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A European biobanking strategy for safeguarding macroalgal genetic material to ensure food security, biosecurity and conservation of biodiversity

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ABSTRACT
Biobanking (also known as germplasm banking) of genetic material is a well-established concept for preserving plant genetic diversity and also contributes to food security, conservation and restoration. Macroalgae currently represent a very small percentage of the strains in publicly accessible European germplasm banks, despite the increasing recognition of their contribution to achieving several of the United Nations Sustainable Development Goals. There is no strategic coordination of existing macroalgal strains, which could have severe ecological and economic implications as species and their genetic diversity disappear rapidly due to local and global environmental stressors. In this opinion paper, we stress the importance of a coordinated European effort for preserving macroalgal genetic diversity and suggest the development of a three-pillared system to safeguard European macroalgal genetic material consisting of (1) a European Board of Macroalgal Genetic Resources (EBMGR) to provide supervision, support and coordination, (2) a network of germplasm banks consisting of currently existing and newly established infrastructures and (3) an interoperable databank integrating existing databanks. While it will be the task of the EBMGR to identify and coordinate priorities, we offer initial recommendations for preserving macroalgal genetic material, discuss the risks of inaction, and highlight the challenges that must be overcome.

HIGHLIGHTS
- A coordinated European effort is crucial to preserve macroalgal genetic diversity, addressing rapid species and genetic loss due to environmental stressors.
- The initiative should include a European Board of Macroalgal Genetic Resources for oversight, a network of existing and new germplasm banks and an interoperable databank integrating current resources.
- The effort supports the United Nations Sustainable Development Goals.

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Introduction

Germplasm banking of genetic material is a well-established concept for breeding, maintaining and protecting crop varieties for agriculture and conserving the gene pool of wild populations (see Box 1). Germplasm banks preserving genetic diversity are repositories that can be leveraged to secure existing or develop novel varieties, which contribute to

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food security, conservation and restoration. As outlined in Wade *et al.* (2020), most germplasm banking efforts have focused on preserving biodiversity of microscopic unicellular algae and terrestrial plant material, the latter for example in botanical gardens, museum herbaria or the Spitsbergen seed vault (Asdal & Guarino, 2018). Globally, 853 culture collections are currently connected in a central network, the World Federation for Culture Collections (https://wfcc.info/), but most are focused on microbial organisms. Among European culture collections, only 37 contain algal cultures, and the vast majority are microalgal strains. The Culture Collection of Algae and Protozoa (CCAP) at the Scottish Association for Marine Science (SAMS) is one of the few public collections with a large variety of seaweed strains, including representatives of commonly cultivated species from the kelp genera *Saccharina* and *Laminaria*, the filamentous brown macroalga *Ectocarpus*, bladed Bangiales (*Porphyra* sensu lato), *Asparagopsis* and the green algal genus *Ulva*. Macroalgal strains in Europe are also maintained in other public repositories, the Culture Collection of Algae at the University of Göttingen (SAG), at the Norwegian Institute for Water Research (NIVA) Culture Collection of Algae, The Spanish Bank of Algae (BEA) and the Roscoff Culture Collection (RCC). Nevertheless, macroalgae represent a very small percentage of strain holdings maintained within publicly accessible algal culture collections. Furthermore, these macroalgal collections as well as the nonpublicly accessible collections located at diverse European research institutions lack a coordinated European strategy for tackling predictable future challenges, such as the need for climate change adaptation and for providing food to the growing global population. In addition to the public collections, macroalgal strains originating from all over the globe are maintained separately by individual researchers, research groups or commercial companies in Europe. Often, these individual germplasm collections are small and lack standardized conditions and information regarding provenance, connectivity and long-term maintenance. In recent years, new national initiatives, such as the Portuguese Blue Biobank (https://www.ciimar.up.pt/platforms/bluebiobank/) and the European Blue Biobank (EBB: https://www.bluebiobank.eu/project/), have started securing the seaweed diversity in local biodiversity hotspots as well as building a network of national marine germplasm banks in order to facilitate sustainable and regulated access to marine biodiversity for science and industry.

While the importance of, and need for, macroalgal germplasm banks have been stressed by several authors in recent years (Barrento *et al.*, 2016; Barbier *et al.*, 2019; Wade *et al.*, 2020; Brakel *et al.*, 2021; Yang *et al.*, 2021), and the first initiatives have started (e.g. technical guidelines developed by the EBB), there is no clear road map or strategy for safeguarding seaweed genetic diversity in Europe. One of the goals of the European Commission's (EC) 'Towards a Strong and Sustainable EU Algae Sector' report was to 'assess the options for an EU-wide approach to conserving seaweed biodiversity by maintaining and documenting European seaweed strains in a centralized germplasm bank network or databank'. There have been recent developments in this direction in the USA, for example the open access kelp germplasm collection Sugar Kelp Base (https://sugarkelpbase.org/) and the European GENIALG project (https://genialgproject.eu/). These projects focused on a few key species important for aquaculture and conservation and generated a large number of new strain accessions from various populations throughout the northern Atlantic, which have been deposited within existing culture collections.

Following the SeaStrains Workshop supported by the Global Seaweed Coalition and hosted at the Alfred Wegener Institute, Helmholtz Center for Polar and Marine Research, in June 2022, representatives from research, academia, culture collections and industry met to lay the foundations for developing a strategy for safeguarding macroalgal genetic diversity in Europe. The resulting 'SeaStrains Network' was the starting point of this opinion paper, which addresses the main issues that were raised and discussed.

The critical importance of safeguarding macroalgal genetic material in germplasm banks to ensure long-term protection of valuable genetic resources in Europe is addressed: (1) We highlight the potential impacts of inaction and provide a suggested strategy to avoid them. The proposed strategy is based on three main pillars, with a foundation in germplasm banking. (2) We discuss the necessary tasks and services that should be provided by a future network of germplasm banks that could best serve all interest groups. (3) We discuss the importance of basing such a strategy on the successes that have already been achieved for germplasm banks that support agriculture. (4) Finally, we discuss the challenges associated with different potential strategies and highlight research priorities that will be necessary in order for this vision to be successfully realized.

Box 1. Macroalgal germplasm banking

We use the term '*macroalgal germplasm bank*' following terminology used by Barrento *et al.* (2016) and Wade *et al.* (2020), for example, to describe the *ex situ* conservation of macroalgal genetic material and associated metadata. Synonyms for this term are '*gene bank*', '*biobank*', '*germplasm collection*', '*genetic resource centre*' or '*biological resource centre*'. The term '*culture collection*' is also frequently used. For land plants, the term '*seed bank*' is often used, referring to the maintenance of the embryo of land plants in its dormant stage. These can be maintained in dry, cold conditions with viability and germination ability ranging from a few years to several decades (De Vitis *et al.*, 2020). In contrast, macroalgal germplasm banking entails maintenance of meristematic tissue (tissue consisting of actively dividing cells forming new tissue) either in the diploid or haploid stage, most often in liquid culture medium or on solid medium plates (see Fig. 1 for examples). These are kept under low light and temperature conditions (relative to natural conditions) but require regular transfer to new medium. Alternatively, macroalgal germplasm can be cryopreserved at ultralow temperatures. For the purpose of clarity, we use the term germplasm bank throughout the remaining text.

The importance of safeguarding macroalgal genetic resources in germplasm banks

The systematic collection, isolation and preservation of macroalgal genetic material in germplasm banks provide a comprehensive repository for maintaining strains that serve as fundamental resources for basic and applied research. Below we briefly describe the widespread loss of macroalgal biodiversity that has been reported throughout Europe and stress the importance of safeguarding genetic macroalgal resources in germplasm banks to conserve and potentially also restore macroalgal biodiversity. We argue that the lack of active and coordinated preservation of macroalgal genetic diversity in sustainable germplasm banks could have severe ecological and economic implications as species and their intraspecific diversity disappear as a consequence of global change. If proper action is not taken, irreversible losses of inter- and intraspecies diversity may occur and restoration and cultivation efforts directed at macroalgal species in Europe will be severely hampered. Furthermore, macroalgal strains for food production and breeding programmes would be limited, resulting in failure to provide additional sources of food for the growing global population. Finally, we describe how germplasm banks not only support basic research and biotechnological applications, but also how they will be essential to scaling up the macroalgal cultivation industry in Europe and simultaneously contributing to the United Nations' Sustainability Goals. Without these activities, the loss of strains used as models for basic research could negatively impact future research efforts, limit experimental reproducibility and hinder bioinnovation.

Vanishing European macroalgal biodiversity

In temperate regions, such as Europe, brown macroalgae belonging to the orders Laminariales, Tilopteridales

Fig. 1. Images of macroalgal germplasm banks maintained at the (A) Alfred Wegener Institute, Helmholtz Center for Polar and Marine Research (photo: Andreas Wagner) and (B, C) Culture Collection of Algae and Protozoa (photos by Cecilia Rad Menéndez).

and Fucales play a pivotal role in marine ecosystem functioning (Lüning, 1990). Due to their size, three-dimensional complexity and the quality of their biomass, they are considered foundation species that improve environmental conditions for a wide variety of organisms (Cheminée *et al*., 2013; Voerman *et al*., 2013; Bermejo *et al*., 2016; Schoenrock *et al*., 2021) and promote biodiversity and productivity compared with communities where these foundation species are absent (Bulleri *et al*., 2002; Steneck *et al*., 2002; Cacabelos *et al*., 2010; Thiriet *et al*., 2016; Teagle *et al*., 2017). Relatively low annual decomposition rates and the resulting stable biomass promote ecosystem functions and services (Viaroli *et al*., 2008; Ramus *et al*., 2017; Cebrian *et al*., 2021). Recent widespread declines in these habitat-forming macroalgae and macroalgal species richness have been recorded from many regions, including Europe, primarily due to the detrimental effects of rising temperature and increasing incidence of marine heatwaves or other local anthropogenic stressors (Mineur *et al*., 2015; Wernberg *et al*., 2016; Rogers-Bennett & Catton, 2019; Filbee-Dexter *et al*., 2020; Smale, 2020). Declines are especially pronounced in regions where macroalgae are situated close to their thermal tolerance limits. In Europe, some fucoids and kelp have declined considerably along the Iberian Peninsula, and the loss of these range-edge kelp and fucoid populations have critical consequences for the species gene pools (Díez *et al*., 2012; Assis *et al*., 2013; Nicastro *et al*., 2013; Neiva *et al*., 2014, 2015, 2020; Martínez *et al*., 2015; Casado-Amezúa *et al*., 2019).

Similarly, several Mediterranean examples of range contractions and local change include the *Cystoseira*, *Ericaria* and *Gongolaria* (*Cystoseira sensu lato*; Fucales, family Sargassaceae) forests (Thibaut *et al*., 2005; Blanfuné *et al*., 2016; Rindi *et al*., 2020), which dominate shallow and mesophotic rocky reefs and represent one of the most endangered habitats in the Mediterranean Sea (Barcelona Convention Annexe II; United Nations Environment Programme/Mediterranean Action PlanUNEP/MAP; Verlaque *et al*., 2019). Declines in these habitat-forming macroalgae (Guidetti *et al*., 2004; Sala *et al*., 2012; Strain *et al*., 2014; Mineur *et al*., 2015; Piñeiro-Corbeira *et al*., 2016; Bianchi *et al*., 2018; Christie *et al*., 2019; Orfanidis *et al*., 2021) result in regime shifts towards turf-dominated ecosystems with a less complex 3D structure, reducing structural habitat for marine organisms (Moy & Christie, 2012; Wernberg *et al*., 2016; Filbee-Dexter & Wernberg, 2018; Feehan *et al*., 2019). Besides the risk of regime shifts, genetically unique populations have been lost (Coleman *et al*., 2022), and severe effects at local scales on fragmented populations of macroalgal species are expected in the future (Verdura *et al*., 2021), which will limit the overall genetic diversity of remaining populations. In addition to kelp forests, other ecosystem engineers such as rhodolith beds (Tuya *et al*., 2023) and calcifying green algae are threatened by climate change, and in some cases have even disappeared from their native ranges (Rilov *et al*., 2020). While *in situ* conservation of macroalgal diversity must be a priority given the ecological importance of brown seaweed forests in ecosystem functions and services, its observed decline and degradation over past decades calls for pressing action for *ex situ* conservation. At the European scale, there is a clear and urgent need to establish coordinated germplasm banks to preserve macroalgal genetic biodiversity.

Conservation and restoration

The conservation of macroalgal forests is crucial to obtain and maintain a good ecological or environmental status, as required by the Marine Framework Strategy Directive (Directive 2000/60/EC) or the Marine Framework Strategy (Directive 2008/56/EC). Many habitat-forming macroalgae are considered indicators of healthy ecosystems when assessing the status of marine ecosystems under these European Directives (Orfanidis *et al*., 2003; Ballesteros *et al*., 2007; Wells *et al*., 2007; Juanes *et al*., 2008; Bermejo *et al*., 2014). Measures for protecting macroalgal forests throughout Europe currently exist (e.g. Annexe II of the Barcelona Convention, COM/2009/0585 FIN; Directive 92/43/EEC; Annexe I; 'Rocky reefs') and 'kelp forests' have been included as threatened habitats within OSPAR (de Bettignies *et al*., 2021; https://www.ospar.org/workareas/bdc/specieshabitats/listofthreateneddecliningspecieshabitats/habitats/kelpforest). Despite a reduction in local anthropogenic pressures and the resulting improvement in water quality (e.g. sewage treatment management, pollutants regulations, limitations on the use of destructive fishing gear, or increases in the number of marine protected areas (MPAs)), the natural recovery of brown macroalgal forests and other ecologically relevant assemblages (e.g. seagrass meadows, oyster reefs) is not always observed (Orth & McGlathery, 2012; Pinedo *et al*., 2013; Gran *et al*., 2022) or can be very slow, especially for species with limited dispersal capacity or recolonization abilities as is the case for many Fucales, Tilopteridales and Laminariales (Billot *et al*., 2003; Schiel *et al*., 2004; Coleman & Brawley, 2005; Buonomo *et al*., 2017). Therefore, restocking or reforestation actions are a promising strategy (Cebrian *et al*., 2021; Gran *et al*., 2022). In this context, the United Nations declared 2021–2030 the 'UN Decade on Ecosystem Restoration' in order to promote restoration actions to fight the climate crisis, enhance food security, provide clean water and protect biodiversity on the planet (Waltham *et al.*, 2020). Seaweed restoration, however, is dependent on local macroalgal resources or seeding material that have survived declines (e.g. Marzinelli *et al.*, 2015; De La Fuente *et al.*, 2019; Layton *et al.*, 2020) and could be complemented in the future by material conserved in germplasm banks. Significant efforts have been made by several EU institutions to research new tools for marine forest restoration and to upscale the process in recent years (e.g. MERCES EU project, AFRIMED, ROCPOP life, FutureMARES, CLIMAREST, RESTORESEAS, FoRESCUE, Green Gravel Action Group). Although restoration has been a highlight of the EU BiodivERsA programme RESTORESEAS, using both the appropriate local genetic lineage and the genetic diversity within the species has been overlooked in many restoration efforts.

Basic macroalgal biological research

Access to well-characterized and diverse macroalgal strains enables scientists to delve into the genetic intricacies of these organisms, unravelling key molecular mechanisms and pathways and driving advances in the field of macroalgal ecology and systems biology. An improved understanding of macroalgal biology, e.g. life cycle and its control, genomes and metabolism is a prerequisite for various undertakings such as macroalga cultivation, biotechnological applications and for future-proofing restoration efforts.

One example of the importance of germplasm banking is the historical trajectory of strains collected by Føyn in 1952, named as *Ulva mutabilis* (Føyn, 1958). Remarkably, since Føyn's initial isolation, the *U. mutabilis* strains have remained in the custodianship of individual researchers, leading to an extensive body of research spanning decades. The strains have been a focal point for numerous investigations into macroalgal reproduction, life cycles, cross-kingdom interactions, symbiotic effects, molecular and taxonomic advancements, and morphogenetic phenomena (Wichard & Oertel, 2010; Spoerner *et al.*, 2012; Oertel *et al.*, 2015; Wichard, 2015; Grueneberg *et al.*, 2016; De Clerck *et al.*, 2018; Steinhagen *et al.*, 2019*a*, 2019*b*; Blomme *et al.*, 2021). These cultures have significantly contributed to research on cell differentiation, growth promoting factors and general macroalgal system biology advancements, underlining the importance of long-term storage, curation and subsequently equitable access to such valuable macroalgal strains (Stratmann *et al.*, 1996; Spoerner *et al.*, 2012; Grueneberg *et al.*, 2016; Ghaderiardakani *et al.*, 2017).

Biotechnology

Bioinnovation also relies on macroalgal strains preserved in germplasm banks (Smith, 2009). Macroalgal polysaccharides and colloids offer various unique features that allow them to be used in cosmetics, tissue engineering, novel biomaterials, food and feed systems and biorefinery processes. Together with other bioactive molecules extracted from marine macroalgae, they show potential for a new generation of active ingredients for diverse industries (Stiger-Pouvreau & Guerard, 2018). To secure the many still unexplored possibilities for the utilization of bioactive compounds from algae, and to support the sustainable use of these marine resources, access to a diverse collection of macroalgal germplasm is needed to support European initiatives.

Aquaculture and food security

The European macroalgal industry will need to scale up cultivation to produce enough biomass for biotechnological innovations and to provide a source of food for the growing world population (Duarte *et al.*, 2021). Large-scale seaweed aquaculture has the potential to serve as a climate change mitigation technology and provide ecosystem services (e.g. provisioning food and feed) that contribute directly to the United Nations Sustainable Development Goals (Duarte *et al.*, 2021; Bermejo *et al.*, 2022; Fricke *et al.*, 2024).

Global macroalgal aquaculture production has increased from 10.6 million tons in 2000 to 35.1 million tons wet weight in 2022, representing an increase from US$4.5 to 16.5 billion with an average yearly growth rate of 6% (The State of World Fisheries and Aquaculture, 2022). Europe currently only produces approximately 0.03% of the global aquaculture-produced macroalgal biomass, but interest in expanding the sustainable macroalgal aquaculture market is growing. A recent report from the European Commission (EC) providing an overview of the industry in Europe showed that there are currently 153 macroalgae-producing enterprises across 23 European countries (Vazquez & Sanchez, 2022), and between 2020 and 2022 investment deals in the industry doubled from 20 to 41 (https://phyconomy.net/articles/2022seaweedreview/). While we acknowledge that there are certainly macroalgal aquaculture enterprises that have not succeeded, the successful number continues to grow. Recent projections have calculated that European producers could increase production from 300 000 tons to 8 million tons by 2030, thereby supplying 30% of the projected €9.3 billion European market from European suppliers (Vincent *et al*., 2020). Nevertheless, several limitations are currently preventing the rapid scale-up of macroalgal production in Europe, including technology, labour costs, competitive pricing and environmental risks (Bermejo *et al*., 2022; Fricke *et al*., 2024). The availability and maintenance of established strains and cultivars in germplasm banks and macroalgal nurseries is one fundamental aspect of the industry that needs to be addressed.

In order to ensure the sustainability of the macroalgal sector, solutions must be found to avoid its dependence upon wild stocks. Several companies have started establishing their own germplasm banks and nurseries to provide starting material to farmers. However, this material will be destined for clients and is generally not available to researchers or the public in general. In addition, company-owned germplasm collections have a stronger focus on selecting for profitable traits rather than ecosystem-relevant traits, the latter of which are relevant to restoration. Nevertheless, recommendations have been submitted to the European Parliament for supporting the development of local cultivars from local strains, not only to select traits of interest, but also to preserve the local genetic background (Barbier *et al*., 2019). This strategy should reinforce the public germplasm banks and involve the private sector in the preservation and restoration of the genetic diversity.

While the investment in breeding of novel macroalgal cultivars will certainly require intellectual property protection, it is essential to ensure fair and open access to the gene pools of commercially and ecologically important species preserved in germplasm banks to support the equitable scaling up of a sustainable cultivation industry in Europe. Open access will foster participatory breeding initiatives helping to develop varietal diversity, particularly if they are conceptualized in close collaboration with seaweed farmers. The year-round access to strains or populations as cultivation starters for biomass production, and access to diverse macroalgal species or cultivars are services that could be provided by germplasm banks to help scale up the cultivation industry. Furthermore, transparency and traceability of source material may provide better consumer acceptance of macroalgal products. This will be particularly important for ensuring future food safety and would help facilitate quality control and tracing. Suggestions for supporting open access and intellectual property protection are provided in the section on facilitating access to macroalgal genetic resources.

Risks of inaction and lessons learned

Learning from mistakes made in agriculture will be essential in order to support food security and protect biodiversity during the scaling up of the macroalgal industry. Researchers have estimated that over 90% of varieties of several vegetables documented in 1903 have been lost due to monocultures and improper conservation of seed, and this now poses a major risk to our food security (Fowler, 2016). A recent report found that our global food system is the primary driver of biodiversity loss (Benton *et al*., 2021). Considering that global fisheries and other marine uses also contribute to marine biodiversity loss (IPBES, 2019), we must place a greater value on protecting marine biodiversity as the production of macroalgae for food and other industries grows, for example by preventing monocultures (Brakel *et al*., 2021), unsustainable harvesting practices (Huanel *et al*., 2022), introductions of non-native species (Mineur *et al*., 2015), and overuse of pesticides and other chemicals (Kumar *et al*., 2023).

The lack of a European sustainable germplasm bank strategy for macroalgae has already led to relevant losses of macroalgal strain collections throughout the past that resided in individual collections, e.g. from retired researchers or researchers who left science, or initiatives who have since folded for a number of reasons (e.g. lack of financial support). In addition to the associated loss in accessible preserved genetic resources and biodiversity, the expertise of personnel and associated operation costs that are needed to obtain macroalgae cultures, such as expeditions to remote places and sampling trips, need to be incorporated into quantifying the monetary and intellectual value of cultures (see Info Box 2). Macroalgae species are not uniform and often isolation of specific groups needs specific expert knowledge. While it is even more difficult to quantify the potential risks and economic losses that may occur if macroalgae genetic diversity is not preserved, the ecosystem services associated with macroalgae have been shown to include high economic value (Bayley *et al*., 2021; Hynes *et al*., 2021; Hu *et al*., 2022; Eger *et al*., 2023). Therefore, it is of utmost importance to develop a long-term European strategy for safeguarding macroalgal genetic material in germplasm banks to ensure food security, biosecurity and the conservation of biodiversity.

Box 2. The monetary value of macroalgal strain collections

Representatives of the SeaStrains Network maintain >2300 macroalgae strains in both institutional and public collections, including a number of small, local collections assembled by individuals. As of December 2024 at the Alfred Wegener Institute (AWI), Helmholtz Center for Polar and Marine Research (Germany), 860 macroalgae strains collected by several macroalgae researchers and associated technicians over the past 50 years exist. The choice of species was driven by the research interests of the scientists. The AWI collection has resulted in >100 peer-reviewed publications between 1975–2022, and >50% of these formed the basis for an understanding of Polar macroalgal autecology. In addition, strains have been given to colleagues worldwide upon request to support general seaweed research.

The authors performed an exercise to estimate the costs accrued by collection, isolation (Table 1) and maintenance (Table 2) of these 860 strains which are preserved in duplicate in separate culture chambers to enhance security. Very conservative estimates are based on personnel costs for 2 working days per strain for sampling in the field and isolation in the laboratory (excluding preparation and travel time and associated expedition costs). For 860 strains, this results in a total of 1720 working days, which extrapolates to 7.8 working years in total (based on a mean of 220 working days per year, excluding holidays; https://www.destatis.de/DE/Presse/Pressemitteilungen/ZahlderWoche/2024/PD24_06_p002.html) and thereby approx. 1.5 working years per decade. Taking a mean annual German salary of approx. €54 000 (before taxes) (https://www.destatis.de/DE/Themen/Arbeit/Verdienste/VerdiensteBrancheBerufe/Tabellen/listebruttomonatsverdienste.html) and excluding inflationary salary increases or currency change during the previous half-century, the personnel costs for establishing the whole collection required a mean investment of at least €8600 per year (Table 1). These annual isolation costs add up to > €400 000 for the whole collection plus the costs of at least 20 polar and other expeditions. In general, collection of strains is often an added value of running projects and depending on the scope of the biobank, associated travel costs may vary considerably.

Currently one technician spends approx. one working month per year to maintain the cultures on the basis of a media exchange twice per year and including other technical service. Adding glassware, diverse laboratory equipment, chemicals and energy consumption of the cultivation cabinets, we calculated approx. €9300 per year (Table 2) for current maintenance costs, while the general investment into infrastructure accounts for approx. €47 000 (value 2024). This germplasm collection only needs four thermocontrolled and illuminated cabinets while other biobanks use walk-in culture rooms, use bigger vessels and change the medium more often, all of which raise maintenance costs. In this respect, the maintenance of a germplasm bank such as this is relatively cost efficient and saves significant investment that would be required to resample strains that are not preserved in germplasm banks. Maintaining seaweed cultures is a sustainable and economical substitute for the significant time and money needed to recollect and reisolate unpreserved strains, especially those that maintain uncommon or difficult to access genotypes or species from isolated or endangered areas.

A European strategy for safeguarding macroalgal genetic resources

Currently existing networks and infrastructures, such as the European Marine Biological Resource Center (EMBRC), the Microbial Resource Research Infrastructure (MIRRI), ELIXIR (European initiative to share infrastructure for biological data) and the Distributed System of Scientific Collections (DiSSCo), serve as excellent examples of how diverse stakeholders like germplasm banks, basic and applied research and biotechnology can be brought together to provide services for all in Europe. These can be used as models for the development of a European concept for safeguarding macroalgal genetic material, and we describe a proposed strategy below.

Table 1. Personnel cost calculation for collecting and isolating seaweed strains held in the Alfred Wegener Institute (AWI) culture collection (CC). The estimated 2 full working days per strain are a conservative estimate and integrate time in the field and the laboratory to establish a clonal isolate (excluding planning and travel time to the sampling location and expedition costs). The personnel costs refer to a mean German salary (before taxes) in 2024 and do not take into account that actual salaries of scientists are higher than the mean, nor the inflationary salary increase or currency change during the previous half-century.

No. of strains in CC	Working days per strain	Mean working days y^{-1} in Germany	Work investment for CC (yrs)	Mean German annual salary (€ yr^{-1})	Age of CC (yrs)	Personnel cost (€yr^{-1})
860	2	220	7.8	~54 000	49	**> 8600**

Table 2. Seaweed culture collection of the Alfred Wegener Institute (AWI, Bremerhaven, Germany). Approximate current investment and maintenance costs based on numbers available for Germany in 2024. The infrastructure consists of four temperature-controlled cabinets with LED illumination (2 × 130 l, 2 × 260 l volume). Irradiance is set to approx. 1–2 µmol photons m^{-2} s^{-1}.

Investment infrastructure		Price per unit in 2024	Investment costs (€)
Cultivation cabinets with LED illumination (130 and 260 l volume)	0/5/10/10°C	€10–12 000 (once per 10–20 years)	45 000
Glassware plus holding boxes	~2000 × 20 ml glass tubes with lid		1600
Access to seawater and sterilization[a]			
Maintenance			**Annual costs** (€ yr^{-1})
Glassware	1000 × 20 ml glass tubes with lid		700
Chemicals[b]	Addition of nutrients		<400
Diverse laboratory ware			500
Energy consumption of 260 l cultivation cabinet set to 5°C	*Hourly consumption* (0.25 kWh/cabinet) × 4 = 1.0 kWh *Daily consumption* 1.0 kWh × 24 h = 24.0 kWh d^{-1} *Annual consumption* 24 × 365 days = 8760 kWh y^{-1}	mean price of kWh: €0.36	3154
Energy consumption LED irradiance			low
Personnel days for maintenance of collection	1 working month y^{-1}	mean German salary: €54 000 y^{-1}	~4500
Total running costs			**~9300**

[a]As access to seawater and facilities to sterilize seawater is extremely dependent on the general logistics of the germplasm bank facility, we cannot provide a meaningful price calculation.
[b]As macroalgal germplasm banks may use a diversity of media for maintenance of cultures and the purchase also is dependent on general logistics of the work environment, exact values are difficult to calculate. The current collection uses 400 ml Provasoli enrichment per year (half-concentration) (Provasoli, 1968). The given price is an estimate over time.

Key tasks and objectives

A European strategy for safeguarding macroalgae genetic resources should deliver three key tasks: (1) the conservation of macroalgal diversity, (2) the development of operational procedures and technical expertise and (3) the promotion of public awareness of the importance of seaweeds (Fig. 2). A diversity of macroalgal stakeholders and their interests must be considered while developing the concept for preserving European macroalgal genetic resources, including producers, breeders, consumers, researchers, NGOs for conservation and society. The key tasks of the strategy should contribute towards (1) ensuring accessibility of macroalgal strains, (2) supporting research, (3) commercial production, (4) breeding and restoration efforts and (5) improving consumer trust in algae products and quality. As with botanical gardens and other biological resource centres, macroalgal germplasm banks can initiate and participate in outreach activities to promote the understanding, appreciation and conservation of macroalgae. A more centralized, interconnected European strategy could contribute more concretely to education and learning and strengthen the European cultural connection to macroalgae. Striving for these objectives within a European concept for macroalgal genetic resources will have broader impacts on economic growth, nature conservation and scientific innovations.

The proposed structure

To address the urgency of counteracting the disappearance of macroalgal biodiversity, with macroalgae being critically important natural resources for the sustainability of basic and applied research, restoration and commercialization efforts, we propose a European strategy including diverse stakeholders (public and private) based on three pillars (Fig. 3): (1) establishment of a European Board of Macroalgal Genetic Resources (EBMGR) in which public partners (scientists and policymakers) and private actors provide supervision, support and coordination for the preservation of macroalgal genetic material in germplasm banks, (2) a network of germplasm banks consisting of existing infrastructure and newly established germplasm banks and (3) an integrated germplasm databank for long-term data storage, preferentially based on or using currently existing databanks.

Following the example used in agricultural research, where the International Board for Plant Genetic Resources (IBPGR) was established in 1974, the proposed EBMGR would lead the network of macroalgal genetic resources and provide recommendations for the collection, conservation, documentation and use of European macroalgal genetic resources. The establishment of the EBMGR could be achieved in close collaboration with the Federation of European Phycological Societies. Under the umbrella of the EBMGR, new initiatives

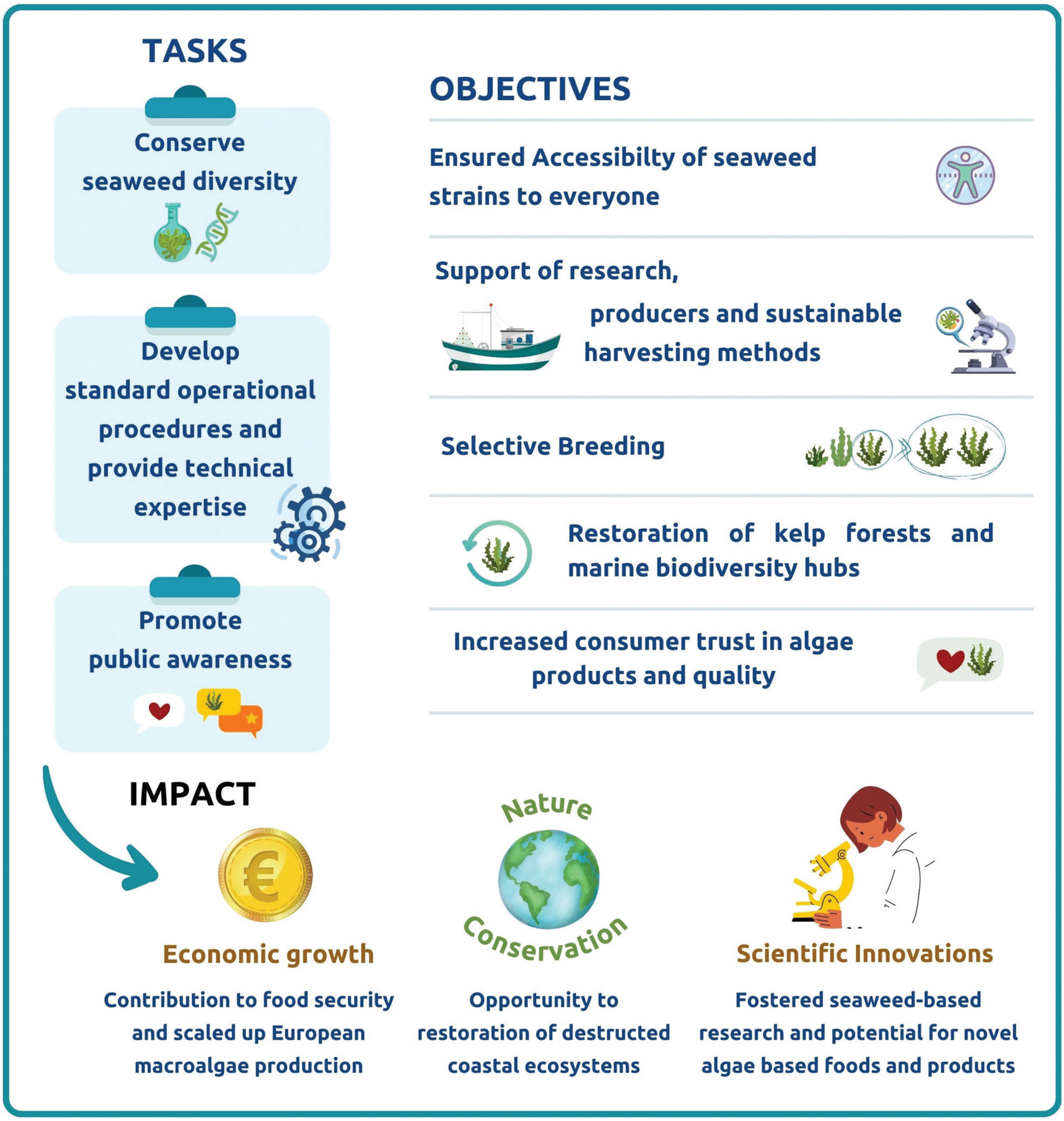

Fig. 2. The tasks and objectives that should be met by a European structure for macroalgal genetic resources.

to foster targeted collections (e.g. Fucales, Cystoseirales), preservation (e.g. infrastructure for cryopreservation) and breeding programmes should be promoted. Breeding programmes could be established in close cooperation with industry stakeholders, research institutes and universities, which could provide further infrastructure required for new cultivar development. Building upon the available infrastructure of existing algal germplasm banks and private collections, the EBMGR could support further developments such as a centralized digital platform with transparent procedures and clear acceptance criteria for the deposition of strains following the guidelines from the OECD Best Practice Guidelines for Biological Resource Centres (OECD, 2007). Additional activities would include securing sources of funding and building new and extending existing infrastructure. Building private-public partnerships could provide a potential solution, but such partnerships must be framed with regulatory tools that clearly define the rights and duties of each partner in order to facilitate the preservation of genetic diversity while simultaneously providing opportunities for new product development (through selection programmes). Existing standard practices, e.g. from the CCAP, for providing patent or confidential depositions to their holdings against fees, can serve as a model to generate income to support the logistics of the germplasm banks.

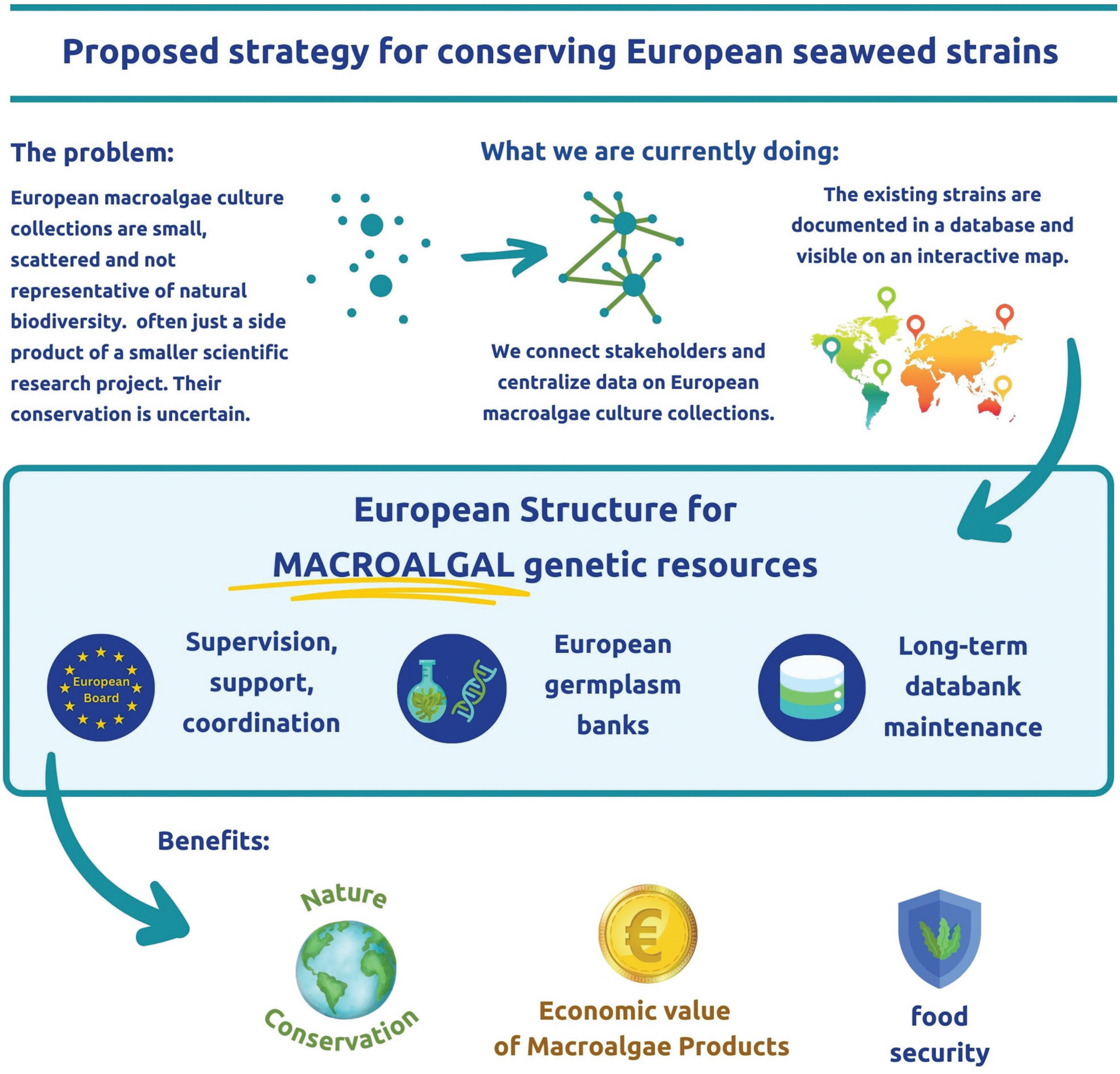

Fig. 3. Proposed European strategy for safeguarding macroalgal genetic material. Currently existing European macroalgal strains are being centralized into a European database by a macroalgal germplasm network (the SeaStrains Network). The next step would be to establish a three-pillar system consisting of a European Board of Macroalgal Genetic Resources, which would provide recommendations to macroalgal germplasm banks for the prioritization, use and conservation of European macroalgal genetic resources, a connected system of germplasm banks consisting of currently existing infrastructure and newly established germplasm banks and a centralized, digital databank for long-term data storage.

Ensuring the sustainability of the germplasm bank infrastructure is one of the major challenges for safeguarding European macroalgal genetic material. The development of novel European infrastructure that uniquely houses macroalgal genetic resources is our long-term vision but would require an immense level of investment and time. As existing germplasm banks for macroalgae in Europe are few and the interest in macroalgae is growing, there are also arguments supporting the need for a novel macroalgae-focused European infrastructure. This could support existing germplasm banks with back-up copies of strains maintained in other banks and provide specialized expertise and infrastructure for certain taxa, technical practices (e.g. cryopreservation) and breeding programmes. Such a long-term vision could also include the transition of macroalgal germplasm banks into European research infrastructures that are eventually linked to form a European Research Infrastructure Consortium (ERIC) for macroalgae.

An additional step towards expanding and improving the preservation of macroalgal genetic diversity in existing germplasm banks would be to specialize in certain areas of expertise. In Fig. 4, we provide examples of potential areas of specialization for macroalgal germplasm banks, and their

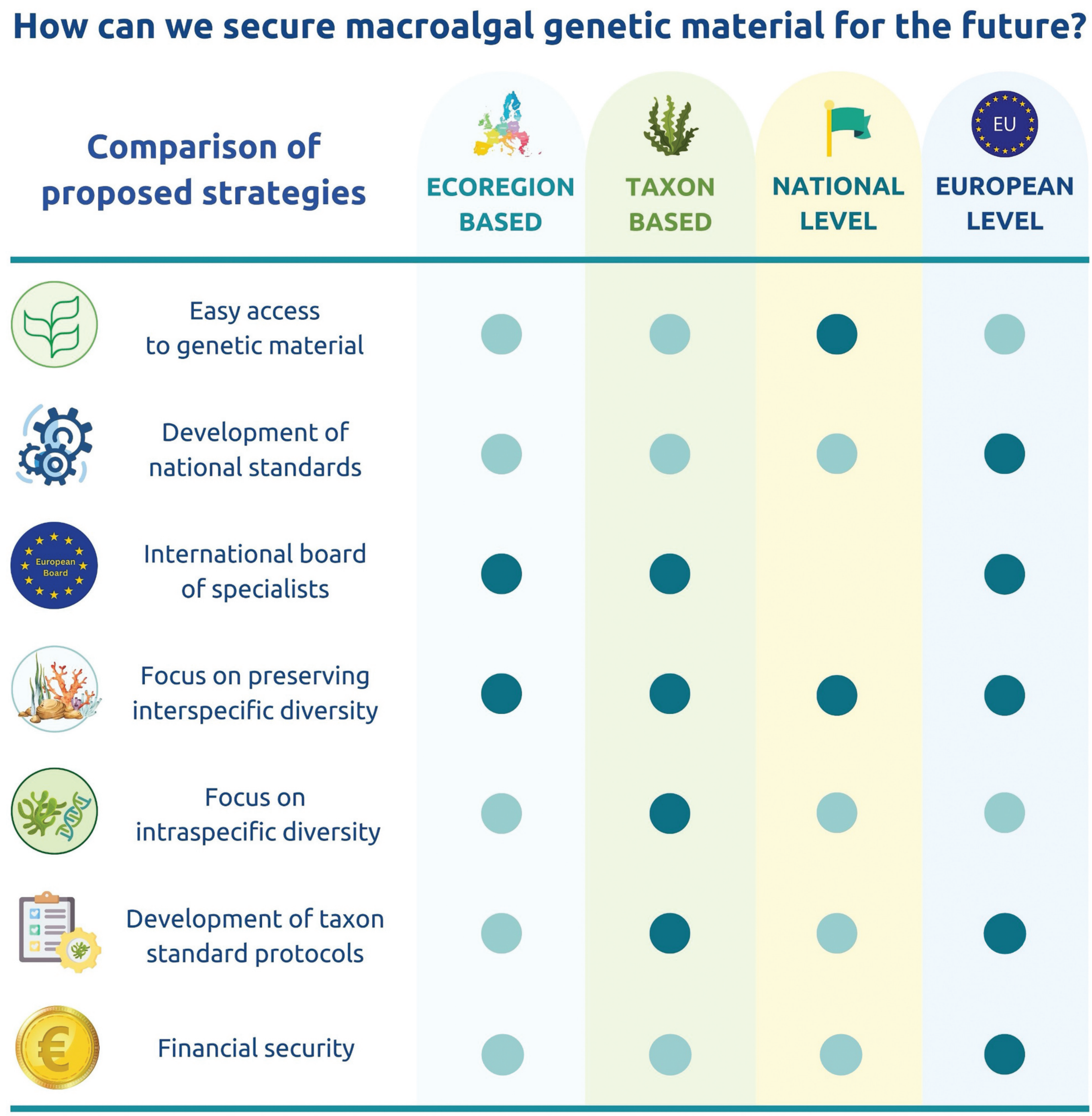

Fig. 4. A comparison of different strategies for the specialization of germplasm banks: by country (national level), taxa or eco-regions (above) or centrally organized via a European germplasm bank. Many of the benefits of a centralized germplasm bank could also be achieved by a decentralized infrastructure network of germplasm banks organized by a centralized governing body (e.g. the suggested European Board for Macroalgal Genetic Resources). Furthermore, it may also be possible for decentralized structures to be supported at the European level or to be part of a European structure located at several sites but under one organizational roof, for example the establishment of a European Research Infrastructure Consortium (ERIC). The degree of shading in the dots represents the relevance of each topic to each of the strategies (dark = high relevance, light = low relevance, absent = no relevance).

associated pros and cons. Some germplasm banks could focus on taxa of interest, for example the Fucales, Laminariales, *Porphyra*/*Pyropia*/*Neopyropia* or macroalgae that are particularly difficult to maintain in culture. The benefits of this model are that experience and know-how would be centralized and the infrastructure would be optimized for the taxa of interest. Alternatively, existing germplasm banks could focus on marine ecoregions (e.g. *sensu* Spalding *et al*., 2007) in an effort to preserve the inter- and intraspecific diversity within a particular European region (e.g. the Baltic, the North Sea, the Mediterranean Sea). We also present the option of national germplasm banks, in which the genetic material within each country is preserved. The benefit of this model is that international exchange and the associated restrictions implemented in the Nagoya protocol of Access and Benefit Sharing (https://www.cbd.int/abs/default.shtml) would not be necessary. Nevertheless, this may not be the best option. Ideally, a combination of these models integrated into a European-wide network overseen by the EMGBR would yield the most benefit. Such a strategy could provide the workforce necessary to set in place material transfer agreements (MTAs) and compliance forms dealing with the Nagoya protocol and to establish common rules that facilitate exchange between European countries, particularly as new cultivars are developed.

A vital issue is the ability of potential users to identify holdings of germplasm banks with specimen availability for various types of use through information systems. However, the rapid accumulation of data from different research areas, such as functional genomics, physiology, ecology and taxonomy, presents a challenge in transforming them into knowledge. In this age of information overload, a problem we frequently encounter is not the need for more data, but the difficulty of integrating complex and rapidly accumulating data in a meaningful way. For this reason, an integrated, interoperable cyber-infrastructure based on currently existing databases (e.g. EMBL/GenBank/DDBJ, GBIF, WoRMs, PubMed, Algaebase) is needed to address the increasing need for informatics support in managing and utilizing stored data. Providing a platform for users to interact and share this information could further help in fostering a collaborative macroalgal research community.

In existing databanks, reference cultures ideally are linked to phenotypic and genetic data as this facilitates macroalgal identification and monitoring. Knowledge of the genetic (DNA barcodes and genomes) and phenotypic variation of macroalgal strains is essential for effectively managing and promoting species' health (Theissinger *et al.*, 2023) and providing correct identifications for regulatory compliance or attribution for cultivation purposes. This is relevant in the context of developing a resilient European industry where researchers and breeders have access to a wide range of information which will contribute to their efforts. Furthermore, such information will be of relevance in the context of conservation as it can be harnessed for informed conservation management strategies and restoration efforts, avoiding inbreeding depression (see section 'Prioritizing intraspecific diversity' below).

Future tasks and challenges

The major challenges for a European germplasm bank strategy are: (1) the lack of financial support for existing and future collections, (2) a decline in well-trained and experienced curatorial staff with expertise across various taxonomic groups, (3) limited infrastructure and resources for germplasm banks to continue to grow and accept new strain deposits unreservedly and (4) a community-wide lack of awareness and understanding of the need for, structure and function of germplasm banks. Below we suggest a strategy for overcoming some of these challenges through targeted prioritization (for both conservation and commercialization) and highlight some of the most pressing issues to be addressed.

Prioritizing macroalgal genetic material for growth of the aquaculture and biotech industries

The GENIALG, Phycomorph, EBB and SeaWheat projects have already made great strides in boosting Europe's macroalgal cultivation and biorefining industries and promoting sustainable farming. Related deliverables from these projects included establishing cultivation and cryopreservation protocols for commercially promising macroalgae, germplasm banking of *Ulva* (Simon *et al.*, 2024) and *Saccharina* strains at the University of Galway and the CCAP (UK), respectively, and the establishment of genomic data for future breeding initiatives. Nevertheless, further prioritization will be necessary to preserve macroalgal biodiversity for targeted commercialization.

Ecosystem services and economic value

Prioritizing species that provide the most significant ecosystem services should be a high priority. A recent report estimating ecosystem services provided by seaweed cultivation found that kelp cultivation provides the highest number of ecosystem services, followed by the agar-producing *Gracilaria* spp., the carrageenan-producing eucheumatoids, and *Porphyra*/*Pyropia*/*Neopyropia* spp. (Bermejo *et al.*, 2022; Fricke *et al.*, 2024). In terms of quantity, the kelp *Saccharina latissima* is the most commonly cultivated species in Europe, followed by *Alaria esculenta, Ulva* spp., *Laminaria* spp., *Palmaria palmata* and *Fucus* spp. (Araújo *et al.*, 2021; Vazquez & Sanchez, 2022, Fig. 5). Similarly, *Saccharina, Laminaria, Alaria, Fucus, Palmaria* and *Ulva* are among the most commonly wild-harvested genera in Europe (Fig. 5). On the other hand, *Chondrus crispus, Ascophyllum nodosum* and bladed Bangiales (=*Porphyra* sensu lato) are commonly harvested in Europe, but there are currently no enterprises cultivating these genera on a large scale. Only two cultivation enterprises are conducting trials for *Porphyra* culture in Europe (Fig. 5), even though it is the fifth biggest macroalgal market in the world, with 2.2 million tons of biomass representing 6% of global production (The State of World Fisheries and Aquaculture, 2022).

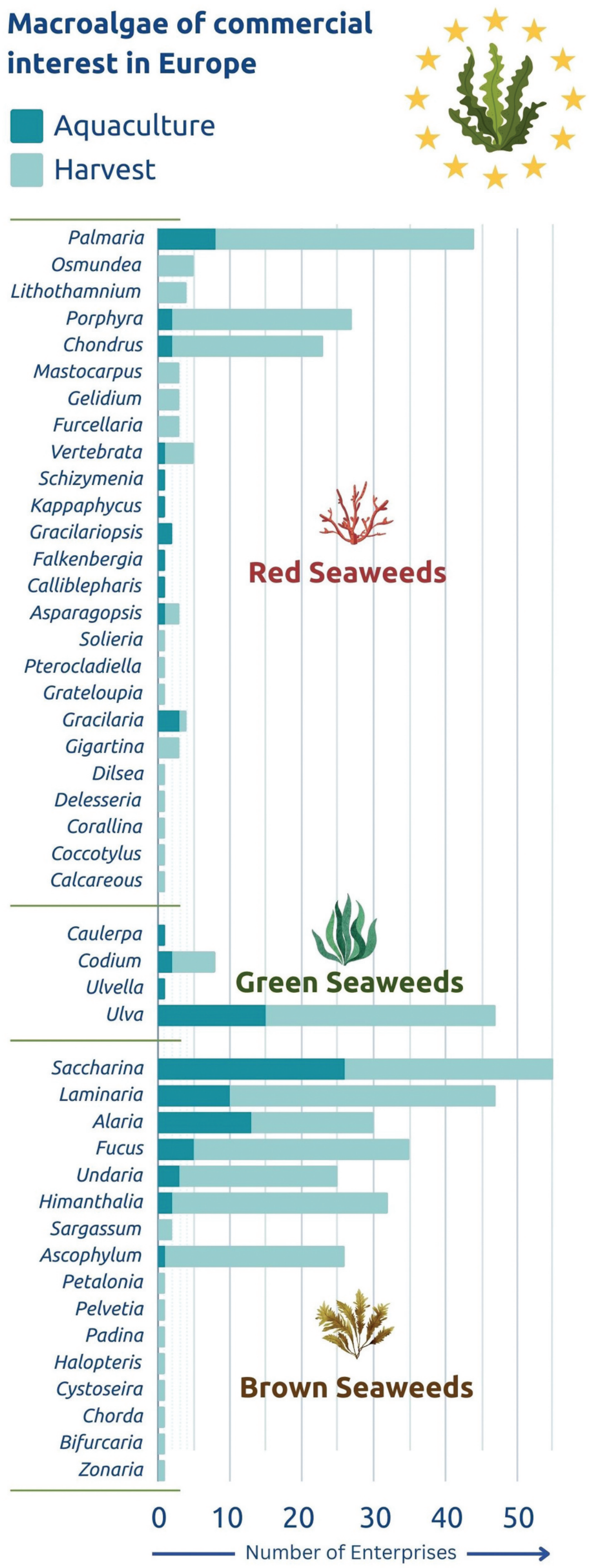

Fig. 5. Overview of cultivated (land- and sea-based; dark blue) and harvested (light blue) macroalgae species in Europe, divided into the categories red seaweeds, green seaweeds and brown seaweeds (data source: https://data.jrc.ec.europa.eu/dataset/fa59f544-bf77-4812-8869-f34d9b096638).

Furthermore, while cultivation of *C. crispus* has been well established as a niche market for Japan and marketed as Hana Tsunomata by Acadian Seaplants (https://www.acadianseaplants.com/), this species is only cultivated by two European companies (Fig. 5). Considering the global interest in these two taxa and the little cultivation activity in Europe, they should be considered high priority for germplasm banks in terms of potential commercial interest.

Another high priority candidate for preservation is *Ascophyllum nodosum*, which is valued for its bioactive compounds, but any attempt to keep this species as a clonal culture collection has failed so far and would need the development of new strategies via vegetative propagation of tissue. This highlights again why more resources and a coordinated European strategy are needed: to support research areas that are essential but too expensive, too long or challenging for single culture collections to pursue. Non-commercial species that provide ecosystem services as ecosystem engineers (as described in Section 2.1), such as *L. hyperborea* and rhodolith beds, should also be prioritized for preservation.

Adaptation to new markets

The economic interest and the associated prioritization of species can change rapidly as new discoveries, applications and compounds of interest are made. A prime example is the genus *Asparagopsis*, which is invasive in the Mediterranean Sea and considered a major threat to biodiversity in Europe (Streftaris & Zenetos, 2006), but there is currently strong interest in the establishment of its large-scale cultivation in Europe due to its ability to reduce methane production in cattle when introduced into their feed (Kinley *et al.*, 2016, 2020; Roque *et al.*, 2019). Other examples are *Chondracanthus teedei* and *Laurencia* spp., the latter used as a model for discovering new bioactive compounds (Monteiro *et al.*, 2023). A European strategy thus needs to adapt to emerging markets, which is only possible through an integrated network such as the proposed EBMGR.

Prioritizing intraspecific genetic diversity

Prioritization and strategic sampling of intraspecific diversity are required to maximize *ex situ* conservation efforts. For restoration purposes, a significant challenge is to preserve local genetic lineages and sufficiently high genetic diversity to facilitate adaptation to rapidly changing conditions and to avoid inbreeding depression (Camus *et al.*, 2021) and subsequent genetic erosion. This becomes even more challenging as the combination of biological invasions and local anthropogenic pressures (Thibaut *et al.*, 2005; Araújo *et al.*, 2011) cause biotic and abiotic stress and reduce the likelihood of recolonization. A major challenge in the conservation of gene pools is knowing the geographical ranges of genetically distinct lineages, because these are usually not visible in the phenotypes. Defining these geographical ranges requires population genotyping throughout the entire biogeographical species distributions, which for a few kelp species of the EU was achieved in the MARFOR project (e.g. Liesner *et al.*, 2020). Advanced techniques of whole genome analysis (Bringloe *et al.*, 2022), ddRAD analysis (Guzinski *et al.*, 2018; Huanel *et al.*, 2022; Reynes *et al.*, 2024) or analysis of species-specific microsatellite markers (Valero *et al.*, 2001) are all currently available to reveal genetic differences between populations on a different resolution and cost level. This knowledge is of particular importance in Europe, where due to the glacial extinction of macroalgal populations in northern Europe, the richest and most diverse gene pools for most investigated species are located near their southernmost ranges, i.e. the trailing edges of populations. This is the case for *Saccorhiza polyschides* (Assis *et al.*, 2016), *Laminaria ochroleuca* (Assis *et al.*, 2018), *Laminaria digitata* (Neiva *et al.*, 2020) and *Laminaria hyperborea* (Barreto 2024). Interestingly, for the trans-Arctic species *Saccharina latissima*, besides the ancient locally differentiated lineages, novel genome recombinations have recently been formed in the Arctic as Pacific lineages have migrated and contacted the Canadian maritimes (Neiva *et al.*, 2018). For the European kelps, any restoration efforts should account for these mapped genetic lineages. The same applies to fucoids of Europe, as most lineages contain richer and/or unique southern genetic types (Neiva *et al.*, 2010, 2012, 2014, 2015; Nicastro *et al.*, 2013; Almeida *et al.*, 2022). Populations at the trailing edges often exhibit better performance under thermal stress caused by climate change, probably because they have genetically adapted to more extreme and stressful conditions (Saada *et al.*, 2016; Martins *et al.*, 2020; Strasser *et al.*, 2022) and may therefore play a crucial role in species survival (Hampe & Petit, 2005). On the other hand, small, fragmented populations already impacted by high rates of genetic drift may not be able to survive climate change due to depauperate genetic diversity (Reynes *et al.*, 2024). Consequently, adaptation along the latitudinal gradient is not uniform (e.g. depending on life-cycle stage, drift and selection pressures) as has been shown in *L. digitata* (Schimpf *et al.*, 2022), pointing to the challenge of considering which genotypes are more or less important for conservation. Careful consideration of all of these factors must be made for future prioritization of intraspecific genetic diversity in macroalgal germplasm banks, and the conservation of a broad intraspecific genotypic diversity will be crucial for future restoration efforts along European coastlines.

Prioritizing genetic material adapted to climate change

The *ex situ* conservation strategy of intraspecific diversity only provides a snapshot at any given time, but does not take into account environmental change and strains that will adapt to the future environment. In plant agronomy, *in situ* management of crop genetic resources, called 'dynamic management' (DM) was proposed in order to integrate the dynamics of genetic diversity in response to environmental changes (Henry *et al.*, 1991). The principle of DM is to maintain natural processes responsible for the diversification and conservation of genetic diversity in subdivided populations grown in different environments. This *in situ* DM was conducted on wheat populations in collaboration with a farmers' network in France, and researchers have shown positive effects of on-farm DM on diversity and adaptation (Enjalbert *et al.*, 2011). Such a DM strategy could be developed in macroalgae in collaboration with local farmers for selected species of interest in Europe to complement the *ex situ* strategy.

Macroalgal material that can genetically tolerate impacts of climate change will be an important resource for successful restoration actions (Wood *et al.*, 2019; Coleman *et al.*, 2020) and for promoting the emerging European aquaculture sector in an ever-changing marine environment (Kim *et al.*, 2017). Different tools can be employed to develop strains resilient to climate change, e.g. by strain selection, selective breeding, genome modification (e.g. emerging CRISPR-Cas9 methodology for macroalgae (Badis *et al.*, 2021) or stress priming (Jueterbock *et al.*, 2021; Gauci *et al.*, 2024)). Selective breeding (i.e. the selection and breeding of tolerant strains to produce offspring with several desirable traits) has been implemented with success for improving tolerance to high irradiance and seawater temperature in *Saccharina* spp. in China (Zhang *et al.*, 2011; Li *et al.*, 2016) and the US (Umanzor *et al.*, 2021). However, care is needed to prevent the impoverishment of genetic diversity by growing those cultivars in large areas as a monoculture. Genome-wide association studies can link DNA regions and traits of interest, such as thermal tolerance, disease resistance or lipid profiles (e.g. see Demirjian *et al.*, 2023), allowing marker-assisted breeding paired with controlled back crosses to maintain high levels of genetic diversity, but it is a very challenging process requiring a lot of resources and is only possible in large consortia. Stress priming is a common non-genetic tool to develop stress-tolerant crops in which stress memory enables plants to become more resilient to a second more severe stress exposure (Liu *et al.*, 2022), and such studies are starting to emerge in macroalgae (Jueterbock *et al.*, 2021). Prior exposure to high or low temperatures has enhanced tolerance in macroalgae when exposed to thermal stress (Li & Brawley, 2004; Kishimoto *et al.*, 2019; Gauci *et al.*, 2022, 2024). Furthermore, associated bacteria, which are co-preserved with the macroalgae in culture collections, can enhance macroalgal resistance under thermal stress (Ghaderiardakani *et al.*, 2024). While the traits of interest are different for macroalgal cultivation and restoration efforts, germplasm banking and the associated infrastructures and methodologies would be the same (see also Filbee-Dexter *et al.*, 2022) so synergies should be sought where possible to achieve resilient and healthy macroalgal ecosystems.

Facilitating access to macroalgal genetic resources

To access and share genetic material of macroalgal species or their derivatives (e.g. DNA), the legal framework of the Nagoya protocol of Access and Benefit Sharing applies (https://www.cbd.int/abs/default.shtml). In the future, digital sequencing information may also fall under this scope. Despite the existence of bilateral agreements ('prior informed consent' (PIC) and 'mutually agreed terms' (MAT)), which are often arranged following the Microbial Resource Research Infrastructure (MIRRI) best practices for germplasm banks, the implementation of this process resulting in material transfer agreements is time- and cost-intensive. Even between member states of the European Union, the exchange of genetic material between partners can be complex and bureaucratic, regardless of the intended use (scientific or commercial). Using the management of plant genetic resources as an example, the International Treaty of Plant Genetic Resources for Food and Agriculture (https://www.fao.org/plant-treaty/en/) regulates access for selected crop species. The treaty is a multilateral legal framework that aims to facilitate access to and protect the privatization of genetic material to support breeding efforts and to safeguard food security. We suggest finding universal rules that facilitate macroalgal genetic material exchange between European countries, particularly as new cultivars are developed.

Plant varieties (i.e. cultivars) can be registered under the framework of Plant Variety Protection (PVP) to strengthen breeders' rights and to encourage breeding activities in many countries. This has only been demonstrated in a few cases for macroalgae. For example, South Korea started to apply a varietal protection system for macroalgae in 2012 under the umbrella of UPOV (International Union for the Protection Of New Varieties of Plants). Since then, 19 macroalgal varieties have been registered (Hwang & Park, 2020), which are held at the Aquatic Plant Variety Centre under the umbrella of the National Institute of Fisheries Science. The European germplasm network under the EBMGR could take similar steps for new macroalgal varieties.

Technical challenges

Species difficult to maintain in culture

The current collections of macroalgae are heavily skewed towards species that are manageable for cultivation. Besides life cycle control, characteristics that enhance the potential for cultivation encompass the presence of a heteromorphic life cycle with a microscopic or filamentous phase, the general feasibility of vegetative propagation and good survival in small vessels and low light, which are often used in germplasm banks. In general, cultivating filamentous life-cycle stages is more straightforward than for (pseudo-) parenchymatous species. Thus, even if only one phase of the life cycle is filamentous, this significantly simplifies the cultivation process. Examples include kelp species which have filamentous gametophytes or bladed Bangiales (*Porphyra, Pyropia*, *Neopyropia*) with a conchocelis phase. Many ecologically important macroalgae unfortunately do not have a filamentous phase which either means one cannot cultivate them or their cultivation requires significantly more effort. For brown macroalgae these include many habitat-forming species such as fucoids which dominate rocky intertidal habitats in cold temperate regions or the shallow subtidal habitats of southern Europe. While there has been some cultivation success at the laboratory scale for Mediterranean *Cystoseira* species (Falace *et al.*, 2018), effective cultivation of such species will require significant research and potential adoption of novel cultivation techniques, including learning from the agriculture sector, e.g. from tropical fruit plants that do not form preservable seeds (Normah *et al.*, 2013). Cultivation of several red algal species as microplantlet suspension cultures has proven successful (e.g. Rorrer *et al.*, 1998; Rorrer & Cheney, 2004).

Cryopreservation

Long-term maintenance of macroalgal strains through serial transfer may cause changes in strain performance, e.g. through genetic drift, changes in the associated microbiome or other poorly understood processes. Continuous handling of strains is also cost and time intensive and prone to human error, e.g. contamination or loss during cultivation. Cryopreservation presents an alternative, where strains are immersed in a cryoprotectant buffer and are often frozen in a two-step freezing process at ultra-low temperatures. Cryopreservation protocols have been developed for various, mainly commercial, macroalgae with mixed results (Lee & Nam, 2016; Day, 2018; Visch *et al*., 2019; Yang *et al*., 2021; Beniers *et al*., 2023; Simon *et al*., 2024). Nevertheless, further investigation and improvement of the protocols are needed for certain taxa, particularly red macroalgae, that cannot be or have poor success when cryopreserved using established methods. The development of such techniques requires specialist knowledge, substantial capital and advanced operational infrastructure. It would therefore be expedient to provide resources on a European scale to develop needed techniques. Also, published studies over the long-term viability of cryopreserved macroalgal strains and their ability to reproduce after thawing are still lacking, although kelp gametophytes of *Saccharina latissima* have been successfully thawed after 3.5 years of cryopreservation in liquid nitrogen (Rad-Menéndez, unpublished data). The fact that some microalgae have been shown to recover after 22 years without loss of viability is promising (Day *et al*., 1997).

Biosecurity and conserving the holobiont

Eukaryotic and prokaryotic microbes form intricate associations with macroalgae, e.g. bacteria, fungi, oomycetes, other micro- and macroalgae (see e.g. Gachon *et al*., 2010; Vallet *et al*., 2018; Bernard *et al*., 2019). Considering that macroalgal aquaculture in some regions has already been devastated by disease (e.g. Ward *et al*., 2020), the aspect of biosecurity in macroalgal germplasm banks is essential and must be further supported and developed (Brakel *et al*., 2021). Taxonomic knowledge and a reference database of relevant macroalgae pathogens and parasites are crucial (Murúa *et al*., 2023). The establishment of a reference germplasm bank of common macroalgal pathogens and pests supporting a progressive management pathway for improving biosecurity (see Cottier-Cook *et al*., 2022) is critical. Biobanking pathogen and pest strains will support highly needed fundamental research on disease resistance and breeding. A reference germplasm bank would also raise awareness about disease and pests and could provide critical information and training for macroalgal producers (see Strittmatter *et al*., 2022). Access to pathogen and pest germplasm would likewise facilitate the development of protocols to monitor and manage their occurrence, e.g. within macroalgae germplasm samples, hatcheries or farms.

The community of bacteria associated with macroalgae (the 'microbiome') can strongly influence the physiology, acclimation potential, defence and reproductive success of the host (Wichard, 2015; Dittami *et al*., 2016; Morris *et al*., 2016; Arnaud-Haond *et al*., 2017; Li *et al*., 2023). These natural microbial communities could potentially provide new sources of biotechnical applications, and the formulation and testing of synthetic communities (SynComs), a well-established tool in human and animal health (Bolsega *et al*., 2021), could further provide new services. Some bacterial strains originating from macroalgal microbiomes (mostly model brown and green macroalgal species) are currently available in public culture collections (e.g. MIRRI and the database from the SIMBA project), but to date there has been limited focus on promoting the visibility and utilization of macroalgae-associated microbial strains. It would undoubtedly be relevant for germplasm banks to provide information on associated microbiomes of non-axenic strains in future, but the erosion of the microbiome with increasing cultivation time due to drift effects presents challenges (Califano *et al*., 2020; van der Loos *et al*., 2021). Cryopreservation of macroalgal strains (along with associated microbiomes) could help preserve a larger part of the diversity of the collected microbiome, albeit probably with some alterations or biases.

Recommendations for next steps

The systematic collection and preservation of macroalgal genetic material in germplasm banks provide a comprehensive repository for maintaining strains that serve as fundamental resources for basic and applied research endeavours. Safeguarding macroalgal genetic resources using a European strategy that builds upon currently existing germplasm bank infrastructure should be built upon three main pillars: (1) a European Board of Macroalgal Genetic Resources (EBMGR), which oversees, supports and coordinates a (2) coordinated network of European germplasm banks connected via a (3) centralized databank. This will be essential for supporting and benefiting conservation, restoration, bioinnovation and aquaculture efforts. The expansion of current and establishment of further germplasm banks for macroalgae is necessary and should be strategically specialized according to ecoregions, taxa or technical expertise identified by the future EBMGR to be of high priority. Building private-public partnerships could provide a potential solution to obtaining financial support, but additional support at the national and EU level (e.g. via programmes such as Biodiversa+, Horizon) will also be necessary.

Once a network of public and private germplasm banks is established under the EBMGR, further steps could include interconnecting them as biological resource centres in a European Research Infrastructure Consortium embedded in existing infrastructure, such as the EMBRC (https://www.embrc.eu/), the European Culture Collection

Organization (ECCO) or the Distributed System of Scientific Collections (DiSSCo), and should be inclusive of all European countries. The establishment of such a structure will most likely require significant financial input to support a central coordination office, including data architects, software developers, project officers, communications and outreach officers, advocacy and engagement officers, and governance affairs specialists. Building the macroalgal germplasm banks into these networks that already exist would save considerable time, resources and effort. The aim should be to serve all interest groups (conservation, restoration, aquaculture, biotechnology, basic research) despite conflicting interests.

Due to the high diversity of macroalgal species and limited resources for their preservation, prioritization will be necessary and will require considering the interests of all stakeholders. While we consider it the task of a future EBMGR to identify and coordinate priorities, we highlight the most pressing issues that are of critical importance in a European strategy for preserving macroalgal genetic resources based on the systematic reasoning provided above. The governance of European macroalgal genetic resources should ensure fair and equal access to genetic material within the framework of the Nagoya Protocol. Species of commercial interest that are currently harvested in Europe, but not yet cultivated, should be prioritized. The establishment of centres of expertise for targeted taxa of high commercial interest (e.g. Fucales, Laminariales, *Porphyra, Palmaria, Ulva, Chondrus*) should be initiated and supported. Furthermore, species that provide the greatest ecosystem services should be given highest priority. Sampling strategies for collecting and preserving wild specimens should be guided by population genetics (e.g. favouring the trailing edges of macroalgal populations). To improve the connectivity of a European germplasm bank network, the development of conservation and propagation protocols, knowledge transfer, training and capacity building should be supported. New infrastructure and training in cryopreservation (potentially centralized) and breeding should be developed, and macroalgae breeding programmes for developing 'future proof' gene pools for restoration and aquaculture should be initiated as a climate change adaptation strategy. Implementing the proposed or similar strategies at the European level, including coordinated efforts, research prioritization and capacity building, will be of critical importance for the long-term stability and protection of European macroalgal genetic resources and hence ensure food security, biosecurity and biodiversity in a rapidly changing climate as we strive for more sustainable use of marine resources.

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Data availability statement

The data underlying this article will be shared on reasonable request to the corresponding author.

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No potential conflict of interest was reported by the author(s).

Author contributions

L.C. Hofmann and J. Brakel: lead authors with equal contribution. L.C. Hofmann, I. Bartsch and J. Brakel: conceptualized and designed the study, collected the data, analysed the findings, and drafted, edited and revised the manuscript. G.M. Arismendi, R. Bermejo, M.I. Parente, E. Creis, O. de Clerck, J. Knoop, M. Lorenz, L.P. Machado, N. Martins, S. Orfanidis, I. Probert, C. Rad-Menéndez, M. Ross, R. Rautenberger, J. Schiller, E.A. Serrao, S. Steinhagen, R. Sulpice, M. Valero and T. Wichard: contributed to writing and revising the manuscript.

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References

Almeida, S.C., Neiva, J., Sousa, F., Martins, N., Cox, C.J., Melo-Ferreira, J., Guiry, M.D. Serrão, E.A. & Pearson, G. A. (2022). A low-latitude species pump: peripheral isolation, parapatric speciation and mating-system evolution converge in a marine radiation. *Molecular Ecology*, **31**: 4797–4817.

Araújo, R., Vázquez Calderón, F., Sánchez López, J., Azevedo, I.C., Bruhn, A., Fluch, S., Garcia Tasende, M. Ghaderiardakani, F., Ilmjärv, T., Laurans, M., Mac Monagail, M., Mangini, S., Peteiro, C., Rebours, C., Stefansson, T. & Ullmann, J. (2021). Current status of the algae production industry in Europe: an emerging sector of the blue bioeconomy. *Frontiers in Marine Science*, **7**: 626389.

Araújo, R., Violante, J., Pereira, R., Abreu, H., Arenas, F. & Sousa-Pinto, I. (2011). Distribution and population dynamics of the introduced seaweed *Grateloupia turuturu* (Halymeniaceae, Rhodophyta) along the Portuguese coast. *Phycologia*, **50**: 392–402.

Arnaud-Haond, S., Aires, T., Candeias, R., Teixeira, S.J.L., Duarte, C.M., Valero, M. & Serrão, E.A. (2017). Entangled fates of holobiont genomes during invasion: nested bacterial and host diversities in *Caulerpa taxifolia*. *Molecular Ecology*, **26**: 2379–2391.

Asdal, Å. & Guarino, L. (2018). The Svalbard global seed vault: 10 years—1 million samples. *Biopreservation and Biobanking*, **16**: 391–392.

Assis, J., Castilho Coelho, N., Alberto, F., Valero, M., Raimondi, P., Reed, D. & Alvares Serrão, E. (2013). High and distinct range-edge genetic diversity despite local bottlenecks. *PLOS ONE*, **8**: e68646.

Assis, J., Coelho, N.C., Lamy, T., Valero, M., Alberto, F. & Serrão, E.Á. (2016). Deep reefs are climatic refugia for genetic diversity of marine forests. *Journal of Biogeography*, **43**: 833–844.

Assis, J., Serrão, E.Á., Coelho, N.C., Tempera, F., Valero, M. & Alberto, F. (2018). Past climate changes and strong oceanographic barriers structured low-latitude genetic relics for the golden kelp *Laminaria ochroleuca*. *Journal of Biogeography*, **45**: 2326–2336.

Badis, Y., Scornet, D., Harada, M., Caillard, C., Godfroy, O., Raphalen, M., Gachon, C.M.M. Coelho, S. M., Motomura, T., Nagasato, C., & Cock, J.M. (2021). Targeted CRISPR-Cas9-based gene knockouts in the model brown alga *Ectocarpus*. *New Phytologist*, **231**: 2077–2091.

Ballesteros, E., Torras, X., Pinedo, S., García, M., Mangialajo, L. & De Torres, M. (2007). A new methodology based on littoral community cartography dominated by macroalgae for the implementation of the European Water Framework Directive. *Marine Pollution Bulletin*, **55**: 172–180.

Barbier, M., Charrier, B., Araujo, R., Holdt, S.L., Jacquemin, B. & Rebours, C. (2019). PEGASUS - PHYCOMORPH European Guidelines for aSustainable Aquaculture of Seaweeds. In *Cost Action Fa1406* (Barbier M. & Charrier B., eds.), Roscoff, France. doi:10.21411/2c3w-yc73

Barrento, S., Camus, C., Sousa-Pinto, I. & Buschmann, A. H. (2016). Germplasm banking of the giant kelp: our biological insurance in a changing environment. *Algal Research*, **13**: 134–140.

Barreto, L. (2024). Intraspecific variation as response to marine heatwaves in two northeast Atlantic kelp species. PhD thesis, University of Algarve, Faro, Portugal, 152 pages

Bayley, D., Brickle, P., Brewin, P., Golding, N. & Pelembe, T. (2021). Valuation of kelp forest ecosystem services in the Falkland Islands: a case study integrating blue carbon sequestration potential. *One Ecosystem*, **6**: e62811.

Beniers, J.E., Bras, S. & Werf, A.K. (2023) Cryopreservation of *Ulva* spp. and *Saccharina latissima*: optimised protocols of cryopreservation, recovery and (long-term) regrowth of *Ulva* spp. and *Saccharina latissima* gametophytes and sporophytes. Stichting Wageningen Research, Wageningen Plant Research, Business Unit Agrosystems research, Wageningen. https://research.wur.nl/en/publications/f44b72ab-8c15-4bf6-bd75-2842f282bc2c (Accessed 5 April 2024).

Benton, T.G., Bieg, C., Harwatt, H., Pudasaini, R. & Wellesley, L. (2021). Food System Impacts On Biodiversity Loss. Three Levers For Food System Transformation In Support of Nature. In *Energy, Environment and Resources Programme*. Chatham House, London

Bermejo, R., Buschmann, A., Capuzzo, E., Cottier-Cook, E., Fricke, A., Hernández, I., Hofmann, L.C. Pereira, R. & van den Burg, S. (2022) State of knowledge regarding the potential of macroalgae cultivation in providing climate-related and other ecosystem services. Report prepared by an Eklipse Working Group https://eklipse.eu/wp-content/uploads/website_db/Request/Macro-Algae/EKLIPSE_DG-Mare-Report-PrintVersion_final.pdf (Accessed 19 May 2022).

Bermejo, R., De La Fuente, G., Ramírez-Romero, E., Vergara, J.J. & Hernández, I. (2016). Spatial variability and response to anthropogenic pressures of assemblages dominated by a habitat forming seaweed sensitive to pollution (northern coast of Alborn Sea). *Marine Pollution Bulletin*, **105**: 255–264.

Bermejo, R., Mangialajo, L., Vergara, J.J. & Hernández, I. (2014). Comparison of two indices based on macrophyte assemblages to assess the ecological status of coastal waters in the transition between the Atlantic and Mediterranean eco-regions. *Journal of Applied Phycology*, **26**: 1899–1909.

Bernard, M.S., Strittmatter, M., Murúa, P., Heesch, S., Cho, G.Y., Leblanc, C. & Peters, A.F. (2019). Diversity, biogeography and host specificity of kelp endophytes with a focus on the genera *Laminarionema* and

Laminariocolax (Ectocarpales, Phaeophyceae). *European Journal of Phycology*, **54**: 39–51.

Bianchi, C.N., Caroli, F., Guidetti, P. & Morri, C. (2018). Seawater warming at the northern reach for southern species: Gulf of Genoa, NW Mediterranean. *Journal of the Marine Biological Association of the United Kingdom*, **98**: 1–12.

Billot, C., Engel, C., Rousvoal, S., Kloareg, B. & Valero, M. (2003). Current patterns, habitat discontinuities and population genetic structure: the case of the kelp *Laminaria digitata* in the English Channel. *Marine Ecology Progress Series*, **253**: 111–121.

Blanfuné, A., Boudouresque, C.F., Verlaque, M. & Thibaut, T. (2016). The fate of *Cystoseira crinita*, a forest-forming Fucale (Phaeophyceae, Stramenopiles), in France (North Western Mediterranean Sea). *Estuarine, Coastal and Shelf Science*, **181**: 196–208.

Blomme, J., Liu, X., Jacobs, T.B. & De Clerck, O. (2021). A molecular toolkit for the green seaweed *Ulva mutabilis*. *Plant Physiology*, **186**: 1442–1454.

Bolsega, S., Bleich, A. & Basic, M. (2021). Synthetic microbiomes on the rise—Application in deciphering the role of microbes in host health and disease. *Nutrients*, **13**: 4173.

Brakel, J., Sibonga, R.C., Dumilag, R.V., Montalescot, V., Campbell, I., Cottier-Cook, E.J., Ward, G. Le Masson, V., Liu, T., Msuya, F.E., Brodie, J., Lim, P.E. & Gachon, C.M.M. (2021). Exploring, harnessing and conserving marine genetic resources towards a sustainable seaweed aquaculture. *Plants, People, Planet*, **3**: 337–349.

Bringloe, T.T., Fort, A., Inaba, M., Sulpice, R., Ghriofa, C. N., Mols, A., Filbee, K. *et al.* (2022). Whole genome population structure of North Atlantic kelp confirms high-latitude glacial refugia. *Molecular Ecology*, **31**: 6473–6488.

Bulleri, F., Benedetti-Cecchi, L., Acunto, S., Cinelli, F. & Hawkins, S.J. (2002). The influence of canopy algae on vertical patterns of distribution of low-shore assemblages on rocky coasts in the northwest Mediterranean. *Journal of Experimental Marine Biology and Ecology*, **267**: 89–106.

Buonomo, R., Assis, J., Fernandes, F., Engelen, A.H., Airoldi, L. & Serrão, E.A. (2017). Habitat continuity and stepping-stone oceanographic distances explain population genetic connectivity of the brown alga *Cystoseira amentacea*. *Molecular Ecology*, **26**: 766–780.

Cacabelos, E., Olabarria, C., Incera, M. & Troncoso, J.S. (2010). Effects of habitat structure and tidal height on epifaunal assemblages associated with macroalgae. *Estuarine, Coastal and Shelf Science*, **89**: 43–52.

Califano, G., Kwantes, M., Abreu, M.H., Costa, R. & Wichard, T. (2020). Cultivating the macroalgal holobiont: effects of integrated multi-trophic aquaculture on the microbiome of *Ulva rigida* (Chlorophyta). Frontiers In Marine Science, **7**: 52.

Camus, C., Solas, M., Martínez, C., Vargas, J., Garcés, C., Gil-Kodaka, P., Ladah, L.B. Serräo, E.A. & Faugeron, S. (2021). Mates matter: gametophyte kinship recognition and inbreeding in the giant kelp, *Macrocystis pyrifera* (Laminariales, Phaeophyceae). *Journal of Phycology*, **57**: 711–725.

Casado-Amezúa, P., Araújo, R., Bárbara, I., Bermejo, R., Borja, Á., Díez, I., Fernández, C. Gorostiaga, J.M., Guinda, X., Hernández, I., Juanes, J.A., Peña, V., Peteiro, C., Puente, A., Quintana, I., Tuya, F., Viejo, R. M., Altamirano, M., Gallardo, T. & Martínez, B. (2019). Distributional shifts of canopy-forming seaweeds from the Atlantic coast of Southern Europe. *Biodiversity and Conservation*, **28**: 1151–1172.

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**: 709219.

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**: 70–79.

Christie, H., Andersen, G.S., Bekkby, T., Fagerli, C.W., Gitmark, J.K., Gundersen, H. & Rinde, E. (2019). Shifts between sugar kelp and turf algae in Norway: regime shifts or fluctuations between different opportunistic seaweed species? *Frontiers in Marine Science*, **6**: 72.

Coleman, M.A., Reddy, M., Nimbs, M.J., Marshell, A., Al-Ghassani, S.A., Bolton, J.J., Jupp, B.P. De Clerck, O., Leliaert, F., Champion, C., Pearson, G.A., Serrão, E.A., Madeira, P. & Wernberg, T. (2022). Loss of a globally unique kelp forest from Oman. *Scientific Reports*, **12**: 5020.

Coleman, M.A., Wood, G., Filbee-Dexter, K., Minne, A.J. P., Goold, H.D., Vergés, A., Marzinelli, E.M. Steinberg, P. D., & Wernberg, T. (2020). Restore or redefine: future trajectories for restoration. *Frontiers In Marine Science*, **7**: 237.

Coleman, M. & Brawley, S. (2005). Spatial and temporal variability in dispersal and population genetic structure of a rockpool alga. *Marine Ecology Progress Series*, **300**: 63–77.

Cottier-Cook, E.J., Cabarubias, J.P., Brakel, J., Brodie, J., Buschmann, A.H., Campbell, I., Critchley, A.T. Hewitt, C.L., Huang, J., Hurtado, A.Q., Kambey, C.S.B., Lim, P. E., Liu, T., Mateo, J.P., Msuya, F.E., Qi, Z., Shaxson, L., Stentiford, G.D., & Bondad-Reantaso, M.G. (2022). A new progressive management pathway for improving seaweed biosecurity. *Nature Communications*, **13**: 7401.

Day, J.G. (2018). Cryopreservation of Macroalgae. In *Protocols For Macroalgae Research* (Charrier, B., Wichard, T. & Reddy, C.R.K., eds.), 79–94. CRC Press Taylor & Francis Group, London and New York.

Day, J.G., Watanabe, M.M., Morris, G.J., Fleck, R.A. & McLellan, M.R. (1997). Long-term viability of preserved eukaryotic algae. *Journal of Applied Phycology*, **9**: 121–127.

de Bettignies, T., De Bettignies, F., Bartsch, I., Bekkby, T., Boiffin, A., Amezúa, P., Christie, H. *et al.* (2021). OSPAR commission 2021 - background document on kelp forest habitat. *Ospar*, **788**(**2021**): 66.

De Clerck, O., Kao, S.-M., Bogaert, K.A., Blomme, J., Foflonker, F., Kwantes, M., Vancaester, E. Vanderstraeten, L., Aydogdu, E., Boesger, J., Califano, G., Charrier, B., Clewes, R., Del Cortona, A., D'Hondt, S., Fernandez-Pozo, N., Gachon, C.M., Hanikenne, M., Lattermann, L., Leliaert, F., Liu, X., Maggs, C.A., Popper, Z.A., Raven, J.A., Van Bel, M., Wilhelmsson, P.K.I., Bhattacharya, D., Coates, J.C., Rensing, S.A., Van Der Straeten, D., Vardi, A., Sterck, L., Vandepoele, K., Van de Peer, Y., Wichard, T., & Bothwell, J.H. (2018). Insights into the evolution of multicellularity from the sea lettuce genome. *Current Biology*, **28**: 2921–2933.e5.

De La Fuente, G., Chiantore, M., Asnaghi, V., Kaleb, S. & Falace, A. (2019). First *ex situ* outplanting of the habitat-forming seaweed *Cystoseira amentacea* var. *stricta* from a restoration perspective. *PeerJ*, **7**: e7290.

Demirjian, C., Vailleau, F., Berthomé, R. & Roux, F. (2023). Genome-wide association studies in plant pathosystems: success or failure? *Trends in Plant Science*, **28**: 471–485.

De Vitis, M., Hay, F.R., Dickie, J.B., Trivedi, C., Choi, J. & Fiegener, R. (2020). Seed storage: maintaining seed viability and vigor for restoration use. *Restoration Ecology*, **28**(**S3**): S249–S255.

Díez, I., Muguerza, N., Santolaria, A., Ganzedo, U. & Gorostiaga, J.M. (2012). Seaweed assemblage changes in the eastern Cantabrian Sea and their potential relationship to climate change. *Estuarine, Coastal and Shelf Science*, **99**: 108–120.

Dittami, S.M., Duboscq-Bidot, L., Perennou, M., Gobet, A., Corre, E., Boyen, C. & Tonon, T. (2016). Host–microbe interactions as a driver of acclimation to salinity gradients in brown algal cultures. *International Society For Microbial Ecology Journal*, **10**: 51–63.

Duarte, C.M., Bruhn, A. & Krause-Jensen, D. (2021). A seaweed aquaculture imperative to meet global sustainability targets. *Nature Sustainability*, **5**: 185–193.

Eger, A.M., Marzinelli, E.M., Beas-Luna, R., Blain, C.O., Blamey, L.K., Byrnes, J.E.K., Carnell, P.E. Choi, C.G., Hessing-Lewis, M., Kim, K.Y., Kumagai, N.H., Lorda, J., Moore, P., Nakamura, Y., Pérez-Matus, A., Pontier, O., Smale, D., Steinberg, P.D., & Vergés, A. (2023). The value of ecosystem services in global marine kelp forests. *Nature Communications*, **14**: 1894.

Enjalbert, J., Dawson, J.C., Paillard, S., Rhoné, B., Rousselle, Y., Thomas, M. & Goldringer, I. (2011). Dynamic management of crop diversity: from an experimental approach to on-farm conservation. *Comptes Rendus Biologies*, **334**: 458–468.

Falace, A., Kaleb, S., De La Fuente, G., Asnaghi, V. & Chiantore, M. (2018). Ex situ cultivation protocol for *Cystoseira amentacea* var. *stricta* (Fucales, Phaeophyceae) from a restoration perspective. Plos ONE, **13**: e0193011.

Feehan, C.J., Grace, S.P. & Narvaez, C.A. (2019). Ecological feedbacks stabilize a turf-dominated ecosystem at the southern extent of kelp forests in the Northwest Atlantic. *Scientific Reports*, **9**: 7078.

Filbee-Dexter, K. & Wernberg, T. (2018). Rise of turfs: a new battlefront for globally declining kelp forests. *Bioscience*, **68**: 64–76.

Filbee-Dexter, K., Wernberg, T., Barreiro, R., Coleman, M. A., de Bettignies, T., Feehan, C.J., Franco, J.N., Hasler, B., Louro, I., Norderhaug, K.M., Staehr, P.A.U., Tuya, F. & Verbeek, J. (2022). Leveraging the blue economy to transform marine forest restoration. *Journal of Phycology*, **58**: 198–207.

Filbee-Dexter, K., Wernberg, T., Grace, S.P., Thormar, J., Fredriksen, S., Narvaez, C.N., Feehan, C.J. & Norderhaug, K.M. (2020). Marine heatwaves and the collapse of marginal North Atlantic kelp forests. *Scientific Reports*, **10**: 13388.

Fowler, C. (2016). *Seeds On Ice: Svalbard and the Global Seed Vault*. Easton Studio Press, Westport CT.

Føyn, B. (1958). Über die Sexualität und den Generationswechsel von *Ulva mutabilis*. *Archiv Für Protistenkunde*, **102**: 473–480.

Fricke, A., Capuzzo, E., Bermejo, R., Hofmann, L.C., Hernández, I., Pereira, R., Van den Burg, S.W.K., Pereira, T., Buschmann, A.H. & Cottier-Cook, E.J. (2024). Ecosystem Services provided by seaweed cultivation: state of the art, knowledge gaps, constraints and future needs for achieving maximum potential in Europe. *Reviews in Fisheries Science and Aquaculture*, **32**: 238–256.

Gachon, C.M., Sime-Ngando, T., Strittmatter, M., Chambouvet, A. & Kim, G.H. (2010). Algal diseases: spotlight on a black box. *Trends in Plant Science*, **15**: 633–640.

Gauci, C., Bartsch, I., Martins, N. & Liesner, D. (2022). Cold thermal priming of *Laminaria digitata* (Laminariales, Phaeophyceae) gametophytes enhances gametogenesis and thermal performance of sporophytes. *Frontiers In Marine Science*, **9**: 862923.

Gauci, C., Jueterbock, A., Khatei, A., Hoarau, G. & Bartsch, I. (2024). Thermal priming of *Saccharina latissima*, a promising strategy to improve seaweed production and restoration in future climates. *Marine Ecology Progress Series*, **745**: 59–71.

Ghaderiardakani, F., Coates, J.C. & Wichard, T. (2017). Bacteria-induced morphogenesis of *Ulva intestinalis* and *Ulva mutabilis* (Chlorophyta): a contribution to the lottery theory. *FEMS Microbiology Ecology*, **93**(**8**): fix094.

Ghaderiardakani, F., Ulrich, J.F., Barth, E., Quartino, M.L. & Wichard, T. (2024). Algal growth and morphogenesis-promoting factors released by cold-adapted bacteria contribute to the resilience and morphogenesis of the seaweed ulva (Chlorophyta) in Antarctica (Potter Cove). *Journal of Plant Growth Regulation*. doi:10.1007/s00344-024-11507-4

Gran, A., Movilla, J., Ballesteros, E., Sales, M., Bolado, I., Galobart, C. & Cefalì, M.E. (2022). Assessing the expansion and success of a restored population of *Gongolaria barbata* (Stackhouse) Kuntze (Fucales, Phaeophyceae) using high-precision positioning tools and size distribution frequencies. *Mediterranean Marine Science*, **23**: 907–916.

Grueneberg, J., Engelen, A.H., Costa, R. & Wichard, T. (2016). Macroalgal morphogenesis induced by waterborne compounds and bacteria in coastal seawater. PLOS ONE, **11**: e0146307.

Guidetti, P., Terlizzi, A. & Boero, F. (2004). Effects of the edible sea urchin, *Paracentrotus lividus*, fishery along the Apulian rocky coast (SE Italy, Mediterranean Sea). *Fisheries Research*, **66**: 287–297.

Guzinski, J., Ballenghien, M., Daguin-Thiébaut, C., Lévêque, L. & Viard, F. (2018). Population genomics of the introduced and cultivated Pacific kelp *Undaria pinnatifida*: marinas-not farms-drive regional connectivity and establishment in natural rocky reefs. *Evolutionary Applications*, **11**: 1582–1597.

Hampe, A. & Petit, R.J. (2005). Conserving biodiversity under climate change: the rear edge matters. Ecology Letters, **8**: 461–467.

Henry, J., Pontis, C., David, J. & Gouyon, P. (1991). An Experiment On Dynamic Conservation of Genetic Resources With Metapopulations. In *Species Conservation: A Population-Biological Approach* (Seitz, A. & Loeschcke, V., eds.), 185–198. Springer, Basel.

Hu, S., Zou, D., He, Q., Shi, X. & Liu, L. (2022). Evaluation for values of ecosystem service functions of cultivated seaweeds in Guangdong Province, China. Algal Research, **63**: 102657.

Huanel, O.R., Quesada-Calderón, S., Ríos Molina, C., Morales-González, S., Saenz-Agudelo, P., Nelson, W.A., Arakaki, N. N., Mauger, S., Faugeron, S., & Guillemin, M.-L. (2022). Pre-domestication bottlenecks of the cultivated seaweed *Gracilaria chilensis*. Molecular Ecology, **31**: 5506–5523.

Hwang, E.K. & Park, C.S. (2020). Seaweed cultivation and utilization of Korea. *Algae*, **35**: 107–121.

Hynes, S., Chen, W., Vondolia, K., Armstrong, C. & O'Connor, E. (2021). Valuing the ecosystem service benefits from kelp forest restoration: a choice experiment from Norway. *Ecological Economics*, **179**: 106833.

IPBES. (2019). The global assessment report of the intergovernmental science-policy platform on biodiversity and ecosystem services. In *IPBES secretariat, Bonn, Germany* (Brondizio E.S. Settele J. Díaz S. & Ngo H.T., eds.), 1148. https://doi.org/10.5281/zenodo.3831673

Juanes, J.A., Guinda, X., Puente, A. & Revilla, J.A. (2008). Macroalgae, a suitable indicator of the ecological status of coastal rocky communities in the NE Atlantic. *Ecological Indicators*, **8**: 351–359.

Jueterbock, A., Minne, A.J.P., Cock, J.M., Coleman, M.A., Wernberg, T., Scheschonk, L., Rautenberger, R. R., Zhang, J., & Hu, Z.-M. (2021). Priming of marine macrophytes for enhanced restoration success and food security in future oceans. *Frontiers In Marine Science*, **8**: 658485.

Kim, J.K., Yarish, C., Hwang, E.K., Park, M. & Kim, Y. (2017). Seaweed aquaculture: cultivation technologies, challenges and its ecosystem services. *Algae*, **32**: 1–13.

Kinley, R.D., De Nys, R., Vucko, M.J., Machado, L. & Tomkins, N.W. (2016). The red macroalgae *Asparagopsis taxiformis* is a potent natural antimethanogenic that reduces methane production during in vitro fermentation with rumen fluid. *Animal Production Science*, **56**: 282.

Kinley, R.D., Martinez-Fernandez, G., Matthews, M.K., De Nys, R., Magnusson, M. & Tomkins, N.W. (2020). Mitigating the carbon footprint and improving productivity of ruminant livestock agriculture using a red seaweed. *Journal of Cleaner Production*, **259**: 120836.

Kishimoto, I., Ariga, I., Itabashi, Y. & Mikami, K. (2019). Heat-stress memory is responsible for acquired thermotolerance in *Bangia fuscopurpurea*. *Journal of Phycology*, **55**: 971–975.

Kumar, P., Kumar, R., Thakur, K., Mahajan, D., Brar, B., Sharma, D., Kumar, S. Sharma, A. K. (2023). Impact of pesticides application on aquatic ecosystem and biodiversity: a Review. *Biology Bulletin*, **50**: 1362–1375.

Layton, C., Coleman, M.A., Marzinelli, E.M., Steinberg, P. D., Swearer, S.E., Vergés, A., Wernberg, T. & Johnson, C.R. (2020). Kelp forest restoration in Australia. *Frontiers In Marine Science*, **7**: 74.

Lee, Y.N. & Nam, K.W. (2016). Cryopreservation of gametophytic thalli of *Ulva prolifera* (Ulvales, Chlorophyta) from Korea. *Journal of Applied Phycology*, **28**: 1207–1213.

Li, J., Weinberger, F., De Nys, R., Thomas, T. & Egan, S. (2023). A pathway to improve seaweed aquaculture through microbiota manipulation. *Trends in Biotechnology*, **41**: 545–556.

Li, R. & Brawley, S.H. (2004). Improved survival under heat stress in intertidal embryos (*Fucus* spp.) simultaneously exposed to hypersalinity and the effect of parental thermal history. *Marine Biology*, **144**: 205–213.

Li, X., Zhang, Z., Qu, S., Liang, G., Zhao, N., Sun, J., Song, S. Cao, Z.M., Li, X., & Pan, J. (2016). Breeding of an intraspecific kelp hybrid Dongfang no. 6 (*Saccharina japonica*, Phaeophyceae, Laminariales) for suitable processing products and evaluation of its culture performance. *Journal of Applied Phycology*, **28**: 439–447.

Liesner, D., Fouqueau, L., Valero, M. Roleda, M.Y., Pearson, G.A., Bischof, K., Valentin, K., & Bartsch, I. (2020). Heat stress responses and population genetics of the kelp *Laminaria digitata* (Phaeophyceae) across latitudes reveal differentiation among North Atlantic populations. *Ecology and Evolution*, **10**: 9144–9177.

Liu, H., Able, A.J. & Able, J.A. (2022). Priming crops for the future: rewiring stress memory. *Trends In Plant Science*, **27**: 699–716.

Lüning, K. (1990). *Seaweeds: Their Environment, Biogeography, and Ecophysiology* John Wiley & Sons, New York.

Martínez, B., Arenas, F., Trilla, A., Viejo, R.M. & Carreño, F. (2015). Combining physiological threshold knowledge to species distribution models is key to improving forecasts of the future niche for macroalgae. *Global Change Biology*, **21**: 1422–1433.

Martins, N., Pearson, G.A., Bernard, J., Serrão, E.A. & Bartsch, I. (2020). Thermal traits for reproduction and recruitment differ between Arctic and Atlantic kelp *Laminaria digitata*. PLOS ONE, **15**: e0235388.

Marzinelli, E.M., Williams, S.B., Babcock, R.C., Barrett, N. S., Johnson, C.R., Jordan, A., Kendrick, G.A. Pizarro, O. R., Smale, D.A., & Steinberg, P.D. (2015). Large-Scale geographic variation in distribution and abundance of Australian deep-water kelp forests. *PLOS ONE*, **10**: e0118390.

Mineur, F., Arenas, F., Assis, J., Davies, A.J., Engelen, A.H., Fernandes, F., Malta, E. E.-J., Thibaut, T., Nguyen Van, 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.

Monteiro, J.R.B., Rodrigues, R.P., Mazzuco, A.C., de Cassia Ribeiro Gonçalves, R., Bernardino, A.F., Kuster, R.M. & Kitagawa, R.R. (2023). In vitro and in silico evaluation of red algae *Laurencia obtusa* anticancer activity. *Marine Drugs*, **21**: 318.

Morris, M.M., Haggerty, J.M., Papudeshi, B.N., Vega, A.A., Edwards, M.S. & Dinsdale, E.A. (2016). Nearshore pelagic microbial community abundance affects recruitment success of giant kelp, *Macrocystis pyrifera*. *Frontiers In Microbiology*, **7**: 1800.

Moy, F.E. & Christie, H. (2012). Large-scale shift from sugar kelp (*Saccharina latissima*) to ephemeral algae along the south and west coast of Norway. *Marine Biology Research*, **8**: 309–321.

Murúa, P., Garvetto, A., Egan, S. & Gachon, C.M.M. (2023). The reemergence of phycopathology: when algal biology meets ecology and biosecurity. *Annual Review of Phytopathology*, **61**: 231-255.

Neiva, J., Assis, J., Coelho, N.C., Fernandes, F., Pearson, G. A. & Serrão, E.A. (2015). Genes left behind: climate change threatens cryptic genetic diversity in the canopy-forming seaweed *Bifurcaria bifurcata*. *PLOS ONE*, **10**: e0131530.

Neiva, J., Assis, J., Fernandes, F., Pearson, G.A. & Serrão, E. A. (2014). Species distribution models and mitochondrial DNA phylogeography suggest an extensive biogeographical shift in the high-intertidal seaweed *Pelvetia canaliculata*. *Journal of Biogeography*, **41**: 1137–1148.

Neiva, J., Paulino, C., Nielsen, M.M., Krause-Jensen, D., Saunders, G.W., Assis, J., Bárbara, I. Tamigneaux, É., Gouveia, L., Aires, T., Marbà, N., Bruhn, A., Pearson, G.A., & Serrão, E.A. (2018). Glacial vicariance drives phylogeographic diversification in the amphi-boreal kelp *Saccharina latissima*. *Scientific Reports*, **8**: 1112.

Neiva, J., Pearson, G.A., Valero, M. & Serrão, E.A. (2010). Surfing the wave on a borrowed board: range expansion and spread of introgressed organellar genomes in the seaweed *Fucus ceranoides* L. *Molecular Ecology*, **19**: 4812–4822.

Neiva, J., Pearson, G.A., Valero, M. & Serrão, E.A. (2012). Drifting fronds and drifting alleles: range dynamics, local dispersal and habitat isolation shape the population structure of the estuarine seaweed *Fucus ceranoides*. *Journal of Biogeography*, **39**: 1167–1178.

Neiva, J., Serrão, E.A., Paulino, C., Gouveia, L., Want, A., Tamigneaux, É., Ballenghien, M. Mauger, S., Fouqueau, L., Engel-Gautier, C., Destombe, C., & Valero, M. (2020). Genetic structure of amphi-Atlantic *Laminaria digitata* (Laminariales, Phaeophyceae) reveals a unique range-edge gene pool and suggests post-glacial colonization of the NW Atlantic. *European Journal of Phycology*, **55**: 517–528.

Nicastro, K.R., Zardi, G.I., Teixeira, S., Neiva, J., Serrão, E. A. & Pearson, G.A. (2013). Shift happens: trailing edge contraction associated with recent warming trends threatens a distinct genetic lineage in the marine macroalga *Fucus vesiculosus*. *BMC Biology*, **11**: 6.

Normah, M., Chin, H.F. & Reed, B.M. (2013). *Conservation of Tropical Plant Species*. Springer, New York.

OECD. (2007). *OECD Best Practice Guidelines For Biological Resource Centres* OECD Publishing, Paris.

Oertel, W., Wichard, T. & Weissgerber, A. (2015). Transformation of *Ulva mutabilis* (Chlorophyta) by vector plasmids integrating into the genome. *Journal of Phycology*, **51**: 963–979.

Orfanidis, S., Panayotidis, P. & Stamatis, N. (2003). An insight to the ecological evaluation index (EEI). *Ecological Indicators*, **3**: 27–33.

Orfanidis, S., Rindi, F., Cebrian, E., Fraschetti, S., Nasto, I., Taskin, E., Bianchelli, S. & Pinedo, S. (2021). Effects of natural and anthropogenic stressors on Fucalean brown seaweeds across different spatial scales in the Mediterranean Sea. *Frontiers in Marine Science*, **8**: 658417.

Orth, R. & McGlathery, K. (2012). Eelgrass recovery in the coastal bays of the Virginia Coast Reserve, USA. *Marine Ecology Progress Series*, **448**: 173–176.

Pinedo, S., Zabala, M. & Ballesteros, E. (2013). Long-term changes in sublittoral macroalgal assemblages related to water quality improvement. *Botanica Marina*, **56**: 461–469.

Piñeiro-Corbeira, C., Barreiro, R. & Cremades, J. (2016). Decadal changes in the distribution of common intertidal seaweeds in Galicia (NW Iberia). *Marine Environmental Research*, **113**: 106–115.

Provasoli, L. (1968). Media and prospects for the cultivation of marine algae. *Proceedings of the US-Japan Conference*, 12-15 September 1966, Hakone, 63-75.

Ramus, A.P., Silliman, B.R., Thomsen, M.S. & Long, Z.T. (2017) An invasive foundation species enhances multifunctionality in a coastal ecosystem. *Proceedings of the National Academy of Sciences*, **114**: 8580–8585.

Reynes, L., Fouqueau, L., Aurelle, D., Mauger, S., Destombe, C. & Valero, M. (2024). Temporal genomics help in deciphering neutral and adaptive patterns in the contemporary evolution of kelp populations. *Journal of Evolutionary Biology*, **37**: 677–692.

Rilov, G., Peleg, O., Guy-Haim, T. & Yeruham, E. (2020). Community dynamics and ecological shifts on Mediterranean vermetid reefs. *Marine Environmental Research*, **160**: 105045.

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**: 2275–2295.

Rogers-Bennett, L. & Catton, C.A. (2019). Marine heat wave and multiple stressors tip bull kelp forest to sea urchin barrens. *Scientific Reports*, **9**: 15050.

Roque, B.M., Brooke, C.G., Ladau, J., Polley, T., Marsh, L.J., Najafi, N., Pandey, P. Singh, L., Kinley, R., Salwen, J.K., Eloe-Fadrosh, E., Kebreab, E., & Hess, M. (2019). Effect of the macroalgae *Asparagopsis taxiformis* on methane production and rumen microbiome assemblage. *Animal Microbiome*, **1**: 3.

Rorrer, G.L. & Cheney, D.P. (2004). Bioprocess engineering of cell and tissue cultures for marine seaweeds. *Aquacultural Engineering*, **32**: 11–41.

Rorrer, G.L., Gerwick, W.H. & Cheney, D.P. (1998). Production of Bioactive Compounds By Cell and Tissue Cultures of Marine Seaweeds In Bioreactor System. In *New Developments in Marine Biotechnology* (Gal, Y.L. & Halvorson, H.O., eds.), 65–67. Springer, Boston.

Saada, G., Nicastro, K.R., Jacinto, R., McQuaid, C.D., Serrão, E.A., Pearson, G.A. & Zardi, G.I. (2016). Taking the heat: distinct vulnerability to thermal stress of central and threatened peripheral lineages of a marine macroalga. *Diversity and Distributions*, **22**: 1060–1068.

Sala, E., Ballesteros, E., Dendrinos, P., Di Franco, A., Ferretti, F., Foley, D., Fraschetti, S. Friedlander, A., Garrabou, J., Güçlüsoy, H., Guidetti, P., Halpern, B.S., Hereu, B., Karamanlidis, A.A., Kizilkaya, Z., Macpherson, E., Mangialajo, L., Mariani, S., Micheli, F., Mourier, J., Planes, S., Rilov, G., & Zabala, M. (2012). The structure of Mediterranean rocky reef ecosystems across environmental and human gradients, and conservation implications. *PLOS ONE*, **7**: e32742.

Schiel, D.R., Steinbeck, J.R. & Foster, M.S. (2004). Ten years of induced ocean warming causes comprehensive changes in marine benthic communities. *Ecology*, **85**: 1833–1839.

Schimpf, N.M., Liesner, D., Franke, K., Roleda, M.Y. & Bartsch, I. (2022). Microscopic stages of North Atlantic *Laminaria digitata* (Phaeophyceae) exhibit trait-dependent thermal adaptation along latitudes. *Frontiers In Marine Science*, **9**: 870792.

Schoenrock, K.M., O'Callaghan, R., O'Callaghan, T., O'Connor, A. & Stengel, D.B. (2021). An ecological baseline for *Laminaria hyperborea* forests in western Ireland. *Limnology and Oceanography*, **66**: 3439–3454.

Simon, C., Fort, A. & Sulpice, R. (2024). Cryopreservation of vegetative thalli of *Ulva* species. *Journal of Applied Phycology*, **36**: 3011–3016.

Smale, D.A. (2020). Impacts of ocean warming on kelp forest ecosystems. *New Phytologist*, **225**: 1447–1454.

Smith, D. (2009). Culture collections and biological resource centres (Brcs). In *Encyclopedia of industrial biotechnology: bioprocess, bioseparation, and cell technology*, and Flickinger, M.C., editor), 1–42. Wiley Online Library.

Spalding, M.D., Fox, H.E., Allen, G.R., Davidson, N., Ferdaña, Z.A., Finlayson, M., Halpern, B.S. Jorge, M.A., Lombana, A., Lourie, S.A., Martin, K.D., McManus, E., Molnar, J., Recchia, C.A., & Robertson, J. (2007). Marine ecoregions of the world: a bioregionalization of coastal and shelf areas. *Bioscience*, **57**: 573–583.

Spoerner, M., Wichard, T., Bachhuber, T., Stratmann, J. & Oertel, W. (2012). Growth and thallus morphogenesis of *Ulva mutabilis* (Chlorophyta) depends on a combination of two bacterial species excreting regulatory factors. *Journal of Phycology*, **48**: 1433–1447.

The State of World Fisheries and Aquaculture (2022). FAO. http://www.fao.org/documents/card/en/c/cc0461en (Accessed 5 April 2024).

Steinhagen, S., Barco, A., Wichard, T. & Weinberger, F. (2019b). Conspecificity of the model organism *Ulva mutabilis* and *Ulva compressa* (Ulvophyceae, Chlorophyta). *Journal of Phycology*, **55**: 25–36.

Steinhagen, S., Weinberger, F. & Karez, R. (2019a). Molecular analysis of *Ulva compressa* (Chlorophyta, Ulvales) reveals its morphological plasticity, distribution and potential invasiveness on German North Sea and Baltic Sea coasts. *European Journal of Phycology*, **54**: 102–114.

Steneck, R.S., Graham, M.H., Bourque, B.J., Corbett, D., Erlandson, J.M., Estes, J.A. & Tegner, M.J. (2002). Kelp forest ecosystems: biodiversity, stability, resilience and future. *Environmental Conservation*, **29**: 436–459.

Stiger-Pouvreau, V. & Guerard, F. (2018). Bio-inspired molecules extracted from marine macroalgae: a new generation of active ingredients for cosmetics and human health. In *Blue biotechnology: production and use of marine molecules* (La Barre, S. & Bates, S.S., eds.), 709–746. Wiley VCH, Hoboken, New Jersey.

Strain, E.M.A., Thomson, R.J., Micheli, F., Mancuso, F.P. & Airoldi, L. (2014). Identifying the interacting roles of stressors in driving the global loss of canopy-forming to mat-forming algae in marine ecosystems. *Global Change Biology*, **20**: 3300–3312.

Strasser, F.-E., Barreto, L.M., Kaidi, S., Sabour, B., Serrão, E.A., Pearson, G.A. & Martins, N. (2022). Population level variation in reproductive development and output in the golden kelp *Laminaria ochroleuca* under marine heat wave scenarios. *Frontiers In Marine Science*, **9**: 943511.

Stratmann, J., Paputsoglu, G. & Oertel, W. (1996). Differentiation of *Ulva mutabilis* (Chlorophyta) gametangia and gamete release are controlled by extracellular inhibitors. *Journal of Phycology*, **32**: 1009–1021.

Streftaris, N. & Zenetos, A. (2006). Alien marine species in the Mediterranean - the 100 'worst invasives' and their impact. *Mediterranean Marine Science*, **7**: 87-118.

Strittmatter, M., Murúa, P., Arce, P., Perrineau, -M.-M. & Gachon, C. (2022). My seaweed looks weird: a community web portal to accelerate pathogen discovery in seaweeds. *Applied Phycology*, **3**: 300–305.

Teagle, H., Hawkins, S.J., Moore, P.J. & Smale, D.A. (2017). The role of kelp species as biogenic habitat formers in coastal marine ecosystems. *Journal of Experimental Marine Biology and Ecology*, **492**: 81-98.

Theissinger, K., Fernandes, C., Formenti, G., Bista, I., Berg, P.R., Bleidorn, C., Bombarely, A. Crottini, A., Gallo, G.R., Godoy, J.A., Jentoft, S., Malukiewicz, J., Mouton, A., Oomen, R.A., Paez, S., Palsbøll, P.J., Pampoulie, C., Ruiz-López, M.J., Secomandi, S., Svardal, H., Theofanopoulou, C., de Vries, J., Waldvogel, A.-M., Zhang, G., Jarvis, E.D., Bálint, M., Kratochwil, C., Primmer, C., Ciofi, C., Waterhouse, R. M., Mazzoni, C.J., Höglund, J., & the European Reference Genome Atlas (ERGA) Consortium. (2023). How genomics can help biodiversity conservation. *Trends In Genetics*, **39**: 545–559.

Thibaut, T., Pinedo, S., Torras, X. & Ballesteros, E. (2005). Long-term decline of the populations of Fucales (*Cystoseira* spp. and *Sargassum* spp.) in the Albères coast (France, North-western Mediterranean). *Marine Pollution Bulletin*, **50**: 1472–1489.

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. (2016). Abundance and diversity of crypto- and necto-benthic coastal fish are higher in marine forests than in structurally less complex macroalgal assemblages. *PLOS ONE*, **11**: e0164121.

Tuya, F., Schubert, N., Aguirre, J., Basso, D., Bastos, E.O., Berchez, F., Bernardino, A.F., Bosch, N.E., Burdett, H.L., Espino, F., Fernández-Gárcia, C., Francini-Filho, R.B., Gagnon, P., Hall-Spencer, J.M., Haroun, R., Hofmann, L.C., Horta, P.A., Kamenos, N.A., le Gall, L. & Tâmega, F.T.S. (2023). Levelling-up rhodolith-bed science to address global-scale conservation challenges. *Science of the Total Environment*, **892**: 164818.

Umanzor, S., Li, Y., Bailey, D., Augyte, S., Huang, M., Marty-Rivera, M., Jannink, J. Yarish, C., & Lindell, S. (2021). Comparative analysis of morphometric traits of farmed sugar kelp and skinny kelp, *Saccharina* spp. strains from the Northwest Atlantic. *Journal of the World Aquaculture Society*, **52**: 1059–1068.

Valero, M., Engel, C., Billot, C., Kloareg, B. & Destombe, C. (2001). Concept and issues of population genetics in seaweeds. *Cahiers De Biologie Marine*, **42**: 53–62.

Vallet, M., Strittmatter, M., Murúa, P., Lacoste, S., Dupont, J., Hubas, C., Genta-Jouve, G. Gachon, C.M. M., Kim, G.H., & Prado, S. (2018). Chemically-mediated interactions between macroalgae, their fungal endophytes, and protistan pathogens. *Frontiers in Microbiology*, **9**: 3161.

Van Der Loos, L.M., D'hondt, S., Willems, A. & De Clerck, O. (2021). Characterizing algal microbiomes using long-read nanopore sequencing. *Algal Research*, **59**: 102456.

Vazquez, C.F. & Sanchez, L.J. (2022). *An Overview of the Algae Industry in Europe* Publications Office of the European Union, Luxembourg.

Verdura, J., Santamaría, J., Ballesteros, E., Smale, D.A., Cefalì, M.E., Golo, R., De Caralt, S. Vergés, A., & Cebrian, E. (2021). Local-scale climatic refugia offer sanctuary for a habitat-forming species during a marine heatwave. *Journal of Ecology*, **109**: 1758–1773.

Verlaque, M., Boudouresque, C.-F. & Perret-Boudouresque, M. (2019). Mediterranean seaweeds listed as threatened under the Barcelona Convention: a critical analysis. *Scientific Reports of Port-Cros National Park*, **33**: 179–214.

Viaroli, P., Bartoli, M., Giordani, G., Naldi, M., Orfanidis, S. & Zaldivar, J.M. (2008). Community shifts, alternative stable states, biogeochemical controls and feedbacks in eutrophic coastal lagoons: a brief overview. *Aquatic Conservation: Marine and Freshwater Ecosystems*, **18**: S105–S11.

Vincent, A., Stanley, A. & Ring, J. (2020) Hidden champion of the ocean: seaweed as a growth engine for a sustainable European future. Seaweed for Europe. https://www.seaweedeurope.com/wp-content/uploads/2020/10/Seaweed_for_Europe-Hidden_Champion_of_the_ocean-Report.pdf (Accessed 25 April 2024).

Visch, W., Rad-Menéndez, C., Nylund, G.M., Pavia, H., Ryan, M.J. & Day, J. (2019). Underpinning the development of seaweed biotechnology: cryopreservation of brown algae (*Saccharina latissima*) gametophytes. *Biopreservation and Biobanking*, **17**: 378–386.

Voerman, S.E., Llera, E. & Rico, J.M. (2013). Climate driven changes in subtidal kelp forest communities in NW Spain. *Marine Environmental Research*, **90**: 119–127.

Wade, R., Augyte, S., Harden, M., Nuzhdin, S., Yarish, C. & Alberto, F. (2020). Macroalgal germplasm banking for conservation, food security, and industry. *PLOS Biology*, **18**: e3000641.

Waltham, N.J., Elliott, M., Lee, S.Y., Lovelock, C., Duarte, C.M., Buelow, C., Simenstad, C. *et al.* (2020). UN decade on ecosystem restoration 2021–2030—What chance for success in restoring coastal ecosystems? *Frontiers in Marine Science*, **7**: 71.

Ward, G.M., Faisan, J.P., Cottier-Cook, E.J., Gachon, C., Hurtado, A.Q., Lim, P.E., Matoju, I. *et al.* (2020). A review of reported seaweed diseases and pests in aquaculture in Asia. *Journal of the World Aquaculture Society*, **51**: 815–828.

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**: 151–161.

Wernberg, T., Bennett, S., Babcock, R.C., De Bettignies, T., Cure, K., Depczynski, M., Dufois, F. Fromont, J., Fulton, C. J., Hovey, R. K., Harvey, E. S., Holmes, T. H., Kendrick, G. A., Radford, B., Santana-Garcon, J., Saunders, B. J., Smale, D. A., Thomsen, M. S., Tuckett, C. A., Tuya, F., Vanderklift, M. A., & Wilson, S. K. (2016). Climate-driven regime shift of a temperate marine ecosystem. *Science*, **353**: 169–172.

Wichard, T. (2015). Exploring bacteria-induced growth and morphogenesis in the green macroalga order Ulvales (Chlorophyta). *Frontiers In Plant Science*, **6**: 86.

Wichard, T. & Oertel, W. (2010). Gametogenesis and gamete release of *Ulva mutabilis* and *Ulva lactuca* (Chlorophyta): regulatory effects and chemical characterization of the "swarming inhibitor". *Journal of Phycology*, **46**: 248–259.

Wood, G., Marzinelli, E.M., Coleman, M.A., Campbell, A. H., Santini, N.S., Kajlich, L., Verdura, J. Wodak, J., Steinberg, P. D., & Vergés, A. (2019). Restoring subtidal marine macrophytes in the Anthropocene: trajectories and future-proofing. *Marine and Freshwater Research*, **70**: 936–951.

Yang, H., Huo, Y., Yee, J.C. & Yarish, C. (2021). Germplasm cryopreservation of macroalgae for aquaculture breeding and natural resource conservation: a review. *Aquaculture*, **544**: 737037.

Zhang, J., Liu, Y., Yu, D., Song, H., Cui, J. & Liu, T. (2011). Study on high-temperature-resistant and high-yield *Laminaria* variety "Rongfu". *Journal of Applied Phycology*, **23**: 165–171.