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Some like it hot: Is the recent presence of the meadow-forming *Penicillus capitatus* in the Azores connected to global warming?

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ABSTRACT

Specimens found in a tide pool on Santa Maria Island (Azores) were identified *in situ* as the green alga *Penicillus capitatus* (Halimedaceae, Bryopsidales). DNA-based analyses of two genetic markers (*rbc*L and *tuf*A) confirmed the identification and indicated that the Azorean population is closely related to those from the Western Atlantic. *P. capitatus* is newly reported for the Azores, with the nearest population in the Madeiran archipelago since 1978. The present record expands the species distribution further north outside the Mediterranean basin. Simulation of particle dispersal indicates that the species could reach the Azores within a year from any place in the North Atlantic where it is known to occur. Therefore, *P. capitatus* most likely arrived by rafting through marine currents, though anthropogenic introduction has not been excluded. While its natural arrival in the Azores may have occurred multiple times, its current successful establishment is likely related to the recent warmer conditions of the Azorean waters, estimated to have increased by 1.05º C over the last four decades. Prospection on sandy bottoms should be performed to assess the distribution of the species in the archipelago. DNA sequence analyses, including representatives of other *P. capitatus* populations, are necessary to enable further studies at a phylogeographical level.

1. Introduction

The genus *Penicillus* (Halimedaceae, Bryopsidales) was established by Lamarck 1813 to accommodate three species of calcified siphonous green algae from American waters, resembling shaving brushes, with a long cylindrical stem terminating in a bundle of numerous branches (Fig. 1, S1). The generitype, *P. capitatus*, is present in Tropical and Subtropical Western Atlantic coasts, from Florida to Southeast Brazil, as well as throughout the Mediterranean, from the Levante States to Spain (Guiry and Guiry, 2023, Fig. 2, Table S1), occurring on sandy bottoms in somewhat exposed to sheltered habitats (Sangil et al. 2010). Additional reports of the species are given for Queensland (Australia) and might represent anthropogenic introductions (Bostock and Holland, 2010) or taxonomic confusion with other co-generic species. In the Eastern Atlantic, *P. capitatus* has been reported close to the Gibraltar Strait in Cadiz, mainland Spain (Seoane-Camba, 1965). It was also reported for the Atlantic islands in the Portuguese archipelago of Madeira (Audiffred and Prud'homme van Reine, 1985, Ribeiro et al. 2019, 2023) and the Spanish archipelago of the Canary Islands (Sangil et al. 2010).

Extensive meadows of *Penicillus capitatus* found in La Palma (Canary Islands) were suggested to be related to recent increased seawater temperatures (Sangil et al. 2010). Further north, recently reported meadows of the siphonous species *Avrainvillea canariensis*, *Caulerpa ashmeadii*, *Halimeda incrassata,* and *Penicillus capitatus* found in Porto Santo Island (archipelago of Madeira) are regarded as a probable "clear sign of climate change effects in the Madeiran benthic communities" (Ribeiro et al. 2019, 2023).

In August 2022, *Penicillus capitatus* was fortuitously found on Santa Maria Island, in the Mid-northern Atlantic archipelago of the Azores, in an artificial tide pool with sand covering the basalt slabs of the bottom (Figs. 1–2, S2; https://youtu.be/9_ECZwN977U). Although several phycologists have reported on the marine flora of the Azores, including

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those from Santa Maria (see revision in Neto et al. 2021), this is the first record of *P. capitatus* for the archipelago.

The present study presents morphological and genetic information from the collected specimens to confirm the species' identity and its relation to other related populations. Sea temperature changes over the last decades, as well as simulations of the natural dispersion of the species, are also presented.

2. Material and methods

2.1. Sample collection

The Azores is located on the Mid-Atlantic ridge, 1200 km west of Europe, within the ecoregion Azores Canaries Madeira of the province Lusitanian (Spalding et al. 2007). The archipelago comprises nine volcanic islands, spreading over 500 km, and is separated into three main groups (Neto et al. 2022; (Fig. 2). Santa Maria is the southernmost island, presenting the warmest water in the archipelago (Lafon et al. 2004).

The alga *Penicillus capitatus* was found in an artificial tide pool in Maia (Santa Maria Island), located in a highly exposed intertidal zone of a Protected Landscape Area. The pool is 1,216 m^2, and its water is partially renewed twice a day during high tides when waves go over its cemented borders. The water quality is monitored during the bathing season (15 June to 15 September), showing pristine conditions (https://servicos-sraa.azores.gov.pt/grastore/BALNEARES/perfis_AB_ID/SantaMaria/2023_perfil_agua_balnear_Maia.pdf).

Specimens were collected from the bottom of the pool, from 1 to 3 m depth, by snorkeling (Table S2). Images were taken with an Olympus Tough TG-5 digital camera (OM Digital Solutions Corporation, Tokyo, Japan) *in situ*, *in vivo* submerged in seawater, and wet on herbarium paper. Samples were dried onto herbarium paper with subsamples kept in 4% formalin/seawater for morphological studies and silica gel for DNA extraction.

2.2. Molecular analyses

Total DNA was extracted using the methods described by Silva et al. (2016). Amplification followed the protocol proposed by Carine et al. (2004), using published primers to amplify the chloroplast-encoded genes *rbc*L (Verbruggen et al. 2009) and *tuf*A (Famà et al. 2002, Haendeler et al., 2010; Table S3). PCR conditions were optimized and described as follows: (1) *rbc*L: initial denaturation at 95°C for 3 min, followed by 35 cycles of 94°C for 45 s, 47°C for 45 s, and 72°C for 90 s, with a final extension of 72°C for 10 min; and (2) *tuf*A: initial denaturation at 94°C for 3 min, followed by 40 cycles of 94°C for 20 s, 52°C for 45 s, and 72°C for 55 s, with a final extension of 72°C for 5 min (Table S3). Sanger DNA sequencing was performed by StabVida (Lisbon, Portugal) using the produced PCR fragments.

DNA sequences were edited and concatenated using Sequencher 5.1 (Gene Codes Corporation, Ann Arbor, MI, USA) and later deposited in GenBank (accession numbers OR665167 - OR665172). Newly generated sequences were aligned with other sequences downloaded from GenBank (Tables S2, S4) in MEGA 11.0.13 (Tamura et al. 2021), using the MUSCLE algorithm (Edgar, 2004) available in the software. Since the genus *Penicillus* is not monophyletic (Lagourgue et al. 2022), only available sequences of *P. capitatus* populations worldwide were included in the alignment. *Udotea conglutinata* was used as an outgroup species based on Lagourgue et al. (2022). Pairwise distances were calculated using MEGA. The phylogeny was inferred in MEGA using the Maximum Likelihood method and Tamura-Nei model, with uniform rates among sites, 1st+2nd+3rd positions included, and tree branches lengths measured in substitution per site. The haplotype network was built using TCS (https://bioresearch.byu.edu/tcs/) with a threshold of 95% connections for 20 *tuf*A sequences (accession numbers KU361926, KU361927, MG784721, MG784723, MG784726, MG784735, MG784740, MG784747, MG784750, MG784765, MG784771, MG784774, MG784776, MG784784, MG784796, MG784799, MG784813, OR665170 - OR665172) trimmed to the same length (442 bp). TCSBu (Santos et al., 2016) was used to improve the network layout.

2.3. Particle Dispersal Model

The particle-tracking model OpenDrift (Dagestad et al., 2018) (available at https://github.com/OpenDrift/opendrift) was used to

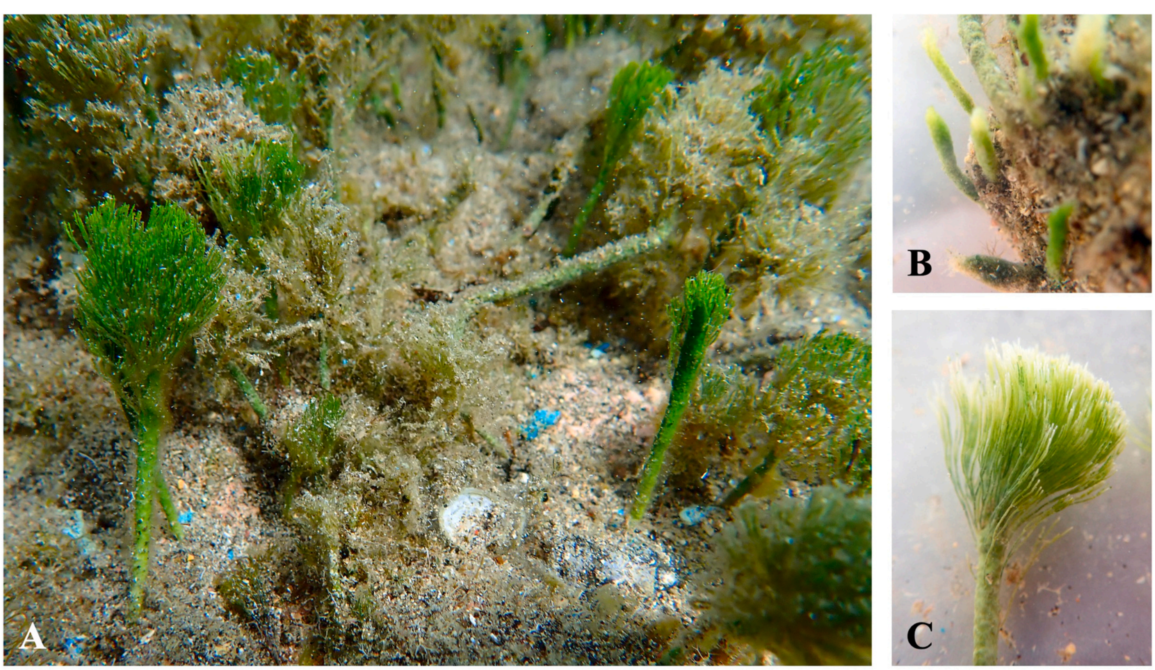

Fig. 1. *Penicillus capitatus* from the Azores. (A) *In situ* image of the species habit and habitat; (B) Stipes growing from the rhizoidal web; (C) Brush-like structure formed by filaments issued from the stip.

simulate the dispersion of particles in the ocean. Open Drift is an open-source model used to simulate the trajectories and fate of objects or substances (e.g., oil drift and weathering, microplastics, larvae drift, etc) drifting in

the ocean. It uses a Runge–Kutta fourth-order time-stepping method whereby particle positions were based on ocean circulation data provided by an ocean model.

The Global Ocean Physics Reanalysis product GLOBAL_-MULTIYEAR_PHY_001_030 (hereafter GLORYS) produced in the framework of the Copernicus Marine Environment Monitoring Service (CMEMS) (Lellouche et al., 2021) was used as the source of the ocean circulation data to the OpenDrift simulations. The GLORYS is a 50 vertical level (from 0 to 5500 m), 0.083 ×0.083° spatial resolution eddy-resolving model that assimilates *in situ* and satellite observations, is forced by 3-hourly surface data from the ECMWF ERA-Interim and uses climatological values for river discharge GLORYS. The GLORYS model is widely used with the OpenDrift Model (Soares et al. 2023, Teixeira et al. 2021) and is already validated for the Atlantic Ocean (Drévillon et al., 2022, Lellouche et al., 2021, Lessa et al. 2021), which supports their application to long-distance dispersal simulations. GLORY surface daily mean values from 2010 to 2019, downloaded from the Copernicus website (https://data.marine.copernicus.eu), were used. Neither winds nor waves have been used in the OpenDrift simulations.

Virtual particles (i.e., simulated algal fragments isolated or connected to floating debris) were released in the Azores once a year on 30 December from 2010 to 2019. The particle trajectories were tracked backward (source search) for 365 days (short-term dispersal) based on 12-hour outputs and for 10 years (long-term dispersal) based on weekly outputs. Each simulation started with 10 mil particles released within 10 km radius centered in the position 38.9°S -28.5° W, at 0.5 m from the sea surface. The configuration used considers that the particles remain close to the sea surface for the entire period used in the simulations. Virtual particles were set to be stranded when they reached the continental coastline or islands. A 180-minute time step with a horizontal turbulent diffusion coefficient Kh = 1 m^2s^{-1} was used to represent the unresolved turbulent motions.

2.4. Sea surface temperature measurements

Monthly blended sea surface temperature data between 1982 and 2018 collected by the Advanced Very High Resolution Radiometer (AVHRR) sensor flying onboard the NOAA-n satellites were downloaded from the NASA Sea Level Portal (https://sealevel.nasa.gov/data-analysis-tool) for western and central groups of the archipelago of the Azores (36.8188 N, 29.2441 W - 39.2798 N, 24.8496 W). Long-term temperature change was estimated using the monthly data.

Monthly blended sea surface temperature data between April 2017 and March 2018 were also downloaded for Santa Maria Island and each ecoregion to which *Penicillus capitatus* is reported (Fig. 2). The maximum and minimum temperatures are provided for the mentioned period (Table S1).

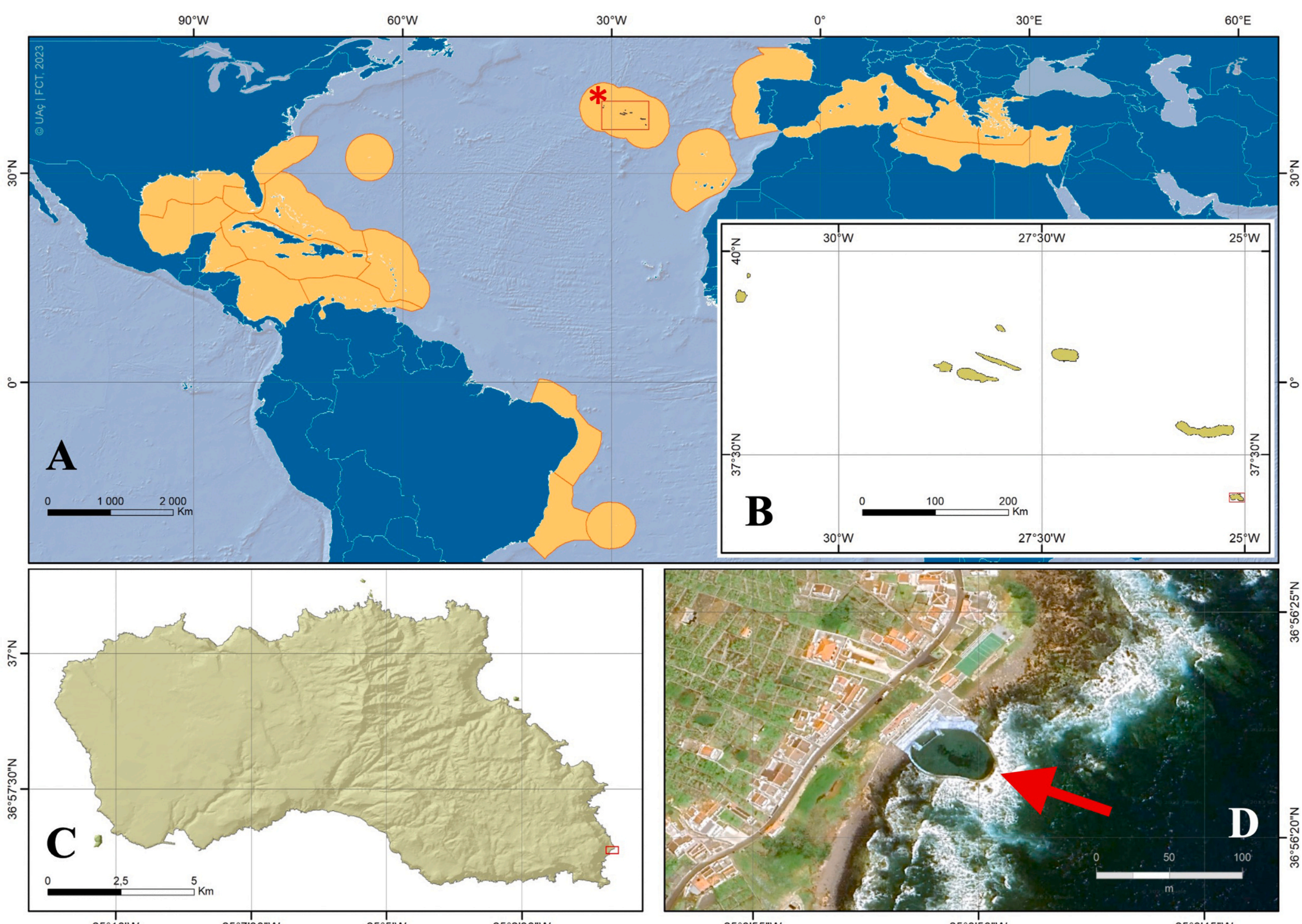

Fig. 2. Study area. (A) Native distribution of *Penicillus capitatus* in the reported ecoregions, with the new record with a "*"; (B) The archipelago of the Azores; (C) Santa Maria Island; (D) Location of the artificial tide pool in Maia (arrow).

3. Results

3.1. Morphology of *Penicillus capitatus* from the Azores

The green alga, newly found in the Azores, agrees with the morphology of *Penicillus capitatus*, namely coenocytic filaments tightly gathered in an upright stipe, which terminates in a brush-like structure in mature individuals (Fig. 1, S1). The alga is up to 10 cm tall and attached to the substratum by fine rhizoidal filaments that form a tight web. Multiple stipes arise from the rhizoidal web that grows between and beneath the sand grains, with the alga vegetatively propagating like *Caulerpa* spp. The stipe is long and cylindrical, simple, or bifurcated. The filaments from the brush-like structure are soft and vary from absent to numerous, with their density probably related to herbivory since the fishes *Sarpa salpa* and *Diplodus sargus* were observed feeding on the algae. *P. capitatus* formed a meadow of separated patches, with more and larger individuals in deeper parts of the pool, probably a location not trampled by the pool users (https://youtu.be/9_ECZwN977U). A few common algae, such as *Asparagopsis* spp. and *Dictyota* spp., were observed growing in this meadow, though further studies are necessary to estimate its biodiversity.

3.2. Genetic variation of *Penicillus capitatus*

DNA-based analyses showed that *Penicillus capitatus* is monophyletic, with transatlantic populations closely related (Figure S3). A single *rbc*L haplotype was detected, i.e., sequences of Azorean specimens are identical to those from the Gulf of Mexico and the Caribbean (Table S5). The haplotype network based on *tuf*A sequences indicates low variation within the Gulf of Mexico and the Caribbean, which differs from the Atlantic populations formed by Bermuda and the Azores (Fig. 3). Pairwise distances among the three *tuf*A haplotypes detected range from 0.01% to 0.03% (Table S6).

3.3. Species dispersion simulations and seawater temperature trends

Simulations of particle dispersal in the backward mode were used to assess possible localities serving as species sources for the archipelago of the Azores. All 365 days backward simulations showed a connection with extensive shorelines in the West Temperate Atlantic and the West Tropical Atlantic basins (Fig. 4a – for the 30 December 2011–30 December 2011 results) within 365 days. Long-term 10 years backward simulations, with particles tracked every week (Fig. 4b – for the 30 December 2019–04 January 2010 results), indicated that all continental regions included in the model present a connectivity with the Azores, except for areas in the East shores of the Atlantic basin above 43ºN (Fig. 4b). All places with known native populations of *Penicillus capitatus* are physically connected to the Azores by surface flows in 1 and 10 years.

Sea Surface Temperature (SST) acquired from satellite measurements between 1982 and 2018 shows an average increase of 0.94º C in 36 years (Fig. 5, Table S7), based on the linear trend $y(t) = 0.00346\,t + 18.2594$ for time t in months. Although the rate of temperature increase has been accelerating worldwide, the collected data showed a decrease between 2013 and 2016, probably due to negative SST anomalies (Fig. 5). Consequently, though a conservative estimate, an increase of 1.05º C in the last 40 years was calculated for the Azorean waters, considering the same trend was maintained over the previous years.

SST in the ecoregions where *Penicillus capitatus* is known to occur

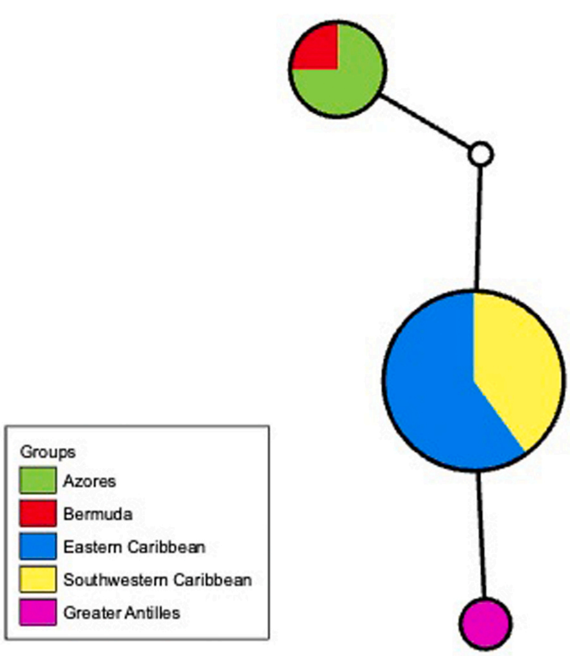

Fig. 3. Haplotype network of *tuf*A sequences of *Penicillus capitatus* from the North Atlantic.

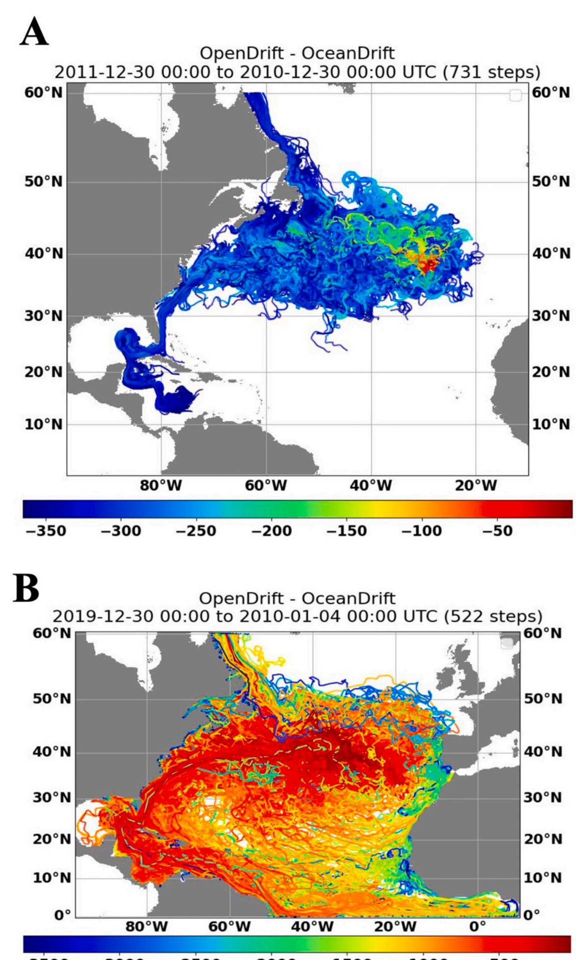

Fig. 4. Backward trajectory of virtual particles released from the Azores, colored according to the time past from release (days). (A) Particles were released on 30/December/2012 and tracked backward for 365 days. Note that North America, Central America, and the Caribbean represent special sources for the Azores in a period of less than a year; (B) Particles released on 30/December/2019 and tracked backward for ten years. Note that all the Atlantic, except for the Eastern Atlantic in latitudes higher than 43ºN, present a connection with the Azores.

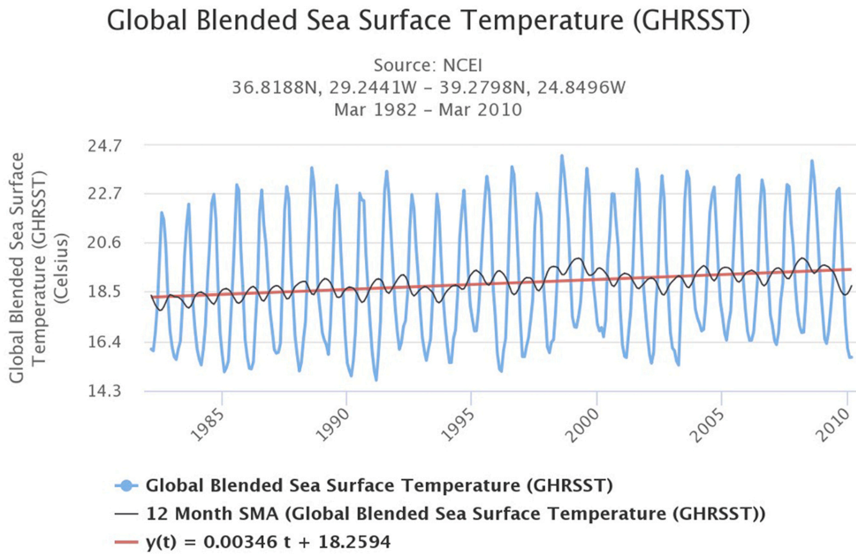

Fig. 5. Monthly blended sea surface temperature data collected by sensors flying onboard the NOAA-n satellites between 1982 and 2018 averaged over the Azores area (blue line). The black line denotes the 12 months running mean filtered data, and the red line represents the linear trend fitted to the monthly data.

ranged from 11.5° C in the winter to 30.0° C in the summer between 2017 and 2018 (Table S1). SST in Santa Maria Island is also within this range, with values between 16.99° C and 24.05° C in the same period (Figure S4).

4. Discussion

The green alga *Penicillus capitatus* is reported for the first time for the archipelago of the Azores, exhibiting a close genetic relationship with populations from the Western Atlantic. Simulations of the species dispersal suggested a connection with all previously known native populations of the species in the short and long term. Although the current seawater temperature in Santa Maria Island is within the temperature range of the regions where *Penicillus capitatus* occurs, the recent success of the species' establishment in the Azores may be related to the current increase of 1.05° C in the archipelagic waters in the last four decades.

4.1. Penicilus capitatus in the ecoregion Azores Canaries Madeira

The first report of *Penicillus capitatus* in the ecoregion Azores Canaries Madeira dates from 1978 when specimens were dredged from 50 to 110 m in the Madeiran Island of Porto Santo (Audiffred and Prud'homme van Reine, 1985). In 2008, this species was observed forming extensive meadows between 20 and 50 m depths on the Canarian Island of La Palma (Sangil et al. 2010), where it is also found in tide pools with a sedimentary bottom (C. Sangil, personal communication). Recently, *P. capitatus* was reported again in the archipelago of Madeira by SCUBA diving at depths beyond 20 m (Ribeiro et al. 2019) in Porto Santo Island and observed in a natural tide pool in Madeira Island (Ribeiro et al. 2023). Additionally, the species has extended its occurrence in the Canary Islands to Tenerife (https://www.biodiversidadcanarias.es/biota/especie/E00834?lang=en) and is also probably in the rest of the western islands in the archipelago (C. Sangil, personal communication). Lastly, *P. capitatus* is here reported to a tide pool with the bottom covered with sand in the Azorean archipelago.

Two general facts arise from such observations: (1) the species previously inhabited deeper waters and is gradually becoming established in intertidal zones; and (2) the species may have been present in these islands longer than reported and may have a wider unknown distribution in subtidal soft bottoms since phycologists scarcely survey those. Sangil et al. (2010), Ribeiro et al. (2019), and Neto et al. (2022) highlighted the lack of knowledge concerning the macroalgae present in this type of subtidal environment for the Canary Islands, Madeira, and the Azores, respectively. For the same reason, it is equally impossible to estimate if *Penicillus capitatus* is a recent colonization in the Azores. In fact, local users of the tide pool where the species was found claim that its occurrence dates back some years and occurs in deeper waters in the proximity of the pool (R. Resende, personal communication). Although it is highly probable that the species is established in deeper waters, the tide pool may provide a climate refuge since its water is warmer than the open sea. The pool also offers sheltered conditions from exposure to waves and larger herbivores' access. Due to the lack of surveys of soft bottoms throughout the archipelago, it is unknown if this is the only population present in these islands. Nonetheless, this species has indeed not been previously reported to other well-studied intertidal habitats of the Azores (Neto et al. 2021).

On the other hand, as *Penicillus capitatus* may also be found in the "*Espera*-phase", i.e., as up to 20 mm long non-consolidated branched siphons (Sangil et al. 2010), studies on herbarium collections are necessary to confirm if the species has been previously found in the Azores with such habit. The "*Espera*-phase" is present all year in the Mediterranean, while the adult phase occurs only occasionally (Sangil et al. 2010). In the Canary Islands, the populations of *P. capitatus* fluctuated, with the adult phase dominant in the summer and the "*Espera*-phase" in the winter (Sangil et al. 2010). Additional prospections in Santa Maria Islands are necessary to assess the population assemblage throughout the year. Further sequencing of individuals from different patches within the tide pool using less saturated genetic markers could also clarify if this population is composed of clones derived from a single founding event.

4.2. Penicillus capitatus in the Atlantic Ocean

The Gulf Stream and the Azores Current are the dominant pathways to the Azores archipelago and can bring macroalgal fragments from the US coast and even from the northwestern Caribbean Sea towards the Azores archipelago in less than one year. Likewise, Cardoso and Caldeira (2021) suggested these currents as the pathway to plastic marine debris to the archipelago of the Azores, with the eddies and meanders from these currents of importance in this transport process. To this end, regions as far as the Brazil Current can be the source of the marine debris arriving at the Azores within 10 years of simulation (Cardoso and Caldeira, 2021).

The relationship between the Western Atlantic and the Azorean populations is confirmed here based on comparative DNA-based analyses of two genetic markers, indicating that the new record has probably arrived in this archipelago by rafting in the main currents, probably attached to, or intertwined with natural or artificial debris. This suggestion is corroborated by the particle dispersal simulations presented here, which show a strong connection with North America, Central America, and the Caribbean. This connection agrees with the simulations presented by Cardigos et al. (2013), which suggested the Gulf Stream as a source to explain the establishment of *Caulerpa prolifera* in the Azores. Based on these simulations, it is also probable that populations of *Penicillus capitatus* occurring in Madeira and the Canary Islands share the same origin as that presently detected in the Azores. Since *P. capitatus* was recorded to Madeira 30 years prior to the Canary Islands and 44 years before the present first report to the Azores, it is unclear if there were multiple introduction events to the different archipelagos or a single introduction event with further flow between those islands. Further collection for molecular studies of other known populations of *P. capitatus* is necessary to confirm the relationship within the ecoregion Azores Canaries Madeira populations and between the Azorean, the Western Atlantic, and the Mediterranean populations. Analyses based on molecular data could help clarify if the species was introduced into those islands through the short-term connection to the Western Atlantic or the long-term connection to the Mediterranean, or even through both connections in multiple introductions events.

The new record of *Penicillus capitatus* in the Azores represents a northern expansion of the species distribution outside the Mediterranean basin (Guiry & Gury 2023). The particle dispersal simulations indicate that the species has probably arrived in the Azores by rafting in the main currents, though human-mediated introduction should not be ignored. Non-native species currently presented in the Azores were mainly introduced by shipping (hull fouling and ballast waters) and escape from confinement (aquarium trade and transport on livestock). *P. capitatus* is a species used in home aquaria and can be easily bought online. Nevertheless, the relative remoteness of Santa Maria Island and the current European law (EU Regulation 1143/2014) affecting customs would affect the success of an online purchase. Another possibility is the transport of germlings in ballast waters, hull fouling, or shellfish. However, with different projects tackling the introduction of non-native species in the Azores (such as ASMAS, PIMA, and BALA), the species would probably have been detected closer to the surveyed areas, such as harbors and marinas (Neto et al. 2022).

4.3. Establishment of Penicilus capitatus in the Azores

Whether *Penicillus capitatus* arrived multiple times through natural dispersal or in a single anthropogenic introduction, the increase of 1.05º C in the sea surface temperature has probably favored the successful establishment of the species in the Azores. As Sangil et al. (2010) suggested, an increase of nearly 2º C between 1973 and 2006 might have promoted the growth of the species when it was first found in the Canary Islands. Various Bryopsidales have been newly reported to this ecoregion and suggested as a sign of marine tropicalization of the region, such as: *Penicillus canariensis* (Sangil et al. 2010) and *Halimeda incrassata* (Sangil et al. 2018) in the Canary Islands; *Caulerpa prolifera* in the Azores (Cacabelos et al., 2018); *Avrainvillea canariensis* in Madeira (Ribeiro et al. 2019) and the Azores (Neto et al. 2022); and *Caulerpa ashmeadii*, *Penicillus capitatus* and *Halimeda incrassata* in Madeira (Ribeiro et al. 2023).

In conclusion, the presence of *Penicillus capitatus* in the Azores is a probable consequence of global warming, increasing the list of species from warmer waters newly reported to the region. Further collection on soft bottoms should be performed to assess the distribution of the recently found species and the presence of other taxa that might have been overlooked. Additional sampling from other known populations is necessary to enable broad studies at a phylogeographical level.

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CRediT authorship contribution statement

Mónica Moura: Funding acquisition, Methodology, Writing – review & editing. **Suzanne Fredericq:** Conceptualization, Writing – original draft, Writing – review & editing. **Carlos Teixeira:** Data curation, Formal analysis, Investigation, Methodology, Writing – original draft, Writing – review & editing. **William Schmidt:** Writing – original draft, Writing – review & editing, Formal analysis, Investigation. **Ana Isabel Ferreira:** Data curation, Formal analysis, Investigation, Writing – review & editing. **Daniela Gabriel:** Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Writing – original draft, 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.

Data availability

The data used in this study are available in the Supplementary Files.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.rsma.2024.103597.

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