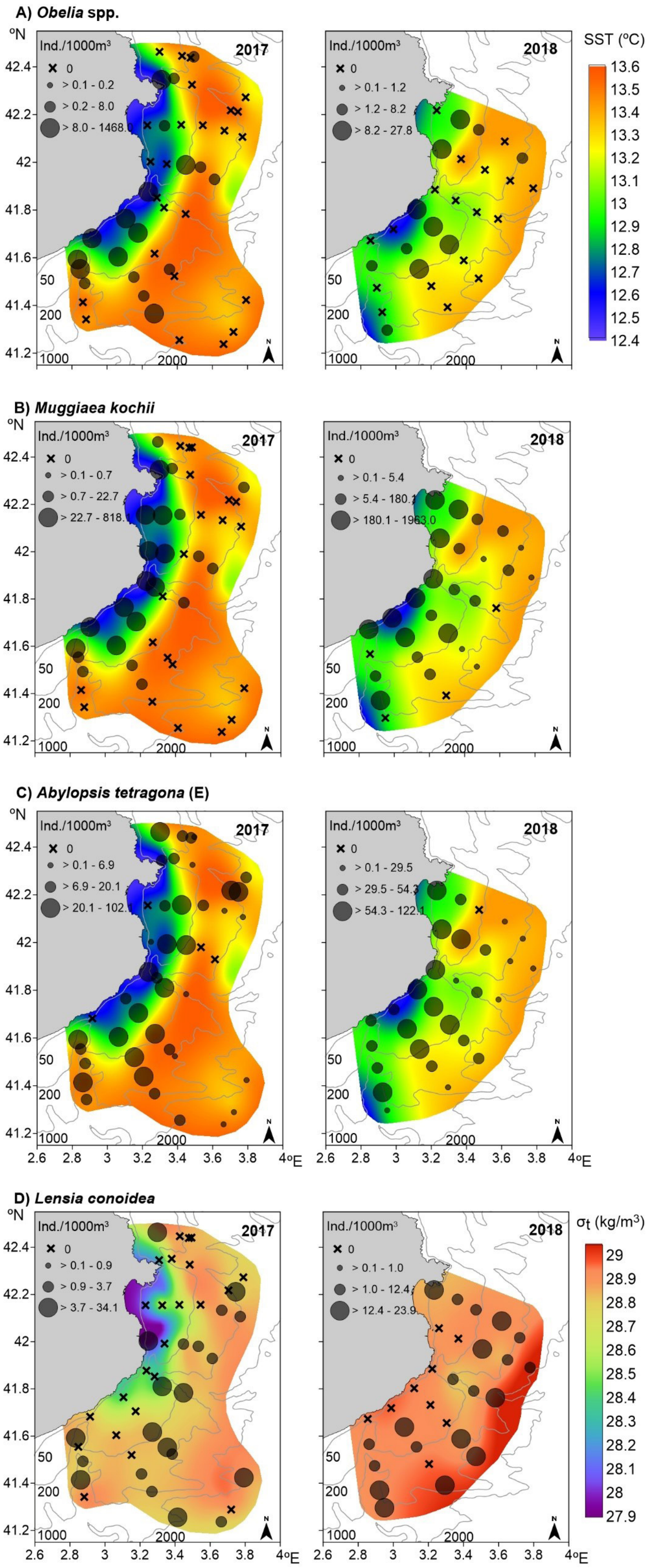

Fig. 7: Spatial distribution of representative cnidarian species of each cluster in the NW Mediterranean during winter. *Obelia* spp. (a) and *Muggiaea kochii* (b) representative of clusters A and B; eudoxid of *Abylopsis tetragona* (c) of cluster D; and *Lensia conoidea* (d) of cluster C. Species distributions are overlaid on surface temperature (ºC) and density (kg/m^3) according to the Redundancy Analysis results (see Fig. 9). Thin grey lines show isobaths (50, 200, 1000 and 2000 m).

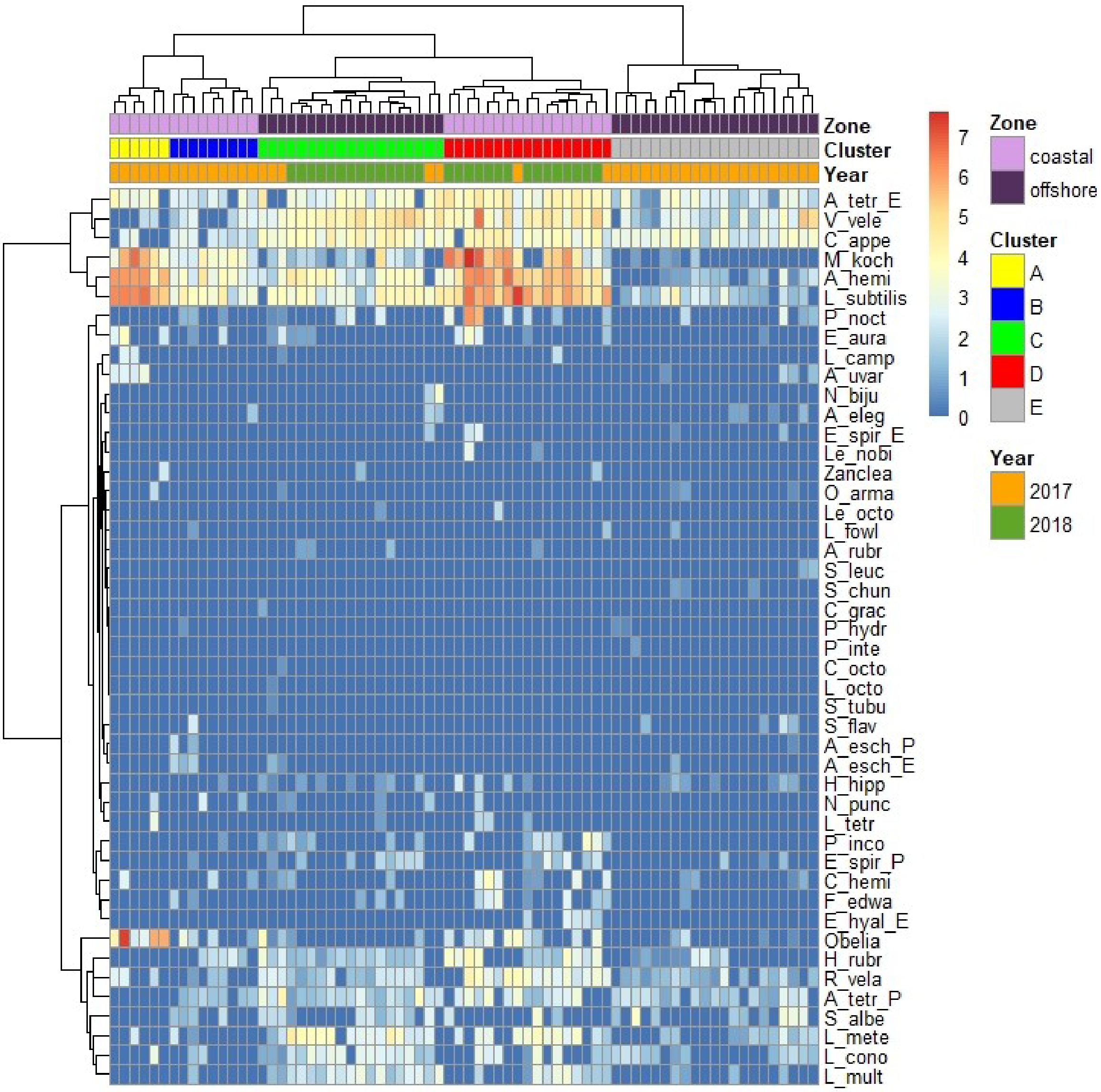

Fig. 8: Hierarchical clustering of stations in winter 2017 and 2018 in the NW Mediterranean and heatmap showing the abundance of species (colour scale shows the ln(x+1) transformed abundance of species, from blue (lower values) to red (higher values)). Different colour scales indicate the zone (coastal, offshore), cluster (A, B, C, D, E) and year of each sampling station.

larvae and *A. tetragona* (eudoxid) were the most abundant species. A distinctive trait of this cluster was the absence of *M. kochii* (Fig. 7b, 8). In general, all clusters were spatially well defined however, it should be noted, that the two submarine canyons presented stations belonging to all clusters (Fig. 6).

The RDA analysis addressing the relationship between cnidarian species and environmental variables, explained 32% of the total variance. The first ordination axis accounted for 79% of the constrained variance and was positively correlated with temperature and bathymetry (significant variables for species ordination) and negatively correlated with chl-*a* (not significant variable, but its inclusion increased the explained variance) (Table II, Fig. 9). *M. kochii*, *A. hemistoma*, *L. subtilis* and *Obelia* spp. were placed on the left side of the axis, where values of temperature and bathymetry were low (Fig. 9). These values correspond to the coastal zone where these species were particularly abundant (Fig, 7a,b, 10a). Some of these species, i.e *M. kochii* and *A. hemistoma*, were practically confined to coastal waters in 2017, while in 2018 presented a wider distribution extending up to the location of the shelf-slope front. Regarding the ordination of the sampling stations, clusters A, B and D were also located at low values of temperature and bathymetry, whereas clusters C and E were placed at the opposite direction, where values of these variables were high (Fig. 9) and are those found in the open sea. The second axis explained 18% of the constrained variance and was negatively correlated with density (significant variable) (Table II, Fig. 9). This variable allowed to separate stations sampled in 2017 (clusters A, B and E), located on the upper part of the RDA diagram (Fig. 9), from those sampled in 2018 (clusters C and D) located on the lower part. *V. velella* larvae, *L. multicristata*, *L. meteori*, and *C. appendiculata* appeared in the lowest part of the diagram, and were more abundant in 2018 than in 2017 (Fig. 8). These species were more abundant offshore, close to the shelf-slope front, where density was high (Fig. 10b, c). Species with a weaker relationship with environmental variables, such as *A. tetragona* (polygastric stage), were located close to the axis origin in the diagram (Fig. 9), and showed either a wide distribution or a lack of spatial pattern (Fig. 11).

Table II: Summary of the results of the Redundancy Analysis (RDA) performed with planktonic cnidarians and the explanatory environmental variables. *α = 0.05; n.s. = non-significant; **bold** indicates those variables correlated with the RDA diagram axis.

Variable	Variance	F - value	P - value	Axis 1	Axis 2
Bathymetry (log)	6.75	17.09	0.0001*	**0.81**	-0.32
Temperature	2.70	6.83	0.0001*	**0.88**	-0.25
Density	2.73	6.91	0.0001*	0.18	**-0.94**
Chlorophyll-*a*	0.35	0.88	0.4705 n.s.	-0.38	-0.22

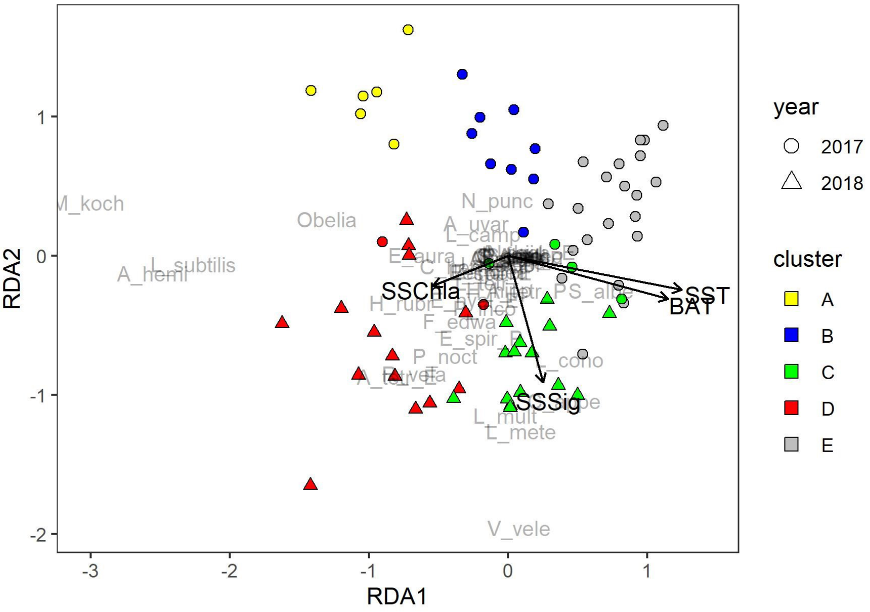

Fig. 9: Redundancy Analysis (RDA) ordination diagram showing the relationships between the cnidarian species, the sampling stations and the explanatory environmental variables (vectors) for winter 2017 and 2018. SST = Temperature; SSSig = density ; SSChla = chlorophyll-*a* and BAT = log transformed bathymetry. Same colour symbols indicate stations with similar species composition. Circles correspond to the stations sampled in 2017 and triangles to the stations sampled in 2018.

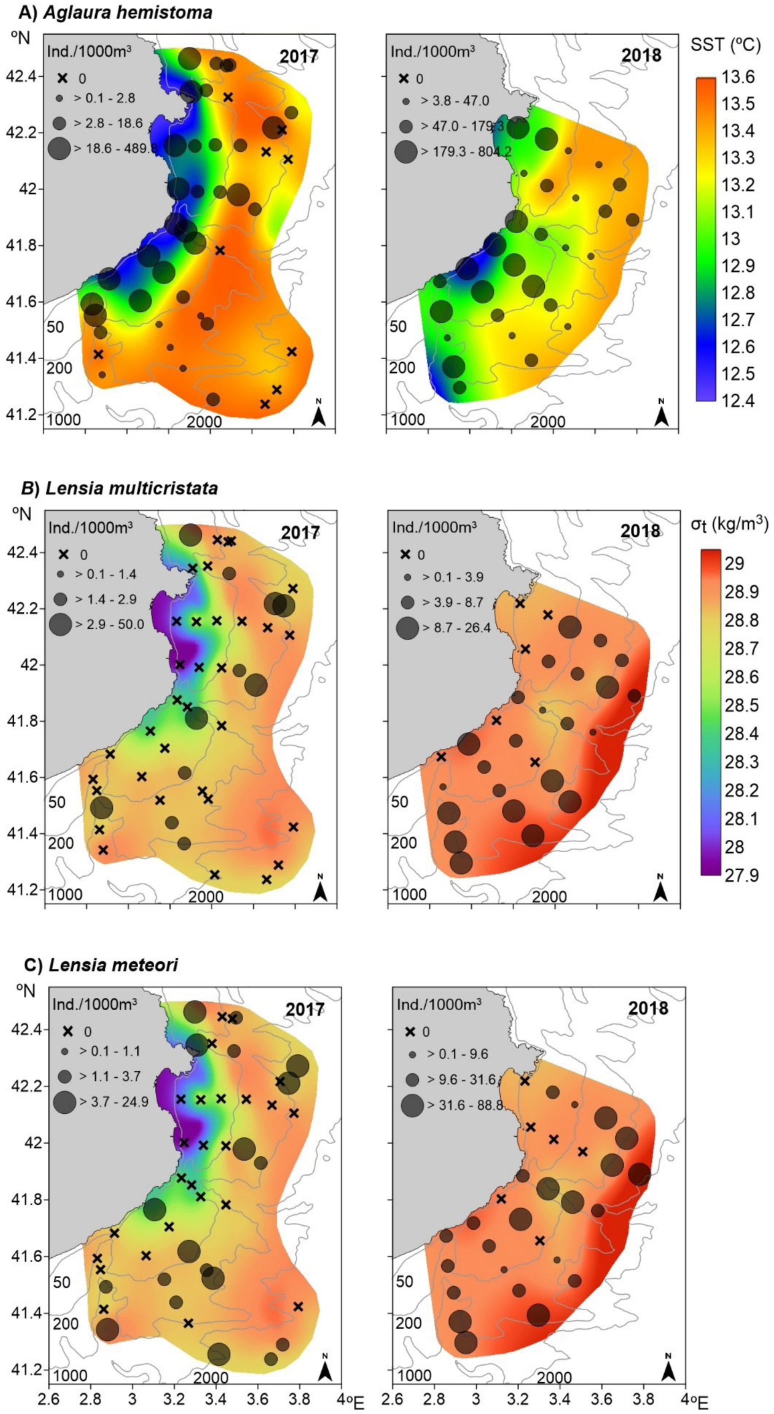

Fig. 10: Spatial distribution of some cnidarian species presenting a strong relationship with environmental variables in the Redundancy Analysis ordination diagram. *Aglaura hemistoma* (a), as example of coastal species associated to low temperature and bathymetry, and *Lensia multicristata* (b) and *Lensia meteori* (c), as examples of species associated to high density values, in 2017 (left) and 2018 (right). Species distributions are overlaid on surface temperature (ºC) and density (kg/m³) according to the Redundancy Analysis results (see Fig. 9). Thin grey lines show isobaths (50, 200, 1000 and 2000 m).

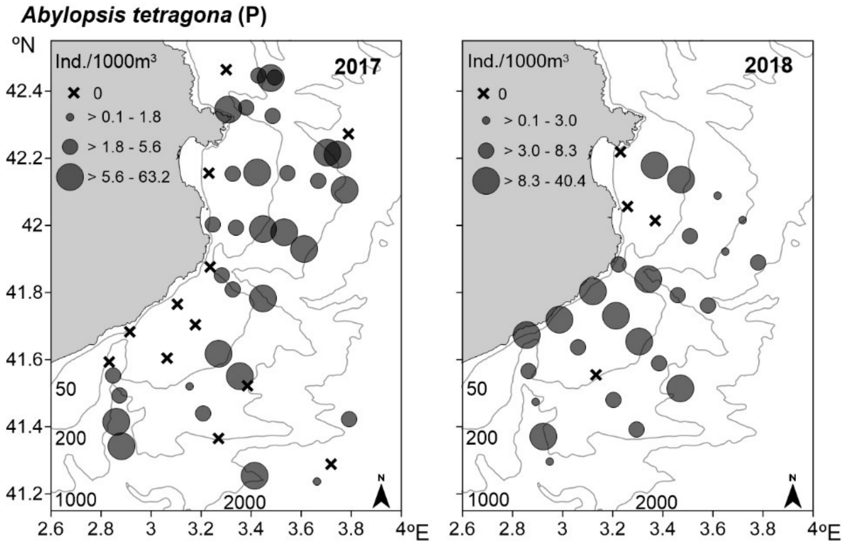

Fig. 11: Spatial distribution of the widespread polygastric stage of *Abylopsis tetragona* in 2017 (left) and 2018 (right). Thin grey lines show isobaths (50, 200, 1000 and 2000 m).

Discussion

This study provides a comprehensive picture of the planktonic cnidarian community structure in two consecutive winters under different environmental scenarios in the NW Mediterranean Sea. The winter period has been scarcely studied for these organisms, as most works have focused on spring and summer, considered *a priori* as those of maximum diversity and abundance of cnidarians (Goy and Thiriot, 1976; Gili et al., 1987a; Gamulin and Kršinić, 1993). The main oceanographic conditions found in the NW Mediterranean during the study were those expected for the season, with a marked coastal-offshore gradient of the main environmental variables (temperature and salinity) and the presence of the shelf-slope density front along the slope (Font, 1987). However, in 2017 the coastal zone was occupied by cold and low saline waters due to the occurrence of heavy rain episodes few days before the cruise that resulted in a marked density gradient over the shelf (Fig. 2). Although sea surface temperatures detected in both cruises were quite similar, winter 2017 was mild and the development of spring conditions and the phytoplankton bloom occurred earlier than in 2018 (Mir-Arguimbau et al., 2022). Thus, the winter scenario in which the samplings were conducted in 2017 was close to the onset of spring conditions, whereas that found in 2018 can be considered as the "typical" winter.

Species composition and abundance

Cnidarian species richness was higher in 2017, whereas the highest abundance was found in 2018 (Table I) which probably is related to the different oceanographic and climatological conditions in both years. The earlier development of spring conditions and the subsequent seasonal phytoplankton bloom in 2017 (Mir-Arguimbau et al., 2022) might have allowed a mixture of winter and spring planktonic cnidarian species. In addition, the high environmental heterogeneity in that first year might have provided more ecological niches favouring an increase in species richness. On the other hand, the "typical" winter oceanographic conditions in 2018 might have allowed the development of the winter species populations, resulting in higher abundances of the cnidarian community. As a result of the higher species richness in 2017 and the higher abundance in 2018, the diversity (H') was quite similar in both years (1.68 in 2017 and 1.84 in 2018) and also slightly higher than that reported in the summer months (0.91 – 1.38) (Guerrero et al., 2018a, b).The species richness recorded in our study (56 species in 2017) was comparable to that obtained during summer (46-59) (Guerrero et al., 2018a, b) and higher to that reported in spring (34 species) and autumn (20 species) (Gili et al., 1988) in a more extensive area of the NW Mediterranean. The cnidarian abundance in both studied winters was, approximately, an order of magnitude lower than that previously reported in summer (Guerrero et al., 2018a, b). It must be taken into account that the abundance peaks of Siphonophorae and Hydromedusae in the western Mediterranean takes place in spring and beginning of summer (Gili et al., 1987a; Fernández de Puelles et al., 2007; Licandro et al., 2012; Touzri et al., 2012).

The higher abundance of Siphonophorae and the higher species richness of Hydromedusae in both years (Fig. 3) is an usual pattern previously found in other studies conducted in the NW Mediterranean (Gili et al., 1988; Sabatés et al., 2010) and in the Atlantic Ocean (D'Ambrosio et al., 2016). The most abundant species in both winters were *L. subtilis*, *M. kochii*, *C. appendiculata*, *A. tetragona* (eudoxid), *A. hemistoma* and *V. velella* larvae, while *Obelia* spp. was especially abundant in 2017. All of these species are common throughout the basin, with abundance peaks at different times of the year (Gili et al., 1987a, b; Gili et al., 1988; Sardou et al., 1996; Batistic et al., 2007; Licandro et al., 2012). In the case of *V. velella*, for which data on larval stages are very scarce in the Mediterranean, the coastal arrivals of planktonic polyp colonies start to occur around March-April in the Ligurian Sea (Purcell et al., 2015; Betti et al., 2019). Thus, we can expect the presence of larvae in the water column during the previous weeks, as observed by Woltereck (1904).

The presence of eudoxid and polygastric stages of *A. tetragona*, *A. eschcholtzii* and *E. spiralis* in our study suggests that the sexual reproduction of these species takes place during the winter months. Previous studies already reported the presence of eudoxid stage of *A. tetragona* in winter (Cervigón, 1958) but also during the rest of the year (Gili et al., 1987a; Dallot et al., 1988; Guerrero et al., 2018b). The production of eudoxids has been associated with high food availability (Purcell, 1982), thus the productivity conditions found during the samplings would be suitable for the sexual reproduction of these species.

It is worth noting the high abundance of *M. kochii* with respect to the congeneric species *Muggiaea atlantica*, that was practically absent in both years. In the NW Mediterranean, *M. kochii* dominated the siphonophore community from late 1960s until early 1980s, when it started to decrease and *M. atlantica* became increasingly dominant (Riera et al., 1986; Carré and Carré, 1991; Licandro et al., 2012). In the Adriatic, a replacement of *M. kochii* by *M. atlantica* was also reported during 1996 (Kršinić and Njire, 2001; Batistic et al., 2007). This shift in species dominance has been associated with hydrological changes which took place in the 1980s in the Mediterranean (Licandro et al., 2012; Batistic et al., 2013). In the Atlantic, this alternation of species was also reported and was related with sea water temperature and food availability (Russell, 1934; Blackett et al., 2014). In our study the dominance of *M. kochii* over *M. atlantica* seems paradoxical since *M. atlantica* is considered a temperate-water species, and *M. kochii* a warm-water species sexually reproducing at <13°C and >13°C, respectively (Alvariño, 1974; Batistic et al., 2013). Unfortunately, the eudoxid stages of these species were not considered in our study and we could not report whether sexual reproduction of these species occurred. In the NW Mediterranean, the maximum abundance of both species takes place in spring-summer (Gili et al., 1987b; Licandro et al., 2012) and it may be that in periods of lower abundance, such as winter, the pattern of species dominance may vary. In any case, we cannot rule out fluctuations in the abundance of both species, which can only be addressed by long-term monitoring.

For both Hydromedusae and Scyphomedusae, the abundance of holoplanktonic medusae increased from 2017 to 2018, while the abundance of meroplanktonic ones decreased (Fig. 4). This would be related to the earlier development of spring conditions and the seasonal phytoplankton bloom in 2017 (Mir-Arguimbau et al., 2022) that would provide suitable conditions for the polyps of meroplanktonic species (e.g. *Obelia* spp.) to release free-swimming medusae. Polyps only release new medusae for sexual reproduction when environmental conditions are optimal (Boero and Bouillon, 1993; Gili et al., 1998). In 2018, when environmental conditions would not be so favourable for medusae release, holoplanktonic species (e.g. *V. velella* larvae, *A. hemistoma*, *P. noctiluca* ephyrae) dominated the medusae community, as already observed by Gili (1986) in autumn and winter.

Spatial distribution

The species richness, total abundance and diversity were more heterogeneously distributed in 2017 than in 2018. In 2017, species richness and diversity presented highest values along the upper slope, beyond the cold and low salinity coastal waters. On the contrary, the highest abundance values were detected in the coastal waters, suggesting that a few, but very abundant species, dominated the coastal community. In 2018, the lack of a clear pattern in the distribution of species richness, abundance and diversity would be related to the more homogeneous distribution of oceanographic variables (Fig. 2).

The cnidarian species assemblages presented a coastal-offshore ordination in both winters as previously observed in the studied area (Gili et al., 1988; Sabatés et al., 2010; Guerrero et al., 2018b) and in other geographic regions (e.g. Gili et al., 1991; Nagata et al., 2014). In both years, the coastal community was defined by a high abundance of *L. subtilis, M. kochii* and *A. hemistoma*, common species in the Mediterranean coastal areas (Gili et al., 1987a; Gili et al., 1988; Sabatés et al., 2010). In 2017, these species were largely retained in the cold, low salinity coastal waters, whose surface density was lower than offshore. *Muggiaea kochii* has also been associated with salinity values < 37.9 (Licandro et al., 2012), as those observed in the coastal zone. The two clusters of stations identified in the coastal zone would be related to the low salinity values detected north of the Palamós canyon (lower abundance of cnidarians) compared to those south of the canyon (higher abundance). *Obelia* spp. was highly abundant in the southern coastal zone, being nearly absent in the low salinity waters of the northern part (Figs. 2, 7a). However, considering that this species is very common in the coastal zone (Gili et al., 1988; Guerrero et al., 2018a), even in brackish waters (Touzri et al., 2012), and that it is present throughout the year (Bouillon et al., 2004), it would be expected to have a high tolerance to environmental variability. Probably, the low salinity would not be the only factor responsible for its scarce presence in the north, which could be related to other factors not considered in this study. In 2018, under more homogeneous oceanographic conditions, the distribution of coastal species extended towards the open sea, being practically absent in the high salinity and density open sea waters close to the shelf-slope front. This suggests, as observed in previous ichthyoplankton studies conducted in the area, that the front would act as a barrier preventing the dispersion of the coastal species towards the open sea (Sabates and Olivar, 1996; Sabatés et al., 2004). However, the lack of sampling beyond the front precludes to know the presence of these species in open sea waters.

The offshore cnidarian community was defined by *L. conoidea*, *L. meteori* and *L. multicristata* that were found over the slope associated with high density values, in the vicinity of the shelf-slope front. Their distribution approached the coast in the submarine canyons of Blanes and Palamós, where great depths are reached close to the coast. *Lensia conoidea* and *L. meteori* have been described as characteristic of offshore waters in the NW Mediterranean (Dallot et al., 1988; Batistic et al., 2007; Guerrero et al., 2018b), and while data on *L. multicristata* are very scarce, the species has been recorded in offshore waters of the Adriatic (Gamulin and Kršinić, 1993) and the North Atlantic (Pugh, 1984). Polygastric stages of *A. tetragona* (Fig. 11) and *C. appendiculata* (not shown) presented a wide distribution all over the study area but with higher abundances offshore in accordance with Gili et al. (1987a) and Sabatés et al. (2010). The distribution of these two species could be related to the increase in salinity towards open sea, as their abundances were associated with salinity > 37.9 (Licandro et al., 2012).

The coastal-offshore ordination in species assemblages found in winter conditions, with *L. subtilis*, *A. hemistoma*, *M. kochii* and *Obelia* spp. in the coastal zone and *L. meteori* and *L. conoidea* offshore, has also been reported in other periods of the year in the NW Mediterranean (Gili et al., 1988; Sabatés et al., 2010;

Guerrero et al., 2018b) suggesting that bathymetry is a determining factor in their distribution. This spatial pattern is probably related to the vertical distribution of the species in the water column. Thus, *L. conoidea* and *L. multicristata* found in the offshore region have a wide vertical distribution, reaching depths of 1000 m depth (Andersen et al., 1992, 2001) and 500-600 m (Pugh, 1984; Mapstone, 2014), respectively. On the other hand, species inhabiting surface waters, such as *M. kochii* (Gili et al., 1987a) and *A. hemistoma* (Berhaut, 1969; Albertini-Berhaut, 1979) are usually found in coastal waters, although *A. hemistoma* has also been reported offshore (Dallot et al., 1988; Touzri et al., 2012). The role of bathymetry in species distribution would help to explain the presence of stations belonging to all clusters in the submarine canyons of Blanes and Palamós (Fig. 6). The presence of the canyons strongly modifies the local circulation generating shelf-slope water exchanges (Alvarez et al., 1996; Flexas et al., 2008) favouring the transport of species from offshore areas to the coast (Alvarez et al., 1996; Masó et al., 1998). Thus, the great depths reached close to the coast over the canyons, would allow the presence of coastal and offshore species, as previously observed in other planktonic organisms (Carreton et al., 2020). The results of the cluster analysis also showed the presence of a station located offshore, northeast of the sampling area, that included a cnidarian coastal community (see Fig. 6). Temperature and salinity values at this station were lower than those of the surrounding area (Fig. 2). As argued by Sabatés et al. (2007), this station would be under the influence of waters from the shelf of the Gulf of Lions, north of study area, that are advected by the Northern Current, probably explaining the presence of this coastal community offshore. The presence of planktonic coastal species, as anchovy larvae, has been widely documented in that area transported by the Northern Current from the spawning grounds in the Gulf of Lions (Sabatés et al., 2007; Maynou et al., 2020).

The Mediterranean is a highly seasonal sea, with a marked phytoplankton bloom in late winter-early spring when surface waters begin to stabilize (Estrada et al., 1985; Saiz et al., 2014). The maximum abundance and species diversity of cnidarians takes place slightly later, in spring and beginning of summer (Gili et al., 1987b; Gamulin and Kršinić, 1993; Licandro et al., 2012). However, our results revealed an "unexpectedly" high species richness and relatively high abundance of cnidarians, suggesting that winter productivity is high enough to sustain a cnidarian community like that found in this study. In winter 2017 the development of spring conditions and the onset of the phytoplankton bloom occurred earlier than in 2018 (Mir-Arguimbau et al., 2022). Under these conditions, samplings were conducted during the winter-spring transition period, resulting in a species-rich cnidarian community. In the "typical" winter conditions of 2018, the specific richness was lower, but the overall abundance was much higher. The combined effect of environmental variables, particularly the bathymetry, and oceanographic structures, as water masses and the shelf-slope density front, resulted in a coastal-offshore ordination of the winter cnidarian species assemblages, that was only disrupted by the presence of the submarine canyons. This study highlights the relevance of studying the planktonic cnidarian community in winter, and during the transition periods of homogeneity and stratification of the water column, to obtain a comprehensive overview of its spatial and temporal variability throughout the annual cycle.

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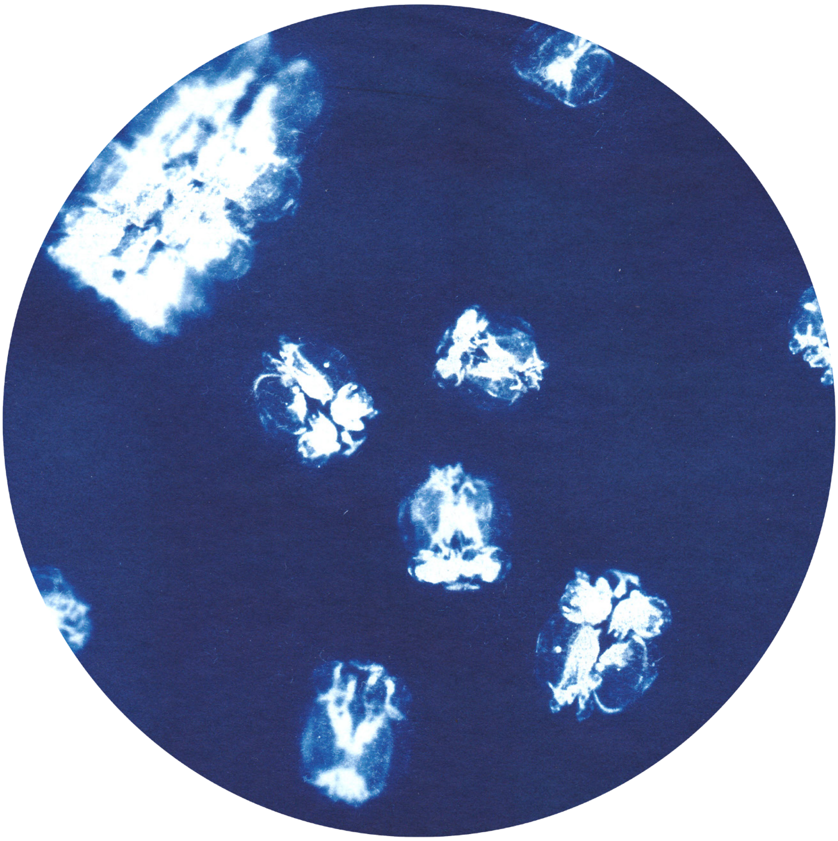


General discussion

Throughout the last decade, information regarding gelatinous zooplankton in the Western Mediterranean has been reported in some general works on zooplankton (Fernández de Puelles et al., 2014; Feuilloley et al., 2020; Fullgrabe et al., 2020), but the greatest effort has been made, especially, on large jellyfish species. This bias is justified by the increasing social and ecological relevance of jellyfish proliferations along the Mediterranean coasts. These studies have focused on a few species and especially on the frequency of blooms and their possible causes (Rosa et al., 2013; Marambio et al., 2021). Furthermore, due to the ecological importance of such proliferations, the trophic ecology (Milisenda et al., 2014; Tilves et al., 2016) and other aspects of these species' biology have been studied both in the field and in the laboratory (Acevedo et al., 2013; Ballesteros et al., 2021). A special effort has also been made to study the socio-economic effects on tourism (Benedetti-Cecchi et al., 2015) and aquaculture (Bosch-Belmar et al., 2017), as well as the role of citizen science in monitoring the frequency of jellyfish blooms on beaches (Gatt et al., 2018; Gueroun et al., 2022).

Salps constitute another relevant group of gelatinous zooplankton capable of forming large blooms and thus, their study has focused especially on their populations dynamics and on the factors shaping their distribution (Pascual et al., 2016, 2017). Other groups of gelatinous zooplankton, such as siphonophorans and hydromedusans, have been mainly studied in periods in which they are, *a priori,* more abundant, such as spring and summer (Guerrero et al., 2018a, b). These studies have mainly considered the relationship between environmental factors and their distribution and abundance patterns in both coastal and offshore areas. In general, gelatinous zooplankton represents an important group of distinct taxa that play different and significant roles in the pelagic food web as efficient filter-feeders or voracious predators. However, they are generally underestimated because standard sampling devices used for zooplankton sampling damage or destroy their fragile bodies and therefore, they are inappropriate for their quantitative estimation. In this sense, some taxa have been little studied, even though they may be of great interest in marine ecosystems. Nonetheless, it is worth mentioning that some recent studies have focussed on species that were little known in the Mediterranean, such as *Gonionemus vertens*, *Rhizostoma luteum* and *Carybdea marsupialis*, and that seem to be abundant or even have a significant socioeconomic impact (Marchessaux et al., 2017; Kienberger et al., 2018; Acevedo et al., 2019). Especial attention has been paid to potential invasive species for the importance of their ecological and social impacts (Killi et al., 2020).

Considering all this recent information, the present Ph.D. thesis aimed to improve the current knowledge on the ecology of the gelatinous zooplankton in the Western Mediterranean Sea, focused on the study of less known areas, species and seasonal periods. The first part of this section addresses the spatial heterogeneity of *Pelagia noctiluca* ephyrae along a wide latitudinal gradient in the Western Mediterranean. The second part examines the oceanographic conditions and colony size shaping the mesoscale distribution of *Pyrosoma atlanticum* in the NW Mediterranean. Finally, the third part analyses the whole planktonic cnidarian community during winter in the NW Mediterranean.

Spatial heterogeneity of *P. noctiluca* ephyrae along a wide latitudinal gradient in the Western Mediterranean

Ephyrae of *P. noctiluca*, the most common jellyfish in the Mediterranean, showed a high variability in their spatial structure linked to the recent and old Atlantic Water masses. Despite their presence in the upper water layer has been previously described (Morand et al., 1992; Buecher and Gibbons, 1999; Ottmann et al., 2021), the occurrence of short-extent diel vertical migrations in these surface levels (upper 50 m) were detected within the frame of this thesis. During the day, ephyrae presented a wide distribution well above and within the thermocline, far from the characteristic DCM that develops during the stratification period (Estrada et al., 1985), while at night they were more concentrated towards the surface. This migration pattern contrasts with that described for the epipelagic zooplankton, characterized by their presence around the DCM depths during the day for feeding and in the upper layers of the water column at night (Alcaraz, 1985; Saiz et al., 2014; Pascual et al., 2017). Some of this epipelagic zooplankton, such as copepods and fish larvae, are prey of *P. noctiluca* ephyrae (Purcell et al., 2014; Tilves et al., 2018), thus the distribution of both, prey and predators, overlaps in surface waters at night, allowing the ephyrae to feed on these prey (Tilves et al., 2018). However, remaining in slightly deeper and colder layers during the day, would decrease their metabolic rates and, consequently, their energy demands (Morand et al., 1987; Lilley et al., 2014). This strategy, together with the transparency of their bodies, that would make them barely visible to predators (Hamner, 1995), would allow *P. noctiluca* ephyrae to survive in such an oligotrophic environment.

The horizontal distribution of *P. noctiluca* ephyrae showed a clear latitudinal gradient with high abundances in the southern part of the study area, south of 40.0º N, and lower abundances in the north, being absent in the northernmost part, north of 41.3º N. This spatial variability was related to different water masses and the resulting mesoscale hydrographic features. The northern half of the area was occupied by the old Atlantic Water flowing through the Northern Current. The absence of ephyrae at the northernmost part, was in accordance to previous studies and coincided with high concentrations of anchovy larvae (Guerrero et al., 2018b; Sabatés et al., 2018). All of this suggests that this area was under the influence of waters coming from the shelf of the Gulf of Lions, an important spawning area for this fish species (Palomera et al., 2007), advected by the Northern Current. Considering the oceanic habitat of *P. noctiluca* (Canepa et al., 2014), the origin of these waters, from the wide shelf of the Gulf of Lions, would be the most likely explanation for the absence of *P. noctiluca* ephyrae in the area. The high abundance of *P. noctiluca* ephyrae south of the study area was associated with the low saline recent Atlantic Water. In summer, the surface Atlantic Water that enters the Mediterranean may reach the Balearic Islands progressing northward across the Eivissa and Mallorca Channels (Pinot et al., 2002; Heslop et al., 2012), forming the warm and low salinity Balearic Current. The ephyrae found in the recent Atlantic Water along the Balearic Current path would have been generated by adults of *P. noctiluca* associated with the entrance of waters from the Atlantic, or trapped by the Atlantic Water flow along its path. The inflowing

Atlantic jet involves high mesoscale activity (Tintoré et al., 1991), generating structures such as fronts and eddies that support high biological productivity (Reul et al., 2005; Vargas-Yáñez and Sabatés, 2007; Macías et al., 2008), favouring gelatinous zooplankton advection and aggregation (Mills, 1984; Graham et al., 2001; Greer et al., 2015). The entrance of gelatinous organisms through the Strait of Gibraltar linked to the inflow of Atlantic Water has been previously reported for other species such as *Rhizostoma luteum* (Prieto et al., 2013). Our results suggest the presence of *P. noctiluca* population connectivity between the Atlantic and the Mediterranean, a key issue to improve the understanding of this species population dynamics and its increasing abundance in the Mediterranean. In this regard, further observational and numerical simulation studies may contribute to better understand this potential connectivity and its seasonal and interannual variability.

The broad spatial scale of this study allowed to detect the hydrodynamic structures determining the spatial heterogeneity of *P. noctiluca* ephyrae in the Western Mediterranean. The basin has a high spatial environmental variability and in some specific areas, such as the northwestern Mediterranean and the Balearic Islands, gelatinous zooplankton has been extensively studied. Future studies on a larger spatial scale would allow to understand the role of hydrodynamic processes in the connectivity amongst different areas.

Oceanographic conditions and colony size shaping the mesoscale distribution of *P. atlanticum* in the NW Mediterranean

Pyrosoma atlanticum has been a poorly studied species in the Mediterranean. Our study, comprising two consecutive winters, shows a high interannual variability in the abundance of *P. atlanticum*. The exceptionally high abundance found in winter 2017 might be related to an earlier development of spring conditions and the subsequent seasonal phytoplankton bloom in that year with respect to winter 2018 (Mir-Arguimbau et al., 2022).

The spatial distribution (vertical and horizontal) of *P. atlanticum* depends on colony size and is ultimately determined by oceanographic and biological structures. The results of mesoscale distribution suggested that large (≥ 7 mm) colonies inhabit over the slope, where reproduction might take place, in association with the shelf-slope front. Their presence close to the front might be related to the enhanced primary and secondary production (Ibanez and Boucher, 1987; Estrada and Margalef, 1988) that makes this area suitable for the development of gelatinous zooplankton (Sabatés et al., 2010; Guerrero et al., 2018b). The front likely aggregates the colonies and prevents their dispersion towards the open sea, as reported for other zooplanktonic organisms in the area (Sabates and Olivar, 1996; Guerrero et al., 2016). On the other hand, small-medium (≤ 6.9 mm) colonies were present over the shelf, probably due to the offshore water intrusions associated with front instabilities (Sabatés et al., 2004), being practically absent in the cold and low salinity coastal waters. Previous studies conducted in the Atlantic and Pacific oceans have also suggested that *P. atlanticum* colonies are mainly located in open sea waters (Angel, 1989; Brodeur et al., 2018) and are likely transported by advection to shelf areas, where they are less abundant (Miller et al., 2019; Schram et al., 2020; Lyle et al., 2022).

The fine-scale analysis of the vertical distribution of *P. atlanticum* allowed us to detect different migration amplitudes as a function of colony size, together with the size range in which the migratory behaviour begins to develop. Small colonies (< 4 mm) were located in the upper 40 m of the water column during day and night, showing no diel vertical migration, as previously reported by Palma (1985). The migratory behaviour, consisting of remaining in the surface layers at night and going to deeper layers during the day, started in medium (4 - 6.9 mm) colonies, but not all colonies of these sizes exhibited such behaviour, suggesting that migration can start at different sizes within this range. Large colonies (≥ 7 mm), increased their migration amplitude reaching the maximum sampling depth (550 m) during the day. The lack of water column stratification typical of winter conditions allowed us to observe the migratory behaviour of this species without the presence of clines, which could influence their vertical movement (Graham et al., 2001). The shallow levels of the water column, where all size classes are found at night, presented the highest values of chlorophyll-*a*, a proxy related to photosynthetic taxa, which are the main prey of the species (Drits et al., 1992; Perissinotto et al., 2007). Thus, the migratory pattern described would allow

P. atlanticum colonies to take advantage of the high phytoplankton abundance found in surface waters at night, before returning to deeper layers during the day to avoid predation in the illuminated layers (Bollens and Frost, 1989; Lampert, 1989; Saiz et al., 2014). The presence of small colonies in the upper productive layers both during day and night suggests a strategy of maximizing the colony growth to reduce the high predation rates of small size organisms (Miller et al., 1988). Furthermore, it must be considered their limited migratory capacity, since their propulsive capacity and migratory amplitude increase with colony size. However, the growth of the colony also enhances its visibility, forcing the colony to migrate deeper to avoid visual predators (Angel, 1979). It remains unclear whether the increase in migration amplitude with colony size is due to higher visibility, increased propulsive capacity, or a combination of the two. The diel vertical migration of *P. atlanticum* colonies might contribute to carbon transport to depth as reported in other geographic areas, as in the Tasman Sea (Henschke et al., 2019). However, our estimates are much lower than those obtained in the latter study, likely due to the smaller size of Mediterranean colonies.

Our results also show a high interannual variability in the abundance of *P. atlanticum* mainly related to the winter environmental conditions, which cause mixing of the water column and the input of nutrients to the surface waters, ultimately modulating the spring phytoplankton bloom (García-Comas et al., 2011; Fullgrabe et al., 2020). The recently observed climatic trends for the Mediterranean Sea, showing an increase in sea water temperature, a lower wind speed and a lengthening of the seasonal stratification period (Rixen et al., 2005; Calvo et al., 2011; Vargas-Yáñez et al., 2017), could modify the intensity and regularity of phytoplankton blooms, eventually altering the abundance, distribution, and species composition of gelatinous zooplankton (Guerrero et al., 2018a). Future studies should address the long-term interannual variability of *P. atlanticum*, as well as relevant aspects of its biology (e.g. feeding and propulsive capacity), to understand its ecological role in the functioning of Mediterranean planktonic ecosystems.

Winter planktonic cnidarian community in the NW Mediterranean

The mesoscale distribution of cnidarians in the NW Mediterranean has been mainly addressed in spring and summer (Gili et al., 1988; Licandro and Ibanez, 2000; Guerrero et al., 2018a), *a priori* considered as periods of maximum diversity and abundance (Goy and Thiriot, 1976; Gili et al., 1987a; Gamulin and Kršinić, 1993). The spatial characterization and species assemblages of the whole cnidarian community (Siphonophorae, Hydromedusae and Scyphomedusae) were studied in two consecutive winters (i.e. 2017 and 2018), in the NW Mediterranean. "Unexpectedly" high species richness was found during the winter of 2017, with values similar or even higher to those reported in spring and summer months (Guerrero et al., 2018a, b).

The earlier development of spring conditions and the subsequent seasonal phytoplankton bloom that occurred in 2017 (Mir-Arguimbau et al., 2022) might have allowed a mixture of winter and spring planktonic cnidarian species to coexist, explaining the high number of species found during that year. On the other hand, the "typical" winter oceanographic conditions observed in 2018 might have allowed the development of winter species populations, resulting in higher abundances of the cnidarian community. Nonetheless, these abundances were an order of magnitude lower than those previously reported for summer months (Guerrero et al., 2018a, b).

Despite the differences observed between years, the most abundant species of the whole cnidarian community during both winter periods were *Lensia subtilis, Muggiaea kochii*, *Chelophyes appendiculata*, *Abylopsis tetragona* (eudoxid), *Aglaura hemistoma*, *Velella velella* larvae and *Obelia* spp., previously considered as common species throughout the whole basin (Gili et al., 1987a, b; Batistic et al., 2007; Licandro et al., 2012). The presence of eudoxid and polygastric stages of *A. tetragona*, *Abylopsis eschcholtzii* and *Eudoxoides spiralis* suggests that the sexual reproduction of these species takes place during winter months. As the production of eudoxids has been associated with high food availability (Purcell, 1982), the productivity conditions found during winter seem to be high enough to allow the sexual reproduction of the species.

During both winters, the cnidarian planktonic community presented a coastal-offshore ordination, with *L. subtilis*, *M. kochii* and *A. hemistoma* defining the coastal community and *Lensia conoidea*, *Lensia meteori* and *Lensia multicristata* the offshore one. This ordination of species assemblages has also been reported for other periods of the year in the same area (Gili et al., 1988; Sabatés et al., 2010; Guerrero et al., 2018b), pointing out that bathymetry would be a determining factor in the planktonic cnidarians distribution. Indeed, this spatial pattern might be related to the vertical distribution of the species in the water column, since those species with a wide vertical distribution, such as *L. conoidea* (Andersen et al., 1992, 2001), were found offshore, while those inhabiting surface waters, such as *M. kochii* (Gili et al., 1987a), were usually detected in coastal areas. The role of bathymetry in species ordination would help to explain the presence of coastal and offshore communities in the Blanes and Palamós submarine canyons. Such geomorphological features modify the local circulation generating shelf-slope water exchanges (Alvarez et al., 1996; Flexas et al., 2008), which favour the transport of species from offshore areas to the coast (Alvarez et al., 1996; Masó et al., 1998).

The Mediterranean is a highly seasonal sea with a marked phytoplankton bloom in late winter-early spring (Estrada et al., 1985; Saiz et al., 2014). Nonetheless, maximum abundance values of cnidarians take place slightly later, during spring and early summer (Gili et al., 1987b; Gamulin and Kršinić, 1993; Licandro et al., 2012). Our results showed an "unexpectedly" high species richness and a relatively high abundance of cnidarians in winter, suggesting that winter productivity might still be high enough to sustain a community like that found. In 2017, due to an earlier onset of spring conditions, sampling was carried out during the winter-spring transitional period, resulting in a species-rich cnidarian community. During the "typical" winter conditions of 2018, the species richness was lower, but the overall abundance was much higher. These findings highlight the relevance of studying the planktonic cnidarian community in winter to obtain a comprehensive view of its spatial and temporal variability along the annual cycle. In particular, sampling during transition periods between homogeneity and stratification of the water column, which determine the availability of nutrients to the surface layers, would allow to better understand the dynamic processes that lead to seasonal changes in the species composition of the gelatinous zooplankton community.

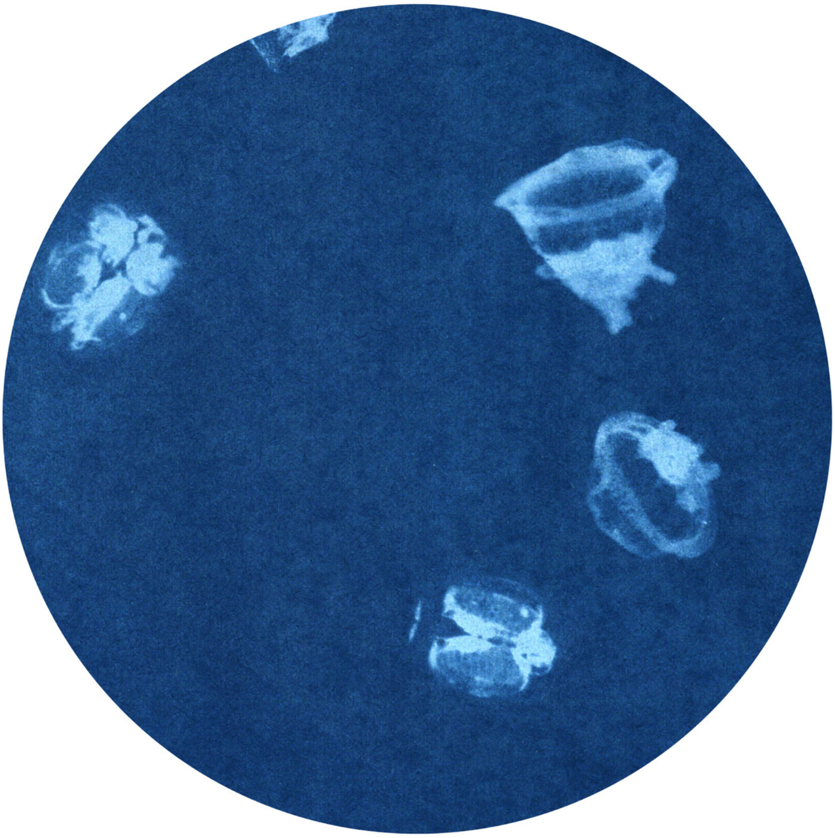
Future research on gelatinous zooplankton in the Western Mediterranean Sea

This Ph.D. thesis provides novel information on the ecology of gelatinous zooplankton in the Western Mediterranean, but at the same time it points out that further research is needed to gain a better understanding of the zooplanktonic community in this temperate sea.

Large-scale studies in other areas of the Mediterranean would provide a basin-wide view on the main hydrodynamic structures that determine the species composition, abundance and distribution, allowing to interconnect separated but well-studied areas, such as the north and south Adriatic Sea (Milos and Malej, 2005; Lucic et al., 2009). So far, most research on the distribution of gelatinous zooplankton, at species or community level, has been conducted in coastal areas, while studies in the open ocean are very limited. Indeed, the development of large-scale studies in open sea areas (e.g. between the Balearic Islands and Sardinia) would provide new information on processes occurring far away from the coast and their potential effects on coastal areas. For instance, numerous studies have been carried out on *P. noctiluca* near the coast, where this species causes high socioeconomic impacts, but the abundance and distribution of its adult phase remains unknown in open sea waters of the Mediterranean.

As stated in the introduction section, most of the research efforts have been biased towards bloom-forming species and large scyphomedusans, while other species such as heteropods and pteropods (planktonic molluscs) have received little attention. Despite a few studies have addressed the vertical distribution of some species (Andersen et al., 1998; Batistic et al., 2004), further research on these less studied taxa is of special interest, as they are often found in sampling events and beaches (e.g. pseudo shells of *Cymbulia* sp.) (Batistic et al., 2007; Nival et al., 2020). In addition, some of these species may also play a relevant role in the zooplanktonic food web through predation of other zooplankton taxa (Lischka and Ossenbrügger, 2017; Nival et al., 2020). Another group that deserves further attention are ctenophores, since they are capable of forming important blooms and can rapidly reduce local zooplankton biomass (Fuentes et al., 2010). However, owed to their fragile body structure, the collection and preservation of ctenophore samples in suitable conditions to allow accurate identification requires specific sampling methods.

Finally, seasonal transition periods between homogeneity and stratification of the water column lead to changes in food availability at the surface layers, that ultimately determine the species composition of the gelatinous zooplankton community. These seasonal transition periods lead to the coexistence of a high number of species and coincide with the end or beginning of many species' life cycle. Therefore, the study of the gelatinous zooplankton communities during these relatively short time periods is necessary to understand how they are structured, especially in highly seasonal seas such as the Mediterranean.



Conclusions

1 Ephyrae of *Pelagia noctiluca* show a heterogeneous spatial distribution in open waters of the Western Mediterranean related to different water masses and the resulting mesoscale hydrographic features.

2 The horizontal distribution of *P. noctiluca* ephyrae presents a clear latitudinal gradient, with high abundances in the south, associated with the recent Atlantic Water entering the Mediterranean through the Strait of Gibraltar, and low abundances in the north, in coincidence with the old Atlantic Water transported by the Northern Current.

3 The association of *P. noctiluca* ephyrae with the recent Atlantic Water suggests the occurrence of population connectivity between the Atlantic and the Mediterranean, a key issue for the understanding of *P. noctiluca* population dynamics in the Mediterranean Sea.

4 Ephyrae of *P. noctiluca* perform diel vertical migrations of short-extent in the first 50 m of the water column. During the day, they present a relatively wide distribution, well above and within the thermocline, without reaching the Deep Chlorophyll Maximum. At night, they concentrate near the surface in coincidence with their potential prey.

5 The mesoscale and vertical distribution of *Pyrosoma atlanticum* in the NW Mediterranean are shaped by the oceanographic and biological structures, as well as by the ontogenetic stage of the colonies.

6 Large colonies (≥ 7 mm long) of *P. atlanticum* inhabit waters over the slope, associated with the shelf-slope density front, which would aggregate them, preventing their dispersion towards the open sea. Small (< 4 mm) and medium (4–6.9 mm) colonies extend their distribution over the shelf owing to instabilities of the front, and being practically absent in the cold, low salinity coastal waters.

7 The higher abundance of P. *atlanticum* colonies in 2017 with regards to that of 2018 was likely related to an earlier onset of spring conditions and the subsequent phytoplankton bloom in 2017.

8 The vertical migratory behaviour of *P. atlanticum* starts when colonies are 4–6.9 mm long, though not all colonies of these sizes exhibit such behaviour. This suggests that migration, as an individual response, can start at any of these sizes.

9 At night *P. atlanticum* colonies of all sizes remain close to the surface, where chlorophyll-*a* levels are high, whereas during the day they migrate to deeper layers, reaching greater depths as colony size increases.

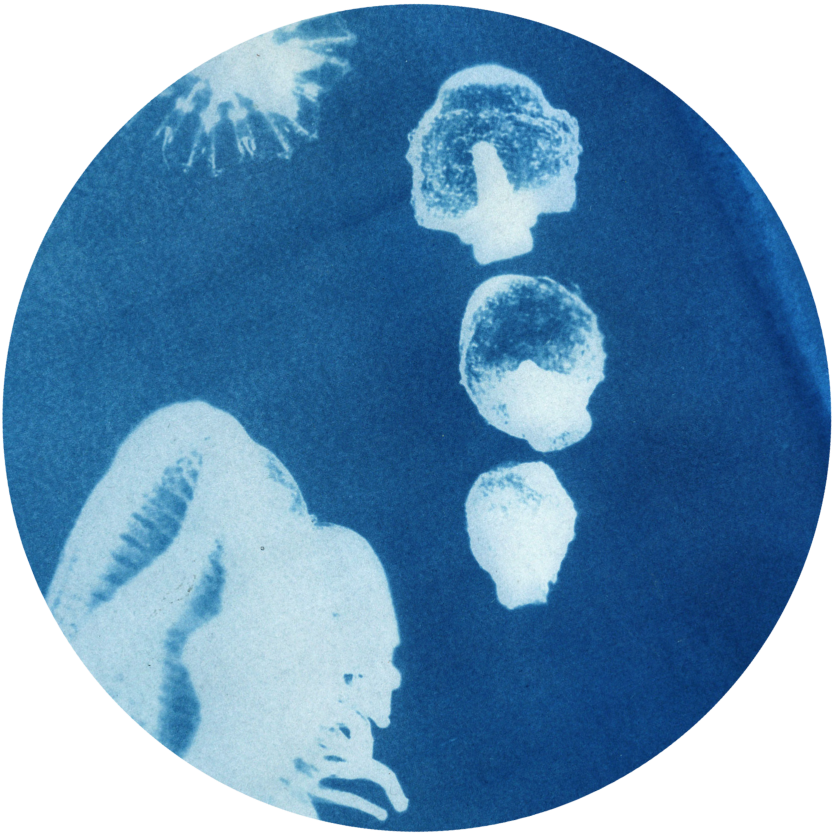
10 The vertical migration performed by *P. atlanticum* might contribute to carbon transport to depth, although the magnitude of this transport is lower than that reported in other geographical areas.

11 The planktonic cnidarian community of the NW Mediterranean during winter reveals an unexpectedly high species richness, comparable to the maximum values reported in spring and summer.

12 The earlier development of spring conditions in 2017 allowed for a mixture of winter and spring planktonic cnidarian species, resulting in a high species richness. The “typical” winter oceanographic conditions that took place in 2018 enabled the development of winter species populations, resulting in a lower number of species and higher abundance of cnidarians.

13 The most abundant planktonic cnidarian species in winter are *Lensia subtilis*, *Muggiaea kochii*, *Chelophyes appendiculata*, *Abylopsis tetragona* eudoxid stage, *Aglaura hemistoma* and *Velella velella* larvae.

14 The planktonic cnidarian assemblages present a coastal-offshore ordination related to the combined effect of environmental variables, particularly bathymetry, and oceanographic features such as water masses and the location of the shelf-slope density front. *Lensia subtilis, Muggiaea kochii* and *Aglaura hemistoma*, define the coastal community, whereas *Lensia conoidea*, *Lensia meteori* and *Lensia multicristata* define the offshore one. This ordination is only disrupted over the submarine canyons, where coastal and offshore cnidarian communities coexist.



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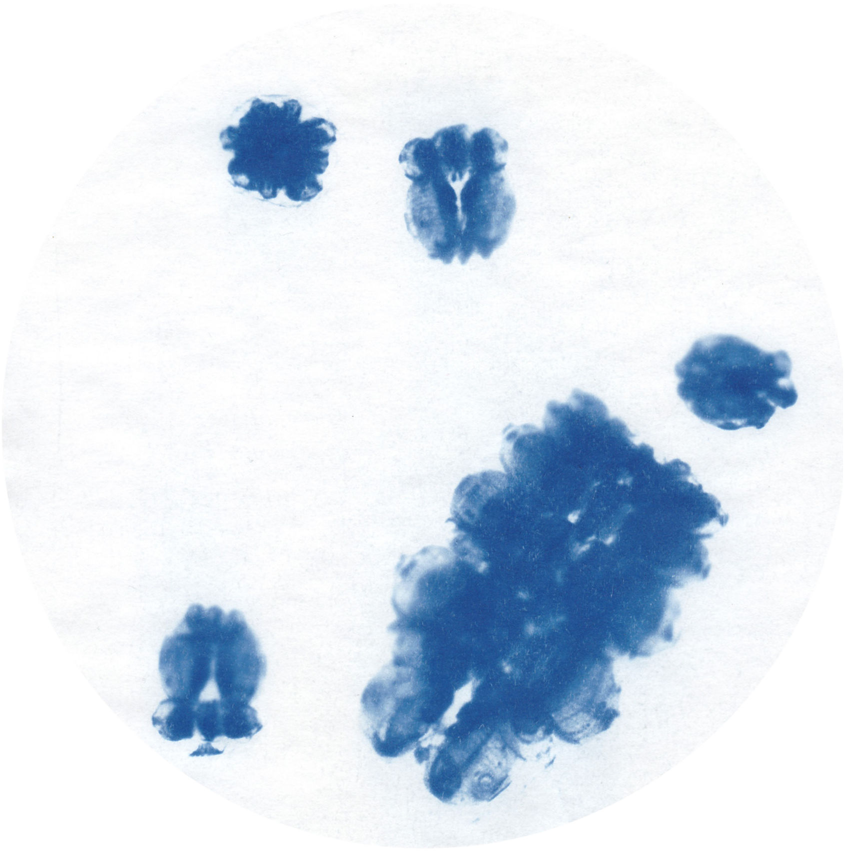
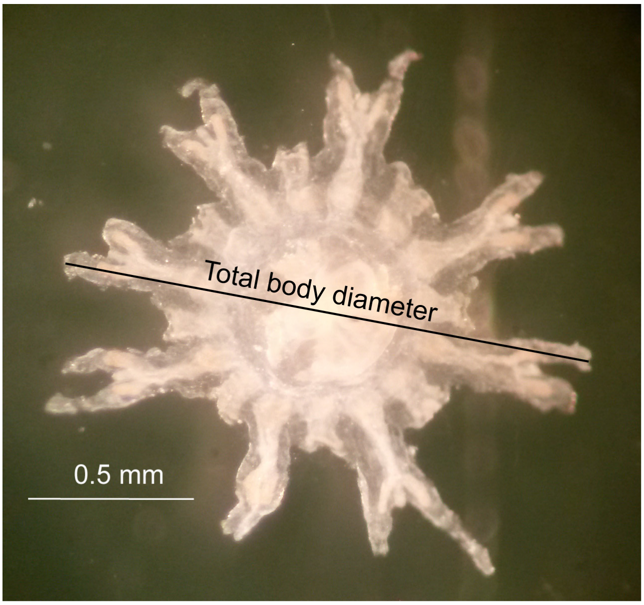


Supporting information

Chapter I



S1 Fig: Measurement of total body diameter taken in *Pelagia noctiluca* ephyrae.

$$NEphyrae_{ij} \sim NB\left(\mu_{ij}, k\right)$$

$$E\left(NEphyrae_{ij}\right) = \mu_{ij} \text{ and } var\left(NEphyrae_{ij}\right) = \mu_{ij} + \frac{\mu_{ij}^2}{k}$$

$$Log\left(\mu_{ij}\right) = Light_{ij} + Depth_{ij} + Light_{ij} \times Depth_{ij} + offset + Station_{ij}$$

$$Station_{ij} \sim N(0, \sigma^2)$$

S1 Equation: Mathematical model formulation for the GLMM analysis on the effect of light (day/night) and depth on the vertical distribution of *P. noctiluca* ephyrae (source (Zuur et al., 2009)).

$$NEphyrae_{ij} \sim NB\left(\mu_{ij}, k\right)$$

$$E\left(NEphyrae_{ij}\right) = \mu_{ij} \text{ and } var\left(NEphyrae_{ij}\right) = \mu_{ij} + \frac{\mu_{ij}^2}{k}$$

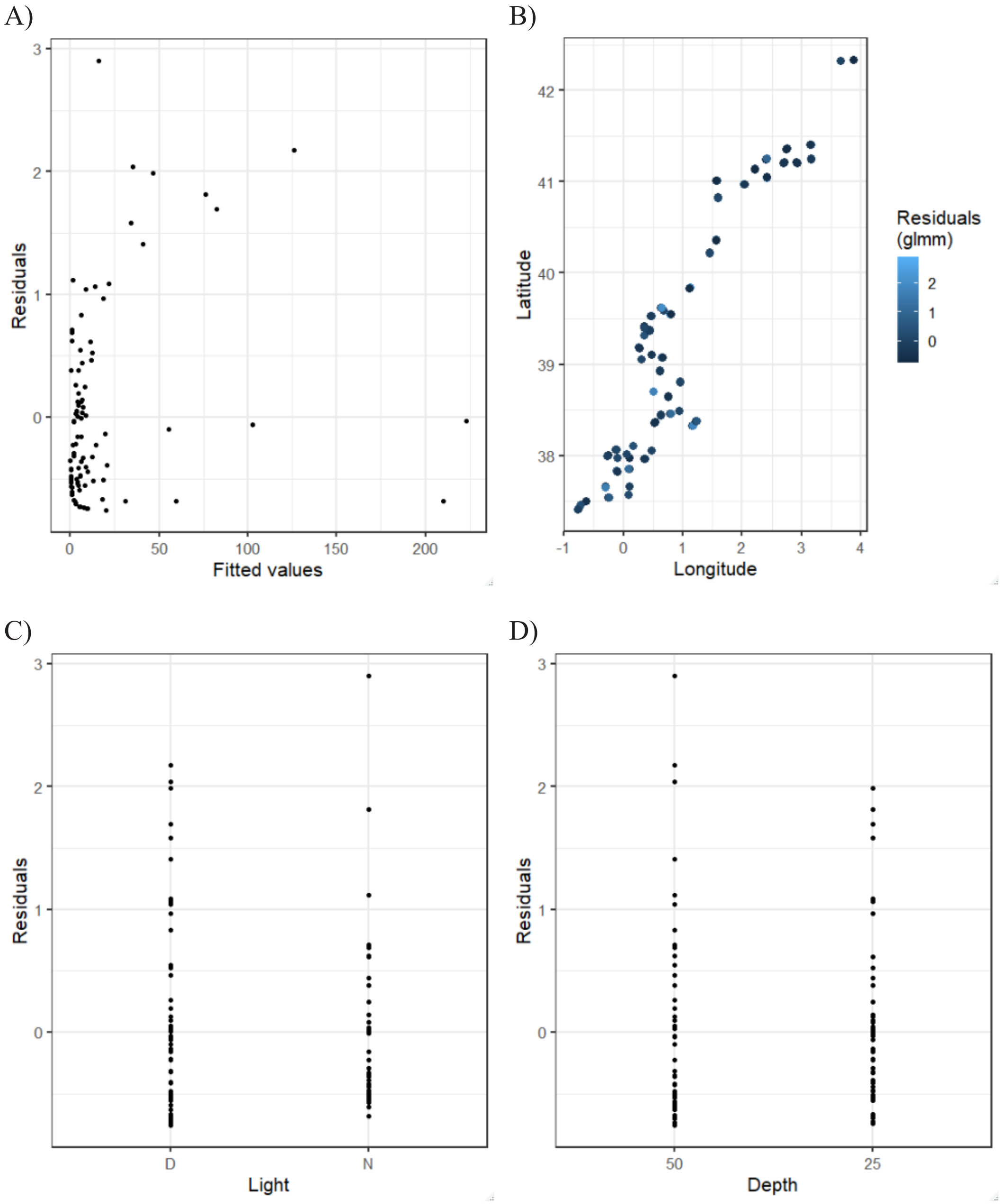
$$Log\left(\mu_{ij}\right) = Temp_{ij} + Sal_{ij} + offset + Station_{ij}$$

$$Station_{ij} \sim N(0, \sigma^2)$$

S2 Equation: Mathematical model formulation for the GLMM analysis on the effect of surface temperature and salinity on the horizontal distribution of *P. noctiluca* ephyrae (source (Zuur et al., 2009)).

S1 Table: Coefficients of GLMM analysis on the effect of light (day/night) and depth on the vertical distribution of *P. noctiluca* ephyrae. n.s. = non significant (p > 0.05).

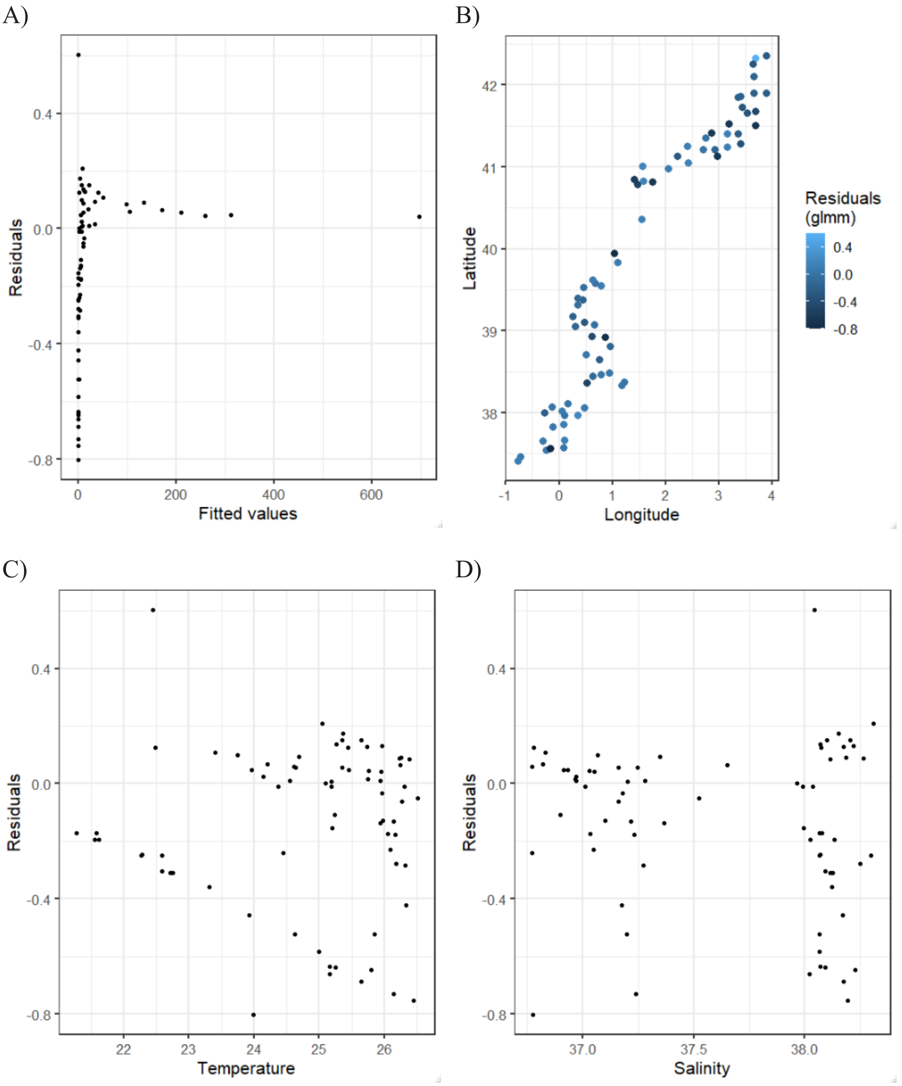
	Estimate	Std. Error	z value	p-value
Intercept	-4.32	0.03	-142.29	< 0.001
Light	-2.04	0.53	-3.85	< 0.001
Depth	0.47	0.36	1.30	0.193 n.s.
Light*Depth	2.07	0.67	3.09	0.002



S2 Fig: Pearson residuals of GLMM analysis on the effect of light (day/night) and depth on the vertical distribution of *P. noctiluca* ephyrae: a) residuals distribution vs. fitted values; b) residuals spatial distribution (missing points in the north correspond to stations where ephyrae were absent); c) residuals distribution vs. light (D = day, N = night); d) residuals distribution vs. depth (m).

S2 Table: Coefficients of GLMM analysis on the effect of surface temperature and salinity on the horizontal distribution of *P. noctiluca* ephyrae.

	Estimate	Std. Error	z value	p-value
Intercept	43.57	13.69	3.18	0.001
Temperature	1.07	0.22	4.82	< 0.001
Salinity	-2.02	0.37	-5.45	< 0.001



S3 Fig: Pearson residuals of GLMM analysis on the effect of surface temperature and salinity on the horizontal distribution of *P. noctiluca* ephyrae: a) residuals distribution vs. fitted values; b) residuals spatial distribution; c) residuals distribution vs. temperature (ºC); d) residuals distribution vs. salinity.

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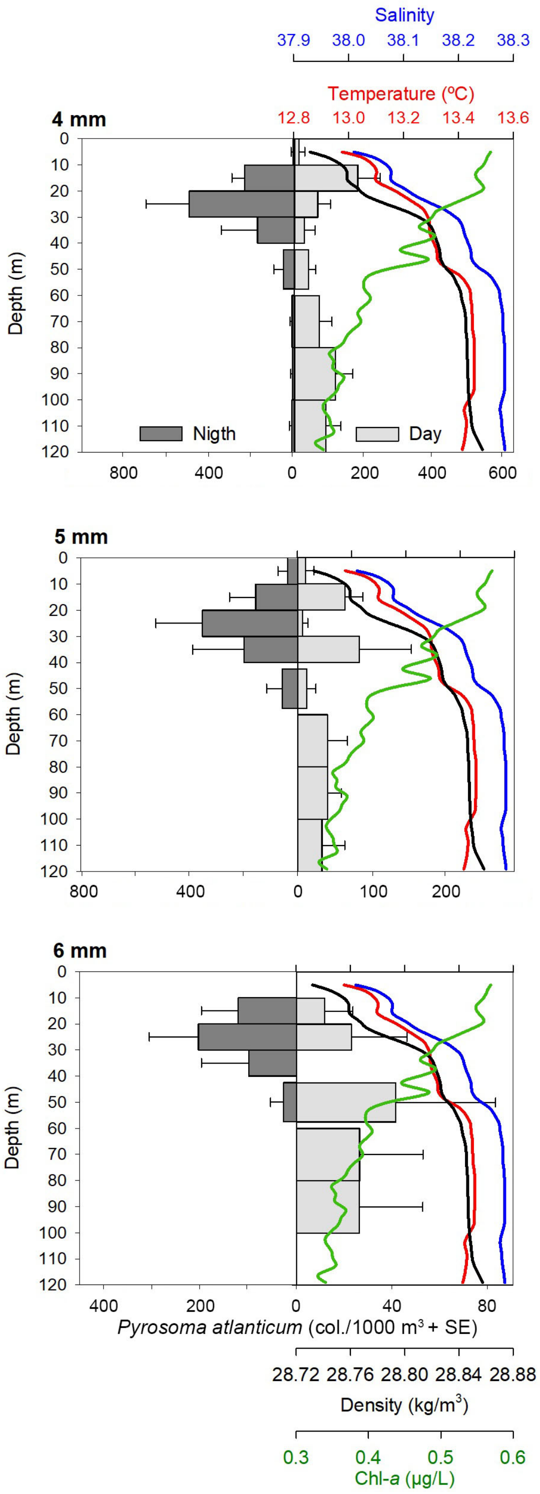

Fig. S1: Mean vertical distribution (+ standard error) of *Pyrosoma atlanticum* by millimetre within the medium size class (4-6.9 mm), in night-time (dark grey bars) and day-time (light grey bars), overlaid on vertical profiles of temperature (red), salinity (blue), density (black) and chlorophyll-*a* (green). Note that the colony abundance scales are different for each colony size. Data correspond to the 48h fixed station sampled in 2017 (see Fig. 1).

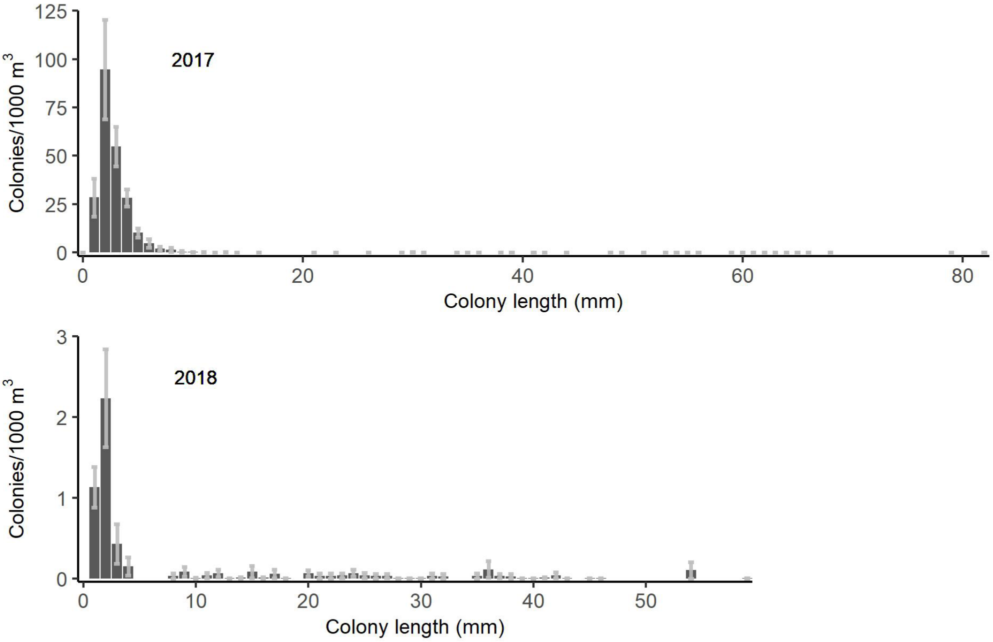

Fig. S2: Size frequency distribution (mean ± standard error) of *Pyrosoma atlanticum* colonies in 2017 (upper panel) and 2018 (lower panel). Note the different axis for colony abundance in each year.

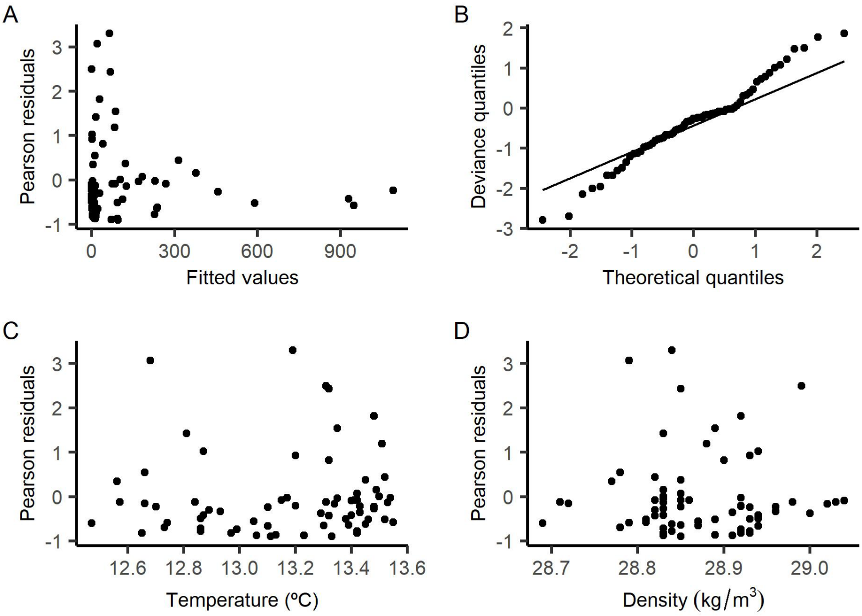

Fig. S3: Residual diagnostics of GLM analysis on the effect of temperature and density on the horizontal distribution of small-medium (≤ 6.9 mm) colonies of *Pyrosoma atlanticum*. Residuals distribution vs. fitted values (a); Q-Q plot (b); residuals distribution vs. temperature (10 m; ºC) (c); residuals distribution vs. density (30 m; kg/m^3) (d).

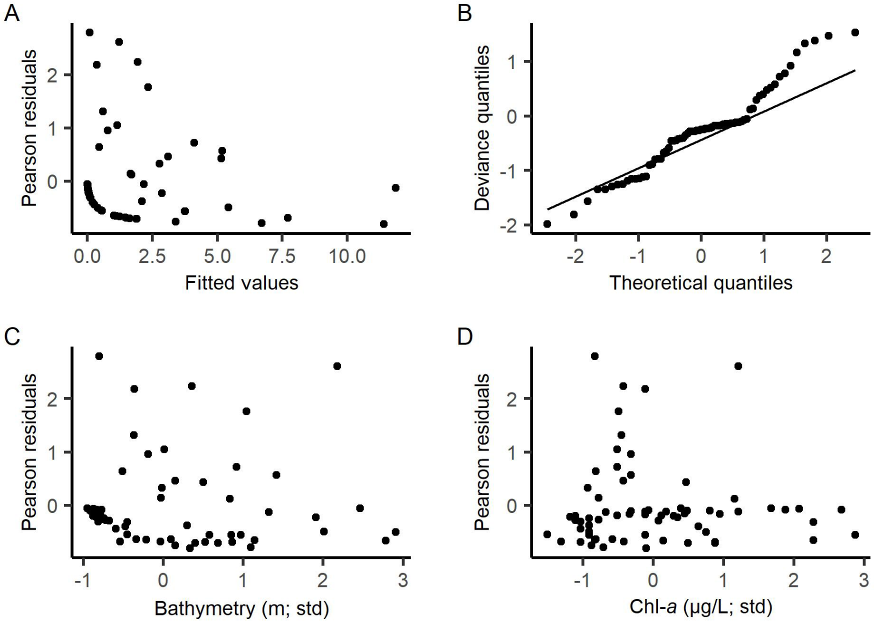

Fig. S4: Residual diagnostics of GLMM analysis on the effect of bathymetry and chlorophyll-*a* on the horizontal distribution of large (≥ 7 mm) colonies of *Pyrosoma atlanticum*. Residuals distribution vs. fitted values (a); Q-Q plot (b); residuals distribution vs. bathymetry (m) (c); residuals distribution vs. chlorophyll-*a* (10 m; µg/L) (d). std = standardized variables.

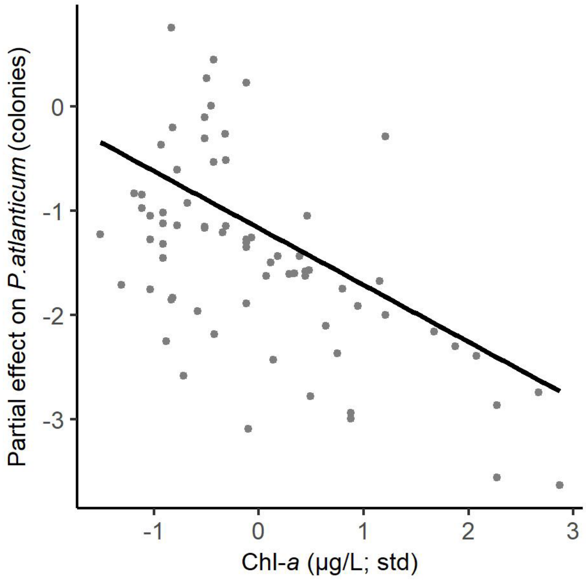

Fig. S5: Partial effect of surface (10 m) chlorophyll-*a* (standardized; non significant) over the large *Pyrosoma atlanticum* colonies (number). Partial effect shows the change in response variable for each value of the variable on the x-axis, holding all other variables constant (median). Bold line show the best fit of the GLMM model and dots correspond to observations.

Estimation of downward active carbon transport by *Pyrosoma atlanticum*

To estimate the active carbon transport by *P. atlanticum* through diel vertical migration we followed the methodology applied in Henschke et al. (2019) for this species. We have only considered the migratory population (52% of medium size colonies and 100% of large size colonies, see results section of the main text).

Wet weight (*WW*; g) of *P. atlanticum* colonies was estimated from the median colony length (l; mm) of the medium and large size colonies each year following the equation:

(1) $$\mathrm{WW}=0.0013l^{2}+0.0151l^{2}$$

Respiration rate (R; ml O_2/col.·h) was expressed by the allometric equation:

(2) $$R=0.0046WW^{1.2284}$$

Where *WW* corresponds to wet weight of the colony (g).

To calculate the respiratory carbon equivalent (RC; µg C/col.·d) from the respiration rate we used the equation from Al-Mutairi and Landry (2001):

(3) $$\mathrm{RC}=\mathrm{R}\cdot\mathrm{RQ}\cdot(12/22.4)$$

where R is the respiration rate (ml O_2/col.·d), RQ is the respiratory quotient (1.16 for salps; see Mayzaud et al., 2005), 12 is the molar weight of carbon (g/mol), and 22.4 is the molar volume (mol/L) of an ideal gas at standard pressure and temperature.

Following Henschke et al. (2019), dissolved organic carbon excretion was assumed to be approximately 31% of the carbon respired (RC). We applied a mortality estimation of 1%/d reported in areas of similar biomass (Henschke et al., 2019). Daily faecal pellet production (FP; mg C/col.·d) was estimated by the equation:

(4) $$\mathrm{FP}=0.25\cdot\mathrm{CW}$$

where daily defecation rates are 25% of body carbon (Henschke et al., 2019) and carbon weight (CW; mg C) was estimated to be 3.92% of wet weight of the colony for *P. atlanticum* (Lebrato and Jones, 2009).

Daily faecal pellet production allows to estimate the gut flux (GF; mg C/ col.·d; i.e.

defecation or nondigested food), where 24 converts daily faecal pellet production to hourly;

(5) $$GF=FP/24\cdot(GPT-DM)$$

A gut passage time (GPT; h) of 1.43h for *P. atlanticum* (Perissinotto et al., 2007) was considered. The time spent in downward migration (DM; h) was estimated using a mean swimming speed of 0.05 m/s (considering the speed range 0.03-0.07 m/s reported in Henschke et al. (2019)) and the distance between weighted mean depth during day and night (migration amplitude). DM was never higher than GPT.

Finally, we estimate the respiratory, excretory, mortality and gut flux contribution to the active carbon transport for *P. atlanctium* (µg C/m^3·d) (Table S1). For the conversion of these values to mg C/m^2·d the migration amplitude of each size class has been considered.

Year	Respiratory flux (µg C/m^3·d)	Excretory flux (µg C/m^3·d)	Mortality flux (µg C/m^3·d)	Gut flux (µg C/m^3·d)	Total carbon flux (µg C/m^3·d)	Total carbon flux (mg C/m^2·d)
2017	0.66	0.21	3.45	0.93	5.26	0.56
2018	0.07	0.02	0.38	0.08	0.54	0.05

Table S1: Estimation of active downward carbon transport for *P. atlanticum* in the NW Mediterranean in 2017 and 2018.

The mean chl-*a* concentration in the upper 70 m of the water column (depth range that covers the weighted mean depth of all colony sizes during the night) was 0.65 ± 0.15 mg chl-*a*/ m^3 in 2017 and 0.86 ± 0.56 mg chl-*a*/ m^3 in 2018). Applying the C:Chl-*a* ratio of 47 (g:g) for the NW Mediterranean (Latasa et al., 2005), the carbon transport by *P. atlanticum* through diel vertical migration represents a 0.01% and a 0.001% of the carbon concentration in the upper water layers in 2017 and in 2018, respectively.

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Chapter III

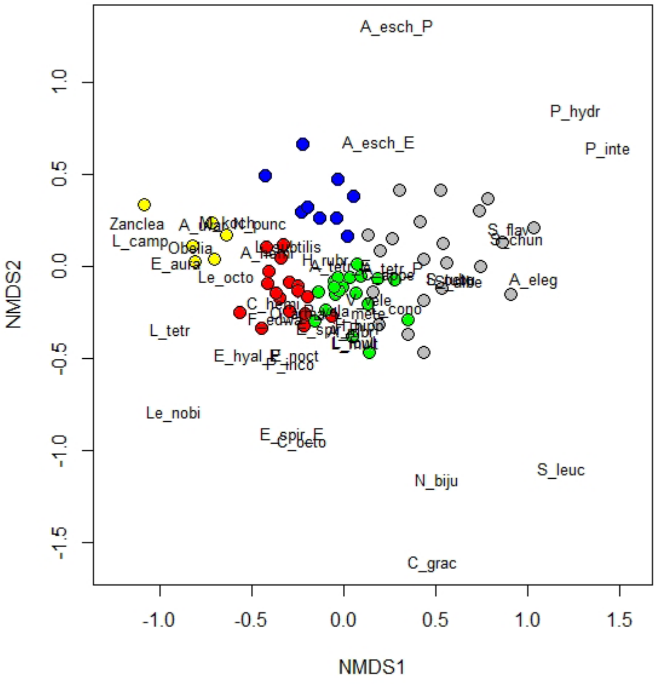
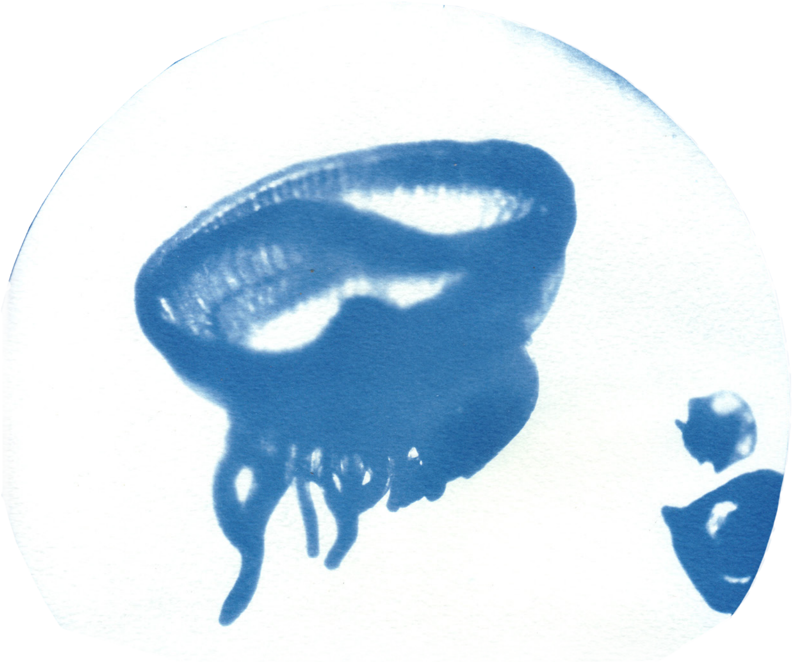


Fig. S1: Non-metric multidimensional scaling (nMDS; stress = 0.16) ordination plot of Bray-Curtis dissimilarity matrix. Species are shown in the plot and sampling stations are coloured according to cluster results.



Publications

PLOS ONE

RESEARCH ARTICLE

Spatial heterogeneity of *Pelagia noctiluca* ephyrae linked to water masses in the Western Mediterranean

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Abstract

Pelagia noctiluca is the most common jellyfish in the Western Mediterranean Sea, living in oceanic waters with a holoplanktonic lifecycle. Frequent outbreaks have been well documented in coastal areas, yet little is known about their offshore distribution. In this study we address the relationship between oceanographic structures and the distribution of *P. noctiluca* ephyrae along the central continental slope of the Western Mediterranean, covering a wide latitudinal gradient, during July-August 2016. The region is characterized by a rich and complex mesoscale surface circulation driven by the inflow of Atlantic Water into the Western Mediterranean through the Strait of Gibraltar. The results revealed a high variability in the ephyrae spatial paterns related with different water masses and the resulting mesoscale hydrographic features. Their horizontal distribution showed a clear latitudinal gradient with high abundances in the south, associated with recent Atlantic Water, and low abundances or absence in the north, in coincidence with the old Atlantic Water transported by the Northern Current. Ephyrae showed diel vertical migrations of short-extent in the first 50 m, with a wide distribution above the thermocline and the Deep Chlorophyll Maximum during daytime, being more concentrated towards the surface at night. The results suggest the population connectivity of *P. noctiluca* between the Atlantic and the Mediterranean. In that case, the abundance variability of the species in the Mediterranean could be modulated by its entrance associated with the inflow of Atlantic Water through the Strait of Gibraltar.

Introduction

Jellyfish are conspicuous components of pelagic communities that show increases in population size often resulting in mass occurrences, or blooms, worldwide [1,2]. While there is a lack of scientific consensus in identifying global trends in jellyfish blooms [3], their negative impacts on human activities in coastal waters are remarkably increasing in frequency and severity [4,5]. These increases in jellyfish abundance have the potential to alter the balance of trophic pathways between smaller zooplankton and their predators in marine ecosystems [6].

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Jellyfish distribution and aggregation are determined by the combination of environmental conditions and life history events resulting in a rapid increase in population numbers [7]. Hydrodynamic structures such as currents, fronts and eddies may act as mechanisms for their transport or confinement [8,9] thereby contributing to an increase in mesoscale spatial heterogeneity. These structures support high levels of biological activity e.g. [10,11] controlling the interactions among organisms with limited horizontal mobility [12] such as jellyfish. Differently, they have the ability to actively swim vertically through sharp clines [13].

The Western Mediterranean Sea (WM) is characterized by a complex physical dynamics with distinctive traits, especially in regard to the thermohaline circulation. The surface circulation is mainly driven by the inflow of Atlantic Water (AW) through the Strait of Gibraltar, its signature being modified as it travels eastward [14]. The input flow of AW in the WM follows the north African coast creating anticyclonic eddies [14,15] which can be trapped by the bottom topography of the Alboran Sea or freely displaced around the Algerian basin and reach the Balearic Islands. The Balearic Islands can be considered a transitional region between the two main WM sub-basins: the Liguro-Provençal and the Algerian basins. Part of the AW flows across the Balearic channels forming the Balearic Current [16,17] that follows the northern side of the Balearic Islands to the west coast of Corsica [18,19]. A surface front, which is not deeper than 200 m, associated with the Balearic Current, separates recent AW brought by the current from the resident waters of the centre of the northern part of the basin [20]. Typically, the salinity of recent AW is nearly 1 unit lower than the older resident AW waters [21]. On the eastern side of the Liguro-Provençal basin, the recent AW flow from the Balearic basin joins the old AW from the Tyrrhenian Sea [22], forming the Northern Current which flows southwestwards along the continental slope, adapted to the bathymetry and contouring the northwestern basin cyclonically [23,24].

Pelagia noctiluca is the most common jellyfish in the Mediterranean Sea, living in oceanic waters [25,26]. It is a holoplanktonic species with a variable reproductive period depending on the region, and the presence of ephyrae has been reported throughout the year [27–29]. In the WM, the highest abundance of *P. noctiluca* occurs during spring and summer [28,30,31] and their blooms appear to be increasing in frequency and duration [26,32,33]. The studies on the spatial distribution of *P. noctiluca* in relation to hydrodynamic structures in open sea waters of the basin are scarce and restricted to some areas of the northwestern region. These studies have shown that the species is particularly abundant in the vicinity of the shelf-slope front associated with the Northern Current [28,34,35]. The particular hydrodynamic conditions of that region enhance and maintain high levels of biological production [36–38] providing ideal conditions for feeding, growth and reproduction of the zooplanktonic organisms. However, the lack of knowledge on the distribution of *P. noctiluca* in open waters further south limits our understanding of a large-scale picture of its spreading patterns in the WM.

Jellyfish are difficult to sample quantitatively [39,40] and the mechanisms of jellyfish transport and aggregation cannot be understood without a large scale sampling of their abundances combined with synoptic environmental measurements. In contrast, ephyrae can be efficiently collected with plankton nets and its distribution can be a good proxy of the global abundance and distribution of the species [35]. Considering this approach, the objective of the present study was to identify how the mesoscale water dynamics shapes the spatial structure of *P. noctiluca* ephyrae along the continental slope of the WM. To this aim, we performed an extensive plankton and hydrographic sampling, with a wide latitudinal and vertical coverage, that will result in a general view of the distribution of the species driven by hydrodynamic processes in open waters of the WM, and provide new insights on its potential populations increase.

Material and methods

Field sampling

The study was conducted on the central continental slope of the WM along a wide latitudinal gradient (37.4˚N—42.3˚N) in a south north direction, between 22nd July and 28th August 2016 on board the R/V García del Cid (Fig 1). A total of 170 hydrographic stations, with plankton sampling at 75 stations (29 at night and 46 during the day) were completed. At each hydrographic station, vertical profiles of basic hydrographic variables (salinity, temperature and fluorescence), from surface to 200 m depth, were obtained by means of conductivity-temperature-depth profilers (CTD) (SBE25 and SBE911), equipped with a fluorometer. At the plankton stations, hydrographic parameters were measured with a CTD (SBE3F) integrated in the plankton net. CTD data were inter-calibrated to make them readily comparable. Afterwards, data were bin averaged at 1 m depth intervals.

Zooplankton was sampled with a Multiple Opening/Closing Net Environmental Sensing System (MOCNESS net) of 1 m^2 opening mouth and a 300 μm mesh. Hauls were oblique from deep to shallow waters, at a vessel speed of 1.2 ± 0.4 knots. The depth strata examined were: 200–100, 100–50, 50–25, 25–0 m, and the volume of filtered water was recorded by a

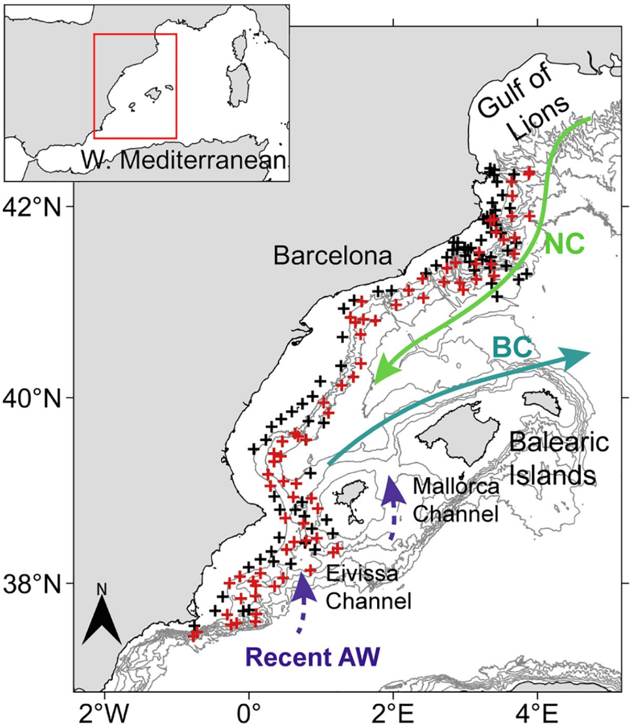

Fig 1. Study area in the Western Mediterranean. Hydrographic (black and red crosses) and plankton (red crosses) stations during the survey. The schematic lines indicate the main currents, Northern Current (NC) and Balearic Current (BC), and recent AW inflow through the Eivissa and Mallorca Channels. Coastline is from Natural Earth [41] and Instituto Hidrográfico de la Marina [42], and isobaths (every 400 m depth) are from European Marine Observation and Data Network (EMODnet, [43]).

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flowmeter attached to the mouth of the net. Immediately after collection, zooplankton samples were fixed in 5% formaldehyde buffered with sodium tetraborate.

Data analyses and sample processing

2D maps showing the latitudinal variation of surface salinity and temperature data were produced by applying Data-Interpolating Variational Analysis (DIVA) gridding to 10 m depth CTD data, using the Ocean Data View (ODV) software [44]. DIVA gridding was also applied using ODV, for creating sections of the depth variation with latitude of the upper 100 m depth from environmental data collected at all the stations. In addition, daily salinity and temperature at 10 m depth reanalysis products from Copernicus Marine Environment Monitoring Service (CMEMS, [45]) were used to estimate mean salinity and temperature values for the surrounding areas during the study period, and were represented with QGIS v3.4.11 [46]. Mean currents data for August 2016, at 10 m depth, from CMEMS were represented through QGIS v2.18.28 [47].

In the laboratory, the zooplankton samples were examined using a stereomicroscope in order to identify and count the ephyrae of *P. noctiluca* (total body diameter: 0.55–3.55 mm, S1 Fig). The number of individuals within each depth strata was standardized to number per 100 m^3 of filtered water.

A preliminary exploration of the ephyrae vertical distribution, from surface to 200 m depth, was carried out for 12 of the 75 sampled stations, randomly selected and distributed along the sampling area. Considering these stations, 99.9% of ephyrae were found between 0–50 m depth. Based on these results, only 0–25 m and 25–50 m depth levels were considered for the vertical distribution analysis. For the mesoscale horizontal distribution, the two depth levels were grouped together (0–50 m). The effect of light (day/night) and depth on the ephyrae vertical distribution was analysed through a Generalized Linear Mixed Model (GLMM) (see S1 Equation in supporting information). A GLMM was also fitted to assess the effects of independent (Pearson's cross-correlation coefficient < 0.5) oceanographic variables (mean surface, 5–10 m depth, salinity and temperature) from CTD data on the horizontal distribution of the ephyrae (see S2 Equation in supporting information). In order to avoid any spatial lack of independence among close sampling stations, the geographical position of each station was included as a random effect in both GLMMs. In addition, in both analyses the error family distribution used was a negative binomial, due to the patchy distribution of ephyrae (a normal condition in plankton ecology [48]), and with a log-link to avoid predicting negative numbers of ephyrae, using the "*glmer.nb*" function from the "MASS" package [49]. To reduce the bias due to different filtered volumes by the nets (mean 471 $m^3 \pm 124$ standard deviation) the (log-transformed) volume of filtered seawater was included as an offset inside GLMMs [50]. The GLMMs were carried out using the statistical programming language R v3.5.3 [51].

Results

Hydrographic conditions

The TS diagram of the upper 100 m showed the more recent AW, characterized by relatively low salinity, and the old and more saline AW transported by the Northern Current, that stayed longer time in the basin (Fig 2).

The spatial distribution of sea surface salinity (10 m) contrasted between the south (≈ 37.1) and the north (≈ 38.1) with a marked gradient between 39.5˚N and 40.0˚N, clearly separating the recent AW to the south and the old AW to the north (Fig 3A). Temperature (10 m) showed values around 24.0˚C (23rd July– 26th July) in the southern part of the area, south of 38.3˚N. Warm waters (≈ 25.2˚C, 27th July - 23rd August) were detected in the central zone, while the

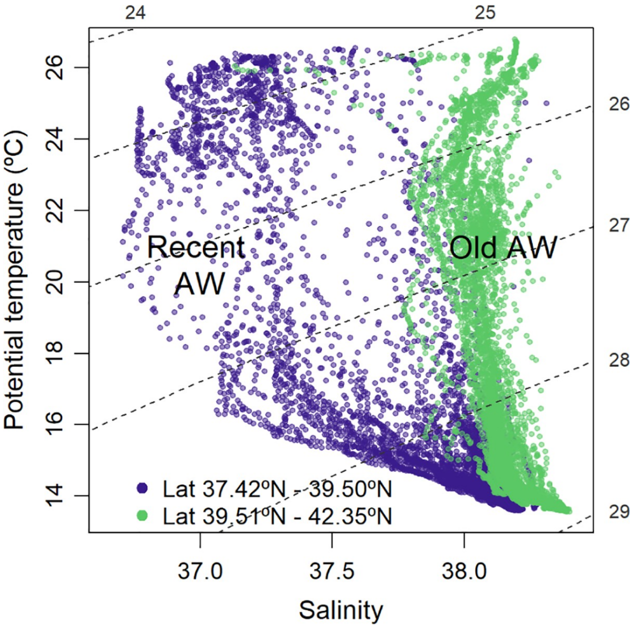

Fig 2. TS diagram of the water layer from 0 to 100 m depth. Recent Atlantic Water (blue dots), south of 39.5˚N; old Atlantic Water (green dots), north of 39.5˚N.

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northernmost part of the area presented the lowest temperatures (≈ 22.0˚C, 24th August– 28th August) (Fig 3B).

The vertical section of salinity (Fig 4A) suggested the presence of a saline front between 39.5˚N and 40.0˚N, delimiting the presence of recent AW in the south and the old AW in the north. The recent AW was detected in the upper 60 m depth in the south and became shallower until 39.5˚N (Fig 4A). The vertical section of temperature along the continental slope showed a surface mixed layer of about 20 m thickness, with temperature values above 25.0˚C between 38.0˚N and 41.0˚N (Fig 4B). This central zone also showed the strongest thermocline gradient below the mixed layer, between 20 and 30 m depth. The thermocline becomes weaker south of 38.0˚N and north of 41.0˚N, with slightly lower surface temperature (Fig 4B). The vertical section of fluorescence was typical of the season with a clear Deep Chlorophyll Maximum (DCM) below the thermocline, between 50 and 90 m (Fig 4C).

The surface currents were characterised by the strong jet of the Balearic Current flowing to the northeast along the northern coast of the Balearic Islands (Fig 5). This current displayed a deflection towards the northwest, at around 4.0˚E, joining the Northern Current path. The presence of the Northern Current was evident in the northern part of the area flowing to the southwest along the continental slope (Fig 5).

Vertical distribution of *P. noctiluca* ephyrae

The preliminary analysis of the vertical distribution of *P. noctiluca* ephyrae revealed that practically all individuals (99.9%) were located in the upper 50 m of the water column (63.3% at 0–25 m and 36.6% at 25–50 m). The remaining 0.1% of ephyrae was found between 50 and

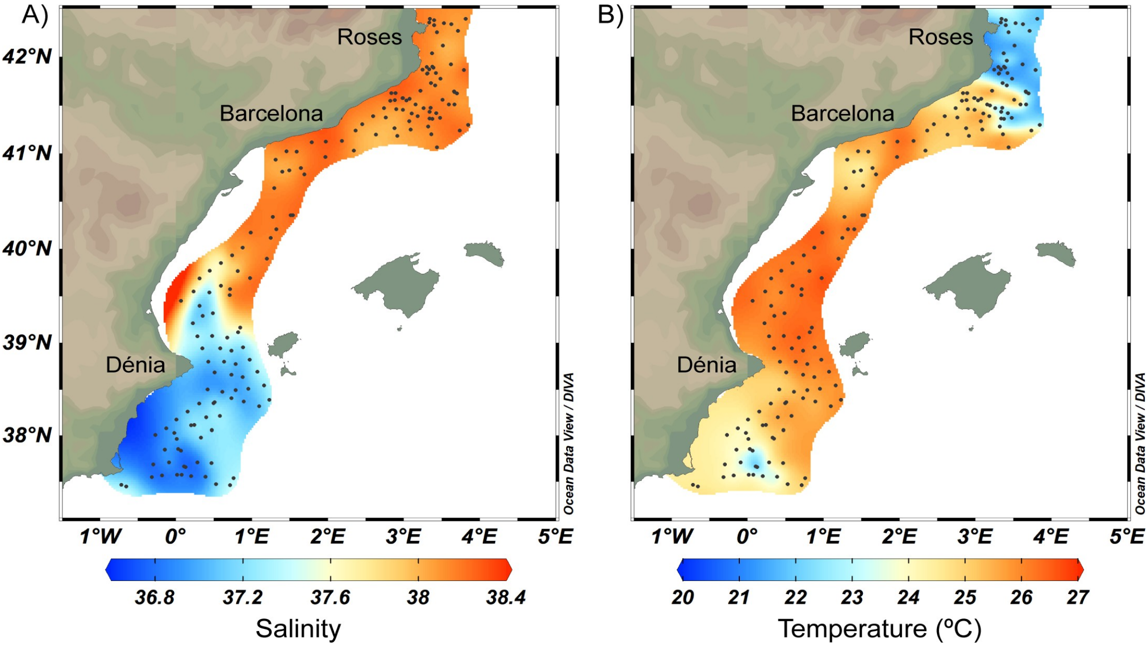

Fig 3. Horizontal distribution of a) salinity and b) temperature at 10 m depth from CTD data. Dots show the sampling stations. Images were created using ODV [44].

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100 m, being absent below 100 m depth. Thus, the subsequent analyses, considering all the sampled stations, were focused on the first 50 metres. The GLMM analysis indicated that the light level (day/night) effect on ephyrae vertical distribution was significant (z = -3.85, p-value < 0.001) and that this effect of the light depended on depth (z = 3.09, p-value = 0.002; see S1 Table and S2 Fig). During the night, the ephyrae were mainly found in the upper 25 m, with low abundances at 25–50 m, whereas during the day they showed a more homogeneous distribution between surface and 50 m (Table 1; Fig 6). The vertical displacement of ephyrae during the day toward deeper water layers never crossed the lower limit of the thermocline and therefore, did not reach the DCM level (Fig 6).

Horizontal distribution of *P. noctiluca* ephyrae

P. noctiluca ephyrae were particularly abundant south of 40.0˚N, in coincidence with the presence of less saline surface water (Fig 7A). These high abundances also fit well with the path of the Balearic Current (Fig 5). In that area, ephyrae were present in almost all stations reaching the maximum abundance value (78 ephyrae 100 m^{-3} per station) slightly south of the Eivissa Channel (around 38.5˚N; Fig 7). However, in the northern half of the area, occupied by the more saline waters, the abundance of ephyrae along the Northern Current path was much lower, being practically absent in the northernmost part characterized by the coldest temperatures (Fig 7B). This low abundance, between 40.0˚N and 41.3˚N, coincided with the mixture of waters from the Northern and Balearic Currents after the deflection of the Balearic Current at 4.0˚E (Fig 5). The GLMM results showed that ephyrae abundance presented a negative association with salinity (z = -5.45, p-value < 0.001) and positive with temperature (z = 4.82, p-

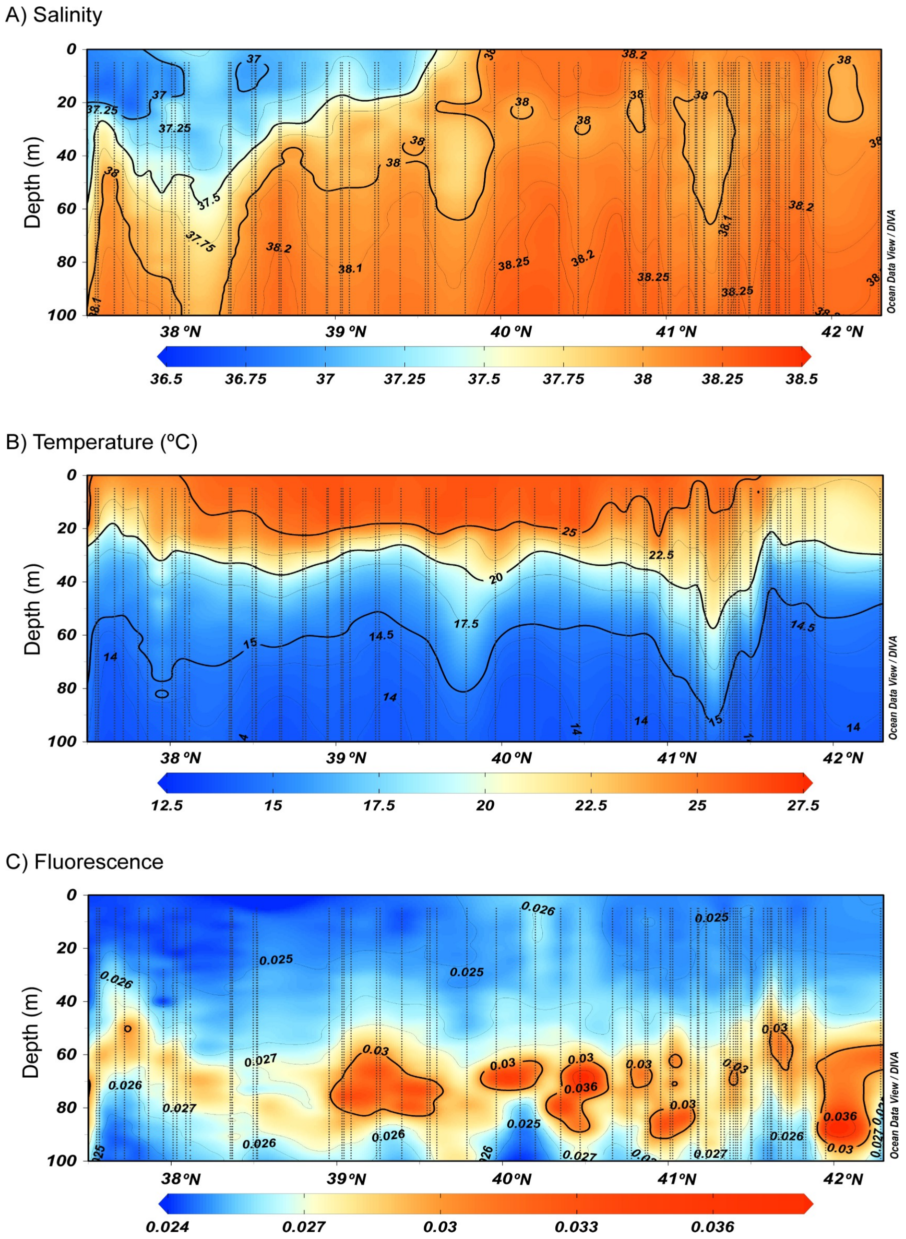

Fig 4. Vertical distribution of a) salinity, b) temperature and c) fluorescence in the upper 100 m depth from CTD data, along the continental slope. Horizontal axis indicates latitude range. Vertical dotted lines represent 1 m binned CTD profiles data.

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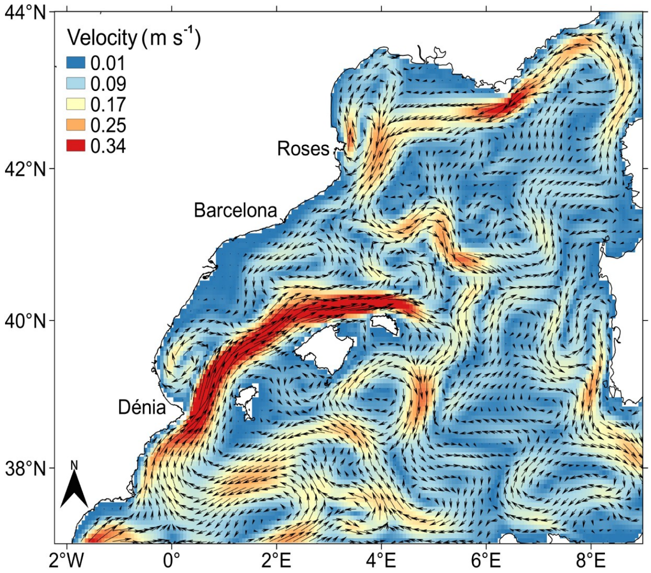

Fig 5. Mean velocity field for August 2016 at 10 m depth from CMEMS reanalysis [45]. The current velocity is depicted through the colour scale and arrows show the current direction. Coastline is from Natural Earth [41] and Instituto Hidrográfico de la Marina [42].

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value < 0.001; see S2 Table and S3 Fig), with the highest values in the warm and low saline waters, between slightly south of the Eivissa Channel and 40.0˚N (Fig 7).

Ephyrae abundance by station superimposed to surface salinity and temperature clearly defines three groups of stations (Fig 8). The highest abundance values were associated with recent AW, characterized by salinities lower than 37.5 and temperatures between 22.5˚C and 26.5˚C. Lower abundances were found associated to old AW (salinity >37.5) at temperatures between 24.0˚C and 26.6˚C, while ephyrae were practically absent in old AW with temperatures lower than 24.0˚C (Fig 8). It is worth noting the high ephyrae abundance in a station not included in any of the three stations groups, located on the boundary between the low and high salinity waters, around 40.0˚N (Fig 7A).

Discussion

The results of the present study revealed a high variability in the spatial structure of *P. noctiluca* ephyrae in surface waters linked to the recent and old AW masses. The presence of *P. noctiluca* ephyrae in the upper water layer is in agreement with previous observations [28,53,54]. In the present study, however, we detected short-extent diel vertical migrations of ephyrae in these surface levels, with a wide distribution well above and within the thermocline during daytime,

Table 1. Ephyrae abundance (mean ± standard error) by day/night and depth stratum.

Ephyrae 100m^{-3}	Night	Day
0–25 m	4.7 ± 2.90	7.6 ± 2.91
25–50 m	1.1 ± 0.91	6.7 ± 3.81

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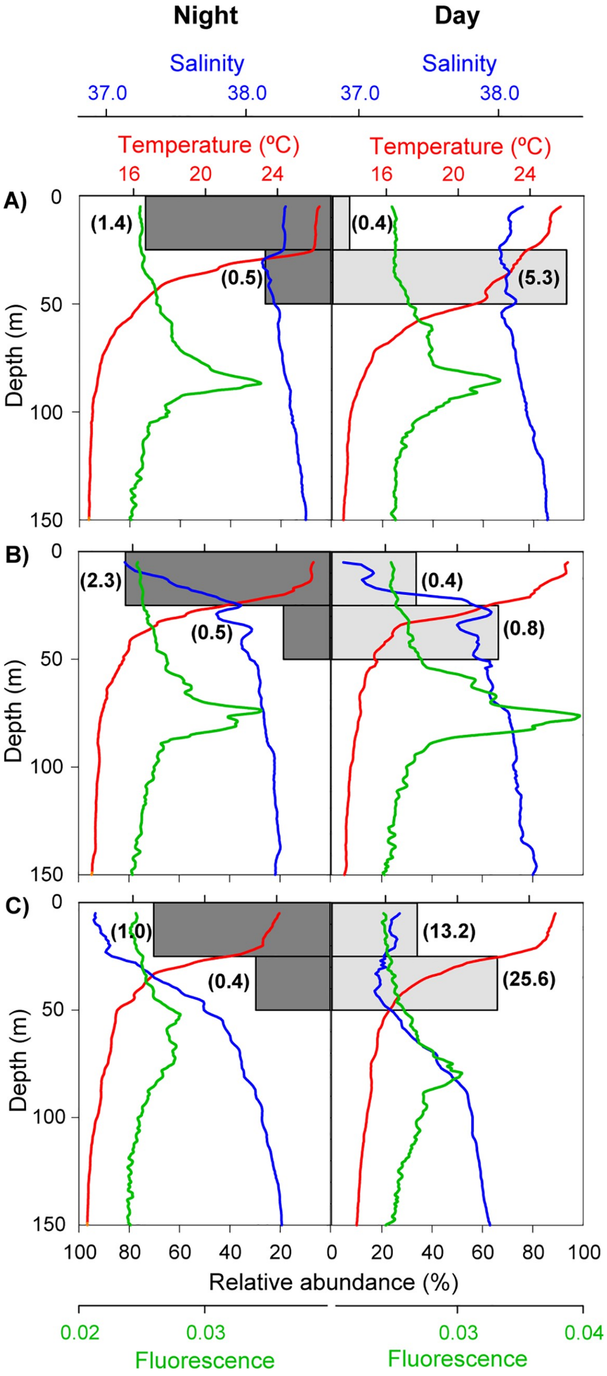
Night
Day
Salinity
37.0
38.0
Temperature (ºC)
16
20
24
A)
B)
C)
Depth (m)
0
50
100
150
(1.4)
(0.5)
(0.4)
(5.3)
(2.3)
(0.5)
(0.4)
(0.8)
(1.0)
(0.4)
(13.2)
(25.6)
100
80
60
40
20
0
20
40
60
80
100
Relative abundance (%)
0.02
0.03
0.04
Fluorescence

Fig 6. Vertical distributions of ephyrae in night time (dark grey bars) and daytime (light grey bars) and temperature (red), salinity (blue), and fluorescence (green). Data of six stations representative of the hydrographic conditions at the a) north (41.0˚N, 2.0˚E), b) centre (39.5˚N, 0.5˚E) and c) south (38.0˚N, 0.2˚E) of the sampling area. Ephyrae relative abundance by station. Values in parenthesis indicate ephyrae abundance 100 m^{-3}.

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being more concentrated towards the surface at night. In any case, their vertical distribution was found far from the characteristic DCM that develops in the Mediterranean during the summer stratification period [55]. This vertical distribution contrasts with that described for the epipelagic zooplankton, characterized by the presence of a zooplankton maximum at approximately the same depths than the DCM during the daytime, whereas at night zooplankton ascends to upper layers [56–58]. This behaviour allows for feeding during the day at the DCM, avoiding the predation at the surface [59]. Taking into account that *P. noctiluca* ephyrae feed on a variety of zooplanktonic prey, such as copepoda, siphonophora, salpida or fish larvae [60,61], the migratory behaviour of the zooplankton would allow the overlap between *P. noctiluca* ephyrae and their prey during the night in surface waters. This would be supported by the high variety of prey detected in the gastric pouches of ephyrae during the night with respect to the day [62]. Moreover, we cannot discard the possibility that ephyrae might feed on microzooplankton, such as ciliates and flagellates, as observed in ephyrae of *Aurelia coerulea* [63]. These microzooplanktonic organisms are very abundant in the upper layers of stratified waters [64] and have been reported to be an important food source for other planktonic organisms, such as cladocerans and fish larvae, living in surface waters [65–67]. We can also consider that the vertical migration to slightly deeper and colder layers during the day would allow ephyrae to save energy, decreasing their metabolic rates and prey requirements [68,69]. The location of ephyrae in the illuminated levels of the water column could make them particularly vulnerable to visual predators such as crustaceans and fish [70,71]. However, the morphology and

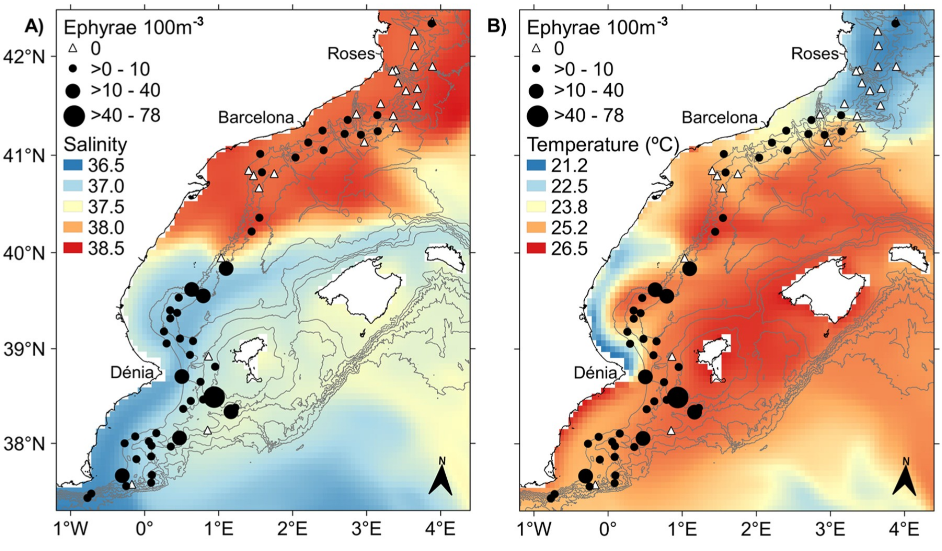

Fig 7. Horizontal distribution of *P. noctiluca* ephyrae overlaid on the mean a) salinity and b) temperature at 10 m depth for the sampling period from CMEMS reanalysis [45]. Coastline is from Instituto Hidrográfico de la Marina [52] and isobaths (every 400 m) are from EMODnet [43].

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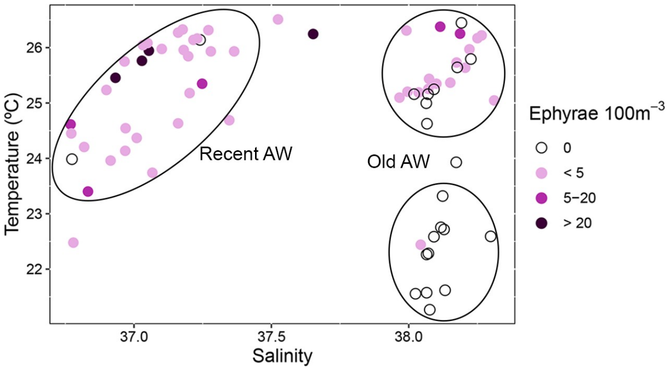

Fig 8. Depth-integrated ephyrae abundances in relation to mean surface (5–10 m depth) salinity and temperature at plankton stations.

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transparency of their bodies would make them barely visible to their predators [72]. All these strategies would allow *P. noctiluca* ephyrae to survive in this oligotrophic environment, avoiding the energy expense to cross the thermocline and reach the DCM zone where, furthermore, they would have to compete with other zooplankton species. The observed vertical migration of ephyrae would probably be constrained by the conditions of water column stratification. As vertical migration in jellyfish is accomplished by swimming [13], the weak swimming capability of ephyrae, in comparison with adult stages [73], may hinder large amplitude migration across the thermocline. *P. noctiluca* adults are strong swimmers that perform extensive vertical migrations from deep waters, below 300 m, during the day to the surface at night [34,74]. Although this migration can be attributed to feeding, following its zooplankton prey, other factors, such as the reproductive behaviour, could determine this migration pattern [34].

The horizontal distribution of *P. noctiluca* ephyrae showed a clear latitudinal gradient with high abundances in the southern part of the area, associated with the low saline recent AW. In summer, the surface AW which enters the Mediterranean may reach the Balearic Islands progressing northward across the Eivissa and Mallorca Channels [16,17] forming the warm fresh core of the Balearic Current. The ephyrae found in the recent AW along the Balearic Current path would have been generated by adults of *P. noctiluca* associated with the entrance of waters from the Atlantic into the Mediterranean, or trapped by the AW flow along its path. The maximum total body diameter of the collected ephyrae was 3.55 mm. According to Ramondenc *et al.* [75] their estimated age would be around 18 days, enough time to come from distant areas. However, we must consider that the instabilities of the current along the continental slope, that generate meanders and eddies [76], will ultimately determine the transport of ephyrae. Further modeling studies implementing individual-based models with a Lagrangian particle-tracking framework using hydrodynamic model outputs, will help to understand the trajectories and potential origin of these ephyrae. The highest abundance of ephyrae was detected in the warm recent AW at the Eivissa Channel, where the currents could have caused a funnel effect. As the recent AW inflow through Eivissa or Mallorca Channel presents not only seasonal [17] but also interannual variability [16], changes in the abundance of the species over time in the study area could be related to the interannual variability of this mechanism. We should consider that other hydrodynamic structures eastwards of the continental slope could also influence the ephyrae observed pattern, but the sampling strategy does not allow to test the possible effect of these processes. The transport of gelatinous organisms through the

Strait of Gibraltar linked to the inflow of the AW into the Mediterranean has been previously reported for other species, such as *Rhizostoma luteum* [77]. The inflowing Atlantic jet involves high mesoscale activity [78], generating structures such as fronts and eddies that support high biological productivity [79–81]. These physical structures would favour gelatinous zooplankton advection and aggregation since, as osmoconformers that adjust to small salinity gradients, they tend to aggregate at density discontinuities [7–9,82].

In the northern half of the area, occupied by the old AW, the abundance of *P. noctiluca* ephyrae along the Northern Current path was much lower, being absent in the northernmost part. The low abundance of ephyrae contrasts with previous observations where high concentrations of *P. noctiluca*, adults and ephyrae, and other gelatinous organisms have been found associated to the Northern Current [9,28,34,35,83] in relation with the high levels of biological production in that area [36–38]. This scarcity of ephyrae together with their absence at the northern end of the area would suggest that the ephyrae found in the Northern Current would not come from areas further north but their presence would be related to the influx of the Balearic Current. The Balearic Current flowing to the northeast, carrying ephyrae, showed a deflection to the west around 4.0˚E and joined the Northern Current probably supplying ephyrae to this current, where the mixture of waters would dilute their abundance. The absence of ephyrae in the northernmost part, characterized by the lowest temperature and more homogeneous upper layer, could suggest that temperatures in that area might have been too low for the development of the species. Nevertheless, taking into account the wide range of temperatures *P. noctiluca* tolerates [25,26] the temperature “per se” would not explain the absence of ephyrae. Previous works already reported the absence of ephyrae in that area in coincidence with high concentrations of anchovy larvae [35,84]. Sabatés *et al.* [35] argued that these colder waters come from further north, advected by the Northern Current, and involved a significant amount of waters from the shelf of the Gulf of Lions, an important spawning anchovy area [85]. Thus given the oceanic habitat of *P. noctiluca* [26], the origin of these waters would be the most likely explanation for the absence of ephyrae in that area.

Licandro *et al.* [31] already suggested that the seasonal occurrence of high densities of *P. noctiluca* adult swarms in the WM followed the progression of the AW surface stream, through the Strait of Gibraltar, along the North African coast before circulating anticlockwise around the WM basin [86]. In the present study, the possible flux of *P. noctiluca* ephyrae towards the north would depend on the seasonality of the currents pattern and on the high mesoscale variability of hydrodynamic processes [14,17]. The entrance of individuals through the Strait of Gibraltar would be supported by the similar genetic structure between *P. noctiluca* from the North Atlantic and the Mediterranean, resulting from an extensive gene flow and a high degree of connectivity between both populations [87,88]. Following the main currents in the WM, and considering the lifespan of this species, between 9 months and 1 year [27,28], individuals entering through the Strait of Gibraltar, or their offsprings, could act as sink populations at different Mediterranean regions (e.g. northern Adriatic, Naples Bay, Tunis Bay and Villefranche Bay [89]).

The frequency of *P. noctiluca* adult blooms in the Mediterranean has increased significantly since the 1990s, particularly in the western basin [26,32,33]. This increase has been related with climatic (mild winters, high temperature, low rainfall and high atmospheric pressure) and anthropogenic factors (lack of predators and decrease of pelagic fish populations, their competitors for food) [1,26,90]. However, we cannot rule out that these population increases could benefit from the contribution of individuals from the Atlantic across the Strait of Gibraltar. The results of the present study suggest the population connectivity of *P. noctiluca* between the Atlantic and the Mediterranean, a key issue for the understanding of the species population dynamics and its increasing abundance in the Mediterranean. Further observational and numerical simulation studies may contribute to better understand this potential connectivity and its seasonal and interannual variability.

Supporting information

S1 Fig. Measurement of total body diameter taken in *Pelagia noctiluca* ephyrae.
(TIF)

S2 Fig. Pearson residuals of GLMM analysis on the effect of light (day/night) and depth on the vertical distribution of *P. noctiluca* ephyrae. a) residuals distribution *vs*. fitted values; b) residuals spatial distribution (missing points in the north correspond to stations where ephyrae were absent); c) residuals distribution *vs*. light (D = day, N = night); d) residuals distribution *vs*. depth (m).
(PDF)

S3 Fig. Pearson residuals of GLMM analysis on the effect of surface temperature and salinity on the horizontal distribution of *P. noctiluca* ephyrae. a) residuals distribution *vs*. fitted values; b) residuals spatial distribution; c) residuals distribution *vs*. temperature (˚C); d) residuals distribution *vs*. salinity.
(PDF)

S1 Table. Coefficients of GLMM analysis on the effect of light (day/night) and depth on the vertical distribution of *P. noctiluca* ephyrae. n.s. = non significant ($p > 0.05$).
(DOCX)

S2 Table. Coefficients of GLMM analysis on the effect of surface temperature and salinity on the horizontal distribution of *P. noctiluca* ephyrae.
(DOCX)

S1 Equation. Mathematical model formulation for the GLMM analysis on the effect of light (day/night) and depth on the vertical distribution of *P. noctiluca* ephyrae (source [50]).
(DOCX)

S2 Equation. Mathematical model formulation for the GLMM analysis on the effect of surface temperature and salinity on the horizontal distribution of *P. noctiluca* ephyrae (source [50]).
(DOCX)

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ORIGINAL ARTICLE

The role of oceanographic conditions and colony size in shaping the spatial structure of *Pyrosoma atlanticum* in the NW Mediterranean Sea

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This study investigates the role of winter oceanographic conditions on the horizontal and vertical spatial structure of *Pyrosoma atlanticum* at different ontogenetic stages. Data were obtained on two oceanographic cruises (February 2017 and 2018) in the NW Mediterranean. Small colonies were exceptionally abundant in 2017, linked to an earlier development of spring conditions and the subsequent seasonal phytoplankton bloom. The mesoscale distribution of *P. atlanticum* differed depending on the colony size. Large colonies ($\geq$7 mm) were found on the slope all along the density front, whereas small ($<$4 mm) and medium colonies (4–6.9 mm) extended their distribution over the shelf because of instabilities of the front, and were mostly absent in the cold, low-salinity coastal waters. The analysis of their vertical distribution showed that at night colonies of all sizes remained close to the surface, where chlorophyll-*a* levels were high, whereas during the day they migrated to deeper layers, reaching greater depths as the colony size increased. The migratory behaviour started when colonies were 4–6.9 mm long. The relative importance of the species in the downward carbon transport is discussed. Our results highlight the need to further study the ecology of this efficient filter feeder in the Mediterranean.

KEYWORDS: diel vertical migration; mesoscale distribution; ontogenetic stage; shelf-slope front; gelatinous zooplankton

INTRODUCTION

Pyrosomes (Greek for "fire bodies" because of their bioluminescence) are colonial pelagic tunicates made up of tens to thousands of zooids encased in a common gelatinous tunic (Godeaux *et al.*, 1998; Madin and Deibel, 1998) ranging from <1 cm to a maximum recorded length of 20 m, depending on the species (Van Soest, 1981). These colonies are holoplanktonic grazers, feeding mainly on phytoplankton of a wide range of types and sizes (Drits *et al.*, 1992; Perissinotto *et al.*, 2007; Décima *et al.*, 2019). As with other pelagic tunicates, pyrosomes have high clearance rates that result in a substantial energy transfer to deep waters (Henschke *et al.*, 2019) through their large production of faecal pellets (Drits *et al.*, 1992) and carcass depositions (Lebrato and Jones, 2009). Pyrosomes are preyed by sea lions, fish, turtles and seabirds in the water column (Harbison, 1998; Childerhouse *et al.*, 2001; Hedd and Gales, 2001), and by arthropods, cnidarians, fish and sharks on the seafloor (Carrassón and Cartes, 2002; Lebrato and Jones, 2009; Archer *et al.*, 2018; Brodeur *et al.*, 2021). These biological traits and trophic interactions give pyrosomes an important role in the marine trophic web and carbon transport (Lebrato and Jones, 2009; Henschke *et al.*, 2019).

Pyrosoma atlanticum is the most widespread and common species. Historically, it has been found in open waters of all oceans between 50°N and 50°S (Van Soest, 1981), but it has recently been reported further north in the Pacific linked to a large marine heat wave (Brodeur *et al.*, 2018; Miller *et al.*, 2019). As found in other gelatinous zooplankton, hydrodynamic structures such as currents, gyres and fronts drive their transport and concentration, ultimately shaping their areas of distribution and abundance (Graham *et al.*, 2001; Guerrero *et al.*, 2016; Bellido *et al.*, 2020). Physical and biological gradients in the water column (e.g. thermoclines and subsurface chlorophyll maxima) determine the vertical distribution of these organisms, limiting their movement or leading to an increase in abundance that results in a patchy distribution (Gibbons *et al.*, 1999; McManus *et al.*, 2003; Nogueira Júnior *et al.*, 2015). *P. atlanticum* is known as a strong migrator that can reach up to 2500 m depth during the day and migrates towards the surface at night (Roe *et al.*, 1987; Angel, 1989). Its short generation time and rapid growth, together with its high filtration rates, allow an exponential population increase of *P. atlanticum* under favourable environmental conditions (Alldredge and Madin, 1982), in some cases leading to large swarms (Angel, 1989; Drits *et al.*, 1992). Unprecedented high densities of large colonies of *P. atlanticum* were reported in the northeast Pacific associated with a warm water mass and a strong El Niño (Brodeur *et al.*, 2018; Sutherland *et al.*, 2018). Despite observations of aggregations in the Tasman Sea (Henschke *et al.*, 2019), southeast Atlantic (Drits *et al.*, 1992), Gulf of Mexico (Archer *et al.*, 2018) and Mediterranean Sea (Braconnot and Goy, 1981), the environmental drivers of these blooms remain unclear.

The Mediterranean Sea has a marked seasonal cycle, with the alternation of stratified (summer) and mixed (winter) periods that confers strong seasonality to primary production (Estrada *et al.*, 1985). Recurrent late winter–early spring blooms are only observed regularly in the northwestern region and intermittently in a few other areas (D'Ortenzio and Ribera d'Alcalà, 2009). The seasonal bloom in the NW Mediterranean is triggered by deep water formation episodes that take place in the Gulf of Lions, driven by evaporation caused by strong, cold and dry northerly winds (MEDOC group, 1970; Schott *et al.*, 1996). Interannual variability in primary production is highly dependent on the extent, intensity and duration of the deep water formation episodes, which increase in colder and drier years (Marty and Chiavérini, 2010; Herrmann *et al.*, 2013). The dynamics of the NW Mediterranean is characterized by the presence of a permanent shelf-slope density front along the slope separating open sea high-salinity waters from coastal low-salinity waters (Font *et al.*, 1988). A geostrophic current (the Northern Current) associated with the front flows from NE to SW, roughly parallel to the coast (Millot, 1999). The front and the associated current are subject to high mesoscale variability that causes oscillations, meandering and eddy generation (Sabatés *et al.*, 2004; Rubio *et al.*, 2005), playing a key role in the distribution and abundance of planktonic organisms (e.g. Sabatés *et al.*, 2004; Guerrero *et al.*, 2016).

Previous studies carried out on gelatinous zooplankton in the NW Mediterranean have shown high spatial variability closely linked to oceanographic dynamics and water mass structure (Guerrero *et al.*, 2016; Sabatés *et al.*, 2018). At a temporal scale, high interannual variability has been reported in abundance and species composition (Licandro and Ibanez, 2000; Guerrero *et al.*, 2018b; Feuilloley *et al.*, 2021), but there is no clear consensus on long-term trends (Molinero *et al.*, 2005; García-Comas *et al.*, 2011; Licandro *et al.*, 2012; Guerrero *et al.*, 2018a). Studies on *P. atlanticum* in the Mediterranean are scarce. Although some sporadic records of the species have been reported in the eastern basin (Galil and Goren, 1994), most of the studies have been conducted in the western basin. These studies have addressed the vertical distribution (Palma, 1985; Andersen and Sardou, 1994; Sardou *et al.*, 1996), seasonality and population dynamics (Franqueville, 1971; Braconnot, 1974) of

P. atlanticum mainly from fixed stations or single transects in which sampling was performed in spring. In this study, we addressed the spatial structure of *P. atlanticum* in the NW Mediterranean during winter oceanographic conditions. The specific objectives were (i) to analyse how the mesoscale water dynamics shape the horizontal distribution of *P. atlanticum* at different ontogenetic stages; and (ii) to determine diel and ontogenetic changes in vertical distributions of *P. atlanticum* in relation to the structure of the water column.

METHOD

Field sampling

Two oceanographic cruises were conducted in the NW Mediterranean (41.3–42.5°N and 2.8–3.8°E) during two consecutive winters (18 February–20 March 2017 and 18–28 February 2018) on board the R/V García del Cid. Sampling stations were placed along transects perpendicular to the coast located at 7–14 km apart and covering the shelf and slope regions (Fig. 1). At each station, vertical profiles of basic hydrographic variables (salinity, temperature and fluorescence) were obtained by means of a conductivity-temperature-depth (CTD) profiler equipped with a fluorometer, and data were interpolated to 1-m depth intervals. Dynamic heights at the stations were calculated with a reference depth level of 500 m. Where station depth was lower, dynamic height was extrapolated using the continuity equation applied to the deepest level of three-station clusters (cf. Hidaka, 1940). Water samples for chlorophyll-*a* (chl-*a*) determination were collected at some stations using a rosette system at three depths down to 80 m throughout the day and night to calibrate the fluorometer. The chl-*a* concentration (μg/L) was determined fluorometrically (Yentsch and Menzel, 1963). Water samples of 150 mL were filtered through Whatman GF/F filters. Chl-*a* was extracted from filters immersed in 6 mL of 90% acetone (24 h at 4°C in darkness). The extract was analysed with a Turner Designs fluorometer calibrated with pure chl-*a*. The relationship between chl-*a* concentration and fluorescence obtained in each survey was used to convert the continuous CTD fluorescence register into the chl-*a* concentration.

Zooplankton mesoscale sampling was conducted at 35 stations in 2017 and at 29 stations in 2018, using a Bongo net (60 cm diameter and 300 μm mesh size) towed obliquely from a maximum depth of 500 m, or 5 m above the seafloor at shallower stations, to the surface and at a vessel speed of 3.7 km/h (Fig. 1). In addition, depth-stratified samplings were performed at selected stations from a maximum depth of 550 m on the shelf and slope during the day (8:30–18:00 h UTC) and night (20:00–06:00 h UTC), avoiding sunset and sunrise. In 2017, these samplings were performed at 13 stations, three of which were fixed stations sampled for 24 or 48 h, and in 2018 two fixed stations were sampled for 24 h (Fig. 1). Depth-stratified samplings were carried out using a Multiple Opening/Closing Net Environmental Sensing System (a MOCNESS net with a 1 m^2 mouth opening consisting of 8 nets with a 300 μm mesh size) towed obliquely at a ship speed of 3.7–4.6 km/h. Depth strata were defined according to the maximum depth at each station (shallow stations 120, 100, 80, 60, 40, 30, 20 and 10 m; deep stations 550, 400, 300, 200, 150, 100, 50 and 25 m). The volume of filtered water was recorded by a flowmeter placed in each net mouth. Immediately after collection, the zooplankton samples were fixed in 5% formaldehyde buffered with sodium tetraborate.

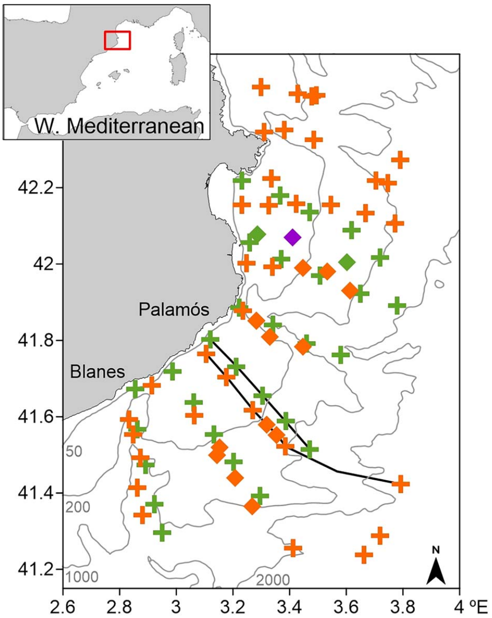

Fig. 1. Study area in the NW Mediterranean. Sampling stations during 2017 (orange) and 2018 (green) surveys. Lines indicate the location of the vertical sections in Fig. 3. Diamonds represent depth-stratified samplings, the purple one corresponds to a fixed station sampled for 48 h in the 2017 survey. Thin grey lines show isobaths (50, 200, 1000 and 2000 m).

Sample processing and data analysis

In the laboratory, colonies of *P. atlanticum* were sorted from zooplankton samples using a stereomicroscope. All *P. atlanticum* colonies were counted, but when samples were estimated to contain >200 colonies, aliquots were taken to obtain at least 100 colonies and extrapolate the count to the whole sample. To determine colony size, all *P. atlanticum* colonies were scanned using a ZooScan (Hydroptic III) (Grosjean *et al.*, 2004) and measured from the diaphragm to the opposite end to the nearest 0.1 mm using the ImageJ software v.1.51j8 (Rasband, 2018). A preliminary exploration of the vertical distribution of *P. atlanticum* colonies (grouped in 1 mm length intervals) revealed that the diel vertical migration did not always initiate at the same colony size but instead was observed in some colonies of 4 mm, some of 5 mm and some of 6 mm (Fig. S1). In addition, colonies of these sizes showed a similar vertical distribution pattern (Fig. S1) and were grouped for the analysis of the vertical distribution. For this analysis, three colony size classes were considered: <4 (including tetrazoids), 4–6.9 and ≥ 7 mm (hereinafter referred to as small, medium and large, respectively). Data from all MOCNESS stations were considered and the number of colonies per size class collected at each depth stratum was standardized to a number per 1000 m^3 of filtered water at each depth stratum. The horizontal distribution of small and medium colonies was similar and quite different from that of the large colonies, so for the analysis of the mesoscale distribution two size classes were considered (≤ 6.9 and ≥ 7 mm; hereinafter referred to as small-medium and large, respectively). This analysis was conducted from data obtained with the Bongo and MOCNESS nets (except at the fixed stations) (Fig. 1). The number of colonies of each size class collected by the Bongo was standardized to a number per 1000 m^3 of filtered water. The number of colonies of each size class collected by the MOCNESS at each depth stratum was pooled and divided by the sum of the filtered water at each depth stratum and standardized to a number per 1000 m^3 of filtered water.

To investigate the effect of environmental variables on the mesoscale horizontal distribution of *P. atlanticum*, the explanatory variables considered were temperature, salinity, density and chl-*a* at 10, 30 and 50 m depth, and bathymetry. Temperature and chl-*a* at 10 m, density at 30 m and bathymetry were selected as independent variables after evaluating collinearity through the Pearson cross-correlation (coefficient $< |0.6|$). A Generalized Linear Model (GLM) was fitted to assess the effect of the independent oceanographic variables on the mesoscale horizontal distribution of small–medium and large *P. atlanticum* colonies. For large colonies, the best model, based on the Akaike information criterion (AIC) (Akaike, 1974) and residual inspection, showed a structure that was included in a Generalized Linear Mixed Model (GLMM), considering the region of the sampling stations ("shelf" when <200 m depth; and "slope" when >200 m depth) as a random effect. In addition, standardized environmental variables [(value-mean)/standard deviation (SD)] were required for the convergence of the GLMM. The number of *P. atlanticum* colonies (counts) of both size classes, which followed a negative binomial distribution, was analysed using the "glm.nb" (for GLM) and "glmer.nb" function (for GLMM) from the "MASS" package and with a log-link to avoid predicting negative numbers of colonies (Venables and Ripley, 2002). The (log-transformed) volume of filtered seawater was included as an offset inside GLM and GLMM to reduce the bias owing to different volumes filtered by the nets (826 m^3 mean, 857 SD) (Zuur *et al.*, 2009; Canepa *et al.*, 2017). In both cases, the optimal model was obtained through a backward selection criterion based on the significance of each explanatory variable ($\alpha = 0.05$), using the AIC comparison and through the inspection of the residuals. Models were carried out using the R statistical programming language v3.5.3 (R Core Team, 2020). Maps of temperature, salinity and chl-*a* at 10 m and density at 30 m for 2017 and 2018 were generated by means of the minimum curvature interpolation method. Vertical sections of temperature, salinity and chl-*a* for both years were obtained using kriging, considering the anisotropy of the water column. All were performed using Surfer® v13.4 (Golden Software, LLC, 2016).

To analyse the vertical distribution of *P. atlanticum* at each size class during day and night, the weighted mean depth (WMD) was calculated for each sampling station (MOCNESS net) by size class and light (day/night) as follows:

$$\mathrm{WMD} = \sum_{i=1}^{n} P_i Z_i$$

where P_i is the proportion of colonies in the ith depth stratum:

$$P_i = \frac{C_i H_i}{\sum_{i=1}^{n} C_i H_i}$$

Z_i is the mean sampling depth of the ith depth stratum; C_i is the concentration of colonies in the ith depth stratum and H_i is the width of the ith depth stratum.

The effect of size class (<4, 4–6.9, ≥ 7 mm), light (day/night) and different oceanographic variables on the vertical distribution of *P. atlanticum* was tested through a GLM. Mean temperature, salinity, density and chl-*a* concentration were calculated for each depth stratum and MOCNESS haul. After evaluating collinearity through the Pearson cross-correlation test, temperature and chl-*a* were selected as independent variables (coefficient $< |0.6|$). The vertical counts of *P. atlanticum*, following a negative binomial distribution, were analysed using the "glm.nb" function from the "MASS" package and with a log-link function (Venables and Ripley, 2002; Zuur *et al.*, 2009). The (log-transformed) volume of filtered seawater at each depth stratum was included as an offset inside GLM to reduce the bias arising from different volumes filtered by the nets (216 m^3 mean, 276 SD)

(Zuur *et al.*, 2009; Canepa *et al.*, 2017), and the oceanographic variables were standardized. The GLM was carried out using the R statistical programming language v3.5.3 (R Core Team, 2020).

RESULTS

Hydrographic conditions

In both years, surface temperature and salinity increased towards the open sea (Fig. 2**A**–**D**). In 2017, the coastal zone showed low temperature (≈12.5°C) and salinity (≈37.2), whereas on the shelf edge and slope, the temperature reached 13.6°C and salinity 38.4. In 2018, coastal waters also showed low temperature (≈12.9°C) and relatively low salinity (≈38.3); on the shelf edge and in the open sea, salinity was similar to that detected in the previous year and temperature was slightly lower, around 13.2°C. Surface chl-*a* did not show a consistent pattern (Fig. 2**E** and **F**). In 2017, relatively high values were detected on the shelf, but also in the open sea (≈1.2 μg/L), whereas in 2018, high chl-*a* concentrations (≈1.9 μg/L) were found in the southwest part of the area. On both cruises, the distribution of density at 30 m increased from near the coast towards the open sea, following a similar pattern to that of salinity. The dynamic height overlaid on the density at 30 m showed the signature of the shelf-slope front associated with the Northern Current (Font *et al.*, 1988) along the continental slope (Fig. 2**G** and **H**). Some detected intrusions onto the shelf were related to the instabilities of the current (Fig. 2G and H). The vertical section of temperature and salinity showed the presence of colder and less saline waters close to the coast, which reached the seafloor up to around 100 m depth in both years and were more evident in 2017 (Fig. **3A**–**D**). Chl-*a* was detected in the first 80 m of the water column, with the highest values in the upper ≈25 m (≈1.15 μg/L in 2017 and ≈0.80 μg/L in 2018) (Fig. 3**E** and **F**).

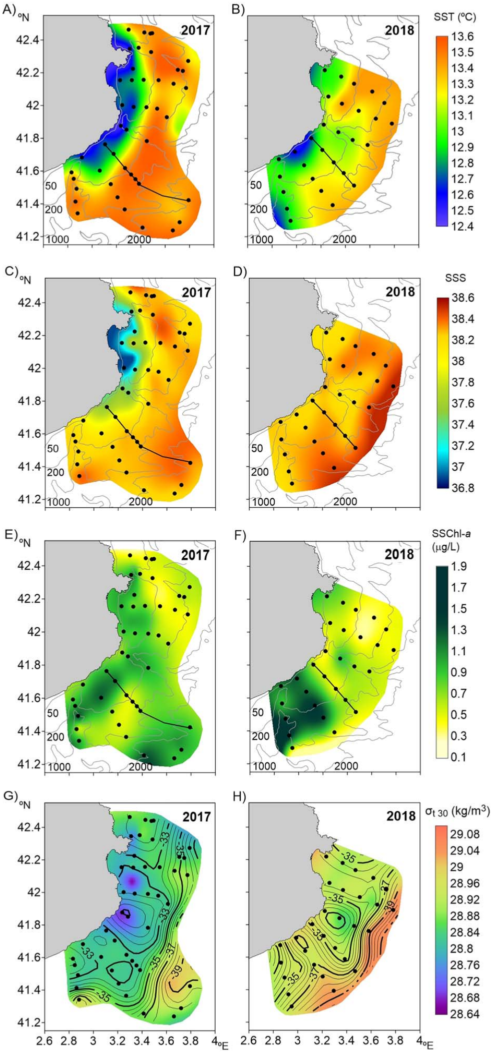

Fig. 2. Maps of surface (10 m) temperature (SST; **A**, **B**), salinity (SSS; **C**, **D**) and chlorophyll-*a* (SSChl-*a*; **E**, **F**) and dynamic height (contour lines, dynamic cm) at 30 m relative to 500 m overlaid on density at 30 m ($\sigma_{t\,30}$; **G**, **H**) in winter 2017 (left panels) and 2018 (right panels). Thin grey lines show isobaths (50, 200, 1000 and 2000 m).

Horizontal distribution of *P. atlanctium*

P. atlanticum colonies were much more abundant in 2017 than in 2018 (mean abundance 228.70 col./1000 m^3, 394.77 SD and 5.12 col./1000 m^3, 6.08 SD, respectively), owing to the massive concentration of small size colonies in 2017. However, small colonies (<4 mm) dominated in both years, 2–3 mm (range: 0.9–82.0 mm) in 2017 and 1–2 mm (range: 1.2–59.0 mm) in 2018 (Fig. S2). The distribution pattern of colonies within the small–medium (≤6.9 mm) and large (≥7 mm) size classes was quite similar in both years. The small–medium colonies were present all over the area, with low abundances or even absence at stations close to the coast and high abundances on the shelf edge (Fig. 4**A** and **B**). The GLM identified surface temperature and density (30 m) as significant variables ($P < 0.05$) related to *P. atlanticum* distribution (Table I, Fig. S3). High abundances were found in warm waters (13.1–13.6°C) and of moderate density (28.7–28.9 kg/m^3) (Fig. 5**A** and **B**). Large colonies were mainly found on the slope at depths greater than

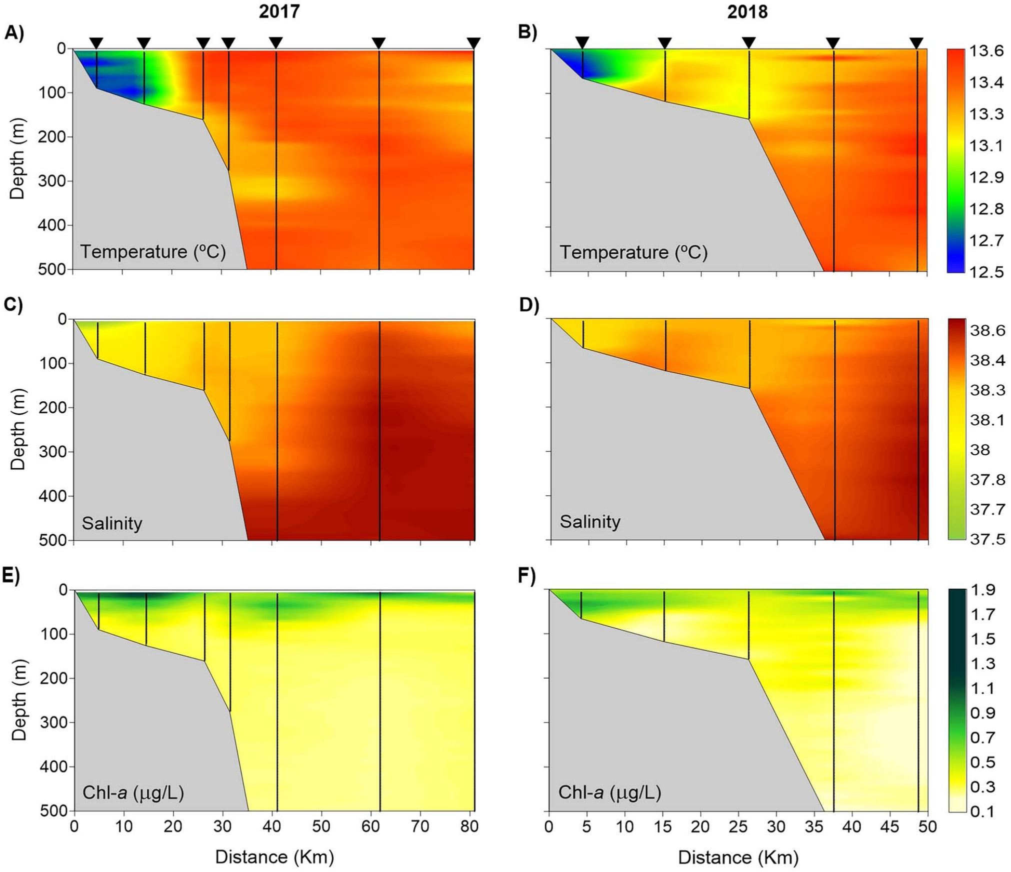

Fig. 3. Vertical distribution of temperature (**A**, **B**), salinity (**C**, **D**) and chlorophyll-*a* (**E**, **F**) in the upper 500 m depth in winter 2017 (left panels) and 2018 (right panels) in the sections marked in Fig. 1. Horizontal axis indicates distance from the coast. Vertical lines represent 1 m binned CTD profile data.

400 m and in relatively low chl-*a* surface waters (0.5–1.0 μg/L) (Figs 2E and F and 6**A** and **B**) in the vicinity of the front throughout the area, but were practically absent in shelf waters. The GLMM identified bathymetry as a significant variable ($P < 0.05$) related to this size class distribution (Table I, Fig. 7, and Fig. S4). Although surface chl-*a* was not a significant variable for the distribution of large colonies (negative relationship, Table I, Fig. S5), it was kept in the GLMM because its inclusion improved the explanatory capacity of the model, providing a lower AIC value (Fig. S4) (Zuur *et al.*, 2009).

Vertical distribution of *P. atlanticum*

The GLM analysis indicated a significant effect ($P < 0.01$) of the colony size class (<4, 4–6.9, ≥7 mm), light level (day/night) and mean chl-*a* concentration by sampling strata on *P. atlanticum* vertical distribution (Table II). During the night, colonies of all size classes were located in the upper part of the water column (WMD was 36, 39 and 67 m for the small, medium and large colonies, respectively; Table III), whereas during the day their distribution varied significantly depending on the colony size. Thus, during daylight hours, small colonies remained in the upper part of the water column (WMD = 69 m), medium size colonies showed a slightly deeper distribution (WMD = 110 m) with a migration amplitude of 71 m and large colonies were located deeper (WMD = 304 m), with a migration amplitude of 237 m (Fig. 8, Table III), reaching a maximum depth of 550 m. The fine-scale vertical distribution obtained at the fixed station performed in 2017 (Fig. 1) followed the pattern

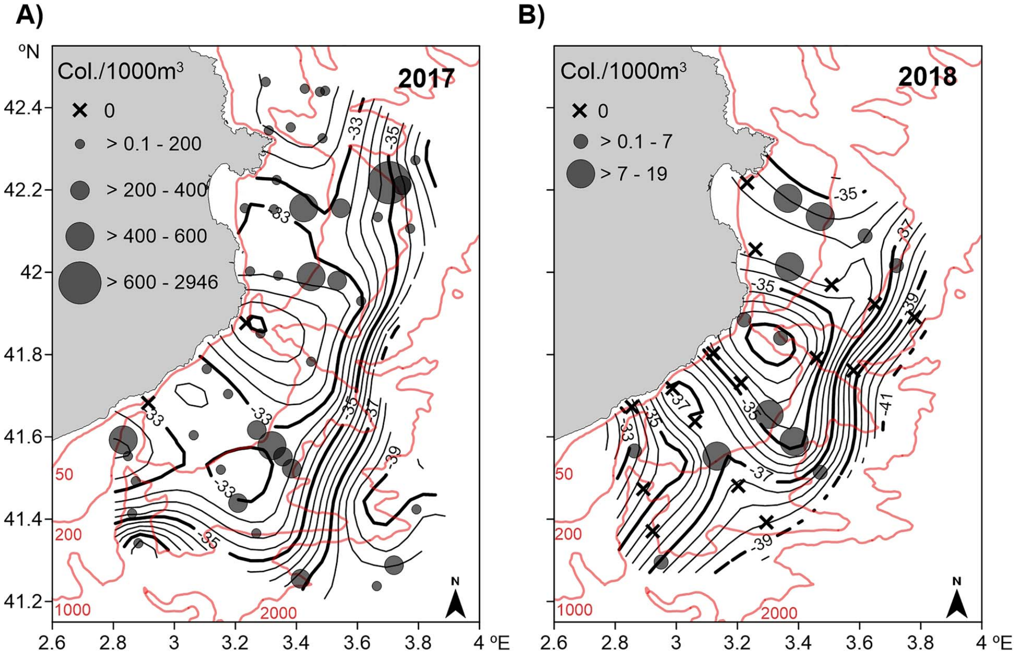

Fig. 4. Horizontal distribution of small-medium ($\leq$6.9 mm) *Pyrosoma atlanticum* colonies overlaid on dynamic height (contour lines; dynamic cm) at 30 m relative to 500 m and bathymetry (in red; 50, 200, 1000 and 2000 m) in 2017 (**A**) and 2018 (**B**).

Table I: Model results for horizontal distribution of small-medium colonies ($\leq$6.9 mm; GLM) and large colonies ($\geq$7 mm; GLMM) of Pyrosoma atlanticum. * $\alpha = 0.05$; std = standardized variables; n.s. = non-significant; + variable still included in the model following AIC criteria

Model	Parameter	Estimate	*z*-value	*P*-value
GLM	Intercept	$-1.50e^5$	−4.95	< 0.01*
	Temperature (10 m)	2.41	3.95	< 0.01*
	Density (30 m)	$1.04e^4$	4.96	< 0.01*
	Density (30 m) ^{2}	$-1.81e^2$	−4.97	< 0.01*
GLMM	Intercept	−6.85	−22.22	< 0.01*
	Bathymetry (std)	2.12	4.22	< 0.01*
	Bathymetry (std)^2	−0.76	−3.01	< 0.01*
	Chlorophyll-*a* (10 m) (std)	−0.54	−1.64	0.101 n.s.$^+$

described above and allowed us to visualize its relation to the chl-*a* concentration in the water column (Fig. 9). Small colonies remained, day and night, in the upper part of the water column (mainly between 10 and 40 m), coinciding with a high chl-*a* concentration in these waters. Medium colonies were also located between 10 and 40 m at night, whereas during the day they showed a wider distribution (between 10 and 120 m), around 52% of the colonies migrating downwards and the rest remaining in the upper layers (Fig. 9). This distribution pattern was followed by colonies of each millimetre (4, 5 and 6 mm) within this medium size class (Fig. S1). Large colonies showed a clearly different distribution between day and night, being located in shallow (10–30 m) productive waters during the night and in deeper waters (below 80 m) during the day (Fig. 9). Overall, the abundance of colonies was higher during the night than during the day, and this pattern was more marked in the largest size class (Figs 8 and 9).

DISCUSSION

Our study evidenced that the spatial distribution (horizontal and vertical) of *P. atlanticum* in the Mediterranean

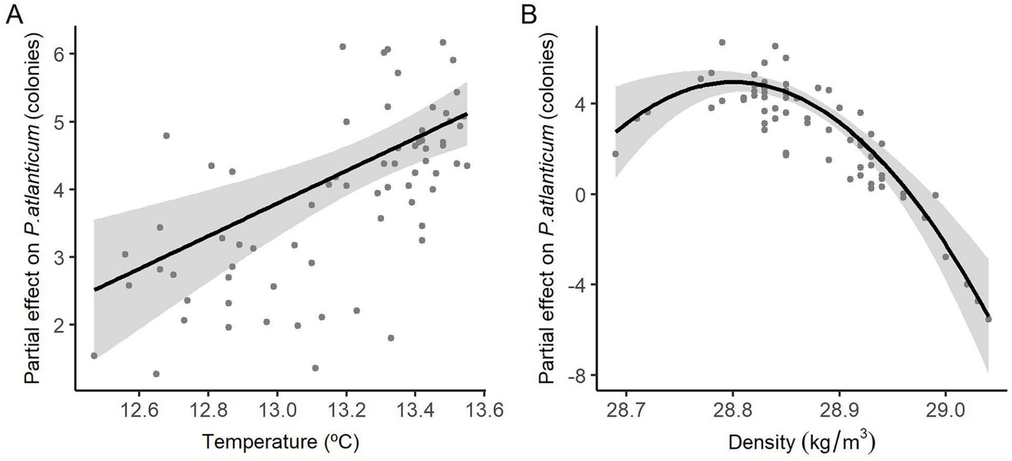

Fig. 5. Partial effect of temperature (10 m; **A**) and density (30 m; **B**) on small–medium (≤ 6.9 mm) *Pyrosoma atlanticum* colonies (number). Partial effect shows the change in response variable for each value of the variable on the *x*-axis, holding all other variables constant (median). Central (bold) lines show the best fit, the shaded areas show the 95% confidence intervals of the GLM model and dots correspond to observations.

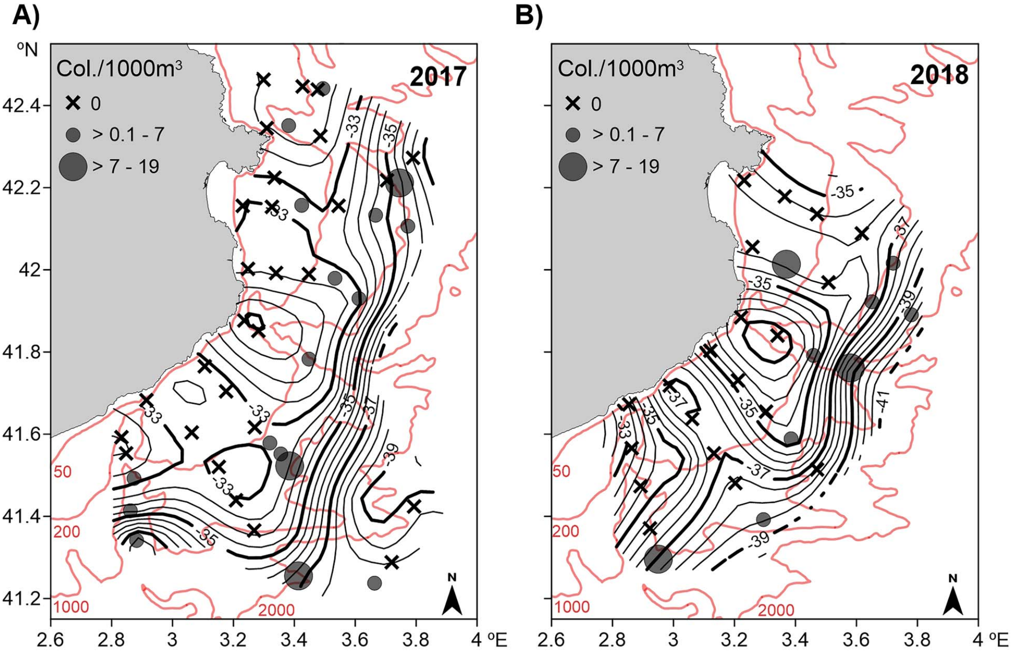

Fig. 6. Horizontal distribution of large (≥7 mm) *Pyrosoma atlanticum* colonies overlaid on dynamic height (contour lines; dynamic cm) at 30 m relative to 500 m and bathymetry (in red; 50, 200, 1000 and 2000 m) in 2017 (**A**) and 2018 (**B**).

Sea depends on the colony size and is ultimately determined by oceanographic and biological structures.

The abundance and size range of *P. atlanticum* colonies found in our study were similar to those recorded

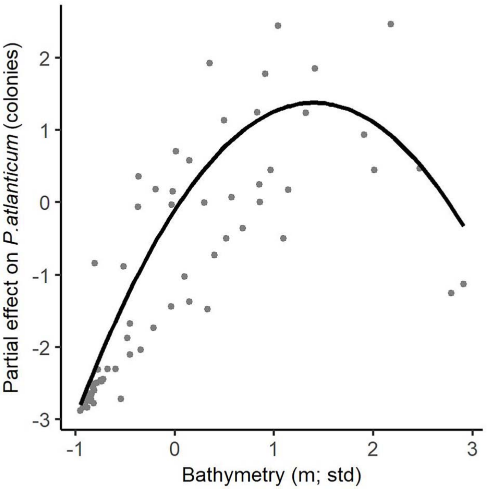

Fig. 7. Partial effect of bathymetry (standardized) on large (≥ 7 mm) *Pyrosoma atlanticum* colonies (number). Partial effect shows the change in response variable for each value of the variable on the *x*-axis, holding all other variables constant (median). Bold line show the best fit of the GLMM model and dots correspond to observations.

Table II: GLM results for chlorophyll-a, colony size class [<4 mm (small), 4–6.9 mm (medium) and ≥7 mm (large)] and light (day-time/night-time) effects on Pyrosoma atlanticum vertical distribution. $^{*}\alpha = 0.05$*; std = standardized variable*

Parameter	Deviance	Pr (>Chi)
Mean chl-*a* (std)	102.52	< 0.01*
Colony size	59.60	< 0.01*
Light (day/night)	8.92	< 0.01*
Colony size: light (day/night)	16.16	< 0.01*

previously in the NW Mediterranean: maximum abundance of 7 col./1000 m^3, 8–88 mm long (Andersen *et al.*, 1992); max. 187 col./1000 m^3, 3–51 mm (Andersen and Sardou, 1994); max. 2000 col./1000 m^3, 20 mm (Braconnot and Goy, 1981); max. 900 col./1000 m^3, 4–6 mm and max. 213 col./1000 m^3, 50 mm long (Granata *et al.*, 2020). In the Atlantic and Pacific oceans, the abundances reported using a similar sampling methodology were much higher and colonies were generally larger, reaching 41 000 col./1000 m^3 for colonies between 50 and 65 mm long (Drits *et al.*, 1992) and 5000 col./1000 m^3 for colonies between 60 and 780 mm long (Schram *et al.*, 2020). In both years studied, the small size classes were dominant (Fig. S2), suggesting that sexual reproduction occurs in winter (Franqueville, 1971; Braconnot, 1974). Several studies carried out in the Mediterranean and northeast Pacific also reported a high abundance of small colonies in late winter and spring (Franqueville, 1971; O'Loughlin *et al.*, 2020; Lyle *et al.*, 2022). Although in both years the sampling was conducted in February, in 2017, the abundance of small–medium (≤6.9 mm) colonies was very high, the largest registered in the Mediterranean (Andersen and Sardou, 1994; Granata *et al.*, 2020). This exceptional abundance might be related to an earlier development of spring conditions and the subsequent seasonal phytoplankton bloom in 2017 in comparison with 2018 (Mir-Arguimbau *et al.*, 2022). The life history traits of *P. atlanticum*, with short generation times and rapid growth, could allow for a rapid population increase during suitable trophic conditions associated with the seasonal production bloom (Alldredge and Madin, 1982).

Horizontal distribution of *P. atlanticum*

The mesoscale distribution of *P. atlanticum* showed that large (≥7 mm) colonies were found on the slope (around 400 m depth), coinciding with the presence of the front all along the area (Fig. 6). This suggests that the species inhabits water over the slope, and the front could aggregate and prevent its dispersion towards the open sea, as reported in other zooplanktonic organisms in the area (Masó *et al.*, 1998; Guerrero *et al.*, 2016). However, the lack of sampling beyond the front precludes any knowledge of the abundance and distribution of *P. atlanticum* in open sea waters, where the species has also been found in the Mediterranean (Bo *et al.*, 2020; Granata *et al.*, 2020). Although it is a filter feeder, a negative but non-significant relationship was found between colony abundance and chl-*a* concentration (Figs 2E and F and 6, Fig. S5). It has been reported that high abundances of phytoplankton prey, usually found in coastal waters, may become harmful because the mucous filters of *P. atlanticum* can become clogged (Harbison *et al.*, 1986; Lyle *et al.*, 2022). Also, it has been suggested that food quality rather than its availability is a determining factor in the species distribution (Schram *et al.*, 2020). However, Henschke *et al.* (2019) reported that chl-*a* concentration was a significant driver of *P. atlanticum* biomass.

In both years studied, small–medium colonies were present throughout the area, with the highest abundances along the edge of the shelf, being very low close to the coast, where the waters were colder and less saline (Figs 2A–D and 4). However, the presence of *P. atlanticum* in colder (7–10°C) (Thompson, 1948; Sutherland *et al.*, 2018) and less saline (31–33) waters than the Mediterranean (Schram *et al.*, 2020) suggests that the temperature and salinity values detected near the coast do not represent a limitation to its distribution, and the low

Table III: Average weighted mean depth (WMD) and standard deviation (SD) during day-time and night-time and migration amplitude of Pyrosoma atlanticum by colony size class

Size class	WMD (m)				Migration amplitude (m)
	Day		Night		
	Mean	SD	Mean	SD	
<4 mm (small)	69	35	36	19	33
4–6.9 mm (medium)	110	55	39	34	71
≥7 mm (large)	304	146	67	64	237

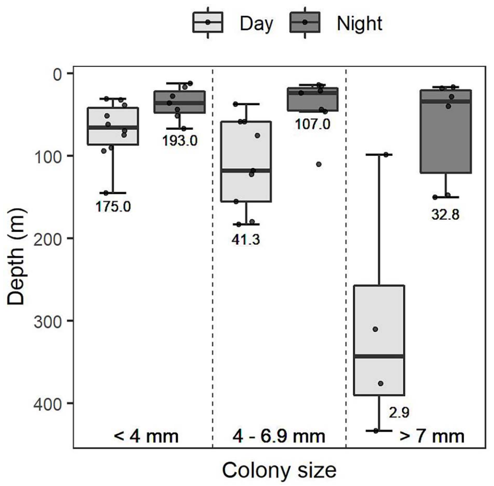

Fig. 8. Weighted mean depth (WMD) of *Pyrosoma atlanticum* by colony size class [<4 mm (small), 4–6.9 mm (medium) and ≥7 mm (large)] during day-time (light grey) and night-time (dark grey). The central marks of each box represent the median of the WMD, the boxes show the interquartile ranges and the whiskers correspond to the ranges of observations. Mean abundance of colonies is indicated below each box (col./1000 m^3).

abundance of *P. atlanticum* in the coastal area is probably associated with the intrusion of a coastal water mass. A high abundance of small-medium colonies was found at the moderate water density values that were found at the shelf edge, close to the highest abundance of large colonies on the slope (Fig. 2G, H, 4, 6). This distribution would support the idea that the young colonies would be offspring of the large ones, taking into account that sexually mature zooids appear in colonies of 40 mm onwards (Van Soest, 1981) and that young colonies grow rapidly (coefficients of exponential growth of 0.24–0.75 per day on a length basis (Andersen and Sardou, 1994)). Overall, the observed distributions suggest that large *P. atlanticum* inhabit waters over the slope, where reproduction might take place, in association with the front, and the presence of young colonies on the shelf could be related to the offshore water intrusions associated with instabilities of the front (Sabatés *et al.*, 2004). Similar observations have been made in this area for other gelatinous organisms. Sabatés *et al.* (2018) reported that adult stages of the Scyphozoan *Pelagia noctiluca* were found along the slope in association with the front. Ephyrae (young stages), which inhabit surface waters (Ottmann *et al.*, 2021; Pastor-Prieto *et al.*, 2021), showed a wider distribution extending over the shelf and their occurrence was associated with offshore water intrusions generated by the oscillatory behaviour of the front. The frontal area is a transitional zone with enhanced primary and secondary production (Estrada and Margalef, 1988; Ibanez and Boucher, 1987; Sabatés *et al.*, 2004) that offers favourable feeding conditions for the reproduction, growth and survival of gelatinous organisms. Nevertheless, it is possible that *P. atlanticum* colonies, as planktonic organisms with limited horizontal mobility, were passively accumulated in that area by physical discontinuities of the ocean, such as fronts and pycnoclines (Graham *et al.*, 2001; Greer *et al.*, 2015, 2018). Studies conducted in the Atlantic and Pacific oceans have suggested that *P. atlanticum* colonies were located in open sea waters (Angel, 1989; Brodeur *et al.*, 2018) and that they may have been transported by advection to the shelf, where they were less abundant (Miller *et al.*, 2019; Schram *et al.*, 2020; Lyle *et al.*, 2022).

Vertical distribution of *P. atlanticum*

The analysis of the vertical distribution of *P. atlanticum* allowed us to detect different migration amplitudes as a function of colony size (Fig. 8). Small colonies showed no diel vertical migration, being mainly located in the upper 40 m of the water column during both day and night, as previously observed by Palma (1985) in the Mediterranean (Fig. 9). The migratory behaviour of remaining in the surface layers during the night and going to deeper layers during the day started in some colonies of 4, 5 and 6 mm (the medium size class), but not all colonies of these sizes exhibited this behaviour (Fig. S1). This would suggest that migration, as an individual response, can start at any of these sizes. The migration amplitude increased from 71 m in medium colonies to 237 m in the large ones. A similar migration amplitude (210 m) for the same size colonies was reported by Sardou *et al.* (1996) in the Mediterranean, whereas other studies described more extensive migrations in that area (515 m) (Andersen *et al.*, 1992) and in the Atlantic Ocean (650 m) (Roe *et al.*, 1987; Angel, 1989; Andersen *et al.*, 1992). Considering that *P. atlanticum* is a strong vertical migrator, being able to reach depths of up to 900 m in the Mediterranean (Sardou *et al.*, 1996) and 2500 m in the Atlantic (Roe *et al.*, 1987), the limited maximum depth reached in our study (550 m) might be related to the lower depth of our samplings (maximum 550 m). The lower abundance of colonies during the day than during the night, particularly in the largest size class, could be due to the location of colonies below the sampling depth (Fig. 8).

In this study, the lack of stratification typical of winter conditions allowed us to observe the migratory behaviour of the species without the presence of clines that could influence their vertical movement (Graham *et al.*, 2001). Peak densities of colonies had been associated with vertical gradients of environmental parameters such as density and fluorescence (Lyle *et al.*, 2022). The shallow levels reached by medium and large colonies during the night correspond to the highest values of chl-*a* in the water column (Fig. 9), a proxy of photosynthetic taxa, the main prey of the species (Drits *et al.*, 1992; Perissinotto *et al.*, 2007). *P. atlanticum* mainly feeds on a wide variety of phytoplankton [e.g. diatoms, dinoflagellates, prymnesiophytes and coccolithophores (Drits *et al.*, 1992; Perissinotto *et al.*, 2007)] by continuous filtration of seawater (Alldredge and Madin, 1982). Thus, colonies would be expected to find higher food availability in surface waters than in deeper ones. On the other hand, pelagic tunicates also exhibit high filtration rates of microbial prey, including heterotrophic bacteria (Sutherland *et al.*, 2010; Sutherland and Thompson, 2021; Thompson *et al.*, 2021), which probably allow them to feed at depth and supplement the food acquired in surface waters. The vertical migration pattern observed in *P. atlanticum* is that followed by most zooplankton, which ascend to upper layers during the night to take advantage of the high phytoplankton abundance at the surface before returning to deeper layers during the day (Lampert, 1989; Saiz *et al.*, 2014) to avoid predation in

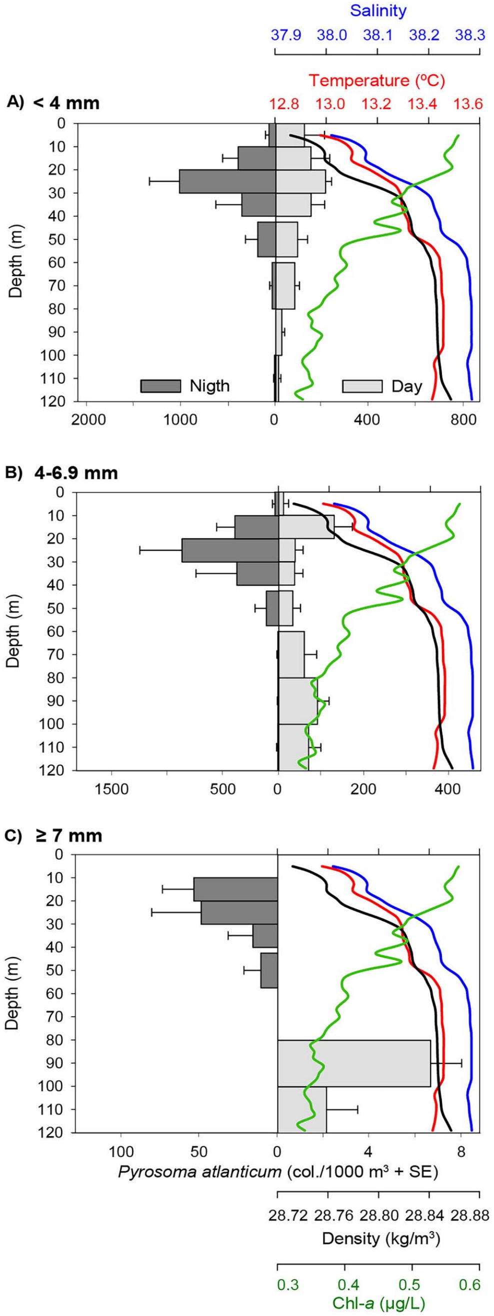

Fig. 9. Mean vertical distribution (+SE) of *Pyrosoma atlanticum* by colony size class [<4 mm (small), **A**; 4–6.9 mm (medium), **B**; ≥7 mm (large), **C**] in night-time (dark grey bars) and day-time (light grey bars), overlaid on vertical profiles of temperature (red), salinity (blue), density (black) and chlorophyll-*a* (green). Note that the colony abundance scales are different for each size class. Data correspond to the 48 h fixed station sampled in 2017 (Fig. 1).

the illuminated layers (Bollens and Frost, 1989). However, other factors such as reproductive behaviour may also play a role, with adults migrating towards the surface to provide a suitable environment for the development of their offspring (Lampert, 1989; Ferraris *et al*., 2012). The location of small colonies both day and night in the upper layers, where chl-*a* levels are highest, suggests a strategy of maximizing the colony growth to reduce the high predation rates of small size organisms (Miller *et al*., 1988). Ontogenetic variations in the vertical distribution are a common trait of other zooplanktonic taxa, such as copepods (Andersen *et al*., 2001) and euphausiids (Pillar *et al*., 1989), with younger stages inhabiting shallower waters and adults performing the typical diel vertical migration pattern. It should also be considered that the permanency of small colonies in surface waters may be related to their limited migratory capacity, since their propulsive capacity—and hence migratory amplitude—increase with colony size. The growth of the colony would not only increase its propulsive capacity, but also enhance its visibility, forcing the colony to migrate deeper to avoid visual predators (Angel, 1979). It is unclear whether the increase in migration amplitude with colony size is due to higher visibility, increased propulsive capacity, or a combination of the two.

Ecological implications

The vertical migration performed by *P. atlanticum* might enhance the vertical transport of carbon to deeper waters. The species shows one of the highest clearance rates of any zooplankton grazer (Perissinotto *et al*., 2007), rapidly producing a high amount of faecal pellets (Drits *et al*., 1992) that are transported to deep waters through diel vertical migration (Henschke *et al*., 2019). It has been reported that mass deposition of *P. atlanticum* may provide an extra input of carbon to benthic consumers (Carrassón and Cartes, 2002; Lebrato and Jones, 2009; Lebrato *et al*., 2013), which rely on the contribution of nutrients from the surface (Smetacek, 1984). In bloom conditions, *P. atlanticum* can exert considerable control over phytoplankton standing stocks (Drits *et al*., 1992; O'Loughlin *et al*., 2020) through competition or direct grazing, playing an important role in the marine food web dynamics (Andersen, 1998; Lavaniegos and Ohman, 2003). Although several *P. atlanticum* bloom events have been reported worldwide, the most impressive was detected in the northeast Pacific, with high abundances of large colonies lasting several years, disrupting marine activities and altering the ecosystem (Brodeur *et al*., 2018, 2019; Schram *et al*., 2020). In the NW Mediterranean, the smaller colonies (Andersen *et al*., 1992; Andersen and Sardou, 1994; this study) and weaker blooms of *P. atlanticum* and other filter-feeding gelatinous taxa than in other regions (Andersen, 1998; Granata *et al*., 2020; O'Loughlin *et al*., 2020) could be related to the oligotrophic nature of this sea. Following Henschke *et al*. (2019), we have estimated that downward carbon transport in our study area would be around 5.26 μg C/m^3 day (0.56 mg C/m^2 day) in 2017 and 0.54 μg C/m^3 day (0.05 mg C/m^2 day) in 2018 (defecation contributing to ≈17% and ≈14%, respectively; see Supplementary Material). These values would be at the lower limit of the estimated ranges of downward carbon transport (0.42–59.57 mg C/m^2 day) by mesozooplankton and macrozooplankton communities in the Mediterranean (Frangoulis *et al*., 2011; Isla *et al*., 2015; Yebra *et al*., 2018). Compared with previous estimates for *P. atlanticum*, our obtained values were two and three orders of magnitude lower than the 363 μg C/m^3 day reported in the Tasman Sea (Henschke *et al*., 2019). However, considering the chl-*a* (i.e. carbon) concentration in the upper water layers observed in both regions (1.33 μg chl-*a*/L in the Tasman Sea, 0.65 μg chl-*a*/L in 2017 and 0.86 μg chl-*a*/L in 2018 in our study area), these differences decrease by one order of magnitude each year (see Supplementary Material). However, the lower values estimated in the present study are probably related to the smaller size of colonies than those observed in the Tasman Sea (range: 11–318 mm) (Henschke *et al*., 2019).

Although our results show a strong difference in the abundance of *P. atlanticum* in the two years studied, longer time series would be necessary to confirm the high interannual variability that has been described for gelatinous zooplankton in the Mediterranean (García-Comas *et al*., 2011;Fullgrabe *et al*., 2020;Feuilloley *et al*., 2021). This high variability has been related to the winter environmental conditions, which cause mixing of the water column and the input of nutrients to the surface waters, ultimately modulating the phytoplankton bloom (García–Comas *et al*., 2011; Fullgrabe *et al*., 2020). The recently observed climatic trends for the Mediterranean, showing an increase in sea water temperature, a lower wind speed and a lengthening of the seasonal stratification period (Rixen *et al*., 2005; Calvo *et al*., 2011; Vargas-Yáñez *et al*., 2017), could modify the intensity and regularity of phytoplankton blooms, altering the abundance, distribution and species composition of gelatinous zooplankton (Guerrero *et al*., 2018a). Future studies should address the long-term interannual variability of *P. atlanticum*, as well as relevant aspects of its biology (e.g. feeding and propulsive capacity) to understand its ecological role in the current context of climate change in the Mediterranean.

CONCLUSIONS

The mesoscale and vertical distribution of *P. atlanticum* in the NW Mediterranean were shaped by the oceanographic and biological structures, as well as by the ontogenetic stage of the colonies. The higher abundance of colonies in 2017 than in 2018 was likely related to an earlier onset of the phytoplankton bloom. Large colonies (≥7 mm) were found on the slope, in association with the shelf-slope front, which would aggregate them, preventing their dispersion towards the open sea. Small (<4 mm) and medium (4–6.9 mm) colonies extended their distribution over the shelf owing to instabilities of the front, and were practically absent in the cold, low-salinity coastal waters. The vertical migration amplitude increased with colony size. At night colonies of all sizes remained close to the surface, where chl-*a* levels were high, whereas during the day they migrated to deeper layers, reaching greater depths as colony size increased. The migratory behaviour started when colonies were 4–6.9 mm long, though not all colonies of these sizes exhibited this behaviour, suggesting that migration can start at any of these sizes. This vertical migration might contribute to carbon transport to depth. Our observations shed light on these gelatinous organisms, scarcely studied in the Mediterranean, which may play a relevant role in the marine trophic web.

SUPPLEMENTARY DATA

Supplementary data is available at *Journal of Plankton Research* online.

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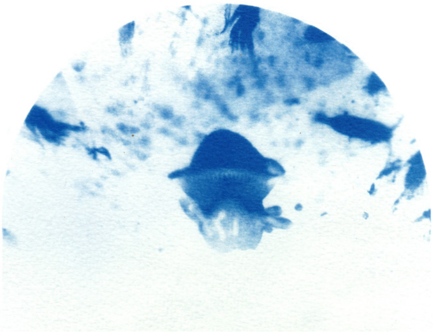

41.3º N - 42.5º N; 2.8º E - 3.8º E
37.4º N - 42.3º N; 0.8º W - 3.9º E