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Links Between Lagrangian Connectivity, Thermal Thresholds and Genetic Structure in the Floating Marine Siphonophore *Physalia*

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ABSTRACT

Aim: To investigate whether genetically distinct species of *Physalia* differ in dispersal behaviour and environmental exposure, and to assess the role of large-scale wind–ocean transport in shaping their genetic structure.

Location: Tropical and subtropical oceans where *Physalia* strandings and distributions overlap.

Time Period: One-year drift simulations, based on recent genetic sampling between 2006 and 2023 and reanalysis datasets.

Major Taxa Studied: *Physalia* (Portuguese Man O' War/Bluebottle), a colonial hydrozoan genus comprising five genetically distinct species.

Methods: We combined genetic identification of 125 individuals from five lineages with numerical Lagrangian particle backtracking. Drift trajectories were simulated using oceanic and atmospheric reanalysis fields, with an experimentally derived drift parameterization that accounts for *Physalia*'s asymmetric morphology and wind-driven motion. Connectivity metrics derived from simulated transport were compared with observed genetic differentiation.

Results: Drift simulations revealed strong lineage-specific differences in dispersal and temperature exposure. Average sea surface temperature along drift paths ranged from 15°C for *Physalia minuta* to 28°C for *Physalia mikazuki*. Genetic differentiation within lineages was significantly associated with dispersal connectivity: the combination of geographic distance and Lagrangian transport explained up to 57% of variance in genetic distance.

Main Conclusions: Wind–ocean transport is a key driver of both environmental exposure and genetic structure in *Physalia*. Differences in dispersal pathways expose lineages to distinct thermal regimes, with implications for ecology and biogeography. As climate change alters wind fields, currents and ocean temperatures, connectivity and thermal habitats will shift in lineage-specific ways, potentially reshaping the distribution and evolutionary trajectories of *Physalia* species.

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1 | Introduction

Patterns of genetic structure in marine species are influenced by the interaction between life history traits and oceanographic variability. Oceanic features such as currents, eddies and frontal zones can reduce gene flow by acting as barriers to dispersal and isolating populations (e.g., Weersing and Toonen 2009; Gilg and Hilbish 2003). At the same time, these features act as long-distance corridors, facilitating dispersal events across remote regions (e.g., Mitarai et al. 2009; Roughan et al. 2011). Additionally, ocean currents influence ocean temperatures, which in turn shape thermal habitats and affect species' physiological thresholds. Approaches to studying seascape connectivity depend on how organisms interact with their environment. Some species, such as benthic invertebrates or demersal fish, live on the sea-floor for part of their life cycle, while many marine vertebrates are active swimmers capable of overcoming or selectively using ocean currents (Hays 2017). In contrast, *Physalia*, also known as Portuguese Man O' War or bluebottle, have little locomotor ability and drift quasi-passively at the air-sea interface, relying mainly on wind, surface currents and wave induced motion for transport (Totton 1960). The lack of strong self-propelled movement in *Physalia* offers a rare opportunity to isolate the role of large-scale physical forcing in shaping genetic connectivity across ocean basins.

Frequent strandings and interactions with fisheries and swimmers make *Physalia* a familiar presence along many coastlines. They often wash ashore in swarms in tropical and subtropical regions, stinging beach-goers (with occasional suspected fatalities; (Burnett and Gable 1989; Prieto et al. 2015)), clogging fishing nets and threatening farmed fish (Mitchell et al. 2021). Yet, despite their visibility and impact, surprisingly little is known about their population dynamics, habitat preferences or open-ocean distributions. The current lack of information on their habitat preferences, particularly their tolerated and optimal temperature ranges, makes it difficult to predict how *Physalia* might respond to changing ocean conditions (e.g., currents and temperatures). This is interesting as recent work links warmer ocean temperatures with increased siphonophore diversity and biomass (Park et al. 2023). Besides, because pathways of *Physalia* are almost entirely dictated by atmospheric and oceanic forces, we can expect the predicted and already observed changes in global wind patterns and ocean currents to strongly impact *Physalia* population dynamics, either by enhancing mixing between previously isolated populations or, conversely, by displacing them into regions they do not typically inhabit.

Observing the drift and dispersal of *Physalia* in the open ocean is extremely challenging. Animal tagging has greatly expanded our understanding of habitat use and movement in large, mobile marine species such as chinstrap penguins and elephant seals (e.g., Carter et al. 2022; Wilson et al. 2025), and more recently in smaller gelatinous organisms (e.g., Sauviat et al. 2025; Diamant et al. 2023). However, these approaches are not applicable to *Physalia*, which are too fragile and lightweight to carry tracking devices without affecting their motion. Drone-based monitoring has been used to detect jellyfish aggregations from the surface, but this method is limited to local observations of short duration, cannot resolve long-distance trajectories and has not been proven successful for *Physalia* detection (Rowe

and Ah Yong 2024; Lehahn et al. 2025). As a result, numerical modelling is the most viable approach to investigate the global dispersal of *Physalia*. Lagrangian tracking is a tool used to model and study pathways of passive particles in the ocean, and it can be adapted to different objects such as plastic debris, oil spills, survival crafts (e.g., Baudena et al. 2022; Sayol et al. 2014; Breivik and Allen 2008) but also larvae of many marine species (e.g., Cetina-Heredia et al. 2019; Coleman et al. 2011; Roughan et al. 2011). Biophysical models have been increasingly used to simulate the transport of various marine organisms and test the influence environmental drivers on spatial patterns of genetic structure (e.g., Quigley et al. 2022; Durrant et al. 2018; Jahnke and Jonsson 2022) and how this might change in the future (e.g., Cetina-Heredia et al. 2015; Coleman et al. 2017).

However, applying this approach to *Physalia* is challenging due to *Physalia*'s complex morphology. Each individual is composed of a gas-filled 'float' that keeps them at the surface, an underwater 'bulge' housing digestive and reproductive zooids, and long trailing tentacles used for prey capture (Totton 1960). This exposes *Physalia* to both ocean and wind forcing simultaneously. In addition, there is a dimorphism in the population, with individuals either left- or right-handed, depending on the position of the submerged bulge relative to the float. This causes them to drift at an angle to the wind direction, to the right- or to the left- of the wind (Woodcock 1956). This drift angle is not fixed, but varies with wind speed: it is large ($\approx 40^\circ$) when winds are weak and decreases ($\approx 0^\circ$) as winds strengthen (Totton 1960). Their complex drift behaviour is therefore not easily captured by traditional particle models. Previous studies have already attempted to simulate *Physalia* drift using Lagrangian tracking that combine ocean currents and wind forcing, typically by applying a fixed fraction of the 10-m wind speed U_{10} to approximate wind-induced drift (Prieto et al. 2015; Ferrer et al. 2015; Ferrer and Pastor 2017; Headlam et al. 2020; Macías et al. 2021). The wide range of studies, from below 1% to 10% of U_{10} , reflects the uncertainty on the influence of wind on *Physalia*'s drift. Most models have also ignored the species' morphological dimorphism, where individuals drift either to the left or right of the wind depending on their handedness. An exception is the study by Ferrer and Gonzalez (2021), which modelled left- and right-handed forms and tested multiple fixed drift angles, though these angles remained constant with wind speed. More recently, a laboratory experiment using 3D-printed replicas of *Physalia* quantified its wind-induced drift while accounting for its asymmetric morphology, dimorphism and the variation of drift angle with wind speed (Bourg et al. 2024). The resulting parameterization can be integrated into Lagrangian tracking models and is expected to greatly improve the accuracy of simulated *Physalia* trajectories.

Despite these advances, all past Lagrangian modelling studies considered *Physalia* as a single species, in line with the taxonomic understanding available at the time. Over the past decades, field observations and morphological descriptions of *Physalia* reported distinct forms and used various names, such as *Physalia physalis* or *Physalia utriculus*. However, without clear evidence of reproductive or genetic separation, these forms were generally treated as synonyms of a single species. The idea that multiple species might exist within the genus was occasionally raised but largely set aside due to the lack of supporting evidence. This assumption was recently revisited by

Church et al. (2025), who conducted a global reassessment of *Physalia* diversity based on genetic and morphological analyses to test the hypothesis of a singular *Physalia* species. They were able to identify four different species: *Physalia physalis* (also referred to as lineage A), *Physalia utriculus* (for which two lineages were found: B1 and B2, B2 remaining unnamed due to lack of morphological data and lower genomic divergence), *Physalia megalista* (lineage C1) and *Physalia minuta* (lineage C2). Later, Yongstar et al. (2025) recognized lineage B2 as a separate species, naming it *Physalia mikazuki*. Accordingly, we refer to B2 as *Physalia mikazuki* and to B1 as *Physalia utriculus* hereafter. Church et al. (2025) quantified the genetic differentiation between species using the fixation index F_{ST} from whole-genome data, which was remarkably high, ranging from 0.3 to 0.6, a level generally interpreted as indicating very high genetic differentiation (Hartl et al. 1997). The morphological characteristics of each species were also described (Church et al. 2025), which enables a systematic identification of individuals from photographs. One such valuable dataset is photographs of beached colonies uploaded to citizen science platforms such as iNaturalist <https://www.inaturalist.org/>. The results revealed that some species appear to be restricted to an ocean basin, such as *Physalia physalis* in the Atlantic Ocean, while others, like *Physalia utriculus*, exhibit a more widespread distribution across the global ocean, occasionally co-occurring with other species while maintaining strong genetic differentiation.

In this study, our objective is to bridge the genetic results of Church et al. (2025) and Yongstar et al. (2025) with environmental exposure and physical connectivity using Lagrangian tracking simulations. Specifically, we ask: How far can individuals drift over the course of a year and what range of temperatures are they exposed to during that period? To address these questions, we backtrack each genetically sampled individual from the time and location of its beaching. We then calculated the Lagrangian connectivity between sampled individuals used in the genetic study and evaluated whether patterns of drift-derived connectivity are consistent with observed genetic structure that defines subpopulations within lineages. In the following sections, we describe the ocean current and wind speed models used in this study, as well as the setup of the Lagrangian particle tracking experiments and the postprocessing analysis. Our results focus on contrasting the trajectories, distribution and temperature exposure between *Physalia* lineages, and exploring to which extent ocean-wind transport can explain the genetic patterns of *Physalia*. We discuss the limitations of our methodology and link our results to the most recent literature on the topic.

2 | Data and Methods

2.1 | Ocean and Wind Data

As *Physalia* are largely passive organisms, moving horizontally at the surface of the ocean through wind and ocean currents (Totton (1960)), we model their drift using wind and ocean velocity data from two global reanalysis products; the European Centre for Medium-Range Weather Forecasts (ECMWF) Reanalysis v5 ERA5 for atmospheric wind forcing (Hersbach et al. 2020) and the Bluelink ReANalysis BRAN2020 for ocean

circulation (Chamberlain et al. 2021). ERA5 provides 10-m hourly wind components (zonal and meridional) on a global grid with a horizontal resolution of 0.25°. For ocean currents, we used daily outputs from the BRAN2020 reanalysis (Chamberlain et al. 2021), which assimilates a wide range of observational datasets, including satellite altimetry, in situ profiles, animal-borne sensors and ship-based measurements, into the Ocean Forecasting Australia Model version 3 (OFAM3) (Oke et al. 2013). OFAM3 is a near-global eddy-resolving hydrodynamic model developed primarily for upper-ocean applications. From BRAN2020, we extracted the shallowest available velocity and temperature fields (which represent the upper 2.5 m of the ocean) with a spatial resolution of 0.1°.

2.2 | Lagrangian Particle Tracking

Lagrangian particle tracking is a useful tool for exploring the movement of mostly passive organisms in the ocean. To understand the relationship between genetic connectivity and patterns of ocean-wind connectivity we conducted Lagrangian backtracking experiments using passive virtual particles seeded at the locations and dates of genetic sampling reported by Church et al. (2025). For each location, we released $N=1000$ particles and followed their trajectories backward in time over 1 year starting from each sample beaching date. This was carried out for 125 out of the 163 *Physalia* samples based on the availability of ocean and wind data (no access to data later than 2023) and the quality of the genetic material. Numerical experiments were run for 32 samples for *P. physalis* (lineage A), 62 samples for *P. utriculus* (lineage B1), 5 samples for *P. mikazuki* (lineage B2), 15 samples for *P. megalista* (lineage C1) and 11 samples for *P. minuta* (lineage C2). The samples were collected between June 2006 and October 2023 and do not uniformly cover years within that period, with for example over 40% of the samples collected in 2023 (detailed list of collection dates can be found in Church et al. (2025)). When the trajectories are less than 100 m from the coast for 3 days or more, we consider that they strand on the coast. These trajectories were already presented as an illustration in Church et al. (2025).

A tracking period of a year was chosen because it aligns with common estimates for many medusozoan jellyfish species, which typically have life spans shorter than a year, with some exceptions (Pitt et al. 2014). Given this uncertainty, the one-year simulation represents a conservative choice, allowing us to assess the upper bounds of potential dispersal and connectivity. The study area is global but restricted to latitudes lower than 60 degrees, as the ocean model was not available at higher latitudes and *Physalia* is unlikely to inhabit polar regions.

Lagrangian tracking experiments were performed using the OpenDrift (v1.12.0) open source package developed by Dagestad et al. (2018). The trajectories of *Physalia* were modelled as a linear combination of oceanic advection, horizontal diffusion and wind-induced drift. The position of particles was computed and updated every hour. Advection was calculated using the Euler integration scheme implemented in OpenDrift. Diffusion was represented as a random walk process to reproduce sub-grid processes, with diffusivity set to $10\text{ m}^2\text{s}^{-1}$ following van der Mheen et al. (2020). The wind-induced drift of *Physalia* was

parameterized based on the results of laboratory experiments carried out in a controlled water tank using 3D-printed replicas of the organism (Bourg et al. 2024). These experiments quantified both the drift angle and the drift speed as a function of wind characteristics. The drift angle α from the wind direction was found to follow an exponential relationship with the 10-m wind speed U_{10} (in m s^{-1}), defined as:

$$\alpha = \pm 50.8 \times e^{-0.15U_{10}} - 0.5. \quad (1)$$

with the angle being positive (counterclockwise) for Right-handed *Physalia*, and negative (clockwise) for Left-handed *Physalia*. A wind drift speed of *Physalia* was estimated to be on average 1.7% of U_{10} . However, this percentage was shown to vary depending on individual size and morphology, with deviations up to $\pm 0.3\%$ (Bourg et al. 2024). To account for this natural variability, we initialized $N=1000$ particles at each seeding location, assigning each one a wind drift speed drawn from a normal distribution with a mean of 1.7% and a standard deviation of 0.13%. To ensure reproducibility of the experiment, a fixed random seed was applied. For all genetic samples in which the handedness of the individual was known ($N=84$), we assigned the corresponding wind-drift orientation in the model. There were both left-handed individuals ($N=55$) which drift to the right of the downwind direction, and right-handed individuals ($N=29$) which drift to the left. For samples in which handedness was not reported ($N=52$), we initialised 500 particles with left-handed drift orientation and 500 particles with right-handed drift orientation.

2.3 | Metrics and Parameters

To analyse temperature exposure, we consider the sea surface temperatures (SST) encountered along the one-year backtracked trajectories as an approximation of the thermal conditions each individual may have experienced over its lifetime and, by extension, could potentially tolerate.

We computed the through-water distance between each pair of sampling sites using the `searoute` Python package (Halili 2025), which estimates the shortest navigable path across the ocean surface. To quantify Lagrangian connectivity, we defined two metrics: the Lagrangian Meeting Probability and the Lagrangian Shortest Distance. The Lagrangian Meeting Probability is defined as the percentage of trajectory pairs that cross the same location (within a 0.5° radius) at any point during their one-year backtracked paths. Furthermore, because some sample pairs are too far from each other and therefore have little probability of connection, we defined the Lagrangian Shortest Distance by looking into the origin points of backtracked trajectories and computing the average distance between the source regions (= position 1 year before stranding) of each sample.

Genetic distances were calculated using the Euclidean distance between samples along principal components of genetic variation. Because our dataset includes sampling within and across species, typical population genomic approaches like estimating asymmetric gene flow may not be appropriate here. In addition, our dataset contains both very large and small spatial and

time scales (across ocean basins as well as collected from the same stranding event). For this reason, we have chosen to estimate genome-scale patterns of variation as calculated with the principal component analysis (PCA). The PCA was performed as described in Church et al. (2025). Briefly, whole genome sequencing data for 141 specimens was mapped to the reference assembly for *P. physalis*, NCBI BioProject PRJNA1040906. Genotype likelihoods were calculated using 'ANGSD', v. 0.935, on a subset of non-repeat sites filtered for quality, coverage and lack of missingness (Korneliussen et al. 2014). PCA was performed using 'PCANGSD', v. 121, with $k=5$ components (Meisner and Albrechtsen 2018). Euclidean distances were calculated over the first ten dimensions. Additional species-specific PCAs were calculated for *P. physalis*, *P. utriculus*, *P. megalista* and *P. minuta*. For these, Euclidean distances were calculated over two or three dimensions, as determined with a scree plot of variation. This was not calculated for *P. mikazuki* because of too little sample size.

Ordinary least-squares (OLS) regression models were run using the `statisticsmodels` Python package. For each regression model, the response variable was the pairwise genetic distance between *Physalia* samples. Each model was run independently so that different predictors could be tested: the Distance through water, the Lagrangian Meeting Probability, the Lagrangian Shortest Distance, and a linear combination of the Distance through water and the Lagrangian Shortest Distance. We used OLS as a simple and interpretable analysis to test the explanatory power of each connectivity metric, which is appropriate given the limited number of predictors and the absence of strong deviations from linear model assumptions.

3 | Results

3.1 | Differences in Distribution, Coastal Proximity and Temperature Exposure Between *Physalia* Lineages

Lagrangian trajectories backtracked from the stranding locations of the *Physalia* samples analysed in Church et al. (2025) were first used to estimate the potential for winds and currents to disperse *Physalia* over the course of a year. The spatial distribution of these one-year backtracked virtual trajectories is shown in Figure 1 (top panels), coloured by lineage. Despite interlineage variability, all trajectories remained broadly confined within the basin they were collected in, although individuals often travelled across the ocean basin. Samples from *P. physalis* remained confined to the North Atlantic, while *P. utriculus* was the most widespread, found across the Pacific, South Atlantic and South Indian Ocean. *P. mikazuki* was found exclusively in the North Pacific. *P. megalista* was restricted to the Southern Hemisphere, spanning much of the South Indian Ocean and the South-West Pacific, with a minor presence in the South-East Pacific. *P. minuta* was the most spatially constrained, mainly concentrated in the South-West Pacific, with a narrow extension westward through the Southern Indian Ocean.

Because different *Physalia* lineages occupy different regions in the ocean, these geographic differences can influence how

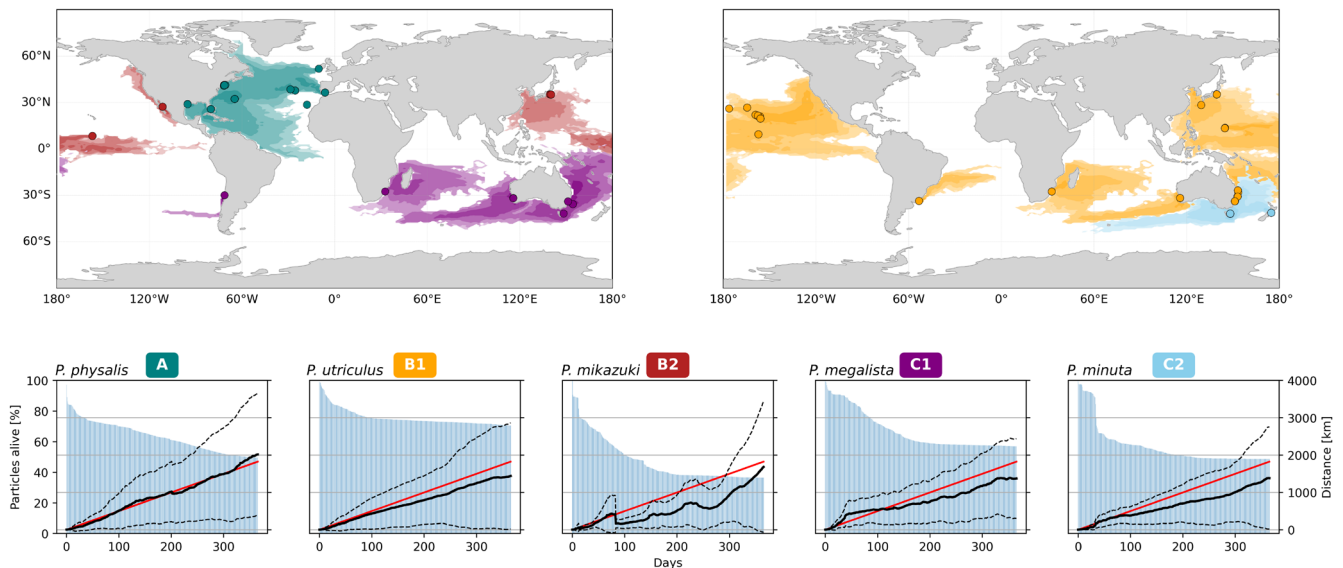


FIGURE 1 | Top panels: Density contours of the distribution of backtracked positions, colour coded as each *Physalia* lineage. Coloured dots indicate sampling collection locations. The five different lineages are shown in two different panels to avoid spatial overlap. On the left panel are shown *Physalia physalis* A: Teal, *Physalia utriculus* 2nd lineage B2: Dark red and *Physalia megalista* C1: Purple. On the right panel are shown *Physalia utriculus* 1st lineage B1: Orange and *Physalia minuta* C2: Cyan. Bottom panels: Time evolution (in days) of displacement (lines, right axis) and percentage of un-stranded particles (bars, left axis) for each lineage. Black lines show the mean (solid line) ± 1 standard deviation (dashed lines) of the distance travelled from their collection point. The red line corresponds to a constant speed of 5 km/day. Lineage labels are colour-coded to match the density maps above.

far individuals can travel and how likely they are to remain at sea without becoming stranded on a beach. To explore this, we looked at the evolution of distance travelled over time and the percentage of particles that remained afloat (i.e., not stranded) throughout the simulation (bottom panels in Figure 1). Overall, *Physalia* can travel several thousand kilometres annually, with clear contrasts in dispersal capacity and stranding tendencies across lineages. After 180 days (≈ 6 months), *P. mikazuki* shows the highest stranding rate (61%), followed by *P. minuta* (49%). In contrast, *P. physalis*, *P. megalista* and especially *P. utriculus* maintain more offshore trajectories, with lower stranding probabilities of 37%, 40% and 26%, respectively. The lineages that experience lower stranding rates also tend to be more dispersive, with greater average displacements. Indeed, after 180 days of simulation, *P. physalis* individuals have travelled the furthest on average (890 km), followed by *P. utriculus* (750 km), *P. megalista* (730 km), *P. minuta* (650 km) and *P. mikazuki* (420 km). *P. physalis* and *P. utriculus* tend to be located in regions where wind and surface current patterns drive relatively fast transport (e.g., in western boundary current regions; see Figure S1), resulting in average drift speeds near 5 km/day (shown by the red reference line in Figure 1, which would correspond for instance to a current of 0.06 m/s). In contrast, particles representing *P. mikazuki* and *P. minuta* move more slowly, around 3.5 km/day on average.

To explore the temperature exposure for each lineage, we first look at the SST on the day and location of collection of each *Physalia* sample (black scatter in Figure 2a). The coldest SST ranges were observed for samples from *P. megalista* (12°C–23°C) and *P. minuta* (16°C–18°C), compared to warmer ranges for *P. physalis* (13°C–28°C), *P. utriculus* (16°C–28°C) and *P. mikazuki* (17°C–27°C). To broaden this result, we consider the SST encountered along the one-year backtracked trajectories. These

along-track SST are broadly consistent with the values observed at the collection location and time, although they show a wider range of exposure, especially for *P. megalista* and *P. minuta*.

Across all lineages, the SST encountered along-track range from 0°C to 30°C, with very few occurrences below 10°C. The mean exposure to SST per lineage falls between 15°C and 27°C. The median exposure to SST per lineage is as follows: 22°C for *P. physalis*, 25°C for *P. utriculus*, 28°C for *P. mikazuki*, 21°C for *P. megalista* and 15°C for *P. minuta*. The differences between lineages are also reflected in the 10th–90th percentile SST ranges: *P. physalis* and *P. megalista* display the broadest thermal extents, spanning 15°C–29°C and 13°C–27°C, respectively. *P. minuta* occupies the coldest range, between 11°C and 19°C. In contrast, *P. utriculus* and *P. mikazuki* are skewed toward warmer waters: *P. utriculus* ranges from 18°C to 29°C, while *P. mikazuki* is restricted to the warmest conditions, between 24°C and 29°C. We note, however, that sample sizes differ among lineages, with *P. mikazuki* and *P. minuta* being represented by fewer records than the other taxa. To assess whether this imbalance could bias the inferred thermal ranges, we performed a subsampling analysis on the more extensively sampled lineages to match the smaller sample sizes. These analyses yielded comparable SST distributions and percentile ranges (see Figure S2), indicating that the observed differences among lineages are unlikely to be driven solely by unequal sampling effort.

Figure 2b shows, for each lineage, the spatial probability that SST falls within these percentile-defined ranges during the whole year of 2023 (chosen as it is the year where most samples were collected). These maps should not be interpreted as probability of presence, but rather as indicative of the different regions of the ocean each lineage could hypothetically inhabit, based

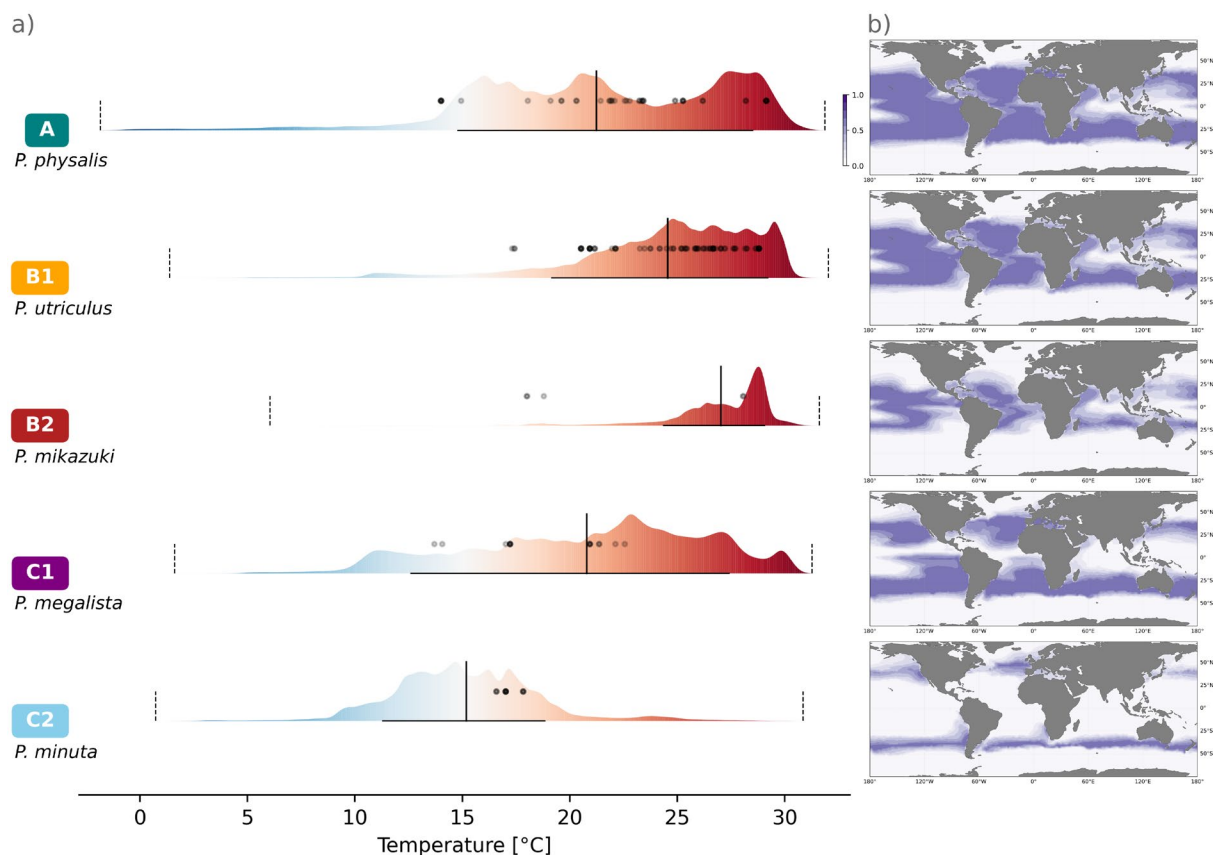


FIGURE 2 | (a) For each lineage: Distribution of along-track SST from all backtracked trajectories, colour-coded by SST value. The solid vertical line marks the average SST for each lineage, dashed lines indicate the minimum and maximum values encountered. The horizontal bar spans the 10th–90th percentile range. Overlaid black scatter points show SST values at the location and time of genetic sampling. (b) For each lineage: Map showing, for each pixel, the probability of being within the 10th–90th percentile SST for the respective lineage range in 2023.

on thermal tolerance alone. The contrast is particularly striking when looking at lineages with narrow SST ranges such as *P. mikazuki* and *P. minuta*, whose potential thermal habitats are very restricted (although the small number of samples might contribute). Interestingly, the SST ranges of *P. mikazuki* and *P. minuta* do not overlap, suggesting that they would likely never co-occur if these thermal conditions were the only constraint. Over 2023, polar oceans are almost entirely colder than the 10th percentile of SST experienced by any lineage, while equatorial regions such as the Indo-Pacific consistently exceed the 90th percentile upper limit across all *Physalia* lineages.

3.2 | Can Ocean-Wind Transport Explain Genetic Similarities Within *Physalia* Lineages?

For each pair of genetic samples belonging to the same lineage, we computed the Lagrangian Meeting Probability based on the one-year back-trajectories of 1000 particles released from each sample location. Then, this metric was compared with the through-water distance between their collection locations. Across all lineages, we observe a negative relationship between distance and Lagrangian connectivity: samples collected in geographic proximity tend to show high Lagrangian Meeting Probability (top left corner in Figure 3), while those farther apart show low values (bottom right corner), with other pairs aligning somewhere in between. All sample pairs collected less than

1680 km apart show non-zero meeting probabilities, whereas all pairs collected beyond 8570 km never connect during the one-year simulation. That corresponds, for example, to the distance between 40° North and 40° South along a meridian.

However, we also observe both ‘close but disconnected’ sample pairs (highlighted in red in the bottom left corner of Figure 3) and ‘far but connected’ ones (highlighted in blue in the top right corner in Figure 3). More specifically, *P. physalis* shows the clearest distance–connectivity relationship, although it still includes some low-probability pairs sampled 1000 km apart. *P. megalista* also generally follows the negative trend, with a few exceptions of low-probability at short distances. In contrast, *P. utriculus* exhibits the broadest spread: some sample pairs located less than 1000 km apart show nearly no probability of meeting, while others collected more than 6000 km from each other reach values of up to 50%. Lineages *P. mikazuki* and *P. minuta*, both represented by fewer samples, fall within the expected region of the plot and do not show strong deviations.

Because subpopulations within lineages have been identified by Church et al. (2025), with samples geographically grouped in the principal component analysis (PCA) of their genetic data, we explore here how these genetic clusters within lineages relate to our Lagrangian connectivity results. To facilitate this comparison, we include their PCA plot in Figure 4. This analysis is not run for *P. minuta* and *P. mikazuki* because of the smaller sample

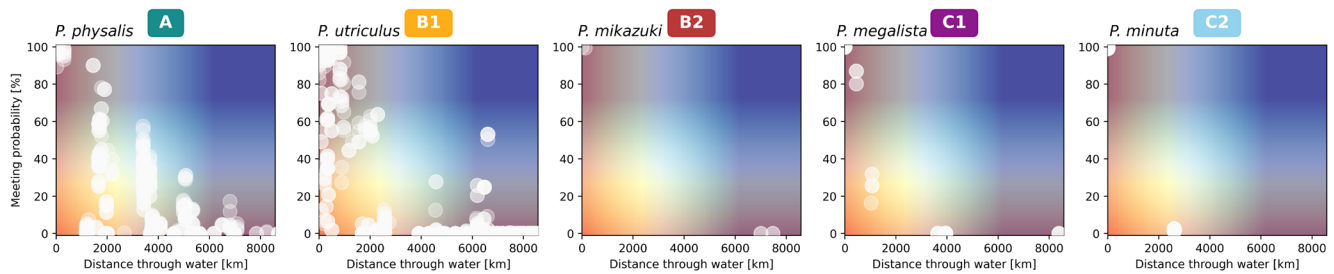


FIGURE 3 | Scatter plot showing Lagrangian Meeting Probability as a function of Distance through water between pairs of genetic samples. Lagrangian Meeting Probability is defined here as the percentage of trajectory pairs that cross the same location (within a 0.5° radius) at any point during their one-year backtracked paths. The distance through water refers to the shortest sea-based route between the sample collection sites, avoiding land. These metrics are computed for each pair of genetic samples belonging to the same lineage. Each subplot displays results for a different lineage. A 2D heatmap is shown beneath the scatter points to highlight key regions: Blue areas indicate pairs that are far apart but highly connected, while red areas highlight pairs that are geographically close but disconnected.

size available for these two species. Within *P. physalis*, there were two distinct genetic clusters: one along the American coast and one along the African-European coast of the North Atlantic. Interestingly, samples from Bermuda and the Azores, though geographically closer to one side, contain representatives from subpopulations on both sides of the ocean basin. A similar pattern emerges in the Lagrangian connectivity results. Samples on each side of the Atlantic show higher Lagrangian Meeting Probability to their respective continental margin (Figure 4a), and insular samples (square and triangle symbols) show strong Lagrangian Meeting Probability with their nearest continental coast but also with each other.

We also examined intra-specific connectivity for *P. utriculus*, for which the samples are spread across very distant locations, and the Lagrangian Meeting Probability metric is no longer sufficient as most sample pairs never connect within 1 year of simulation. To address this, we introduced the Lagrangian Shortest Distance: the average distance between the source points of backtracked trajectories. Shorter distances between origin points suggest a higher potential for connectivity, while larger distances indicate a lower likelihood of connectivity. This metric is shown for *P. utriculus* in the central panels of Figure 4. Several of the short-distance links (blue lines) correspond to sample pairs that are genetically close in the PCA from Church et al. (2025) as shown in the left panel. For example, Japan and Guam, Japan and eastern Australia, eastern Australia and the North Pacific islands, and South Africa and Western Australia all appear relatively close in the two dimensional PCA projection, and these same regions show the shortest distances between origins in our analysis. In contrast, regions that are genetically distant in the PCA also tend to have high values of Lagrangian Shortest Distance. In particular, sample pairs such as Western Australia and the North Pacific, South America and Japan, or South Africa and the Pacific islands occupy opposite ends of the PCA and show the longest distances between origins in our analysis (red lines in Figure 4). For *P. megalista*, the agreement between PCA structure and Lagrangian Shortest Distance is less clear, but some consistent patterns remain. For example, South Africa and western Australia are still relatively close and Chile, which is genetically far from most samples in the genetic analysis, displays only high Lagrangian Shortest Distance values to other samples.

To verify the link between genetic differentiation and drift-derived connectivity, we use an Ordinary Least Square regression model. For each pair of samples of the same lineage, the Euclidian distance on the PCA is predicted using different predictors: the distance through water (D) which corresponds to the shortest route through water between two samples, the Lagrangian Meeting Probability, the Lagrangian Shortest Distance and a combination of the Distance through water and the Lagrangian Shortest Distance. The results are presented in Table 1. When looking at all intra-lineage samples together (2nd column in Table 1), the models explain a substantial proportion of the variance, between 27% and 57%, with all p -values below 0.05, confirming that both geographic separation and ocean-wind connectivity are meaningful predictors of genetic differentiation within lineages. Among predictors, the term $D \times \text{LSD}$ (57%) explains more variance than D (42%), LMP (27%) or LSD (51%) alone. This shows that accounting for both large-scale separation and Lagrangian connectivity improves our ability to predict genetic similarity. LMP explains less variance than the other metrics, likely because it drops to zero for very distant pairs and therefore underrepresents longer-range dispersal patterns.

Applying the same methodology with Euclidian distance calculated from species specific PCAs separately (columns 3–6 in Table 1), we see some variability in the strength of the relationship between genetic distance and our connectivity predictors. *P. utriculus* and *P. minuta* are those for which the models explain the highest proportion of genetic variance: up to 55% and 46%, respectively. For both lines, the predictor that performs best is the combination of distance through water and Lagrangian Shortest Distance ($D \times \text{LSD}$). In contrast, for *P. physalis*, distance through water alone performs as well as the combined metric $D \times \text{LSD}$ (both explaining 29% of variance). For *P. megalista*, the best predictor is the Lagrangian Meeting Probability (LMP), which explains 26% of the variance.

4 | Conclusions and Discussion

In this study, we addressed two main questions: how do *Physalia* lineages differ in their dispersal trajectories and thermal exposure; and to what extent can wind–ocean transport help explain

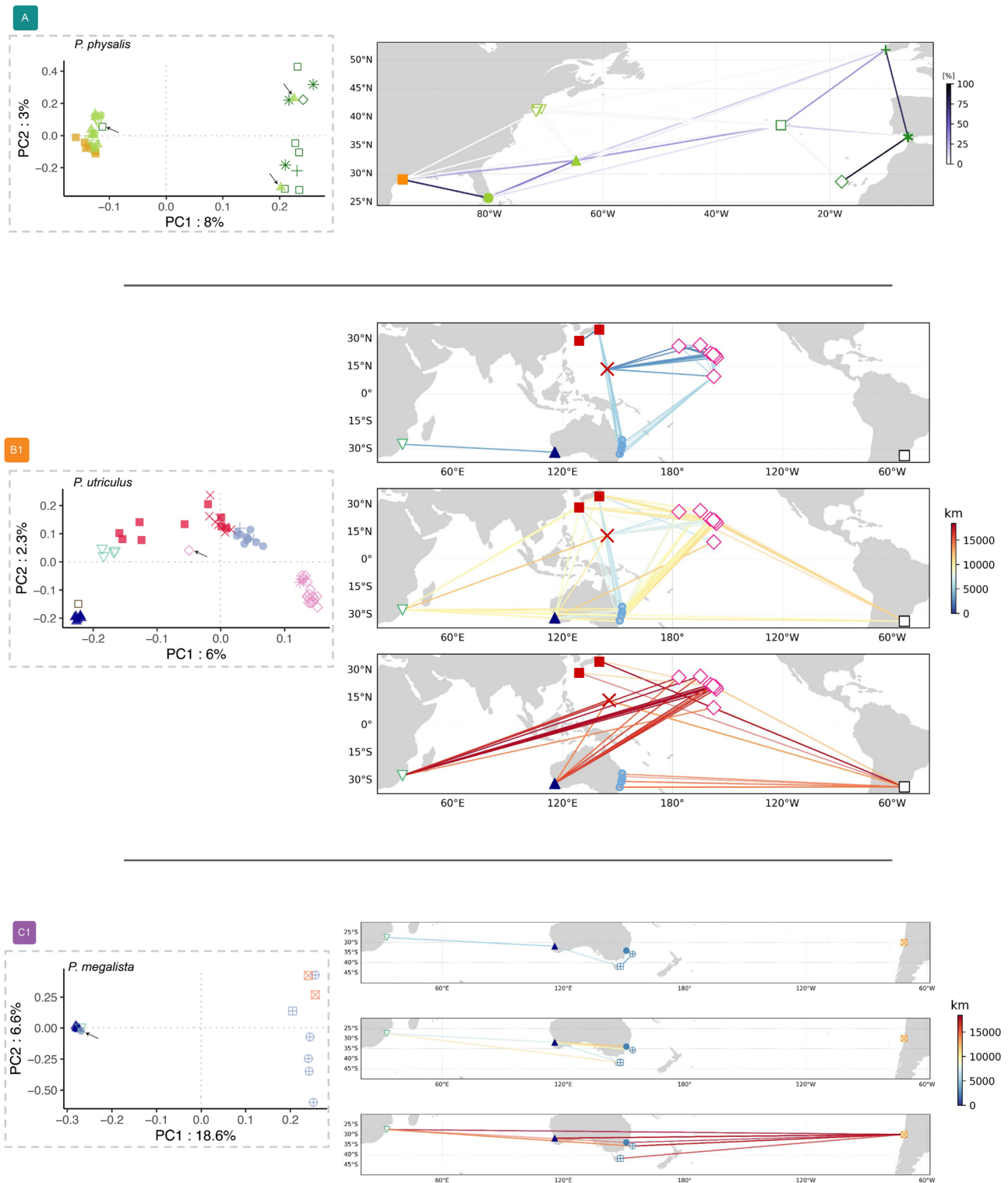


TABLE 1 | Ordinary least squares regression results (r^2 and p -values) for models predicting pairwise genetic distance between *Physalia* samples.

Predictors	Intra-lineages r^2 p -value	<i>P. physalis</i> r^2 p -value	<i>P. utriculus</i> r^2 p -value	<i>P. megalista</i> r^2 p -value	<i>P. minuta</i> r^2 p -value
Distance through water (D)	0.42 0.00	0.29 0.00	0.39 0.00	0.07 0.00	0.20 0.00
Lagrangian Meeting Probability (LMP)	0.27 0.00	0.08 0.00	0.36 0.00	0.26 0.00	0.20 0.00
Lagrangian Shortest Distance (LSD)	0.51 0.00	0.10 0.00	0.53 0.00	0.12 0.00	0.44 0.00
D $\times$ LSD	0.57 0.00; 0.00; 0.00	0.29 0.00; 0.09; 0.05	0.55 0.00; 0.00; 0.00	0.17 0.18; 0.00; 0.00	0.46 0.02; 0.00; 0.03

Note: Analyses were performed across all intra-lineage pairs and within each lineage individually. The rows show results from a model including Distance through water, Lagrangian Meeting Probability, Lagrangian Shortest Distance and combined Distance through water and Lagrangian Shortest Distance (D $\times$ LSD). For the latter, three p -values are listed: for D, LSD and their interaction.

the genetic structure observed within lineages? To address these questions, we simulated the trajectories of 125 genetically identified *Physalia* individuals presented in Church et al. (2025), backtracking from their stranding locations using a wind- and current-driven numerical Lagrangian model, assuming a one-year lifespan.

Our results show clear inter-lineage variability in dispersal capacity, coastal proximity and temperature exposure. Because all lineages follow the same drift behaviour in our model, these results evidence the influence of the environments the different *Physalia* lineages occupy (i.e., tropical vs. high-latitude distribution, coastal vs. insular samples, highly dynamic vs. quiet ocean). For example, we noticed that individuals collected on islands tended to strand earlier in the backtrack (not shown), remaining closer to the coast, while samples from continental coasts generally stranded later. Most individuals remained broadly confined within their ocean basin, but *P. physalis* and *P. utriculus* show the highest displacement rates, the lowest stranding rates and the largest range of SST exposure. In contrast, *P. mikazuki* and *P. minuta* display slower drift speeds, are more frequently stranded and have smaller ranges of SST exposure. *P. minuta* occupies the coldest waters of all lineages, while *P. mikazuki* is present in the warmest waters. We also find contrasting SST exposure ranges between *P. utriculus* and *P. mikazuki*, the two lineages with the lowest genetic differentiation (Church et al. 2025). In particular, the lower limit of the SST range (10th percentile) of *P. mikazuki* is almost equal to the average SST encountered by *P. utriculus*.

Globally, the spatial probability of SST to fall within the ranges of temperature maps shown in Figure 2 shows that, according to our analysis, different *Physalia* lineages likely occupy different latitudes and temperatures, with for example *P. mikazuki* being more likely to be tropical and *P. minuta* more likely to be present only in high latitude regions, similarly to other medusozoans (e.g., the genus *Aurelia*). In addition, Figure 2 can be compared with the distribution patterns derived from the iNaturalist dataset used in Church et al. (2025). The maximum latitudinal extents of lineages *P. physalis* and *P. megalista* match well between our SST-based estimates and the iNaturalist records. Observations of *P. minuta* on iNaturalist are few, but all fall within the narrow latitudinal band

predicted by the SST range experienced by *P. minuta* in our experiments. Interestingly, *P. utriculus* is widely observed in mid- and low-latitude regions, but is largely absent from Maritime Southeast Asia, a region also excluded by its estimated SST range in Figure 2. These correspondences suggest that the SST ranges inferred from Lagrangian backtracking align, at least in part, with observational data and could offer an interesting basis for further exploration of potential lineage distributions. In this study, we look into the temperature potentially experienced by the *Physalia* samples we have access to, acknowledging that this may not directly reflect the thermal tolerance limits of the species. Still, it provides a useful starting point for exploring the potential role of temperature in shaping habitat boundaries. Interestingly, Yongstar et al. (2025) observed the presence of *P. mikazuki* in the Tohoku region of Japan coinciding with record-breaking sea surface temperature changes over the previous 2 years.

When comparing physical transport to genetic structure, we found several lines of agreement. Cross-species connectivity show that samples with low genetic similarity (e.g., *P. utriculus*, *P. megalista* and *P. minuta*) exhibit limited Lagrangian connectivity, even when located in close spatial proximity. In contrast, the only pair of lineages with relatively low genetic differentiation (*P. utriculus* and *P. mikazuki*) displays the highest long-distance connectivity in our simulations, with some sample pairs over 6000 km apart still showing up to 50% overlap in particle trajectories. Within-lineage patterns also partly mirror the spatial genetic clustering found by Church et al. (2025). For *P. physalis*, individuals on opposite sides of the North Atlantic (American vs. African–European coastlines) show stronger connectivity within their own basin margin than across it, and island samples (e.g., Bermuda, Azores) act as potential connectors. For *P. utriculus*, where samples span large oceanic distances, direct Lagrangian connectivity becomes sparse. Yet, using average distances between backtracked origin points, we found that genetically similar regions (e.g., Japan–Guam and Eastern Australia–Japan, or South Africa–Western Australia) also tend to have short inferred distances. Accordingly, genetically distant regions (e.g., Western Australia–North Pacific and Eastern Australia–Atlantic South America, or South Africa–North Pacific) are separated by the longest dispersal distances in our framework.

The role of Lagrangian connectivity in shaping genetic differentiation is further supported by our statistical regression results. Intra-lineage pairwise genetic distances were better explained when incorporating connectivity metrics derived from our Lagrangian simulations. Although distance alone accounted for 42% of the variance, including the interaction between distance and Lagrangian Shortest Distance increased the variance explained by the model by 15 percentage points, reaching up to 57% of the explained variance. This is striking given that the model only disperses over a single generation and relies on a relatively small sample size. For *P. physalis*, distance through water alone performs as well as the combined metric DxLSD, indicating that genetic differentiation in this lineage may be shaped by more stable or older processes, less influenced by present-day drift. For *P. megalista*, the best predictor is the Lagrangian Meeting Probability, which may be due to the pronounced genetic split observed between the Indian and Pacific Ocean populations, a pattern stronger than in any other lineage. For such distant populations, LMP often drops to zero, whereas continuous distance metrics may not reflect this barrier as clearly. For inter-lineage comparisons, the model explained only 11% of the variance (not shown), likely reflecting that the genetic divergence between lineages is shaped by deeper evolutionary histories and processes over multiple generations beyond the scope of our initial simulations.

This study comes, however, with limitations. First, sample sizes differ between species, and although we attempted to account for this through subsampling (see Figure S2), we cannot exclude the possibility that it may bias some of our results. To the best of our knowledge, however, this represents the most comprehensive dataset currently available. It is also possible that some species are genuinely less abundant, which could contribute to the smaller number of samples collected. Besides, the genetic dataset, although geographically widespread, remains sparse, with fewer than 200 individual samples worldwide. Sampling is particularly biased toward the Northern Hemisphere, with very few samples collected from Africa, South America and Southeast Asia. The Southern Hemisphere presents fewer large-scale geographic barriers to dispersal, which may allow for broader connectivity than what is reflected in our results. Hence, given the sampling bias, we cannot draw firm conclusions about distributions or connectivity in the Southern Hemisphere and the Southern Ocean. Besides, while our Lagrangian tracking runs incorporate wind-induced drift calibrated from laboratory experiments, it does not account for wave effects or non-linear interactions between wind, waves and currents, which may strongly influence drift behaviour in the ocean. Our ocean and wind fields are also derived from model products which, although state-of-the-art, inevitably smooth out fine-scale processes that may be relevant for the transport of *Physalia*, whose float size typically ranges from a few to thirty centimetres.

Additionally, the drift parameterization likely oversimplifies a wide range of biological and morphological variability. While we have used a range of parameters informed by laboratory experiments, Bourg et al. (2024) showed that variations in float morphology (such as sail height, sail length and float curvature) can influence the drift speed and drift angle of *Physalia*. Because these morphological traits differ between species (Church et al. 2025), it would be important to explore this

variability. Moreover, *Physalia* individuals can actively retract their tentacles, bend their float or erect their sail (Totton 1960), but the frequency and conditions under which these behaviours occur and the extent to which they alter drift trajectories remain unknown. We also limited this study to single generation surface simulations because the early life stages of *Physalia* are believed to occur below the surface, yet there is currently no information on how long individuals remain submerged or at what depth (Munro et al. 2019). We ran our simulations over 1 year, consistent with what is currently believed to be their approximate lifespan, although this remains uncertain and largely undocumented in the literature.

Despite these limitations, we believe that this study brings together the best available knowledge on both the genetic structure and the parameterization of *Physalia* drift. Interestingly, we know that *Physalia* species can differ in body size and venom potency, with *P. physalis* generally being the largest and considered the most dangerous to humans. We find here that, under present-day ocean circulation, *P. physalis* is unlikely to drift more than approximately 2000 km within a year. Consequently, dispersal from the Atlantic Ocean to another ocean basin appears unlikely under current connectivity. Other regions are exposed to multiple *Physalia* species. Understanding the species's respective venom potency and when they are likely to strand could help mitigate the risk of stings to humans and farmed fish.

Across lineages, we find clear differences in thermal exposure and stranding tendencies. Such differences in thermal exposure should prompt further investigation into the physiological tolerances of each lineage, as they may reflect lineage-specific thermal niches. Consequently, the results of the present study raise important questions about how different *Physalia* species could respond to changing temperature. For example, *P. mikazuki* appears to inhabit the narrowest range and the warmest waters. If our observed range is indicative of its thermal limits, its distribution may need to shift poleward to remain within suitable conditions. How such shifts may be constrained by physical barriers to dispersal remains an open question. Because *Physalia* disperses passively via winds and currents, its capacity to track suitable environmental conditions may be limited. In areas where species distributions overlap or may do so in the future, we can imagine that species already adapted to warmer conditions could potentially be more resilient.

Beyond thermal exposure, we also find strong similarities between the physical connectivity derived from Lagrangian tracking and the genetic differentiation reported by Church et al. (2025). That these concordances emerge despite the simplifications of our model suggests that large-scale wind-current transport plays a strong role in shaping *Physalia* population structure. As changes in global wind and current patterns have already been observed and are projected to continue under climate change, this could eventually modify connectivity among populations, either increasing or decreasing genetic exchange depending on the region. While such changes would likely occur over long timescales, they represent an important avenue for future research to determine how the habitat suitability, distribution and gene flow of *Physalia* may evolve under ongoing climate change.

Author Contributions

Natacha Bourg: conceptualization, methodology, formal analysis, writing – original draft, writing – review and editing. **Amandine Schaeffer:** conceptualization, methodology, funding acquisition, supervision, writing – review and editing. **C. Gabriela Mayorga-Adame:** conceptualization, methodology, formal analysis, writing – review and editing. **Samuel H. Church:** data curation, formal analysis, writing – review and editing. **Moninya Roughan:** supervision, writing – review and editing. **Kylie A. Pitt:** supervision, writing – review and editing. **Mary Beth Decker:** data curation, writing – review and editing. **Casey W. Dunn:** data curation, writing – review and editing. **Jasmin C. Lawes:** writing – review and editing.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

Ocean current and sea surface temperature data were obtained from the BRAN2020 ocean reanalysis, produced by CSIRO and available at <https://research.csiro.au/bluelink/>. Wind data are from the ERA5 reanalysis produced by ECMWF, accessible at <https://www.ecmwf.int/en/forecasts/dataset/ecmwf-reanalysis-v5>. The code used to generate the particle tracking outputs and the figures and analyses in this study can be found at <https://github.com/natachabourg/JBiogeography2026Bourg>. The outputs of the Lagrangian particle tracking simulations are available on demand. No fieldwork permits were required for this study.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Figure S1:** For each lineage, using a random sub-sampling to match the same number of samples for each lineage: distribution of along-track SST from all backtracked trajectories, colour-coded by SST value. The solid vertical line marks the average SST for each lineage, dashed lines indicate the minimum and maximum values encountered. The horizontal bar spans the 10th–90th percentile range. Each subplot shows this but subsampled randomly six times. On each y-axis, the lineage A corresponds to *Physalia physalis*, B1 is *Physalia utriculus*, B2 is *Physalia mikazuki*, C1 is *Physalia megalista* and C2 is *Physalia minuta*. **Figure S2:** 2023 average maps of sea surface temperature (BRAN2020 data), surface ocean currents (BRAN2020 data) and winds at 10 m (ERA5 data).