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**Phytobenthic communities of Aegean Sea under the
impact of climatic warming.**

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Περίληψη

Οι φυτοβενθικοί οργανισμοί, ιδιαίτερα τα μακροφύκη και τα θαλάσσια φυτά, είναι θεμελιώδους σημασίας για την παράκτια ζώνη. Παρέχουν κυρίως τροφή και προστασία σε πολλούς οργανισμούς που συνδέονται με τα φυτοβενθικά οικοσυστήματα. Η παρουσία και η κατανομή τους εξαρτάται από το υπόστρωμα και τη διαθεσιμότητα των απαραίτητων θρεπτικών, τη θερμοκρασία, τη διαπερατότητα του φωτός και άλλων βιοτικών παραγόντων, ενώ επηρεάζονται όλο και περισσότερο από ανθρωπογενής πιέσεις. Τα μακροφύκη, ιδιαίτερα τα kelp forests και τα θαλάσσια φυτά, όπως τα θαλάσσια λιβάδια του είδους *Posidonia oceanica*, παρέχουν καταφύγιο και τροφή σε άλλους οργανισμούς προσφέροντας πολλές οικοσυστημικές υπηρεσίες στον άνθρωπο. Το θαλάσσιο φυτοβένθος απειλείται σε παγκόσμιο επίπεδο, ενώ οι μεταβολές και οι επιπτώσεις στο παράκτιο οικοσύστημα δεν έχουν μελετηθεί αρκετά. Η παρούσα πτυχιακή εργασία, αποσκοπεί στην περιγραφή της παρούσας κατάστασης του φυτοβένθους στη Μεσόγειο, σε συσχέτιση με την άνοδο της θαλάσσιας θερμοκρασίας. Πραγματοποιήθηκε ανάλυση δεδομένων επιφανειακής θερμοκρασίας για τη χρονοσειρά 1948-2023 και εξαγωγή της εποχικής διακύμανσης, της κλιματολογίας, της μέσης ετήσιας SST και των ιστογραμμάτων της περιοχής μελέτης (Αιγαίο Πέλαγος). Η θαλάσσια επιφανειακή θερμοκρασία (SST) χαρακτηρίζεται από μια αυξητική τάση, συνοδευόμενη από μεταβολές στην κλιματολογία και στη συχνότητα ακραίων τιμών. Μέγιστες και ελάχιστες τιμές της SST πιθανώς να συνδέονται με την παρουσία ακραίων καιρικών φαινομένων για την περιοχή μελέτης. Κατά τη διάρκεια των τελευταίων δεκαετιών παρατηρείται θέρμανση των επιφανειακών υδάτων, ιδιαίτερα από το 1990 και μετά. Με βάση την κλιματολογία της περιοχής μελέτης, σημαντική αύξηση της θερμοκρασίας παρατηρήθηκε κατά τους μήνες Ιούλιο και Αύγουστο, ξεπερνώντας τη διαφορά του 1°C κατά τη διάρκεια των τελευταίων 25 ετών. Η εποχική διακύμανση της περιόδου 1998-2023, χαρακτηρίζεται από μια αυξητική τάση, ιδιαίτερα για τους μήνες Φεβρουάριο, Σεπτέμβριο και Νοέμβριο, με μέγιστη διαφορά τους 0.95°C. Η αύξηση της θαλάσσιας θερμοκρασίας φαίνεται να επηρεάζει άμεσα την αναπαραγωγική ικανότητα του φυτοβένθους, ενώ έμμεσα ωφελούνται τα εισβολικά είδη. Με την αύξηση της θαλάσσιας θερμοκρασίας αυξάνεται η τρωτότητα του φυτοβένθους και σε συνδυασμό με άλλες πιέσεις μειώνεται η ικανότητα επιβίωσης του. Ο κατακερματισμός του φυτοβενθικών ενδιαιτημάτων με υψηλή βιοποικιλότητα δεν έχει κατανοηθεί σε μεγάλο βαθμό, ενώ χρειάζεται περισσότερη ενημέρωση, έρευνα και επαρκής χρηματοδότηση.

Λέξεις κλειδιά: φυτοβένθος, λιβάδια ποσειδωνίας, Αιγαίο, κλιματική αλλαγή, επιφανειακή θερμοκρασία

Abstract

Phytobenthic communities, particularly macroalgae and seagrasses, are fundamental for the coastal zone, mainly by providing food and shelter to associated species. Their presence and distribution, naturally depends on substrate and nutrient availability, temperature, light penetration, and various biotic factors, and are being increasingly affected by various human pressures. Macroalgae, particularly and seagrasses such as *Posidonia oceanica*, provide shelter and feeding grounds for many marine organisms, as also multiple ecosystem services to human communities. Marine phytobenthos is threatened worldwide, and there is limited knowledge about their response and consequent impacts on coastal ecosystems. This master thesis aims to describe the present status of phytobenthos within global warming in the Mediterranean and especially the Eastern part. Sea surface temperature data for the period 1948-2023 were analyzed to extract seasonal variability, climatology, mean SST (annually), and histogram characteristics of the study area (Aegean Sea). Analysis of sea surface temperature (SST) data from 1983 to 2023 reveals an increasing trend in annual mean SST, along with changes in climatology and the frequency of high temperatures, with both maximum and minimum SST values closely linked to extreme weather events. The data from 1948 to 2023 indicate long-term warming, with a clear upward shift in temperatures over recent decades, particularly from the late 1990s and afterwards. Climatology analysis highlights a consistent increase in SST during the summer months, especially in July and August, with a rise of at least 1°C in the past 25 years. Seasonal variability from 1998 to 2023 further demonstrates an accelerating increase in SST, particularly in February, September, and November, with temperature differences reaching up to 0.95°C. Climate warming directly impacts recruitment and indirectly promotes antagonistic species, jeopardizing the long-term survival of phytobenthic communities. Temperature rise seems to increase the overall stress and therefore the vulnerability of these communities, especially when other stress factors act synergistically. As a conclusion, the decline of marine habitat-forming species still remains poorly understood, and largely hindered by limited awareness, research and funding.

Key Words: phytobenthic communities; *Posidonia oceanica*; canopy forming species; Aegean; climate warming; sea surface temperature.

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1. Introduction

1.1 Coastal zone and macroalgae

Ecosystem is a term describing the total number of organisms that are organized biologically, the interactions among organisms, and the interactions of the organisms and the abiotic environment, resulting in a certain trophic structure and material cycles. Comparing terrestrial and marine ecosystems shows that marine ecosystems are characterized by higher functional diversity due to unique functional patterns. Phyletic diversity in marine ecosystems is higher than in terrestrial ecosystems, answering the question “why more complex functional diversity can be observed in marine ecosystems” ([Langar et al., 2014](#)). Seaweeds are substantial for the coastal zone, considering their structural and functional role, ranging from turfs to kelp forests worldwide. Especially in Europe, seaweed assemblages are among the most diverse ecosystems, supporting over 1500 species (nearly 500 genera). Several studies based on biodiversity and ecosystem functional patterns underline the positive effects of seaweeds on the coastal zone. These benefits include photosynthetic rate, biomass accumulation, nutrient uptake, invasion resistance, and stability, especially when multiple ecosystem functions are considered together ([Mineur et al., 2015](#)). Primary production constitutes a crucial parameter for coastal ecosystems and the survival of marine organisms and therefore the whole food chain. Primary production is comprised of planktonic unicellular algae, benthic unicellular algae, and benthic multicellular algae, also referred to as phytoplankton, microphytobenthos, and macrophytobenthos, respectively. Microphytobenthos and macrophytobenthos are estimated to possess about 10% of the total marine primary production for the world ocean, while on the continental shelf alone, benthic and planktonic algae are about equivalent ([Charpy-Roubaud & Sournia, 1990](#)). Macroalgae are estimated to cover about 3.4 million km^2 and are able to support a net primary production of $1.5 Pg C yr^{-1}$ globally, dominating the coastal zone as primary producers ([Krause-Jensen et al., 2018](#)).

1.1.1 Seagrass vs Macroalgae similarities and differences

Seagrass and macroalgae are among the most productive of the earth’s ecosystems and can be found all over the world’s ocean coastal zone (excluding Antarctica in the case of seagrasses), supporting a variety of resident and transient species that can be harvested and also support fisheries. Both seagrass and macroalgae are benthic photosynthetic organisms and are often grouped together, providing many similar ecosystem services, such as food and shelter for fauna, changes in the biotic and abiotic environment, water oxygenation, recycling of nutrients, trapping and stabilizing sediments, and finally providing nursery ground to many marine organisms (particularly fish). The main differences between macroalgae and seagrass are i) the

absence of vascular tissues while nutrients are diffused through the cell surface for uptake and transport, ii) the lack of underground tissues, iii) in general their wall cells have a fibrillar skeletal framework and extensive polysaccharide matrix and lack lignin, iv) they are characterized by complex and diverse life cycles and reproduction, v) they have five different chlorophyll pigments and a variety of other accessory pigments availing a wide range of wavelengths, resulting in the advantage of growing to light environments with as little as 0.12% of incident light and vi) they are more nutritious and energetically favorable for consumption by herbivores due to lower C:N ratio and lack of lignocellulose tissue ([Macreadie et al., 2017](#)).

1.1.2 Depth and macroalgae

Marine macroalgae can take advantage of a wide range of wavelengths, allowing them to survive up to a maximum depth of 200 m, while they can be categorized into three zones based on depth and surface light (SI). The first distinct zone is composed mainly of leathery algae with a depth limit at about 0.5 % SI, followed by an intermediate zone of foliose and delicate algae with depth limits at 0.1 % SI and a lower zone of encrusted algae extended down to 0.01 % SI. The decrease in thallus specific carbon when the depth increases is often notable, resulting in a thin thallus that is essential for the growth and survival of marine macroalgae at great depths ([Markager & Sand-Jensen, 1992](#)). The mesophotic zone extends from 30 to 150 m beneath the surface, where sunlight gradually fades until its absence. Mesophotic macroalgae assemblages is estimated to be over 100 species per site, while most algae species with similar morphological characteristics are grouped together (when molecular techniques are not applied), leading to an underestimation of true diversity. In contrast to the intertidal and shallow subtidal zones, marine macroalgae haven't been described in detail for the mesophotic zone, mainly due to the advanced technical requirements needed in order to access these depths. Mesophotic environments are considered to be less impacted by industrial and urban development and may represent the last remaining partially preserved continental shelf habitats, where species observed in shallow waters may also be present. The main threats that lead to degradation of the mesophotic zone assemblages in the case of macroalgae are abiotic (tropical cyclones, sedimentation, global warming, and ocean acidification) and anthropogenic factors (mining, fishing, oil and gas activities, invasive species, and eutrophication) ([Spalding et al., 2019](#)).

1.1.3 Temperature and macroalgae

Temperature is one of the most important factors affecting the biogeographical distribution of macroalgae, while direct impacts of ambient temperature on macroalgae composition disturbances are rarely reported. Physiological changes (such as carbon assimilation) and

nutrient uptake rate alteration are documented, while seasonal, spatial, and genetic variability, along with associated responses, have been established for the majority of algae groups. Higher water temperatures can decrease levels of phenolics, and temperature stress can indirectly increase other stress and antioxidant response mechanisms associated with salinity and irradiance, often leading to increased production of stress metabolites ([Stengel et al., 2011](#)). Temperature variation can strongly affect the survival, recruitment, growth, and reproduction of seaweeds, such as marine heatwaves, which negatively affect intertidal macroalgae (growth, nutrient uptake, and photosynthetic performance). Atmospheric heatwaves can also decrease photosynthetic activity, resulting in oxidative stress when direct exposure to intense sunlight leads to increased air temperature, affecting the physiological performance of macroalgae. Both marine and atmospheric heatwaves are the most important drivers in the global distribution of canopy-forming macroalgae, considering temperature, resulting in species decline and range shifts expanding to the structural and functional characteristics of these communities and to the entire ecosystem ([Román et al., 2020](#)).

1.1.4 Threats to macroalgae

Changes in the environment, such as reductions in water quality (depth and photic zone implications), often lead to the loss of macroalgal habitats, and ramifications may occur in other aspects of biodiversity in associated communities. Habitat alienation, which occurs from the development of the coastline (construction of ports, marinas, groynes, and housing developments), may pose threats to macroalgal habitats and biodiversity. Pollution can also result in major changes to water quality by adding nutrients and other chemicals (including industrial developments and their effluents), especially when wastewater treatment is absent. Water quality variables affecting macroalgal habitats are i) nutrients (results in eutrophication increasing frequency, duration, and extent of phytoplankton and macroalgae blooms, low oxygen concentrations, shifts in species compositions, loss of diversity, and an increase in fish diseases and water flow), ii) light penetration (is often reduced), iii) siltation (affecting abundance and % cover of macroalgae), iv) toxic chemicals, and v) introduction of alien species. Nevertheless, human activities on the coast alter little direct evidence on macroalgae diversity, but further (long-term and multidisciplinary) effort is needed in order to estimate the influence of anthropogenic activities on the whole community ([Walker & Kendrick, 1998](#)).

1.2 Macroalgae evolution

Marine benthic macroalgae are chronologically estimated since the Proterozoic (2500 to 853 Ma), while for the Precambrian period, the available data, both in morphological and

evolutionary terms, are incomplete. In order to categorize macroalgae into morphological and evolutionary patterns, the available data can be analyzed using non-parametric multidimensional scaling (NMDS) and functional form group (FFG) approaches. The research of [Bykova et al. \(2020\)](#) shows a progressive increase in thallus size, morphospace range, and aspects of ecological complexity such as canopy heights, surface area/volume ratios, and functional-form groups through time. Despite the gradual increase of evolutionary characteristics through time, a maximization of morphological diversity and size is altered in the Neoproterozoic (Tonian and Ediacaran periods, respectively) and Ordovician. On the other hand, in the terminal Ediacaran Stage (~550-539 Ma) during the Kotlinian crisis, macroalgae were declined, notably interconnecting both Ediacaran-type macro-organisms.

1.3 Macroalgae types

Macroalgae species can be classified into three types named green, red, and brown algae and can be distinguished based on their structural characteristics (sexual reproduction), type of photosynthetic pigments, and food products they store. Green algae are estimated to include 7000 and 1800 unicellular and multicellular marine species respectively, while they are characterized by a simple thallus form in contrast to brown and red algae. Despite the low species number, they are very common in some sea environments (mostly on rocky coasts), and their structural form varies from a single giant cell (*Caulerpa*) to numerous segments with deposits of calcium carbonate. Brown algae are vital in temperate and polar rocky coasts in terms of primary production and are the largest and most complex macroalgae type. The records of species are estimated to be over 1800 marine species, with kelps being the most complex and largest of brown algae, reaching up to 100 m in length while they provide food and shelter for many other organisms and show very high primary production. Finally, red algae are essentially marine (only 6000 live in fresh water or soil), and their number of marine species surpasses green and brown algae combined. They are characterized by simple structural form and, in some cases, heterotrophic behavior (absence of chlorophyll), while they parasitize their hosts. In general, most red algae are filamentous, but thickness, width, and arrangement vary a great deal, and they are able to tolerate a wide range of temperature, salinity, and light. Some species can deposit carbonate calcium within their cell walls, and their calcified thallus can be found in i) thin disks growing over other macroalgae, ii) branches with many joints, and iii) smooth or rough encrusting growths on rocks ([Castro & Huber, 2012](#)). A very important type of macroalgae is seaweed forests, which can be spotted in the infralittoral and circalittoral zones of temperate and cold seas. They are considered to be ecosystem engineers, and they generally belong to Phaeophyceae, especially Fucales (*Cystophora*, *Cystoseira*, *Sargassum*) and Laminariales (*Agarum*, *Laminaria*, *Macrocystis*, *Saccharina*). Within seaweed forests, sessile and mobile animals (Metazoa) are abundant in terms of species richness, and the number of individuals increases the functional role of these ecosystems, but they are not considered to be

ecosystem engineers. Canopy-forming species vary into a wide range of ages, from short-lived species (up to 6 years) to long-lived ones such as *Cystoseira spp.*, which can exceed 50 years and probably much more. These ecosystems are mainly dependent on i) available light, ii) temperature, iii) water movement, iv) nutrients, v) herbivore pressure, and vi) overall ecosystem functioning (distinguished into crustose coralline and sponges, turf macroalgae, low stands of erect macroalgae, canopy-forming seaweed forests, and canopy-forming animal forests). Despite the importance of macroalgae communities (e.g., seaweed forests and algal turfs), they are only considered second-rate communities or degraded stages of the iconic ones (bioconstructions by blade-forming corallines) and animal forests of gorgonians, erect sponges (coralligenous ecosystems), and hexacorallians (coral reefs) (Charles F. Boudouresque et al., 2016).

1.4 Importance of macroalgae

The number of macroalgae species is estimated to be over 7,000, and 700, 265, and 500 genera of red, brown, and green algae, respectively, noting, however, the dynamic and controversial taxonomy, particularly when molecular data analysis is applied. Macroalgae are very important in coastal habitats, creating a potential habitat and foraging area for the total of the faunal community, such as fish, octopuses, squids, snails, oysters, sponges, shrimps, urchins, anemones, worms, polychaetas, crabs, and clams. In addition, macroalgae are characterized by great palatability, nutrition values, and ease of digestion by grazers in comparison to seagrass (e.g., *Posidonia*). Macroalgae beds act like a nursery ground for juveniles of many marine fisheries, and large macroalgae (e.g., kelps) provide substratum for direct spawning, alter local hydrodynamic conditions, promote planktonic larval settlement, and reduce predation pressure ([Macreadie et al., 2017](#)). Seasonal variability is affecting macroalgae, and when under pressure, it may result in habitat loss, where species richness and density of fish seem to decline across seasons in contrast to marine habitats where the density of canopy-forming macroalgae (holdfast and coverage) is high. The latter leads to the fact that high structural complexity can preserve key ecological processes across seasons, leading to advanced conservation attention within spatial management frameworks ([Wilson et al., 2014](#)). In some ecosystems, such as coral reefs, benthic macroalgae assemblages are dynamically determined by the association of algae production (some macroalgae species can take advantage of high nutrient availability, often driven by anthropogenic factors) and grazing pressure. The latter results in an increase in the abundance of macroalgae in coral reefs, affecting benthic communities ([Schaffelke et al., 2005](#)).

1.4.1 Ecology and biodiversity

The three protistan groups of macroalgae, Rhodophyta, Chlorophyta, and Phaeophyceae, are estimated to have 17,000 species (7,000, 2,000, and 8,000, respectively, for every group), and marine algae registered to algbase.org is 2,013 globally (seagrasses are included). Kelp forests can assist species of macrofauna, and the study of [Włodarska-Kowalczyk et al. \(2009\)](#) in the Arctic Ocean results that Bryozoa, Polychaeta, and Hydrozoa consist of the highest numbers of species (70, 52, and 37, respectively) of a total of 208 species for over 403 samples. The number of species ranged from 1 to 47, with a mean sample species richness of 11.5 species per sample +/- 8.8 SD, while most species associated with kelps were concentrated on holdfasts (all holdfasts were colonized with fauna in contrast to blades and stipes, with 54% and 9% of them being colonized by animals) and a total number of 200 species. The data about kelp forests and those of other latitudes cannot be compared easily, mainly due to reduced sampling efforts and the different methodologies applied. Likewise, most studies are restricted to less than 150 samples, and colonial taxa (Bryozoa, Hydrozoa) are neglected, despite the fact that they comprise about half of all macrofaunal species in the latter study.

1.4.2 Economical and industrial benefits

Macroalgae, besides their ecological importance, provide goods and services for humans, such as harvesting for consumption, fertilizers, animal feed activities, pet foods, and cosmetics, such as in the case of Canada, where artisanal and commercial harvesting occurs in all five Atlantic provinces ([Khan et al., 2018](#)). The interest in exploiting macroalgae as biofuels is rising due to fast-growing rates and carbohydrate-rich biomass over other biofuel feedstocks. The main advantages are the reduced land dependence and freshwater requirements in order to assist sustainable, eco-friendly, and carbon-neutral energy alternatives. Bioethanol consists of a biofuel, and green algae is considered to be an alternative in order to achieve energy sustainability, and green macroalgae has been found to exhibit growth during all seasons and the highest total carbohydrate ([Ramachandra & Hebbale, 2020](#)). Micro and macroalgae are under investigation for numerous applications, mainly for commercial food, agriculture and horticulture, pharmaceuticals, cosmetics, and bioenergy use. The increasing interest in macroalgae species, which can benefit the industrial and economic aspects, occurs due to the high diversity between and within taxa and the chemical composition of natural algae populations, introducing many potential uses. The chemical composition of macroalgae species is furthermore influenced by spatial and temporal changes of the environment, including light, temperature, nutrients, and salinity, as well as biotic interactions. Commercially employed algae molecules are not yet fully described, despite the fact that they have been known since 1950. *Cystoseira* species are in the center of attention among macroalgae species, which are difficult to categorize by their morphological characteristics, and it is found that some species

contain a wider range of pigments than previously thought ([Schmid et al., 2017](#); [Stengel et al., 2011](#)).

1.4.3 Macroalgae as bioindicators

Good ecological status of the water body is vital for the ecosystems, while the preservation of the functional and structural characteristics of the associated biological communities (e.g., macroalgae) is considered as a bioindicator in order to assess ecological status. Global climate change and anthropogenic pressures can affect the water quality status, and the need to observe, preserve, and recover the disturbed ecosystems into pristine environments is a key issue. Through the last decades, public policies (Habitats Directive 92/43/EEC) and international agreements aiming to protect biodiversity have been adopted. Seaweeds, or macroalgae, were primarily recognized as a biological quality element for the classification of coastal waters, and afterwards the Water Framework Directive (WFD 2000/60/E.C.) was included by using different indices, such as CFR in Spain, MarMAT in Portugal, and HPI in Germany ([Ar Gall et al., 2016](#)). The EC Water Framework Directive (WFD) is fundamental in order to assess ecological quality classification of the rocky seashores, taking advantage of the abundance and species composition of intertidal macroalgae communities. The restrictions detected refer to i) the differences observed when examining the sensitivity of macroalgae in different locations and ii) the absence of ecological quality assessments between very large changes in abundance of common species. Advanced expertise to identify macroalgae species is critical, and in order to achieve maximum effectiveness, a similar sampling methodology must be carried out, ensuring a uniform level of thoroughness ([Wells et al., 2007](#)).

1.4.4 Macroalgae and blue carbon

In coastal ecosystems, blue carbon can be stored in both plants and sediments, mainly by mangroves, salt marshes, and seagrasses (seagrass meadows can store in the soil over 95% of the carbon). Macroalgae may also be an important source of allochthonous carbon through exportation to the open ocean and open sea, so their contribution should be considered in Blue Carbon assessments. Calculations of the macroalgal carbon exportation to the ocean require a well-determined ratio between carbon and DNA per taxon, which are unknown for the majority of macroalgae ([Ortega et al., 2019](#)). Macroalgae (almost all haptophytic) global net primary production (NPP) is estimated between 80 and 210 Tmol C yr^{-1} , and the global carbon sequestration range is 0.8 and 22 Tmol C yr^{-1} , (including local sediments plus export), while calcified macroalgae are unlikely to be involved in net CO₂ sequestration (11 Tmol C yr^{-1} , which are overestimated by calcified macroalgae) ([Raven, 2018](#)). Nevertheless, blue carbon referencing to macroalgae is recently considered in blue carbon literature and requires specific

management to deliver its potential as a C donor. Noticeable is the fact that searching the term blue carbon and macroalgae on 8 February 2018 (Web of Science) retrieved 16 publications, and an increase of 18-fold citations (between 2011 and 2017) grew from 5 to 92 citations, resulting in incremental interest in macroalgae as potential blue carbon resources ([Krause-Jensen et al., 2018](#)).

1.5 Key role of *Posidonia oceanica* meadows

Posidonia oceanica is an endemic species to the Mediterranean Sea and is considered to be a high-importance habitat by forming dense and extensive green meadows. They provide several ecological functions and services and harbor highly diverse communities. Nutrient-poor waters, transparency, and sediments with reduced organic matter are essential for the survival of *P. oceanica* ([Díaz-Almela & Duarte, 2008](#)). Marine environmental management and protection in the Mediterranean Sea of *P. oceanica* is a major issue due to the fundamental characteristics for the quality of the coastal environment. Socio-economic benefits are provided, especially to artisanal fishing and tourism development, reinforcing the need to protect and manage these habitats ([Boudouresque et al., 2012](#)).

1.5.1 Ecological role

P. oceanica, which is endemic in the Mediterranean Sea, is a key species in coastal waters and is ideal in order to assess the ecological status of the coastal waters. It is the most abundant seagrass in the Mediterranean Sea, forming extensive meadows from the surface down to 40 m depth; therefore, they conclude a major ecological role ([Montefalcone, 2009](#)). They tend to increase the abundance for many associated biota (macroinvertebrates, fish, amphipods, and polychaetes), especially at the 'edge' of this habitat type, while living and dead matte have positive effects on different species. *Sarpa salpa*, *Paracentrotus lividus*, and *Pinna nobilis* are highly affected in a positive way by living matte, and to the edge, while on naturally occurring dead matte, the abundance of the amphipods *Leptocheirus guttatus* Grube and *Maera grossimana* Montagu and the polychaeta *Nereis rava* Ehlers shows an increasing trend ([Abadie et al., 2018](#)). In fact, herbivores don't consume directly the primary production of the *P. oceanica* meadows, but dead roots, rhizomes, leaves, and drifts of epibionts result in i) sequestration within the matte, ii) consumption by detritus-feeders within the meadows, and iii) exportation towards other marine ecosystems, where it constitutes a source for food webs ([Charles F. Boudouresque et al., 2016](#)).

1.5.2 Blue carbon

P. oceanica appears to be the most efficient seagrass in carbon fixation and storage. The average annual carbon fixation of the blades, sheaths, and rhizomes is estimated at 1024, 220, and 58 t C.ha⁻¹.yr⁻¹ respectively (total fixation rate of 1302 t C.ha⁻¹.yr⁻¹), while the sequestration rate is 278 t C.ha⁻¹.yr⁻¹. A major advantage of the *P. oceanica* is its capacity to store carbon from annual carbon sequestration for centuries to millennia, which can be compared to several terrestrial ecosystems ([Pergent-Martini et al., 2021](#)). Organic carbon trapped in the matte may reach up to 711 Mg C ha⁻¹, with a mean matte thickness of 210 cm. Mean fixation is estimated to 1.62 Mg C ha⁻¹ yr⁻¹. with a sequestration rate of 27 to 30% taking place for at least 1580 years, which is confirmed by radiocarbon analysis. Total stock of organic carbon, considering a mean matte thickness of 210 cm and coverage of 1 to 1.5 million hectares, might be as much as 711 to 1067 million Mg C ([Monnier et al., 2021](#)).

1.5.3 Geological and hydrodynamic interactions

P. oceanica, except for the high ecological benefits, is able to affect geomorphological processes in shallow waters, mitigating flood and erosion risks. Wave energy attenuation can reduce water flows, leading to an increase in sediment deposition and accumulation, positively affecting beach stability ([Ruju et al., 2018](#)). Dead leaves in autumn form wedge, and layered structures ranging from a few centimeters to several meters in thickness (banquettes) and may reduce the impact from waves. Nevertheless, the protection from seagrass banquettes at semi-closed sandy beaches should be reconsidered because during the winter season they used to be removed, and when storms arrive, the organic barrier is almost absent ([Gómez-Pujol et al., 2013](#)). Hydrodynamic forces of waves and bottom currents are reduced between 10% and 75% under the leaves and by 20% a few centimeters over the meadows, while similar effects have also been reported for other marine coastal habitats (kelp forests, tidal marshes, and coral reefs) ([Vacchi et al., 2017](#)).

1.5.4 Economic benefits and ecosystem services

Economic valuation associated with the human well-being of *P. oceanica* meadows can be estimated by locating their presence in coastal development and assessment of the provided ecosystem services. The ecosystem services may count up to 25, and the economic value of goods and benefits is estimated between 25.3 million and 45.9 million €/year. Furthermore, lack of available data leads to undervaluation, and as a final result, coastal development policies and protection of these habitats are crucial ([Campagne et al., 2014](#)). The most important

ecosystem services are related to i) primary production, ii) sediment retention and hydrodynamic attenuation, iii) increased biodiversity, iv) recreational and touristic activities, and v) carbon sequestration. In fact, the most common keywords between “*P. oceanica*” and “ecosystem services” are “biodiversity,” “environmental monitoring,” and “conservation,” but further efforts are necessary to evaluate the values of ecosystem services ([Capasso et al., 2024](#)).

2. The Mediterranean and Aegean Sea

2.1 Mediterranean biodiversity and habitats of macroalgae

The Mediterranean covers an area of 2,969,000 km^2 , and the maximum depth is 5,267 m (average depth 1,460 m), and it is the biggest enclosed sea in the world (Figure 1). It is estimated that over 17,000 species are identified in the Mediterranean Sea, while seaweeds and seagrasses cover 22% of benthic macroscopic (macrophytobenthic species, including 854 species of chlorophyta, rhodophyta, and magnoliophyte taxonomic groups) primary producers and invertebrates. The rate of species description is not expected to increase significantly, but the fact that a large number of macroalgae are poorly known, morphological studies, and molecular tools are essential to describe the taxonomy of several genera (*Ectocarpus*, *Cystoseira*, *Acrochaetium*, *Polysiphonia*, and *Ulva*, among others) ([Coll et al., 2010](#)). Temperature is a very important factor affecting macroalgae, and the maximum temperature of the eastern Mediterranean may reach up to 32 °C (Israeli shelf) during the summer months, compared to the western Mediterranean, which has a maximum temperature of 22.3 °C (northwest African region from Gibraltar south to 20 °N latitude). This temperature alteration results in a solid thermic barrier that isolates the species pool of the Mediterranean from the geographically adjacent West African tropical species pool ([Albano et al., 2021](#)). In the Mediterranean Sea, *Cystoseira* species are crucial, resulting in highly diverse communities supporting many associated species and creating a complex spatial structure. Despite the benefits provided by *Cystoseira* species, their presence has recently been described (even in the most studied sites, such as MPAs), and deep-water communities are highly endangered or face total extinction, basically due to catastrophic events (such as storms), anthropogenic disturbances (fishing nets, anchoring, and diving), and invasive species, resulting in up to 80% adult mortality of *Cystoseira* canopy-forming algae ([Langar et al., 2014](#)).

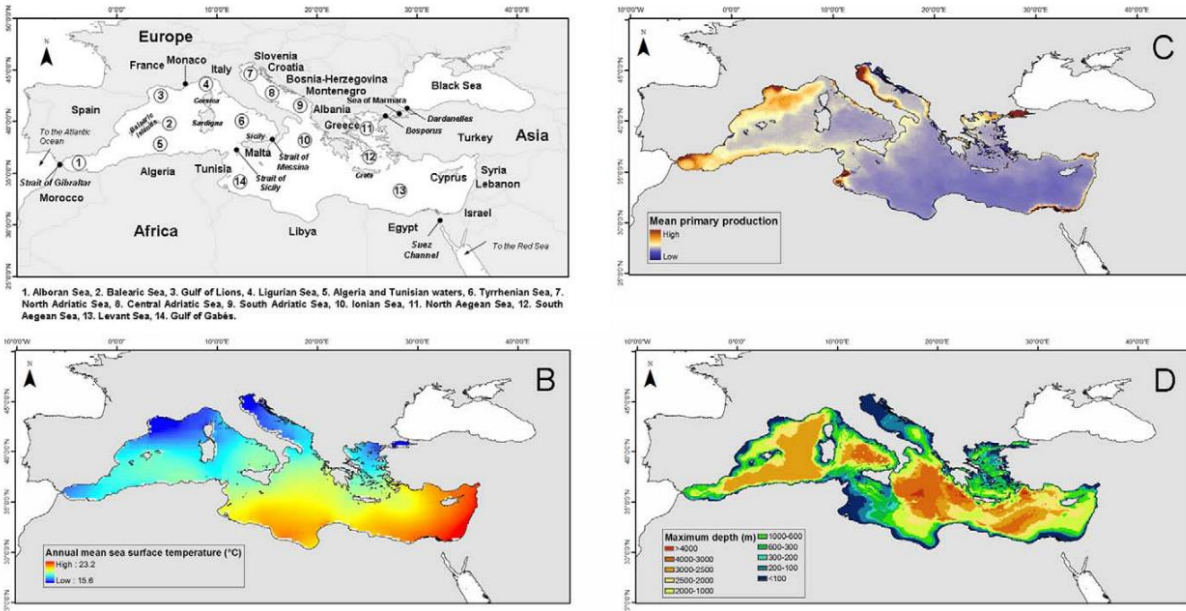


Figure 1. Biogeographic regions and oceanographic features of the Mediterranean Sea. A) Main biogeographic regions, basins, and administrative divisions of the Mediterranean Sea, B) Annual mean sea surface temperatures (°C), C) Annual mean relative primary production, and D) Maximum average depth ([Coll et al., 2010](#)).

2.1.1 Cystoseira and water quality status

The Mediterranean Sea and macroalgae communities in the upper sublittoral zone are affected in a great deal, especially in the areas with high nutrient loads, such as sewage outfalls, resulting in changes to species composition and structure in these habitats. In general, a gradient is observed where nitrophilous species dominate the area close to sewage outfalls (*Ulva* spp.), followed by *Corallina*-dominated communities at intermediate levels of nutrient enrichment, and finally *Cystoseira*-dominated communities, where a decrease in nutrient enrichment occurs. In general, *Cystoseira* species thrive in anthropogenically undisturbed areas, but some species (e.g., *C. mediterranean* and *C. elongata*) can tolerate a certain degree of pollution. Nevertheless, different impacts may be observed by industrial effluents or run-off waters of agricultural areas on macroalgae communities, which can assist in the assessment of the water quality status ([Arévalo et al., 2007](#); [Orfanidis et al. 2003; 2011](#)).

2.1.2 Most important species and habitats

Macroalgae forests are worldwide threatened, and the Mediterranean is not an exception, such as habitat-forming species (*Cystoseira* forests), which have been declining over the last decades

in the Mediterranean ([Tamburello et al., 2019](#)). In general, Mediterranean shorelines are characterized by the presence of turf algae, but *Cystoseira* species can dominate the littoral and lower sublittoral zones, while obtaining accurate and detailed records of seaweed species is challenging, and many distribution records may be inaccurate ([Mineur et al., 2015](#)). *Cystoseira* species are the most important of the canopy-forming algae in the Mediterranean, but species classification is varying a lot, especially when advanced techniques are applied. *Cystoseira* forests (e.g., *C. crinita* and *C. balearica*) provide nursery ground for juveniles such as *Symphodus* spp., supporting 9 to 12 times more juveniles when compared to habitats with less complexity. Nevertheless, more research is needed to estimate the effects of *Cystoseira* canopy-forming algae on the entire food web (e.g., fish assemblage) and the ecological and economical benefits provided by these habitats ([Cheminée et al., 2013](#)).

2.1.3 Threatened species

In the Mediterranean Sea, most species of Fucales are threatened or endangered, while regression of *Carpodesmia crinita*, *Treptacantha elegans*, *T. sauvageanuana*, and *T. barbata f. aurantia* has been observed, and two taxa are facing local extinction (*Cystoseira foeniculacea*, *Treptacantha barbata f. barbata*) ([Mariani et al., 2019](#)). The IUCN is a list that classifies species into 10 categories depending on the degree of threat, including 16 species of macroalgae (other than *Cystoseira* taxa, where 31 species are registered except *C. compressa*), and approximately 1200 to 1300 macroalgae species are estimated to be present in the Mediterranean. Despite the fact that macroalgae are threatened worldwide within the IUCN Red List, along with the European Union (EU) Habitats Directive and international conventions, they are largely ignoring marine species. Additionally, the list of threatened macroalgae contains species that are far from extinction (*Cystoseira amentacea*) or species that could take advantage of human impacts and global warming (*Caulerpa prolifera*) and, on the other hand, ignores species facing extinction (e.g., *Sargassum acinarium* and *S. hornschurchii*) ([Verlaque et al., 2019](#)).

2.1.4 Alien species

Alien species constitute another important threat to native macroalgae, as they reduce the number of macroalgae species, which results in lower diversity and furthermore affects the populations of sea urchins, fish, amphipods, and polychaetes. In the Mediterranean Sea, *Caulerpa taxifolia* was first observed in 1984 and outcompetes native macroalgae through i) high growth rate, ii) total substrate occupation, iii) improved light access, iv) increased sedimentation rates, and v) synthesis of secondary metabolites, while a strong decrease of eco-diversity (and perhaps bio-diversity) will occur if expansion continues at present rates (Boudouresque et al., 1995). The total number of species described as alien species in the

Mediterranean is estimated to be 986 (775, 249, 190, and 308, for eastern, central, Adriatic, and western Mediterranean, respectively, until 2012), while macrophytic alien species are increasing by 2-3 species every year (Figure 2. Cumulative number of NIS of the main taxa by MSFD subregion (Zenetos et al., 2012).

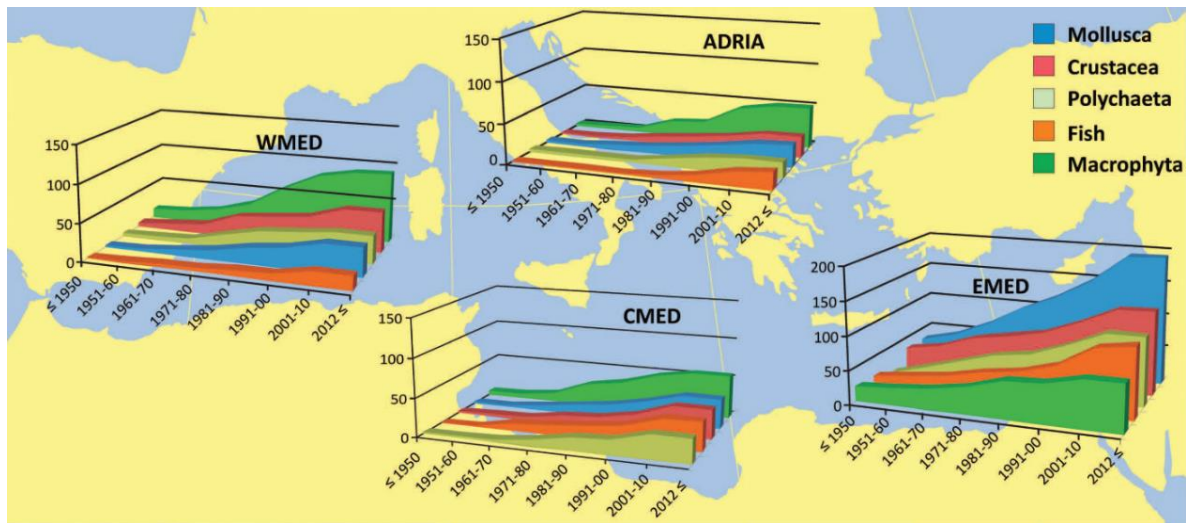


Figure 2. Cumulative number of NIS of the main taxa by MSFD subregion (Zenetos et al., 2012).

Macrophytic alien species (128 taxa in the Mediterranean) may have negative effects on ecosystem structure and function, with characteristic examples being the species *Stryopodium schimperi*, *Caulerpa taxifolia*, and *C. racemosa*. The introduction of alien species is a result of corridors (54%), shipping (44.9%), aquaculture (12%), aquarium trade (2%), and others (0.4%), but focusing on macroalgae, the vector of introduction is aquaculture and trade (import of shellfish products) (Figure 3) (Zenetos et al., 2012).

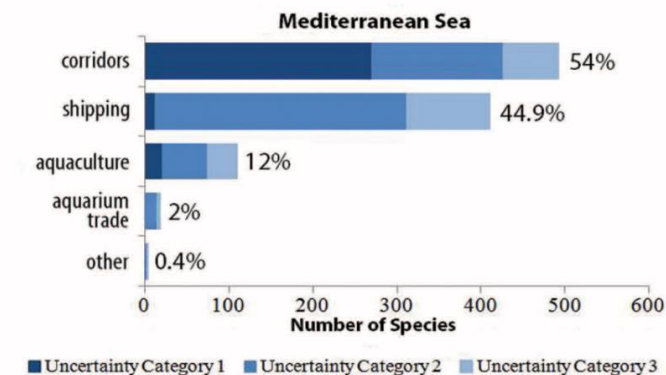


Figure 3. Pathways of Mediterranean alien species (Zenetos et al., 2012)

2.2 East Mediterranean macroalgae habitats

2.2.1 East Mediterranean status

The Mediterranean Sea differentiates on a large scale when compared from West to East in a lot of aspects, such as temperature and species composition ([Albano et al., 2021](#)). The Mediterranean Sea in general is considered to be one of the most oligotrophic regions of the world, particularly the Eastern Basin, both in terms of primary productivity and chlorophyll α concentrations. Differentiations are observed in the hydrographic characteristics of the Eastern Mediterranean, such as the Ionian, Aegean, and Cretan Seas ([Psarra et al., 2000](#)). In the Eastern Mediterranean, there is a gradient of benthic community complexity from turfs or barrens to canopy-forming macroalgae communities of the genus *Cystoseira* sensu lato (which accounts for most of the biomass and production of the shallow rocky reef assemblages with high biodiversity). Increased biomass and high biodiversity of invertebrates are observed in relation to high algae biomass, and a decrease in *Cystoseira* coverage occurs either by sea urchins *A. lixula* and *P. lividus* ([Giakoumi et al., 2012](#)) or other overpopulated herbivores ([Tsiamis et al., 2013](#); [Salomidi et al., 2016](#)). In the Eastern Mediterranean, the macroalgae species can be divided into three major categories: chlorophyta (*Ulva* sp. and *Cladophora pellucida*), rhodophyta (*Nemalion helminthoides*, *Galaxaura rugosa*, and *Gracilaria* sp.), and ochrophyta (brown algae) (*Padina pavonica* and *Sargassum vulgare*). Macroalgae are crucial to preserving the normal functions of marine coastal ecosystems, but there is also a contribution as biorefineries of raw materials. It is estimated that *Ulva* sp. has the highest economic potential in comparison to all photosynthetic organisms (ranging from \$1733 kg^{-1} to \$3140 kg^{-1}), despite the fact that *Ulva* sp. is considered to compete with native macroalgae species ([Robin et al., 2017](#)).

2.2.1 East Mediterranean seaweed diversity

In the entire Eastern Mediterranean Sea, a total of 1200 seaweed species is estimated, and 300 species are recognized in Israel, which is very high considering the small maritime area. Nevertheless, 16% of marine flora characterized as invasive or exotic species to the Israeli shores originated from the Indo-Pacific and migrated through the Suez Canal (115 seaweed species in the Levant basin since 1890) ([Israel et al., 2020](#)). In Cyprus, there is limited research interest in seaweeds, and the marine environment is considered highly oligotrophic. In the upper subtidal zone, 51 taxa have been recorded in Vasiliko Bay (South Cyprus), and the species *Cladophora nigrescens* and *Laurencia caduciramulosa* are the most recent records as non-

native species. *Cystoseira* species (such as *Cystoseira barbulata*) are abundant on shorelines with limited human activity, forming dense forests, and a decline is observed around bathing waters, while in heavy industrial areas they are almost absent ([Kletou et al., 2018](#)). Alien species are recently targeted by phycologists and marine biologists, especially those that exhibit invasive behavior (*Caulerpa racemosa* var. *cylindraceae*) and can affect the sea bottom and indigenous vegetation. Since 1970, an increase of alien marine macroalgae has been observed, introduced by shipping, aquaculture, aquaria, and via the Suez Canal (Lessepsian immigrants), which are spreading westwards and northwards associated with global warming. *Hypnea anastomosans* was initially considered a Red Sea immigrant and a Lessepsian invasive species, while the discovery of *Hypnea valentiae* at Rhodes Island confirms its introduction in the Eastern Mediterranean Sea. The latter introduction indicates that the marine alien flora is still spreading in the Eastern Mediterranean, and further molecular analyses may assist the taxonomical linkage between native and non-indigenous species (identifying the origination of alien species) ([Tsiamis & Verlaque, 2011](#)). In the Eastern Mediterranean, a classification of the ecological status is a main goal based on the Water Framework Directive, and it is estimated that 6 sampling sites are characterized as “good,” 15 as “fair,” and 2 as “bad” water quality (based on demersal fish fauna) ([Langar et al., 2014](#)).

2.3 Aegean Sea

2.3.1 Aegean Sea macroalgae assemblages

The Aegean Sea is located in the Eastern Mediterranean and covers an area of about 215,000 km^2 and the maximum depth is 2,639 m to the west of Karpathos, while the coastline length is 13,676 m the largest in the Mediterranean basin (Figure 4).



Figure 4. Map of the Aegean Sea and MPAs ([Sini et al., 2017](#))

The Aegean Sea represents a stronghold for marine biodiversity, but marine habitats and species lack spatial information, and further research is needed in order to elucidate the distribution patterns and conservation status of several ecological features, especially in deep areas (depth > 40 m). The existing protection measures are unable to safeguard biodiversity, and only 2.3% are conservatively manageable (41 ecological features are also represented in these areas), while the high complexity of geomorphological and transitional characteristics of the Aegean is hampering the efforts of systematic conservation ([Sini et al., 2017](#)). Marine macroalgae species of the Aegean Sea have shown an increasing interest during the last decades, especially in the North Aegean, Saronikos Gulf, and Dodecanese complex, scaling up

the species richness of macroalgae while new species are registered, such as *Mesophyllum macedonis*. In general, the overall macroalgae diversity of the upper sublittoral zone is similar between Aegean islands, and total species number and coverage per sampling unit are typical when compared to other Greek coasts ([Tsiamis et al., 2013](#)). Brown algae are considered key species of macroalgae communities hosting high biodiversity of marine life, and large brown algae of the genera *Cystoseira* and *Sargassum* show a decreasing trend (especially *Cystoseira* species) in the Saronikos and Korinthiakos Gulfs. *Cystoseira* species (non-plastic) are dominating the oligotrophic and highly transparent pristine rocky coasts through efficient use of stored nutrients to support growth during periods of nutrient shortage, while *Cystoseira compressa* and *C. barbata* (plastic species) are distributed from pristine to moderately degraded coastal waters of shallow waters ([Orfanidis et al., 2011](#)). *Cystoseira spinosa* and *C. compressa* show a unique composition locally, reflecting differences in the trophic status, while there is no specific pattern of epiphytic algae distribution on hosts. Epiphytic algae on *Cystoseira* species can negatively affect their survivorship mainly due to reduction of photosynthetic tissues and high epiphytic densities ([Belegratis et al., 1999](#)). Despite the decline of *Cystoseira* spp., rare and poorly known deep-water species of the genus *Sargassum* have been detected (growing on small stones and pebbles at about 40-50 m depth) and identified to be close to *Sargassum acinarium*.

2.3.2 New macroalgae species in Aegean

Macroalgae species in the Aegean have been studied since 1775, and they are considered to be a very interesting field due to the geographical position, vast coastline, and great depths. The knowledge of seaweed species is mainly registered in the form of checklists, excluding morphological descriptions, resulting in taxonomic confusion, and the Aegean is considered to be the poorest in terms of macroalgae diversity when compared to the eastern Mediterranean basin. However, studies in the Aegean about macroalgae species are limited, underestimating the number of species, and large areas are still unexplored. At least 30 alien species have been registered since 2010, while 10 macroalgae taxa are reported that are new or rare to the Aegean Sea. The new macroalgae species that have been reported to the Aegean indicate that eastern Mediterranean macroalgae flora is also underestimated, especially at deep-water habitats ([Tsiamis et al., 2010](#)). New species registrations are added to the Aegean Sea, such as *Cystoseira foeniculaceae* f. *schiffneri* and *Cystoseira funkii*, and both of them are described for the first time in the Eastern Mediterranean Sea. Both taxa are considered to include rare species that are under protection by the Barcelona Convention, while they have been found within three Natura 2000 marine sites of community importance, strengthening the need for establishing and reinforcing site-specific management measures in order to protect the endemic and little-known taxa of the Mediterranean Sea ([Tsiamis et al., 2016](#)). In Greece, at least 35 non-native species have been registered, while an increasing trend of new algae

introductions and further expansion has been observed. In the Aegean Sea specifically, the red algae *Botryocladia madagascariensis* and *Neosiphonia harveyi* have been reported recently for the first time (2015), while *Asparagopsis taxiformis* is expanding towards the North Aegean. In April 2013, the brown algae *Scytosiphon* cf. *dotyi* was found in Crete (located in the South Aegean Sea) for the first time, and new regional records of marine alien macroalgae species (*Asparagopsis taxiformis*, *Botryocladia madagascariensis*, *Codium fragile*, *Hypnea spinella*, *Neosiphonia harveyi*, and *Strypodium schimperi*) have been found ([Tsiamis & Panayotidis, 2015](#)). Additionally, the red algae *Cryptonemia tuniformis* has been found, which is very rare and has been reported only once before ([Tsiamis et al., 2012](#)).

2.3.3 Posidonia oceanica meadows

The first surface area coverage of *P. oceanica* was attempted in 2001 within the context of the Habitat Directive (92/43/EEC), and despite an increase in scientific efforts over the last decades, the knowledge about *P. oceanica* meadows remains unclear. Growth patterns of *P. oceanica* meadows are differentiated at local and sub-ecoregional scales, and in terms of morphological and demographic descriptors, the North and South Aegean are characterized by significant differences. Light limitation is considered to be the main driver affecting distribution, demography, and biometric characteristics of the North Aegean coastal zone ([Gerakaris et al., 2021](#)). *P. oceanica* meadows is estimated to extend by approximately 70% of the Greek coastline, covering 2749.07 km². Meadows highest coverage (996 km²) is observed in the North Aegean Sea, while seagrass coverage of the South Aegean is estimated at 850 km². Nevertheless, an underestimation of total coverage due to low spatial resolution should be highlighted, especially when satellite data are not followed by acoustic remote sensing techniques and *in situ* methodologies ([Panayotidis et al., 2022](#)). Estimation of seagrass coverage for the Greek coastline through satellite multispectral images is 2510.1 km² between 0 and 40 m depth ([Traganos et al., 2018](#)); therefore 238,97 km² less when compared to combined methodologies with satellite data. Regardless of the underestimation of seagrass coverage by satellite images, it comprises a very useful survey field for large-scale ecological and conservation studies considering the spatial distribution of seagrass meadows ([Topouzelis et al., 2018](#)). Satellite image spatial processing is applicable for *P. oceanica* meadows, such as maritime spatial planning within the directive 2014/89/EE. In Greece, between 2014 and 2020, the project INTERREG V-A, with the support of Greece and Cyprus national authorities, quantified *P. oceanica* meadows spatial distribution (<https://ypen.gov.gr/chorikos-schediasmos/thal-chor2/>). Free access to *P. oceanica* in Greece is available (<https://thalchor-2.ypen.gov.gr/>) for 62 Natura 200 locations with total coverage of 2619 km² and total accuracy of 76.3%.

2.4 The case of Saronikos Gulf

The Saronikos Gulf is located between Attica and Argolis and covers an area of about 83km^2 and a maximum depth of 416m, located westwards of Methana volcano, but it is considered to be one of the most polluted areas in the Eastern Mediterranean, mainly due to urban pollution through the last decades of the 20th century. Saronikos Gulf communicates with the Aegean Sea through an eastern channel (12m depth) and a western channel (8m depth), while the Western and Eastern basins of Saronikos Gulf (inner and outer Saronikos, respectively) are separated, considering an imaginary line between the islands Aigina and Salamina (Figure 5). In 1987, sampling efforts took place in order to monitor the biological and physicochemical parameters, followed by a monitoring pollution project (MED-POL project) through seasonal cruises until 1998, sponsored by UNEP. The first studies of phytobenthic communities were carried out at the beginning of the 20th century, and the most recent studies (1983, 1987) increased the knowledge of the composition and abundance of hard bottom communities related to urban and industrial pollution of Athens ([Siokou-Frangou, 1999](#)).

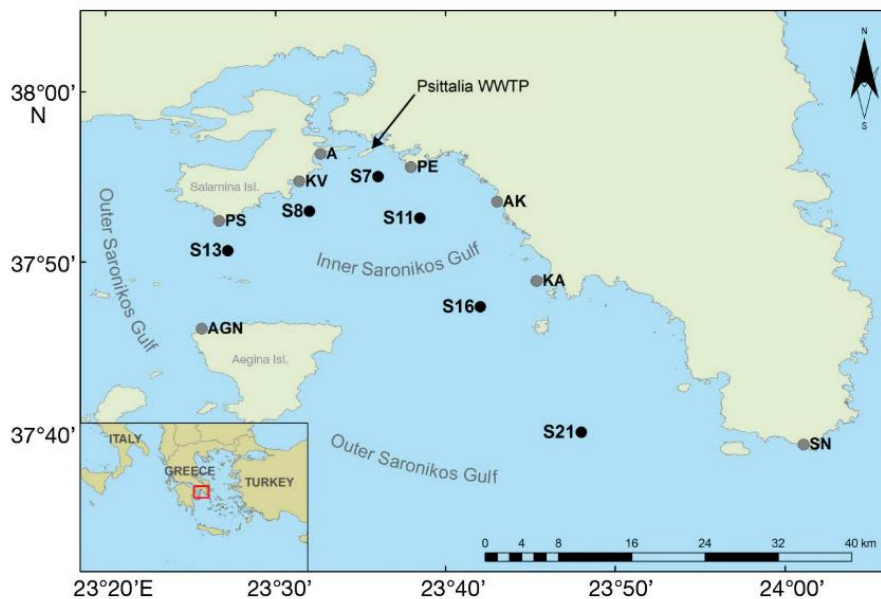


Figure 5. Inner and outer Saronikos gulf (sampling sites for macroalgae) ([Tsiamis et al., 2013](#)).

In 1990, the Sewage Primary Treatment Plant was established, and research about macroalgae species took place, assessing the ecological status at Saronikos Gulf. Through 13 years of monitoring (1998–2011), a total of 213 taxa were identified and classified into Chlorophyceae, Phaeophyceae, and Rhodophyceae, including 47, 36, and 130 taxa, respectively. During 2001 and 2005, the number of species increased by 2 times, and an increasing trend at lower rates continued until 2008. Thereafter, the number of macroalgae species decreased by 5% and total

coverage by 40% between 2010 and 2011. Large brown macroalgae, and especially *Cystoseira spp.*, during 1998 and 2011 showed a decreasing trend of total coverage from 100% to 40% on the outer Saronikos Gulf sampling sites, while on the inner Saronikos Gulf total coverage and abundance were insignificant. Nevertheless, the nutrient loads decreased after the Treatment Plant resulting in a decrease of nitrophilous macroalgae species (such as *Ulva spp.*, *Cladophora spp.*, and *Enteromorpha spp.*) and their total coverage. Besides the eutrophic conditions and their impacts on macroalgae, other factors seem to affect macroalgae assemblages in the Saronikos Gulf, such as habitat destruction and sea urchin overgrazing ([Balanika et al., 2011](#)).

2.4.1 Saronikos alien species

Saronikos Gulf is considered to be a hub for introduced species, and a total of 89 alien species (15% of them are phytobenthic) have been reported, while more than 70% were established successfully or became invasive (55 and 8 species, respectively) (Figure 6).

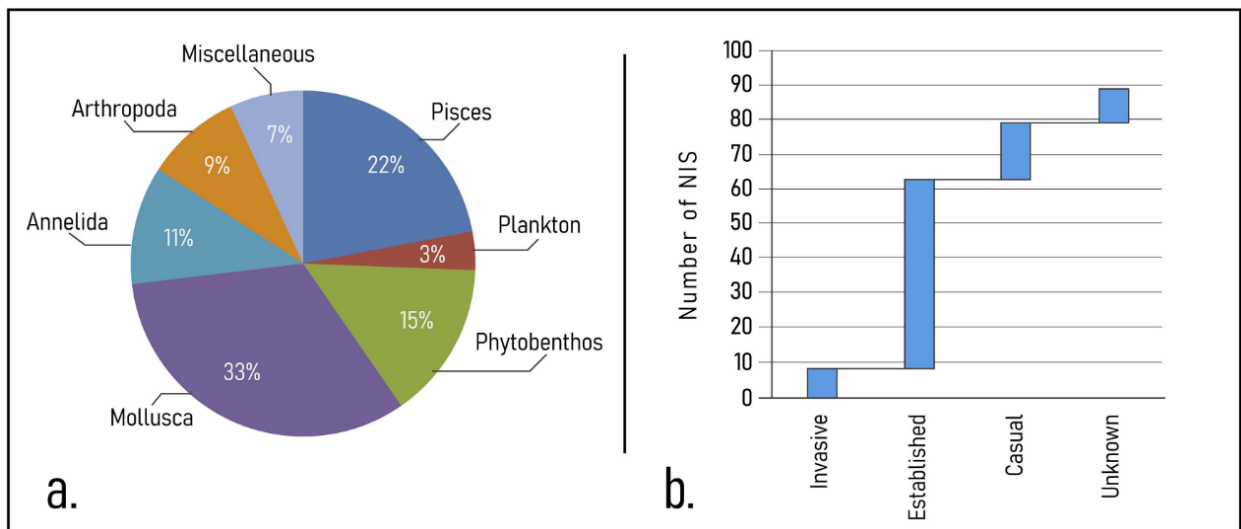


Figure 6. a) Contribution of major taxonomic/eco-functional groups to the diversity of marine NIS of the Saronikos Gulf, b) establishment success [Zenetos et al., 2020](#).

After 2000, an increasing trend of alien species has been reported, mainly due to new scientific efforts in the area, and 13 phytobenthic macroalgae species were registered. The green algae *Caulerpa cylindraceae*, *Codium fragile*, and the brown algae *Styopodium schimperi* exhibit invasive behavior. The species *C. fragile* and *C. schimperi* show a more limited distribution, but they can monopolize the sea bottom (a characteristic example of Salamina Island), and *Caulerpa cylindraceae* is extensively found along Saronikos Gulf coasts. Most recently, the

species *Halophila decipiens* was registered for the first time in the Saronikos Gulf and the whole Mediterranean Sea. The primary introduction of alien species in the Saronikos Gulf occurs mainly due to international shipping and aquaculture, while recreational vessels can spread the already introduced species ([Zenetos et al., 2020](#)). Besides the fact that Saronikos Gulf is considered to be a hotspot of alien species, the spatial distribution patterns are still incomplete, such as in the case of *Caulerpa C. racemosa (=cylindracea)*. The latter species invaded and expanded into the entire Mediterranean Sea during the last 30 years, and a higher probability of occurrence is observed at shallow areas <4 m deep and at depths between 15 and 30 m. The density of *C. cylindracea* is higher at rocky bottoms (compared to *P. oceanica* beds or on sandy/muddy bottoms) and also in the southeastern part of the Gulf, which is the initial establishment area, indicating that time favors the steady expansion and further dominance over native species ([Katsanevakis et al., 2010](#)).

2.4.2 Biological quality elements through WFD

Macroalgae (along with macroinvertebrates and phytoplankton) can be used as biological quality elements to assess water quality status through the application of some indexes, such as the Ecological Evaluation Index (EEI). EEI is based on the classification of macroalgae species through their morphological and functional characteristics, and in general, disturbed marine environments are dominated by species with high growth rates and reproduction in contrast to undisturbed areas, where species with low growth rates and reproductive potential are abundant. The ecological status based on EEI is classified as high, good, moderate, poor, and bad, ranging between 2 and 10, based on the percentage of the mean macroalgae abundance-coverage of the represented taxa. In the Saronikos Gulf, sample efforts took place at 14 stations in order to assess the ecological quality status of the water body based on zoobenthos, phytoplankton, and macroalgae. Ecological quality status of macroalgae species took place in 6 stations, ranging from poor (4 stations) to moderate (2 stations) status, while a gradient from poor to moderate status occurs away from Psittalia (outfall). Overall, the Ecological Quality Status is estimated from moderate to good status except for 1 sampling station (closest to the Psittalia outfall), which was found to be in poor status (AMBI and BENTIX indexes) (Table 1, Figure 7) ([Simboura et al., 2005](#)).

Table 1. Comparison between the BENTIX and the AMBI index in Saronikos gulf benthic data Stations (*Simboura et al., 2005*).

Stations	BENTIX	EcoQ-BENTIX	AMBI	BI	EcoQ-AMBI
S3	3.36	M	2.6	2	G
S7	2.20	P	5.3	5	P
S39Z	2.74	M	3.1	2	G
S8	2.71	M	3.4	3	M
S46Z	3.04	M	2.9	2	G
S13	3.25	M	2.4	2	G
S26	2.95	M	3.3	2	G
S26A	3.25	M	2.5	2	G
S26B	4.37	G	1.4	2	G
S11	3.70	G	2.5	2	G
S11A	3.87	G	1.9	2	G
S16	3.49	G	2	2	G
S16A	3.48	G	1.9	2	G
S16B	4.21	G	1.8	2	G

EcoQ: Ecological Quality Status. Station rows with controversial results are shaded.

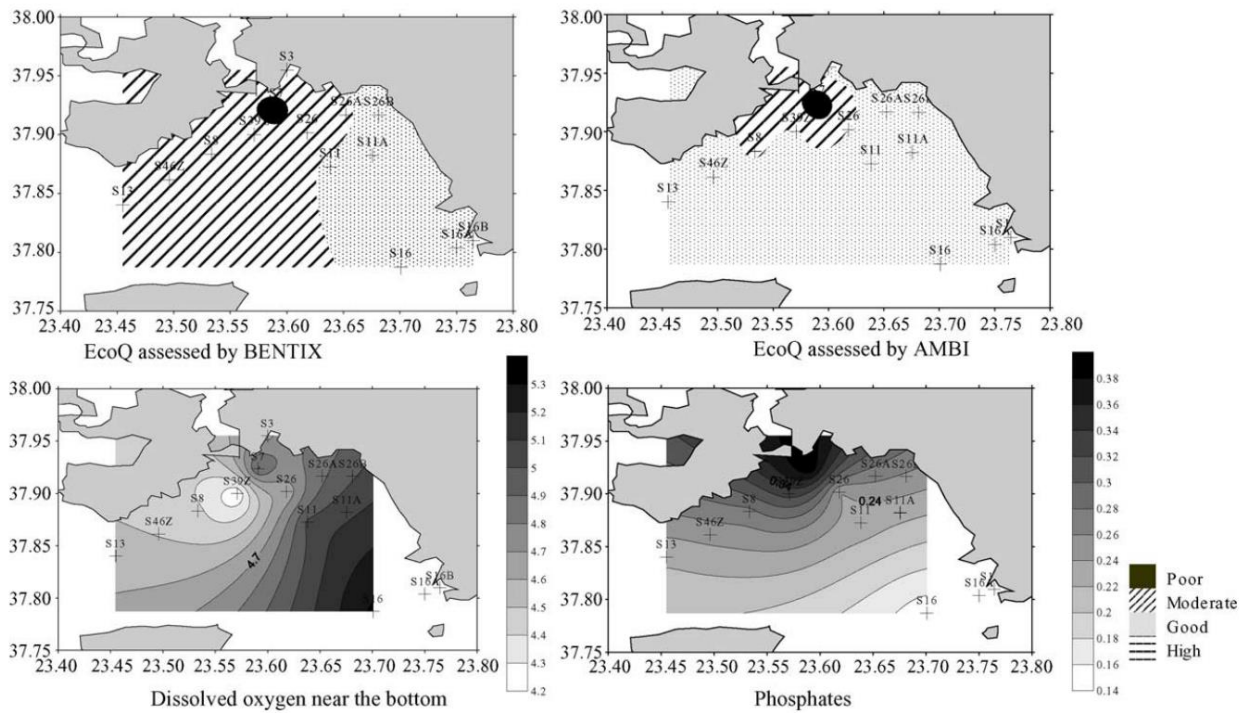


Figure 7. Ecological quality status by BENTIX and AMBI, dissolved oxygen near the bottom and Phosphates classification (*Simboura et al., 2005*).

2.4.3 Re-oligotrophication of Saronikos Gulf

Saronikos Gulf after the wastewater treatment plant in Psittalia switched from eutrophic to oligotrophic status in a very short period where nutrient and organic loads declined, resulting in a rapid re-oligotrophication. Since 2004, both total nitrogen and phosphorus levels decreased by 75% and 25%, respectively (Figure 8), while total nitrophilous green algae coverage reduced by 100% to 23% until 2009 (cold season) (Figure 9).

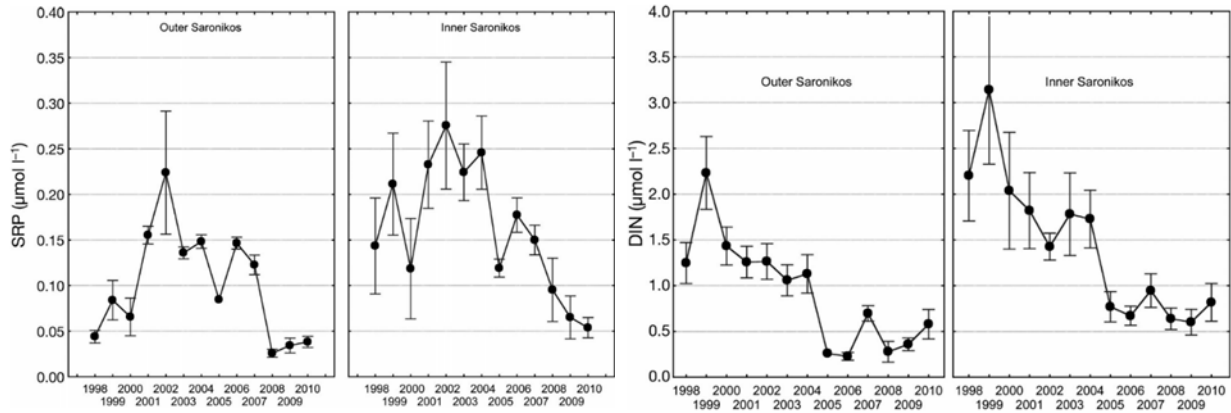


Figure 8. Annual values of Surface soluble reactive phosphorus (SRP) and surface Dissolved Inorganic Nitrogen (DIN), for Saronikos Gulf (Inner and Outer) ([Tsiamis et al., 2013](#)).

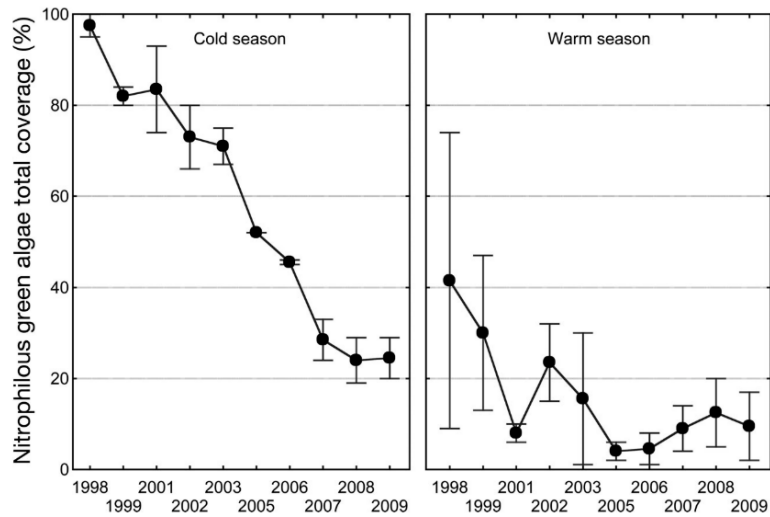


Figure 9. Annual nitrophilous green algae coverage for the Inner Saronikos gulf for the cold (March) and warm (September) seasons ([Tsiamis et al., 2013](#)).

The lower total abundance of nitrophilous green algae gradually decreased, resulting in areas with more diverse communities and an increase in species richness since opportunistic and ephemeral species inhabited the new available space. It is noteworthy that *Cystoseira* and *Sargassum* spp. were expected to increase in terms of abundance but instead declined. This decline in the inner Saronikos Gulf may be a result of the absence of parental *Cystoseira* species, or the water quality threshold did not reach the required status to support these sensitive species. On the other hand, the outer Saronikos Gulf had never been affected by high nutrient and organic loads, and as a result, other causes are responsible for the decline of *Cystoseira* forests, such as coastal interferences (construction of sailing and maritime sport facilities (2004 Olympic Games), recreational buildings, and installations), an increase in heavy metals and persistent organic compound concentrations, and overgrazing (by overpopulated sea urchins and herbivorous fish species) ([Tsiamis et al., 2013](#)).

2.4.4 Environmental status

Environmental status of the Saronikos Gulf is based on the Water Framework Directive and Marine Strategy Framework Directive (WFD and MSFD, respectively) according to European legislation, including the criteria and standards on Good Environmental Status (physical damage and condition of the benthic community of Sea Floor Integrity). In order to describe the condition of benthic communities, the following indicators were applied: i) the presence of sensitive and tolerant species; ii) species diversity and richness and the proportion of opportunistic to sensitive species; iii) the proportion of biomass or the number of individuals above a specified length/size; and iv) parameters describing the size spectrum of benthic communities. After the wastewater Treatment Plant, an upgrade of benthic communities was observed (BENTIX and diversity indices mostly), especially in the areas adjacent to the outfall zones and after the advanced secondary biological treatment plant in 2004. Moderate and good ecological and environmental status gradually improved as distance increased from WWTP outfalls. Elefsis Bay is characterized by more complex patterns and low environmental conditions of benthic communities due to shallow depth, local pressures, and enclosed physiography ([Simboura et al., 2014](#)). Most recently in the Saronikos Gulf, an integrated assessment of the status of marine waters was applied using the holistic Nested Environmental Status Assessment Tool (NEAT), using 9 biological and chemical ecosystem components, 24 indicators, and 8 descriptors of MSFD. Benthic vegetation, along with benthic fauna, sediment, mammals, and alien species, were found to be the most impacted components, and the overall quality status of Saronikos was classified into good status. Elefsis Bay and Psittalia Outfall are classified as having poor and moderate environmental status, respectively, and as a conclusion, the application of the NEAT tool may be very useful in order to assess the environmental status on spatial and temporal scales and integrate data from different sources under MSFD ([Pavlidou et al., 2019](#)).

3. Materials and methods

Temperature is considered a high-importance factor for seagrass and macroalgal assemblages, affecting their geographic distribution and functional patterns. Over the last decades, sea surface temperature data has been available from satellites, providing long-term temperature observations. Sea surface temperature data were downloaded from the Physical Science Laboratory (<https://psl.noaa.gov/cgi-bin/data/timeseries/timeseries1.pl>) for the closest latitudes (39.0N to 35.2N) and longitudes (22.5E to 24.4E) of the study area (figure 10). Chronologically, the SST monthly mean values time series were downloaded from 1948 until 2023. The time series were separated into 3 different groups: 1948-1972, 1973-1997, and 1998-2023, in order to identify the alternations of the sea surface temperature dataset. Afterwards, every 25-year period was analyzed to extract seasonal variability, climatology, mean SST (annually), and histogram characteristics of the study area. Winter and summer seasons refer to the months January, February, and March, and July, August, and September, respectively. This region was chosen because Saronikos Gulf (which has been studied extensively) is included within the study area, and the limitation of spatial resolution availability for the dataset (calculating closest latitudes and longitudes to the given study area).

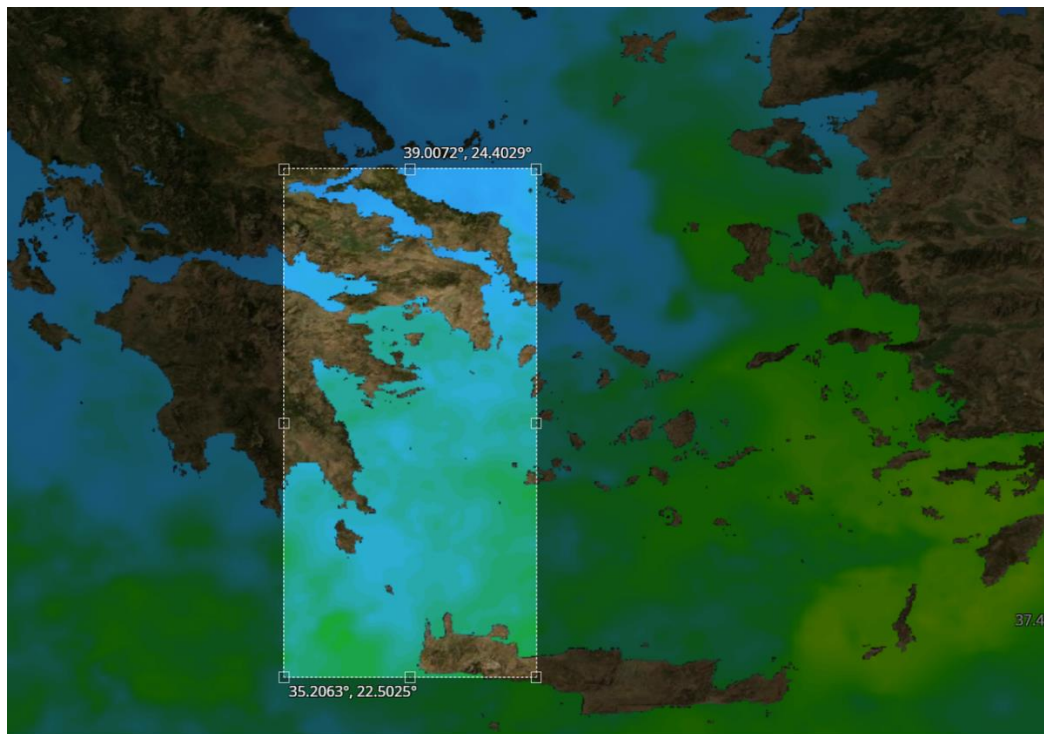


Figure 10. Coordinates for the closest latitudes (39,0 N to 35,2 N) and longitudes (22,5 E to 24,4 E) of the study area (<https://soto.podaac.earthdatacloud.nasa.gov>).

4. Results

SST monthly mean temperature ranges from 10.7 to 26.9°C in February 2003 and in August 2010, respectively, for the time series 1948-2023. The annual mean SST lowest temperature is observed in 1976 at 17.4°C and the highest in 2018 at 19.3°C. The coldest months for the time series are January, February, and March, and the warmest months are July and August. The mean SST temperature for the latter months is 12.71, 12.47, 13.21, 24.91, and 25.30°C, respectively. A total of 912 observations are counted, and 185 (20%) of them are between 13 and 14°C.

4.1 Climatology

Climatology is considered to be a great field of research to determine weather patterns and temperatures over time, while the average period is at least 30 years long. The available SST data for the period 1948-2023 indicate that at the most recent time series (1998-2023), there is an increasing trend for the months June to December in comparison to the other two time series (1948-1972 and 1973-1997). It is worth noting that there is an increase of at least 1 °C for the months of July and August for the last 25 years (figure 11).

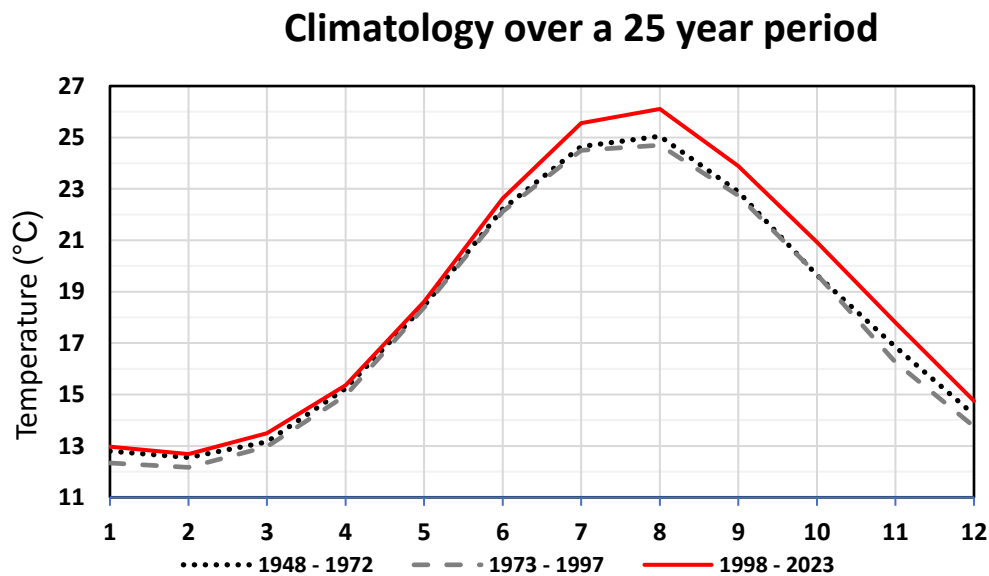


Figure 11. Climatology from 1948-2023 divided into 3 different periods 1948-1972, 1973-1997, 1998-2023.

4.2 Annual mean SST and anomalies

Annual mean SST and anomalies for the period 1948-2023 indicate an increasing trend after the year 1998 (figure 12). The highest temperature occurred in 2018 with a mean of 19.26°C and is the highest for the whole time series. Since 1998, considering anomalies, it turns out that all annual mean SST are positive, except 2006. In contrast, from 1964 to 1997, all the anomaly values were negative except 1994.

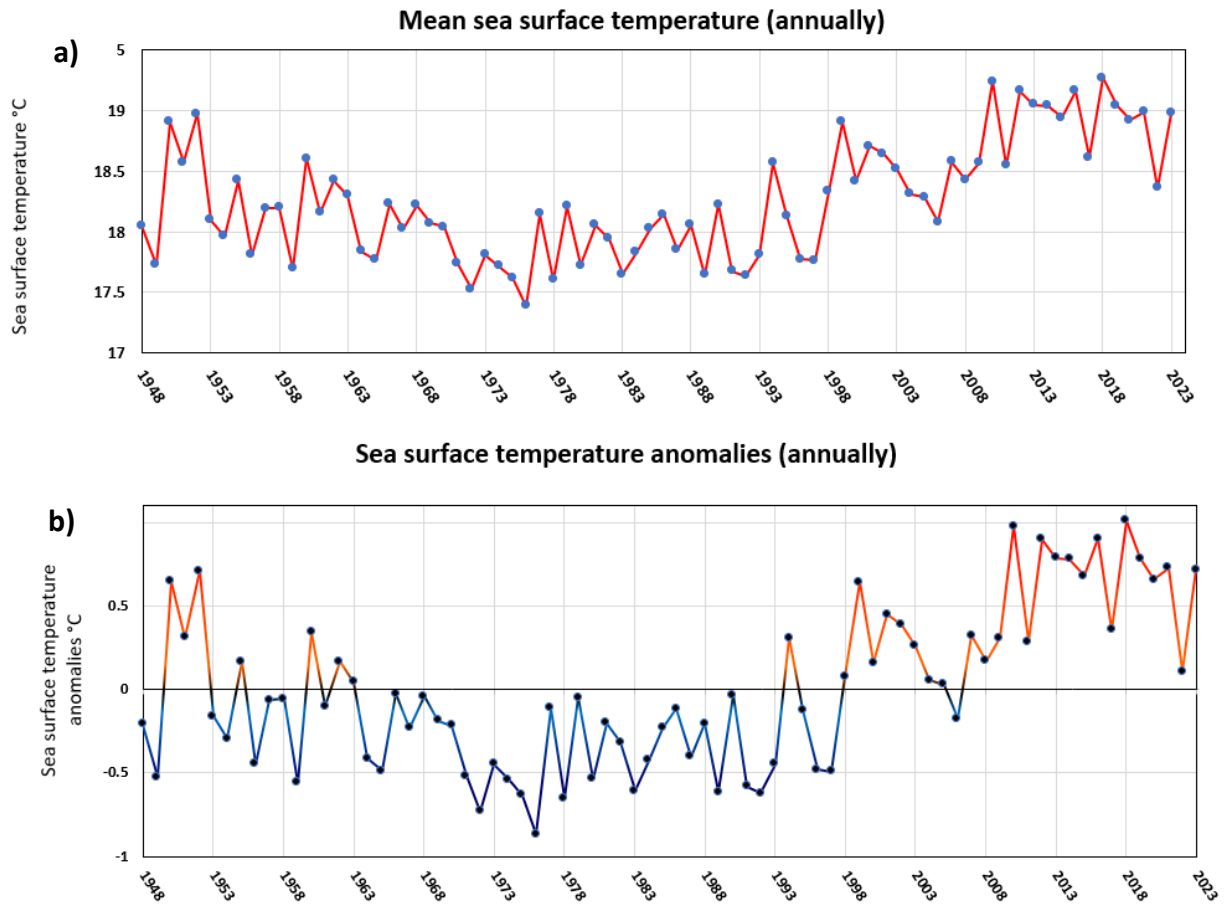


Figure 12. The upper panel, figure a and b show the annual mean SST and the anomalies respectively from 1948 – 2023.

4.3 SST seasonal variability

The seasonal variability for the last 25 years is characterized by an increasing trend of the SST, divided into two periods: 1998-2009 and 2010-2023. The latter period has a higher monthly SST, and only in June is it negligible, while the highest differences occurred for the months February, September, and November (0.95, 0.79, and 0.68°C, respectively) (figure 13).

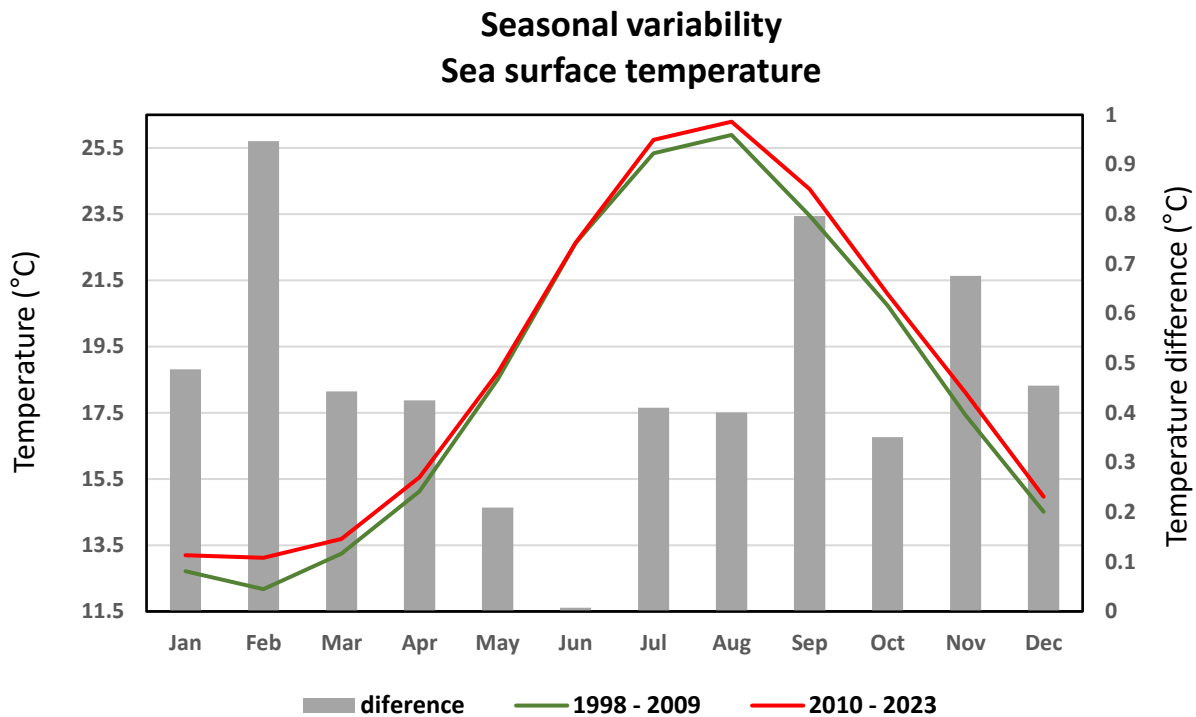


Figure 13. Monthly mean SST for the periods 1998-2009 and 2010–2023 are represented with green and red line. On the right side the difference of the mean values for every month corresponds with the gray bars on the figure.

4.4 Summer and Winter seasons SST

During the summer season (July, August, and September), an increasing trend of the mean SST is obvious, and 2 peaks in the dataset occur for the years 2012 and 2021 at 25.90°C. The winter season (January, February, and March) is characterized by more stability, although after 2010 there is a rise in mean SST temperature. The highest SST was 13.96°C and 14.80°C for the years 2014 and 2016, respectively. In 2022, the SST dropped down 11.52°C, and it is the lowest value since 1948.

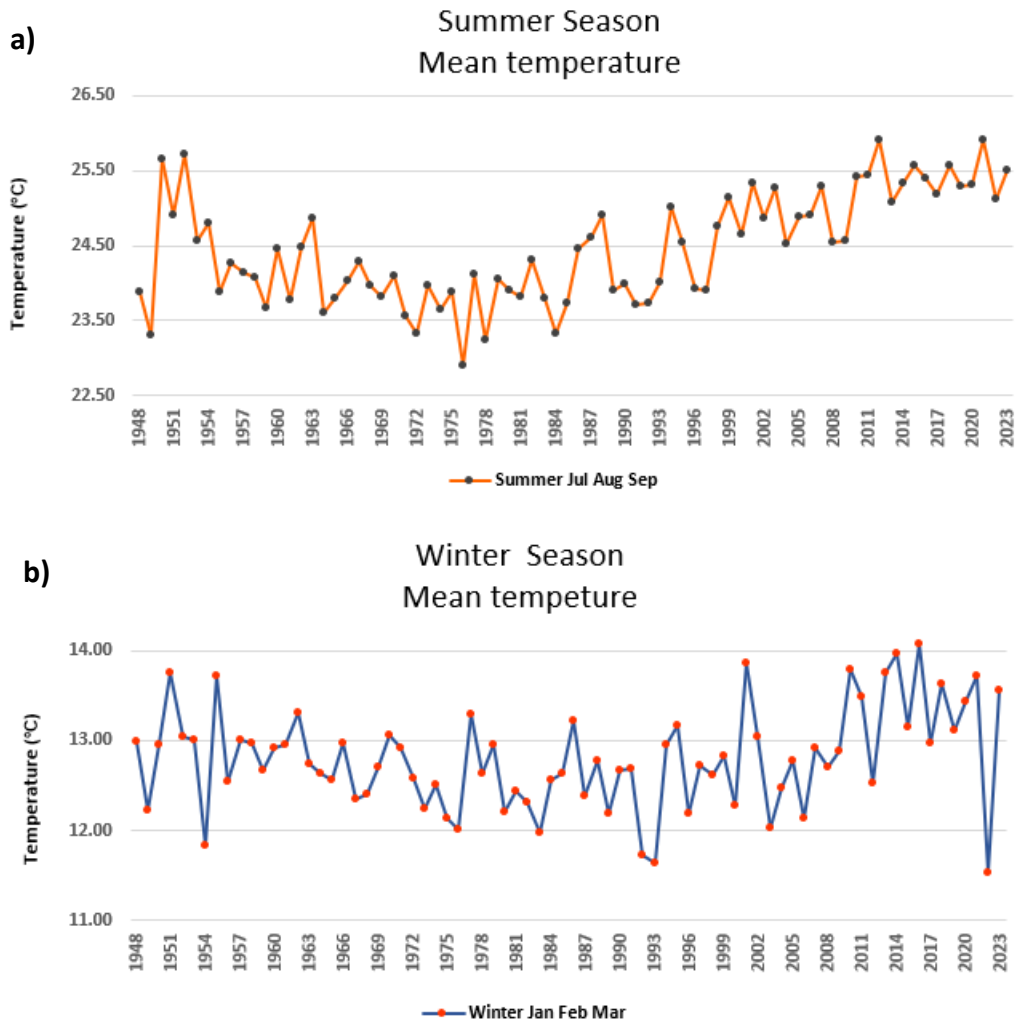


Figure 14. Annually mean SST for the summer season is shown on panel a) and the winter season on panel b). Summer season is for the months July, August and September and winter season for the months January, February and March.

4.5 SST histograms

Monthly mean SST for the dataset was separated chronologically into 3 histogram graphs in order to identify the frequency of the observations. Each histogram is grouped into 9 SST ranges for every 2°C, while the most important findings are about [11, 13] and [25, 27]°C. The edging ranges of the latest period, 1998-2023, show the lowest and highest frequencies with 22 and 43 entries (figure 15, a). In contrast, the mean SST values frequencies for the first and second periods (1948-1972, 1973-1997) were 57 and 46, and 22 and 26, for the minimum and maximum ranges, respectively (figure15, a and b).

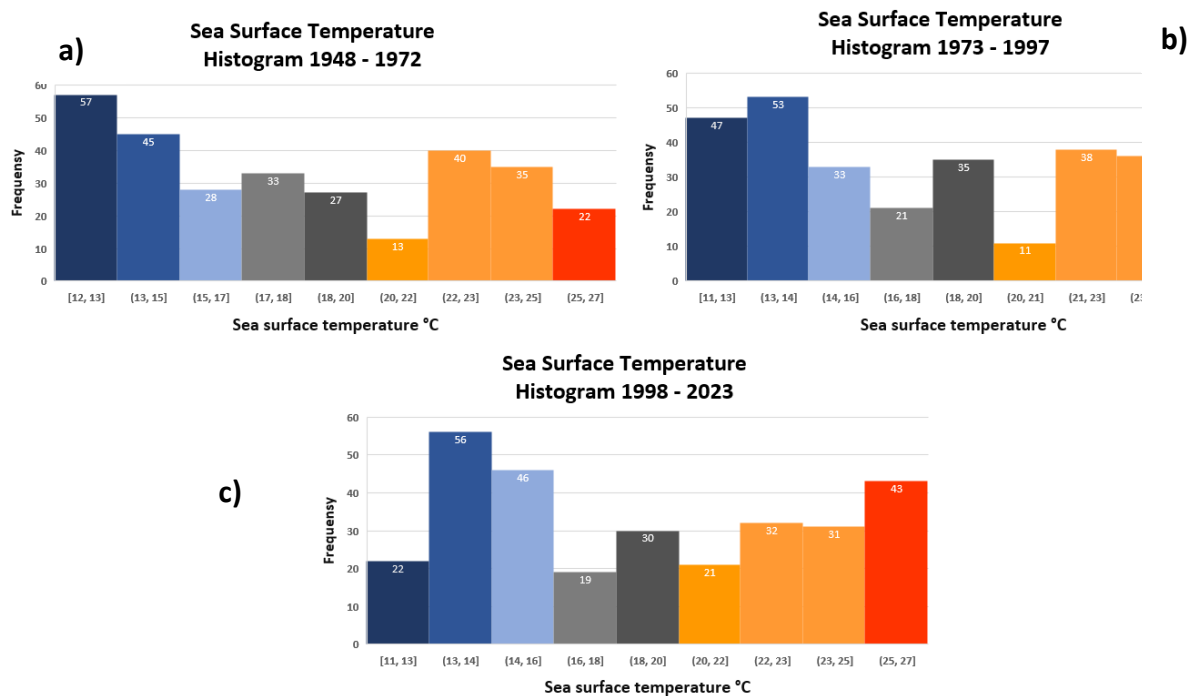


Figure 15. Monthly mean SST values correspond to the periods 1948-1972 (panel a), 1973-1997 (panel b) and 1998-2023 (panel c).

5. Discussion and conclusions

Pristine rocky habitats in the Mediterranean are characterized by structural and biological complexity, supporting the highest mean species richness and abundance of juvenile fish due to different macroalgal assemblages. *Cystoseira* forests are considered to be habitats of high importance, providing nursery ground for juvenile fish (*Symphodus* spp., *Labrus* spp., and *Serranus* spp.), while *C. julis* and *T. pavo* are more abundant at the edge of these forests. Nevertheless, the nursery ground provided by shallow rocky habitats is a result of macroalgae assemblages that are connected to each other (throughout separated patches), providing a complex mosaic that is more efficient when examined holistically ([Cheminée et al., 2021](#)). *Cystoseira* forests show an increase in abundance of associated fauna of the families Labridae and Seranidae (necto-benthic fish) and Blenniidae, Cliniidae, Gobiidae, Trypterigiidae, and Scorpaeniidae (crypto-benthic fish), but no total biomass differences are alerted when compared to barren areas. In contrast, the taxa *Diplodus* spp. and *Thalassoma pavo* are estimated to be more abundant in barrens than *Cystoseira* forests ([Thiriet et al., 2016](#)). Canopy-forming algae are declining on a global scale, and sea urchin grazing is considered to be the main driver, while the complexity of these habitats and the mechanisms aren't fully understood. Human impacts are considered to be a very important factor affecting canopy-forming macroalgae species, resulting in the fact that sea urchin grazing alone can't provide sufficient conservation plan management in order to manage and preserve subtidal canopies ([Bulleri et al., 2018](#)). Long-term studies indicate that urbanization can lead to a general environmental deterioration affecting macroalgae, such as the case of Ancona, where 25-30 species have disappeared between the years 1940-1960, and in addition, 9 invasive species have been introduced by maritime traffic ([Fabbrizzi et al., 2020](#)). The decline of seaweed, and especially canopy-forming species, by anthropogenic disturbances, even after mitigation (such as sewage treatment management), in most cases cannot recover, and typical species of pristine environments (*Cystoseira* spp. mainly) are not abundant, but instead an increase of stress-tolerant species (e.g., *Corallina elongate*), occurs ([Pinedo et al., 2013](#)). Pressures by human activities that can erode marine biodiversity of macroalgae assemblages include i) overexploitation of large predators or ecosystem engineers, ii) nonindigenous species moving across biogeographic barriers, iii) chemical pollution, and iv) coastal development, while natural variability in synergy with human pressures can lead to different trends of decline in alpha and beta diversity ([Piazzi & Ceccherelli, 2020](#)). Despite the importance of macroalgae assemblages, these habitats haven't yet been described in detail, especially deep-water habitats where species composition and abundance of the identified morphological groups differ from shallow habitats, and additionally, a greater number of species occurs ([Balata & Piazzi, 2008](#)). Deep-water macroalgal species (especially *Cystoseira* spp.) and their dispersal abilities and population dynamics haven't been studied on a great scale, while their slow population dynamics and the limited population connectivity are the main causes of decline, along with anthropogenic pressures ([Capdevila et al., 2018](#)). In the Mediterranean, the knowledge of *Cystoseira* species

distribution is available for about 14% of the coastline, and large gaps of data emerge in the eastern and southern parts. Furthermore, predictions about the distribution of *Cystoseira* species show high accuracy, affected mainly by geomorphological conditions and secondarily by anthropogenic variables (pollution and urbanization) ([Fabbrizzi et al., 2020](#)). Macroalgae assemblages and their importance in coastal rocky areas should be examined diligently, and more research must be carried out in order to protect, conserve, and manage coastal areas as an integrative ecosystem ([Sini et al., 2017](#)). Minding that anthropogenic pressures can affect macroalgal assemblages, marine protected areas (MPAs) and no-take zones are demarcated as protective measures, but good knowledge of natural community dynamics is necessary in order to assess the drivers leading to a decline of macroalgal assemblages. The composition and total coverage of macroalgae in protected areas do not differ when compared with areas outside the protected zone, but some species, such as the canopy-forming macroalgae *Treptacantha elegans*, show a positive effect by applying protection measures ([Medrano et al., 2020](#)). Climate change can affect macroalgae assemblages, and the main factors include i) temperature, ii) nutrient supply ([Muquerza et al., 2022](#)), iii) ocean acidification (72% reduction in calcareous species and community structure shifts) ([Porzio et al., 2011](#)), and iv) sea level ([Macreadie et al., 2017](#)). Extreme weather conditions can affect macroalgae assemblages, and climatic change is expected to increase the severity and frequency of heat waves and sea temperature extremes (extreme weather events affecting macroalgae). Sea level rise in association with increased storminess (resulting in increased waves) can affect macroalgae assemblages mainly due to i) high concentration of nutrients and import of freshwater, ii) dislodge of canopy-forming algae, and iii) sedimentation ([Macreadie et al., 2017](#)). Increasing temperature, which is the main driver of climate change, is also favoring alien species expansion all over the world ocean and in the Mediterranean Sea, suggesting that an ecosystem management approach should contain climate change and biological invasions ([Corrales et al., 2018](#); [Raitsos et al., 2010](#)). Managing the water environment has been lately described as of high importance, and in Europe the EU Water Framework Directive took place in order to establish a holistic and integrated approach (<https://environment.ec.europa.eu/>). Achieving good ecological status is the main goal of WFD, and macroalgae can be very useful as bioindicators in order to describe the coastal zone ecological status, while different indexes have been applied, such as the Ecological Evaluation Index ([Orfanidis et al., 2011](#)). Furthermore, the Marine Strategy Framework Directive and Good Environmental Status (GES) is based on 11 qualitative descriptors related to biological diversity, non-indigenous species, commercially exploited fish, and food webs, among others (<https://eba.eu.com/environmental/msfd-and-wfd/>), and when focusing on coastal habitats, macroalgae should be considered of high importance. In addition, the high structural complexity of macroalgae assemblages is leading to the opinion that these habitats should be observed in a holistic view in order to protect and sufficiently manage these ecosystems and, furthermore, to benefit human activities related to macroalgae directly (e.g., scuba diving, harvest) or indirectly (e.g., supporting fishing stock). On a global scale, the Aichi Target 11 of the Convention on Biological Diversity dictates that 10% of the sea should be protected by 2020, while only 20% worldwide is meeting the target.

The Aegean Sea is considered to be a stronghold of marine biodiversity of the Mediterranean but still lacks spatial information, both in marine habitats and species (especially deep water), while large areas are understudied. Existing conservation of the Aegean and the measures applied are considered to be insufficient to safeguard biodiversity, while only 2.3% correspond to designated areas for conservation ([Sini et al., 2017](#)). Saronikos Gulf has been studied extensively, and more recent results indicate that macroalgae assemblages have increased in terms of biodiversity (species richness and total coverage values), but canopy-forming algae decline was addressed despite the better water quality after Sewage Primary Treatment in 2004. The re-oligotrophication of Saronikos and the decline of canopy-forming algae may be a result of i) absence of parental *Cystoseira* population, ii) lower water quality required and iii) overgrazing by overpopulated marine herbivores ([Tsiamis et al., 2013](#)). It is worth noting that on a global scale, when eutrophicated areas shift to an oligotrophic state, perennial macroalgae cannot recover, and the overall status shifts are mainly unknown ([Le Fur et al., 2019](#); [Pinedo et al., 2013](#)). Considering that urbanization is the main driver leading to canopy-forming species decline, it is secondarily supported that non-indigenous species are also of high importance (mostly through marine trafficking) ([Rindi et al., 2020](#)), and the Saronikos Gulf is also considered to be an alien species hotspot ([Zenetos et al., 2020](#)). Nevertheless, when focusing on macroalgae forests, the drivers leading to a decline or even absolute absence remain unknown, and natural recovery is rarely documented ([Cebrian et al., 2021](#)). The Saronikos Gulf has lately been examined in a holistic approach, and the most impacted ecological components are i) organic sedimentation, ii) benthic fauna and vegetation, iii) mammals, and iv) alien species, while the whole Saronikos Gulf basin is categorized into GOOD status ([Pavlidou et al., 2019](#)). Future anthropogenic threats to macroalgae assemblages of the Saronikos Gulf may oppose the increase of tourism (in Attica, 5.5 million tourists in 2018, up from 2.6 million in 2012 (<https://www.greeceinvestorguide.com/regions/attica/>)) and infrastructure investments (such as The Ellinikon, with a threshold of 1 million tourists to be hospitalized annually (<https://theellinikon.com.gr/en/invest/>)) during their construction and afterwards. Global warming and extreme weather conditions can affect macroalgae, mainly due to the expansion of alien species and the competition with native species.

The sea surface temperature of the study area shows an increasing trend during the last 25 years (1998-2023). Extreme weather conditions may affect SST in various ways, while notable weather and climate events in Greece (2022) ([HNMS, 2022](#)) are associated with alternations to temperature (figure 14b). In 2022, heavy snowfall occurred by “Elpis” on January 22 to 25 (Aegean, Evia, and Attica region) and also on March 9 to 16 by “Filippos” (Attica and Viotia region). As a result of these extreme weather conditions, March 2022 was the 3rd coldest March since 1960, and considering the analysis of the SST dataset in this thesis, the winter season of the year 2022 was the coldest with a mean temperature of 11.52°C (figure 14b). The highest mean annual SST (19.26°C) of the study area for the dataset occurred in 2018, and a marine temperature extreme event (marine heat wave) with high activity was observed in the eastern Mediterranean Sea ([Simon et al., 2022](#)). Warming and extreme heatwaves have increased since

the 1990s in the Mediterranean Sea, leading to the “tropicalization” of the fauna and flora, mainly by the spread of tropical non-indigenous species ([Balzan et al., 2022](#)). Marine heatwaves impacts on marine biodiversity are highlighted globally, and the Mediterranean Sea is not an exception, while monitoring and forecasting efforts are necessary to understand these events ([Darmaraki et al., 2024](#)). Nevertheless, *P. oceanica* meadows can tolerate temperature increases within their thermal limits (up to 28-30°C), but metabolic and physiological dysfunction is observed in the seeds after a temperature threshold of 26-28°C ([Rinaldi et al., 2023](#)). Despite the high tolerance of *P. oceanica* meadows to temperature increase, when natural or cultural eutrophication events are combined, present and future persistence is affected, particularly under eutrophic conditions ([Pazzaglia et al., 2020](#)). Some canopy-forming species (e.g., *Gongolaria barbata*) show high adaptability to future climate conditions related to marine heat waves ([Fabbrizzi et al., 2023](#)), and, on the other hand, the persistence and integrity of macroalgae forests (such as kelp forests) are threatened by ocean warming ([Smale, 2020](#)). In the Mediterranean Sea, macroalgal forests formed by *Cystoseira sensu lato* are affected by thermal anomalies and ocean warming at their reproductive phenology, germling growth, and viability, leading to increased mortality in the recruitment stages, rendering them vulnerable to further stresses ([Falace et al., 2021](#)). Ocean warming impacts on phytobenthic communities indicate that recruitment stages are affected the most, and long-term threats to the survival of these high-importance phytobenthic habitats are expected. Furthermore, ocean warming increases the stress of phytobenthos, and when other factors act synergistically, high-importance habitats (e.g., *P. oceanica* meadows and macroalgae forests) are highly threatened. The overall alterations to marine diversity and human benefits by the loss of coastal phytobenthic ecosystems are still under question, but the fact that nowadays they are considered to be valuable and the need to protect, conserve, and preserve these ecosystems is highlighted.

Ocean warming is the most severe threat among global climate change factors for the phytobenthic communities and is the most important range-limiting factor. Ongoing climatic changes are expected to alter physiological responses and the survivability of early life changes (both seeds and spores) of macroalgae and seagrasses. Additionally, symbiotic relations between microbiome communities and their hosts and biochemical changes in macrophytes are affected, which can have severe impacts on trophic levels feeding on seagrass-derived organic matter (e.g., reduced carbon fixation leading to reduced energy transfer and severe reduction of essential fatty acid production) ([Duarte et al., 2018](#)). For the study area, analysis of sea surface temperature (SST) data from 1983 to 2023 reveals an increasing trend in annual mean SST, along with changes in climatology and the frequency of high temperatures. Both maximum and minimum SST values are closely linked to extreme weather events. The data from 1948 to 2023 indicate long-term warming, with a clear upward shift in temperatures over recent decades, particularly from the late 1990s and afterwards. Climatology analysis highlights a consistent increase in SST during the summer months, especially in July and August, with a rise of at least 1°C in the past 25 years. Seasonal variability from 1998 to 2023 demonstrates an

accelerating increase in SST, particularly in February, September, and November, with temperature differences reaching up to 0.95°C (Figure13). The highest monthly mean SST for the latter period is 26.29°C in August, followed by July at 25.74°C. Marine macroalgal forests, mainly formed by *Cystoseira sensu lato* species, are affected in both the pre- and post-zygotic phases by thermal anomalies. The period of sexual maturity is June and July, while in the study area, July is the month with the highest mean SST. Thermal anomalies result in low culture efficiency, lower fertilization of eggs, and slower embryo growth, leading to lower percent cover of seedlings on the tiles and lower survival rate ([Cimini et al., 2024](#)). If ocean warming continues, the optimal temperature for the growth of *P. oceanica*, *Cystoseira compressa*, *Padina pavonica*, *Caulerpa prolifera*, and *Halimeda tuna* will be affected negatively. *P. oceanica* has an upper lethal limit of 28.9°C and is the most vulnerable among the other macrophytic organisms ([Savva et al., 2018](#)). In the study area, the highest mean monthly SST almost reaches 27°C (e.g., 26.93°C in August 2010, 26.92°C in August 2021, and 26.69°C in July 2021), and therefore the early life stages are already negatively affected. Further temperature increase will challenge the survival of *P. oceanica*, especially when other pressures are combined, such as direct erosion by anchoring and fishing, water and sediment eutrophication, coastline transformation effects, and expansion of alien species. Climate change will affect macrophytic communities in the next decades, and long-term monitoring and a holistic approach are necessary to identify the alterations and impacts to macrophytic assemblages.

References

1. Abadie, A., Pace, M., Gobert, S., & Borg, J. A. (2018). Seascape ecology in *Posidonia oceanica* seagrass meadows: Linking structure and ecological processes for management. *Ecological Indicators*, 87(September 2017), 1–13. <https://doi.org/10.1016/j.ecolind.2017.12.029>
2. Albano, P. G., Steger, J., Bošnjak, M., Dunne, B., Guifarro, Z., Turapova, E., Hua, Q., Kaufman, D. S., Rilov, G., & Zuschin, M. (2021). Native biodiversity collapse in the eastern Mediterranean. *Proceedings of the Royal Society B: Biological Sciences*, 288(1942), 1–9. <https://doi.org/https://doi.org/10.1098/rspb.2020.2469>
3. Ar Gall, E., Le Duff, M., Sauriau, P. G., De Casamajor, M. N., Gevaert, F., Poisson, E., Hacquebart, P., Joncourt, Y., Barillé, A. L., Buchet, R., Bréret, M., & Miossec, L. (2016). Implementation of a new index to assess intertidal seaweed communities as bioindicators for the European Water Framework Directory. *Ecological Indicators*, 60(January), 162–173. <https://doi.org/10.1016/j.ecolind.2015.06.035>
4. Arévalo, R., Pinedo, S., & Ballesteros, E. (2007). Changes in the composition and structure of Mediterranean rocky-shore communities following a gradient of nutrient enrichment: Descriptive study and test of proposed methods to assess water quality regarding macroalgae. *Marine Pollution Bulletin*, 55(1–6), 104–113. <https://doi.org/10.1016/j.marpolbul.2006.08.023>
5. Balanika, K., Konida, K., Tsiamis, K., Salomidi, M., & Panayotidis, P. (2011). *Long-Term Changes of Marine Macroalgae Saronikos Gulf: Data From the Years 1998-2011*. https://oceanos-dspace.hcmr.gr/bitstream/handle/123456789/1051/035_tel_MPALANIKA_TEXT.pdf?sequence=1
6. Balata, D., & Piazzì, L. (2008). Patterns of diversity in rocky subtidal macroalgal assemblages in relation to depth. *Botanica Marina*, 51(6), 464–471. <https://doi.org/10.1515/BOT.2008.068>
7. Balzan, M. V., El, A., Hassoun, R., Aroua, N., Baldy, V., Dagher, M. B., Branquinho, C., Dutay, J., El, M., Médail, F., & Mojtahid, M. (2022). *First Mediterranean Assessment Report – Chapter 4: Ecosystems*. <https://doi.org/10.5281/zenodo.7101090>
8. Belegreatis, M. R., Bitis, I., Economou-Amilli, A., & Ott, J. A. (1999). Epiphytic patterns of macroalgal assemblages on *Cystoseira* species (Fucales, Phaeophyta) in the east coast of Attica (Aegean Sea, Greece). *Hydrobiologia*, 412, 67–80. <https://doi.org/10.1023/A:1003852300198>
9. Boudouresque, C. F., Bernard, G., Bonhomme, P., Charbonnel, E., Diviacco, G., Meinesz, A., Pergent, G., Pergent-Martini, C., & Ruitton, S. T. L. (2012). *Protection and conservation of Posidonia oceanica meadows. RAMOGE and RAC/SPA publisher. Tunis, pp. 1–202.* (p. 202).
10. Boudouresque, Charles F., Pergent, G., Pergent-Martini, C., Ruitton, S., Thibaut, T., & Verlaque, M. (2016). The necromass of the *Posidonia oceanica* seagrass meadow: fate, role, ecosystem services and vulnerability. *Hydrobiologia*, 781(1), 25–42. <https://doi.org/10.1007/s10750-015-2333-y>
11. Boudouresque, Charles F., Blanfuné, A., Harmelin-, M., Personnic, S., Ruitton, S., Thibaut, T., & Verlaque, M. (2016). Where Seaweed Forests Meet Animal Forests: the Examples of Macroalgae in Coral Reefs and the Mediterranean Coralligenous Ecosystem. *Marine Animal Forests*. <https://doi.org/10.1007/978-3-319-17001-5>
12. Boudouresque, Charles F., Meinesz, A., Ribera, M. A., & Ballesteros, E. (1995). Spread of the green alga *Caulerpa taxifolia* (Caulerpales, Chlorophyta) in the Mediterranean: possible consequences of a major ecological event. *Scientia Marina*, 59(1), 21–29.
13. Bulleri, F., Cucco, A., Dal Bello, M., Maggi, E., Ravaglioli, C., & Benedetti-Cecchi, L. (2018). *The role of wave-exposure and human impacts in regulating the distribution of alternative habitats on shallow rocky reefs in the NW Mediterranean*. 1–31.
14. Bykova, N., LoDuca, S. T., Ye, Q., Marusin, V., Grazhdankin, D., & Xiao, S. (2020). Seaweeds through time: Morphological and ecological analysis of Proterozoic and early Paleozoic benthic macroalgae. *Precambrian Research*, 350. <https://doi.org/10.1016/j.precamres.2020.105875>
15. Campagne, C. S., Salles, J. M., Boissery, P., & Deter, J. (2014). The seagrass *Posidonia oceanica*: Ecosystem services identification and economic evaluation of goods and benefits. *Marine Pollution Bulletin*, 97(1–2), 391–400. <https://doi.org/10.1016/j.marpolbul.2015.05.061>
16. Capasso, L., Buonocore, E., Franzese, P. P., & Russo, G. F. (2024). The scientific literature on *Posidonia*

- oceanica meadows and related ecosystem services. *Ecological Questions*, 35(1), 1–14. <https://doi.org/10.12775/EQ.2024.003>
17. Capdevila, P., Linares, C., Aspillaga, E., Riera, J. L., & Hereu, B. (2018). Effective dispersal and density-dependence in mesophotic macroalgal forests: Insights from the Mediterranean species *Cystoseira zosteroides*. *PLoS ONE*, 13(1), 1–15. <https://doi.org/10.1371/journal.pone.0191346>
 18. Castro, P., & Huber, M. E. (2012). *Marine Biology 10th Edition* (Vol. 53, Issue 9). McGraw-Hill Education. <https://doi.org/10.1017/CBO9781107415324.004>
 19. Cebrian, E., Tamburello, L., Verdura, J., Guarnieri, G., Medrano, A., Linares, C., Hereu, B., Garrabou, J., Cerrano, C., Galobart, C., & Fraschetti, S. (2021). A Roadmap for the Restoration of Mediterranean Macroalgal Forests. *Frontiers in Marine Science*, 8(October), 1–14. <https://doi.org/10.3389/fmars.2021.709219>
 20. Charpy-Roubaud, C., & Sournia, A. (1990). The comparative estimation of phytoplanktonic, microphytobenthic and macrophytobenthic primary production in the oceans. *Marine Microbial Food Webs*, 4(April 1988), 31–57.
 21. Cheminée, A., Le Direach, L., Rouanet, E., Astruch, P., Goujard, A., Blanfuné, A., Bonhomme, D., Chassaing, L., Jouvenel, J. Y., Ruitton, S., Thibaut, T., & Harmelin-Vivien, M. (2021). All shallow coastal habitats matter as nurseries for Mediterranean juvenile fish. *Scientific Reports*, 11(1), 1–17. <https://doi.org/10.1038/s41598-021-93557-2>
 22. Cheminée, A., Sala, E., Pastor, J., Bodilis, P., Thiriet, P., Mangialajo, L., Cottalorda, J. M., & Francour, P. (2013). Nursery value of *Cystoseira* forests for Mediterranean rocky reef fishes. *Journal of Experimental Marine Biology and Ecology*, 442(November 2018), 70–79. <https://doi.org/10.1016/j.jembe.2013.02.003>
 23. Cimini, J., Asnaghi, V., Chiantore, M., Kaleb, S., Onida, A., & Falace, A. (2024). Can thermal anomalies impair the restoration of *Cystoseira* s.l. forests? *Marine Environmental Research*, 198(May). <https://doi.org/10.1016/j.marenvres.2024.106537>
 24. Coll, M., Piroddi, C., Steenbeek, J., Kaschner, K., Lasram, F. B. R., Aguzzi, J., Ballesteros, E., Bianchi, C. N., Corbera, J., Dailianis, T., Danovaro, R., Estrada, M., Frogli, C., Galil, B. S., Gasol, J. M., Gertwage, R., Gil, J., Guilhaumon, F., Kesner-Reyes, K., ... Voultsiadou, E. (2010). The biodiversity of the Mediterranean Sea: Estimates, patterns, and threats. *PLoS ONE*, 5(8). <https://doi.org/10.1371/journal.pone.0011842>
 25. Corrales, X., Coll, M., Ofir, E., Heymans, J. J., Steenbeek, J., Goren, M., Edelist, D., & Gal, G. (2018). Future scenarios of marine resources and ecosystem conditions in the Eastern Mediterranean under the impacts of fishing, alien species and sea warming. *Scientific Reports*, 8(1), 1–16. <https://doi.org/10.1038/s41598-018-32666-x>
 26. Darmaraki, S., Denaxa, D., Theodorou, I., Livanou, E., Rigatou, D., E., D. R., Stavrakidis-Zachou, O., Dimarchopoulou, D., Bonino, G., McAdam, R., Organelli, E., Pitsouni, A., & Parasyris, A. (2024). Marine Heatwaves in the Mediterranean Sea: A Literature Review. *Mediterranean Marine Science*, 25(3), 586–620. <https://doi.org/10.12681/mms.38392>
 27. Díaz-Almela, E., & Duarte, C. M. (2008). Management of Natura 2000 habitats_Posidonia beds (Posidonium oceanica) 1120. In *Ecosystems*.
 28. Duarte, B., Martins, I., Rosa, R., Matos, A. R., Roleda, M. Y., Reusch, T. B. H., Engelen, A. H., Serrão, E. A., Pearson, G. A., Marques, J. C., Caçador, I., Duarte, C. M., & Jueterbock, A. (2018). Climate change impacts on seagrass meadows and macroalgal forests: An integrative perspective on acclimation and adaptation potential. *Frontiers in Marine Science*, 5(JUN). <https://doi.org/10.3389/fmars.2018.00190>
 29. Fabbri, E., Munari, M., Fraschetti, S., Arena, C., Chiarore, A., Cannavacciuolo, A., Colletti, A., Costanzo, G., Soler-Fajardo, A., Nannini, M., Savinelli, B., Silvestrini, C., Vitale, E., & Tamburello, L. (2023). Canopy-forming macroalgae can adapt to marine heatwaves. *Environmental Research*, 238(P2), 117218. <https://doi.org/10.1016/j.envres.2023.117218>
 30. Fabbri, E., Scardi, M., Ballesteros, E., Benedetti-Cecchi, L., Cebrian, E., Ceccherelli, G., De Leo, F., Deidun, A., Guarnieri, G., Falace, A., Fraissinet, S., Giommi, C., Mačić, V., Mangialajo, L., Mannino, A. M., Piazzini, L., Ramdani, M., Rilov, G., Rindi, L., ... Fraschetti, S. (2020). Modeling macroalgal forest distribution at mediterranean scale: Present status, drivers of changes and insights for conservation and management. *Frontiers in Marine Science*, 7(February), 1–18. <https://doi.org/10.3389/fmars.2020.00020>
 31. Falace, A., Marletta, G., Savonitto, G., Candotto Carniel, F., Srijemsi, M., Bevilacqua, S., Tretiach, M., & Alongi, G. (2021). Is the South-Mediterranean Canopy-Forming *Ericaria giacconeii* (= *Cystoseira hyblaea*) a

- Loser From Ocean Warming? *Frontiers in Marine Science*, 8(November), 1–12. <https://doi.org/10.3389/fmars.2021.760637>
32. Gerakaris, V., Papathanasiou, V., Salomidi, M., Issaris, Y., & Panayotidis, P. (2021). Spatial patterns of *Posidonia oceanica* structural and functional features in the Eastern Mediterranean (Aegean and E. Ionian Seas) in relation to large-scale environmental factors. *Marine Environmental Research*, 165(July 2020), 105222. <https://doi.org/10.1016/j.marenvres.2020.105222>
 33. Giakoumi, S., Cebrian, E., Kokkoris, G. D., Ballesteros, E., & Sala, E. (2012). Relationships between fish, sea urchins and macroalgae: The structure of shallow rocky sublittoral communities in the Cyclades, Eastern Mediterranean. *Estuarine, Coastal and Shelf Science*, 109, 1–10. <https://doi.org/10.1016/j.ecss.2011.06.004>
 34. Gómez-Pujol, L., Orfila, A., Álvarez-Ellacuría, A., Terrados, J., & Tintoré, J. (2013). *Posidonia oceanica* beach-cast litter in Mediterranean beaches: a coastal videomonitoring study. *Journal of Coastal Research*, 165(65), 1768–1773. <https://doi.org/10.2112/si65-299.1>
 35. HNMS. (2022). *Notable weather and climate events in Greece 2022*.
 36. I.Siokou-Frangou. (1999). *National Centre for Marine Research Monitoring of the Saronikos Gulf Ecosystem Affected By the Psittalia Monitoring of the Saronikos Gulf. November*. [https://oceanos-dspace.hcmr.gr/xmlui/bitstream/handle/123456789/3395/TEE\(243\).pdf?sequence=1](https://oceanos-dspace.hcmr.gr/xmlui/bitstream/handle/123456789/3395/TEE(243).pdf?sequence=1)
 37. Israel, A., Golberg, A., & Neori, A. (2020). The seaweed resources of Israel in the Eastern Mediterranean Sea. *Botanica Marina*. <https://doi.org/10.1515/bot-2019-0048>
 38. Katsanevakis, S., Salomidi, M., & Panou, A. (2010). Modelling distribution patterns and habitat preference of the invasive green alga *Caulerpa racemosa* in the Saronikos Gulf (Eastern Mediterranean). *Aquatic Biology*, 10(1), 57–67. <https://doi.org/10.3354/ab00267>
 39. Khan, A. H., Levac, E., van Guelphen, L., Pohle, G., & Chmura, G. L. (2018). The effect of global climate change on the future distribution of economically important macroalgae (seaweeds) in the northwest Atlantic. *Facets*, 3(1), 275–286. <https://doi.org/10.1139/facets-2017-0091>
 40. Kletou, D., Savva, I., Tsiamis, K., & Hall-Spencer, J. M. (2018). Opportunistic seaweeds replace *Cystoseira* forests on an industrialised coast in Cyprus. *Mediterranean Marine Science*, 19(3), 598–610. <https://doi.org/10.12681/MMS.16891>
 41. Krause-Jensen, D., Lavery, P., Serrano, O., Marba, N., Masque, P., & Duarte, C. M. (2018). Sequestration of macroalgal carbon: The elephant in the Blue Carbon room. *Biology Letters*, 14(6). <https://doi.org/https://doi.org/10.1098/rsbl.2018.0236>
 42. Langar, H., Bouafif C., & A, O. (2014). Proceedings of the 5th Mediterranean Symposium on Marine Vegetation. *UNEP/MAP – RAC/SPA, 2014. Proceedings of the 5th Mediterranean Symposium on Marine Vegetation (Portorož, Slovenia, 27-28 October 2014)*. LANGAR H., BOUAFIF C., OUERGI A., Edits., RAC/SPA Publ., Tunis: 251 P, October, 251.
 43. Le Fur, I., De Wit, R., Plus, M., Oheix, J., Derolez, V., Simier, M., Malet, N., & Ouisse, V. (2019). Re-oligotrophication trajectories of macrophyte assemblages in Mediterranean coastal lagoons based on 17-year time-series. *Marine Ecology Progress Series*, 608, 13–32. <https://doi.org/10.3354/meps12814>
 44. Macreadie, P. I., Jarvis, J., Trevathan-Tackett, S. M., & Bellgrove, A. (2017). Seagrasses and Macroalgae: Importance, Vulnerability and Impacts. In *Climate Change Impacts on Fisheries and Aquaculture* (Issue November). <https://doi.org/10.1002/9781119154051.ch22>
 45. Mariani, S., Cefali, M. E., Chappuis, E., Terradas, M., Pinedo, S., Torras, X., Jordana, E., Medrano, A., Verdura, J., & Ballesteros, E. (2019). Past and present of *Fucales* from shallow and sheltered shores in Catalonia. *Regional Studies in Marine Science*, 32. <https://doi.org/10.1016/j.rsma.2019.100824>
 46. Markager, S., & Sand-Jensen, K. (1992). Light requirements and depth zonation of marine macroalgae. *Marine Ecology Progress Series*, 88(1), 83–92. <https://doi.org/10.3354/meps088083>
 47. Medrano, A., Linares, C., Aspillaga, E., Capdevila, P., Montero-Serra, I., Pagès-Escolà, M., Zabala, M., & Hereu, B. (2020). Long-term monitoring of temperate macroalgal assemblages inside and outside a No take marine reserve. *Marine Environmental Research*, 153(July). <https://doi.org/10.1016/j.marenvres.2019.104826>
 48. Mineur, F., Arenas, F., Assis, J., Davies, A. J., Engelen, A. H., Fernandes, F., Malta, E. Jan, Thibaut, T., Van Nguyen, T., Vaz-Pinto, F., Vranken, S., Serrão, E. A., & De Clerck, O. (2015). European seaweeds under pressure: Consequences for communities and ecosystem functioning. *Journal of Sea Research*, 98, 91–

108. <https://doi.org/10.1016/j.seares.2014.11.004>
49. Monnier, B., Pergent, G., Boudouresque, C. F., Monnier, B., Pergent, G., Boudouresque, C. F., Mateo, M. Á., & Posidonia, T. (2021). *The Posidonia oceanica matte : a unique coastal carbon sink for climate change mitigation and implications for management*.
50. Montefalcone, M. (2009). Ecosystem health assessment using the Mediterranean seagrass *Posidonia oceanica*: A review. *Ecological Indicators*, 9(4), 595–604. <https://doi.org/10.1016/j.ecolind.2008.09.013>
51. Muguerza, N., Arriaga, O., Díez, I., Becerro, M. A., Quintano, E., & Gorostiaga, J. M. (2022). A spatially-modelled snapshot of future marine macroalgal assemblages in southern Europe: Towards a broader Mediterranean region? *Marine Environmental Research*, 176(March), 105592. <https://doi.org/10.1016/j.marenvres.2022.105592>
52. Orfanidis, S., Panayotidis, P., & Ugland, K. I. (2011). Ecological Evaluation Index continuous formula (EEI-c) application: A step forward for functional groups, the formula and reference condition values. *Mediterranean Marine Science*, 12(1), 199–231. <https://doi.org/10.12681/mms.60>
53. Ortega, A., Gernaldi, N. R., Alam, I., & Kamau, A. A. (2019). *Important contribution of macroalgae to oceanic carbon sequestration*. https://digital.csic.es/bitstream/10261/192545/3/Ortega_et_al_2019_preprint.pdf
54. Panayotidis, P., Papatthasiou, V., Gerakaris, V., Fakiris, E., Orfanidis, S., Papatheodorou, G., Kosmidou, M., Georgiou, N., Drakopoulou, V., & Loukaidi, V. (2022). Seagrass meadows in the Greek Seas: Presence, abundance and spatial distribution. *Botanica Marina*, 65(4), 289–299. <https://doi.org/10.1515/bot-2022-0011>
55. Pavlidou, A., Simboura, N., Pagou, K., Assimakopoulou, G., Gerakaris, V., Hatzianestis, I., Panayotidis, P., Pantazi, M., Papadopoulou, N., Reizopoulou, S., Smith, C., Triantaphyllou, M., Uyarra, M. C., Varkitzi, I., Vassilopoulou, V., Zeri, C., & Borja, A. (2019). Using a holistic ecosystem-integrated approach to assess the environmental status of Saronikos Gulf, Eastern Mediterranean. *Ecological Indicators*, 96(January), 336–350. <https://doi.org/https://doi.org/10.1016/j.ecolind.2018.09.007>
56. Pazzaglia, J., Santillán-Sarmiento, A., Helber, S. B., Ruocco, M., Terlizzi, A., Marín-Guirao, L., & Procaccini, G. (2020). Does Warming Enhance the Effects of Eutrophication in the Seagrass *Posidonia oceanica*? *Frontiers in Marine Science*, 7(December), 1–15. <https://doi.org/10.3389/fmars.2020.564805>
57. Pergent-Martini, C., Pergent, G., Monnier, B., Boudouresque, C. F., Mori, C., & Valette-Sansevin, A. (2021). Contribution of *Posidonia oceanica* meadows in the context of climate change mitigation in the Mediterranean Sea. *Marine Environmental Research*, 165, 1–20. <https://doi.org/10.1016/j.marenvres.2020.105236>
58. Piazzì, L., & Ceccherelli, G. (2020). Alpha and beta diversity in Mediterranean macroalgal assemblages: relevancy and type of effect of anthropogenic stressors vs natural variability. *Marine Biology*, 167(3), 1–10. <https://doi.org/10.1007/s00227-019-3631-0>
59. Pinedo, S., Zabala, M., & Ballesteros, E. (2013). Long-term changes in sublittoral macroalgal assemblages related to water quality improvement. *Botanica Marina*, 56(5–6), 461–469. <https://doi.org/10.1515/bot-2013-0018>
60. Porzio, L., Buia, M. C., & Hall-Spencer, J. M. (2011). Effects of ocean acidification on macroalgal communities. *Journal of Experimental Marine Biology and Ecology*, 400(1–2), 278–287. <https://doi.org/10.1016/j.jembe.2011.02.011>
61. Psarra, S., Tselepides, A., & Ignatiades, L. (2000). Primary productivity in the oligotrophic Cretan Sea (NE Mediterranean): Seasonal and interannual variability. *Progress in Oceanography*, 46(2–4), 187–204. [https://doi.org/10.1016/S0079-6611\(00\)00018-5](https://doi.org/10.1016/S0079-6611(00)00018-5)
62. Raitos, D. E., Beaugrand, G., Georgopoulos, D., Zenetos, A., Pancucci-Papadopoulou, A. M., Theocharis, A., & Papatthasiou, E. (2010). Global climate change amplifies the entry of tropical species into the eastern Mediterranean Sea. *Limnology and Oceanography*, 55(4), 1478–1484. <https://doi.org/10.4319/lo.2010.55.4.1478>
63. Ramachandra, T. V., & Hebbale, D. (2020). Bioethanol from macroalgae: Prospects and challenges. *Renewable and Sustainable Energy Reviews*, 117(February 2019), 109479. <https://doi.org/10.1016/j.rser.2019.109479>
64. Raven, J. (2018). Blue carbon: Past, present and future, with emphasis on macroalgae. *Biology Letters*, 14(10), 1–5. <https://doi.org/https://doi.org/10.1098/rsbl.2018.0336>
65. Rinaldi, A., Martínez, M., Badalamenti, F., D’Anna, G., Mirto, S., Marín-Guirao, L., Procaccini, G., &

- Montalto, V. (2023). The ontogeny-specific thermal sensitivity of the seagrass *Posidonia oceanica*. *Frontiers in Marine Science*, *10*(July), 1–11. <https://doi.org/10.3389/fmars.2023.1183728>
66. Rindi, F., Gavio, B., Díaz-Tapia, P., Di Camillo, C. G., & Romagnoli, T. (2020). Long-term changes in the benthic macroalgal flora of a coastal area affected by urban impacts (Conero Riviera, Mediterranean Sea). *Biodiversity and Conservation*, *29*(7), 2275–2295. <https://doi.org/10.1007/s10531-020-01973-z>
 67. Robin, A., Chavel, P., Chemodanov, A., Israel, A., & Golberg, A. (2017). Diversity of monosaccharides in marine macroalgae from the Eastern Mediterranean Sea. *Algal Research*, *28*(October), 118–127. <https://doi.org/10.1016/j.algal.2017.10.005>
 68. Román, M., Román, S., Vázquez, E., Troncoso, J., & Olabarria, C. (2020). Heatwaves during low tide are critical for the physiological performance of intertidal macroalgae under global warming scenarios. *Scientific Reports*, *10*(1), 1–14. <https://doi.org/10.1038/s41598-020-78526-5>
 69. Ruju, A., Ibba, A., Porta, M., Buosi, C., Passarella, M., & Muro, D. (2018). *The role of hydrodynamic forcing, sediment transport processes and bottom substratum in the shoreward development of Posidonia oceanica meadow*. <https://doi.org/10.1016/j.ecss.2018.06.025>. This
 70. Savva, I., Bennett, S., Roca, G., Jorda, G., & Marbà, N. (2018). *Thermal tolerance of Mediterranean marine macrophytes Vulnerability to global warming*.
 71. Schaffelke, B., Mellors, J., & Duke, N. C. (2005). Water quality in the Great Barrier Reef region: Responses of mangrove, seagrass and macroalgal communities. *Marine Pollution Bulletin*, *51*(1–4), 279–296. <https://doi.org/10.1016/j.marpolbul.2004.10.025>
 72. Schmid, M., Guihéneuf, F., & Stengel, D. B. (2017). Ecological and commercial implications of temporal and spatial variability in the composition of pigments and fatty acids in five Irish macroalgae. *Marine Biology*, *164*(8). <https://doi.org/https://doi.org/10.1007/s00227-017-3188-8>
 73. Simboura, N., Panayotidis, P., & Papatthanassiou, E. (2005). A synthesis of the biological quality elements for the implementation of the European Water Framework Directive in the Mediterranean ecoregion: The case of Saronikos Gulf. *Ecological Indicators*, *5*(3), 253–266. <https://doi.org/10.1016/j.ecolind.2005.03.006>
 74. Simboura, N., Zenetos, A., & Pancucci-Papadopoulou, M. A. (2014). Benthic community indicators over a long period of monitoring (2000–2012) of the Saronikos Gulf, Greece, Eastern Mediterranean. *Environmental Monitoring and Assessment*, *186*(6), 3809–3821. <https://doi.org/10.1007/s10661-014-3659-z>
 75. Simon, A., Plecha, S. M., Russo, A., Teles-Machado, A., Donat, M. G., Auger, P. A., & Trigo, R. M. (2022). Hot and cold marine extreme events in the Mediterranean over the period 1982–2021. *Frontiers in Marine Science*, *9*(August), 1–12. <https://doi.org/10.3389/fmars.2022.892201>
 76. Sini, M., Katsanevakis, S., Koukourouvli, N., Gerovasileiou, V., Dailianis, T., Buhl-Mortensen, L., Damalas, D., Dendrinou, P., Dimas, X., Frantzis, A., Gerakaris, V., Giakoumi, S., Gonzalez-Mirelis, G., Hasiotis, T., Issaris, Y., Kavadas, S. G., Koutsogiannopoulos, D. D., Koutsoubas, D., Manoutsoglou, E., ... Zotou, M. (2017). Assembling ecological pieces to reconstruct the conservation puzzle of the aegean sea. *Frontiers in Marine Science*, *4*(NOV), 1–22. <https://doi.org/10.3389/fmars.2017.00347>
 77. Smale, D. A. (2020). Impacts of ocean warming on kelp forest ecosystems. *New Phytologist*, *225*(4), 1447–1454. <https://doi.org/10.1111/nph.16107>
 78. Spalding, H. L., Amado-filho, G. M., Bahia, R. G., Ballantine, D. L., Fredericq, S., Leichter, J. J., Nelson, W. A., Slattery, M., & Tsuda, R. T. (2019). *Mesophotic Coral Ecosystems. Coral Reefs of the World, vol 12. Springer, Cham.* (Issue May). <https://doi.org/10.1007/978-3-319-92735-0>
 79. Stengel, D. B., Connan, S., & Popper, Z. A. (2011). Algal chemodiversity and bioactivity: Sources of natural variability and implications for commercial application. *Biotechnology Advances*, *29*(5), 483–501. <https://doi.org/10.1016/j.biotechadv.2011.05.016>
 80. Tamburello, L., Papa, L., Guarnieri, G., Basconi, L., Zampardi, S., Scipione, M. B., Terlizzi, A., Zupo, V., & Frascchetti, S. (2019). Are we ready for scaling up restoration actions? An insight from Mediterranean macroalgal canopies. *PLoS ONE*, *14*(10), 1–23. <https://doi.org/10.1371/journal.pone.0224477>
 81. Thiriet, P. D., Di Franco, A., Cheminée, A., Guidetti, P., Bianchimani, O., Basthard-Bogain, S., Cottalorda, J. M., Arceo, H., Moranta, J., Lejeune, P., Francour, P., & Mangialajo, L. (2016). Abundance and diversity of crypto- and necto-benthiccoastal fish are higher in marine forests than in structurally less complex macroalgal assemblages. *PLoS ONE*, *11*(10), 1–24. <https://doi.org/10.1371/journal.pone.0164121>
 82. Topouzelis, K., Makri, D., Stoupas, N., Papakonstantinou, A., & Katsanevakis, S. (2018). Seagrass mapping

- in Greek territorial waters using Landsat-8 satellite images. *International Journal of Applied Earth Observation and Geoinformation*, 67(December 2017), 98–113. <https://doi.org/10.1016/j.jag.2017.12.013>
83. Traganos, D., Aggarwal, B., Poursanidis, D., Topouzelis, K., Chrysoulakis, N., & Reinartz, P. (2018). Towards global-scale seagrass mapping and monitoring using Sentinel-2 on Google Earth Engine: The case study of the Aegean and Ionian Seas. *Remote Sensing*, 10(8), 1–14. <https://doi.org/10.3390/rs10081227>
 84. Tsiamis, K., & Panayotidis, P. (2015). New record and further expansion of alien macroalgae in Greece. *11th Panhellenic Symposium on Oceanography and Fisheries, April 2013*, 601–604. http://elnais.hcmr.gr/wp-content/uploads/2015/05/Tsiamis_Panagiotidis.pdf
 85. Tsiamis, K., Panayotidis, P., Peters, A. F., Kawai, H., Salomidi, M., Nikolic, V., Taskin, E., Balanika, A., Konida, A., Tsigirigi, A., Küpper, F. C., & Katsaros, C. (2012). Recent Highlights in the Exploration of East Mediterranean Brown Algal Biodiversity and Ecology. *10th Panhellenic Symposium on Oceanography and Fisheries, Athens, 7-11 May, 2012. Athens: HCMR, (e-Book)*, 1–6. http://oceanos-dspace.hcmr.gr/xmloi/bitstream/handle/123456789/1209/098_tel_Tsiamis_revised.pdf?sequence=1
 86. Tsiamis, Konstantinos, Economou-Amilli, A., Katsaros, C., & Panayotidis, P. (2013). First account of native and alien macroalgal biodiversity at Andros Island (Greece, Eastern Mediterranean). *Nova Hedwigia*, 97(1–2), 209–224. <https://doi.org/10.1127/0029-5035/2013/0109>
 87. Tsiamis, Konstantinos, Panayotidis, P., Salomidi, M., Pavlidou, A., Kleinteich, J., Balanika, K., & Küpper, F. C. (2013). Macroalgal community response to re-oligotrophication in Saronikos Gulf. *Marine Ecology Progress Series*, 472, 73–85. <https://doi.org/10.3354/meps10060>
 88. Tsiamis, Konstantinos, Salomidi, M., Kytinou, E., Issaris, Y., & Gerakaris, V. (2016). On two new records of rare Cystoseira taxa (Fucales, Phaeophyceae) from Greece (Eastern Mediterranean). *Botanica Marina*, 59(1), 73–77. <https://doi.org/10.1515/bot-2015-0084>
 89. Tsiamis, Konstantinos, & Verlaque, M. (2011). A new contribution to the alien red macroalgal flora of Greece (Eastern Mediterranean) with emphasis on Hypnea species. *Cryptogamie, Algologie*, 32(4), 393–410. <https://doi.org/10.7872/crya.v32.iss4.2011.393>
 90. Tsiamis, Konstantinos, Verlaque, M., Panayotidis, P., & Montesanto, B. (2010). New macroalgal records for the Aegean Sea (Greece, eastern Mediterranean Sea). *Botanica Marina*, 53(4), 319–331. <https://doi.org/10.1515/BOT.2010.041>
 91. Vacchi, M., De Falco, G., Simeone, S., Montefalcone, M., Morri, C., Ferrari, M., & Bianchi, C. N. (2017). Biogeomorphology of the Mediterranean Posidonia oceanica seagrass meadows. *Earth Surface Processes and Landforms*, 42(1), 42–54. <https://doi.org/10.1002/esp.3932>
 92. Verlaque, M., Boudouresque, C., & Perret-boudouresque, M. (2019). Mediterranean seaweeds listed as threatened under the Barcelona Convention: A critical analysis. *Sci. Rep. Port-Cros Natl. Park*, 33(January), 179–214.
 93. Walker, D. I., & Kendrick, G. A. (1998). Threats to macroalgal diversity: Marine habitat destruction and fragmentation, pollution and introduced species. *Botanica Marina*, 41(1), 105–112. <https://doi.org/10.1515/botm.1998.41.1-6.105>
 94. Wells, E., Wilkinson, M., Wood, P., & Scanlan, C. (2007). The use of macroalgal species richness and composition on intertidal rocky seashores in the assessment of ecological quality under the European Water Framework Directive. *Marine Pollution Bulletin*, 55(1–6), 151–161. <https://doi.org/https://doi.org/10.1016/j.marpolbul.2006.08.031>
 95. Wilson, S. K., Fulton, C. J., Depczynski, M., Holmes, T. H., Noble, M. M., Radford, B., & Tinkler, P. (2014). Seasonal changes in habitat structure underpin shifts in macroalgae-associated tropical fish communities. *Marine Biology*, 161(11), 2597–2607. <https://doi.org/10.1007/s00227-014-2531-6>
 96. Włodarska-Kowalczyk, M., Kukliński, P., Ronowicz, M., Legeżyńska, J., & Gromisz, S. (2009). Assessing species richness of macrofauna associated with macroalgae in Arctic kelp forests (hornsund, svalbard). *Polar Biology*, 32(6), 897–905. <https://doi.org/10.1007/s00300-009-0590-9>
 97. Zenetos, A., Gofas, S., Morri, C., Rosso, A., Violanti, D., García Raso, J. E., Çinar, M. E., Almogi-Labin, A., Ates, A. S., Azzurro, E., Ballesteros, E., Bianchi, C. N., Bilecenoglu, M., Gambi, M. C., Giangrande, A., Gravili, C., Hyams-Kaphzan, O., Karachle, P. K., Katsanevakis, S., ... Verlaque, M. (2012). Alien species in the Mediterranean Sea by 2012. A contribution to the application of European Union's Marine Strategy Framework Directive (MSFD). Part 2. Introduction trends and pathways. *Mediterranean Marine Science*, 13(2), 328–352. <https://doi.org/10.12681/mms.327>

98. Zenetos, Argyro, Ovalis, P., Giakoumi, S., Kontadakis, C., Lefkadiou, E., Mpazos, G., Simboura, N., & Tsiamis, K. (2020). Saronikos gulf: A hotspot area for alien species in the mediterranean sea. *BioInvasions Records*, 9(4), 873–889. <https://doi.org/10.3391/bir.2020.9.4.21>