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The role of species thermal plasticity for alien species invasibility in a changing climate: A case study of *Lophocladia trichoclados*

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ABSTRACT

The Mediterranean Sea provides fertile ground for understanding the complex interplay between invasive species and native habitats, particularly within the context of climate change. This thermal tolerance study reveals the remarkable ability of *Lophocladia trichoclados,* a red algae species that has proven highly invasive, to adapt to varying temperatures, particularly thriving in colder Mediterranean waters, where it can withstand temperatures as low as 14 °C, a trait not observed in its native habitat. This rapid acclimation, occurring in less than a century, might entail a trade-off with high temperature resistance. Additionally, all sampled populations in the Mediterranean share the same haplotype, suggesting a common origin and the possibility that we might be facing an exceptionally acclimatable and invasive strain. This high degree of acclimatability could determine the future spread capacity in a changing scenario, highlighting the importance of considering both acclimation and adaptation in understanding the expansion of invasive species' ranges.

1. Introduction

Invasive alien species (IAS) are those that are introduced to a new area outside of their native range, with negative impacts on the local ecosystem, economy and human health (Pyšek and Richardson, 2010). The ability of IAS to establish and spread in a new area depends on diverse factors, such as their physiological tolerance, life history traits and competitive abilities (Devin and Beisel 2007; Van Kleunen et al., 2015; Lee 2002; Whitney and Gabler 2008). One of the most important factors that define the geographical range or future spread of a species is temperature (Adey and Steneck, 2001, Amundrud and Srivastava 2020; Schweiger and Beierkuhnlein 2016), influencing the ability to invade and spread of many species, such are some invasive fish (e.g. *Micropterus dolomieu* and *Salmo trutta*) or plants (e.g. *Impatiens glandulifera*) (Lawrence et al. 2015; Willis and Hulme 2002; Wood and Budy 2009). In this line, thermal width is highly related with temperature tolerance in invasive species, giving to the IAS a higher ability to acclimate or adapt to new environmental conditions than native species (Kelley, 2014; Parker et al. 2013)

Acclimation and adaptation are two mechanisms through which some species can cope with changes in their environment (Hoffmann and Parsons 1991; Liang et al. 2019; Narum et al. 2013; Somero 2010). Briefly, acclimation is a reversible physiological response of an organism to a change in its environment that occurs within an individual's lifetime and can happen relatively quickly, often within days or weeks (Sinclair and Roberts 2005). Adaptation refers to the long-term genetic changes that allow a species to better survive and reproduce in a particular environment. It is a slow process that takes place over many generations and involves changes in the genetic makeup of a population, providing a selective advantage in a particular environment. Adaptation, however, is irreversible, as it involves genetic changes that are passed on to future generations (Hoffmann et al. 2003; Kuebler et al. 1991).

Thermal requirements may also vary greatly among species and populations since they are determined by species-specific traits, including the organism's metabolic rate, behaviour and adaptation to heat and cold (Gaston 2003, 2009; Jeffree and Jeffree 1994; Kearney and Porter 2009). Within species, a population or group of organisms can be adapted to a specific set of environmental conditions or ecological niche. These populations typically exhibit distinct genetic, physiological and/or behavioural characteristics that allow them to thrive in their specific habitat. These adaptations enable the populations to be better suited to their local environment than other populations of the same species (Hereford 2009; Turesson 1922). However, the ability of populations to acclimate or adapt to climate change is not universal and

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depends on multiple variables that interact in intricate ways. For example, some species with short generation times and high genetic diversity may adapt better and faster to changing conditions than species with long generation times and low genetic diversity (Byrne et al., 2019; Calosi et al., 2013; Pespeni et al., 2013; Reusch and Boyd, 2013; Van Dijk and Hautekeete 2007). Additionally, the speed and magnitude of climate change can outpace the ability of some populations to acclimate, leading to range shifts, declines in population size or even local extinctions (Jump et al., 2006; Peng et al., 2004; Sage et al., 2008; Sykes and Prentice 1995).

The implications of population acclimation or adaptation for the dynamics of species are of special interest when invasive species are involved. For example, if IAS are better able to acclimate to changing climate conditions than native species, they may become even more successful at establishing and spreading in new areas (Beckmann et al., 2009; Lejeusne et al., 2014; Schaffelke et al., 2006; Theoharides and Dukes 2007). In the case of a species with a wide distribution range, it may have an increased probability of finding optimal environmental conditions for its establishment in a potential new area (Lind and Parker 2010; Pyšek and Richardson, 2007; Van Kleunen et al., 2010). In fact, in numerous invasion events, the capacity for acclimation, also known as phenotypic plasticity, has been demonstrated to play a crucial role in the ultimate success of IAS over native populations (Davidson et al., 2011; Lockwood and Somero, 2011; Richards et al., 2006; Santamaría et al., 2021; Tepolt and Somero 2014). Algae and plants possess the capacity to modulate distinct traits, including photosynthetic capacity (Molina-Montenegro et al., 2012; Zanolla et al., 2015), leaf area or shoot allocation (Arenas et al., 2002; Liu and Su 2016) and growth form (Monro and Poore 2009, Santamaría et al., 2021; Van Kleunen et al., 2010), as adaptive responses to prevailing environmental alterations (Lewis et al., 1987; Monro and Poore 2005; Nicotra et al., 2010). This is especially significant considering the pace of environmental changes induced by climate change, where acclimation appears to take precedence over genetic adaptation. Climate change may also create new opportunities for IAS to establish in new areas, either by making the areas hospitable or by altering the distribution range of the native species. In this line, understanding the thermal requirements and species/population specific plasticity of the species that may have invasive behaviour is important for predicting how they will respond to future warming scenarios (Breeman 1990; Ehrlén and Morris, 2015; Osland et al., 2017; Rutterford et al., 2023). This information can be essential to manage species or priority areas for conservation and to predict future outbreaks of more temperature tolerant species (Hobbs 2000; Simberloff et al., 2005).

The Mediterranean Sea stands as one of the most invaded marine ecosystems worldwide, facing a significant influx of non-indigenous species (Galil, 2009; Occhipinti-Ambrogi 2007), mainly due to a high heterogeneity of environmental conditions at regional scale, its direct connection with the contrasting oceanographic conditions of the Atlantic Sea and the Red Sea, and the high influence of climate change in the region, with an average warming rate, more than three times higher than the global average (Garrabou et al., 2022; Pörtner et al., 2019). Therefore, it presents an ideal context to investigate the interplay between invasive and native species, along with the implications of climate change. Among Mediterranean Sea invaders, *Lophocladia trichoclados* (previously misidentified as *Lophocladia lallemandii* (Golo et al., 2023)), is noteworthy for its expansive geographical distribution. This red alga boasts a significantly extensive spatial range, suggesting either a wide thermal tolerance or a considerable capability for adaptation and acclimation (Pakker et al., 1996). In the Mediterranean, it was first reported in the 1990s (Petersen 1918) and has become invasive in several locations along the Mediterranean coast (Katsanevakis et al., 2011; Tiberti et al., 2021), leading to changes in the composition of benthic communities (Ballesteros et al., 2007; Cebrian et al., 2018; Tiberti et al., 2021; Zrelli et al., 2021). Remarkably, it has been suggested that its invasion pattern might be potentially mediated by alterations in the thermal regime within the Northwestern Mediterranean zone (Golo et al., 2023).

To investigate the impact of acclimation plasticity on the expansion capacity of marine IAS, we undertook a thermotolerance study, which aimed to explore potential variations in acclimation plasticity among populations of *Lophocladia trichoclados* from both the invaded and the native regions. Due to its cryptic taxonomic nature (Golo et al., 2023; Golo et al., 2024), molecular analyses were needed to ensure accurate species identification. As a species naturally growing in high contrasting environmental conditions, we related thermal tolerance of populations, the thermal regime they thrive in, and the molecular population variability within populations.

2. Material and methods

2.1. Target species

Lophocladia is a genus within the Rhodomelaceae family, currently comprising eight recognised species (Guiry and Guiry, 2023). One of the most widely distributed species within this genus is the type species, *Lophocladia trichoclados*, found along coastlines globally in warm to temperate regions (Fig. 1). In the Mediterranean Sea, *L. trichoclados* stands out as one of the most notorious invaders (Zenetos et al., 2005). Its presence was first documented in the early 1900s (Aysel 1981; Cormaci et al., 1992; Feldmann and Feldmann, 1939; Petersen 1918), and it was initially considered a Lessepsian invader, originating from the Red Sea. However, it has since been reclassified as an invasive species originating from the Atlantic Ocean (Golo et al., 2023). The invasive behaviour of *L. trichoclados* was first observed in 1994 (Patzner 1998), and since then it has been known to dominate local ecosystems, attaining coverages of up to 100%. This dominance has had a profound impact on the highly diverse ecosystems of the Mediterranean Sea (Fig. 2) (Ballesteros et al., 2007; Cebrian et al., 2018; Tiberti et al., 2021; Zrelli et al., 2021).

2.2. Experimental set-up

To investigate the potential conservation of thermal tolerance we conducted a laboratory-based study among native populations from the Canary Islands (Atlantic Ocean), and from three introduced populations from Cabrera and Menorca (the Balearic Islands) and the Columbretes Islands, both in the Mediterranean Sea (Fig. 3). Thermal tolerance of this species was studied by Pakker in 1996, comparing populations from the Canary Islands and the Caribbean. For further comparison, we adopted similar experimental conditions to those used by Pakker, but extending the duration of the experiments to 45 days in contrast to the two-weeks' duration of Pakker's study. Growth rates were daily standardised in all experiments. In cases where, after 4 weeks, all tissue had perished, we adjusted the growth rate to 0. This adjustment was made because prolonged exposure to these conditions invariably resulted in a survival rate of 0.

The specimens (45 per population) were collected through diving or snorkelling at a depth of 5–10m in each location and were then transported to our laboratory. To minimise stress, all individuals were gathered the day before transfer and kept in a cool and moist environment without submersion. Upon arrival at the laboratory, each population sample was placed in separate 5-L aquaria filled with sterilised seawater and Von Stosch medium at a concentration of 1 ml per L (Von Stosch 1964). The aquaria were then placed in incubators set at a constant temperature of 21 °C and provided with a light intensity of 15 μmol/m2 for a duration of one week to allow for acclimatisation. By subjecting individuals from different populations to identical thermal regimes in a controlled laboratory environment, we aimed to determine whether thermal tolerance is conserved among these populations. This experimental setup would provide valuable insights into the potential adaptability and ecological implications of thermal tolerance in the context of

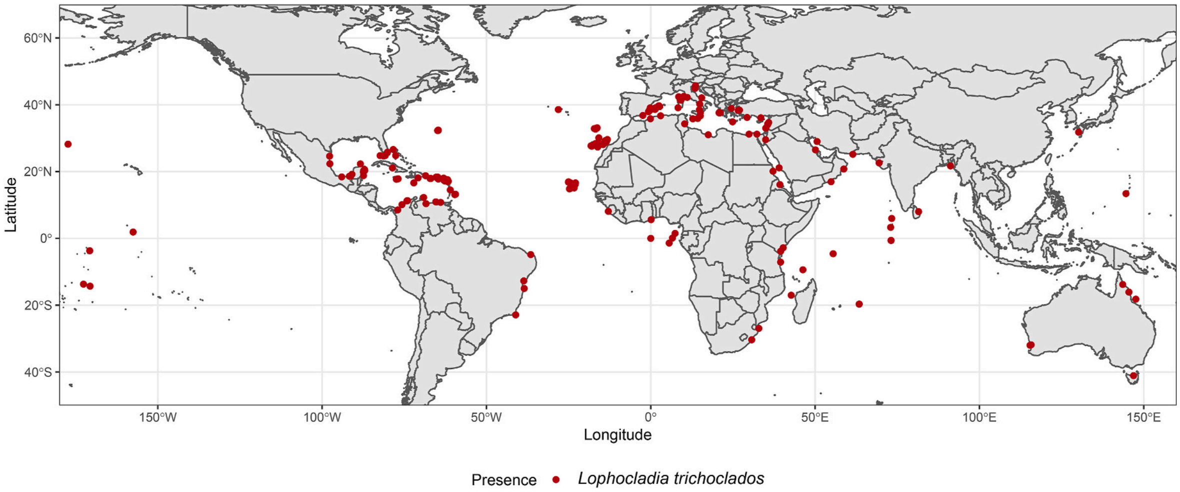

Fig. 1). Global distribution of *Lophocladia trichoclados* (Golo et al. 2023).

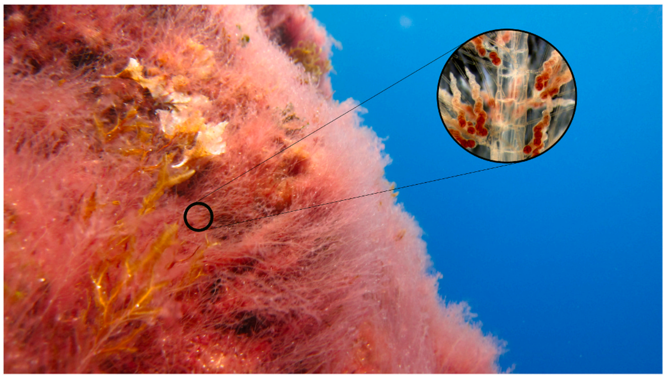

Fig. 2). *Lophocladia trichoclados* covering a habitat dominated by photophilous algae in the Balearic Islands. In detail the thallus and tetrasporangia of *Lophocladia* sp. (photographies by Capdevila P., and Huissman J.M.)

the introduced range of the species.

After the acclimatisation period, we randomly selected five individuals from each population and exposed them to nine different temperature treatments (12, 14, 16, 21, 24, 26, 27, 28, 29 °C). From each individual, one small fragment (0.5 cm–1 cm) was placed in a Petri dish containing 5 ml of water with Von Stock medium (Pakker et al., 1996). Each temperature treatment was carried out in a Radiber incubator (same model) and individuals (5 per population and temperature) were gradually acclimatised to the desired temperature by increasing or decreasing the temperature by one degree every two days (Supplementary Fig. 1). To assess the effect of thermal conditions, we evaluated the relative growth rate of the individuals using a methodology adapted from Pakker (1996). Measurements were taken every four days for 10 time points (approximately 45 days) using a stereoscopic microscope (stereomicroscope Stemi, 2000-C, Carl Zeiss, Berlin, Germany) equipped with an AxioCam ERc 5s camera). Photographs were captured using a specific microscope and camera (Zeiss AXIO Imager A.2 (Carl Zeiss, Berlin, Germany) equipped with an AxioCam MRc5 camera), and the images were analysed using the Zen2011 software (Blue Edition) to obtain measurements in millimetres. The daily growth of each individual was calculated using the following formula, and the average growth rate was computed for each location and time point.

Relative Growth rate = (Gf - Gi) / Gi

The difference in algal length (mm) between the final time point (Gf) and the initial time point (Gi) was used to calculate the growth rate. The difference value was divided by the total duration of the experiment (45 days) to obtain the daily growth rate for each temperature and location. This approach allowed for the comparison of growth patterns across different locations. Although the growth measurements of *L. trichoclados* samples were recorded in millimetres, the application of the formula described above results in relative growth rates in relation to the initial measurement. This range encompasses values from −1, indicating complete tissue death of the sample, to 0, representing no growth, while the positive values indicate the number of growth occurrences relative to the initial size (e.g., once, twice, and so on).

2.3. *Statistical analysis*

The effect of temperature on growth was evaluated using linear mixed models (LMM). The experimental design incorporated 9 fixed temperature levels and 5 populations, while time was treated as a random factor, with 10 measurements. To assess growth variations among populations, analysis of variance (ANOVA) was performed, followed by the post-hoc Tukey's test for all models. All the data were analysed in the statistical environment R (R version 3.6.3) (R Core Team, 2018), while the packages *car* and *emmeans* were used for the Anova and the post-hoc tests, respectively.

2.4. *Thermal environmental conditions*

To gain a comprehensive insight into the thermal regime of the sampling locations, temperatures during the warmest and coldest days were extracted using satellite data from 2014 to 2019. Satellite-derived sea surface temperatures (SST) are frequently employed as a substitute for coastal temperatures due to their strong correlation with in situ sea temperature (IST), as demonstrated by Brewin et al. (2018). The temperature data derived from satellites were acquired from the NOAA's OISST dataset (Reynolds et al., 2002) for the period in question. Several temperature thresholds were established to align with the conditions in the thermal-tolerance experiment (12, 14, 16, 17, 24, 25, 26, 27, 28, and 29 °C). These thresholds were used to determine the number of days in each population that fell below or exceeded the specified temperature conditions.

2.5. *Molecular analyses*

Distinguishing morphological characteristics among species can be subtle, and in cases where fertile material is absent, identifying species within the *Lophocladia* genus can be challenging, often resulting in uncertainties (Abbott et al., 2010; Huisman 2018; Womersley and Parsons,

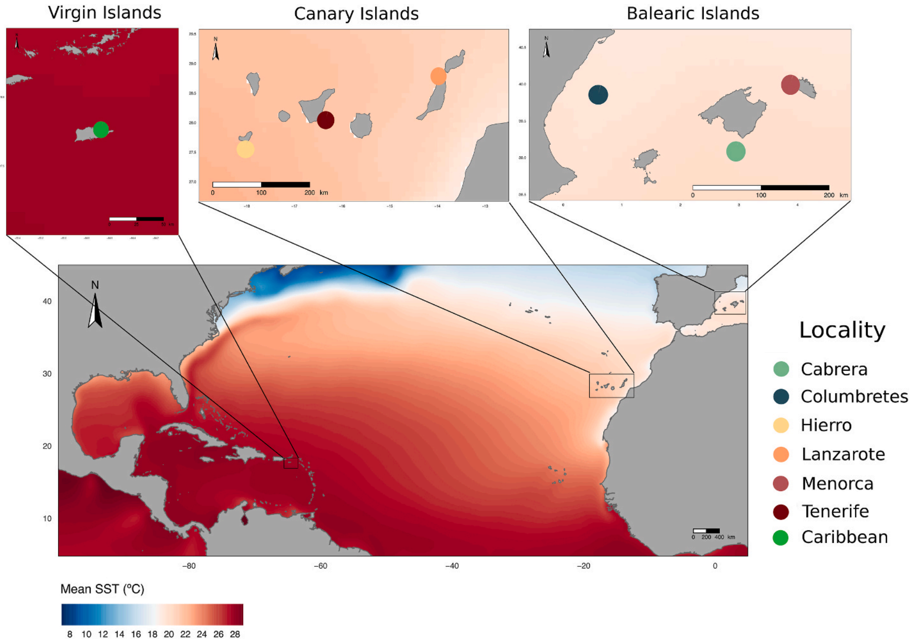

Fig. 3). The map illustrates the geographic locations selected for thermotolerance experiments and genetic analysis of the populations sampling. The Atlantic populations encompass El Hierro, Tenerife, and Lanzarote within the Canary Islands and Caribbean Islands, while the western Mediterranean populations include Cabrera, Columbretes, and Menorca. The map background provides a visual representation of the thermal regimes in the Atlantic and Mediterranean regions.

2003). In such situations, molecular-assisted identification methods become valuable tools for reevaluating species delineation and identification within the *Lophocladia* genus (Golo et al., 2024).

DNA extraction was carried out using the DNeasy Plant Mini Kit (QiaGen) following the supplier's protocol. Fragments of the *rbc*L gene were amplified using an Applied Biosystems 2720 Thermal Cycler and the primer pairs FrbcL – R1150 and F2 – R1464 or R1452 (Díaz-Tapia et al., 2018; Freshwater et al., 1994). The PCR master mix (25 μL) comprised 2 μL of each dNTP (10 μM), 10 × reaction buffer, 2 μL of each primer (10 μM), 2 μL of MgCl2, and 1 unit of Taq DNA polymerase (Thermo Scientific Taq). The PCR protocol consisted of an initial denaturation step (93 °C for 3 min), followed by 35 cycles of denaturation (94 °C for 30 s), primer annealing (45 °C for 30 s), extension (74 °C for 90 s) and a final extension (74 °C for 5 min) (Díaz-Tapia et al., 2018). Subsequently, the PCR products were purified and sequenced by Macrogen Inc. (Madrid, Spain).

A total of 23 new sequences were obtained, and only sequences meeting the criteria of having no ambiguous bases and a length greater than 600 bp were included in the final alignment for phylogenetic analysis. Sequence alignment was conducted using MUSCLE in R v3.6.0. The subsequent phylogenetic analysis was performed using the R packages ape v5.3 (Paradis and Schliep 2019) and phangorn v2.5.5 (Schliep 2011). Both Maximum Likelihood (ML) and Bayesian (MrBayes) approaches were employed for tree generation. The branch support was evaluated using 1000 replicates for ML and 20,000 replicates for Bayesian analysis.

The genetic diversity among populations of *Lophocladia trichoclados* was investigated by haplotyping all sequences obtained in this study. The analysis of *rbc*L sequences was performed using the R package "pegas" (Paradis, 2010). Furthermore, all available *rbc*L sequences of *L. trichoclados* were utilised to assess genetic variations within and outside the Mediterranean region.

3. Results

During the experimental period, *Lophocladia trichoclados* displayed a significant growth rate under optimal temperature conditions (between 16 and 21 °C), reaching values of 11 times the initial measurement in Columbretes, 8 times in Cabrera and Tenerife, and 5 times in Menorca. Notably, no mortality was observed among the samples in either temperature treatment until T5 (day 20) (Fig. 4).

The growth rate of *Lophocladia trichoclados* showed a significant variation among populations and temperatures throughout the experiment (Supplementary Fig. 2; Fig. 4). The Menorca population exhibited the lowest growth rate, while the Cabrera, Columbretes and Tenerife populations displayed similar and higher growth rates (Supplementary Table 1, Fig. 4). Extreme low temperatures (12-14 °C) and high temperatures (28 and 29 °C) seemed to inhibit growth, causing tissue loss in all populations at the end of the experiment period (time 10, 45th day) (Supplementary Table 2; Fig. 4). However, at 16 °C, positive thallus growth was observed in all populations except for the Tenerife one, while at 21 °C, all populations exhibited substantial and significant growth (Fig. 4). The positive growth rate persisted until reaching temperatures of 26 °C, except for the Menorca population, where almost no growth was observed (Supplementary Table 2; Fig. 5). Furthermore, at 27 °C, all populations from the Mediterranean region stabilised or showed a decline in growth, whereas the population from Tenerife continued to grow (Supplementary Table 2; Fig. 5). In summary, although growth rates were slightly different among populations, all the Mediterranean populations displayed a similar thermal tolerance trend, with optimal growth observed at moderate temperatures ranging from 16 °C to 26 °C. This thermal range is comparable to that found for the Atlantic population, which demonstrated adaptation to slightly warmer conditions, ranging from 21 °C to 27 °C (Fig. 5). The thermal tolerance trend observed in our experiment for the Tenerife population closely resembles that reported by Pakker (1996) in the Canary Island (Tenerife) and Caribbean populations (St. Croix) (Fig. 5).

The analysis of temperature data reveals that all three populations from the Mediterranean Sea experience more than 80 days per year with temperatures exceeding 24 °C (Fig. 6). At the 25-degree threshold, we observe slight variations among the populations. Specifically, Cabrera and Columbretes have an annual count of 75 days exceeding this limit, whereas Menorca shows a slightly lower average of 60 days per year (Fig. 6). However, a significant disparity emerges at the 27-degree threshold. While the Cabrera and Columbretes populations encounter between 9 and 13 days per year, respectively, above this threshold, the

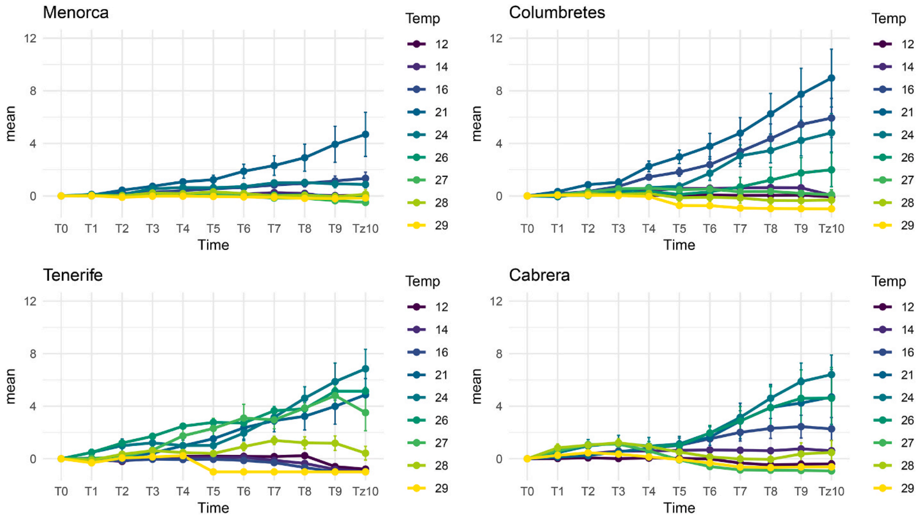

Fig. 4). Growth patterns of the studied populations under various temperature treatments. The growth range is represented on the y-axis, ranging from −1 (indicating complete mortality of the initial biomass) to values above 0, indicating an increase in size relative to the initial biomass. The bars on the graph represent the standard error (SE) among the five replicates at each time point. The experiment duration spanned approximately 45 days, with measurements taken every four days to assess the growth progression.

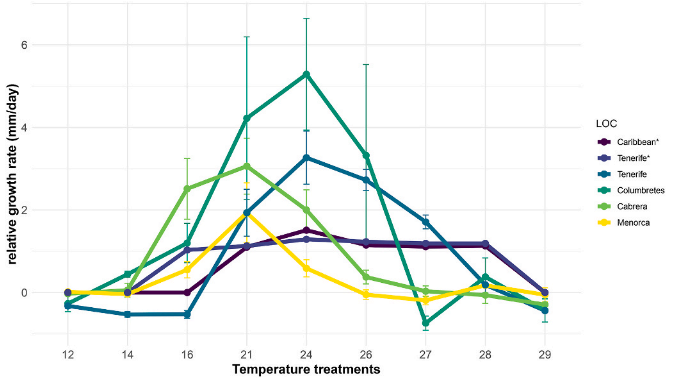

Fig. 5). Growth rate per day for each temperature treatment across all locations. The y-axis represents the relative growth rate measured in mm/day. The bars on the graph indicate the standard deviation between samples for each temperature and population. It is important to note that the Caribbean* and Tenerife* data from Pakker (1996) was included in the analysis but adapted to fit the 45-day duration of our experiment. Additionally, for temperatures above 28°, the growth rate was adjusted to zero, taking into account the total duration of our experiment (45 days) compared to Pakker's study, which had a shorter duration of only 15 days.

Menorca populations are only occasionally subjected to these temperatures (from 0 to 4 days) (Fig. 6).

Based on the analysis of the phylogenetic tree, no genetic differences were detected among the species inhabiting the surveyed localities (Fig. 7), but four distinct haplotypes were identified among them (Fig. 8). While all haplotypes were found in the Canary Islands population (Atlantic Ocean), only one of them (haplotype A; Fig. 8) was found in all the Mediterranean Sea localities.

4. Discussion

Lophocladia trichoclados has extended its range from the Atlantic Ocean, characterised by consistent and warm temperatures, to the Mediterranean Sea, known for its high seasonal temperature fluctuations. Interestingly, there is a slight disparity in the optimal temperature range for growth between the Mediterranean (16–24 °C) and Atlantic (21–27 °C) populations. Although caution should be taken when

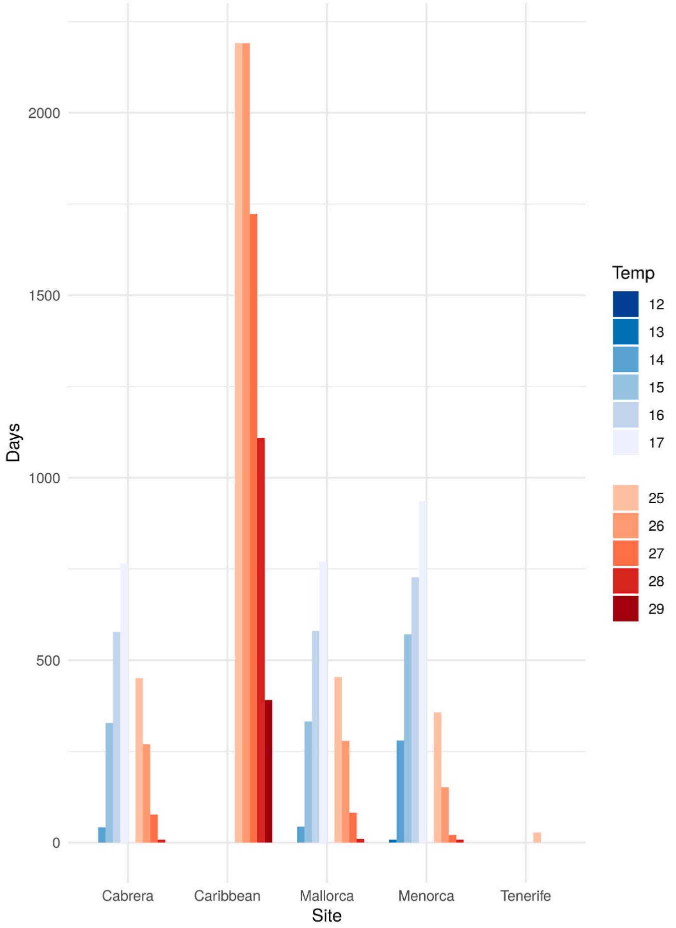

Fig. 6). Average occurrence of days exceeding temperature thresholds (24, 25, 26, 27, 28, and 29 °C) between 2014 and 2019, highlighted in red, for the studied locations (Cabrera, Columbretes, Menorca, Tenerife, and Caribbean). Correspondingly, data pertaining to days falling below thresholds of 12, 14, 16, and 17° are presented in blue. This data originates from the NOAA sea surface temperature database.

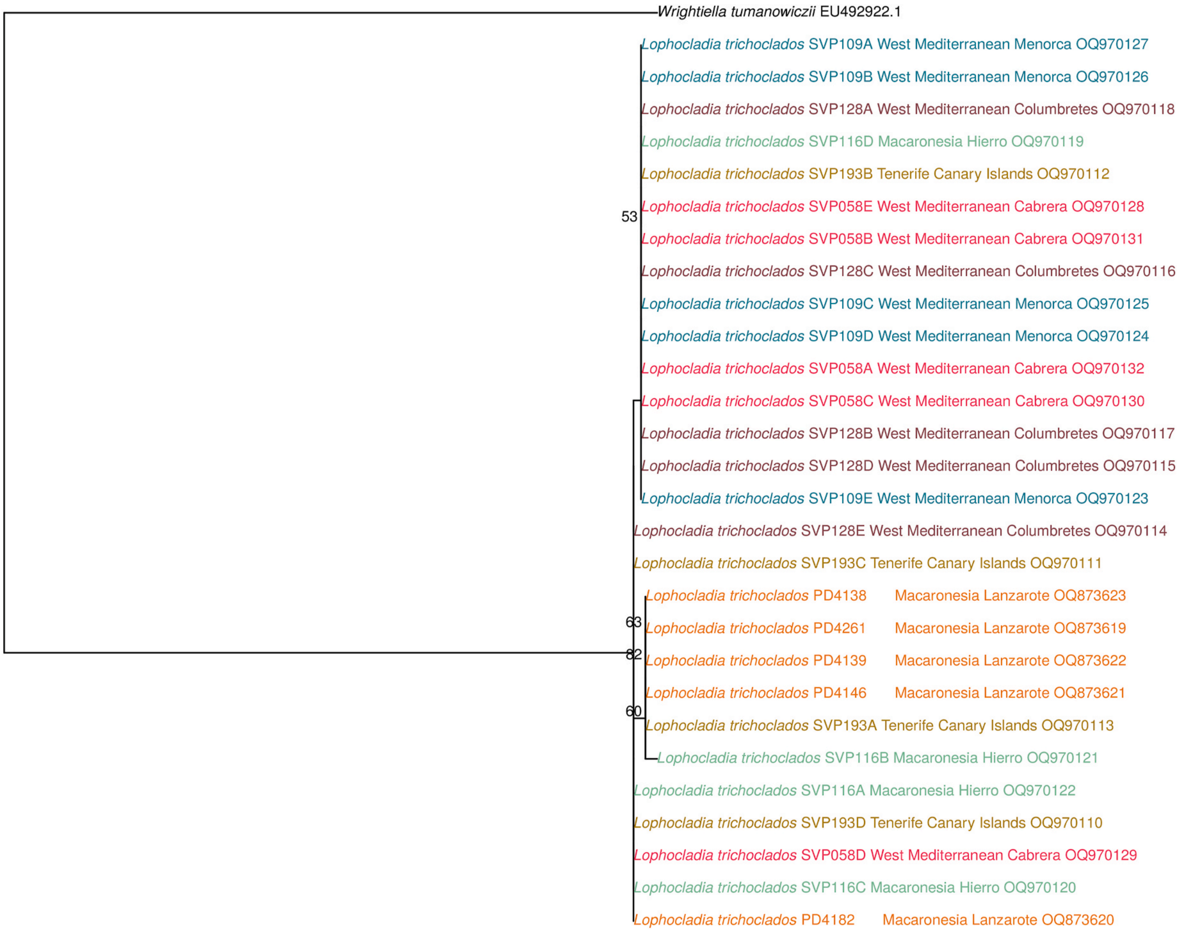

Fig. 7). A maximum likelihood tree and Mr. Bayes analysis were performed using *Lophocladia rbc*L sequence data. The bootstrap values presented indicate the number of bootstrap re-samplings (1,000) and the support percentage after 20,000 cycles in the Bayesian analysis. Nodes with bootstrap support values greater than 70 are indicated. The sequences are color-coded based on their geographic origin. *Wrightiella tumanowiczii* from GenBank was used as an outgroup in the analysis.

comparing experiments, our results are in accordance with those found by Pakker in 1996 for his Atlantic populations (the Canary Islands and the Caribbean). The Eastern Atlantic populations, allegedly originated from long-range colonisation events from the Caribbean (Pakker et al., 1996), where they naturally experience warm temperatures (up to 30 °C) and encounter a relatively narrow and consistent thermal range (Chollett et al., 2012; Kaufmann and Thompson, 2005) (Fig. 3), have not needed to develop significant temperature plasticity. This lack of variability is evident in the absence of substantial differences in the thermal tolerances observed within Atlantic populations. Notably, none of the studied populations in our work grew at temperatures exceeding 28°, probably because such extreme conditions are not encountered in their natural environments.

Significantly, the Mediterranean populations displayed diminished growth beyond 27° in comparison to their Atlantic counterparts. Furthermore, their growth started at 16°, which was slightly lower than the 18–21° required for the Atlantic populations to initiate growth. Invasive Mediterranean populations have probably undergone acclimation to survive the colder Mediterranean environmental conditions, with the ability to grow at temperatures <18 °C. This acclimation to lower temperatures for winter survival in the Mediterranean Sea, where water temperatures can reach 14 °C and lower, is potentially at the cost of reduced tolerance to higher temperatures, suggesting a trade-off with losing resistance at higher temperatures to increase survival ability at low temperatures, as has been observed for other species (Willett, 2010). Remarkably, low species tolerance to cold temperatures (<14 °C) might explain its restricted distribution in the Western Mediterranean Sea, where populations thrive in the warmest areas such as the Balearic Islands and Columbretes, but are absent in areas more influenced by colder waters such as the Gulf of Leon, where temperatures can reach 10 °C.

Interestingly, and bearing in mind that consistent thermal tolerance ranges of *L. trichoclados* have been sustained over millennia in the Atlantic Ocean (Pakker et al., 1996), our results suggest that only a short time frame of less than a century since its introduction has been enough to alter the thermal tolerance of this species to efficiently cope with the colder winters of the Mediterranean Sea. This finding definitively suggests that *L. trichoclados* is a highly acclimatable species when needed, and this could explain its success as an invader. Species with broad distribution ranges (such is *Lophocladia trichoclados*) are more prone to become invasive, possibly because they possess ancestral adaptations enabling them to survive in various habitats (Kelley 2014). Another common characteristic among invasive species is their ability to tolerate higher temperatures than necessary in their native habitat (Hofmann and Somero 1996; Zerebecki and Sorte 2011). While this holds true for *L. trichoclados* in the Canary Islands, our findings suggest a trade-off in the Mediterranean Sea, where it acclimatizes to withstand colder winters. Whereas, research on invasive species usually emphasizes their tolerance to higher temperatures fewer explore their resilience to colder temperatures. Here we show that invasiveness and spread can be also due to acclimatation on the other way around, being the ability to withstand colder temperatures, the factor that provides to the IAS the ability to spread to new areas. In line with our results, other species, such as *Bromus tectorum*, a grass species invading North America from the

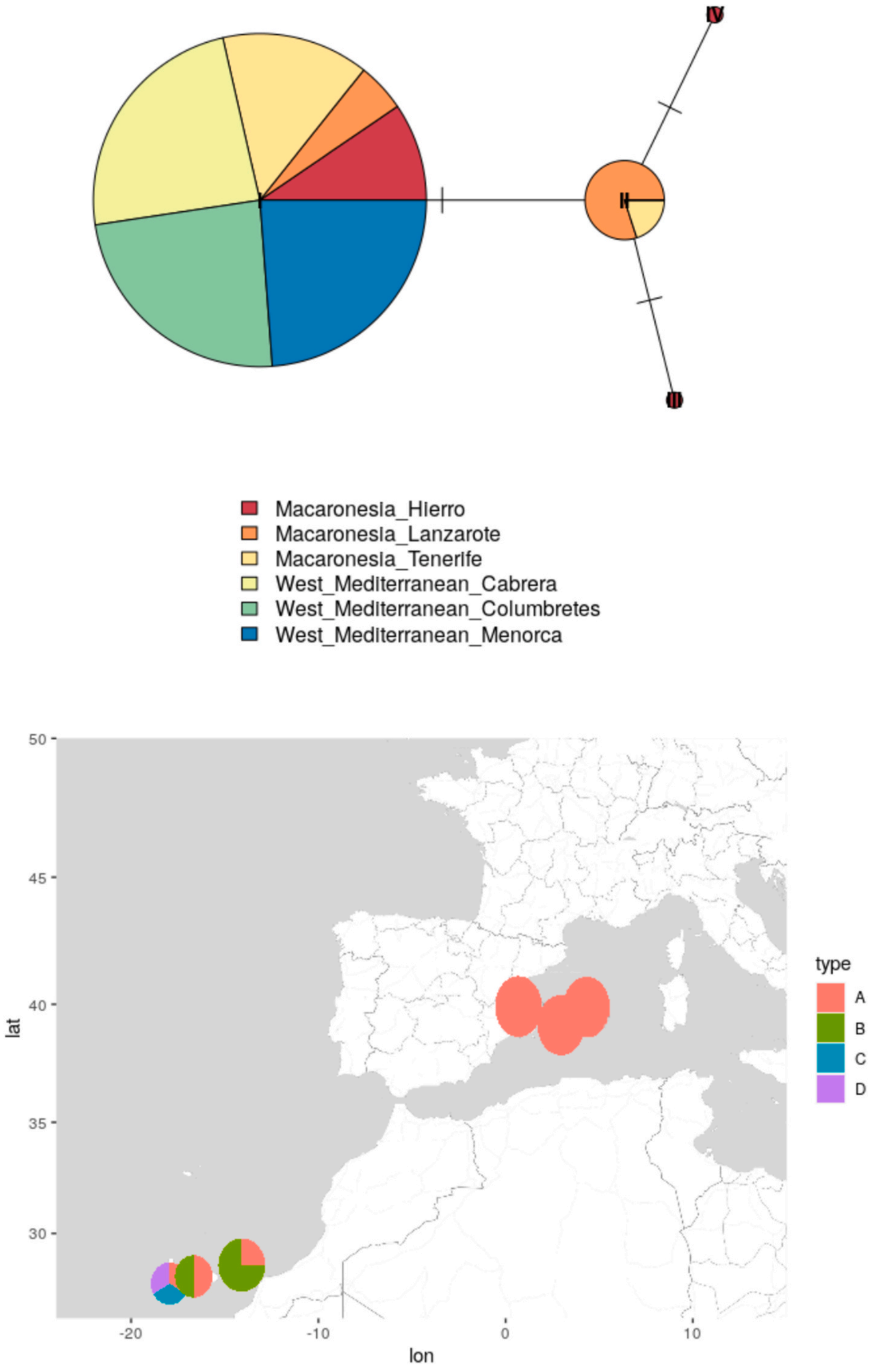

Fig. 8). The haplotypes observed in the four studied localities (Cabrera, Columbretes, Menorca, and Canary Islands) are shown. In the Canary Islands population, samples were collected from three different islands (Tenerife, El Hierro, and Lanzarote), resulting in the identification of haplotypes A, B, C, and D. Conversely, only haplotype A was detected in the Mediterranean populations. The size of each pie chart corresponds to the number of samples, while the colors represent the percentage of each haplotype within each island.

Mediterranean, it's able to invade new areas because invasive populations can endure much harsher winters than those in its native habitat (Bykova and Sage 2012).

As for thermal tolerance, growth rates were generally consistent across populations, although some slight variability was observed, with the Menorca population displaying lower growth rates. Given that the Menorca population inhabits a slightly cooler thermal environment compared to other Mediterranean populations studied, this observation might explain why Menorca has the lowest abundance and expansion of *Lophocladia* among Mediterranean populations (Santamaría et al., 2022). However, apart from temperature, variations in growth rates observed within populations can occur due to other factors such as algae age and size, nutrient availability and interspecific competition. For instance, algal growth rates can fluctuate with age due to alterations in physiological processes like photosynthesis, nutrient uptake, and metabolic activity. Young algal thalli may prioritize resource allocation towards growth, while older individuals may focus more on maintenance and defense mechanisms (Cronin and Hay 1996; Duffy and Hay 1990). However, it's important to note that we always worked with thalli of uniform size and appearance. On the other hand, nutrient concentrations in the surrounding water can also significantly impact macroalgal growth (Mayakun et al., 2013; Ross et al., 2018). In his sense, although nutrient concentrations remained consistent between populations during the experiment, differences in growth rates could also be attributed to varying nutrient availability in their respective original habitats. It's worth mentioning that all Mediterranean populations are situated in areas characterized by oligotrophic conditions (Bosc et al., 2004; Estrada 1996), and as such, significant differences in nutrient availability are not expected.

At the molecular level, although all populations used in the experiments belong to the same species, four distinct haplotypes were identified. All of them were present in the Canary Islands, whereas in the Balearic Islands only one of the haplotypes was detected. The reduced genetic diversity observed in the invaded locality reinforces the theory of a successful invasion following a genetic bottleneck from the Atlantic (Dlugosch and Parker 2008; Golani et al., 2007; Schmid-Hempel et al., 2007). Although the number of samples is small, and despite the species probably arriving in multiple introduction events, it appears that there is only one strain in the Western Mediterranean. The presence of only one strain across Mediterranean populations leads to the hypothesis that the thermal lower temperature tolerance of the Mediterranean populations may be associated with its specific strain capacity, potentially contributing to its proliferation throughout the Mediterranean Sea, where seawater temperatures are lower than in the Atlantic areas where *L. trichoclados* thrives.

An intriguing aspect of Mediterranean *Lophocladia trichoclados* populations is the apparent absence of sexually reproductive individuals (Cebrian and Ballesteros, 2010), suggesting that sexual reproduction is either rare or has remained undetected thus far in this region. In contrast, reproductive structures have been documented in other native areas. To this effect, it appears that asexual reproduction predominates in the Mediterranean Sea, limiting the genetic exchange between populations. This phenomenon, while constraining genetic diversity, may actually favour the proliferation of a single strain that is exceptionally well-adapted to the local Mediterranean conditions or that possesses a high capacity for rapid acclimation to temperature fluctuations.

With climate change driving an increase in the mean temperature of the Mediterranean region (Lionello and Scarascia, 2018; Zittis et al., 2022), one might question the long-term utility *of L. trichoclados* acclimation to colder temperatures. However, it is evident that this species possesses a remarkable capacity for rapid acclimation to abrupt changes. Therefore, in species like this, the focus should shift from whether the adaptation to lower temperatures is advantageous in the present to whether this high acclimation capacity will confer the invasive species a competitive advantage over native species vis-à-vis ongoing climate change. Specific knowledge on species attributes leading to greater heat stress resistance or rapid acclimation (Dong et al., 2022; Liu et al., 2014; Lockwood and Somero, 2011; Somero 2010), usually disregarded in marine macroalgae ecology, could be of great utility to understand future trends of native and invasive macroalgae species and thereby provide effective management strategies aimed at prioritising conservation areas.

In conclusion, the spread of *Lophocladia trichoclados* from its native Atlantic habitat to the entire Mediterranean Sea highlights its remarkable adaptability to diverse thermal environments. The disparities in temperature environments between populations reflect their ability to acclimate to new conditions, with Mediterranean populations exhibiting adaptations to colder temperatures potentially at the expense of heat tolerance. Despite concerns regarding the long-term implications of climate change on its dynamics, the species' demonstrated capacity for rapid acclimation underscores its competitive advantage in a changing environments. Understanding the mechanisms driving such adaptations is crucial for informing conservation efforts and managing the impacts of invasive species in the face of climate change. By incorporating insights from studies on heat stress resistance and acclimation, we can better anticipate the future dynamics of marine ecosystems and implement effective conservation strategies.

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CRediT authorship contribution statement

R. Golo: Writing – review & editing, Writing – original draft, Methodology, Formal analysis, Data curation. **J. Santamaría:** Writing – review & editing, Formal analysis, Data curation. **A. Vergés:** Writing – review & editing, Supervision, Resources, Methodology, Funding acquisition, Conceptualization. **E. Cebrian:** Writing – review & editing, Writing – original draft, Supervision, Resources, Methodology, Funding acquisition, Conceptualization.

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

Data will be made available on request.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.marenvres.2024.106642.

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