



HAL
open science

Distribution, health and threats to Mediterranean macroalgal forests: defining the baselines for their conservation and restoration

Jana Verdura, Lluc Rehues, Luisa Mangialajo, Simonetta Frascchetti, Zahira Belattmania, Silvia Bianchelli, Aurélie Blanfuné, Brahim Sabour, Antonia Chiarore, Roberto Danovaro, et al.

► To cite this version:

Jana Verdura, Lluc Rehues, Luisa Mangialajo, Simonetta Frascchetti, Zahira Belattmania, et al.. Distribution, health and threats to Mediterranean macroalgal forests: defining the baselines for their conservation and restoration. *Frontiers in Marine Science*, 2023, 10, 10.3389/fmars.2023.1258842 . hal-04531131

HAL Id: hal-04531131

<https://amu.hal.science/hal-04531131>

Submitted on 4 Apr 2024

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.



Distributed under a Creative Commons Attribution 4.0 International License



OPEN ACCESS

EDITED BY

Joao M. Neto,
University of Coimbra, Portugal

REVIEWED BY

Sarah Caronni,
University of Milan Bicocca, Italy
Elisabetta Manea,
UMR8222 Laboratoire d'Ecogéochimie
des Environnements Benthiques
(LECOB), France

*CORRESPONDENCE

Jana Verdura
✉ jana.verdura@univ-cotedazur.fr

[†]These authors have contributed
equally to this work and share
first authorship

RECEIVED 14 July 2023

ACCEPTED 27 October 2023

PUBLISHED 20 November 2023

CITATION

Verdura J, Rehues L, Mangialajo L,
Fraschetti S, Belattmania Z, Bianchelli S,
Blanfuné A, Sabour B, Chiarore A,
Danovaro R, Fabbrizzi E, Giakoumi S,
Iveša L, Katsanevakis S, Kytinou E, Nasto I,
Nikolaou A, Orfanidis S, Rilov G, Rindi F,
Sales M, Sini M, Tamburello L, Thibaut T,
Tsirintanis K and Cebrian E (2023)
Distribution, health and threats to
Mediterranean macroalgal forests:
defining the baselines for their
conservation and restoration.
Front. Mar. Sci. 10:1258842.
doi: 10.3389/fmars.2023.1258842

COPYRIGHT

© 2023 Verdura, Rehues, Mangialajo,
Fraschetti, Belattmania, Bianchelli, Blanfuné,
Sabour, Chiarore, Danovaro, Fabbrizzi,
Giakoumi, Iveša, Katsanevakis, Kytinou,
Nasto, Nikolaou, Orfanidis, Rilov, Rindi, Sales,
Sini, Tamburello, Thibaut, Tsirintanis and
Cebrian. This is an open-access article
distributed under the terms of the [Creative Commons Attribution License \(CC BY\)](https://creativecommons.org/licenses/by/4.0/). The
use, distribution or reproduction in other
forums is permitted, provided the original
author(s) and the copyright owner(s) are
credited and that the original publication in
this journal is cited, in accordance with
accepted academic practice. No use,
distribution or reproduction is permitted
which does not comply with these terms.

Distribution, health and threats to Mediterranean macroalgal forests: defining the baselines for their conservation and restoration

Jana Verdura^{1*†}, Lluc Rehues^{2†}, Luisa Mangialajo¹,
Simonetta Fraschetti^{3,4}, Zahira Belattmania⁵, Silvia Bianchelli^{4,6},
Aurélie Blanfuné⁷, Brahim Sabour⁵, Antonia Chiarore⁸,
Roberto Danovaro^{4,6}, Erika Fabbrizzi^{3,4}, Sylvaine Giakoumi⁹,
Ljiljana Iveša¹⁰, Stelios Katsanevakis¹¹, Eleni Kytinou¹¹,
Ina Nasto¹², Athanasios Nikolaou¹¹, Sotiris Orfanidis¹³,
Gil Rilov¹⁴, Fabio Rindi^{4,6}, Marta Sales¹⁵, Maria Sini¹¹,
Laura Tamburello^{4,9}, Thierry Thibaut⁷, Konstantinos Tsirintanis¹¹
and Emma Cebrian¹⁶

¹UMR 7035 ECOSEAS, Université Côte d'Azur, CNRS, Nice, France, ²GRMAR, Institut of Aquatic Ecology, University of Girona, Girona, Spain, ³Department of Biology, University of Naples Federico II, Naples, Italy, ⁴National Biodiversity Future Centre, Palermo, Italy, ⁵Research Unit (RU) Phycology, Blue Biodiversity & Biotechnology, URL CNRST 10 – Laboratory of Plant Biotechnology, Ecology and Ecosystem Valorization, Faculty of Sciences, University Chouaib Doukkali, El Jadida, Morocco, ⁶Dipartimento di Scienze della Vita e dell'Ambiente, Università Politecnica delle Marche, Ancona, Italy, ⁷Aix-Marseille University, Mediterranean Institute of Oceanography (MIO), CNRS/INSU, IRD, UM 110, Marseille, France, ⁸Department of Integrative Marine Ecology, Stazione Zoologica Anton Dohrn, Naples, Italy, ⁹Sicily Marine Centre, Stazione Zoologica Anton Dohrn, Lungomare Cristoforo Colombo (complesso Roosevelt), Palermo, Italy, ¹⁰Center for Marine Research, Ruder Bošković Institute, Rovinj, Croatia, ¹¹Department of Marine Sciences, University of the Aegean, Mytilene, Greece, ¹²Department of Biology, University "Ismael Qemali", Vlora, Albania, ¹³Fisheries Research Institute, Hellenic Agricultural Organization-Demeter, Kavala, Greece, ¹⁴National Institute of Oceanography, Israel Oceanographic and Limnological Research (ILOR), Haifa, Israel, ¹⁵Institut Menorquí d'Estudis, Maó, Spain, ¹⁶Department Ecologia Marina, Centre d'Estudis Avançats de Blanes-CSIC, Blanes, Spain

The worldwide decline of macroalgal forests is raising major concerns for the potentially negative consequences on biodiversity and ecosystem functions, pushing for the definition of specific conservation and restoration measures. Protecting and restoring these habitats requires detailed information on their distribution, ecological status, and drivers of decline. Here, we provide the most updated available information on the distribution of Mediterranean *Cystoseira s.l.* forests by conducting a comprehensive bibliographic survey of literature published from 2009 to 2021, complemented by unpublished data. We also provide insights into the ecological status of these forests and the stressors affecting them across the Mediterranean basin. Our results show that most Mediterranean coasts remain un(der)studied and that the available information is concentrated in spatially limited coastal areas, restricted to very few species. When the ecological status is reported, data is highly heterogeneous, making any comparisons problematic, what claims for the description and use of easy and standardized monitoring methods for comparative purposes. Drivers of decline

of *Cystoseira s.l.* forest have been even less investigated and, therefore, still poorly characterized. Our results highlight that our current knowledge is still insufficient to implement effective conservation and restoration strategies at the basin scale but also regionally. We call for the urgent need for mapping and standardized monitoring of *Cystoseira s.l.* forests to obtain baseline information for future management strategies involving their conservation, the mitigation of the stressors threatening them and the restoration of the degraded forests.

KEYWORDS

Cystoseira sensu lato, Mediterranean marine forests, marine threats, macroalgal restoration, macroalgal conservation, macroalgal distribution, ecological status, site prioritization

1 Introduction

Marine algal forests are typically dominated by brown canopy-forming macroalgae from the Orders Laminariales, Fucales, Tilopteridales and Desmarestiales. These habitats produce important biomass and create 3D structures of high fractal complexity that host and feed a myriad of associated species (e.g., Cheminée et al., 2013; Teagle et al., 2017). Thus, these forests represent some of the most productive and biodiverse coastal marine ecosystems in temperate and polar regions on the planet (Mann, 1973; Steneck et al., 2002) while also providing essential ecosystem goods and services for human society (Smale et al., 2013). Canopy-forming macroalgal species exhibit a great diversity of growth forms, life strategies and environmental requirements; therefore, forest-forming species vary among regions worldwide. Temperate and Arctic rocky coastlines are mostly dominated by different species of kelps (Laminariales) (Wernberg et al., 2019). In the Mediterranean Sea, different macroalgal (Fucales) species, mainly of the genera *Cystoseira*, *Ericaria* and *Gongolaria* (Orellana et al., 2019; Molinari-Novoa and Guiry, 2020) (hereafter reported as *Cystoseira s.l.*) shape rocky seascapes from the upper infralittoral to the upper circalittoral zones (Giaccone and Bruni, 1973).

Globally, many brown canopy-forming macroalgal species are increasingly affected in several regions by the cumulative impacts of local and global anthropogenic stressors which raises major concern for their conservation (e.g., Johnson et al., 2011; Smale and Wernberg, 2013; Wernberg et al., 2013; Thibaut et al., 2015; Araújo et al., 2016; Smale, 2020). Their loss often triggers a transition towards less diverse and productive habitats, such as sea urchin barrens or turf-dominated grounds, in which stabilizing feedback processes reinforce their persistence (Thibaut et al., 2005; Ling et al., 2015; Filbee-Dexter and Wernberg, 2018). Specifically, *Cystoseira s.l.* species are highly vulnerable to several human disturbances. Indeed, widespread declines in their distribution throughout the Mediterranean basin have been reported, mainly linked to habitat destruction, overgrazing and deterioration in water quality (Munda, 1993; Thibaut et al., 2005; Bianchi et al., 2014; Mariani et al., 2019). Some (if not many) species may also be

sensitive to global change, for example, ocean warming (e.g., Verdura et al., 2021; Mulas et al., 2022). In response, since the 1980s and 1990s, some efforts aimed at the conservation of *Cystoseira s.l.* forests have been made, such as establishing protection status (e.g., being listed as threatened or endangered species in the Annex II of the Barcelona Convention; UNEP/MAP, 2013), or requiring the local mitigation of human pressures (e.g., sewage treatment management plans; Pinedo et al., 2013). However, despite these efforts, the natural recovery of *Cystoseira s.l.* forests is frequently unachievable. Although isolated instances of natural recolonization have been documented (Iveša et al., 2016; Zavodnik et al., 2020), the overall limited dispersal ability of these species and the scarcity of nearby propagules likely impede this process (Iveša et al., 2016; Zavodnik et al., 2020), suggesting the need for active restoration.

With the increasing awareness of the need for natural ecosystems conservation and concern about human threats, ecological restoration has been included in the policy agenda at global, regional, and national levels, especially following the objectives of different initiatives, such as the UN decade on Ecosystem Restoration (Waltham et al., 2020) or the EU Biodiversity Strategy for 2030 (EC, 2020) and the proposed UE Nature Restoration Law (EC, 2022). Macroalgal restoration attempts are less common than those for other marine habitats (Duarte et al., 2020; Frascchetti et al., 2021). However, during the last decade, macroalgae restoration knowledge has significantly progressed through an increasing number of funded projects in the Mediterranean Sea (e.g., AFRIMED, ROC-POPLife or MERCES EU projects), as well as in other areas of the world (e.g., the Green Gravel or Operation Crayweed projects). These projects have provided different methodologies and protocols leading to the recovery of structural habitat-forming species (e.g., *Cystoseira s.l.*, *Phyllospora comosa* or *Saccharina latissima*) as a herald for the recovery of overall associated biodiversity and ecosystem functions, showing active restoration as a potential successful tool to recover marine forests (Layton et al., 2020; Cebrian et al., 2021; Eger et al., 2022; Galobart et al., 2023).

Site prioritization is one of the first challenges for successful restoration outcomes (McDonald et al., 2016). Site selection can be

crucial in marine ecosystems to achieving the restoration targets and reducing costs (Bayraktarov et al., 2016; Frascchetti et al., 2021). The primary eligibility criteria for spatial prioritizing restoration sites should be based on the historical presence of the habitat or species targeted for restoration. Equal importance should be given to assessing the suitability of the current and future biotic conditions, such as the presence of potentially harmful invasive species or herbivory pressure, as well as abiotic conditions, such as bottom type, hydrodynamics, or sea-water temperature, within the selected area (Fabrizzi et al., 2023; Smith et al., 2023). Crucial information to consider thus includes fine-scale data on the past and present distribution of the species, as well as the ecological status of populations. It is also important to identify the causal stressor/s responsible for population declines (Gann et al., 2019). Nonetheless, comprehensive knowledge concerning marine forests is generally limited to a few species and regions with mostly short-time data series, primarily due to the scarcity of long-term monitoring and limited cartographic information about these habitats (Krumhansl et al., 2016).

The Mediterranean Sea is not exempt from this prevailing trend. Remarkable efforts have been dedicated to the compilation of historical and contemporary records in specific regions of France (Thibaut et al., 2005; Thibaut et al., 2014; Thibaut et al., 2015; Thibaut et al., 2016; Blanfuné et al., 2016a, Blanfuné et al., 2019), Catalonia (Mariani et al., 2019), Italy (Tamburello et al., 2022; Rendina et al., 2023), Croatia (Iveša et al., 2014, Iveša et al., 2016) and Montenegro (Mačić and Antolić, 2015). The information acquired holds significant value; however, the process of data acquisition is often arduous due to the need for screening technical reports, monitoring programs, herbarium specimens, scientific literature, and unpublished data from experts and projects. Regrettably, the only studies collecting and mapping all available data (considering historical and present records from 1985 to 2018) regarding the occurrences of *Cystoseira s.l.* forests across the Mediterranean Sea, indicate that such knowledge is only accessible for approximately 15% of the Mediterranean coasts (Fabrizzi et al., 2020; Fabrizio et al., 2023). In this context, despite having a broad view of the historical and current distribution knowledge, a comprehensive overview of the available and updated knowledge on *Cystoseira* species' current distribution, ecological status, and the stressing factors contributing to their decline across the Mediterranean basin is lacking. Furthermore, the distribution and intensity of local and global stressors responsible for population collapse have rarely been validated on case-by-case (Mancuso et al., 2018; Mariani et al., 2019). Finally, this critical knowledge gap across Mediterranean regions hampers our capacity to effectively manage and restore these habitats in a rapidly changing ocean.

In this context, through a systematic scientific literature review and the exploitation of unpublished data together with expert judgment, this work provides a picture of the updated (from 2009) and accessible knowledge about *Cystoseira s.l.* forests at the Mediterranean scale. More especially, we aim to (1) provide a complete overview of the updated available information on the distribution and ecological status of *Cystoseira s.l.* forests, (2) identify the drivers of *Cystoseira s.l.* forests loss, and (3)

determine any geographic pattern of these drivers. With the final aim to optimize future management, conservation, and restoration efforts on these ecosystems, our results may be used as an essential baseline to determine which features (e.g., species, stressors, etc.) and areas show major gaps, allowing the identification of where more investments are needed to allocate funds, monitoring and sampling effort (e.g., mapping; Fabrizio et al., 2020; Fabrizio et al., 2023). Moreover, it can also assist in determining where to focus on impact mitigation and where restoration and conservation plans should be prioritized.

2 Materials and methods

2.1 Information search

2.1.1 Systematic bibliographic assessment

We performed a systematic literature review consisting of (1) relevant article identification, (2) eligibility evaluation and (3) detailed revision of selected articles. The article identification was conducted using three databases: Web of Science (WoS), SCOPUS, and ScienceDirect, limiting the search to peer-reviewed articles published from 2009 to 2021 (cut-off dates 1st January 2009 and 31st December 2021 specifically). The starting cut-off date was decided according to the aim of assessing the current state of *Cystoseira s.l.* forests, and thus, avoiding older publications that might contain outdated data. WoS facilitates access to different databases and searches the parameters screening in the Title, the Abstract and the Keywords. SCOPUS and ScienceDirect were used to search the parameters within the Title, the Abstract, the Keywords, and the Text. The search query used was the same for the three databases. It was designed to return generic results:

“*Cystoseira*” AND “Mediterranean”) OR (“Canopy” AND “Algae” AND “Mediterranean”).

Given the fact that the taxonomy of *Cystoseira s.l.* has been in constant change during the last few years (Orellana et al., 2019; Molinari-Novoa and Guiry, 2020; Neiva et al., 2022), we performed four consecutive searches each time replacing the word “*Cystoseira*” by “*Carpodesmia*”, “*Treptacantha*”, “*Ericaria*” and “*Gongolaria*”. Due to this reinstatement, most of the species' names used in the revised publications before 2020 are no longer accepted, and thus accepted species names, according to AlgaeBase (Molinari-Novoa and Guiry, 2020), are used in the present study.

The articles identified by the different searches and databases were combined, and duplicates were excluded manually using the EndNote software. After that, we conducted an eligibility evaluation to assess the articles' suitability for data extraction. This step consisted of screening the abstract, where a first assessment was carried out, and if favourable, an in-depth check of the articles followed. Articles were excluded when: (a) the study area was not within the Mediterranean Sea, (b) the article studied canopy-forming algae other than *Cystoseira s.l.*, (c) no specific geographical information of *Cystoseira s.l.* populations was provided, and (d) authors used the same sampling site to conduct different studies and published more than one article. When the latter was detected, the articles were regarded as duplicates; hence,

only one of the different articles was kept for data extraction. As a result, 138 articles were used for data extraction.

2.1.2 Complementary search and personal communications

Some areas of the Mediterranean Sea were underrepresented in terms of data availability. This unbalance might be due to certain studies being published in local or regional journals (often non-indexed) or/and in the country's official language and, therefore, may have gone unnoticed by the databases used in the first systematic search. To balance these differences, subsequent searches using Google Scholar and targeting those specific areas were carried out. Citations in the articles reviewed were also checked when considered relevant. This search added 15 articles to those previously selected.

Lastly, all authors contributed data, encompassing extensions of existing datasets from prior publications or technical reports. These data sources encompassed a broad spectrum, including information from monitoring programs and frequently sampled areas from various national and international projects.

2.2 Data extraction

To map the reported knowledge on the distribution, ecological status, and stressors of *Cystoseira s.l.* forests, key information was extracted from each article when available: *Cystoseira s.l.* species, geographical information (including coordinates, site name, region, country), ecological status (Good, Moderate, Bad), presence of stressors and stressor type, dynamics of the population (Increased, Stable, Decreased abundance) and sampling year.

When coordinates were not provided, location names were searched on websites and georeferenced using QGIS 3.26 software, allowing the extraction of coordinates with the same program. When sampling points were only provided in a figure map, points were manually georeferenced using QGIS 3.26 software. To identify regional geographical differences, the Mediterranean Sea was divided into eight sub-basins, following the framework proposed by Teruzzi et al. (2011) with a few minor modifications. These adjustments were made considering the regional identification from our bibliographic research, where Adriatic Sea is considered as a single sub-basin and the entire Balearic archipelago is considered into the same sub-basin.

The ecological status of populations was derived from different types of variables. Some articles used numerical variables, while others used categorical ones. Categorical data consisted of descriptions and were highly heterogeneous. As a rule, if a population was described as “forest”, “continuous belt”, or “dominant”, it was classified as Good; if it was described as “patches”, it was classified as Moderate; and if it was described as “Scattered individuals”, “Barren ground”, or “Absent after a population extinction” it was classified as Bad. The georeferenced points reporting the absence of *Cystoseira s.l.* species but not specifying the reason, were excluded from this analysis. The numerical variables were wet weight per unit area, density (number of thalli per surface), or percentage cover of individuals,

the latter being the most common. Different thresholds were set for each of these variables to classify the numeric values into the three established categories in this study. The criteria details used to classify the extracted data into the three categories of ecological status (Good, Moderate, or Bad) are described in Table 1.

Information about the presence or absence and the type of stressors affecting *Cystoseira s.l.* populations were also extracted from the articles, when available. Different types of stressors were classified into different categories, defined in Table 2.

2.3 Data processing and representation

The resulting database consisted of georeferenced points with different attributes. These points were projected into a map using the Geographic Information System (GIS) software QGIS 3.26. The coordinate representation system used was WGS84 (EPSG: 4326). The spatial data were processed using ArcGIS Pro 3.0.0 software, and all graphics were generated using ggplot2 package (Wickham, 2016) in the statistical environment R (R Core Team, 2019). The spatial analysis consisted of assessing (1) data availability, (2) ecological status, and (3) stressor occurrence.

2.3.1 Data availability

To study the spatial availability of the compiled data, a grid of 10 km x 10 km was projected on a map of the Mediterranean Sea, and then only the cells that intersected with the coastline were kept. Each cell was assigned a distinct colour based on the number of georeferenced points it encompassed (Figure 1). The number of occurrences (presence, absence, and extinction) per *Cystoseira s.l.* species was also represented in a bar plot (Figure 2).

2.3.2 Ecological status

The points that contained information about the ecological status of *Cystoseira s.l.* assemblages were classified as Poor, Moderate or Good (Table 1), as explained above. A numerical value was given for each ecological status category; the locations with “Poor” ecological status were given a value of 1, “Moderate” a value of 2, and “Good” a value of 3. Using the same grid described in

TABLE 1 Criteria used to classify the different data obtained through different variables within the three ecological states established in this study: Poor, Moderate, and Good.

Measure	Ecological status		
	Poor	Moderate	Good
Cover (%)	0-10	10-50	50-100
Wet weight (g/m ²)	0-100	100-500	≥ 500
Density (Individuals/m ²)	0-1	2-3	≥ 4
Descriptive	“Scattered individuals” “Absent after population extinction” “Barren ground”	“Patches”	“Forest” “Continuous belts” “Dominant”

TABLE 2 Classification of the different reported stressors within the established “stressor categories” in this study.

Stressor categories	Reported stressors that have been included within each category
Water quality	Sewage outfall/chemical pollution, water turbidity, sedimentation, eutrophication (e.g., aquaculture farming or mariculture), freshwater inputs, agriculture, eutrophication, anthropization
Habitat destruction	Habitat destruction, harbour facilities, urbanisation, trawling, anthropization
Overgrazing by sea urchins	Overgrazing by <i>Paracentrotus lividus</i> and/or <i>Arbacia lixula</i>
Overgrazing by native fish	Overgrazing by <i>Sarpa salpa</i>
Overgrazing by invasive fish	Overgrazing by <i>Siganus</i> spp.
Climate change	Seawater warming, marine heatwaves, acidification*, and/or storms
Others	Species competence (including, invasive algae, mussels, turf species); Natural events (including hydrodynamics, strong winds, hydrothermal activity); Mechanical damage (including boat anchoring, ghost nets).
No-Stressor	Absence of stressor confirmed
Unknown/Not reported	Stressor either not reported in the study or unknown

*Ocean acidification on *Cystoseira s.l.* species are uncertain (Celis-Plà et al., 2017; Porzio et al., 2011), although negative effects have been observed in laboratory experiments on early life stages (Monserrat et al., 2022).

the Data availability section (2.3.1), the average ecological status was calculated in each cell (Figure 3). The values obtained were rounded to the closest integer. Supplementary Materials S4 contains more detailed maps of occurrences with associated ecological information. Specifically, for regions exhibiting a higher density of points, the ecological value attributed to each individual point is presented. Finally, the number of points of each ecological status category and the number of points without ecological status information (Unknown category) were also represented per sub-basins in a bar plot (Figure 4).

2.3.3 Stressor occurrence and expected trends

We identified 590 points reporting information about stressors (or their absence) impacting *Cystoseira s.l.* populations. It is worth noting that one point could be impacted by more than one stressor category. To study the density of each stressor at a Mediterranean scale, we conducted a Kernel density estimation of each stressor. Kernel density estimation is a technique used to estimate the probability density function of a set of data points (Silverman, 1998). It fits a smoothly curved surface over each point, where the surface value is the highest at the point location and decreases moving away from it until reaching the Search radius (r). The search radius defines the area around each point considered statistically significant for the analysis.

The density at a given location (x,y) is calculated by adding the values of all the kernel surfaces overlaying that location. The result is a continuous surface representing the data points’ density, with higher densities represented by higher surface values (Silverman, 1998).

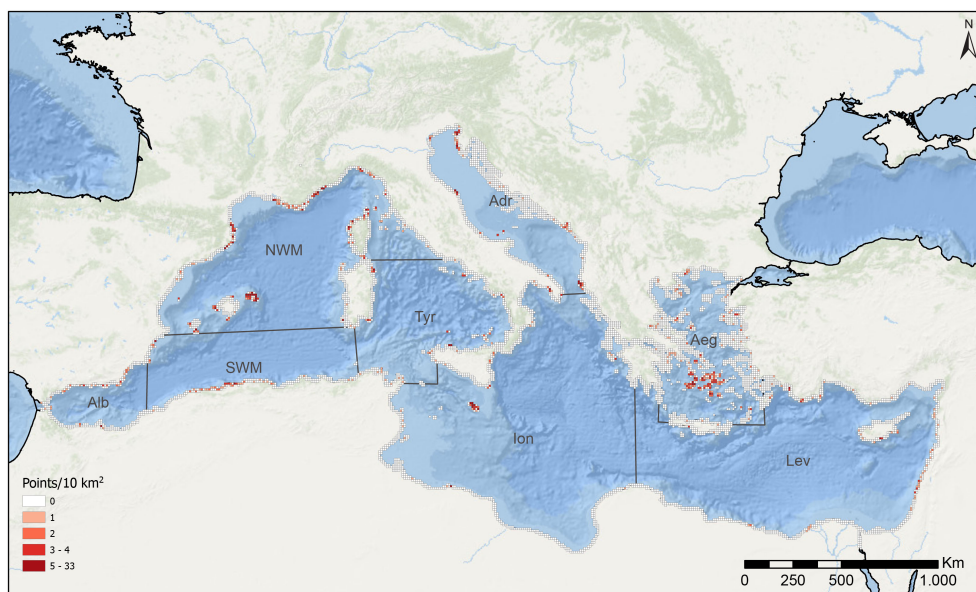


FIGURE 1 Data availability. Distribution of all sampled points of *Cystoseira s.l.* populations along the Mediterranean basin that have been obtained in the data extraction process. In the map, each square encompasses an area of 10 km², the colour of which represents the number of sampling points within the given area. The different divisions represent the Mediterranean sub-basins defined in this study (modified from Terruzi et al., 2011): Alb: Alboran Sea, NWM: North-Western Mediterranean, SWM: South-Western Mediterranean, Tyr: Tyrrhenian Sea, Adr: Adriatic Sea, Ion: Ionian Sea, Aeg: Aegean Sea, Lev: Levantine Sea.

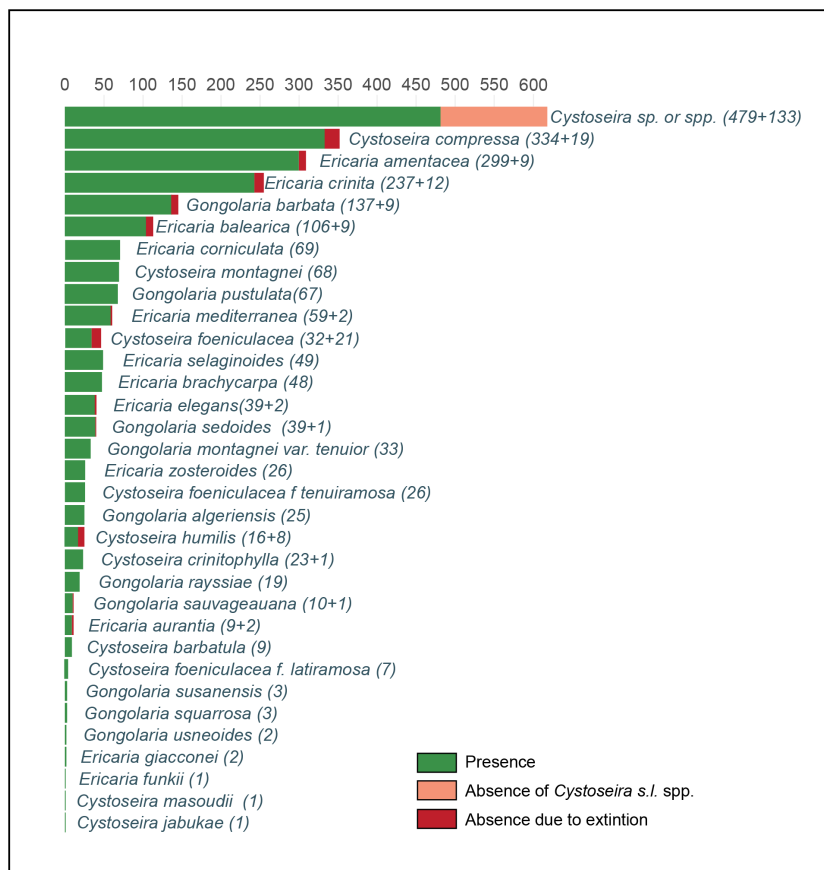


FIGURE 2 Number of reported occurrences (including past and present presence and absence) of *Cystoseira s.l.* species, based on the available data.

The analysis was conducted using the “Kernel Density” tool, included in the “Spatial Analyst Tools” package of ArcGIS Pro 3.0.0, which is based on the quartic kernel function described in Silverman, 1998 [(Silverman, 1998), p.76, equation 4.5].

The formula determining the density in a particular location (x, y) is defined as follows:

$$Density = \frac{1}{r^2} \sum_{i=1}^n \left[\frac{3}{\pi} \cdot \left(1 - \left(\frac{d_i}{r} \right)^2 \right)^2 \right]$$

For $d_i < r$

Where d_i is the distance between point i and the location (x,y). To calculate the search radius around each point, the following formula was used:

$$r = 0.9 \cdot \min \left(SD, \sqrt{\frac{1}{\ln(2)} \cdot D_m} \right) \cdot n^{-0.2}$$

Where SD is the standard distance, D_m is the median distance from the mean centre, and n is the number of points.

The Standard Distance is calculated using the following formula:

$$SD = \sqrt{\frac{\sum_{i=1}^n (x_i - \bar{X})^2}{n} + \frac{\sum_{i=1}^n (y_i - \bar{Y})^2}{n}}$$

Where n is the number of points, x_i, y_i are the coordinates for feature i , and \bar{X}, \bar{Y} are the coordinates of the mean centre of the group of points.

The representation of the results was restricted to 25 km from the coastline for a better interpretation.

Finally, we illustrate the occurrence of primary stressors (those frequently reported or considered to have substantial implications) in each sub-basin and outline their expected impact trends over the next 50 years (referred to as the mid-term). To do so, we combined the information collected in the present study with expert consensus in each sub-basin. Further details on collecting and evaluating expert perceptions of stressors’ future trends can be found in Supplementary Materials S1.

3 Results

The information search, including the bibliographic search and the personal information from 2009 to 2021, resulted in 1536

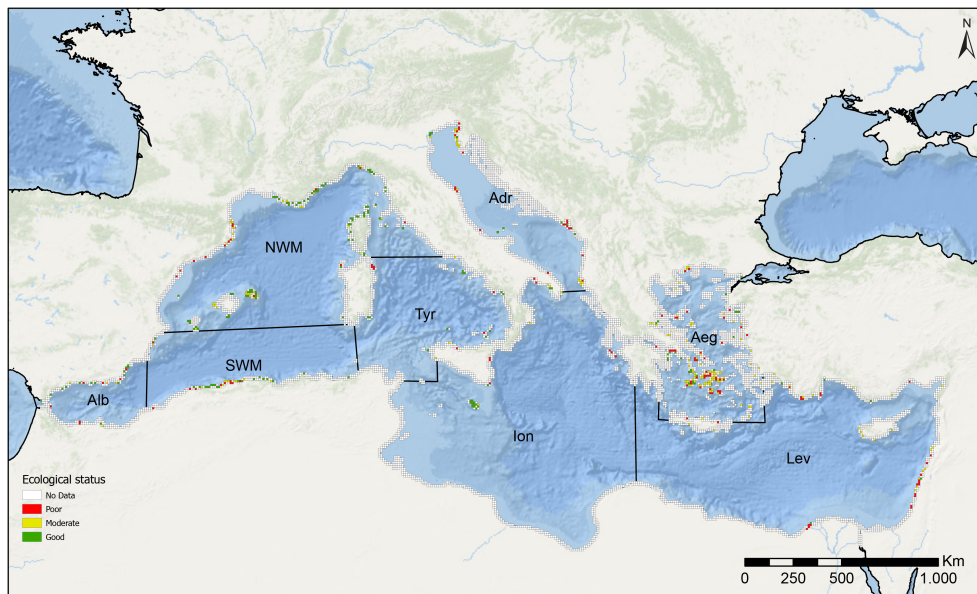


FIGURE 3
 Ecological status. Distribution of the sampling points reporting information regarding the ecological status of *Cystoseira s.l.* populations along the Mediterranean basin that have been obtained in the data extraction process. Each square encompasses an area of 10 km², the colour of which shows the mean ecological status value of the different points within the given area. The mean ecological status value has been obtained from the average value of the ecological status of the different sampling points that are located within the area of each square. The different divisions represent the Mediterranean sub-basins defined in this study (modified from Terruzi et al., 2011): Alb: Alboran Sea, NWM: North-Western Mediterranean, SWM: South-Western Mediterranean, Tyr: Tyrrhenian Sea, Adr: Adriatic Sea, Ion: Ionian Sea, Aeg: Aegean Sea, Lev: Levantine Sea.

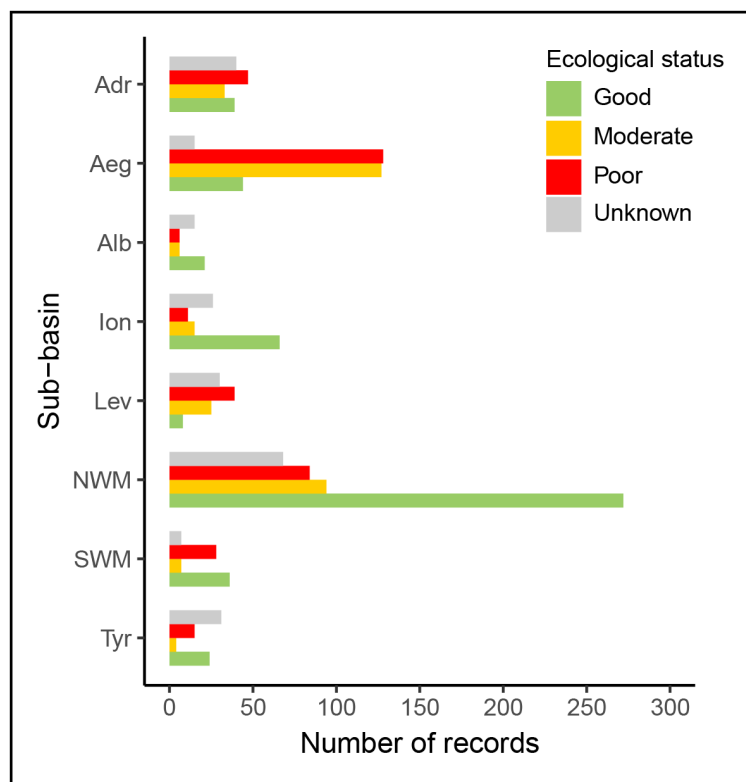


FIGURE 4
 Number of points reporting the past or present presence of *Cystoseira s.l.* forest in the different sub-basins classified within the different categories of ecological status (Good, Moderate and Poor), based on the extracted data. Those points reporting the presence of *Cystoseira s.l.* forest but not mentioning the ecological status of the forest are classified within "Unknown" category in the graph. Alb: Alboran Sea, NWM: North-Western Mediterranean, SWM: South-Western Mediterranean, Tyr: Tyrrhenian Sea, Adr: Adriatic Sea, Ion: Ionian Sea, Aeg: Aegean Sea, Lev: Levantine Sea.

geographical points reporting the occurrence of *Cystoseira s.l.* species. The complete list of the articles reviewed is presented in [Supplementary Materials S2](#). Based on the number of records in the literature and personal information, our results indicate that *Cystoseira s.l.* forests have been increasingly studied through the years ([Supplementary Materials S3](#)). However, our data also show that available information is still scarce, characterized by geographic and taxonomic bias, with a concentration in specific areas and on a limited number of species. For most Mediterranean coasts, there are no available or updated (after 2008) data on the presence or absence of *Cystoseira s.l.* forests. When available, data are concentrated especially in the Catalan and the Balearic coasts, some regions of the French Mediterranean coast, the north-west coasts of Corsica (NWS sub-basin), the Istrian coast (northern Adriatic Sea), and the coasts of Cyclades Islands (Aegean Sea) and Malta (Ionian Sea). Some information is available in other areas, such as the central region of the Algerian coast, some parts of the Italian, Lebanese and Cyprus coasts, and the southern shores of Spain, although with fewer reports ([Figure 1](#)). On the other hand, with few exceptions, such as the Aegean Sea, the Island of Malta, and the Israeli coast, the eastern part of the basin is the most underrepresented, especially the Ionian Sea, and the southern coasts of the Levantine Sea, which present a scarcity of sampled points ([Figure 1](#)).

Of the 1536 georeferenced points, 1361 reported the presence of at least one *Cystoseira s.l.* species. The absence of *Cystoseira s.l.* species was explicitly mentioned in 175 points. Among these, 50 points specifically indicated the absence of *Cystoseira s.l.* spp. as a result of local extinction, while the remaining 125 data points do not provide explicit information regarding whether the absence is attributable to natural factors or population decline. Concerning the taxonomic data quality, it is worth noting that 32% of the georeferenced points reporting past or present *Cystoseira s.l.* presence (450 out of 1411), are not based on species-level identification but are reported simply as *Cystoseira sp.* or spp. The remaining points (961 out of 1411) reported the presence or absence (due to decline) of at least one *Cystoseira s.l.* species, with several points reporting the occurrence of more than one species. This resulted in a total of 2382 past or present occurrences. Out of 36 *Cystoseira s.l.* species present in the Mediterranean Sea ([Oliveras-Pla and Gómez-Garreta, 1989](#)), we obtained occurrences for 32 species. *Cystoseira compressa*, *Ericaria amentacea*, and *E. crinita* were the most frequently reported species (with 353, 308 and 249 records, respectively), representing 48% of the total obtained occurrences reporting species-level information (1895 records), while 86% was reached by records of only 14 species ([Figure 2](#)). *Ericaria funkii*, *Cystoseira masoudii* and *C. jabukae* were the species least frequently reported, each reported only in one location ([Figure 2](#)).

Of the 1411 points reporting the present or past presence of *Cystoseira s.l.* forests, 1179 (83%) had available information on the ecological status of the *Cystoseira s.l.* populations (concerning any of the variables previously described, [Table 1](#)), among which 510 (36%) were classified as in Good ecological status, 311 (22%) Moderate, and 358 (25%) Poor ([Figures 3, 4](#)). Generally, forests in different ecological status categories have been reported in all sub-basins. However, in some sub-basins, such as the Adriatic Sea, the

Aegean Sea and the Levantine Sea, the number of forests in poor ecological status predominates ([Figure 4](#)). Conversely, in the NWM, the sub-basin containing the highest number of occurrences, forests considered good ecological status are the most reported ([Figure 4](#)). For a more comprehensive view with a higher resolution of occurrences reporting ecological information and the ecological value assigned to each individual point, please refer to [Supplementary Materials S4](#).

Information regarding stressors was the least reported in articles or personal communications. Only 590 (38%) of the occurrences (1536) provided specific information on the presence and/or the type of stressors affecting the population, while in only 5% (76) of the cases *Cystoseira s.l.* populations were recognized as not being threatened by any stressor. Multiple stressors were identified and grouped into different categories (see [Table 2](#)). Impacts related to water quality and habitat loss were the most reported, followed by overgrazing by sea urchins and overgrazing by invasive fishes (i.e., *Siganus* spp.). Despite increasing in recent years, impacts associated with climate change were reported less if compared to the aforementioned stressors, as well as other impacts, such as overgrazing by native fishes (e.g., *Sarpa salpa*), species competition, strong winds, and mechanical damage.

Certain spatial patterns can be observed when looking at the Kernel Density Estimations (KDE) of the reported stressors ([Figure 5](#)). Some stressors, such as water quality and habitat loss, have low-density values and are widespread along the Mediterranean coasts and follow a fairly comparable distribution: their highest occurrence was detected in the western part of the Mediterranean Sea (SWM and NWM sub-basins), but some cases were also detected at the easternmost part of the Mediterranean Sea, and in the western part of the Aegean sub-basin in the case of water quality. Despite being also somewhat scattered, the heat map indicated a higher concentration of reports on overgrazing by sea urchins in some regions of the NWM, southeastern Adriatic Sea, and the southern parts of the Aegean Sea. Finally, stressors related to climate change and overgrazing by invasive species showed a strong zonation pattern, especially the latter, which was restricted to a small area of the Cyclades Islands (Aegean Sea) and the northern Israeli coast. KDE values of overgrazing are not necessarily representative of the true extent of grazing pressure and are associated with the high availability of data in the Cyclades Islands ([Sala et al., 2011](#); [Nikolaou et al., 2023](#)). KDE values show that climate change has higher density values in the Levantine part of the Mediterranean Sea, but also in the northern part of the Adriatic Sea, coinciding with the northernmost and coldest part of the Mediterranean Sea ([Bianchi and Morri, 2000](#)) and of the distribution of *Cystoseira s.l.* species. It is imperative to emphasize that in [Figure 5](#), the areas depicted as lacking a specific stressor do not necessarily indicate its absence, as this outcome may also be attributed to the lack of documentation of the said stressor.

In terms of stressor presence and their expected impacts, none of the sub-basins is expected to witness an amelioration in any of the considered stressors, except for overgrazing by *Sarpa salpa* in the Aegean sub-basin, likely due to the out-competence with invasive fish species ([Figure 6](#)). Furthermore, there is a prevailing perception that the effects of global stressors will intensify across the

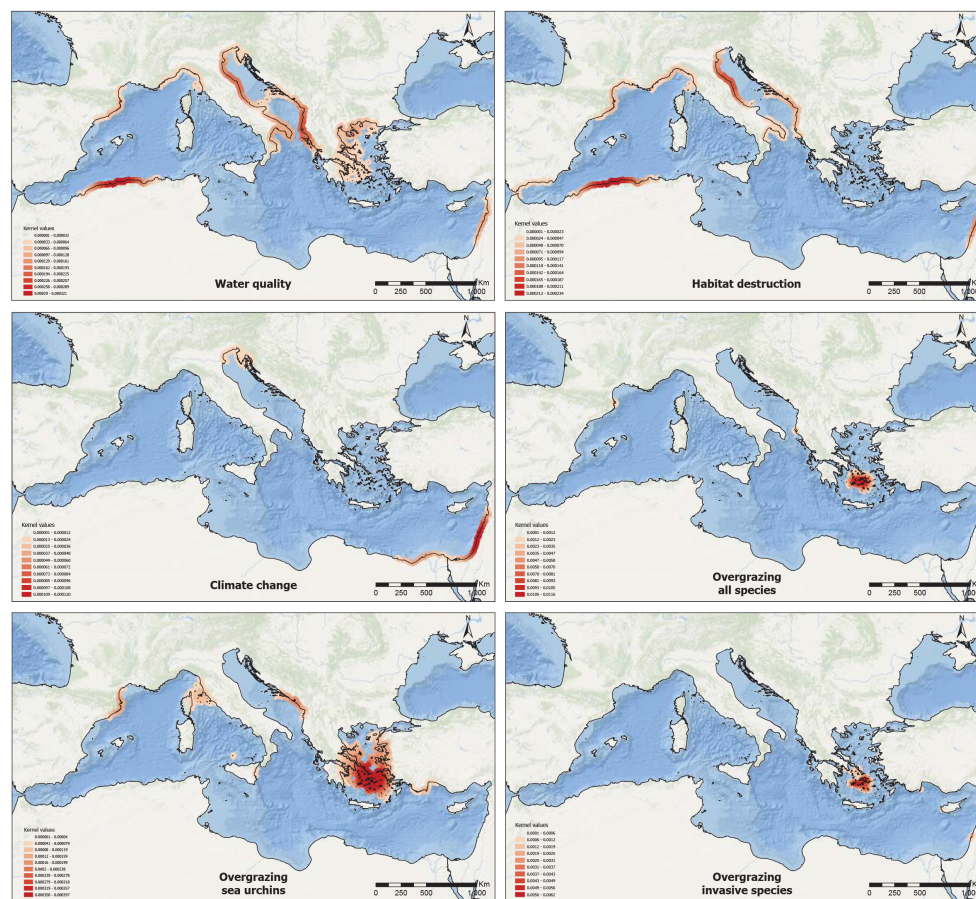


FIGURE 5

Stressors. Kernel density map of the main reported stressors of *Cystoseira s.l.* population along the Mediterranean Sea, based on the available data. The red colour on each map indicates the highest density associated with the areas with the highest reporting frequency and intensity of each stressor, from left to right and from top to bottom: Water quality, Habitat destruction, Climate change, Overgrazing by all species, Overgrazing by sea urchins and Overgrazing by invasive fish species. It is important to note that areas depicted as lacking a specific stressor do not necessarily indicate its absence, as this outcome may also be attributed to the lack of documentation of the said stressor.

entire Mediterranean Sea, with particular emphasis on the easternmost basins (Figure 6).

4 Discussion

4.1 The need for cross-basin monitoring efforts

This study highlighted the challenge of establishing reliable baselines of the present distribution, ecological status, and stressors currently threatening *Cystoseira s.l.* forests in the Mediterranean Sea. Although essential for any regional conservation or restoration action, this information is generally scarce. Our results indicated that knowledge is highly limited, spatially skewed and biased to a few species. Although certain regions have received more attention in terms of research effort [e.g. Italy (Porzio et al., 2020; Tamburello et al., 2022; Rendina et al., 2023), Catalonia (Mariani et al., 2019) and the Mediterranean French coast (Thibaut et al., 2014; Thibaut et al., 2015; Blanfuné et al., 2016a), respective information and long-term monitoring for much of the remaining Mediterranean

coastline is lacking (Rilov et al., 2020). Indeed, most available information mainly relies on surveys that provide scattered spatial data without information on the population area/extension (e.g., X, Y coordinates of sampling points; Giakoumi et al., 2012). Frequently, the reported data points exhibited a low spatial resolution. For instance, sampling sites were often represented as dots on image maps of the study area. Furthermore, these data points were frequently derived from studies with objectives unrelated to the distribution of *Cystoseira s.l.* forests (e.g., Sales et al., 2012).

Additionally, regardless of the overall diversity of *Cystoseira s.l.* species found in the Mediterranean Sea, a significant portion of the existing information focuses on a few broadly distributed, shallow-water species that are more easily accessible to researchers, such as *C. compressa*, *E. crinita*, and *E. amentacea* (Sales and Ballesteros, 2010; Thibaut et al., 2014; Blanfuné et al., 2016a). A large part of the available information concerning shallow *Cystoseira s.l.* species, such as the case of *E. amentacea*, is frequently derived from the widespread implementation of the CARLIT Index throughout the Mediterranean Sea (e.g., Asnaghi et al., 2009; Bermejo et al., 2013; Nikolic et al., 2013; Torras et al., 2016; Blanfuné et al., 2016b;

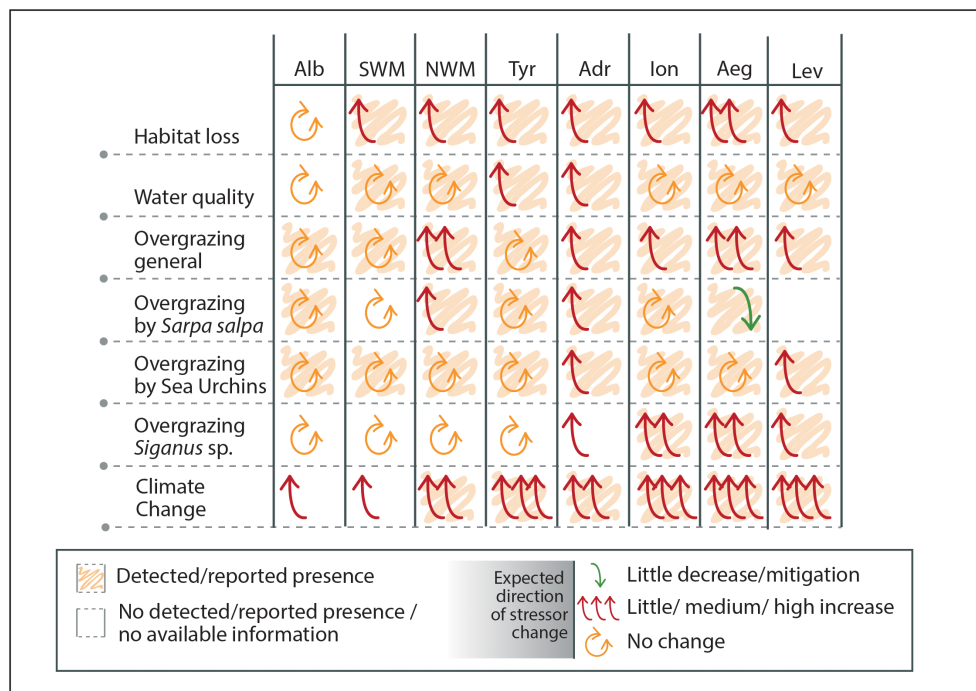


FIGURE 6

Presence of the reported stressors per sub-basin and expected direction of change based on the extracted data and expert judgment. Alb: Alboran Sea, NWM: North-Western Mediterranean, SWM: South-Western Mediterranean, Tyr: Tyrrhenian Sea, Adr: Adriatic Sea, Ion: Ionian Sea, Aeg: Aegean Sea, Lev: Levantine Sea.

Badreddine et al., 2018; De La Fuente et al., 2018). The CARLIT method uses the cartography of littoral upper-sublittoral macroalgal-dominated communities along rocky shores to assess the ecological status of coastal waters (Ballesteros et al., 2007). Nevertheless, these studies primarily report the obtained ecological status at the surveyed locations, while the detailed data encompassing information on macroalgal communities (e.g., occurrence and abundance) is often not included in the findings (Asnaghi et al., 2009; Nikolic et al., 2013). The creation or the use of existing databases (e.g. EMODnet) should be considered to consolidate data obtained through the widespread application and standardized methodology of this approach. At the same time, public repositories (eventually centralized) would facilitate data sharing, collaboration, and transparency among researchers. By making the database accessible to the public or upon request, it would serve as a valuable resource for the scientific community, policymakers, and stakeholders involved in research, restoration, conservation, and decision-making processes.

Information regarding the ecological status of the targeted populations was obtained from most of the collected occurrences. Overall, we found great variability in the ecological status of the populations within all sub-basins, suggesting that changes or alterations in the ecological status of analyzed populations are mainly attributed to local stressors rather than processes acting at the Mediterranean basin scale. However, these data must be considered carefully since the collected information is sourced from studies with vastly differing objectives, sampling periods, and ecological variables (e.g., density, cover, or descriptive

variables), making comparisons difficult. It is also crucial to bear in mind that the ecological status map (Figure 3) does not depict the current ecological status of *Cystoseira s.l.* forests in the Mediterranean Sea, but instead reflects the restricted scope of knowledge currently made accessible.

4.2 Threats to *Cystoseira s.l.* Mediterranean forests

Overall, the lack of baseline knowledge on the distribution, health and threats of *Cystoseira s.l.* forests hinders our ability to detect present or future changes in the ecological status of the populations, such as population decline or recovery. It also makes it challenging to identify the stressors leading to these alterations. This raises the need to develop coordinated and standardized methods, user-friendly, to evaluate and compare these habitats' ecological status through regions and time. In this line, the limited availability of mid/long-term monitoring studies may account for the fact that only a third of the existing research provides information on stressors affecting *Cystoseira s.l.* forests. Moreover, even among the studies that do address this aspect, the causal relationship between the identified factors and population declines is generally lacking. As a result, despite efforts to experimentally understand the direct effects of different stressors on *Cystoseira s.l.* species and life stages (Irving et al., 2009; Sala et al., 2011; de Caralt et al., 2020; Monserrat et al., 2022), in general, cause-effects relationships behind population declines remain unknown, unproven, or

poorly understood, with interactive and/or cumulative effects, probably being the most likely drivers of population loss (Tamburello et al., 2022; Cebrian et al., 2021).

Among the available information, as it has been historically mentioned, habitat destruction (e.g., Mangialajo et al., 2008; Rindi et al., 2020), changes in water quality such as sedimentation or pollution (e.g., Pinedo et al., 2015), and overgrazing by native species (e.g., Sala et al., 1998; Vergés et al., 2009; Giakoumi et al., 2012; Gianni et al., 2017), are the most frequently attributed stressors to the deforestation of the Mediterranean Sea (Gros, 1978; Munda, 1982; Thibaut et al., 2005). Such stressors, driven mainly by the lack of optimal local management practices, can result in local-level effects. Nevertheless, as they have been extensively documented across the entire Mediterranean basin, they pose a significant challenge to the basin-wide conservation of these habitats. More recently, overgrazing by invasive species (e.g., Sala et al., 2011; Giakoumi, 2014; Vergés et al., 2014; Nikolaou et al., 2023) has been added to this list, along with the direct effects of climate-driven impacts (e.g., marine heatwaves; Verdura et al., 2021; Mulas et al., 2022). Specifically, the effects of invasive alien species are concentrated in the eastern Mediterranean Sea, where *Cystoseira s.l.* population declines due to overgrazing by the Lessepsian fishes *Siganus luridus* and *Siganus rivulatus* are pronounced. *Siganus* spp. are thermophilous species; thus, their distribution is restricted by temperature (Ragkousis et al., 2023). In contrast to the extensively documented mass mortality events related to marine heatwaves for benthic invertebrates (Garrabou et al., 2022), reports of temperature-induced collapses of *Cystoseira s.l.* forests are relatively scarce and primarily reported in the easternmost and warmest regions of the Mediterranean basin, although some isolated cases have also been reported in the northern Adriatic Sea and the Gulf of Lions (NWM) (Verdura et al., 2021; Iveša unpublished obs.). To make predictions on the vulnerability of *Cystoseira s.l.* species to further ocean warming (and marine heatwaves), experimental work is needed, but so far, this has been extremely scarce (but see Capdevila et al., 2019; Verdura et al., 2021; Monserrat et al., 2022). Recent experimental work did, however, show the high thermal vulnerability of *Gongolaria rayssiae*, a species endemic only to the coasts of Lebanon and Israel, the hottest and fastest-warming part of the Mediterranean, where this species may become (globally) extinct under business-as-usual climate change scenarios (Mulas et al., 2022).

Although global stressors, such as ocean warming, have received less attention, their interaction with pre-existing local stressors is expected to have far-reaching consequences (Strain et al., 2014). In this context, the effects of marine heatwaves on already locally threatened populations have been identified as a critical driver for *Cystoseira s.l.* forest collapse, even in the coldest locations of *Cystoseira s.l.* species distribution (e.g., Verdura et al., 2021; Iveša unpublished obs.). These results are consistent with other studies that suggest global stressors on temperate macroalgal forests can be modulated by other factors or processes at the local scale (Bennett et al., 2015; Krumhansl et al., 2016). Therefore, given the current context of climate change (Lejeusne et al., 2010), studies examining the combined effects of local and global stressors on the resistance and resilience of these species are crucial for preserving these habitats (Gissi et al., 2021; Monserrat et al., 2022).

Based on the compiled expert opinions (Figure 6), there is a prevailing consensus that locally manageable stressors are likely to maintain their current impact levels or experience marginal increases in the near future. This trend is exemplified by the case of water quality, which has witnessed significant improvements in many regions over the past few decades (Soltan et al., 2001; Pinedo et al., 2013; Iveša et al., 2016). Concerning habitat destruction, although coastal urbanization is expected to persist, environmental considerations are foreseen to accompany this process, resulting in a slight increase in its impact. In line with numerous scientific studies (Lejeusne et al., 2010) there is also a consensus that climate change will intensify its effects throughout the entire Mediterranean Sea, particularly in the easternmost basins. The perception of herbivory patterns among the asked experts is not consistently uniform. In certain sub-basins, a slight or medium increase is anticipated, possibly attributed to an increase in herbivore abundance (Gianni et al., 2017) or alterations in herbivory-plant interaction influenced by temperature increase (Mannino et al., 2016; Buñuel et al., 2021). However, no change or even a reduction in herbivory is expected in other sub-basins. Further research should be conducted to understand better the impact of overgrazing on *Cystoseira s.l.* forests, particularly by Salemas. Moreover, the impact of invasive fish species, such as *Siganus* spp., is projected to increase in sub-basins where they are already present. In the Adriatic region, where these species are currently uncommon, there is a growing perception that they may become more prevalent in the near future. However, in the western basins, these species are not expected to arrive within the given timeframe. Nevertheless, niche modelling studies provide evidence that *Siganus* spp. will likely spread across the Mediterranean Sea by the end of the century under different climatic scenarios (Schickele et al., 2021). Therefore, lessons learned from their impacts in the eastern basin should be considered before this almost certain invasion occurs in the west.

The limited available knowledge on *Cystoseira s.l.* forests could be attributed to several contributing factors. On one hand, despite international agreements, such as the Barcelona Convention (UNEP/MAP, 2013) and European legislation such as the European Union's Habitats Directive Habitats Directive 1992 (92/43/E; Habitats Directive 1992) and the Marine Strategy Framework Directive (MSFD, 2009), encouraging the mapping and monitoring of priority habitats, *Cystoseira s.l.* forests were not identified as priority habitats by the Habitat Directive (Verlaque et al., 2019). This fact means that Mediterranean canopy-forming macroalgae (as well as kelp beds in temperate oceanic coasts) are not distinguished from other marine habitats, such as erect macroalgae, turfs or barren grounds, and are all included in the same habitat type: Reefs (Habitat Type 1170). As a result, while existing cartographies are helpful for mapping EU-defined macrophyte-dominated habitats, such as *Posidonia oceanica* meadows [Habitat type 1120: *P. oceanica* beds – *Posidionion oceanicae*; (Telesca et al., 2015)], they do not provide accurate information, nor do they offer high-resolution maps about other habitats, such as *Cystoseira s.l.* forests. On the other hand, difficulties in taxonomic identification within the *Cystoseira s.l.* complex (Neiva et al., 2022) may also contribute to the lack of spatial and ecological-related data on these habitats.

By considering both the previously published habitat suitability map for *Cystoseira s.l.* species (Fabbrizzi et al., 2020) and the updated map of *Cystoseira s.l.* forest distribution that we present in this study (Figure 1), it becomes apparent that there is a compelling need to explore and investigate understudied areas within the basin in the future. Excluding areas identified as unsuitable for the growth of these forests, such as the Gulf of Lion, Gulf of Venice, and Gulf of Gabes (Fabbrizzi et al., 2020), numerous regions of almost all sub-basins necessitate more comprehensive surveys. Remarkably, there is a pressing need to prioritize thorough investigations in the south Ionian and Levantine sub-basins. Additionally, attention should be given to other areas, including the Eastern Adriatic Sea's central part, Italy's western coasts, and Corsica and Sardinia's eastern coasts. Moreover, significant efforts should be dedicated to mapping and surveying deep-water *Cystoseira s.l.* species across the Mediterranean basin, as limited information about these species exists (but see, Ballesteros, 1990; Ballesteros et al., 1998; Hereu et al., 2008; Ballesteros et al., 2009; Capdevila et al., 2015).

Only by gathering this knowledge together with an accurate understanding of the stressors currently threatening these populations we will be able to establish ecosystem-based management of marine forests, in which mitigation of both local and global stressors, such as water quality and herbivory pressure, should be a critical step of the process. Appropriate management and threats mitigation are pre-requisite in any conservation and restoration plan, and we can draw inspiration from the few examples of naturally recovered *Cystoseira s.l.* populations after reduced eutrophication or pollution levels in seawater (Iveša et al., 2016; Ricart et al., 2018) and herbivory (Guarnieri et al., 2020). Climate change already affects some populations and represents a challenging factor that cannot be easily mitigated (Bevilacqua et al., 2019). However, promoting the resilience of healthy *Cystoseira s.l.* populations, more tolerant species and populations, localizing potential areas that can serve as climate change refugia for thermally sensitive species or determining which areas are expected to be more severely impacted by human activities, are among the leading research challenges in conserving macroalgal forests.

There is a need to allocate efforts and resources to accurately collect distributional, ecological and environmental data for mapping and monitoring *Cystoseira s.l.* populations and assessing their ecological status. Acquiring this knowledge is crucial for achieving the EU's Biodiversity Strategy 2030 goals, aiming to protect and restore biodiversity and enhance ecosystem resilience to climate change. As previously highlighted (Verlaque et al., 2019; Tamburello et al., 2022), it is urgent to prioritize *Cystoseira s.l.* forests as one of the main objectives of the protection and management of the Mediterranean marine environment. We also recommend reconsidering the inclusion of *Cystoseira s.l.* species in international and European agreements and conventions. Legal protection measures would be critical for implementing conservation and restoration strategies for these canopy-forming macroalgae and their associated marine habitats.

Author contributions

JV: Conceptualization, Data curation, Formal Analysis, Investigation, Methodology, Writing – original draft, Writing – review & editing. LR: Data curation, Formal Analysis, Methodology, Software, Writing – original draft, Writing – review & editing. LM: Funding acquisition, Investigation, Writing – review & editing. SF: Investigation, Writing – review & editing. ZB: Investigation, Writing – review & editing. SB: Investigation, Writing – review & editing. AB: Investigation, Writing – review & editing. BS: Writing – review & editing. AC: Investigation, Writing – review & editing. RD: Funding acquisition, Investigation, Writing – review & editing. EF: Investigation, Writing – review & editing. SG: Investigation, Writing – review & editing. LI: Investigation, Writing – review & editing. SK: Investigation, Writing – review & editing. EK: Investigation, Writing – review & editing. IN: Investigation, Writing – review & editing. AN: Investigation, Writing – review & editing. SO: Investigation, Writing – review & editing. GR: Investigation, Writing – review & editing. FR: Investigation, Writing – review & editing. MSa: Investigation, Writing – review & editing. MSi: Investigation, Writing – review & editing. LT: Investigation, Writing – review & editing. TT: Investigation, Writing – review & editing. KT: Investigation, Writing – review & editing. EC: Conceptualization, Funding acquisition, Investigation, Supervision, Writing – original draft, Writing – review & editing.

Funding

The author(s) declare financial support was received for the research, authorship, and/or publication of this article. This work is supported by the AFRIMED EU project funded by the Executive Agency for Small and Medium Enterprises (EASME) and European Maritime and Fisheries Fund (EMFF) under grant agreement No. EASME/EMFF/2017/1.2.1.12/S4/01/SI2.789059; by the FoRestA project from the Spanish Ministry of Science and Innovation (Grant/Award No. PID2020-112985GB-I00); and by Biodiversa+ (FORESCUE project), the European Biodiversity Partnership under the 2021-2022 BiodivProtect joint call for research proposals, co-funded by the European Commission (GA N°101052342) and with the funding organisations, Agencia Estatal de Investigación AEI/10.13039/501100011033/NextGenerationEU/PRTR (PCI2022-135070-2, PCI2022-135052-2) and the French Agence Nationale de la Recherche. This research was also funded by the European Union – NextGeneration EU – as part of the MITECO program for the Spanish Recovery, Transformation and Resilience Plan (Recovery and Resilience Facility of the European Union established by the Regulation (EU) 2020/2094), and was entrusted to CSIC, AZTI, SOCIB, and the universities of Vigo and Cadiz. This work has also been supported by the French government, through the UCAJEDI Investments in the Future project managed by the National Research Agency (ANR) with the reference number ANR-15-IDEX-01).

Acknowledgments

The authors would thank Enric Ballesteros, Miriam Benali, Lamia Bahbah, Sultana Tsioli and Vasilis Papatthanasios for personal communications and data clarification. This is a contribution from the Consolidated Research Group “Medrecover; www.medrecover.org”, SGR2017-1521 (Catalan Government).

Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

The author(s) declared that they were an editorial board member of Frontiers, at the time of submission. This had no impact on the peer review process and the final decision.

The reviewer SC declared a shared affiliation with the author IN to the handling editor at the time of review.

Publisher's note

All claims expressed in this article are solely those of the authors and do not necessarily represent those of their affiliated

organizations, or those of the publisher, the editors and the reviewers. Any product that may be evaluated in this article, or claim that may be made by its manufacturer, is not guaranteed or endorsed by the publisher.

Supplementary material

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fmars.2023.1258842/full#supplementary-material>

SUPPLEMENTARY MATERIALS S1

Procedure and set of questions developed to construct, which captures the experts' perceptions of different stressors in each sub-basin.

SUPPLEMENTARY MATERIALS S2

List of the reviewed papers.

SUPPLEMENTARY MATERIALS S3

Number of scientific papers reporting spatial data on *Cystoseira s. l.* species per year.

SUPPLEMENTARY MATERIALS S4

Ecological status. Detailed maps of the distribution of the sampling points reporting information regarding the ecological status of *Cystoseira s.l.* populations along the Mediterranean basin that have been obtained in the data extraction process.

References

- Araújo, R. M., Assis, J., Aguillar, R., Airoidi, L., Bárbara, I., Bartsch, I., et al. (2016). Status, trends and drivers of kelp forests in Europe: an expert assessment. *Biodivers. Conserv.* 25, 1319–1348. doi: 10.1007/s10531-016-1141-7
- Asnaghi, V., Chiantore, M., Bertolotto, R. M., Parravicini, V., Cattaneo-Vietti, R., Gaino, F., et al. (2009). Implementation of the European Water Framework Directive: Natural variability associated with the CARLIT method on the rocky shores of the Ligurian Sea (Italy). *Mar. Ecol.* 30, 505–513. doi: 10.1111/j.1439-0485.2009.00346.x
- Badreddine, A., Abboud-Abi Saab, M., Gianni, F., Ballesteros, E., and Mangialajo, L. (2018). First assessment of the ecological status in the Levant Basin: Application of the CARLIT index along the Lebanese coastline. *Ecol. Indic.* 85, 37–47. doi: 10.1016/j.ecolind.2017.10.006
- Ballesteros, E. (1990). Structure and dynamics of the assemblage of *Cystoseira zosteroides* (Turner) C. Agardh (Fucales, Phaeophyta) in the northwestern Mediterranean. *Scientia Marina* 54, 217–229.
- Ballesteros, E., Garrabou, J., Hereu, B., Zabala, M., Cebrian, E., and Sala, E. (2009). Deepwater stands of *Cystoseira zosteroides* C. Agardh (Fucales, Ochrophyta) in the Northwestern Mediterranean: insights into assemblage structure and population dynamics. *Estuar. Coast. Shelf Sci.* 82, 477–484. doi: 10.1016/j.ecss.2009.02.013
- Ballesteros, E., Sala, E., Garrabou, J., and Zabala, M. (1998). Community structure and frond size distribution of a deep water stand of *Cystoseira spinosa* (Phaeophyta) in the Northwestern Mediterranean. *Eur. J. Phycol.* 33 (2), 121–128. doi: 10.1080/09670269810001736613
- Ballesteros, E., Torras, X., Pinedo, S., García, M., Mangialajo, L., and de Torres, M. (2007). A new methodology based on littoral community cartography dominated by macroalgae for the implementation of the European Water Framework Directive. *Mar. Pollut. Bull.* 55, 172–180. doi: 10.1016/j.marpolbul.2006.08.038
- Bayraktarov, E., Saunders, M. I., Abdullah, S., Mills, M., Beher, J., Possingham, H. P., et al. (2016). The cost and feasibility of marine coastal restoration. *Ecol. Appl. Ecol. Appl.* 26, 1055–1074. doi: 10.5061/dryad.rc0jn
- Bennett, S., Wernberg, T., Joy, B. A., De Bettignies, T., and Campbell, A. H. (2015). Central and rear-edge populations can be equally vulnerable to warming. *Nat. Commun.* 6, 10280. doi: 10.1038/ncomms10280
- Bermejo, R., de la Fuente, G., Vergara, J. J., and Hernández, I. (2013). Application of the CARLIT index along a biogeographical gradient in the Alboran Sea (European Coast). *Mar. Pollut. Bull.* 72, 107–118. doi: 10.1016/j.marpolbul.2013.04.011
- Bevilacqua, S., Savonitto, G., Lipizer, M., Mancuso, P., Ciriaco, S., Srijemsi, M., et al. (2019). Climatic anomalies may create a long-lasting ecological phase shift by altering the reproduction of a foundation species. *Ecology* 100, e02838. doi: 10.1002/ecy.2838
- Bianchi, C. N., Corsini-Foka, M., Morri, C., and Zenetos, A. (2014). Thirty years after; dramatic change in the coastal marine habitats of Kos Island (Greece), 1981–2013. *Mediterr. Mar. Sci.* 14, 482–497. doi: 10.12681/mms.678
- Bianchi, C. N., and Morri, C. (2000). Marine biodiversity of the Mediterranean Sea: Situation, problems and prospects for future research. *Mar. Pollut. Bull.* 40, 367–376. doi: 10.1016/S0025-326X(00)00027-8
- Blanfuné, A., Boudouresque, C. F., Verlaque, M., Beqiraj, S., Kashta, L., Nasto, I., et al. (2016b). Response of rocky shore communities to anthropogenic pressures in Albania (Mediterranean Sea): Ecological status assessment through the CARLIT method. *Mar. Pollut. Bull.* 109, 409–418. doi: 10.1016/j.marpolbul.2016.05.041
- Blanfuné, A., Boudouresque, C. F., Verlaque, M., and Thibaut, T. (2016a). The fate of *Cystoseira crinita*, a forest-forming Fucale (Phaeophyceae, Stramenopiles), in France (North Western Mediterranean Sea). *Estuar. Coast. Shelf Sci.* 181, 196–208. doi: 10.1016/j.ecss.2016.08.049
- Blanfuné, A., Boudouresque, C. F., Verlaque, M., and Thibaut, T. (2019). The ups and downs of a canopy-forming seaweed over a span of more than one century. *Sci. Rep.* 9, 5250. doi: 10.1038/s41598-019-41676-2
- Buñuel, X., Alcoverro, T., Romero, J., Arthur, R., Ruiz, J. M., Pérez, M., et al. (2021). Warming intensifies the interaction between the temperate seagrass *Posidonia oceanica* and its dominant fish herbivore *Sarpa salpa*. *Mar. Environ. Res.* 165, 105237. doi: 10.1016/j.marenvres.2020.105237
- Capdevila, P., Hereu, B., Salguero-Gómez, R., Rovira, G. L., Medrano, A., Cebrian, E., et al. (2019). Warming impacts on early life stages increase the vulnerability and delay the population recovery of a long-lived habitat-forming macroalga. *J. Ecol.* 107 (3), 1129–1140. doi: 10.1111/1365-2745.13090
- Capdevila, P., Linares, C., Aspillaga, E., Navarro, L., Kersting, D. K., and Hereu, B. (2015). Recruitment patterns in the Mediterranean deep-water alga *Cystoseira zosteroides*. *Mar. Biol.* 162, 1165–1174. doi: 10.1007/s00227-015-2658-0
- Cebrian, E., Tamburello, L., Verdura, J., Guarnieri, G., Medrano, A., Linares, C., et al. (2021). A roadmap for the restoration of Mediterranean macroalgal forests. *Front. Mar. Sci.* 8. doi: 10.3389/fmars.2021.709219

- Celis-Plá, P. S.M., Martínez, B., Korbee, N., Hall-Spencer, J. M., and Figueroa, F. L. (2017). Ecophysiological responses to elevated CO₂ and temperature in *Cystoseira tamariscifolia* (Phaeophyceae). *Climate Change* 142, 97–81. doi: 10.1007/s10584-017-1943-y
- Cheminée, A., Sala, E., Pastor, J., Bodilis, P., Thiriet, P., Mangialajo, L., et al. (2013). Nursery value of *Cystoseira* forests for Mediterranean rocky reef fishes. *J. Exp. Mar. Biol. Ecol.* 442, 70–79. doi: 10.1016/j.jembe.2013.02.003
- de Caralt, S., Verdura, J., Vergés, A., Ballesteros, E., and Cebrian, E. (2020). Differential effects of pollution on adult and recruits of a canopy-forming alga: implications for population viability under low pollutant levels. *Sci. Rep.* 10, 17825. doi: 10.1038/s41598-020-73990-5
- De La Fuente, G., Chiantore, M., Gaino, F., and Asnaghi, V. (2018). Ecological status improvement over a decade along the Ligurian coast according to a macroalgae based index (CARLIT). *PLoS One* 13 (12), e0206826. doi: 10.1371/journal.pone.0206826
- Duarte, C. M., Agustí, S., Barbier, E., Britten, G. L., Castilla, J. C., Gattuso, J.-P., et al. (2020). Rebuilding marine life. *Nature* 580, 39–51. doi: 10.1038/s41586-020-2146-7
- EC (2020). “EU Biodiversity Strategy for 2030,” in *EU Biodiversity Strategy for 2030* (Brussels). Available at: <https://eur-lex.europa.eu/legal-content/EN/TXT/?qid=1590574123338&uri=CELEX%5A52020DC0380>. ed. 380 final. Nature Back into Our Lives. E. Commission.
- EC (2022) *Proposal for a Regulation of the European Parliament and of the Council on Nature Restoration: E. Commission* (Brussels). Available at: <https://eur-lex.europa.eu/legal-content/EN/TXT/?uri=CELEX%3A52022PC0304>.
- Eger, A. M., Marzinelli, E. M., Christie, H., Fagerli, C. W., Fujita, D., Gonzalez, A. P., et al. (2022). Global kelp forest restoration: past lessons, present status, and future directions. *Biol. Rev.* 97 (4), 1449–1475. doi: 10.1111/brv.12850
- Fabbrizzi, E., Giakoumi, S., De Leo, F., Tamburello, L., Chiaroni, A., Colletti, A., et al. (2023). The challenge of setting restoration targets for macroalgal forests under climate changes. *J. Environ. Manage.* 326, 116834. doi: 10.1016/j.jenvman.2022.116834
- Fabbrizzi, E., Scardi, M., Ballesteros, E., Benedetti-Cecchi, L., Emma, C., Ceccherelli, G., et al. (2020). Modeling macroalgal forest distribution at Mediterranean scale: Present status, drivers of changes and insights for conservation and management. *Front. Mar. Sci.* 7. doi: 10.3389/fmars.2020.00020
- Filbee-Dexter, K., and Wernberg, T. (2018). Rise of turfs: A new battlefield for globally declining kelp forests. *BioScience* 68, 64–76. doi: 10.1093/biosci/bix147
- Fraschetti, S., McOwen, C., Papa, L., Papadopoulou, N., Bilan, M., Boström, C., et al. (2021). Where is more important than how in coastal and marine ecosystems restoration. *Front. Mar. Sci.* 8. doi: 10.3389/fmars.2021.626843
- Galobart, C., Ballesteros, E., Golo, R., and Cebrian, E. (2023). Addressing marine restoration success: evidence of species and functional diversity recovery in a ten-year restored macroalgal forest. *Front. Mar. Sci.* 10. doi: 10.3389/fmars.2023.1176655
- Gann, G. D., McDonald, T., Aronson, J., Nelson, C. R., Jonson, J., Hallett, J. G., et al. (2019). International principles and standards for the practice of ecological restoration (Summary). *Second edition: September 2019* (Washington D.C. 20005 U.S.A.: Society for Ecological Restoration). doi: 10.1111/rec.13035
- Garrabou, J., Gómez, D., Medrano, A., Cerrano, C., Ponti, M., Schlegel, R., et al. (2022). Marine heatwaves drive recurrent mass mortalities in the Mediterranean Sea. *Glob. Change Biol.* 28, 5708–5725. doi: 10.1111/gcb.16301
- Giaccone, G., and Bruni, A. (1973). Le *Cystoseira* e la vegetazione sommersa del Mediterraneo. *Atti Istituto Veneto Scienze Lettere ed Arti* 131, 59–103.
- Giakoumi, S. (2014). Distribution patterns of the invasive herbivore *Siganus luridus* (Rüppell 1829) and its relation to native benthic communities in the central Aegean Sea, Northeastern Mediterranean. *Mar. Ecol.* 35, 96–105. doi: 10.1111/maec.12059
- Giakoumi, S., Cebrian, E., Kokkoris, G. D., Ballesteros, E., and Sala, E. (2012). Relationships between fish, sea urchins and macroalgae: The structure of shallow rocky sublittoral communities in the Cyclades, Eastern Mediterranean. *Estuar. Coast. Shelf Sci.* 109, 1–10. doi: 10.1016/j.ecss.2011.06.004
- Gianni, F., Bartolini, F., Pey, A., Laurent, M., Martins, G. M., Airoldi, L., et al. (2017). Threats to large brown algal forests in temperate seas: The overlooked role of native herbivorous fish. *Sci. Rep.* 7, 6012. doi: 10.1038/s41598-017-06394-7
- Gissi, E., Manea, E., Mazaris, A. D., Frascchetti, S., Almpandou, V., Bevilacqua, S., et al. (2021). A review of the combined effects of climate change and other local human stressors on the marine environment. *Sci. Total Environ.* 755, 142564. doi: 10.1016/j.scitotenv.2020.142564
- Gros, C. (1978). *Le genre Cystoseira sur la côte des Albères. Répartition, écologie, morphogénèse* PhD thesis., Paris: Université Pierre et Marie Curie.
- Guarnieri, G., Bevilacqua, S., Figueras, N., Tamburello, L., and Frascchetti, S. (2020). Large-scale sea urchin culling drives the reduction of subtidal barren grounds in the Mediterranean Sea. *Front. Mar. Sci.* 7. doi: 10.3389/fmars.2020.00519
- Habitats Directive (1992). Council Directive 92/43/EEC of 21 May 1992 on the conservation of natural habitats and of wild fauna and flora. *Off. J. Eur. Union* L206, 7–50.
- Hereu, B., Mangialajo, L., Ballesteros, E., and Thibaut, T. (2008). On the occurrence, structure and distribution of deep-water *Cystoseira* populations in the Port-Cros National Park (North-western Med-iterranean). *Eur. J. Phycol.* 43, 263–273. doi: 10.1080/09670260801930330
- Irving, A. D., Balata, D., Colosio, F., Ferrando, G. A., and Airoldi, L. (2009). Light, sediment, temperature, and the early life-history of the habitat-forming alga *Cystoseira barbata*. *Mar. Biol.* 156, 1223–1231. doi: 10.1007/s00227-009-1164-7
- Iveša, L., and Devescovi, M. (2004). Distribution and composition of *Cystoseira* stands along the west Istrian coast (northern Adriatic, Croatia) and comparison with historical data. in *5th Mediterranean Symposium on Marine Vegetation*.
- Iveša, L., Djakovac, T., and Devescovi, M. (2016). Long-term fluctuations in *Cystoseira* populations along the west Istrian Coast (Croatia) related to eutrophication patterns in the northern Adriatic Sea. *Mar. pollut. Bull.* 106, 162–173. doi: 10.1016/j.marpolbul.2016.03.010
- Johnson, C. R., Banks, S. C., Barrett, N. S., Cazassus, F., Dunstan, P. K., Edgar, G. J., et al. (2011). Climate change cascades: Shifts in oceanography, species’ ranges and subtidal marine community dynamics in eastern Tasmania. *J. Exp. Mar. Biol. Ecol.* 400, 17–32. doi: 10.1016/j.jembe.2011.02.032
- Krumhansl, K. A., Okamoto, D. K., Rassweiler, A., Novak, M., Bolton, J. J., Cavanaugh, K. C., et al. (2016). Global patterns of kelp forest change over the past half-century. *Proc. Natl. Acad. Sci.* 113, 13785–13790. doi: 10.1073/pnas.1606102113
- Layton, C., Coleman, M. A., Marzinelli, E. M., Steinberg, P. D., Swearer, S. E., Vergés, A., et al. (2020). Kelp forest restoration in Australia. *Front. Mar. Sci.* 7. doi: 10.3389/fmars.2020.00074
- Lejeune, C., Chevaldonné, P., Pergent-Martini, C., Boudouresque, C. F., and Pérez, T. (2010). Climate change effects on a miniature ocean: the highly diverse, highly impacted Mediterranean Sea. *Trends Ecol. Evol.* 25, 250–260. doi: 10.1016/j.tree.2009.10.009
- Ling, S. D., Scheibling, R. E., Rassweiler, A., Johnson, C. R., Shears, N., Connell, S. D., et al. (2015). Global regime shift dynamics of catastrophic sea urchin overgrazing. *Philos. Trans. R. Soc B* 370, 20130269. doi: 10.1098/rstb.2013.0269
- Mačić, V., and Antolić, B. (2015). Distribution of rare *Cystoseira* species along the Montenegrin coast (South-Eastern Adriatic Sea). *Period. Biol.* 117, 441–447. doi: 10.18054/pb.2015.117.3.2995
- Mancuso, F. P., Strain, E. M. A., Piccioni, E., De Clerck, O., Sarà, G., and Airoldi, L. (2018). Status of vulnerable *Cystoseira* populations along the Italian infralittoral fringe, and relationships with environmental and anthropogenic variables. *Mar. pollut. Bull.* 129, 762–771. doi: 10.1016/j.marpolbul.2017.10.068
- Mangialajo, L., Chiantore, M., and Cattaneo-Vietti, R. (2008). Loss of fucoid algae along a gradient of urbanisation, and structure of benthic assemblages. *Mar. Ecol. Prog. Ser.* 358, 63–74. doi: 10.3354/meps07400
- Mann, K. (1973). Seaweeds: their productivity and strategy for growth. *Science* 224, 347–353. doi: 10.1126/science.177.4047.410
- Mannino, A. M., Vaglica, V., Cammarata, M., and Oddo, E. (2016). Effects of temperature on total phenolic compounds in *Cystoseira amentacea* (C. Agardh) Bory (Fucales, Phaeophyceae) from southern Mediterranean Sea. *Plant Biosyst.* 150, 152–160. doi: 10.1080/11263504.2014.941033
- Mariani, S., Cefali, M. E., Chappuis, E., Terradas, M., Pinedo, S., Torras, X., et al. (2019). Past and present of Fucales from shallow and sheltered shores in Catalonia. *Reg. Stud. Mar. Sci.* 32, 100824. doi: 10.1016/j.rsma.2019.100824
- McDonald, T., Gann, G., Jonson, J., and Dixon, K. (2016). International standards for the practice of ecological restoration – including principles and key concepts. *Soc. Ecol. Restor.* doi: 10.2139/ssrn.3645563
- Molinari-Novoa, E., and Guiry, M. (2020). Reinstatement of the genera *gongolaria* boehmer and *ericaria* stackhouse (Sargassaceae, phaeophyceae). *Notulae Algarum* 172, 1–10.
- Monserrat, M., Comeau, S., Verdura, J., Alliouane, S., Spennato, G., Priouzeau, F., et al. (2022). Climate change and species facilitation affect the recruitment of macroalgal marine forests. *Sci. Rep.* 12, 1–12. doi: 10.1038/s41598-022-22845-2
- MSFD (2009). *Marine Strategy framework Directive (MSFD) Marine Strategy Coordination Group*.
- Mulas, M., Silverman, J., Guy-Haim, T., Noè, S., and Rilov, G. (2022). Thermal vulnerability of the Levantine endemic and endangered habitat-forming macroalga, *Gongolaria rayssiae*: implications for reef carbon. *Front. Mar. Sci.* 9. doi: 10.3389/fmars.2022.862332
- Munda, I. M. (1982). The effects of organic pollution on the distribution of fucoid algae from the Istrian coast (vicinity of Rovinj). *Acta Adriat.* 23, 329–337.
- Munda, I. M. (1993). Changes and degradation of seaweed stands in the Northern Adriatic. *Hydrobiologia* 260–261, 239–253. doi: 10.1007/BF00049025
- Neiva, J., Bermejo, R., Medrano, A., Capdevila, P., Milla-Figueras, D., Afonso, P., et al. (2022). DNA barcoding reveals cryptic diversity, taxonomic conflicts and novel biogeographical insights in *Cystoseira s.l.* (Phaeophyceae). *Eur. J. Phycol.* 00, 1–25. doi: 10.1080/09670262.2022.2126894
- Nikolaou, A., Tsirintanis, K., Rilov, G., and Katsanevakis, S. (2023). Invasive fish and sea urchins drive the status of canopy forming macroalgae in the eastern Mediterranean. *Biology* 12, 763. doi: 10.3390/biology12060763
- Nikolic, V., Zuljevic, A., Mangialajo, L., Antolic, B., Kuspilic, G., and Ballesteros, E. (2013). Cartography of littoral rocky-shore communities (CARLIT) as a tool for ecological quality assessment of coastal waters in the Eastern Adriatic Sea. *Ecol. Indic.* 34, 87–93. doi: 10.1016/j.ecolind.2013.04.021
- Oliveras-Pla, M., and Gómez-Garreta, A. (1989). Corología del género *Cystoseira* C. Agardh (Phaeophyceae, Fucales). *Anales del Jardín Botánico Madrid* 46, 89–97.
- Orellana, S., Hernández, M., and Sansón, M. (2019). Diversity of *Cystoseira sensu lato* (Fucales, Phaeophyceae) in the eastern Atlantic and Mediterranean based on morphological and DNA evidence, including *Carpodesmia* gen. emend. and

- Treptacantha* gen. emend. *Eur. J. Phycol.* 54, 447–465. doi: 10.1080/09670262.2019.1590862
- Pinedo, S., Arévalo, R., and Ballesteros, E. (2015). Seasonal dynamics of upper sublittoral assemblages on Mediterranean rocky shores along a eutrophication gradient. *Estuar. Coast. Shelf Sci.* 161, 93–101. doi: 10.1016/j.ecss.2015.05.004
- Pinedo, S., Zabala, M., and Ballesteros, E. (2013). Long-term changes in sublittoral macroalgal assemblages related to water quality improvement. *Bot. Mar.* 56, 461–469. doi: 10.1515/bot-2013-0018
- Porzio, L., Rech, D., and Buia, M. C. (2020). Long-term changes, (1800–2019) in marine vegetational habitats: Insights from a historic industrialised coastal area. *Mar. Environ. Res.* 161, 105003. doi: 10.1016/j.marenvres.2020.105003
- Ragkousis, M., Zenetos, A., Souissi, J.B., Hoffman, R., Ghanem, R., Taşkın, E., et al. (2023). Unpublished Mediterranean and Black Sea records of marine alien, cryptogenic, and nonnative species. *BioInvasions Rec.* 12 (2), 339–369. doi: 10.3391/bir.2023.12.2.01
- R Core Team (2019). *R: A Language and Environment for Statistical Computing* (Vienna, Austria: R Foundation for Statistical Computing).
- Rendina, F., Falace, A., Alongi, G., Buia, M. C., Neiva, J., Appolloni, L., et al. (2023). The lush fucales underwater forests off the Cilento coast: An overlooked Mediterranean biodiversity hotspot. *Plants* 12, 1–12. doi: 10.3390/plants12071497
- Ricart, A. M., García, M., Weitzmann, B., Linares, C., Hereu, B., and Ballesteros, E. (2018). Long-term shifts in the north western Mediterranean coastal seascape: The habitat-forming seaweed *Codium vermilara*. *Mar. Pollut. Bull.* 127, 334–341. doi: 10.1016/j.marpolbul.2017.12.019
- Rilov, G., Peleg, O., Guy-Haim, T., and Yeruham, E. (2020). Community dynamics and ecological shifts on Mediterranean vermetid reefs. *Mar. Environ. Res. Mar. Environ.* 160, 105045. doi: 10.1016/j.marenvres.2020.105045
- Rindi, F., Gavio, B., Díaz-Tapia, P., Di Camillo, C. G., and Romagnoli, T. (2020). Long-term changes in the benthic macroalgal flora of a coastal area affected by urban impacts (Conero Riviera, Mediterranean Sea). *Biodivers. Conserv.* 29, 2275–2295. doi: 10.1007/s10531-020-01973-z
- Sala, E., Boudouresque, C. F., and Harmelin, M. (1998). Fishing, trophic cascades, and the structure of algal assemblages: evaluation of an old but untested paradigm. *Oikos* 82, 425–439. doi: 10.2307/3546364
- Sala, E., Kizilkaya, Z., Yildirim, D., and Ballesteros, E. (2011). Alien marine fishes deplete algal biomass in the Eastern Mediterranean. *PLoS One* 6, e17356. doi: 10.1371/journal.pone.0017356
- Sales, M., and Ballesteros, E. (2010). Long-term comparison of algal assemblages dominated by *Cystoseira crinita* (Fucales, Heterokontophyta) from Cap Corse (Corsica, North Western Mediterranean). *Eur. J. Phycol.* 45, 404–412. doi: 10.1080/09670262.2010.498585
- Sales, M., Ballesteros, E., Anderson, M. J., Iveša, L., and Cardona, E. (2012). Biogeographical patterns of algal communities in the Mediterranean Sea: *Cystoseira crinita*-dominated assemblages as a case study. *J. Biogeogr.* 39, 140–152. doi: 10.1111/j.1365-2699.2011.02564.x
- Schickele, A., Guidetti, P., Giakoumi, S., Zenetos, A., Francour, P., and Raybaud, V. (2021). Improving predictions of invasive fish ranges combining functional and ecological traits with environmental suitability under climate change scenarios. *Glob. Change Biol.* 27, 6086–6102. doi: 10.1111/gcb.15896
- Silverman, B. W. (1998). *Density estimation for statistics and data analysis (1st ed.)* (Routledge: CRC press). doi: 10.1201/9781315140919
- Smale, D. A. (2020). Impacts of ocean warming on kelp forest ecosystems. *New Phytol.* 225, 1447–1454. doi: 10.1111/nph.16107
- Smale, D. A., Burrows, M. T., Moore, P., O'Connor, N., and Hawkins, S. J. (2013). Threats and knowledge gaps for ecosystem services provided by kelp forests: A northeast Atlantic perspective. *Ecol. Evol.* 3, 4016–4038. doi: 10.1002/ece3.774
- Smale, D. A., and Wernberg, T. (2013). Extreme climatic event drives range contraction of a habitat-forming species. *Proc. R. Soc. B: Biol. Sci.* 280, 20122829. doi: 10.1098/rspb.2012.2829
- Smith, C. J., Verdura, J., Papadopoulou, N., Frascchetti, S., Cebrian, E., Fabbri, E., et al. (2023). A decision-support framework for the restoration of *Cystoseira* sensu lato forests. *Frontiers in Marine Science* 10, 1159262.
- Soltan, D., Verlaque, M., Boudouresque, C. F., and Francour, P. (2001). Changes in macroalgal communities in the vicinity of a Mediterranean sewage outfall after the setting up of a treatment plant. *Mar. Pollut. Bull.* 42, 59–70. doi: 10.1016/S0025-326X(00)00116-8
- Steneck, R., Graham, M. H., Bourque, B. J., Corbett, D., and Erlandson, J. M. (2002). Kelp forest ecosystems: Biodiversity, stability, resilience and future. *Environ. Conserv.* 29, 436–459. doi: 10.1017/S0376892902000322
- Strain, E. M. A., Thomson, R. J., Micheli, F., Mancuso, F. P., and Airoldi, L. (2014). Identifying the interacting roles of stressors in driving the global loss of canopy-forming to mat-forming algae in marine ecosystems. *Glob. Change Biol.* 20, 3300–3312. doi: 10.1111/gcb.12619
- Tamburello, L., Chiarore, A., Fabbri, E., Colletti, A., Franzitta, G., Grech, D., et al. (2022). Can we preserve and restore overlooked macroalgal forests? *Sci. Total Environ.* 806, 150855. doi: 10.1016/j.scitotenv.2021.150855
- Teagle, H., Hawkins, S. J., Moore, P. J., and Smale, D. A. (2017). The role of kelp species as biogenic habitat formers in coastal marine ecosystems. *J. Exp. Mar. Biol. Ecol.* 492, 81–98. doi: 10.1016/j.jembe.2017.01.017
- Telesca, L., Belluscio, A., Criscoli, A., Ardzizzone, G., Apostolaki, E. T., Frascchetti, S., et al. (2015). Seagrass meadows (*Posidonia oceanica*) distribution and trajectories of change. *Sci. Rep.* 5, 12505. doi: 10.1038/srep12505
- Teruzzi, A., Salom, S., Bolzon, G., Lazzari, P., Campagna, S., Ficarella, F., et al. (2011). Operational forecasts of the biogeochemical state of Mediterranean Sea. *Mercator Ocean Q. Newslett.* 40, 15–25.
- Thibaut, T., Blanfuné, A., Boudouresque, C.-F., Cottalorda, J.-M., Hereu, B., Susini, M.-L., et al. (2016). Unexpected temporal stability of *Cystoseira* and *Sargassum* forests in Port-Cros, one of the oldest Mediterranean marine National Parks. *Cryptogamie Algologie* 37, 61–90. doi: 10.7872/crya/v37.iss1.2016.61
- Thibaut, T., Blanfuné, A., Boudouresque, C., and Verlaque, M. (2015). Decline and local extinction of Fucales in French Riviera: the harbinger of future extinctions? *Mediterr. Mar. Sci.* 16, 206–224. doi: 10.12681/mms.1032
- Thibaut, T., Blanfuné, A., Markovic, L., Verlaque, M., Boudouresque, C. F., Bottin, L., et al. (2014). Unexpected abundance and long-term relative stability of the brown alga *Cystoseira amentacea*, hitherto regarded as a threatened species, in the north-western Mediterranean Sea. *Mar. Pollut. Bull.* 89, 305–323. doi: 10.1016/j.marpolbul.2014.09.043
- Thibaut, T., Pinedo, S., Torras, X., and Ballesteros, E. (2005). Long-term decline of the populations of Fucales (*Cystoseira* spp. and *Sargassum* spp.) in the Albères coast (France, North-western Mediterranean). *Mar. Pollut. Bull.* 50, 1472–1489. doi: 10.1016/j.marpolbul.2005.06.014
- Torras, X., Pinedo, S., García, M., Weitzmann, B., and Ballesteros, E. (2016). “Environmental quality of Catalan coastal waters based on macroalgae: the interannual variability of CARLIT index and its ability to detect changes in anthropogenic pressures over time,” in *Experiences from ground, coastal and transitional water quality monitoring: The EU Water Framework Directive implementation in the Catalan river basin district (Part II): 183–199. The Handbook of Environmental Chemistry*, vol. 43. Eds. A. Munné, A. Ginebreda and N. Prat (Switzerland: Springer International Publishing).
- UNEP/MAP (2013). “Protocol concerning specially protected areas and biological diversity in the Mediterranean,” in *List of endangered species* (Athina: UNEP/MAP).
- Verdura, J., Santamaria, J., Ballesteros, E., Smale, D. A., Cefali, M. E., Golo, R., et al. (2021). Local-scale climatic refugia offer sanctuary for a habitat-forming species during a marine heatwave. *J. Ecol.* 109, 1758–1773. doi: 10.1111/1365-2745.13599
- Vergés, A., Alcoverro, T., and Ballesteros, E. (2009). Role of fish herbivory in structuring the vertical distribution of canopy algae *Cystoseira* spp. in the Mediterranean Sea. *Mar. Ecol. Prog. Ser.* 375, 1–11. doi: 10.3354/meps07778
- Vergés, A., Tomas, F., Cebrian, E., Ballesteros, E., Kizilkaya, Z., Vergé, A., et al. (2014). Tropical rabbit fish and the deforestation of a warming temperate sea. *J. Ecol.* 102, 1518–1527. doi: 10.1111/1365-2745.12324
- Verlaque, M., Boudouresque, C., and Perret-Boudouresque, M. (2019). Mediterranean seaweeds listed as threatened under the Barcelona Convention: A critical analysis. *Sci. Rep. Port-Cros Natl. Park* 33, 179–214.
- Waltham, N. J., Elliott, M., Lee, S. Y., Lovelock, C., Duarte, C. M., Buelow, C., et al. (2020). UN decade on ecosystem restoration 2021–2030—What chance for success in restoring coastal ecosystems? *Front. Mar. Sci.* 7. doi: 10.3389/fmars.2020.00071
- Wernberg, T., Krumhansl, K., Filbee-Dexter, K., and Pedersen, M. F. (2019). “Status and Trends for the World’s Kelp Forests,” in *World seas: An environmental evaluation* (Amsterdam: Elsevier), 57–78. doi: 10.1016/b978-0-12-805052-1.00003-6
- Wernberg, T., Smale, D., Tuya, F., Thomsen, M. S., Langlois, T. J., de Bettignies, T., et al. (2013). An extreme climatic event alters marine ecosystem structure in a global biodiversity hotspot. *Nat. Clim. Change* 3, 78–82. doi: 10.1038/nclimate1627
- Wickham, H. (2016). *ggplot2: Elegant graphics for data analysis* (New York: Springer-Verlag).
- Zavodnik, E., Ivesa, L., and Travizi, A. (2020). Note on recolonisation by fucoial algae *Cystoseira* spp. and *Fucus virsoides* in the North Adriatic Sea. *Acta Adriatica* 43, 25–32.