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 (≥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

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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 (Carrasón 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 (Bracq, 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’Alcalá, 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 Chiavellini, 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 (Moliner 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 (Franquéville, 1971; Bracq, 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 RV 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 m² 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.

**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 (Hydrotic III) (Grosjean et al., 2004) and measured from the diaphragm to the opposite end to the nearest 0.1 mm using the ImageJ software v1.51j8 (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 seawater. 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-α at 10, 30 and 50 m depth, and bathymetry. Temperature and chl-α 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 (α = 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-α 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-α 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:

$$ \text{WMD} = \frac{\sum_{i=1}^{n} P_i \cdot \bar{Z}_i}{\sum_{i=1}^{n} P_i}$$

where $P_i$ is the proportion of colonies in the $i$th depth stratum:

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

$\bar{Z}_i$ is the mean sampling depth of the $i$th depth stratum; $C_i$ is the concentration of colonies in the $i$th depth stratum and $H_i$ is the width of the $i$th 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-α concentration were calculated for each depth stratum and MOCNESS haul. After evaluating collinearity through the Pearson cross-correlation test, temperature and chl-α 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).
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–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. 2E 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. 2G 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. 3E and F).

Horizontal distribution of P. atlanticum

P. atlanticum colonies were much more abundant in 2017 than in 2018 (mean abundance 228.70 col./1000 m³, 394.77 SD and 5.12 col./1000 m³, 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 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/m³) (Fig. 5A and B). Large colonies were mainly found on the slope at depths greater than...
The role of oceanographic conditions and colony size

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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 6A 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 (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 (≤ 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 | −1.50e5  | −4.95   | < 0.01* |
|       | Temperature (10 m) | 2.41 | 3.95 | < 0.01* |
|       | Density (30 m) | 1.04e6 | 4.96 | < 0.01* |
|       | Density (30 m)² | −1.81e2 | −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
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./1000 m³, 8–88 mm long (Andersen et al., 1992); max. 187 col./1000 m³, 3–51 mm (Andersen and Sardou, 1994); max. 2000 col./1000 m³, 20 mm (Braconnot and Goy, 1981); max. 900 col./1000 m³, 4–6 mm and max. 213 col./1000 m³, 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 m³ for colonies between 50 and 65 mm long (Drits et al., 1992) and 5000 col./1000 m³ 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

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**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 | 56.90 | < 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

| 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 m³).

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 (Aldredge 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; Lavaniegoz 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/m² day (0.56 mg C/m² day) in 2017 and 0.54 μg C/m² day (0.05 mg C/m² day) in 2018 (delegation 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/m² day) by mesozooplankton and macrozooplankton communities in the Mediterranean (Frangoulis et al., 2011; Isla et al., 2015; Yebr 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/m² 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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REFERENCES

Akaike, H. (1974) A new look at the statistical model identification. IEEE Trans. Automat. Cont., 19, 716–723. https://doi.org/10.1109/TAC.1974.1100705.

Alldredge, A. L. and Madin, L. P. (1982) Pelagic tunicates: unique herbivores in the marine plankton. Bioscience, 32, 655–663. https://doi.org/10.2307/1308815.
Calvo, E., Simó, R., Comes, R., Ribes, M., Pascual, J., Sabatés, A., Gili, J. M. and Polječko, C. (2011) Effects of climate change on Mediterranean marine ecosystems: the case of the Catalan Sea. *Clim. Res.*, 50, 1–29. https://doi.org/10.3354/cr01040.

Canepa, A., Fuentes, V., Bosch-Belmar, M., Acevedo, M., Toledo-Guedes, K., Ortiz, A., Durá, E., Bordohore, C. et al. (2017) Environmental factors influencing the spatio-temporal distribution of *Carybdea maritimus* (Linne, 1758, Cubozoa) in South-Western Mediterranean coasts. *PLoS One*, 12, e0181611. https://doi.org/10.1371/journal.pone.0181611.

Carras, M. and Cartes, J. E. (2002) Trophic relationships in a Mediterranean deep-sea fish community: partition of food resources, dietary overlap and connections within the benthiic boundary layer. *Mar. Ecol. Prog. Ser.*, 241, 41–55. https://doi.org/10.3354/meps241041.

Chidlerhouse, S., Bis, B. and Gales, N. (2001) Diet of New Zealand Sea Ions (*Phacodactylus hookeri*) at the Auckland Islands. *Wildl. Res.*, 28, 291–298. https://doi.org/10.1071/WR00063.

D’Ortenzio, F. and Ribera, D’Alçà, M. (2009) On the trophic regimes of the Mediterranean Sea: a satellite analysis. *Biogeochemistry*, 6, 139–148. https://doi.org/10.1016/j.biorto.2009.02.003.

Décima, M., Stukel, M. R., López-López, L. and Landry, M. R. (2019) The unique ecological role of pyrosomes in the eastern tropical Pacific. *Limnol. Oceanogr.*, 64, 728–743. https://doi.org/10.1002/lno.11071.

Drits, A. V., Arashkevich, E. G. and Semenova, T. N. (1992) *Pyrosoma atlanticum* (Tunicata, Thaliacea): grazing impact on phytoplankton standing stock and role in organic carbon flux. *J. Plankton Res.*, 14, 799–809. https://doi.org/10.1002/jplankt.14_6.799.

Estrada, M. and Margalef, R. (1988) Supply of nutrients to the Mediterranean photic zone along a persistent front. *Oceanol. Acta, SP*, 133–142.

Estrada, M., Vives, F. and Alcazar, M. (1985) Life and productivity of the open sea. In Margalef, R. (ed.), *Western Mediterranean*, Pergamon Press, Oxford, p. 363.

Ferraris, M., Berline, I., Lombard, F., Guidi, I., Elineau, A., Mendoza-Vera, J. M., Lilley, M. K. S., Taillardier, V. et al. (2012) Distribution of *Pelagia noctiluca* (Cnidaria, Scyphozoa) in the Ligurian Sea (NW Mediterranean Sea). *J. Plankton Res.*, 34, 874–885. https://doi.org/10.1002/jplankt.0497.

Feuilloley, G., Fromentin, J.-M., Saravia, C., Irissen, J.-O., Jalabert, I. and Lemmarié, L. (2021) Temporal fluctuations in zooplankton size, abundance, and taxonomic composition since 1995 in the northwestern Mediterranean Sea. *ICES J. Mar. Sci.*, 78, 882–900.

Font, J., Salat, J. and Tintorié, J. (1988) Permanent features of the circulation in the Catalan Sea. *Oceanol. Acta, SP*, 51–57.

Franquelin, C., Squires, N., Lepoint, G., Elkayal, K., Goffart, A., Pinnegar, J. K. and Hecq, J. H. (2011) Importance of copepod carcases versus faecal pellets in the upper water column of an oligotrophic area. *Estuar. Coast. Shelf. Sci.*, 92, 456–463. https://doi.org/10.1016/j.ecss.2011.02.005.

Franqueville, C. (1971) *Macroplacita profunda* (Invertébrés) de la Méditerranée Nord-occidentale. *Tethys*, 3, 11–55.

Fulgrabe, L., Grosjean, P., Gobert, S., Lejeune, P., Lebucq, M., Engels, G., Dauby, P., Boissery, P. et al. (2020) Zooplankton dynamics in changing environments: a 13-year survey in the northwestern Mediterranean Sea. *Mar. Environ. Res.*, 159, 104962. https://doi.org/10.1016/j.marenvres.2020.104962.

Gabi, B. S. and Goren, M. (1994) The deep sea Levantine fauna. New records and rare occurrences. *Sonneken Marit.*, 25, 41–52.

García-Comas, C., Steffan, L., Ibáñez, E., Berline, L., Mazzocchi, M. G., Gasparini, S., Picheral, M. and Gorsky, G. (2013) Zooplankton long-term changes in the NW Mediterranean Sea: decadal periodicity forced by winter hydrographic conditions related to large-scale atmospheric changes? *J. Mar. Syst.*, 87, 216–226. https://doi.org/10.1016/j.jmarsys.2011.04.003.

Gibbons, M. J., Gagushe, N., Boyd, A. J., Shannon, L. J. and Mitchell-Innes, B. A. (1999) Changes in the composition of the non-copepod zooplankton assemblage in St Helena bay (southern Benguela ecosystem) during a six day drague study. *Mar. Ecol. Prog. Ser.*, 180, 111–120. https://doi.org/10.3354/meps180111.

Godeaux, J., Bone, Q. and Bracconnot, J.-C. (1998) Anatomy of Thaliacea. In Bone, Q. (ed.), *The Biology of Pelagic Tunicates*, Oxford University Press, New York, pp. 1–24.

Golden Software, LLC (2016) *Surfer for Windows. Contouring and 3-D Surface Mapping*, Golden, CO, USA, www.goldensoftware.com.

Graham, W. M., Pagès, F. and Hammer, W. M. (2001) A physical context for gelatinous zooplankton aggregations: a review. *Hydrobiologia*, 451, 199–212. https://doi.org/10.1023/A:1011876004427.

Granata, A., Bergamasco, A., Battaglia, P., Masienda, G., Pansera, M., Bonamzingo, V., Arena, G., Andaloro, F. et al. (2020) Vertical distribution and diel migration of zooplankton and micronekton in Polcevera submarine canyon of the Ligurian mesopelagic zone (NW Mediterranean Sea). *Pelag. Oceanogr.*, 183, 102298. https://doi.org/10.1016/j.pocean.2020.102298.

Greer, A. T., Chiaverano, L. M., Luo, J. Y., Cowen, R. K. and Graham, W. M. (2018) Ecology and behaviour of holoplanktonic scyphomedusae and their interactions with larval and juvenile fishes in the northern Gulf of Mexico. *ICES J. Mar. Sci.*, 75, 751–763. https://doi.org/10.1093/icesjms/fsx168.

Greer, A. T., Cowen, R. K., Guigand, C. M. and Hare, J. A. (2015) Fine-scale planktonic habitat partitioning at a shelf-slope front revealed by a high-resolution imaging system. *J. Mar. Syst.*, 142, 111–125. https://doi.org/10.1016/j.jmarsys.2014.10.008.

Grojsecan, P., Picheral, M., Warembourg, C. and Gorsky, G. (2004) Enumeration, measurement, and identification of net zooplankton samples using the ZOOSCAN digital imaging system. *ICES J. Mar. Sci.*, 61, 518–525. https://doi.org/10.1016/j.icesjms.2004.03.012.

Guerrero, E., Gili, J.-M., Grinyó, J., Raya, V. and Sabatés, A. (2018a) Long-term changes in the planktonic cnidarian community in a mesoscale area of the NW Mediterranean. *PLoS One*, 13, e0196431. https://doi.org/10.1371/journal.pone.0196431.

Guerrero, E., Gili, J.-M., Maynou, F. and Sabatés, A. (2018b) Diversity and mesoscale spatial changes in the planktonic cnidarian community under extreme warm summer conditions. *J. Plankton Res.*, 40, 178–196. https://doi.org/10.1093/plankt/fby001.

Guerrero, E., Marrodán, A., Sabatés, A., Orejas, C. and Gili, J.-M. (2016) High spatial heterogeneity of two planktonic cnidarian species related to the variability of a shelf-slope front at short time scales. *Sci. Mar.*, 80, 487–497. https://doi.org/10.3989/scimar.04452.03A.

Harbison, G. R. (1998) The parasites and predators of Thaliacea. In Bone, Q. (ed.), *The Biology of Pelagic Tunicates*, Oxford University Press, New York, pp. 187–214.

Harbison, G. R., McAlister, V. L. and Gilmer, R. W. (1986) The response of the salp, *Pyrosoma communica*, to high levels of particulate material:
starvation in the midst of plenty. Limnol. Oceanogr., 31, 371–382. https://doi.org/10.4319/lo.1986.31.2.0371.

Heed, A. and Gales, R. (2001) The diet of shy albatrosses (Thalassarche cauta) at Albatross Island, Tasmania. J. Zool., 253, 69–90. https://doi.org/10.1017/S0952836901008067.

Henschke, N., Pakhomov, E. A., Kwong, L. E., Everett, J. D., Laiolo, L., Coghlán, A. R. and Suthers, I. M. (2019) Large vertical migrations of Pyrosoma atlanticum play an important role in active carbon transport. J. Geophys. Res. Biogosci., 124, 1056–1070. https://doi.org/10.1029/2018JB019418.

Herrmann, M., Díaz, F., Estournel, C., Marsaleix, P. and Ueses, C. (2013) Impact of atmospheric and oceanic interannual variability on the Northwestern Mediterranean Sea pelagic planktonic ecosystem and associated carbon cycle. J. Geophys. Res. Oceans., 118, 5792–5813. https://doi.org/10.1002/jgrc.20405.

Hidaka, K. (1940) Absolute evaluation of ocean currents. Proc. Imp. Acad., 16, 391–393. https://doi.org/10.2183/pjab.1912.16.391.

Ibanez, F. and Boucher, J. (1987) Anisotropie des populations zooplanctonnes dans la zone frontale de Mer Ligure. Oceanol. Acta, 10, 205–216.

Isla, A., Scharek, R. and Latasa, M. (2015) Zooplankton diel vertical migration and contribution to deep active carbon flux in the NW Mediterranean. J. Mar. Syst., 143, 86–97. https://doi.org/10.1016/j.marsys.2014.10.017.

Lampert, W. (1989) The adaptive significance of diel vertical migration of zooplankton. Funct. Ecol., 3, 21–27. https://doi.org/10.2307/2390671.

Lavaniegos, B. E. and Ohman, M. D. (2003) Long-term changes in pelagic tunicates of the California current. Deep. Res. Part II Top. Stud. Oceanogr., 50, 2473–2498. https://doi.org/10.1016/S0967-0645(03)01132-2.

Lebrato, M. and Jones, D. O. B. (2009) Mass deposition event of Pyrosoma atlanticum carcases off Ivory Coast (West Africa). Limnol. Oceanogr., 54, 1197–1209. https://doi.org/10.4319/lo.2009.54.4.1197.

Lebrato, M., Molinero, J.-C., Cartes, J. E., Lloris, D., Mélin, F. and Beni-Casadella, L. (2013) Sinking jelly-carbon unveils potential environmental variability along a continental margin. PLoS One, 8, e82070. https://doi.org/10.1371/journal.pone.0082070.

Lacandón, P. and Ibáñez, F. (2000) Changes of zooplankton communities in the Gulf of Tigullio (Ligurian Sea, Western Mediterranean) from 1985 to 1995. Influence of hydroclimatic factors. J. Plankton Res., 22, 2223–2233. https://doi.org/10.1016/plankt.8212.2223.

Lacandón, P., Souissi, S., Ibáñez, F. and Garré, C. (2012) Long-term variability and environmental preferences of calycopean siphonophores in the bay of Villefranche (north-western Mediterranean). Prog. Oceanogr., 97, 152–163.

Lyle, J. T., Cowen, K. K., Sponaugle, S. and Sutherland, K. R. (2012) Fine-scale vertical distribution and diel migrations of Pyrosoma atlanticum in the northern California current. J. Plankton Res., 44, 298–302. https://doi.org/10.1093/plankt/bfr006.

Madin, L. P. and Deleu, D. (1998) Feeding and energetics of Thaliacea. In Bone, Q. (ed.), The Biology of Pelagic Tunicates of Pelagic Tunicates, Oxford University Press, New York, pp. 81–104.

Marty, J. C. and Chiavérini, J. (2010) Hydrological changes in the Ligurian Sea (NW Mediterranean, DYFAMED site) during 1993–2007 and biogeochemical consequences. Biogeosciences, 7, 2117–2128. https://doi.org/10.5194/bg-7-2117-2010.

Masó, M., Sabatés, A. and Olivar, M. P. (1998) Short-term physical and biological variability in the shelf-slope region of the NW Mediterranean during the spring transition period. Cont. Shelf Res., 18, 661–675. https://doi.org/10.1016/S0278-4343(98)00011-9.

McManus, M. A., Alldredge, A. L., Barnard, A. H., Boss, E., Case, J. F., Cowles, T. J., Donnaghy, P. L., Eiser, L. B. et al. (2003) Characteristics, distribution and persistence of thin layers over a 48 hour period. Mar. Ecol. Prog. Ser., 261, 1–19. https://doi.org/10.3354/meps261001.

MEDOC Group (1970) Observation of formation of deep water in the Mediterranean Sea. Nature, 227, 1037–1040. https://doi.org/10.1038/2271037a0.

Miller, R. R., Santora, J. A., Auth, T. D., Sakuma, K. M., Wells, B. K., Field, J. C. and Brodeur, R. D. (2019) Distribution of pelagic thaliaceans, Thysys vagina and Pyrosoma atlanticum, during a period of mass occurrence within the California current. CalCOFI, 69, 94–108.

Miller, T. J., Crowder, L. B., Rice, J. A. and Marschall, E. A. (1988) Larval size and recruitment mechanisms in fishes: toward a conceptual framework. Can. J. Fish. Aquat. Sci., 45, 1657–1670. https://doi.org/10.1139/f88-197.

Millot, C. (1999) Circulation in the western Mediterranean Sea. J. Mar. Syst., 20, 423–442. https://doi.org/10.1016/S0924-7963(99)00078-5.

Mir-Arguinb, J., Flexas, M., Salat, J., Martín, P., Balecels, M., Raventós, N. and Sabatés, A. (2022) Severe winter conditions improve recruitment success of blue whiting (M.JpaRepositorys poutassou), a temperate water fish species, in the NW Mediterranean Sea. Prog. Oceanogr., 205, 102818. https://doi.org/10.1016/j.pocean.2022.102818.

Molinero, J. C., Ibáñez, F., Nival, P., Buccher, E. and Souissi, S. (2005) North Atlantic climate and northwestern Mediterranean plankton variability. Limnol. Oceanogr., 50, 1213–1220. https://doi.org/10.4319/lo.2005.50.4.1213.

Nogueira Júnior, M., Brandini, F. P. and Codina, J. C. U. (2015) Diel vertical dynamics of gelatinous zooplankton (Cnidaria, Ctenophora and Thaliacea) in a subtropical stratified ecosystem (south Brazilian bight). PLoS One, 10, e0144161. https://doi.org/10.1371/journal.pone.0144161.

O’Loughlin, J. H., Bernard, K. S., Daly, E. A., Zeman, S., Fisher, J. L., Brodeur, R. D. and Hurst, T. P. (2020) Implications of Pyrosoma atlanticum range expansion on phytoplankton standing stocks in the northern California current. Prog. Oceanogr., 188, 102424. https://doi.org/10.1016/j.pocean.2020.102424.

Ottmann, D., Álvarez-Berastegui, D., Prieto, L., Balbin, R., Alemany, F., Fiksen, O., Gordoa, A. and Reglero, P. (2021) Absence of Pelagia noctiluca early life stages in the western Mediterranean Sea scales with surface chlorophyll. Mar. Ecol. Prog. Ser., 658, 75–88. https://doi.org/10.3354/meps13423.

Palma, S. (1985) Migration nictameral del macrooplanton gelatinosio de la bahía de Villefranche-Sur-Mer, Mediterráneo Noroccidental. Investig Pesq., 49, 261–274.

Pastor-Prieto, M., Bahamón, N., Sabatés, A., Canepa, A., Gili, J. M., Carreton, M. and Company, J. B. (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.

Pirisinotto, R., Mayzaud, P., Nichols, P. D. and Labat, J. P. (2007) Grazing by Pyrosoma atlanticum (Tunicata, Thaliacea) in the South Indian Ocean. Mar. Ecol. Prog. Ser., 330, 1–11. https://doi.org/10.3354/meps330001.
