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Relationship between dimorphism and drift in the Portuguese man-of-war

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A B S T R A C T

One interesting feature of the Portuguese man-of-war (*Physalia physalis*) is its dimorphism, with the existence of two distinct forms (left- and right-handed individuals). The worldwide distribution of this dimorphic wind-propelled siphonophore is a much discussed but poorly understood phenomenon. Here we investigate the most likely region of origin and routes of more than 3,500 individuals of this species that were collected along the Basque coast (southeastern Bay of Biscay) in August 2010. We also test the hypothesis that most of these individuals were right-handed. To do this, we used the Sediment, Oil spill and Fish Tracking model (SOFT). From our model results, we can conclude that the region of origin of these individuals was probably located in the northern part of the North Atlantic Subtropical Gyre. The findings also suggest that our hypothesis is very likely to be correct.

1. Introduction

The Portuguese man-of-war (*Physalia physalis*) is a colonial organism that lives in warm tropical and subtropical waters (Totton and Mackie, 1960; Bardi and Marques, 2007; Mapstone, 2014; Ferrer et al., 2015; Munro et al., 2019). One interesting feature of the Portuguese man-of-war is the existence of two distinct forms (i.e., dimorphism). These two forms are mirror images of one another but otherwise identical. The dimorphism in the Portuguese man-of-war has been discussed by several researchers (e.g., Totton and Mackie, 1956, 1960; Woodcock, 1956, 1971, 1997; Bieri, 1959; Shannon and Chapman, 1983). Their observations reveal that under the influence of the wind one form (left-handed) moves to the right of the downwind direction, while the other (right-handed) to the left (see Fig. 1). Several years later, Iosilevskii and Weihs (2009) observed that the Portuguese man-of-war sailed with its float aligned with the wind direction in strong winds.

In 2010, the Atlantic and Mediterranean coasts of the Iberian Peninsula and the Canary Islands experienced their largest recorded number of Portuguese man-of-war. In August 2010, beach cleaning services collected more than 3,500 individuals along the Basque coast (southeastern Bay of Biscay). Unfortunately, there is no information on whether these individuals were left- or right-handed. Prieto et al. (2015) concluded that the meteorological and oceanographic conditions were very favourable for the occurrence of the 2010 swarm event along the Mediterranean coast. This conclusion agrees with the results obtained by Ferrer and Pastor (2017) for the Basque coast. Ferrer et al. (2015) suggested the use of a simple model based only on wind information to estimate the drift of the Portuguese man-of-war. This model was applied by Ferrer and Pastor (2017) to investigate the most likely region of origin as well as the routes of the Portuguese man-of-war that were collected along the Basque coast in August 2010 (hereafter referred to as the 2010 PMW, for simplicity). These authors concluded that the region of origin was located in the North Atlantic Subtropical Gyre (NASG, see Fig. 2(a)). In their numerical simulations, they did not consider the dimorphism in the Portuguese man-of-war.

Although many studies have been done on the Portuguese man-of-war, little information is available on issues such as its life cycle (including growth and reproduction rates, and lifespan), behaviour, ecology and dimorphism. Here we repeat the numerical simulations carried out by Ferrer and Pastor (2017) but considering the dimorphism in the Portuguese man-of-war (i.e., left- and right-handed individuals). Using a Lagrangian particle tracking model, we test the hypothesis that most of the 2010 PMW were right-handed. The results obtained from this study will improve our understanding of the distribution of this colonial organism in the North Atlantic Ocean.

2. Methods

The region of origin and routes of the 2010 PMW were estimated using the Sediment, Oil spill and Fish Tracking model (SOFT). This Lagrangian particle tracking model includes a new version of the equation used by Ferrer and Pastor (2017), in which the drift of a Portuguese man-of-war can be estimated by:

$$\mathbf{U}_D = C_D \cdot \mathbf{U}_{W,\theta} = C_D \cdot U_{W,\theta} + C_D \cdot V_{W,\theta} \quad (1)$$

where $\mathbf{U}_D = (U_D, V_D)$ is the drift velocity vector, C_D is the wind drag

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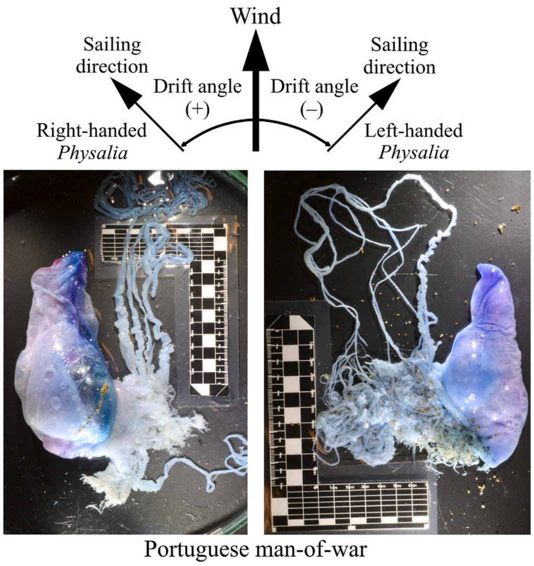


Fig. 1. Sailing directions of right- and left-handed *Physalia*. Photographs by Nagore Zaldua-Mendizabal.

coefficient and $\mathbf{U}_{W,\theta} = (U_{W,\theta}, V_{W,\theta})$ is the wind velocity vector at 10 m height rotated a drift angle θ about the wind direction. The direction of rotation is anticlockwise if θ is positive (for right-handed individuals) and clockwise if θ is negative (for left-handed individuals).

In our numerical simulations with SOFT, we used Eq. (1) with the hourly wind fields provided by the operational forecasting system developed by MeteoGalicia (meteorological agency of Galicia) for the years 2009 and 2010. These wind fields, with a spatial resolution of 36 km (see the oceanic grid points of the model domain in Fig. 2(b)), were obtained using the Weather Research and Forecasting model (WRF). More detailed information about WRF is available in Skamarock et al. (2005). We also used a C_D value of 0.045, which is the maximum value proposed by Ferrer and Pastor (2017) in their numerical simulations. Recent results obtained with SOFT using data from small surface drifting buoys (not shown) indicate that this proposed C_D value may be appropriate for studies assessing the drift of small floating objects.

Regarding the drift angle, eight values were used considering the results previously obtained by other researchers (Totton and Mackie, 1956, 1960; Woodcock, 1956, 1997): $+45°$, $+33.75°$, $+22.5°$ and $+11.25°$ for right-handed (left-sailing) individuals, and $-11.25°$, $-22.5°$, $-33.75°$ and $-45°$ for left-handed (right-sailing) individuals. To summarize the model results, those obtained using drift angles of $+45°$, $+22.5°$, $-22.5°$ and $-45°$ are shown and described in depth in the following section, while those obtained using drift angles of $+33.75°$, $+11.25°$, $-11.25°$ and $-33.75°$ are briefly discussed. SOFT was run backwards in time to estimate the most likely region of origin and routes (or trajectories) of the 2010 PMW. In the simulations, two virtual individuals were released every day in August 2010 at 00:00 and 12:00 UTC, respectively. The initial location of these individuals (at about 10 km from the Basque coast) is shown in Fig. 2(b).

The full details of the reproduction and growth rate of the Portuguese man-of-war are still unknown. The maximum lengths of the float and tentacles of the few individuals examined in the 2010 event were 20 cm and 50 cm, respectively. If its growth rate is approximately 3 cm per month (Kennedy, 1972), its lifespan could be around one year. This means that its reproduction could occur between summer and autumn. For this reason, each virtual Portuguese man-of-war was moved backwards in time using SOFT for one year. Therefore, the simulation period lasted from the end of August 2010 to the beginning of August 2009.

The trajectories obtained with SOFT from the end of August to the beginning of January 2010 were plotted separately from those obtained from the end of December to the beginning of August 2009. The end points of these trajectories in August 2009 are the locations of our virtual individuals at the initial stage of development (i.e., at the age of 0 days). The end points located in the open North Atlantic Ocean were used to approximately delimit the region of origin of the 2010 PWM, while those located on the coast were discarded as possible points of origin.

3. Results

In total, 62 trajectories of virtual Portuguese man-of-war were obtained in each simulation, starting near the Basque coast. The trajectories obtained with SOFT using a wind drag coefficient of 0.045 and drift angles of $+45°$ and $+22.5°$ for right-handed (left-sailing) individuals are shown in Fig. 3, while those obtained using drift angles of $-22.5°$ and $-45°$ for left-handed (right-sailing) individuals are displayed in Fig. 4. The end points of these trajectories are shown in Figs. 5 and 6. The trajectories of the second part of the simulation period (Fig. 3(b), (d), 4(b) and (d)) start at the end points of the trajectories of the first part of the simulation period (Fig. 5(a), (c), 6(a) and (c)).

During the first part of the simulation period (i.e., from the end of August to the beginning of January 2010) and with drift angles of $+45°$ and $+22.5°$, the routes of the virtual Portuguese man-of-war released near the Basque coast covered a large geographical area, which included the Bay of Biscay, the Celtic Sea and a small part of the open Atlantic Ocean (43.2°–52.2° N, 2.7°–14.5° W, see Fig. 3(a) and (c)). With a drift angle of $-22.5°$, the drift occurred in a slightly different area, which also included the English Channel and the northwest coast of France (43.4°–51.8° N, 0.7°–13.7° W, see Fig. 4(a)). However, with a drift angle of $-45°$, this drift was confined to a smaller area in the eastern part of the Bay of Biscay, which included much of the French coast (43.3°–48.2° N, 1.5°–5.4° W, see Fig. 4(c)).

During the second part of the simulation period (i.e., from the end of December to the beginning of August 2009), there was a change in the drift velocity of our virtual Portuguese man-of-war due to a change in the wind velocity. At the end of the simulation period and with drift angles of $+45°$ and $+22.5°$, all the virtual Portuguese man-of-war released near the Basque coast were located in the open North Atlantic Ocean (37.8°–43.8° N, 18.6°–24.7° W, see Fig. 5(b) and (d)). However, with drift angles of $-22.5°$ and $-45°$, 45.2% and 4.8% of the virtual Portuguese man-of-war, respectively, were located in the open North Atlantic Ocean (46.1°–52.1° N, 14.7°–35° W) and the rest on the coasts of the British Isles and France (46.4–51.8° N, 0.7–8.1° W, see Fig. 6(b) and (d)). In these latter two cases, 30.6% and 3.2% of the virtual Portuguese man-of-war, respectively, were located at 35° W, with ages between 5.3 and 41.6 days. This means that their region of origin was probably located much farther west.

For the virtual Portuguese man-of-war released on 31 August 2010 at midday, we analysed the drift and wind velocities from the end of August 2009 to the end of August 2010 along the trajectory obtained using a drift angle of $+45°$ (Fig. 7). This right-handed individual was located at 40° N and 19.1° W on the last simulation day. The zonal and meridional components of its drift velocity, U_D and V_D, respectively, are displayed in Fig. 8. The values of U_D and V_D ranged between -88 cm s^{-1} and 96 cm s^{-1}. The mean values of these components were higher in the second part of the simulation period (8 cm s^{-1} and 10 cm s^{-1},

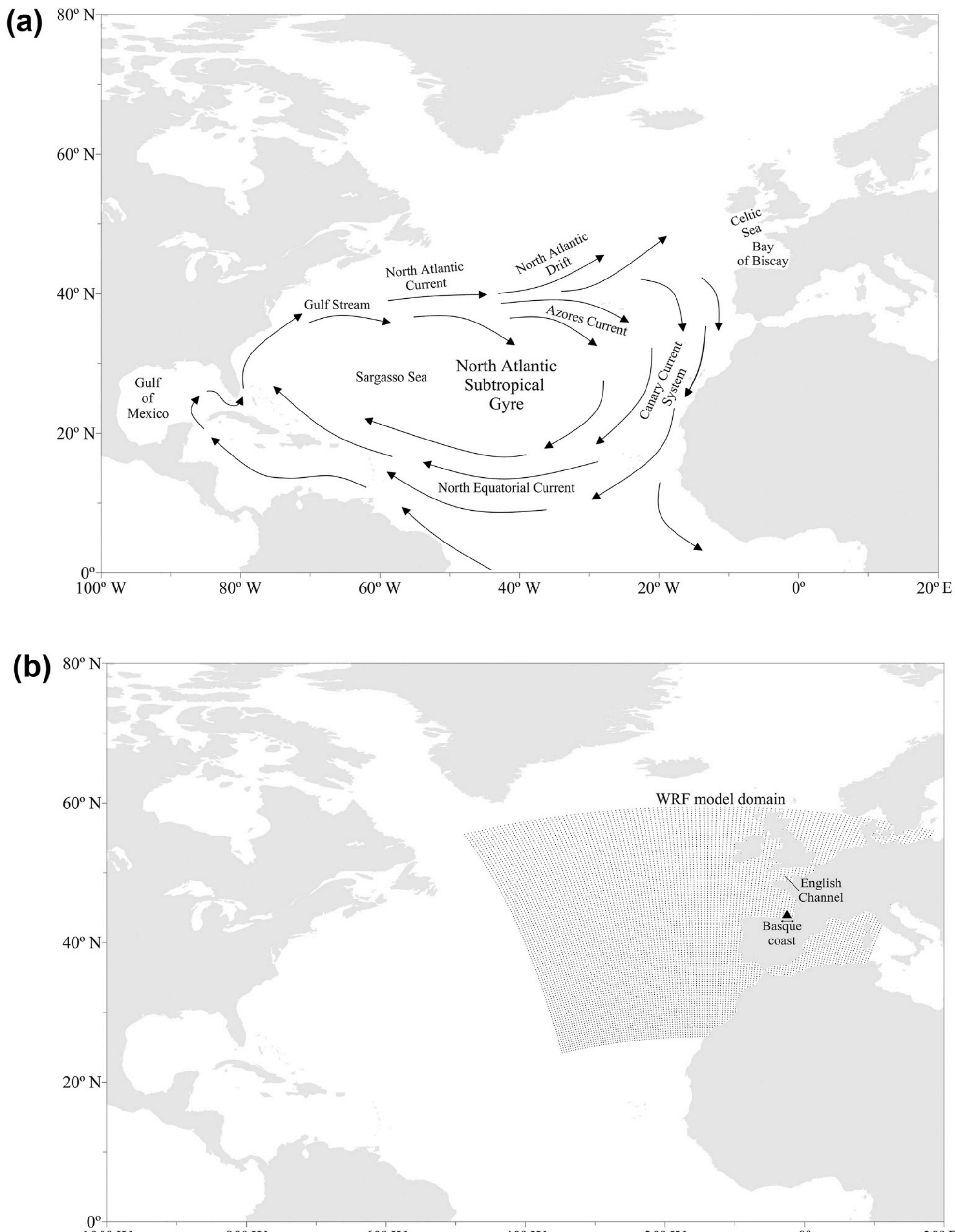


Fig. 2. (a) General surface ocean circulation in the North Atlantic Subtropical Gyre, adapted from Ferrer and Pastor (2017). (b) Oceanic grid points of the WRF model domain. The black triangle indicates the initial location (near the Basque coast) of the virtual Portuguese man-of-war used in SOFT.

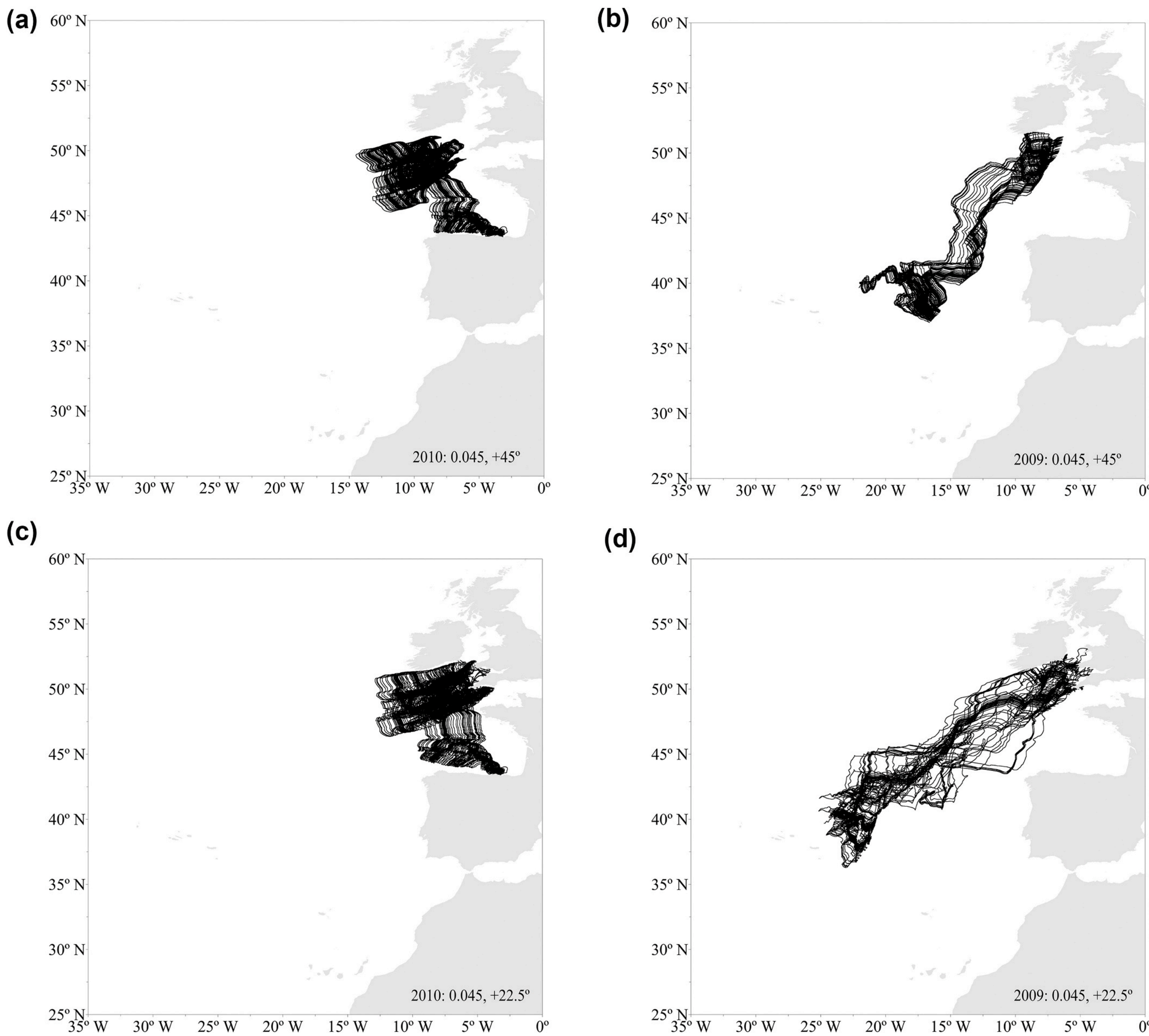


Fig. 3. Trajectories of 62 virtual Portuguese man-of-war obtained with SOFT using a wind drag coefficient of 0.045 and the following drift angles: (a, b) +45°; and (c, d) +22.5°. The results obtained from the end of August to the beginning of January 2010 (a, c) are plotted separately from those obtained from the end of December to the beginning of August 2009 (b, d).

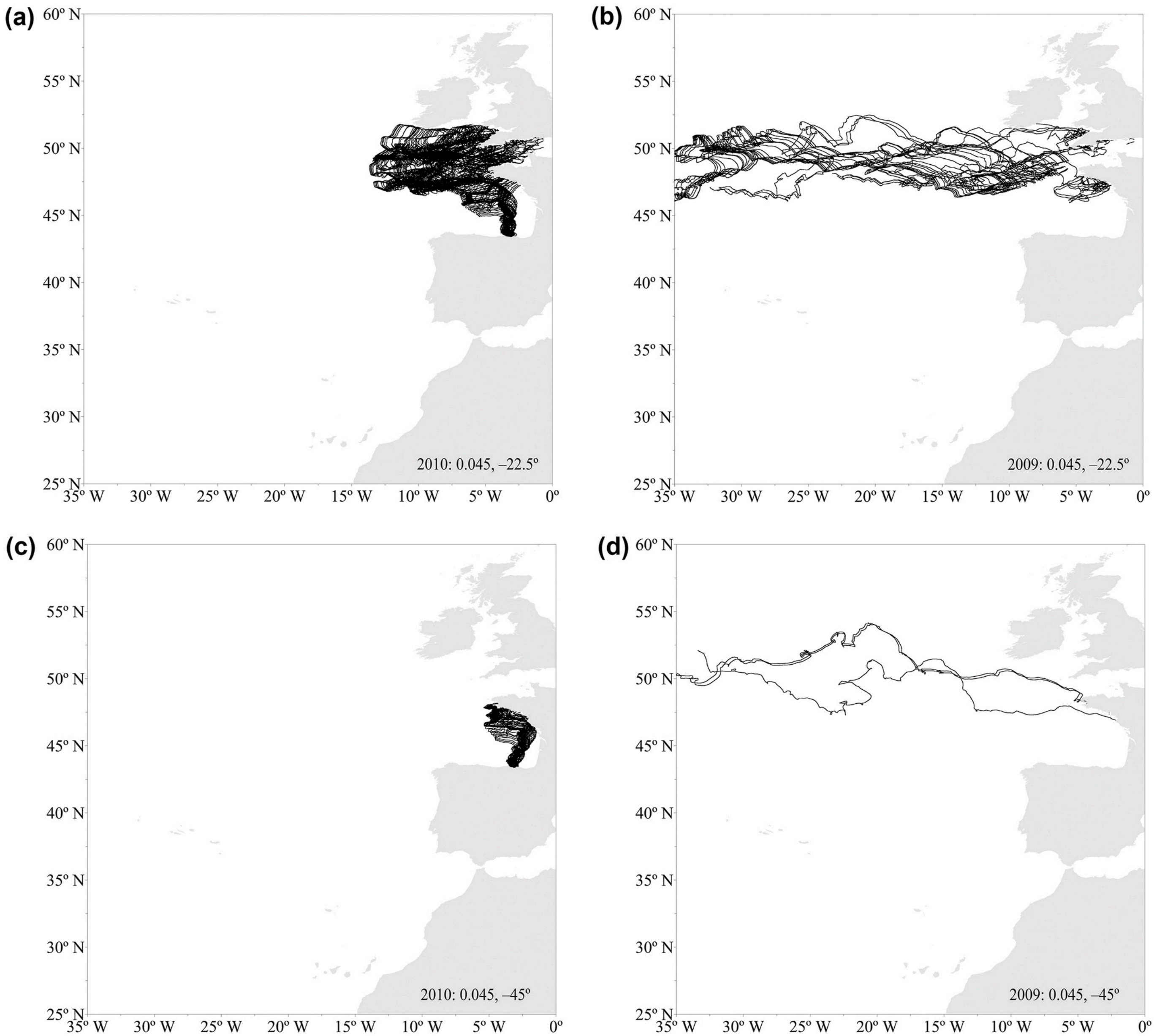


Fig. 4. As in Fig. 3, but using the following drift angles: (a, b) $-22.5°$; and (c, d) $-45°$.

respectively) than in the first part (2 cms^{-1} and –3 cms^{-1}, respectively), reflecting the aforementioned change in the drift velocity.

Regarding the values of $U_{W,+45°}$ and $V_{W,+45°}$ along the trajectory shown in Fig. 7, these ranged between -70.4 kmh^{-1} and 76.8 kmh^{-1}. The mean values of $U_{W,+45°}$ and $V_{W,+45°}$ were higher in the second part of the simulation period (6.2 kmh^{-1} and 8 kmh^{-1}, respectively) than in the first part (1.9 kmh^{-1} and –2.3 kmh^{-1}, respectively), showing a change in the wind velocity. On average, the right-handed individual of Fig. 7 drifted northeastwards from the end of August to the end of December 2009, and then drifted southeastwards from the beginning of January to the end of August 2010. The distance (total length of the trajectory) travelled by this Portuguese man-of-war from the open North Atlantic Ocean to the Basque coast was about 11,121 km. For the same virtual Portuguese man-of-war and with a drift angle of 0°, Ferrer and Pastor (2017) obtained a value for this distance of 11,798 km.

The end points of the simulated trajectories in August 2009 (Fig. 5 (b), (d), 6(b) and (d)), and those obtained using drift angles of $+33.75°$, $+11.25°$, $-11.25°$ and $-33.75°$, are displayed in Fig. 9. Only the end points located in the open North Atlantic Ocean are shown in this figure. The analysis of the data used in Fig. 9 show that the number of virtual right-handed individuals in open waters, N_R, was about 2.5 times larger than the number of virtual left-handed individuals, N_L. This N_R/N_L ratio was obtained assuming that the region of origin of the Portuguese man-of-war was located somewhere below latitude 52.1° N (the maximum latitude of the end points). If this region were located far below this latitude, N_L would decrease, and the N_R/N_L ratio would increase substantially.

From our model results, we can conclude that the region of origin of the 2010 PMW was probably located in the northern part of the NASG. In this region, the number of Portuguese man-of-war was strongly dependent on the latitude: the lower the latitude, the larger the number of Portuguese man-of-war. At lower (higher) latitudes, the individuals were right-handed (left-handed). Assuming that the Portuguese man-of-war is especially common in warm tropical and subtropical waters

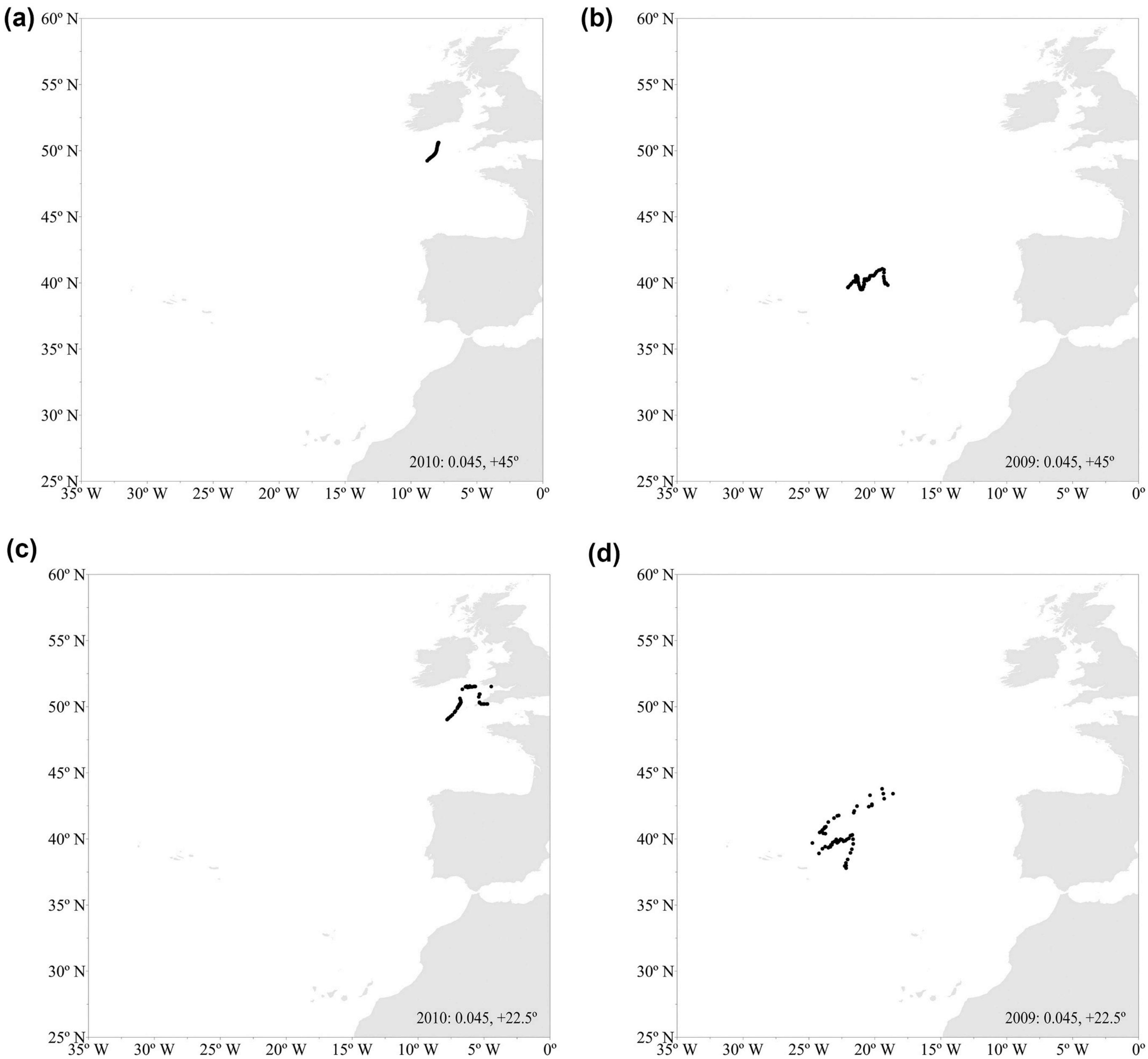


Fig. 5. End points of the trajectories obtained with SOFT using a wind drag coefficient of 0.045 and the following drift angles: (a, b) +45°; and (c, d) +22.5°. The results obtained at the beginning of January 2010 (a, c) are plotted separately from those obtained in August 2009 (b, d).

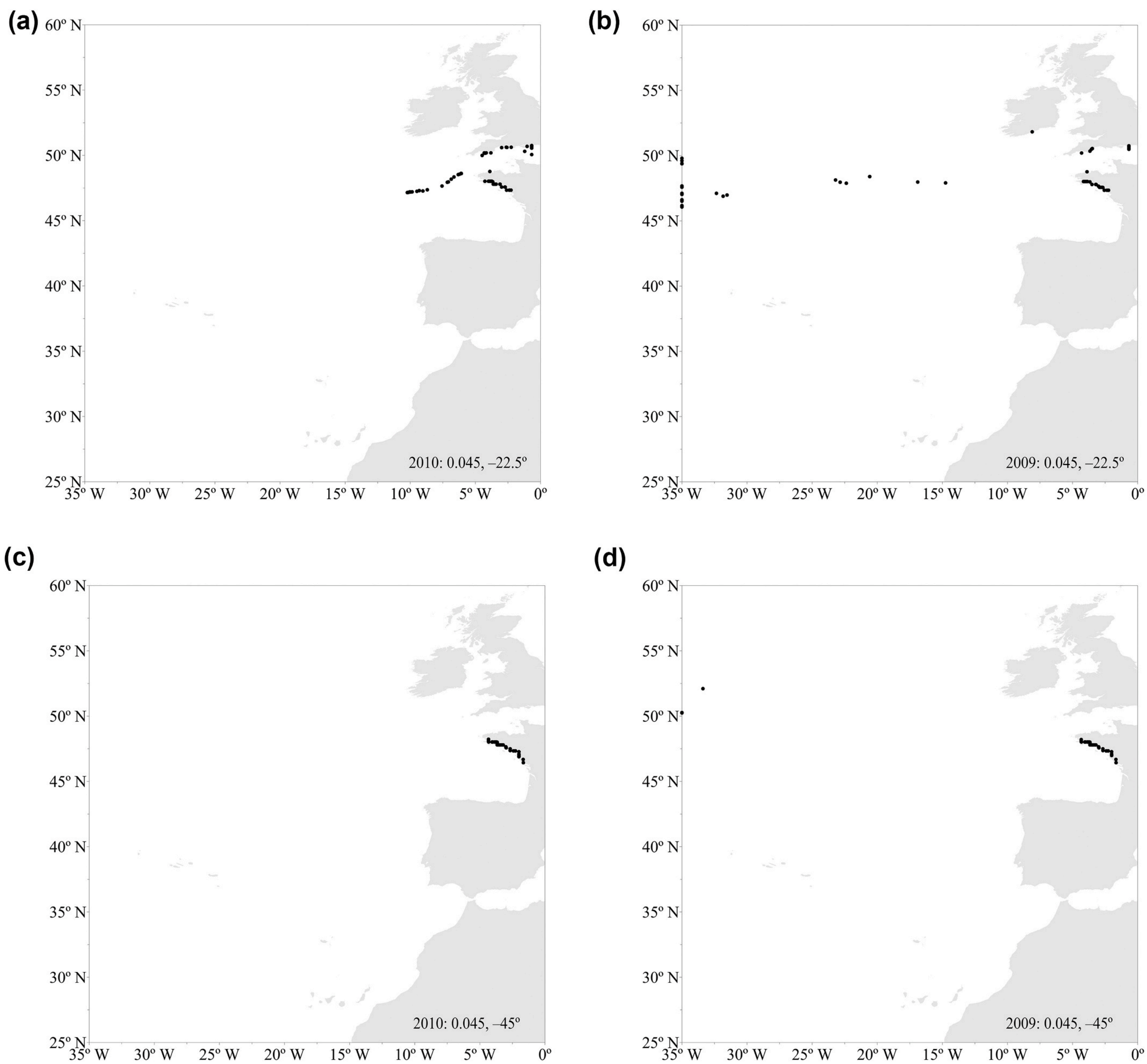


Fig. 6. As in Fig. 5, but using the following drift angles: (a, b) −22.5°; and (c, d) −45°.

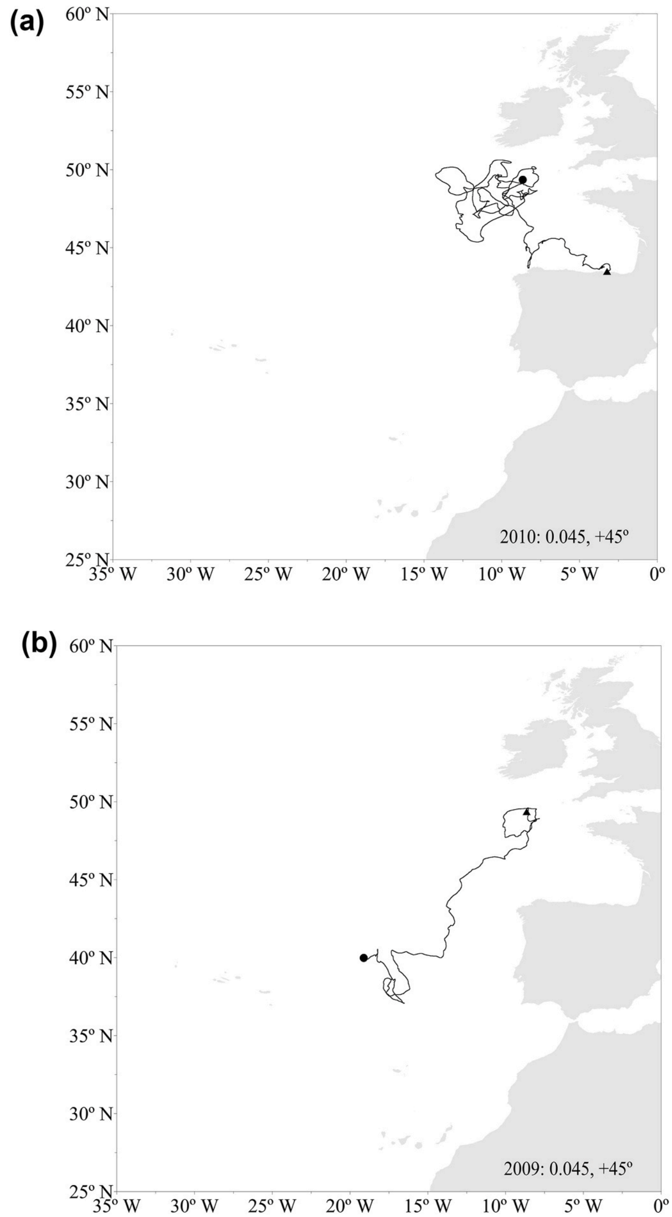


Fig. 7. Trajectory of the virtual Portuguese man-of-war released on 31 August 2010 at midday, obtained with SOFT using a wind drag coefficient of 0.045 and a drift angle of +45°: (a) from the end of August (black triangle) to the beginning of January 2010 (black circle); and (b) from the end of December (black triangle) to the end of August 2009 (black circle).

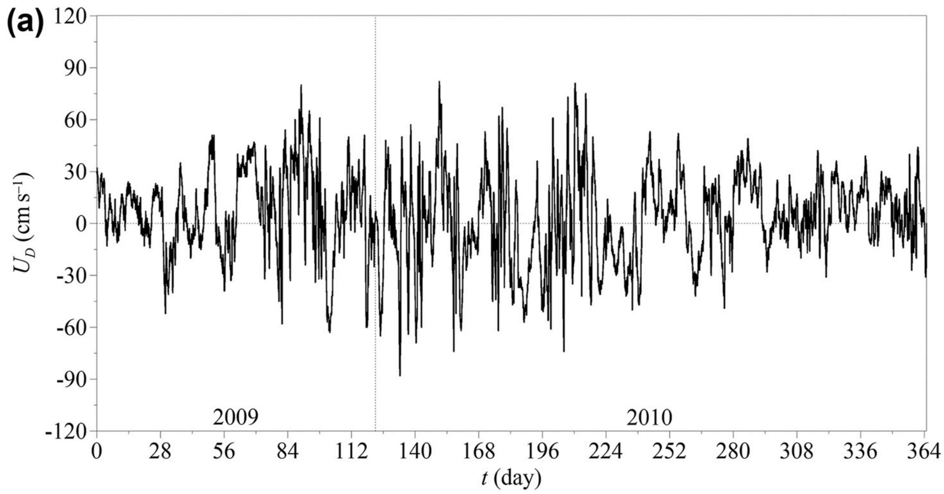
(i.e., from the Equator to latitude 40° N in the North Atlantic Ocean), our findings also suggest that most of the 2014 PMW were right-handed.

4. Discussion

Several studies have demonstrated the complexity of surface ocean currents (e.g., Ursell, 1950; Longuet-Higgins, 1953, 1960; Hasselmann, 1970; Pollard, 1970; Huang, 1979; Wu, 1983; Jenkins, 1989; Perrie et al., 2003; Tang et al., 2007; Sotillo et al., 2008; Song, 2009; Abascal et al., 2009, 2012; Ferrer et al., 2015). The main conclusion of these studies is that the effects of winds and waves on these currents are significant and can substantially change the nature of the Ekman layer (Ekman, 1905).

Following the suggestion of Ferrer et al. (2015), here we used a simple model based only on wind information to investigate the most likely region of origin as well as the routes of the 2010 PMW. We simulated the drift of virtual left- and right-handed individuals in order to test our initial hypothesis.

The first conclusion we can draw from our results is that the region of origin of the 2010 PMW was probably located in the northern part of the NASG. This conclusion agrees with the results obtained by Ferrer and Pastor (2017). In our case, the region of origin is larger than the one obtained by these authors, because in our numerical simulations we considered the dimorphism in the Portuguese man-of-war. The general surface ocean circulation in the NASG (Laiz et al., 2012; Putman and He, 2013) supports this conclusion, because the wind is the main mechanism controlling this circulation in the upper centimetres of the water column. In their discussion, Ferrer and Pastor (2017) pointed out that the Sargasso Sea, which is located entirely within the NASG (see Fig. 2(a)), could probably be a region with a high concentration of Portuguese man-of-war. From here, the Portuguese man-of-war would drift towards the shores of America and Europe. Many researchers have confirmed



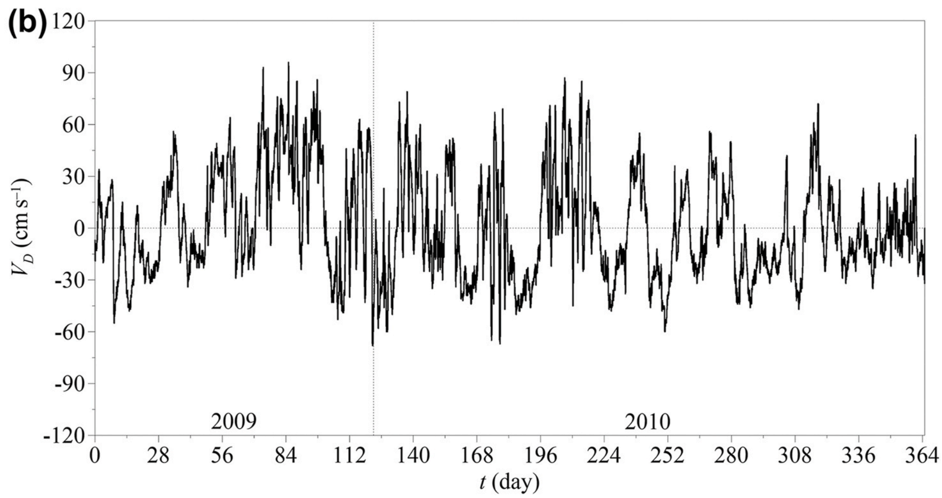


Fig. 8. Drift velocity along the trajectory shown in Fig. 7, from the end of August 2009 to the end of August 2010: (a) zonal component, U_D; and (b) meridional component, V_D.

that the wind plays a central role in the drift of the Portuguese man-of-war. For example, the occurrence of Portuguese man-of-war on the coast of the British Isles in March and the early part of April 1912 and in the summer of 1945 was analysed and discussed by Orton (1913) and Wilson (1947), respectively. These authors concluded that the wind was the main factor in transporting the swarms of Portuguese man-of-war towards the British Isles. Wilson (1947) considered it likely that the 1945 swarms came from the Azores-mid-Atlantic region rather than from the Canaries-Gibraltar district. Other surface organisms (*Lepas fascicularis*, *Lepas pectinata* and some *Velella velella*) and a few turtles (*Caretta caretta*) were associated with these swarms and could have come under the same meteorological influences as the Portuguese man-of-war. *Velella* is another dimorphic wind-propelled sea animal (Bieri, 1959; Francis, 1991).

The second conclusion of this study is that our initial hypothesis (i.e., most of the 2010 PMW were right-handed) is very likely to be correct. This conclusion is based on the numbers of virtual left- and right-handed individuals (N_L and N_R, respectively) located in the open North Atlantic Ocean at the end of the simulation period. With negative drift angles (i.e., left-handed individuals), N_L decreased substantially. In the future, the visual inspection of the Portuguese man-of-war coming from the open ocean will allow us to corroborate this conclusion. Obviously, the numbers of left- and right-handed individuals in a specific coastal area depends on the drift angle. If this drift angle is around 0°, these numbers will be similar. Considering the results reported by Iosilevskii and Weihs (2009), it seems reasonable to expect the drift angle to vary with the wind speed and over the lifespan of the Portuguese man-of-war, because there will be a significant increase in the size of this colonial organism.

This investigation was undertaken to gain more precise knowledge of the effect of dimorphism on the drift of the Portuguese man-of-war. The findings obtained after running SOFT backwards in time for a year support our initial hypothesis and highlight the growing importance of using numerical models in science. Although little information exists on the life cycle of the Portuguese man-of-war, some progress has been made over the last decade (Mapstone, 2014; Prieto et al., 2015; Ferrer et al., 2015; Ferrer and Pastor, 2017; Munro et al., 2019). However, there is still a long way to go before the behaviour of this colonial organism is fully understood.

5. Conclusions

In August 2010, beach cleaning services collected more than 3,500 Portuguese man-of-war along the Basque coast (southeastern Bay of Biscay). Using the Sediment, Oil spill and Fish Tracking model (SOFT), we investigated the most likely region of origin and routes of these individuals. In our numerical simulations, we considered the dimorphism in the Portuguese man-of-war. From our model results, we can conclude

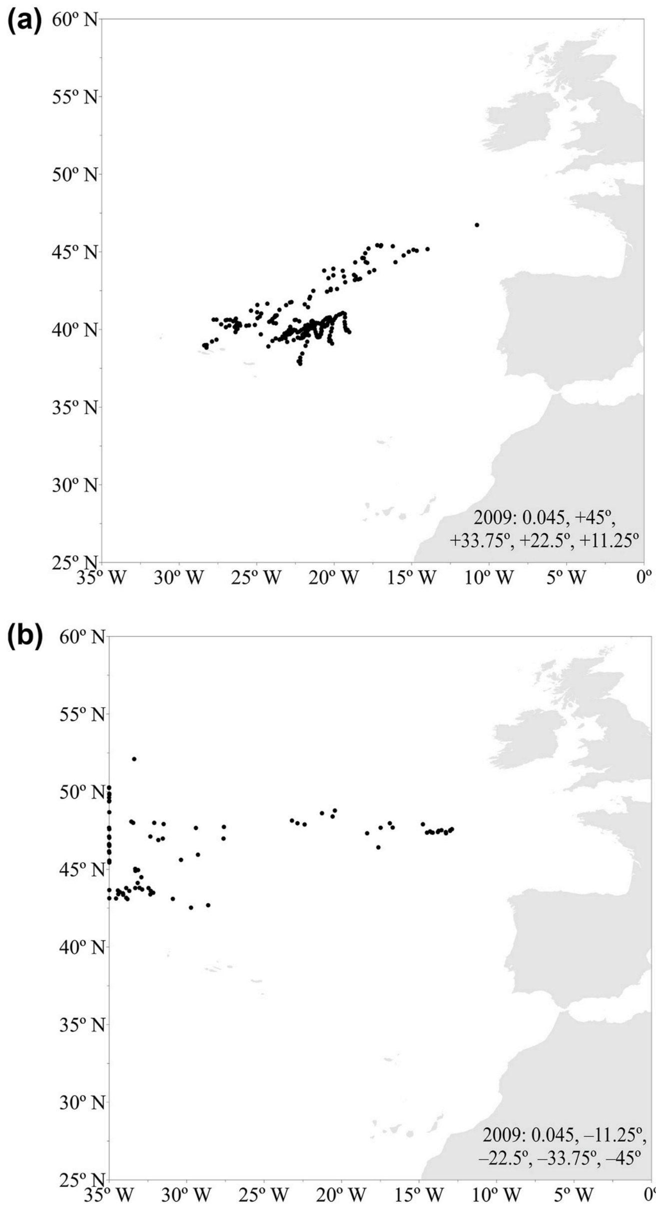


Fig. 9. End points of the trajectories obtained with SOFT using a wind drag coefficient of 0.045 and the following drift angles: (a) +45°, +33.75°, +22.5° and +11.25°; and (b) −11.25°, −22.5°, −33.75° and −45°. Only the end points located in the open North Atlantic Ocean in August 2009 are shown here.

that the region of origin of these individuals was probably located in the northern part of the North Atlantic Subtropical Gyre. Our findings also suggest that most of these individuals were right-handed. Further research with field data should be conducted in the future to investigate the dimorphism in the Portuguese man-of-war coming from the open North Atlantic Ocean.

CRediT authorship contribution statement

Luis Ferrer: Conceptualization, Methodology, Software, Formal analysis, Investigation, Writing - original draft, Writing - review & editing, Visualization, Supervision. **Manuel González:** Methodology, Software, Formal analysis, Resources, Data curation, Writing - review & editing.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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