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Massive strandings of *Velella velella* (Hydrozoa: Anthoathecata: Porpitidae) in the Ligurian Sea (North-western Mediterranean Sea)

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Abstract
Velella velella, the so-called by-the-wind sailor, is a common member of the open-ocean pleustonic fauna, worldwide distributed in tropical and temperate regions. Thanks to their sail protruding above the sea surface, floating polymorphic colonies of this hydrozoan are carried by winds, and tend to aggregate in large swarms, that often get stranded along the shores. Although these events are commonly observed in springtime along the Ligurian coasts (North-western Mediterranean Sea), no quantitative characterization was ever made. The aim of this study was to characterize the stranding events that occurred in spring 2016 along the Ligurian coast, by evaluating the influence of the local sea conditions and by quantifying the abundance of the stranded colonies in each event. Their size-frequency distribution and biomass were examined, and the associated mollusc fauna identified and counted. The magnitude of these episodes was so relevant that, along the Ligurian coasts, the *V. velella* strandings constitute one of the most important biological deposition of organic matter; nevertheless, the ecological role of these remarkable and stochastic accumulations of chitin along the coast is still unexplored.

Keywords: *Pleuston, blooms, pelagic snails, zooplankton, swarms*

Introduction

Velella velella (Linnaeus, 1758), commonly known as by-the-wind sailor, is a cosmopolitan holoplanktonic, free-floating marine hydrozoan living in open waters at tropical and temperate latitudes (Daniel 1976; Bieri 1977; McGrath 1985, 1994; Evans 1986; Mianzan & Girola 1990; Flux 2008; Gershwin et al. 2010; Purcell et al. 2015; Gershwin 2016; Pires et al. 2018). The polymorphic colony, up to 120 mm long (Bieri 1977), is enclosed in an oval chitinous pneumatophore, positively buoyant and characterized by an upright and triangular dorsal sail. A central, large gastrozooid hangs below the pneumatophore, surrounded by hundreds of small gonozooids involved in reproduction and a peripheral ring of dactylozooids (Brinckmann-Voss 1970; Kirkpatrick & Pugh 1984; Schuchert 2010).

The sail is constituted by chitinous layers that form a sort of triangular fin, whose main axis is partially shifted respect to that of the pneumatophore. Two mirror-symmetric forms were described (Gul 2015): the right-left asymmetry was associated with a tendency to sail at an angle to the downwind direction. It was hypothesized that when these organisms are transported onshore by winds, only those with one orientation will be blown, depending on the wind direction (Francis 1991; Gershwin 2016).

Floating colonies accumulate in enormous offshore swarms, often constituted by hundreds of millions of colonies (Purcell et al. 2012). Winds may strand such swarms on beaches, causing what can probably be considered one of the most relevant events of organic matter deposition of animal origin on tropical and temperate beaches (Kemp 1986). The large swarms are known to largely influence the planktonic trophic web, with *V. velella* being an active predator of zooplankton, including fish eggs and juveniles (Purcell et al. 2015). In turn, *V. velella* is preyed by some pleustonic gastropods belonging

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to the genus *Janthina* Röding, 1798, nudibranchs as *Glaucus atlanticus* (Forster, 1777) and *Fiona pinnata* (Eschscholtz, 1831), as well as sea turtles like *Caretta caretta* (L., 1758) and the sunfish *Mola mola* (L., 1758) (Bayer 1963; Parker et al. 2005; Purcell et al. 2012; Betti et al. 2017).

Because of its open-ocean holoplanktonic life, little is known about the biology and ecology of *V. velella*. Each colony produces a large number of medusae with associated symbiotic zooxanthellae (Schuchert 2010), but the complete life cycle of this species has not been delineated yet. Swarms are known to form offshore (Daniel 1976; Evans 1986; Purcell et al. 2012), in particular over deep basins (Purcell et al. 2015), suggesting that the larval cycle of this species is carried out in deep waters (Woltereck 1904). On the other hand, thanks to massive accumulations on beaches, some information is available on *V. velella* strandings around the world (Bieri 1977; McGrath 1985, 1994; Kemp 1986; Purcell et al. 2015). Particularly, their occurrence in the Mediterranean basin is known since ancient times (Imperato 1599; Colonna 1616; Carburi 1757; Costa 1843).

In the western Mediterranean Sea, blooms show an annual periodicity, with a spring peak and, along the southern coasts, also a minor autumnal one; blooms of *V. velella* along the Italian coasts have been monitored in the last years by the University of Salento (Lecce, Italy) with the help of the citizen science METEOMEDUSE Project (Boero 2013). The Ligurian Sea, located in the northernmost part of the western Mediterranean Sea, experiences extremely relevant blooms from the quantitative point of view (Brian 1923; Issel 1928; Betti et al. 2017). These high biomasses may have important consequences on the entire planktonic trophic web of the basin. However, despite their relevance, with the exception of the work by Purcell et al. (2015) regarding the diel-feeding patterns and digestion periods of *V. velella*, the species is only reported secondarily, as part of studies on other organisms in the scientific literature available for the region (Brian 1923; Issel 1928). Indeed, recently, Betti et al. (2017) described the occurrence of *V. velella* colonies along the Ligurian coasts, within exceptional strandings of the pelagic snail *Janthina pallida* W. Thompson, 1840, occurred during persistent southerly winds.

Main purpose of this study was to quantify for the first time the stranding events, both in terms of biomass and abundance of the colonies, estimating the organic matter deposited along the Ligurian beaches in order to understand the ecological implications of the phenomenon. Moreover, the role of the local sea conditions in driving the dynamics of these events was evaluated. Finally, the chance given by the strandings to observe an otherwise elusive species was used to extrapolate biological information regarding *V. velella*, such as growth rate and relation with associate fauna.

Materials and methods

In order to quantitatively characterize the *V. velella* swarms stranded along the Ligurian coasts during spring 2016, a total of six samplings were conducted in three sites distributed along the coast (Figure 1): i) Noli Cape, in the western Ligurian Riviera, ii) the beach of Arenzano, a locality placed in the center of the Ligurian Arc (32 km eastward from Noli Cape), and iii) Santa Margherita Ligure, in the eastern Ligurian Riviera (44 km eastward from Arenzano). All the three sites are characterized by linear sandy coasts, roughly facing E.

On 11 April, a first swarm of *V. velella* was observed by fishermen operating few miles off Arenzano, over a bottom of 100 m depth. Since then, and for the following months, the authors daily checked the chosen sites, in order to record the eventual stranding episodes. During that period, the swarms repeatedly stranded along the Ligurian coasts; the first day of each stranding, all the *V. velella* specimens and their associated predators on each site were collected within five replicates of 40 × 40 cm squares, randomly placed on the strip of stranded colonies, to estimate the abundance of the organisms (Figure 2(a,b)). Within an hour from the collection, samples were preserved at −20°C until the laboratory analysis. The length of the pneumatophores of all the colonies present in each square (up to 2,000 specimens) was measured with a calliper. From these data, average length and size-frequency distributions were obtained. For the same specimens, the right-left asymmetry of the sails was also noted.

The total wet weight (WW) of each replicate was obtained through an electronic scale measurement. Finally, the dry weight (DW) was obtained after drying the samples at 50°C for 3 days. For each sample, the associated organisms, when present, were counted and weighted separately. The sites where abundance and biomass of beached *V. velella* was quantified were chosen among sandy beaches, where the floating material tends to accumulate, due to the convergence of wave energy (Tucker & Pitt 2001; Burcharth 2003). In the two considered sectors of the Ligurian Arc (Noli-Arenzano and Arenzano-Santa Margherita Ligure), the sandy littorals cover approximately 20 km and 5 km of coastline, respectively. In each chosen locality, samplings were made in April and

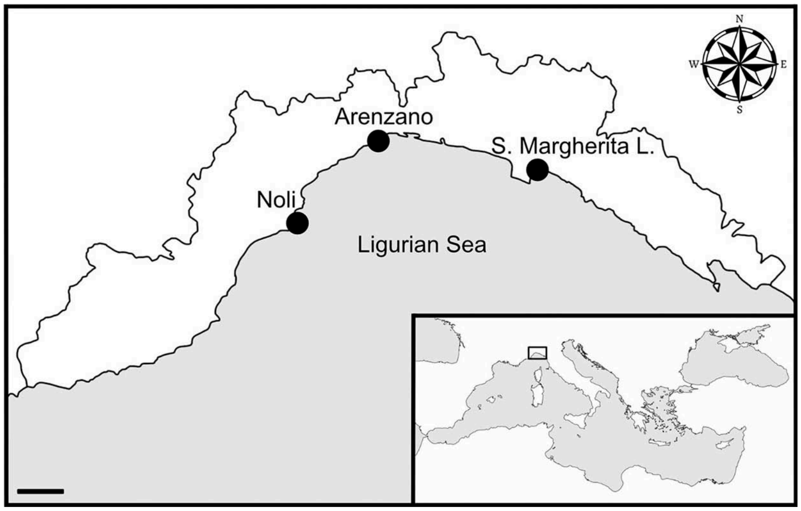

Figure 1. Map of the Ligurian Sea showing the study sites. Scale bar = 10 km.

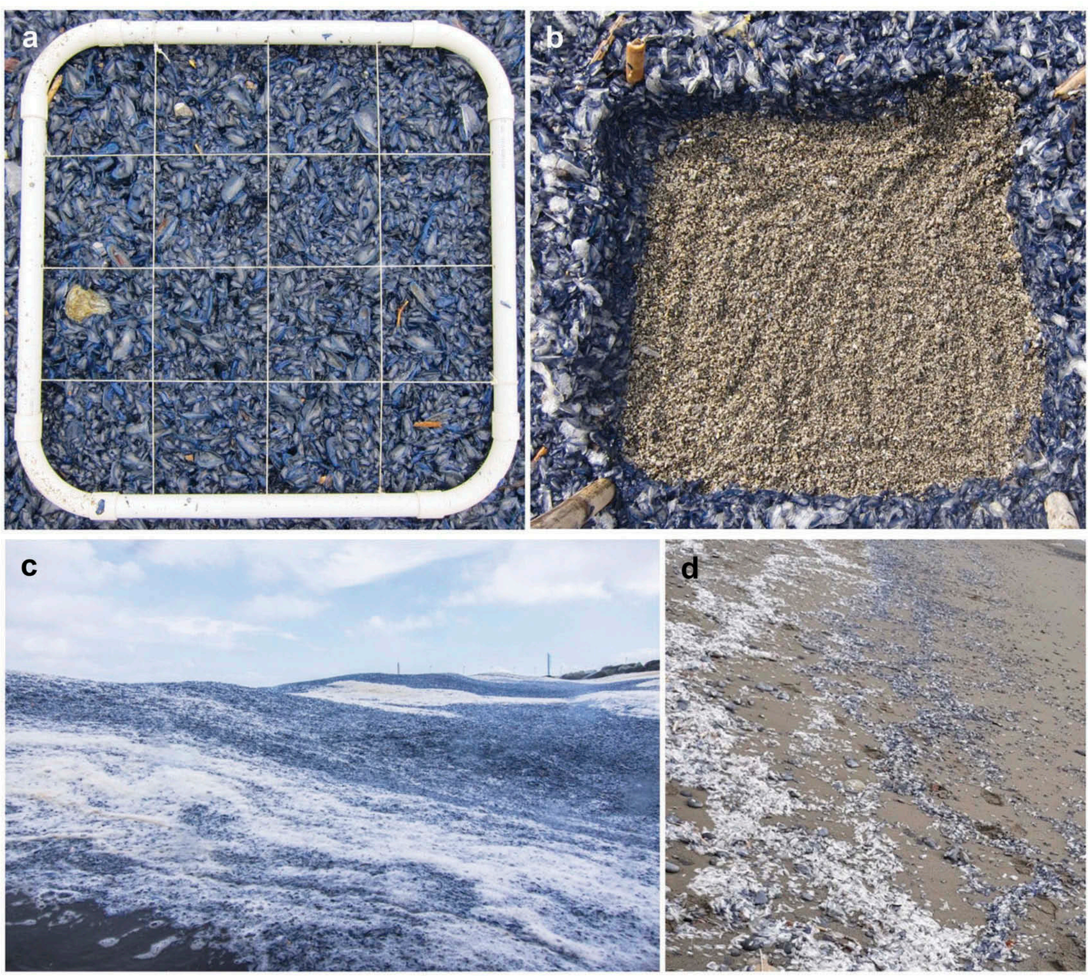

Figure 2. Stranding *of Velella velella* on the beach of Arenzano during the spring 2016. (a) A standard surface used to obtain quantitative data on the biomass of beached organisms. (b) The appearance of the beach after the collection of the organisms present in the standard surface. (c) A dense swarm on the sea surface close to the beach: the colonies completely cover the sea surface. (d) Numerous old (white) and freshly beached (blue) *V. velella* colonies in long bands along the shore.

May/June in correspondence to each recorded stranding episode (Table I). Thanks to consecutive strandings, it was possible to estimate the growing trend of the *V. velella* population, by comparing lengths and weights of colonies collected in different periods.

Information about the percent persistence of the wind direction (hours week^{-1}) and intensity (m s^{-1}) from April to June 2016, recorded by the sea stations at Portofino (5 km westward of S. Margherita Ligure) and Noli Cape, were obtained from the Regione Liguria data set (www.mareografico.it).

The associated fauna was lately analyzed for taxonomic identification and quantification. Three specimens of the poorly known pelagic nudibranch *Fiona pinnata* associated with *V. velella* were collected in Arenzano on the 12th of April 2016 and preserved in formalin 4%, with the objective of ascertaining if the nudibranch uses cleptodefences acquired from its prey, a strategy well known in aeolid nudibranchs (e.g. Conklin & Mariscal 1977; Day & Harris 1978; Greenwood & Mariscal 1984; Martin 2003). Hence, some cerata were removed from the body with tweezers and squeezed on a slide to search for nematocysts, following the descriptions of the cnidome provided by Russell (1939). Samples were observed under a 100x magnification and pictures were taken with the Leica LAS EZ software. No other specimens were recorded in the other samples.

Results

Dynamics of the strandings

The day after the record of offshore swarms by fishermen (12 April), a first stranding occurred on the Arenzano beach, followed by others, observed at Noli Cape (13 April) and Santa Margherita Ligure beaches (15 April). A new stranding was observed on 29 April only at Santa Margherita Ligure. One month later, on 27 May and 1 June, other *Velella* swarms beached at Noli and Arenzano, respectively (Table I).

In the considered periods, wind regime along the Ligurian coast was dominated by an alternation of winds blowing from SE and N. This trend was very similar in both the considered meteorological stations of Portofino and Noli Cape (Figure 3). In particular, a first peak of persistence of winds from southern quadrants reaching 85.1% and 75.6%, respectively, for Portofino and Noli Cape, was evident in the second and third weeks of the studied period. These winds reached a maximal intensity of about 18 m s^{-1}. A second peak was observed two months later, from 6 to 12 June with a persistence of 88.4% and 66.7%, respectively, for Portofino and Noli Cape. Between these two peaks, a span of time mainly characterized by northerly winds occurred. The maximal recorded intensity of the northern winds reached 19 m s^{-1}. Each stranding occurred in days characterized by winds blowing persistently from the southern quadrants (Figure 3).

Characteristics of the strandings

The April 2016 strandings were extremely intense from a quantitative point of view with the sea surface close to the studied beaches completely covered by *V. velella* colonies (Figure 2(c)). When the organisms beached, they formed bands parallel to the coast (Figure 2(d)) sometimes up to 10 cm thick (Figure 2(b)).

Densities and biomass of the stranded colonies were different, according to the localities (Table I, Figure 4(a,b)): the highest values were recorded at Santa Margherita Ligure, with an average density of about 114,000 colonies m^{-2} and a biomass of about 3,900

Table I. Estimated abundances, in terms of number of specimens, length and biomass of *Velella velella* and its predator *Janthina pallida* in the three study localities during the 2016 strandings.

Localities	Santa Margherita Ligure		Arenzano		Noli	
Coordinates	44° 20′ 09″ N 09° 13′ 27″ E		44° 24′ 28″ N 08° 41′ 32″ E		44° 12′ 14″ N 08° 25′ 01″ E	
Dates	15/04	29/04	12/04	01/06	13/04	27/05
Velella velella						
Densities (colonies m^{-2})	114,559 ± 18,289	41,674 ± 10,730	24,719 ± 6022	623 ± 125	7,460 ± 1277	811 ± 200
Length (mm)	11.5 ± 0.2	21.3 ± 0.2	11.9 ± 0.3	30.6 ± 0.4	20.5 ± 0.2	34.9 ± 0.3
WW (g m^{-2})	3,902.2 ± 543.9	5,731.2 ± 1,533.6	770.63 ± 191.7	159.8 ± 32.3	939.1 ± 326.9	191.2 ± 94.7
DW (g m^{-2})	223.3 ± 30.5	611.2 ± 260.3	46.25 ± 12.9	23.5 ± 2.4	43.1 ± 9.7	32.8 ± 7.3
Janthina pallida						
Densities (shells m^{-2})	523.0 ± 97		241.0 ± 51		204.0 ± 47	
WW (g m^{-2})	550.7 ± 79.8		218.8 ± 40.7		72.6 ± 14.5	
DW (g m^{-2})	178.6 ± 39.6		56.7 ± 9.4		18.1 ± 3.7	

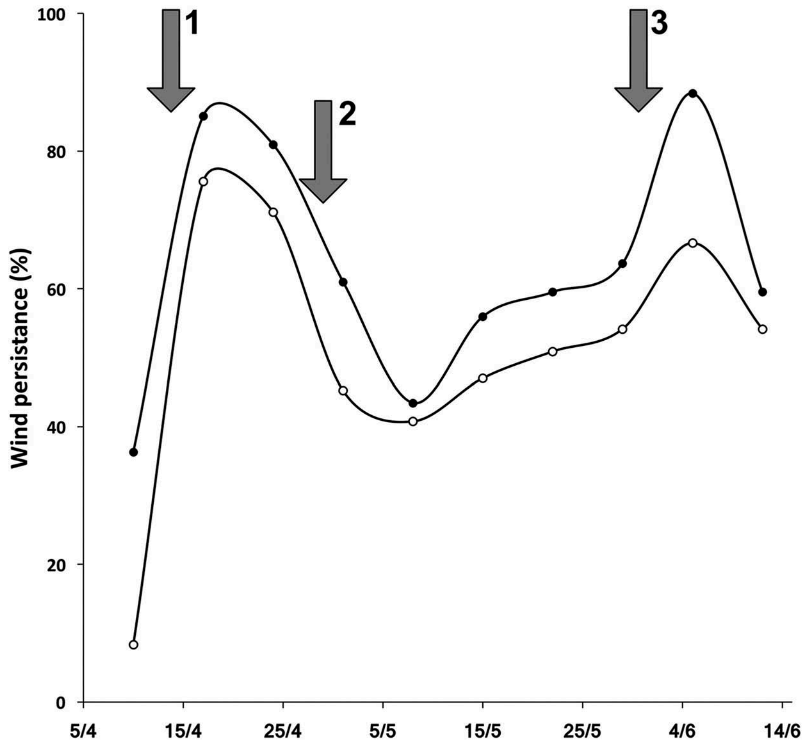

Figure 3. Percent persistence of the southern wind direction as recorded at the meteorological station of Portofino (black spots) and Arenzano (white spots). The arrows indicate the recorded strandings (1, Arenzano, Noli Cape and Santa Margherita Ligure 12-15/4/2016; 2, Santa Margherita Ligure 29/4/2016; 3, Arenzano, Noli, 27/5/2016-1/6/2016).

g WW m^{-2} corresponding to 223 g DW m^{-2}. In Arenzano and Noli, values were from 5 to 10 times lower. At Santa Margherita Ligure, 14 days after (29 April), a new stranding was recorded, with densities of about 41,000 colonies m^{-2} (Figure 4(a,b)). Although the densities were lower than half of the previous ones, the wet biomass increased to 5,700 g WW m^{-2} and the DW reached about 600 g m^{-2}. At the end of May, 44–50 days after the first appearance, other strandings occurred again at Arenzano and Noli. Also in these cases, beached colonies were fewer than in April. In Arenzano, the density was about 600 colonies m^{-2} with a WW of about 160 g m^{-2}, and a DW of 23 g m^{-2}. A similar situation was recorded in Noli Cape, with about 800 colonies m^{-2} with a WW of about 190 g m^{-2}, corresponding to 32 g m^{-2} DW (Figure 4(a,b)). No other stranding episodes were observed in 2016 in the selected sites; few days after each stranding episodes, the combination of high tides, waves and the northern winds action removed all the dead colonies from the shore.

The colony lengths, measured during the different strandings, indicated that the size-frequency distributions of the beached specimens were always unimodal in the three localities and in all considered periods, but consistently increased in the second stranding (Figure 5). From these data, it was possible to estimate the growing trend of the *V. velella* population present in the Ligurian Sea. The average size increased quickly, with an average estimated growth rate of 0.4 ± 0.02 mm per day (Figure 6). All the analyzed specimens presented the same sail orientation, left to right.

Associated fauna

During the April 2016 strandings, several specimens of two *V. velella* predators, the gastropods *Janthina pallida* (Figure 7(a,b)) and *Fiona pinnata* (Figure 7(c,d)), were recorded. The abundance of the stranded shells of *J. pallida* (at times, exceeding 500 shells m^{-2}) was strongly related with the corresponding amounts of the beached colonies of *V. velella* (Table I, Figure 8). Shell size ranged from 0.4 to 30 mm and the younger specimens were as numerous as 14 shells per each *Velella* colony (on average 4.3 ± 0.4). The nudibranch *F. pinnata* resulted much rarer, ranging from 14 ± 6 specimens m^{-2} in Arenzano to 5 ± 3 specimens m^{-2} in Santa Margherita Ligure. The cnidome analysis of the cerata, blue in color, confirmed the presence of rare intact, undischarged stenotele nematocysts, 10.3 ± 0.1 × 8.5 ± 0.2 μm in size.

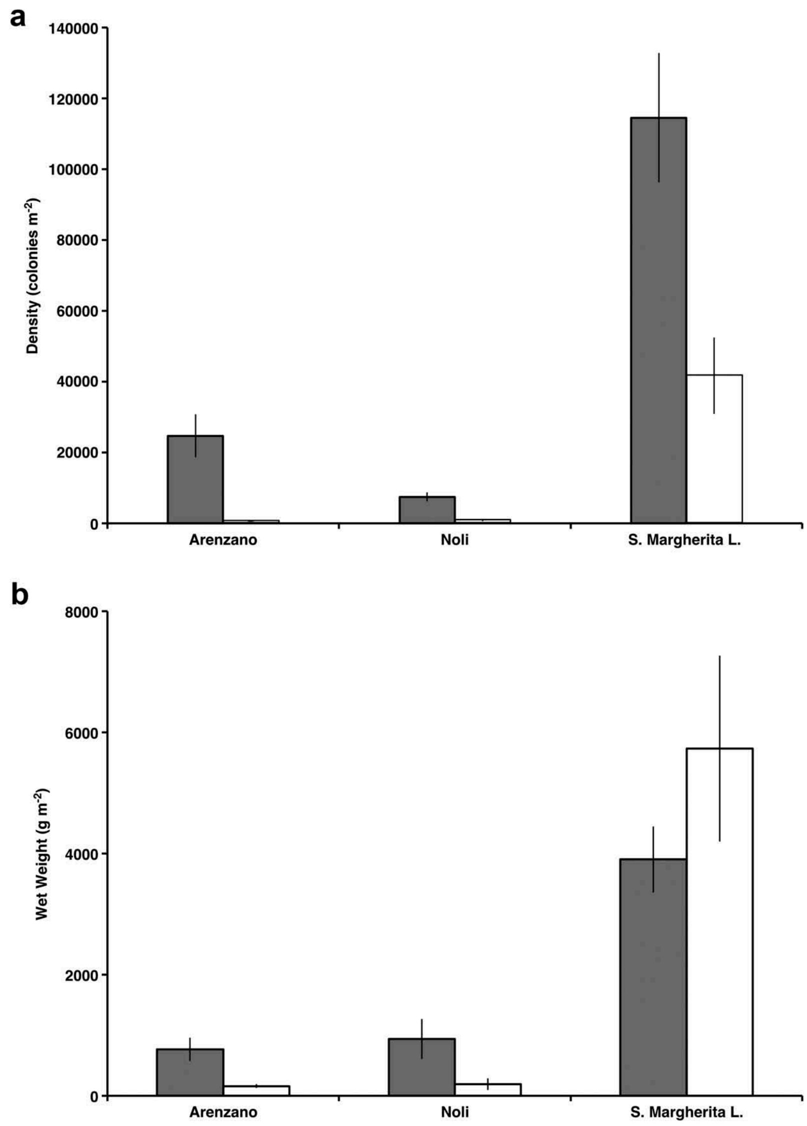

Figure 4. Average density (colonies m^{-2}) (a) and average biomass (WW m^{-2}) (b) of colonies of *Velella velella* in the studied localities during the stranding of April 2016 (grey bars) and May–June 2016 (white bars).

Discussion

The massive strandings of the hydroid *Velella velella* are driven by complex biological, oceanographic and meteorological processes, which affect its life cycle and are still largely unknown (Bieri 1977; McGrath 1994; Betti et al. 2017; Pires et al. 2018). Stochastic events, as local wind persistence in terms of intensity and direction, as well as surface circulation variability, are considered to be able to drive the structure and composition of gelatinous zooplankton assemblages and pleustonic *V. velella* in particular (Boero 1994; Benedetti-Cecchi et al. 2015; Bologna et al. 2018; Pires et al. 2018).

In the Ligurian Sea, the seasonal and spatial distributions of zooplankton are related to the physical structure of the Ligurian-Provençal Front: the main annual coastal current in the basin, up to 30 km from the shore, flows westward (Bethoux et al. 1982; Casella et al. 2011), from the Tuscany coasts towards France; it is possible to distinguish coastal and offshore zooplankton, the latter able to remain in the convergence area between the open sea and the coastal current (Boucher et al. 1987; Sournia et al. 1990; Astraldi & Gasparini 1992; Violette 1995; Millot 1999). Based on the collected data, we hypothesize that large swarms, consisting of a single cohort of colonies, may gather

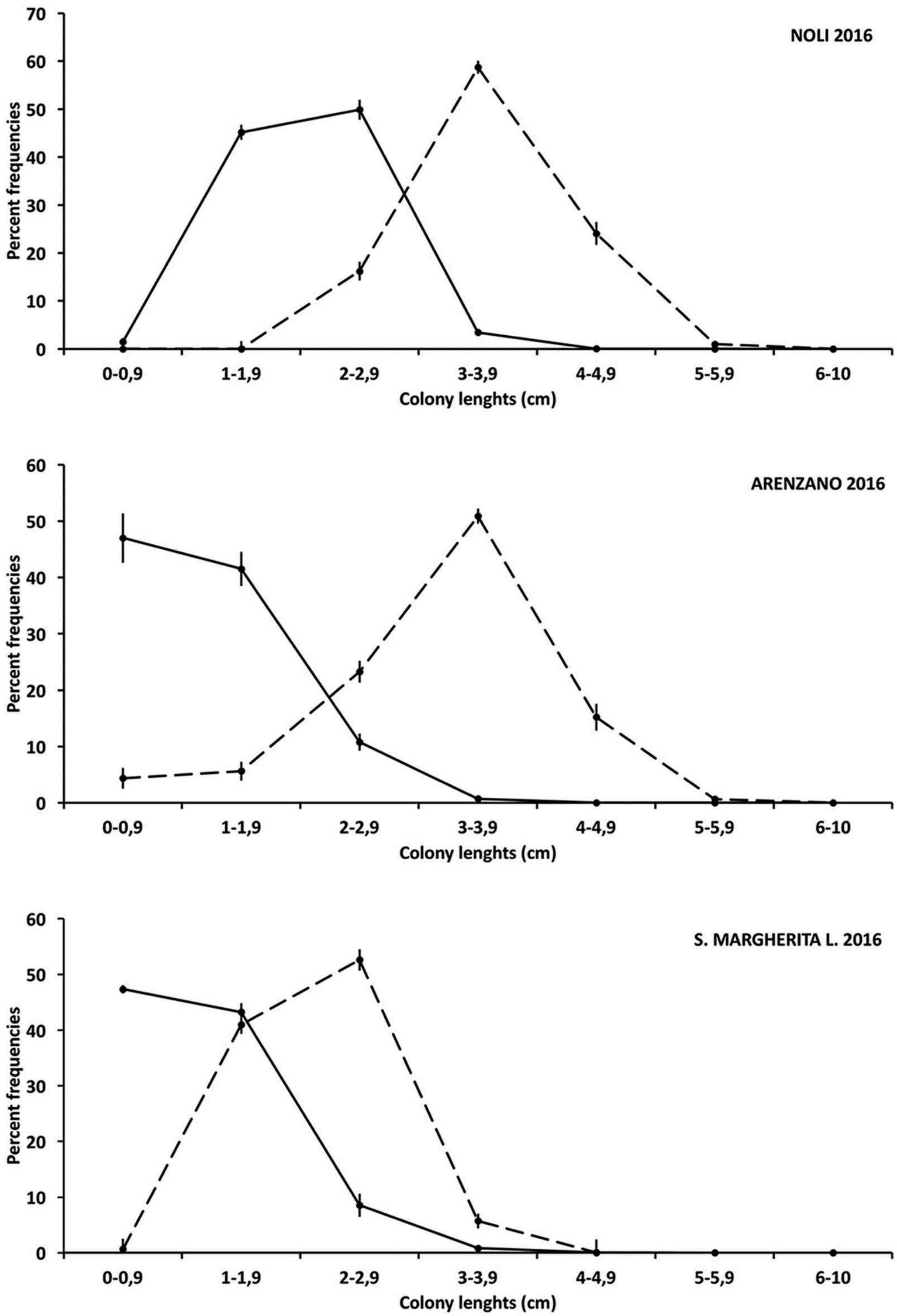

Figure 5. Percent size-frequency distributions of the pneumatophore length of beached *Velella velella* in the three studied localities. Continuous line, first beaching; dotted line, second beaching.

along this hydrological front in early spring (February–March) and be transported onshore, not subjected to the main East to West current, but moving according to the seasonal direction patterns of the predominant winds that, in the Ligurian basin, from March to June usually blow alternately from SE and N (Pensieri et al. 2018). Under these conditions, the swarms may be divided in sub-clusters, spreading out in different

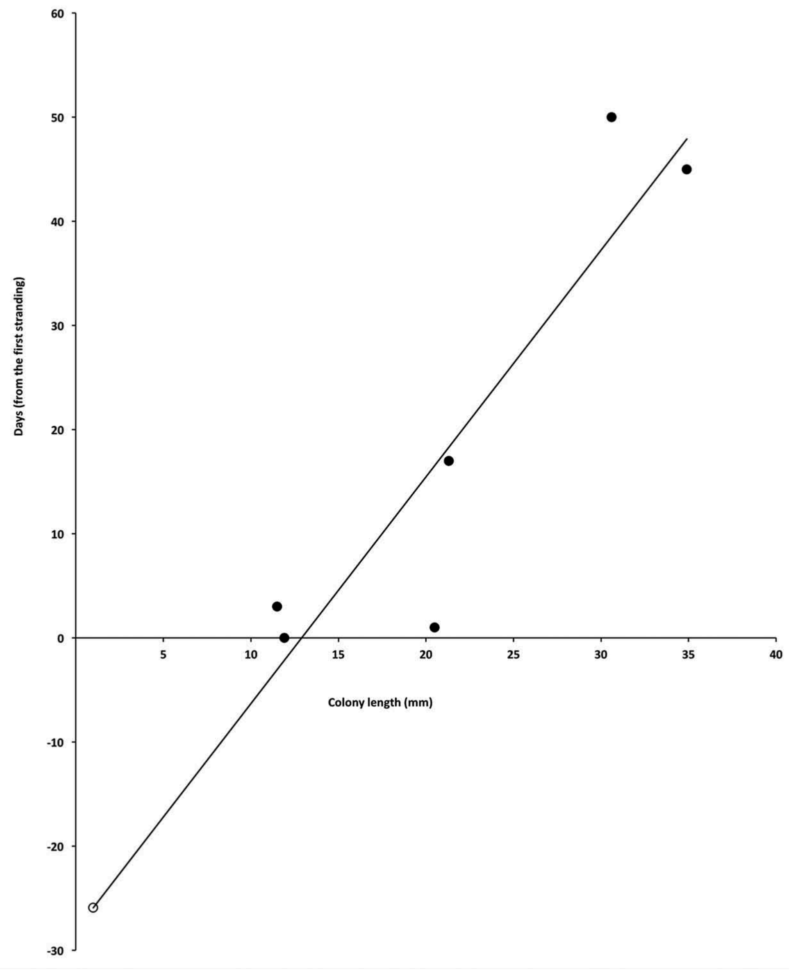

Figure 6. Average size of the colonies in all the recorded strandings (black spots) and regression line (r = 0.98) against the days from the first event. The white spot indicates the theoretical starting point of the colony growth.

periods and locations, depending on the local weather and hydrodynamic conditions (Figure 3). Seasonal strandings are punctual in this region, always under persistent southern wind conditions, but their extent is variable among years (unpublished data), due to hydrological and meteorological conditions, but plausibly also to biological constraints, which occasionally results in high biomass of other species, such as *Janthina pallida* (Betti et al. 2017).

Peaks of abundance of *V. velella* in the northern oceans are usually recorded in March (a data comparable to what is reported in the present paper), and again in August (Bieri 1977); the general lack of strandings in fall along the Ligurian coasts may be related to the different wind condition, as from July to February the dominant winds in the area come from the northern quadrant (Pensieri et al. 2018), preventing the swarms to get close to the shores.

The growing pattern of the colonies within the offshore swarm is deductible from the dimensional shift observed in the size-frequency distribution of the strandings indicating that a maximal length of 35 mm is reached in about 44–50 days. The average size of the *V. velella* colonies beached in April 2016 (11.5 ± 0.2 mm) suggests that this first stranding mainly includes young colonies, while the last stranding (end May) includes mainly adults. This trend can be also seen comparing the two consecutive strandings in Santa Margherita Ligure. The average size of the last stranded colonies is in agreement with that recorded from the Atlantic Ocean (Purcell et al. 2015) in 2013 and 2014, (33 mm and 32 mm, respectively), and slightly larger in respect to that measured by Flux (2008) from New Zealand (average 26 mm).

The colony growth rate measured in the Ligurian Sea is about 0.4 ± 0.02 mm per day, values in according with those reported by Bieri (1977) for colonies from California, with an average length increase of about 0.3–0.9 mm per day. Considering

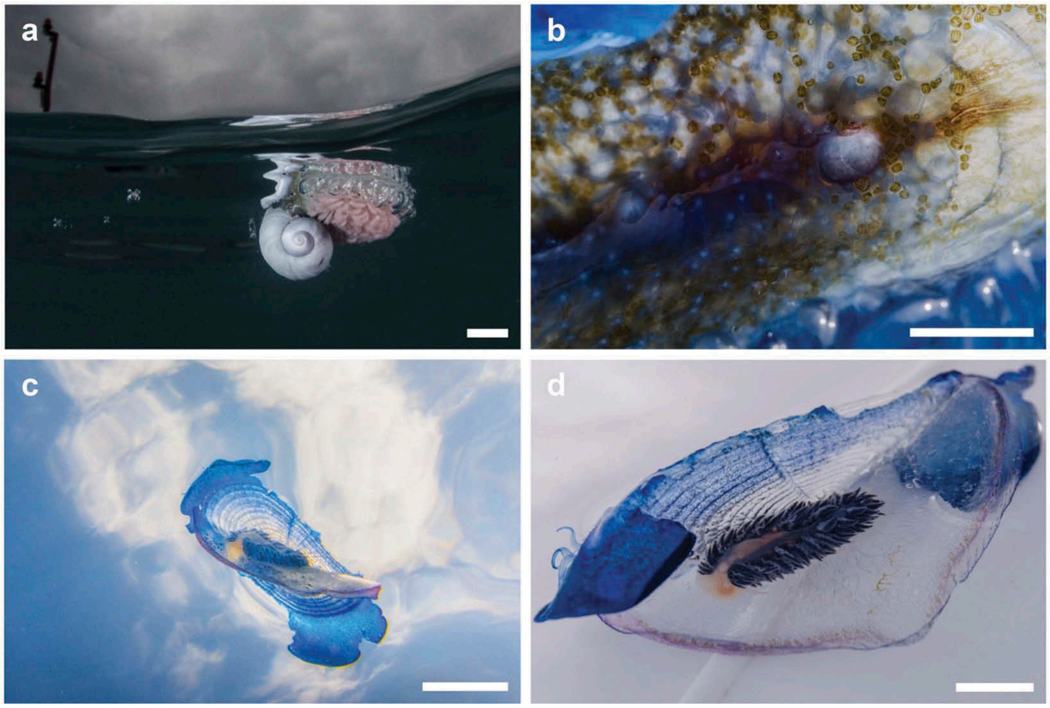

Figure 7. *Velella velella* predators. (a) *Janthina pallida* floating below its own raft. (b) A young *J. pallida* attached to the lower side of a *V. velella* colony. (c) *Fiona pinnata* eating a *V. velella* colony. (d) *F. pinnata* on *V. velella* in aquarium. Scale bars = 1 cm.

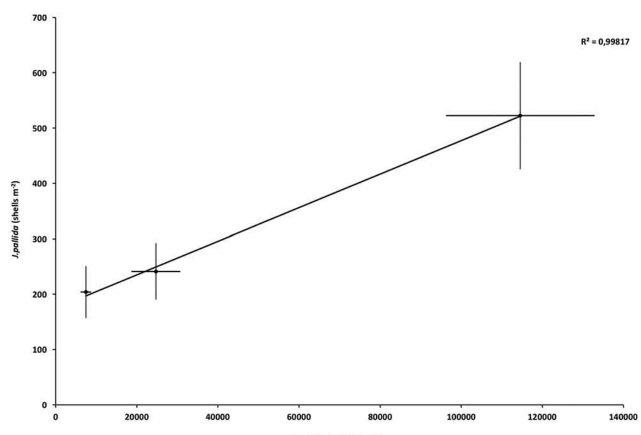

Figure 8. Relationship between the abundance of the beached colonies of *Velella velella* and that of its predator, *Janthina pallida*, in the three studied localities. *J. pallida* was observed only during the first episode.

this growth rate, it is possible to estimate that the colonies started to growth about 1 month before the first stranding, around the beginning of March (Figure 6), probably a bit later than the North Atlantic colonies (Bieri 1977).

Since all the observed colonies showed a left to right orientation of the sail, it might be possible that only that symmetry brings the specimens to the Ligurian shores, while the ones characterized by different morphologies might remain in open sea, as suggested by laboratory studies and in-field observations for other areas (Francis 1991; Gershwin 2016).

The biomasses of the Ligurian beached *V. velella* were very high, even if with lower values than the ones recorded on Pacific beaches, which reached 2.5 kg AFDW/m^2 (Kemp 1986). A relatively relevant contribution to the stranded biomass of *V. velella* is given by the associated fauna, particularly *J. pallida*. Both associated species were confirmed as important predators of the hydrozoan, with

Fiona pinnata here proven for the first time as using cleptodefences.

In conclusion, along the Ligurian coasts, excluding the accumulations of *Posidonia oceanica* dead leaves, the *V. velella* strandings appear to constitute the most important biological deposition of organic matter (mainly represented by chitin) for the entire sandy coastlines, estimated in about 250 kg DW km^{-1} and 27 kg DW km^{-1} respectively, in April and May. This impressive amount of organic matter does not remain for a long time on the beach; in fact, it is quickly dispersed by winds or washed up offshore, from night to day (Authors, pers. obs.). The possible ecological role of these remarkable and stochastic accumulations of chitin along the coast, consequently, remains unexplored.

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Disclosure statement

No potential conflict of interest was reported by the authors.

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