

Untangling *Velella velella* (Cnidaria: Anthoathecatae) transport: a citizen science and oceanographic approach

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ABSTRACT: *Velella velella* is a pleustonic colonial organism found in temperate and tropical oceanic waters worldwide. During certain periods of the year, large numbers of the species can wash up on coastal beaches. However, little information exists on the ecology and dispersal patterns of this cosmopolitan species, especially on their distribution at sea. How *V. velella*'s at-sea distribution changes with respect to local oceanographic conditions is important to determine their impact on zooplankton communities and the entire marine food web. Zooplankton samples collected off the northwestern Portuguese shelf during a spring oceanographic survey revealed considerable abundance of *V. velella* specimens, mostly in the pelagic phase. Drifters released in the sampling area were remotely followed to examine surface currents, and current velocities were registered, allowing the characterization of the oceanic conditions in the region. Sightings of *V. velella* collected through the 'GelAvista' program, a Portuguese citizen science initiative, were used complementarily, and provided important indications on periods of high abundance and probable areas of occurrence. Local wind regimes were the main driver of *V. velella* distribution and onshore transport, taking into account the direct exposure to the wind and surface circulation variability. The observed occurrences followed the predominant local alongshore currents and are discussed according to local ocean dynamics, enhancing the knowledge on the at-sea ecology of these organisms.

KEY WORDS: Jellyfish · Zooplankton · Transport · Distribution · Upwelling · Portugal

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INTRODUCTION

Gelatinous organisms are important components of marine ecosystems, with many forming remarkable blooms in coastal waters as part of their life history (CIESM 2001, Mills 2001, Lucas & Dawson 2014). Blooms may be more related to inherent population fluctuations rather than long-term expansion of the species (Graham et al. 2001, Condon et al. 2013). Indeed, enhanced productivity and environmental or biotic variability may pro-

mote adequate conditions for blooms of gelatinous plankton (Mills 2001, Condon et al. 2013). However, the passive transport of these organisms from established populations can induce a false bloom in coastal areas (Graham et al. 2001). The difficulty with predicting and assessing the distribution patterns, abundances or occurrence periods of gelatinous organisms is due to the irregularity and short duration that characterize blooms and beach stranding events (Kemp 1986, Graham et al. 2001, Mills 2001).

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For neustonic gelatinous organisms, knowledge and prediction of occurrence and dispersal patterns is often limited by the difficulty in repeatedly collecting data on such widely dispersed animals. Furthermore, the dynamic nature of shelf areas and the patchiness usually associated with zooplanktonic communities adds to this difficulty (Bieri 1977, Shenker 1988). The strong association between the distribution of these organisms and wind conditions may also contribute (Bieri 1977, Graham et al. 2001, Marshall & Burchardt 2005).

Velella velella is a common pleustonic Anthomedusa of temperate and tropical oceanic waters, and an important component of the food web (Purcell et al. 2012). Given their propensity to occur in large blooms that can be driven ashore, they can also significantly contribute to coastal systems (Savilov 1968, Bieri 1977, Purcell et al. 2015). Their distinct life cycle includes a colony (asexual polyp) from which pelagic medusae (sexual phase) are released, a stage easily overlooked in zooplankton samples (Larson 1980). The medusae sink in the water column during summer to reproduce (a process that can last up to 4 mo), reaching depths of 600 to 1000 m (Lebour 1947, Bieri 1977, Purcell et al. 2012). The medusae release pelagic larvae (conaria) that must ascend to surface waters and develop a floating sail-like structure, which allows the colony to float above the water surface (Bieri 1977, Purcell et al. 2012, 2015). *V. velella* distribution is considered to be driven not only by these migrations, but also by the ocean circulation and wind regimes (Bieri 1977). Spring and fall are the main periods of occurrence, growth and reproduction for *V. velella* (Bieri 1977, Purcell et al. 2012), a seasonality that contributes to the unpredictability of their occurrence. These peaks are probably related to food availability, wind conditions and the light necessary to support the associated zooxanthellae (Bigelow 1911, Bieri 1977, Purcell et al. 2015).

The Western Iberian Margin circulation is characterized by highly variable seasonal dynamics, strongly associated with the occurrence of frequent wind-driven upwelling events (Peliz et al. 2007). Northerly winds (upwelling-favourable) dominate during spring/summer, while during winter the warm, salty northward Iberian Poleward Current, driven by south and southwestern winds, is more intense, favouring coastal convergence and downwelling processes (Peliz et al. 2005, 2007, Bartilotti et al. 2014). Our study region represents an area of high fluvial discharge from the Douro and Mondego rivers, but also the Ria de Aveiro coastal lagoon, creating the Western Iberian Buoyant Plume, a surface layer of low salinity (Peliz

et al. 2002, 2007). The short time scales of these processes, together with the vertical migrations performed by zooplanktonic organisms, result in highly complex dispersal patterns that can favour coastal retention even during upwelling events (e.g. Marta-Almeida et al. 2006, dos Santos et al. 2008, Bartilotti et al. 2014).

Citizen science programs such as GelAvista can provide important long-term biodiversity data on the occurrence, abundance and population dynamics of several organisms (Dickinson et al. 2010). These programs encompass wide areas at a scale that would be difficult for researchers to cover, contributing to the identification of invasive or new species and helping to understand the influence of environmental parameters on their distribution (Conrad & Hilchey 2011, Jordan et al. 2011). Other advantages include the connection between the scientific community and the general audience, and the enhancement of ocean literacy and species conservation (Conrad & Hilchey 2011, Jordan et al. 2011). For gelatinous plankton, these programs also give indications on their transport by ocean currents (e.g. Boero 2013, Pikesley et al. 2014).

The lack of oceanic data on gelatinous organisms from plankton samples, but also the scarce data on *V. velella* (e.g. Purcell et al. 2012, 2015), particularly in Portuguese waters, were some of the reasons behind the present work. This study examined the hypothesis that wind regimes are the dominant factor driving *V. velella* transport, and it contributes to the at-sea knowledge on the ecology of this poorly studied species, as well as other similar neustonic organisms.

MATERIALS AND METHODS

Fieldwork and sample processing

Zooplankton samples were collected along the northwestern Portuguese shelf, off the Aveiro coastal lagoon (Fig. 1), during a 2013 spring survey (19–24 May) aboard the RV 'Noruega'. Sampling took place in a south–north direction, with the southern sites sampled first. A total of 52 sampling sites were covered using neuston (0.2 × 1 m mouth aperture, 200 µm mesh), Bongo (60 [BO60] and 90 [BO90] cm mouth diameter, 335 and 500 µm mesh, respectively) and epibenthic nets (EB; 0.8 × 0.6 m mouth aperture, 500 µm mesh). Surface and bottom horizontal hauls (3–5 min duration) were performed with the neuston and epibenthic nets, respectively, while the Bongo nets were utilized to collect water

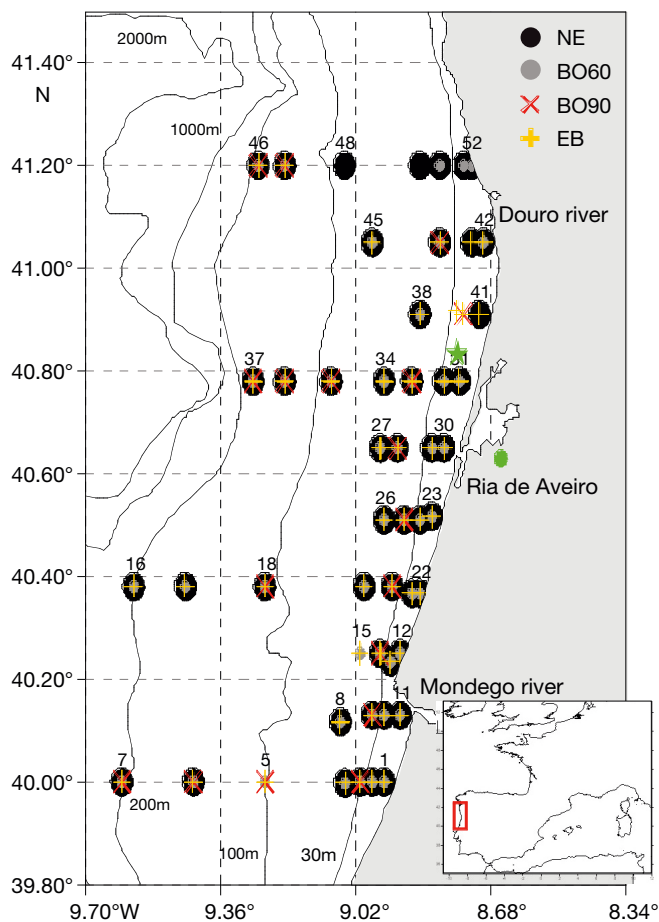


Fig. 1. Northwestern coast of Portugal (eastern Atlantic) showing the sampling sites covered in the survey, nets employed at each sampling station (NE: neuston; BO60: Bongo 60; BO90: Bongo 90; EB: epibenthic) and main hydrographic features. The acoustic Doppler current profiler (ADCP) and drifter release position, and the wind station at the physics department of University of Aveiro are highlighted with a green star and circle, respectively

column data in depth-integrated double-oblique hauls from the surface to 5 m above the bottom (Fig. 1). The water volume filtered during each haul was calculated using flowmeters fixed on the neuston and Bongo nets, whereas for the EB net this calculation was made using the mouth aperture area of the net, haul duration and the distance travelled by the net. Sea conditions during net deployment did not surpass level 6 on the Beaufort scale. Physical parameters of temperature, salinity and chlorophyll *a* (chl *a*) (Fig. 2) were gathered vertically with a SBE 911p CTD and a Chelsea Aqua Tracka III fluorometer.

After preservation of the zooplankton samples in 4 % borax-buffered formaldehyde, biovolume values were determined (except for the BO90 samples) by

the displacement method (Postel et al. 2000) and converted into biomass applying the Wiebe (1988) equations. *Velella velella* specimens were sorted from the samples and their development stage analysed. Individual sail length was measured longitudinally for 552 *V. velella* individuals and they were separated into size categories according to development stage. Hence, individuals <3 mm were considered an early post-conaria phase (Fig. 3a,b), those between 3.1 and 7.5 mm a late post-conaria phase (Fig. 3c–e), and those with a sail >7.5 mm a pre-colonial stage, very close to the adult form (Fig. 3f) (e.g. Langstroth & Langstroth 2000). Abundances were standardized to number of ind. 10 m⁻³ (Postel et al. 2000) and normalised (Ibanez 1971). Kruskal-Wallis analyses were performed on the spatial distribution to evaluate the statistical significance of observed abundance differences among sites and according to distance from coast. The correlation with physical parameters was also explored.

Citizen science data

In February 2016, IPMA (Portuguese Sea and Atmosphere Institute) introduced the GelAvista citizen science program, which aims to gather information about gelatinous species present in Portuguese waters by compiling beach stranding records and data collected at sea. GelAvista observers are prompted to email any available information (old or new) on gelatinous organisms, providing the date, time and location of the sighting, and to include photos with visual scale to enable species confirmation. GelAvista observers are also encouraged to report null sightings, which gives confidence that the lack of sightings is related to a period of low abundance. The number of sighted *V. velella* individuals is provided by observers in category intervals of <5, 5–10, 10–50, 50–100, 100–1000 and >1000. These numbers are then processed by an approximation to an average value. The quality of the GelAvista data is always validated according to the information received and the status of the observers. Thus, a confidence level of 1 (high confidence) is attributed for sightings that include time, date and location, but also if the number of individuals and photos are included. If no photo is attached, but the observer is frequent and reliable (e.g. participated in workshops of the project) confidence level 2 is attributed (medium confidence). A confidence level 3 (low confidence) is assigned when no photo is provided or the information is incomplete.

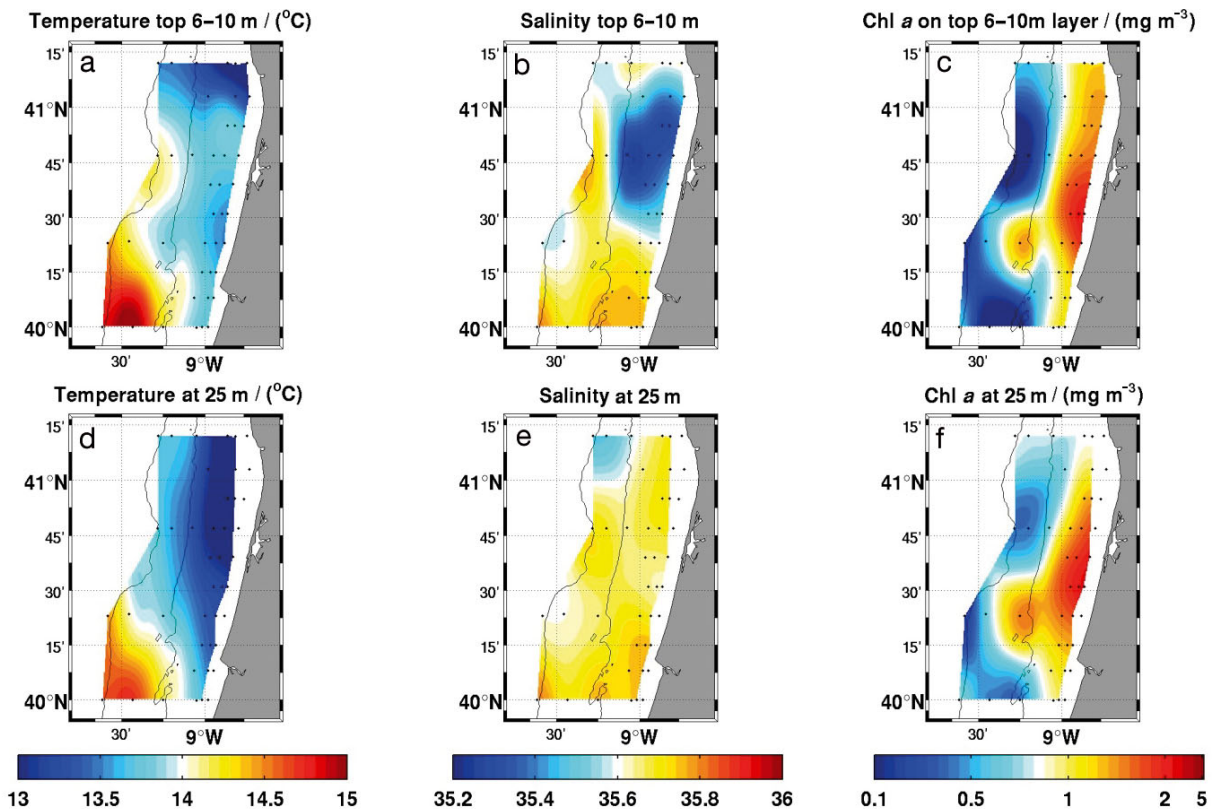


Fig. 2. (a,d) Temperature ($^{\circ}\text{C}$), (b,e) salinity and (c,f) chl *a* (mg m^{-3}) values registered by the CTD between (a-c) 6–10 and (d-f) 25 m depth at the northwestern coast of Portugal (Fig. 1). The black dots represent the positions of the sampling stations

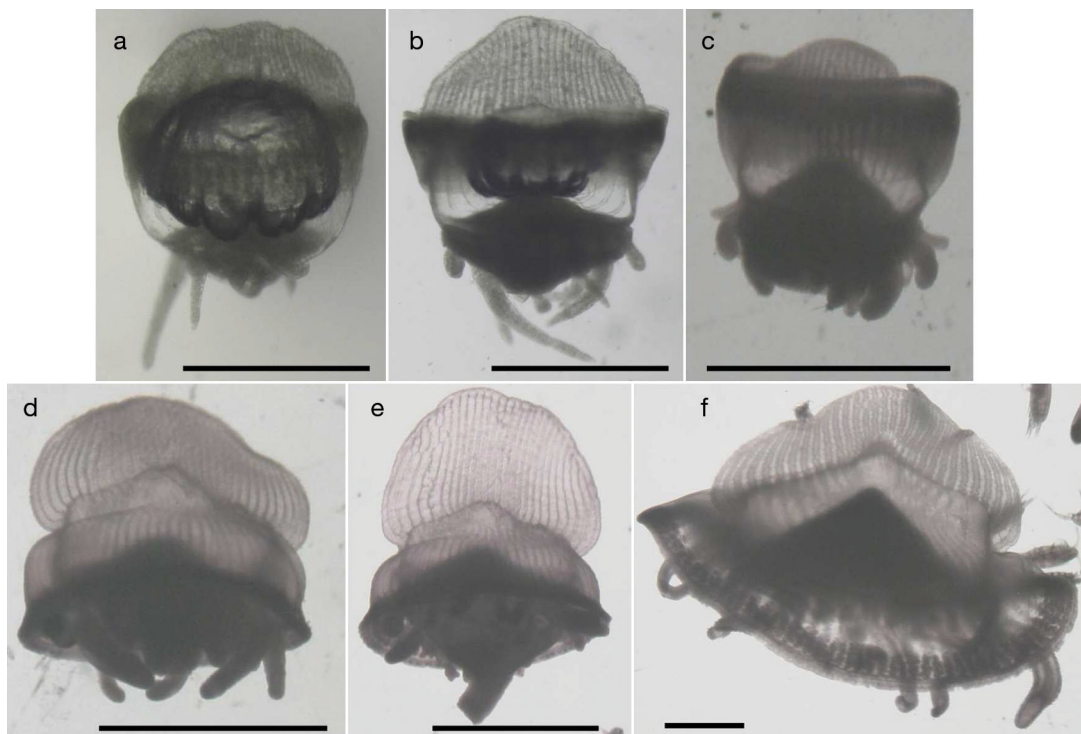


Fig. 3. Different *Velella velella* forms sorted from the collected zooplankton samples, designated as (a,b) early post-conaria, (c–e) late post-conaria and (f) pre-colonial phases. Scale bar: (a,b) 1 mm, (c–f) 2 mm

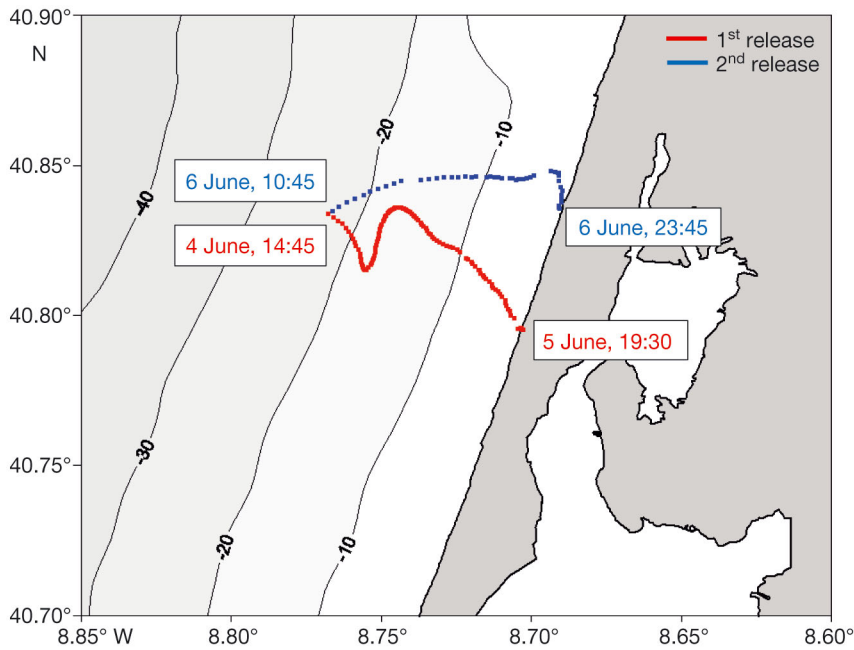


Fig. 4. GPS positions registered during the experiment with ecological drifters and buoys through time for the 1st and 2nd release events (red and blue lines, respectively) off Ria de Aveiro (Fig. 1). Experiment started at 14:45 h GMT on 4 June and ended at 23:45 h GMT on 6 June. Depth contours (meters) are represented relative to the hydrographic zero (e.g. –10 corresponds to 10 m depth)

GelAvista data on *V. velella* for 2016 and early 2017 (January to April) were examined and validated for the present study, and both the periods of higher abundance and the most probable occurrence areas for the Portuguese coast were extracted. For comparative purposes, data for 2013 and 2014, although limited, were also cautiously included, complementing the spatial and temporal occurrence information. Null sightings were also analysed, corresponding to periods of low abundance of gelatinous organisms.

a short period covering only the sampling cruise (20 May to 1 June) to register vertical profiles of current velocity (Fig. 5b). The objective was to explore the local currents and associated oceanographic mechanisms that influence the observed abundance patterns, allowing the analysis of plankton dispersal. Due to the ADCP limitation, the 7 m depth currents were the closest to surface to be registered, and were compared with spatial abundances of *V. velella*.

Physical data

In order to explain the oceanographic structures influencing the biological patterns observed during the survey, an assessment of coastal oceanographic conditions was conducted after the survey period, from 4 to 6 June 2013. The experiment focused on obtaining information about surface currents that have strong influence on neustonic organisms. Thus, ca. 2000 ecological drifters (oranges) were released in 2 distinct events (4 and 6 June), together with a real-time GPS drifting buoy (iSphere current tracking buoy), 5.3 km off the Aveiro coastal lagoon (40.83° N, 8.77° W) and 15 km north of the lagoon mouth (Fig. 1). The path of the drifting buoy, launched in both release events, is presented in Fig. 4.

An acoustic Doppler current profiler (ADCP) was deployed at about 25 m depth off Aveiro (at the same position of the drifter experiment) for

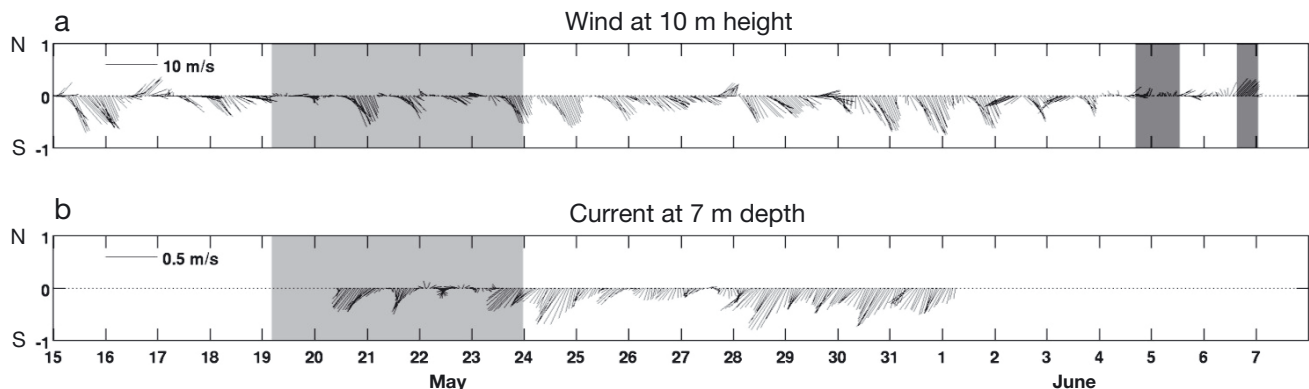


Fig. 5. (a) Wind intensity (m s^{-1}) and direction for the period between 15 May and 7 June at the wind station at the physics department of University of Aveiro (40° 37' 39" N, 8° 39' 24" W). (b) Current velocities (m s^{-1}) and direction for 7 m depth registered by the acoustic Doppler current profiler (ADCP) deployed at 25 m depth off Ria de Aveiro (Fig. 1). Grey bands: survey (19–24 May) and drifter experiment (4–6 June) periods

Time series of wind speed and direction (Fig. 5b) measured every 10 min at the physics department of University of Aveiro (40.63°N, 8.66°W) (Fig. 1) were obtained between 15 May and 6 June 2013, covering the survey, ADCP deployment and drifter experiment periods.

RESULTS

Physical data

Low temperatures and high chl *a* values were found in the nearshore waters of the sampling region compared with the offshore area, confirming an upwelling event (Fig. 2a,c). The presence of a surface plume front of lower salinity values was evident in the neighbourhood of Ria de Aveiro, associated with river outflow, extending south-westward from the Douro River (Fig. 2b). This surface plume was not visible in subsurface waters at 25 m depth (Fig. 2e). The offshore spreading of recently upwelled coastal waters is suggested by the chl *a* values at 40° 20' N extending 35 km from the coast (Fig. 2c,d).

Northerly winds (upwelling-favourable) dominated during the sampling period (Fig. 5a), with higher intensities in the offshore area (data not shown). A relative relaxation period with the occurrence of rainstorms was registered just before the survey and lasted until 20 May, when winds were again more intense (average of 5 m s^{-1}), maintaining a northerly direction throughout most of the cruise period (Fig. 5a). Thus, the southern sampling sites were under distinct oceanographic conditions. During the release of the ecological and drifting buoys (4 to 6 June), winds were mainly weak southerlies (velocities below 5 m s^{-1}) (Fig. 5a).

The drifter experiments, although short in duration, showed a persistent cross-shore transport by surface currents towards the coast for both the ecological and mechanical drifters (Fig. 4). In the first release event, the drifters moved first towards the southeast, then deflected north for a brief period before resuming cross-shore transport and reaching the coast ~28 h after deployment. In the second release event, the drifters were transported northeast and then southward, travelling very close to shore and for a brief period. Contrasting wind conditions were registered during the survey and drifter experiments. The weak winds during the drifter experiment, in contrast to the scenario registered during the survey, resulted in a strong zonal (west–east) onshore transport. The wind direction is closely followed by the drifter trajectory (Figs. 4 & 5a).

Currents registered by the ADCP followed the predominant local northerly wind regime, with prevailing offshore and southward motion in the surface layer (Fig. 5). Currents in the lower layer were onshore and the front interface was registered around 15 to 20 m depth (data not shown). Thus, the upwelling influence off the continental shelf was evident during the survey. However, these upwelling conditions were disrupted during 2 episodes of relative wind relaxation (22 and 27 May), which coincided with a more westerly direction and a weakening of the current intensities (Fig. 5). This produced brief coastal convergence periods in the upper layers (Fig. 5b). Considering the cross-shore direction of the surface currents, the inner shelf circulation and the upwelling events in the area are thus strongly driven by the velocity and direction of the local winds.

Biological data

A total of 560 *Veleva velella* individuals were sorted from all the samples, and consisted mainly of late post-conaria stages (Fig. 3c–e), with sails measuring between 2.1 and 5 mm length. The sail size range of the collected *V. velella* individuals is presented in Fig. 6. Most of the collected specimens were in young pelagic stages. Abundances registered during the survey were relatively high and mainly limited to the neuston samples (Fig. 7a). For this net, the highest abundances were found in the southern sampling sites, especially on the outer shelf between 43 and 60 km off the coast, corresponding to a maximum of $6.8 \text{ ind. } 10 \text{ m}^{-3}$. However, the species

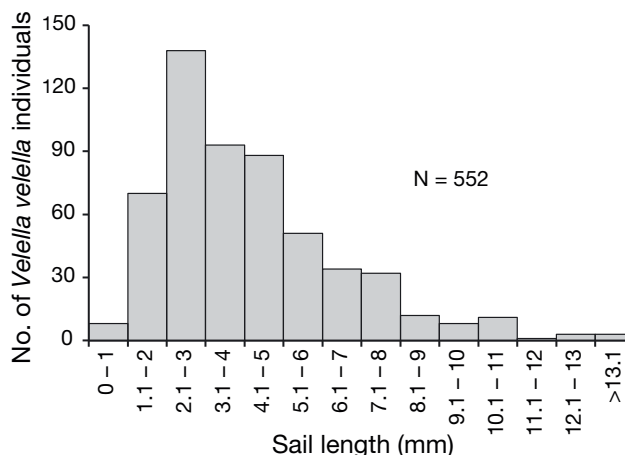


Fig. 6. *Veleva velella* sail size range (mm) versus number of *V. velella* individuals collected in each sail length category

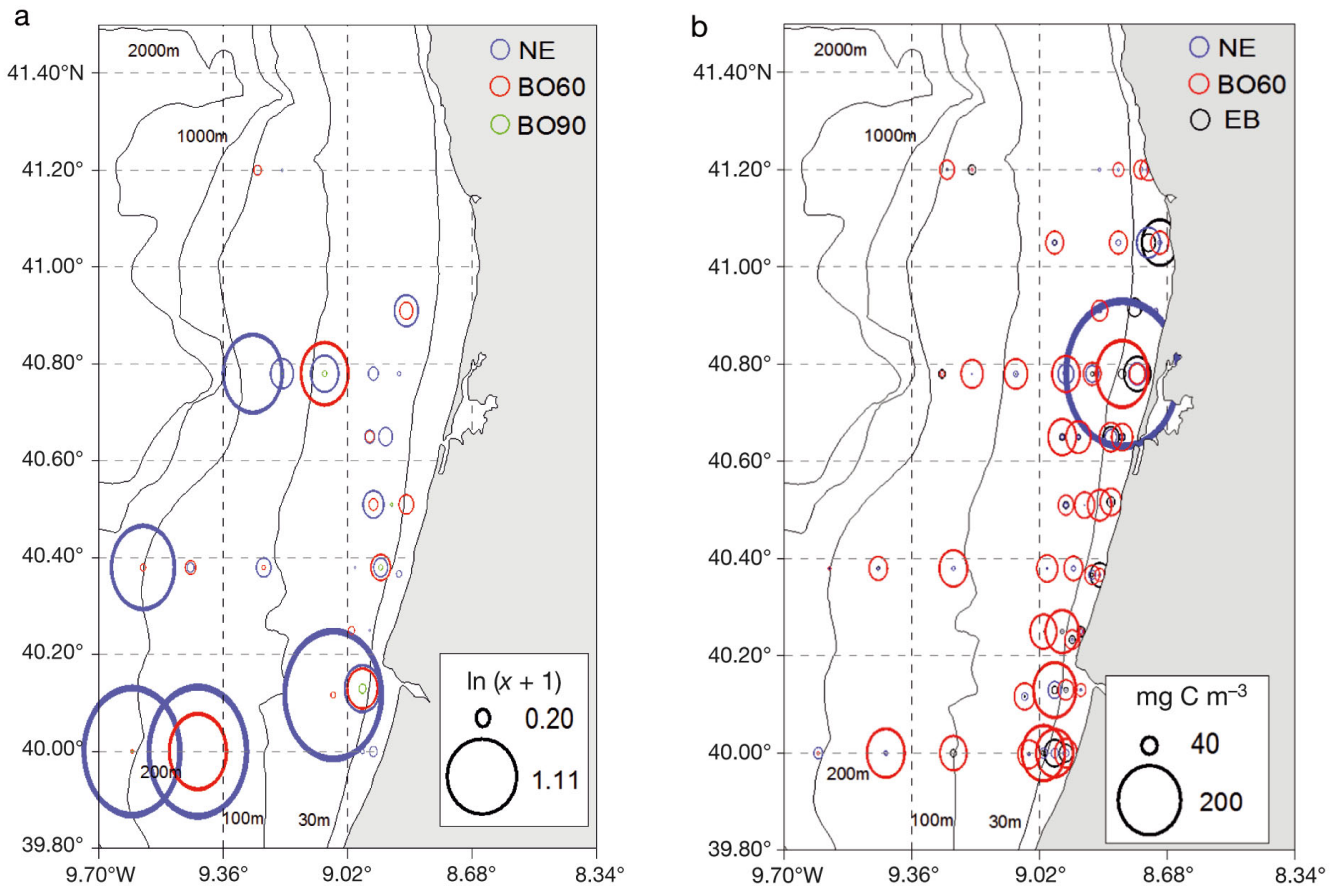


Fig. 7. Spatial biological patterns at the northwestern Portuguese coast. (a) *Velella velella* abundances in $\ln(x + 1)$ (where $x = \text{ind. } 10 \text{ m}^{-3}$) collected with neuston (NE), Bongo 60 (BO60) and Bongo 90 (BO90) nets. (b) Spatial zooplankton biomass (mg C m^{-3}) for each sampling site for the NE, BO60 and epibenthic (EB) nets. Biomass values for the BO90 net were not measured. *V. velella* specimens were not found in the epibenthic samples

was also present at one inner shelf site (13 km from the coast), at an abundance of $6.7 \text{ ind. } 10 \text{ m}^{-3}$ (Fig. 7a). At the middle sites, an abundance maximum of $2.8 \text{ ind. } 10 \text{ m}^{-3}$ was registered offshore. The species was almost absent from the northern sites. Lower abundances were found in the Bongo samples, with a maximum of $0.8 \text{ ind. } 10 \text{ m}^{-3}$ offshore and $0.2 \text{ ind. } 10 \text{ m}^{-3}$ in the inner shelf for the BO60 and BO90 nets, respectively (Fig. 7a). No *V. velella* specimens were detected in the EB samples.

The highest abundances of *V. velella* did not coincide with the highest zooplankton biomass registered for the neuston net (Fig. 7b). However, their occurrence was correlated with high temperatures and low chl *a* levels ($p < 0.05$), despite the non-significant relationship with salinity values. Significant differences in abundances were also registered among sampling sites in the first 10 km off the coast and the outer shelf (30–50 km) (Kruskal-Wallis $H = 19.72$, $p = 0.01$).

A total of 39 sightings were transmitted by GelAvista observers for the years 2013 to early 2017, with the exception of 2015, in which there were no reported sightings. Of the total sightings, 95% were validated with the maximum level of confidence (level 1). Data collected in the scope of the GelAvista citizen science program (Fig. 8) confirmed the presence of *V. velella* specimens on the Portuguese coast during spring 2013 (Fig. 8a), close to the time of the survey. One sighting reported a concentration of >100 individuals of different sizes (from <1 to 7 cm, approximately) several weeks before the survey in a beach near Lisbon, south of the study area (Fig. 8). Sightings for the 2013, 2014, 2016 and 2017 years revealed that *V. velella* were mostly sighted in the north and central western Portuguese coast, close to the survey area, usually in high numbers (Fig. 8a). Sightings were limited to fall and spring months (Fig. 8d).

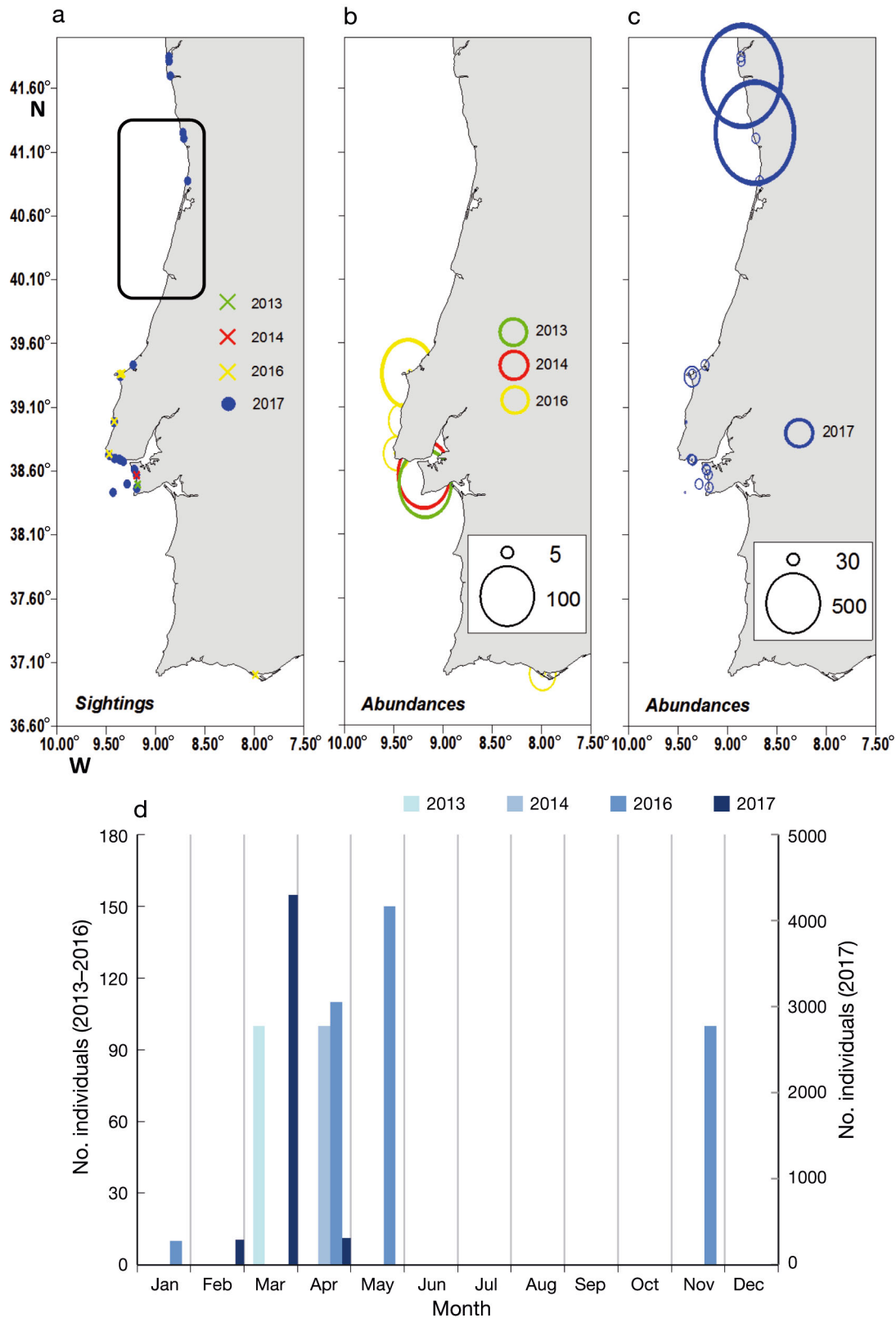


Fig. 8. (a) Portuguese coast map (eastern Atlantic) showing the GelAvista occurrences of *Velella velella* registered in terms of (a) sightings (only) for the years 2013, 2014 (one each), 2016 and 2017, and respective abundances (total no. of ind.) for the years (b) 2013, 2014 and 2016, and (c) 2017. Survey area is also demarcated by a black rectangle in (a). (d) Total number of *V. velella* sighted per month and year

DISCUSSION

Neustonic communities, usually occupying the first centimetres of the water column (Zaitsev 1997), experience highly variable and extreme conditions, both daily and seasonally, due to the constant disturbances acting on the sea surface (Marshall & Burchardt 2005). The pleustonic position of *Velella velella* (Hardy 1997) makes them especially vulnerable to sea–air interactions. In fact, winds, biological exchanges and physical structures such as fronts, currents, eddies and upwelling events drive the distribution of neustonic organisms (Zaitsev 1997, Marshall & Burchardt 2005). Conditions in the neuston layer are completely distinct from the deeper waters, but can influence the communities found therein, since many neustonic organisms descend in the water column during their development (Zaitsev 1997).

Most of the *V. velella* specimens found in the present survey were young, suggesting an advection of recent colonies to the surface (Purcell et al. 2012) and that a snapshot of the spring reproduction period was probably captured in the sampling. Young specimens are usually detected in offshore regions (Lebour 1947) and our results comply with this pattern, with *V. velella* being driven ashore due to the upwelling currents (see discussion below). GelAvista sightings agree with the seasonal marked occurrence suggested for the species, with periods of high abundance during spring and fall months—favourable periods for *V. velella* reproduction and growth (Bieri 1959, 1977, Purcell et al. 2012). In the western Mediterranean Sea, closely associated with the southern Portuguese coast, several records of *V. velella* blooms were also reported during the 2013 spring period both at sea and on beaches (Purcell et al. 2015). Summer months were the poorest in terms of *V. velella* sightings. Summer migrations performed by the pelagic larvae can generate this pattern, as a dispersal control mechanism to remain in productive areas during a more fragile phase of their life cycle and to manage the usually weaker winds of the season (e.g. Bieri 1977). However, considering the short duration of the survey, continuation of the GelAvista program will allow clarification of the occurrence patterns of *V. velella*.

Abundance values registered during the present study are somewhat low in terms of number of individuals compared to the typically large numbers encountered during beach strandings. Our results may be expected, considering that Larson (1980) suggested that the species is probably distributed in low densities at sea, eventually being concentrated by local wind regimes and transported to shore. In fact,

an extensive volume of water was sampled at sea during the survey and only low densities were found. According to Omori & Hamner (1982), aggregations of zooplankton usually comprise an abundance increase of 100 to 1000 times relative to normal population numbers. This also concurs with the patchy nature of most neustonic and zooplanktonic organisms (Shenker 1988).

For the study area, results suggest predominant local wind regimes as being the main drivers of the observed *V. velella* distribution. ADCP results showed that the upper layer currents were strongly driven by the alongshore wind component. The predominant local spring regimes (mainly north to south), which are strongly seasonal (Fiúza 1983, Peliz et al. 2002, 2005), will favour an alongshore distribution of the species. In periods of upwelling relaxation, these currents would promote an onshore convergence (Fiúza 1983, Peliz et al. 2002, 2007). Similar alongshore distribution and retention have been found in the area for crustacean decapod and cirripedia larvae (e.g. dos Santos et al. 2007, 2008, Bartilotti et al. 2014). These patterns are related to wind-driven currents and behavioural mechanisms adopted by the species (i.e. vertical migrations; Marta-Almeida et al. 2006, Peliz et al. 2007). The strong association with surface waters expose *V. velella* to particular wind-driven currents that define their distribution extent (Bieri 1977, Purcell et al. 2012). Thus, factors such as wind velocity, direction and duration are essential to understand the transport of the species (Bingham & Albertson 1974). This is particularly evident when considering the near-shore occurrence in the southern sampling sites, and that the species usually occupies central water masses and is rarely observed in shallow waters (Bieri 1977, Purcell et al. 2015). The disruption of the upwelling regime before and during the first days of survey explains the onshore transport of *V. velella* occurring in the outer shelf. Similar scenarios of near-shore retention on alongshore aggregations for decapod larvae in periods of upwelling relaxation were modelled by Peliz et al. (2007) for the area. The near-shore occurrence of *V. velella* was previously considered as an indication of wind drift of surface waters (Russell & Kemp 1932) and high onshore transport of adult specimens during spring months was previously reported by Tregouboff & Rose (1957). Lebour (1947) reported higher blooms and beach strandings of the species after storm periods that indeed occurred just before our sampling survey, contributing to the nearshore accumulation of *V. velella* specimens in the first sampling days at the southern sites.

The drifter experiment occurred under totally different oceanic conditions than the survey, but reproduced the brief upwelling relaxation events occurring before and during the survey, with surface currents quickly promoting onshore transport.

V. velella distribution appears to be related to the oceanic front created by the wind-upwelled waters in the study area, in light of the spatial differences between the inner and outer shelf abundances. Data for *V. velella*, as with other neustonic organisms, suggest that they usually concentrate at offshore surface convergence areas characterized by high trophic activity (Bieri 1977, Marshall & Burchardt 2005, Purcell et al. 2012, 2015). The intrusion of warmer and more saline waters towards the coast at the southern sampling sites can also favour the nearshore occurrence of *V. velella*, particularly considering the low temperatures and high chl *a* levels that characterize the upwelling events in the inner shelf. Cold waters can even induce the occurrence of a single reproduction period (Purcell et al. 2012). This inner shelf intrusion of warm slope waters during upwelling relaxation periods and northward currents is a common pattern in the local circulation (e.g. Peliz et al. 2002, 2007, Bartilotti et al. 2014). Physical parameters are, indeed, considered important triggers of gelatinous plankton aggregations (Graham et al. 2001).

High zooplankton biomass values appear to be less important to the observed distribution patterns, as they were not followed by *V. velella* abundances. However, the species was registered before in productive areas, associated with zooplankton migrations (Purcell et al. 2015) and is usually more abundant during highly productive periods (Bieri 1977). For the Portuguese coast, spring months comprise high seasonal peaks of zooplankton abundance and diversity (dos Santos 1999, Peliz et al. 2007), adequate conditions to trigger blooms of the species. However, the short survey may have caught only the beginning of a reproductive period. One idea is that the vertical migrations performed by *V. velella* pelagic larvae may limit the cross-shore transport by being retained nearshore and escaping the offshore upwelling transport, a pattern registered for decapod larvae in the area (e.g. dos Santos et al. 2008). Ascending back to the surface in a more developed stage may promote an offshore transport where the adults are usually found. Productive waters may be more important for the young larvae than for the adults.

In the future, long-term data eventually provided by the GelAvista program continuation can help to clarify the spring/fall occurrence patterns and the

likely common occurrence of the species in Portuguese waters. As a transition zone between temperate and tropical environments, and as the northern/southern distribution limit of many species (Lima et al. 2007), the Portuguese coast is a strategic area in which to study the patterns and impact of *V. velella* on coastal habitats. Then the Portuguese coast can be used to understand the connectivity with the Celtic Sea and northeastern Atlantic where the species is also found (Purcell et al. 2012, Pikesley et al. 2014; see also www.JellyWatch.org online world data).

The present study provides a first step towards understanding *V. velella* distribution patterns and transport mechanisms in Portuguese waters. It gives important indications for the dispersal and spatial distribution of other gelatinous species, such as *Physalia physalis* which is exposed to similar conditions, that can be utilized to develop physical-ecological models and examine species transport. It also exemplifies the usefulness of plankton surveys in untangling gelatinous plankton distribution.

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