Regional Studies in Marine Science 90 (2025) 104466

Contents lists available at ScienceDirect

Regional Studies in Marine Science

journal homepage: www.elsevier.com/locate/rsma

First record of *Caulerpa prolifera* (Bryopsidales, Chlorophyta) beyond 60m depth in the SW Tenerife Island, Spain

S. Fraissinet [a,*], J. Blanco [b], R. Aguilar [b], S. Rossi [a,c,d]

[a] Department of Biological and Environmental Science and Technology (Di.S.Te.B.A.), University of Salento, Campus Ecotekne, Lecce 73100, Italy
[b] Oceana, Madrid, Spain
[c] CoNISMa Consorzio Nazionale Interuniversitario per le Scienze del Mare, Rome 00196, Italy
[d] Institute of Marine Sciences (LABOMAR), Federal University of Ceará, Fortaleza 60440-900, Brazil

ARTICLE INFO

Keywords:
Caulerpa prolifera
Tenerife Island
Atlantic Ocean
ROV survey

ABSTRACT

The genus *Caulerpa* J. V. Lamouroux, 1809 (Bryopsidales, Chlorophyta) includes more than 100 species worldwide and, due to its morphological variation and dispersal mechanism, can colonize different substrates. As part of scientific surveys, a Remotely Operated Vehicle (ROV) recorded video transects along the southwest side of Tenerife Island (30000 m,^{2} depth range 6.7–156 m). Out of 55 videos recorded, 24 over sandy bottom were found with patches of *C. prolifera*. This represents a first record of *C. prolifera* in a depth range of 25–83 m in the Canary Islands, Spain.

1. Introduction

The genus *Caulerpa* J. V. Lamouroux, 1809 (Bryopsidales, Chlorophyta) has more than 100 species in shallow waters globally distributed, from circum-tropical to warm temperate geographic area (Zubia et al., 2020). The highest *Caulerpa* diversity has been registered in the Caribbean, Indo-Malay rand in the South of Australia (Zubia et al., 2020), but species-level identification is still under debate due to multiple challenges in the identification (Jacobs, 1994; Cacabelos et al., 2019). This seaweed indeed is characterized by high phenotypic plasticity that leads to the overlap of morphological traits among different species; these morphological traits, such as thallus appearance or branch shape, can be strongly influenced by environmental factors, increasing the blur among species boundaries. In addition, the use of historical names based on the morphology creates confusion when integrated with molecular data as in some case the old nomenclature may not correspond to genetically distinct/same species (Belton et al., 2014; de Senerpont Domis et al., 2003; Fernández-García et al., 2015; Verbruggen et al., 2013; Zubia et al., 2020). This genus exhibits remarkable adaptability, occupying diverse environmental niches, that sometimes can overlap with seagrasses like *Cymodocea nodosa* (Olivé et al., 2021; Zubia et al., 2020). These niches vary significantly with temperature, light availability, season, depth, and water movement. The composition and texture of the benthic substrate also play a crucial role in their establishment (Crockett and Keough, 2014; Fernández-García et al., 2015; Ohba et al., 1992; Zubia et al., 2020). These factors can affect growth and nutrient uptake causing different responses even at the species and population levels, showcasing their ecological versatility in various marine environments. *Caulerpa* can spread and colonize various habitats rapidly, thanks to its dispersal mechanisms, which include fragmentation expansion and stolon elongation (Parreira et al., 2021), creating patches or meadows over mud or sandy bottoms but also rocky or mixed substrata (Cunha et al., 2013). *Caulerpa prolifera* as other Bryopsidales is a siphonous green alga (SGA). These algae depend on a non-cellular cylindrical structure (siphonous), which consists of one large tubular cell containing a central vacuole, filled with water and ions that exert pressure against the walls, resulting in a characteristic plump appearance, with the other cellular components (e.g. multiple nuclei or a macronucleus, chloroplasts, etc.) arranged around it (Del Cortona et al., 2020; Vroom and Smith, 2003). Moreover, the distinctive biology and structural arrangement of *Caulerpa* species play a significant role in the proliferation of these macroalgae, complicating their detection through conventional environmental DNA methods, which have recently been employed to swiftly identify the presence of invasive species, thereby exacerbating the challenge in the eradication (Waters et al., 2023). *Caulerpa* spp are responsible to declining seagrasses population, increasing sulfide concentration in the sediments and altering their biogeochemical composition caused ecological disturbances in the

* Corresponding author.
E-mail address: silvia.fraissinet@unisalento.it (S. Fraissinet).

https://doi.org/10.1016/j.rsma.2025.104466
Received 5 May 2025; Received in revised form 1 September 2025; Accepted 2 September 2025
Available online 3 September 2025

Mediterranean Sea, Australia, and California (Parreira et al., 2021; Waters et al., 2023; Holmer et al., 2009). *Caulerpa prolifera* is distributed globally across three primary geographical regions: the West Atlantic, the East Atlantic, and the Mediterranean Sea. Higher diversity and older ancestral types have been documented in the West Atlantic, implying that this population may be more ancient than the others (Varela-Álvarez et al., 2015). Similar to the congeneric *Caulerpa cylindracea* and *Caulerpa taxifolia*, *C. prolifera* can also be considered highly invasive, outside its native range and in particular within it, by replacing seagrasses after a disturbance event, modifying the substrate, and consequently making the recovery almost impossible (Holmer et al., 2009).

Populations of *Caulerpa* from the Mediterranean Sea and the Atlantic Ocean exhibit slight differences, primarily due to their surrounding environmental conditions; specifically, Atlantic populations are more adapted to cooler water temperatures compared to their Mediterranean counterparts (Olivé et al., 2021). *C. prolifera* in low light conditions, can increase the leaves surface to improve light exposition in shady zones but has a limited ability to photoprotect (Collado-Vides, 2002; Brewton and Lapointe, 2023; García-Sánchez et al., 2012), is indeed, commonly found in sheltered areas with high organic matter content and low hydrodynamisms, preferring habitats between 1 and 20 m of depth (Cacabelos et al., 2019; Emilio Sánchez-Moyano et al., 2001). Its presence (highly sparse) has been reported down to 50 m in Tenerife Island in 2005, reporting this depth as the lower limit. Twenty years later, we found *Caulerpa prolifera* again at 50 m depth in Tenerife Island (in the same area), not thinned but abundant. Moreover, its presence extends to depths greater than 80 m, beginning to thin out at depths greater than 60 m. This is the first record of *C. prolifera* in water depths deeper than generally known in the Canarians, reaching 83.2 m in the southwest Tenerife Islands.

2. Materials and Methods

2.1. Study area

The study area is on the west side of Tenerife Island, between La Arena (28,22785° N, 16,84197° W) and the southern part of San Juan Beach (28.172931° N, 16.807127° W). The coast mainly consists of rocky cliffs with some sandy beaches along the shoreline. Four polygons and their surrounding areas were explored to map benthic habitats and evaluate the conservation and health status of the site selected for restoration within the Ocean Citizen project framework (Fig. 1).

2.2. ROV survey

On board the OCEANA Catamaran, the ROV survey was carried out between June 16th and 25th, 2024. ROV transects were performed using Sibiu Pro Nido Robotics ROV, able to submerge down to −300 m, improved with a 4 K camera with a tilt angle of 60 degrees. The ROV had 1500-lumen LED lights, 8 motors, and long-lasting batteries. The ROV was not equipped with a sampling arm; thus, collecting samples was not

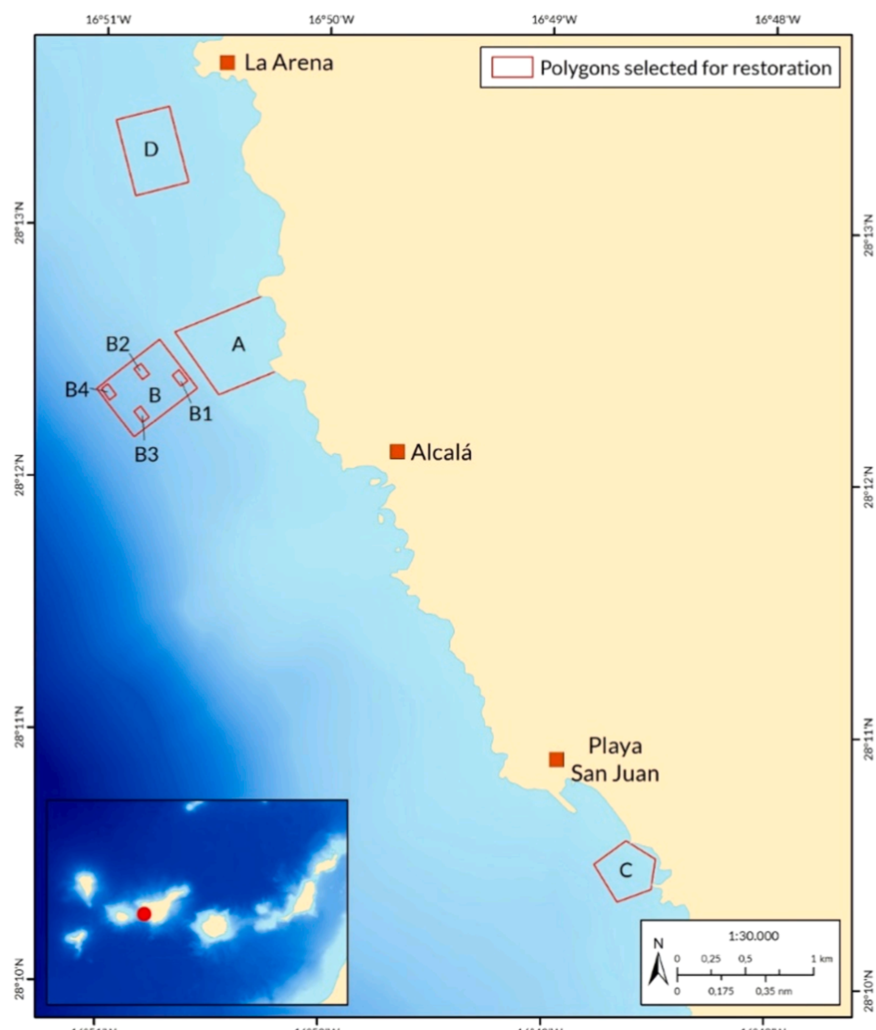

Fig. 1. Map of the study area, with the red polygons indicating the areas selected for restoration in the Ocean Citizen project.

possible during the campaign. Transects were performed by drifting together with the boat along the surveyed area. During the last 3 days of the cruise, laser pointers (20 cm intra-laser distance) were used. The average speed during the surveys was 0.2/0.3 knots, while the average width pathway of the ROV's camera view was 185 cm. The depths of the ROV dives ranged from 6.7 to 156.8 m. 55 ROV transects were successfully performed, covering approximately 31217 m^2.

2.3. ROV video analysis and map production

The ROV videos were analyzed using VLC software. The area of each transect was calculated by QGIS software using the length of the transect and the width of the pathway defined by the camera view. The density of the *Caulerpa* laminae was calculated by dividing their number by the sampled surface of each transect, covered by the seaweed, to provide the percentage of occupancy.

3. Results and discussion

Caulerpa prolifera was detected in 24 out of 55 transects, and in 13 of these transects (54 %), its presence was registered over 50 m in depth, in a range between 25.7 m and 82.4 m (Fig. 2). It was mainly observed in the sandy bottom and on mixed sediments, occasionally associated with *Cymopolia barbata* and *Heteroconger longissimus.* Most of the time, this co-occurrence was at an average depth of 51 m for both species.

C. prolifera presence at 50 m depth is not new for the SW side of Tenerife island, Barquín-Diez and coworkers reported it in 2005, the same area surveyed in this work, noticing that the percentage of substrate occupied by the seaweed was decreasing from 27 m down to 50 m, where it start to disappear completely, they also assumed the possibility that *C. prolifera* presence stand down to 60 m (Barquín-Diez et al., 2005). In contrast to what was observed 20 years ago, this survey revealed medium-dense *C. prolifera* patches at depths of 50 and 60 m (Fig. 3). *C. prolifera* now appears to start decreasing in the number of laminae and thus in the surface area of substrate occupied at a depth of 65 m, indicating a shift toward greater depths.

The number of laminas counted in each transect ranged from a few dozen to several hundred, with varying densities throughout the study area. Higher values were registered in the bathymetric range between 45 and 55 m, followed by the 25–35 m depth (Fig. 4A-4B). In Cabrera National Park, deeper populations of *C. racemosa* (30 m) thrive better than those in shallower areas (10 m), with higher values of biomass, frond and stolon length, and number of laminae. However, the opposite trend was observed in the Northern Tyrrhenian Sea along the Italian coast with denser *C. racemosa* populations in the shallow areas (Cebrian, Ballesteros, 2009; Piazzi et al., 2001). Seawater temperature, light conditions, season, and depth all affect populations in different ways. This is particularly true for *Caulerpa* species that show a lot of variety in their shape and function, whether among different species or within the same species in different conditions (Cebrian, Ballesteros, 2009).

Light plays a significant role in the spatial distribution of *C. prolifera*. A recent study (Olivé et al., 2021) compared two populations of this seaweed: one from the Mediterranean Sea and its counterpart in the Atlantic region; the former displayed increased photosynthetic rates. Conversely, the population from the Atlantic region, specifically in the Canary Islands, exhibited high photosynthetic efficiency adapted to lower saturation irradiance levels (Olivé et al., 2021). This seaweed has been demonstrated to be a shade-adapter (García-Sánchez et al., 2012; Olivé et al., 2021; Sangil and Juan, 2020). In addition, *C. prolifera* can change its morphological lamina shape as a response to different light intensities; laminae from a shade environment are elongated, while in high light conditions, laminae become shorter and broader, respectively increasing and reducing the lamina surface area (Collado-Vides, 2002). The clear waters of the Canary Islands probably let the light filter down to 90 m of depth, with low irradiance, resulting in the lamina's adaptation in a slender and thinner shape of the ramets in deeper waters (as shown in Fig. 2).

Temperature is also a crucial factor in determining the distribution of species in seawater. In 2024, global sea surface temperature (SST) and upper 2000 m ocean heat content reached unprecedented record highs, a result of a continuous (and recently accelerated) ocean warming trend observed over the last decades (Cheng et al., 2025). The genus *Caulerpa* spp. is known for its adaptability, and local conditions can influence how populations acclimate to temperature changes (Schoepf et al., 2015). Increases in seawater temperature may affect populations of the same species differently, especially if they are adapted to different thermal environments (Vinagre et al., 2018). For instance, *C. prolifera* communities from Mar Menor have a threshold above 30 °C for both photosynthesis and metabolism (Terrados and Ros, 1992). The Mediterranean ones instead are adapted to mean sea surface temperatures (SST) ranging from 25 to 27 °C in Summer, compared to around 24 °C in the Atlantic near the Canary Islands (Garcias-Bonet et al., 2019; Tuya et al., 2014).

In the Canary basin, a warming trend has been registered over decades both in the oceanic and coastal areas, even if it is highly more evident in the open ocean with respect to near-shore stations, probably due to the upwelling region, which can influence the values (Vélez-Belchí et al., 2015; Varela et al., 2022). As a result, *C. prolifera* populations in the Mar Menor and Mediterranean Sea may be better equipped to handle changes in temperature than their Atlantic counterparts. The ocean warming and the variation in SST in the North Atlantic region are the result of complex multifactor interactions (e.g. winds, oceanic currents, upwelling phenomenon, global climate change), which can lead to a reorganization of biological communities (Taboada, Anadón, 2012; Haroun et al., 1993). This vegetational shift toward deeper waters was already reported for the Canary Islands in the early 1990s, due to the more stable conditions of deeper water (Haroun et al., 1993). The updated distribution records can further reinforce the idea that the deep-water flora of the Canary Islands is closely connected to the warm-temperate flora of the western Atlantic and the western Mediterranean (Haroun et al., 1993), with the Macaronesia archipelago serving as a bridge among them. Additionally, the recent discoveries of *C. prolifera* population in the Azores with a West Atlantic origin may also lend support to this idea, suggesting an expansion towards northern areas and supporting the hypothesis that the Western Atlantic still can represent an origin of this species (Cacabelos et al., 2019; Varela-Álvarez et al., 2015). However, as it is well known that during periods of glaciation, a temperature change could shift the northern boundaries of

Fig. 2. *C. prolifera* detected at 82.4 m (A), 77.1 m (B), 71.3 m (C).

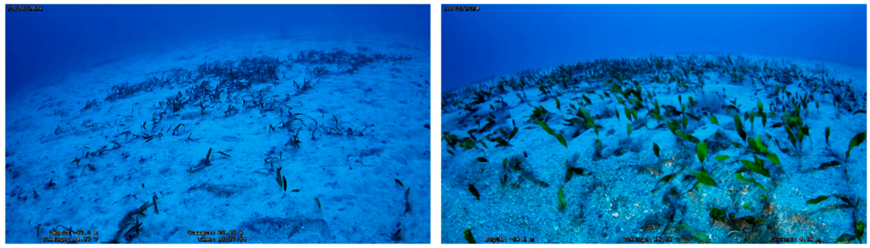

Fig. 3. Frame from the videos of ROV dive 13 and 24. Patches of *C. prolifera* were found at depths of 62 m (left) and 49.1 m (right).

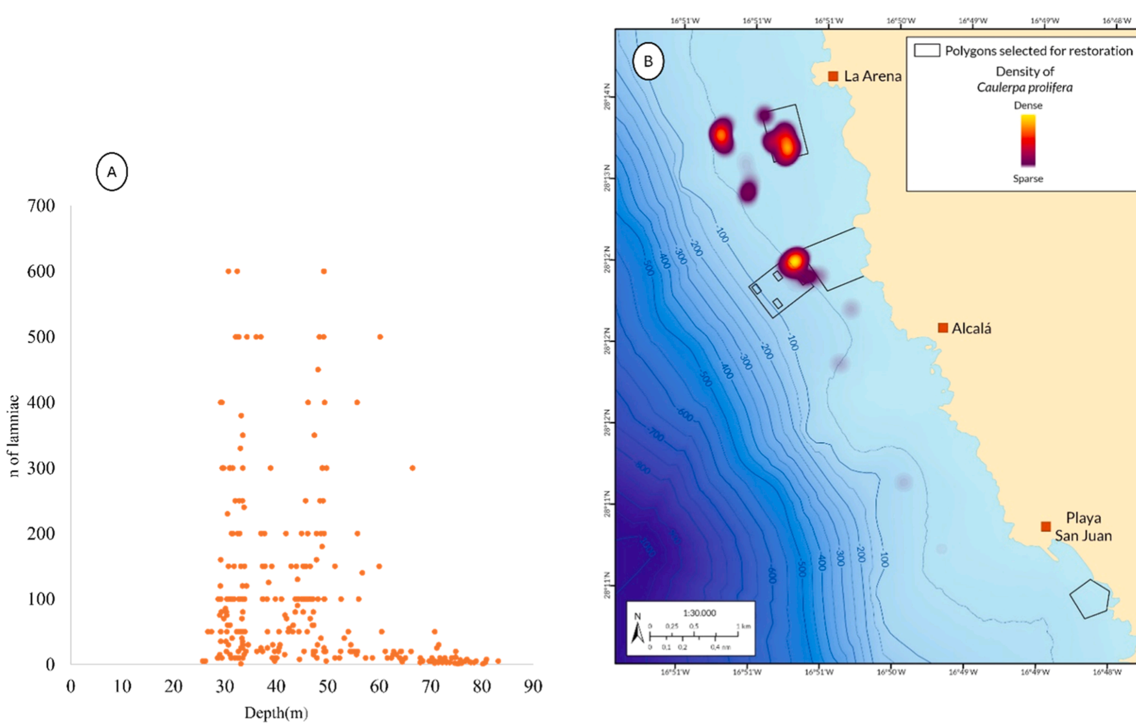

Fig. 4. A. Dispersion graph of the recorded number of *C. prolifera* leaves at different depths in the survey area. B. The data plotted as a concentration map referred to the transects performed in the study area.

some strictly subtropical or tropical-subtropical species south of the Macaronesia islands (Haroun et al., 1993), global warming could shift boundaries northward or to deeper waters.

4. Conclusions

This is the first record of *C. prolifera* down to more than 80 m, in the Canarian archipelago. Our data indicate the presence of *C. prolifera* in Atlantic waters (SW Tenerife Island) at a higher depth than previously observed. This could represent a concerning condition if linked to climate change, as seawater temperatures are rising, indicating a possible shift of seaweed to deeper waters compared to 20 years ago. The study presents a snapshot of the actual situation. Further studies are needed to expand knowledge about the ecology of these algae, including collecting samples from the field to characterize it at laboratory level and improving effort in broaden the area of study, investigating other sites in the Tenerife Island with focus on different depths, to understand any possible distribution scenario around the island, and if there are any possible linkage with the ocean warming.

CRediT authorship contribution statement

Silvia Fraissinet: Conceptualization, Investigation, Writing original draft, Writing—review and editing. **Jorge Blanco:** Investigation, Data curation, Visualization, Writing—review and editing. **Ricardo Aguilar:** Conceptualization, Investigation, Resources, Supervision, Writing—review and editing, Project administration. **Sergio Rossi:** Conceptualization, Resources, Writing—review and editing, Supervision, Project administration, Funding acquisition.

Funding

This paper belongs to the project OCEAN CITIZEN (“Marine forest coastal restoration: an underwater gardening socio-ecological plan”, Horizon Europe HORIZON-MISS-2021-OCEAN-02-01, Contract Number 101093910).

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.

Acknowledgments

The authors would also like to thank all the OCEANA crew members on the catamaran (Ranger) for their invaluable help and daily dedication in sampling and mapping activities.

Data availability

Data will be made available on request.

References

Barquín-Diez, J., González-Lorenzo, G., Martín-García, L., Gil-Rodríguez, M.C., Brito-Hernández, A., 2005. Distribución espacial de las comunidades bentónicas submareales de los fondos someros de canarias. I: las comunidades de sustrato blando de las costas de tenerife. Vieraea 33, 435–438.

Belton, G.S., van Reine, W.F.P.H., Huisman, J.M., Draisma, S.G., D. Gurgel, C.F., 2014. Resolving phenotypic plasticity and species designation in the morphologically challenging caulerpa racemosa–peltata complex (Chlorophyta, Caulerpaceae). J. Phycol. 50 (1), 32–54. https://doi.org/10.1111/jpy.12132.

Brewton, R.A., Lapointe, B.E., 2023. The Green macroalga *Caulerpa prolifera* replaces seagrass in a nitrogen enriched, phosphorus limited, urbanized estuary. Ecol. Indic. 156, 111035. https://doi.org/10.1016/j.ecolind.2023.111035.

Cacabelos, E., Faria, J., Martins, G.M., Mir, C., Parente, M.I., Gabriel, D., Sánchez, R., Altamirano, M., Costa, A.C., Prud'homme Van Reine, W., Neto, A.I., 2019. First record of *Caulerpa prolifera* in the azores (NE Atlantic). Bot. Mar. 62, 155–160. https://doi.org/10.1515/bot-2018-0075.

Cebrian, E., Ballesteros, E., 2009. Temporal and spatial variability in shallow-and deep-water populations of the invasive *Caulerpa racemosa* var. Cylindracea in the Western Mediterranean. Estuar. Coast. Shelf Sci. 83 (4), 469–474. https://doi.org/10.1016/j.ecss.2009.04.026.

Cheng, L., Abraham, J., Trenberth, K.E., Reagan, J., Zhang, H.M., Storto, A., Gues, F., 2025. Record high temperatures in the ocean in 2024. Adv. Atmos. Sci. 1–18.

Collado-Vides, L. (2002). Morphological plasticity of *Caulerpa prolifera* (Caulerpales, Chlorophyta) in relation to growth form in a coral reef lagoon.

Crockett, P.F., Keough, M.J., 2014. Ecological niches of three abundant *Caulerpa* species in port phillip bay, southeast Australia. Aquat. Bot. 119, 120–131. https://doi.org/10.1016/j.aquabot.2014.08.007.

Cunha, A.H., Varela-Alvarez, E., Paulo, D.S., Sousa, I., Serrao, E.A., 2013. The rediscovery of Caulerpa prolifera in Ria Formosa, Portugal, 60 years after the previous record. Cah. Biol. Mar. 54, 359–364.

de Senerpont Domis, L.N., Famà, P., Bartlett, A.J., Prud'homme van reine, W.F., Espinosa, C.A., Trono Jr., G.C., 2003. Defining taxon boundaries in members of the morphologically and genetically plastic genes *Caulerpa* (caulerpales, chlorophyta). J. Phycol. 39 (6), 1019–1037.

Del Cortona, A., Jackson, C.J., Bucchini, F., Van Bel, M., D'hondt, S., Škaloud, P., Leliaert, F., 2020. Neoproterozoic origin and multiple transitions to macroscopic growth in Green seaweeds. Proc. Natl. Acad. Sci. 117 (5), 2551–2559. https://doi.org/10.1073/pnas.1910060117.

Emilio Sánchez-Moyano, J., Estacio, F.J., García-Adiego, E.M., Carlos García-Gómez, J., 2001. Effect of the vegetative cycle of *Caulerpa prolifera* on the spatio-temporal variation of invertebrate macrofauna. Aquat. Bot. 70, 163–174. https://doi.org/10.1016/S0304-3770(00)00144-3.

Fernández-García, C., Cortés, J., Alvarado, J.J., Nivia-Ruiz, J., 2015. Physical factors contributing to the benthic dominance of the alga *Caulerpa sertularioides* (Caulerpaceae, Chlorophyta) in the upwelling Bahía culebra, north pacific of Costa Rica. RBT 60, 93. https://doi.org/10.15517/rbt.v60i2.19970.

García-Sánchez, M., Korbee, N., Pérez-Ruzafa, I.M., Marcos, C., Domínguez, B., Figueroa, F.L., Pérez-Ruzafa, Á., 2012. Physiological response and photoacclimation capacity of *Caulerpa prolifera* (Forsskål) J.V. Lamouroux and *Cymodocea nodosa* (Ucria) ascherson meadows in the mar menor lagoon (SE Spain). Mar. Environ. Res. 79, 37–47. https://doi.org/10.1016/j.marenvres.2012.05.001.

Garcias-Bonet, N., Vaquer-Sunyer, R., Duarte, C.M., Marbà, N., 2019. Warming effect on nitrogen fixation in Mediterranean macrophyte sediments. Biogeosciences 16, 167–175. https://doi.org/10.5194/bg-16-167-2019.

Haroun, R.J., Prud'homme Van Reine, W.F., Müller, D.G., Serrao, E., Herrera, R., 1993. Deep-water macroalgae from the canary islands: new records and biogeographical relationships. Helgoländer Meeresunters. 47 (2), 125–143.

Holmer, M., Marbà, N., Lamote, M., Duarte, C.M., 2009. Deterioration of sediment quality in seagrass meadows (*Posidonia oceanica*) invaded by macroalgae (*Caulerpa* sp.). Estuaries Coasts 32 (3), 456–466. https://doi.org/10.1007/s12237-009-9133-4.

Jacobs, W.P., 1994. *Caulerpa*. Sci. Am. 271 (6), 100–105.

Ohba, H., Nashima, H., Enomoto, S., 1992. Culture studies on *Caulerpa* (Caulerpales, Chlorophyceae) III. Reproduction, development and morphological variation of laboratory-cultured *C. racemosa var. peltata*. Bot. Mag.= Shokubutsu-gaku-zasshi 105 (4), 589–600.

Olivé, I., Varela-Álvarez, E., Silva, J., Serrão, E., Santos, R., 2021. Physiological potential of the chlorophyte *Caulerpa prolifera* for proliferation across the Mediterranean-Atlantic basins in a warmer ocean. Mar. Ecol. Prog. Ser. 668, 73–84. https://doi.org/10.3354/meps13719.

Parreira, F., Martínez-Crego, B., Lourenço Afonso, C.M., Machado, M., Oliveira, F., Manuel Dos Santos Gonçalves, J., Santos, R., 2021. Biodiversity consequences of *Caulerpa prolifera* takeover of a coastal lagoon. Estuar. Coast. Shelf Sci. 255, 107344. https://doi.org/10.1016/j.ecss.2021.107344.

Piazzi, L., Ceccherelli, G., Cinelli, F., 2001. Threat to macroalgal diversity: effects of the introduced Green alga *Caulerpa racemosa* in the Mediterranean. Mar. Ecol. Prog. Ser. 210, 149–159.

Sangil, C., Juan, A.P.-S., 2020. Spread of *Caulerpa cylindracea* impacts: the colonization of atlantic intertidal communities. Reg. Stud. Mar. Sci. 34, 100989. https://doi.org/10.1016/j.rsma.2019.100989.

Schoepf, V., Stat, M., Falter, J.L., McCulloch, M.T., 2015. Limits to the thermal tolerance of corals adapted to a highly fluctuating, naturally extreme temperature environment. Sci. Rep. 5, 17639. https://doi.org/10.1038/srep17639.

Taboada, F.G., Anadón, R., 2012. Patterns of change in sea surface temperature in the North Atlantic during the last three decades: beyond mean trends. Clim. Change 115, 419–431. https://doi.org/10.1007/s10584-012-0485-6.

Terrados, J., Ros, J.D., 1992. The influence of temperature on seasonal variation of *Caulerpa prolifera* (Forsskal) lamouroux photosynthesis and respiration. J. Exp. Mar. Biol. Ecol. 162, 199–212. https://doi.org/10.1016/0022-0981(92)90201-K.

Tuya, F., Png-Gonzalez, L., Riera, R., Haroun, R., Espino, F., 2014. Ecological structure and function differs between habitats dominated by seagrasses and green seaweeds. Mar. Environ. Res. 98, 1–13. https://doi.org/10.1016/j.marenvres.2014.03.015.

Varela, R., Rodríguez-Díaz, L., De Castro, M., Gómez-Gesteira, M., 2022. Influence of canary upwelling system on coastal SST warming along the 21st century using CMIP6 GCMs. Glob. Planet. Change 208, 103692. https://doi.org/10.1016/j.gloplacha.2021.103692.

Varela-Álvarez, E., Balau, A.C., Marbà, N., Afonso-Carrillo, J., Duarte, C.M., Serrão, E.A., 2015. Genetic diversity and biogeographical patterns of *Caulerpa prolifera* across the Mediterranean and Mediterranean/Atlantic transition zone. Mar. Biol. 162, 557–569. https://doi.org/10.1007/s00227-014-2605-5.

Vélez-Belchí, P., González-Carballo, M., Pérez-Hernández, M.D., Hernández-Guerra, A., 2015. Open ocean temperature and salinity trends in the canary current large marine ecosystem. Cent. Oceanogáfico De Canar. ⟨http://www.unesco.org/new/en/ioc/ts115⟩.

Verbruggen, H., Tyberghein, L., Belton, G.S., Mineur, F., Jueterbock, A., Hoarau, G., De Clerck, O., 2013. Improving transferability of introduced species' distribution models: new tools to forecast the spread of a highly invasive seaweed. PLOS One 8 (6), e68337. https://doi.org/10.1371/journal.pone.0068337.

Vinagre, C., Mendonça, V., Cereja, R., Abreu-Afonso, F., Dias, M., Mizrahi, D., Flores, A. A.V., 2018. Ecological traps in shallow coastal waters: potential effect of heat-waves in tropical and temperate organisms. PLOS One 13, e0192700. https://doi.org/10.1371/journal.pone.0192700.

Vroom, P.S., Smith, C.M., 2003. Life without cells. Biologist 50 (5), 222–226.

Waters, T., Langlois, K., Gold, Z., Theroux, S., Eagle, R.A., 2023. Hidden in plain sight: the invasive macroalga *Caulerpa prolifera* evades detection by environmental DNA methods due to negligible shedding. BioRxiv 07, 2023. https://doi.org/10.1101/2023.07.31.551316.

Zubia, M., Draisma, S.G.A., Morrissey, K.L., Varela-Álvarez, E., De Clerck, O., 2020. Concise review of the genus *Caulerpa* J.V. Lamouroux. J. Appl. Phycol. 32, 23–39. https://doi.org/10.1007/s10811-019-01868-9.