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Habitat features and their influence on the restoration potential of marine habitats in Europe

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

Author contribution statement

As part of the MERCES WP1 work, an expert group selected the marine habitats and features to be included in this paper. TB, NP and CS lead the focus workshop of experts. TB, CG, CL, NP, CS, TM, DF, KG, SF, CM, EB and EC were all part of this process and earlier analyses. At a later stage, more people were added to the expert group in order to ensure expertise on all habitats and regions, and to support the new analyses. ER, GA, CF and HG were included in the work on the kelp forests, CB on seagrass meadows, MC-S, TM and MB on cold-water coral habitats, CC and SK on the coralligenous assemblages, RD and ER-L on deep-sea habitats and JK and HO on habitat ecology in general. TB, NP, DF, CM, ER, CB, MC-S and CL were responsible for the Table 3 "scoring", but all authors listed have contributed to the discussions and conclusions, and in writing of the manuscript.

Keywords

Degraded habitats, Restoration success, Recovery, seagrass, Kelp, macroalgae, Coralligenous assemblages, Cold-water Corals, coral reefs, Coral gardens

Abstract

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To understand the restoration potential of degraded habitats, it is important to know the key processes and habitat features that allow for recovery after disturbance. As part of the EU (Horizon 2020) funded MERCES project, a group of European experts compiled and assessed current knowledge, from both past and ongoing restoration efforts, within the Mediterranean Sea, the Baltic Sea, and the North-East Atlantic Ocean. The aim was to provide an expert judgement of how different habitat features could impact restoration success and enhance the recovery of marine habitats. A set of biological and ecological features (i.e. life-history traits, population connectivity, spatial distribution, structural complexity and the potential for regime shifts) were identified and scored according to their contribution to the successful accomplishment of habitat restoration for five habitats: seagrass meadows, kelp forests, Cystoseira macroalgal beds, coralligenous assemblages and cold-water coral habitats. The expert group concluded that most of the kelp forests features facilitate successful restoration, while the features for the coralligenous assemblages and the cold-water coral habitat did not promote successful restoration. For the other habitats the conclusions were much more variable. The lack of knowledge on the relationship between acting pressures and resulting changes in the ecological state of habitats is a major challenge for implementing restoration actions. This paper provides an overview of essential features that can affect restoration success in marine habitats of key importance for valuable ecosystem services

Contribution to the field

Human activities exert considerable pressure on ecosystems and resources through pollution, over-exploitation of resources, introduction of invasive species and habitat clearance and fragmentation. In an attempt to reverse the current level of degradation within European seas, the EU Biodiversity Strategy 2020 aims to restore at least 15% of degraded ecosystems by 2020. However, whilst marine restoration actions are common in many areas of the world, their success rate is highly variable. To understand the restoration potential of degraded habitats, it is important to know the key processes and habitat features that allow for recovery after disturbance. This paper provides an overview of the essential biological and ecological features for a range of marine habitats (ecosystem engineers) that can affect restoration success, highlighting the key factors for a successful restoration. Moreover, we provide some best practice guidelines to improve restoration success. Even though habitat restoration is much more complicated than that which has been discussed here, it is hoped that our discussions and recommendations will be useful when designing and executing future marine restoration.

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Habitat features and their influence on the restoration potential of marine habitats in Europe

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Keywords: degraded habitats, restoration success, recovery, seagrass, kelp, macroalgae, coralligenous assemblages, cold-water corals, coral reefs, coral gardens

Abstract

To understand the restoration potential of degraded habitats, it is important to know the key processes and habitat features that allow for recovery after disturbance. As part of the EU (Horizon 2020) funded MERCES project, a group of European experts compiled and assessed current knowledge, from both past and ongoing restoration efforts, within the Mediterranean Sea, the Baltic Sea, and the North-East Atlantic Ocean. The aim was to provide an expert judgement of how different habitat features could impact restoration success and enhance the recovery of marine habitats. A set of biological and ecological features (i.e. life-history traits, population connectivity, spatial distribution, structural complexity and the potential for regime shifts) were identified and scored according to their contribution to the successful accomplishment of habitat restoration for five habitats: seagrass meadows, kelp forests, *Cystoseira* macroalgal beds, coralligenous assemblages and cold-water coral habitats. The expert group concluded that most of the kelp forests features facilitate successful restoration, while the features for the coralligenous assemblages and the cold-water coral habitat did not promote successful restoration. For the other habitats the conclusions were much more variable. The lack of knowledge on the relationship between acting pressures and resulting changes in the ecological state of habitats is a major challenge for implementing restoration actions. This paper provides an overview of essential features that can affect restoration success in marine habitats of key importance for valuable ecosystem services.

1. Introduction: Degradation and restoration of habitats in European seas

For centuries humans have been reliant upon the ocean as a source of food, transport, and leisure. As resources become increasingly scarce and populations continue to grow, we are progressively turning to the coasts and oceans to drive the global economy and stimulate innovation and growth (EC 2018). The potential for economic opportunities in the coastal region is great, resulting in convergence of different activities, such as shipping, tourism and energy production, alongside traditional resource-based activities, such as coastal fisheries, seaweed harvesting, and aquaculture. There is now ample evidence that such opportunities come with significant environmental risk and costs (e.g. Halpern et al., 2015, Ramirez-Llodra et al. 2011). Human activities exert considerable pressure on ecosystems and resources through pollution, over-exploitation of resources, introduction of invasive species and habitat clearance and fragmentation (Dailianis et al. 2018, Gerovasileiou et al. 2019). Together, such activities are resulting in a decline in biodiversity, a reduction in the capacity of the oceans to provide ecosystem goods and services (Worm et al. 2006, EEA 2015) and increased vulnerability of marine ecosystems to additional pressures such as climate change and ocean-acidification stressors (Folke et al. 2004).

In an attempt to reverse the current level of degradation within European seas, the EU Biodiversity Strategy 2020 aims to restore at least 15% of degraded ecosystems by 2020, in accordance with the 2010 Aichi targets and the UN 2030 Agenda for Sustainable Development (A/RES/70/1). However, whilst marine restoration actions are common in many areas of the world, their success rate is highly variable. For instance, whilst 65% of tropical coral reef and salt marsh restoration projects successfully achieved their goals, seagrass restoration has had a success rate of only 38% (Bayraktarov et al. 2016, van Katwijk et al. 2016). Variation in restoration success stems from different sources, including the inherent biology and ecology of species, including their interactions (Kilminster et al. 2015) and how, where and when restoration is conducted (Montero-Serra et al. 2018a). This variation leads to uncertainty in terms of conservation outcomes and economics. Consequently, there is a need to develop robust methodologies to effectively restore habitats and deliver the full range of conservation and socioeconomic benefits that can be derived (Elliot et al. 2007).

Historically, research on restoration best practices and methods has mainly focused on terrestrial, rather than on marine ecosystems. Even though several of the basic principles developed in terrestrial systems can be used in the marine realm (van Dover et al. 2014, Da Ros et al. 2019), the knowledge on which factors are enhancing or limiting restoration success is very limited for the marine environment. The H2020 MERCES project (www.merces-project.eu) aims to enhance the European Union's capacity to restore degraded marine ecosystems and habitats and the ecosystem services they provide. As part of this effort, the present paper seeks to structure and discuss the existing knowledge amongst leading European experts on the restoration potential of some important marine habitats within Europe. The discussion includes the biological and ecological features that determine the habitats' sensitivity to human pressures and thereby modulate the success of restoration actions. This information will provide the basis for knowledge-based guidelines of how to advance marine ecosystem restoration and increase the political and management willingness to initiate restoration actions.

2. The approach

A total of 25 experts representing 11 European countries, from Norway and Finland in the north to Crete in Greece in the south, was part of a MERCES initiated workshop to discuss habitat restoration activities. The group had expertise on species biology and ecology, covering key habitats found within the Mediterranean Sea, the Baltic Sea, and the NE Atlantic Ocean. A set of focal habitats were selected (section 2.1), and the experts were asked to suggest and agree on a set of key biological and ecological features (section 2.2) that were important to the recovery of these habitats. Following this discussion, each feature was discussed in terms of their relevance to the recovery potential, in general and for each habitat separately. The agreed-on features and characteristics were based on knowledge from both past and ongoing restoration efforts, within the European seas. The aim was to provide a consensual judgement (a "scoring", section 2.2) on how different biological and ecological features impact restoration success and the recovery of habitats.

Throughout this paper, the term "restoration" refers to an intentional activity (i.e. active intervention or manipulation) that initiates or accelerates the recovery of an ecosystem with respect to its health, integrity, and sustainability (SER 2004). Active approaches, also referred to as assisted regeneration (McDonald et al. 2016), include seedling of spores, transplantation, the removal of grazers, etc. The recovery of the ecosystem is defined as the reinstatement of ecosystem attributes, such as composition, structure, and function, back to a level identified for a reference ecosystem (McDonald et al. 2016). We do not include passive restoration (natural re-generation), where restoration goals are achieved by allowing the ecosystem to recover once the source of disturbance has been removed.

2.1.Selection and description of the target habitats

The five marine habitats chosen for this paper were selected by the expert group at the workshop because they are considered to have highly ecological and economic important, are sensitive to human activities and are relevant in conservation. Different directives and list were used as guidance when making the agreed-on list of target habitats: EU Habitats Directive 92/43/EEC, OSPAR List of Threatened and/or Declining Species and Habitats, OSPAR 2008, HELCOM List of Threatened and/or Declining Species and biotopes/habitats in the Baltic Sea, HELCOM 2007, UNEP/MAP-SPA/RAC 2018 Annex II List of Endangered or threatened species. The selected habitats cover shallow and deep areas and soft and hard substrates in the Mediterranean Sea, the Baltic Sea and NE Atlantic Ocean (see Figure 1 for habitat examples).

Seagrass meadows are found on soft bottoms down to a maximum depth of 50 m (Duarte 1991a). Seagrasses are important ecosystem engineer, i.e. they create, modify and maintain habitats (Boström et al. 2014, Jahnke et al. 2016), and provide multiple ecosystem services through stabilizing sediments, sequestering carbon, filtering nutrients and providing food and shelter for invertebrates, fish and birds (Hemminga & Duarte 2000). Different human pressures are responsible for the decline of seagrasses in Europe (Airoldi & Beck 2007). Whilst seagrass loss has been accelerating through decades (Waycott et al. 2009), recent assessment demonstrates a more positive trend in Europe (de los Santos et al. 2019).

Kelp forests are found on rocky seabed down to a depth of about 30 m, with single individuals (i.e. not forests) growing even deeper. Kelps are habitat-forming species, providing food, shelter and habitat for many species (Christie et al. 2009, Leclerc et al. 2013). They play a major role in the carbon cycle (Krause-Jensen & Duarte 2016) and coastal protection, along with a long list of other ecosystem services (Gundersen et al. 2016). The kelp forest distribution is decreasing in many areas around the world (Filbee-Dexter & Wernberg 2018) but is also showing increasing trends in some parts (e.g. recovering in the Norwegian NE Atlantic, Araujo et al. 2016, Krumhansl et al. 2016).

Cystoseira macroalgal beds are found down to a maximum depth of 50 m. *Cystoseira* spp. are habitat-forming species found in rocky intertidal and subtidal coastal areas and are recognized as hot spots of biodiversity. They provide food and habitat to diverse assemblages of understory species and enhance coastal primary productivity (Ballesteros 1990, Ballesteros et al. 1998, Cheminée et al. 2013). Shallow beds (mainly down to 10 m depth) have a different community composition and different life history traits than deeper ones (10-50 m depth, Capdevila et al. 2016). The decline in *Cystoseira* over vast areas has been documented in many regions (Bianchi et al. 2014, Thibaut et al. 2015) and natural recovery has been recorded only occasionally (Perkol-Finkel & Airoldi 2010, Iveša et al. 2016)

Coralligenous assemblages can be found down to maximum depth of about 120 m (Laborel 1961). Coralligenous outcrops are mainly produced by the accumulation of calcareous encrusting algae. This habitat supports high biodiversity (approximately 10-20% of the Mediterranean species) and structural complexity (Ballesteros 2006), and the most abundant species are long-lived algae and sessile invertebrates with an important role as habitat-formers (Linares et al. 2007, Cerrano et al. 2010 Teixidó et al. 2011). Coralligenous assemblages have been lost or degraded in several areas across the Mediterranean Sea (Bevilacqua et al. 2018, Ingrosso et al. 2018).

Cold-water coral habitats are major ecosystem engineers in the deep sea, mostly occurring in the depth range of 200-1500 m where they can form large and extensive habitats, such as coral reefs formed mostly by *Scleractinia* species (stony corals) and coral gardens primarily composed by octocorals and black corals (Roberts 2009, Buhl-Mortensen & Buhl-Mortensen 2018). They create a complex three-dimensional habitat and support high levels of biodiversity, providing refuge, feeding opportunities, and spawning and nursery areas for a wide range of organisms (Buhl-Mortensen et al. 2010). Cold-water corals grow extremely slowly (a few to several mm per year) and can live for hundreds or thousands of years (e.g. Roberts et al. 2009, Watling et al. 2011, Carreiro-Silva et al. 2013). The limited knowledge on the distribution and extent of cold-water coral habitats makes it difficult to assess changes. Nevertheless, cold-water coral habitats have been defined as Vulnerable Marine Ecosystems (VMEs, FAO 2009) and international management and conservation policies (e.g. FAO, OSPAR) are expected to contribute to the recovery of impacted sites and the protection of the remaining pristine coral communities.

2.2. Selection of habitat features and assessment ("scoring") of the restoration potential

The recovery potential of habitats depends upon their resilience, which is strongly influenced by the biology and ecology of their component species. The expert group identified and agreed on the biological and ecological features of greatest relevance through discussion and by structuring information from literature reviews (Perkol-Finkel & Airoldi 2010, McDonald et al. 2016, Abelson et al. 2016a, b). This resulted in the selection of five features relevant to restoration success, namely: life-history traits, population connectivity, spatial distribution, structural complexity, and the potential for regime shifts. The features' general relevance to the recovery potential of habitats is described in Table 1.

By using the features, the expert group assessed the restoration potential of the selected habitats based on 1) evidence in the published literature, 2) experiences obtained from ongoing restoration projects and actions, and 3) expert knowledge of the habitats' or species' biology and ecology. The discussion ended up with agreed-on characteristics of the biological and ecological features for each habitat (Table 2). Based on these characteristics, each feature was given a score from 1 (low) to 5 (high), according to its potential contribution to the successful accomplishment of restoration for each of the habitats (Table 3). We chose five levels to ensure that enough variability could be included in the assessment to distinguish restoration potential amongst habitats, but that did not have too many levels that would hide emerging patterns. This number of levels have also been considered suitable for defining conservation status of habitats and species (from favourable to unknown under the EU Habitats Directive) and ecosystem health status of marine waters (from high to bad under the Water Framework Directive). When a feature may lead to both restoration failure and success, the scoring was given as a range or a set of values, rather than one single score. As shallow *Cystoseira* beds have a different community and different life history traits than deeper beds, these communities were scored separately.

3. The assessment of the habitat features and the resulting "scoring"

The characteristics of the biological and ecological features relevant for assessing the recovery potential is described in Section 3.1-3.5 and summed up in Table 2. Table 2 provides the information needed for the agreed-on scoring in Table 3, in which the features of the different habitats are considered according to their contribution to successful restoration.

3.1.Seagrass meadows

As life-history traits of seagrass may lead to restoration failure or success, depending on the species in question, it is difficult to assess this feature`s importance for habitat restoration in general (Kilminster et al. 2015). For example, *Posidonia oceanica* is a slow-growing species (Duarte 1991) forming enduring meadows (Kilminster et al. 2015), while *Cymodocea nodosa* and *Zostera marina* exhibit faster clonal growth (Olesen and Sand-Jensen 1993, Cancemi et al. 2002) forming more transient meadows (Kilminster et al. 2015). As slow-growing species will need more time to recover than fast-growing species (Montero-Serra et al. 2018a), the time scale needed for recovery should be assessed carefully depending on the species in question. In general, populations with high connectivity (dispersal and gene flow) have higher genetic diversity, which makes them more resilient to environmental perturbations (Reusch et al. 2005, Jahnke et al. 2018). However, especially at the extreme ends of the geographical range of eelgrass, clonal growth dominates, creating vulnerable and isolated populations with limited connectivity (Olsen et al. 2004). Several species may spread both asexual (clonal) and through seed production (McMahon et al. 2014). Thus, different geographical regions and species naturally possess different capacities for local and large-scale dispersal (gene flow), from less than 15 m to up to 1000 km (Orth et al. 1994, Källström et al. 2008, Jahnke et al. 2018). The distribution of the species is also crucial, as a wide spatial distribution implies easier access to donor populations during restoration, which increases the probability of recovery success. In general, large-scale planting has been identified as an important method for increasing restoration success (van Katwijk et al. 2016).

Seagrass meadows are extremely vulnerable to anthropogenic pressures, such as habitat destruction, eutrophication, pollution, and climate change (Orth et al. 2006). It is important that pressures, such as eutrophication (which limits light availability and growth, Burkholder et al. 2007, Moksnes et al. 2018) and habitat destruction (Erftemeijer & Lewis 2006), are removed and appropriate sediment conditions are re-established, as sediment conditions tend to become unsuitable for re-establishment following seagrass loss (de Boer 2007, Carr et al. 2016, Moksnes et al. 2018). Seagrass meadows are prone to regime shifts (Maxwell et al. 2016, Moksnes 2018), characterised by a transition into an algal dominated or a barren state. Understanding drivers, interactions and thresholds in these regime shifts is crucial before any restoration action can take place.

After restoration action has taken place, seagrass meadows should be sustained in the long-term through positive feedback mechanisms (Suykerbuyk et al. 2016, Maxwell et al. 2017). As part of restoration it is therefore important to ensure (and possibility reintroduce) healthy populations of associated species, especially top predators, which can control algal (over)growth through trophic cascades (Jahnke et al. 2018, Moksnes et al. 2008, 2018).

3.2.Kelp forests

All of the selected features associated with kelp forests promote successful restoration. Fertile kelp produces a high number of propagules that can be dispersed for several days with coastal currents (Reed et al. 1992, Andersen 2013b), and the release is relatively synchronous among populations (Andersen et al. 2011). Connectivity between kelp populations is reinforced by reproductive synchrony because higher abundance of spores in the currents increases the probability of long-distance dispersal (Reed et al. 1997), which also facilitates recovery. Kelp colonizes hard substrate such as bedrock, boulders, and rocks, forming forests with a wide spatial distribution. Kelp forests are structurally very complex, with a heterogeneous understory of younger plants and associated flora and fauna. Kelp forests generally support food webs with a high number of species at different trophic levels (e.g. Steneck et al. 2002, Smale et al. 2013, Krause-Jensen & Duarte 2014) contributing to ecosystem resilience.

Restoration actions may be implemented at large spatial scales and transplanted or recovered kelp plants can quickly become spore donors to adjacent barren areas. The major threats for kelp (reviewed in Filbee-Dexter & Wernberg 2018) are eutrophication, temperature increase (in the North Sea, Moy & Christie 2012, Bekkby & Moy 2011) and grazing by sea urchins (in the Norwegian and Barents Sea, Araujo et al. 2016), but kelp forests show high level of recovery when these pressures are removed. Consequently, removing pressures, such as sea urchins and nutrients, should be the priority before any additional actions (such as planting kelp or seeding spores). Despite the documented regime shift and widespread collapse of kelp forests (Ling et al. 2015), such as for the *Laminaria hyperborea* forests, some forests have had a back-and-forth shift between kelp and turf algae, without it being a regime shift (e.g. *Saccharina latissima*, Christie et al. 2019). Before any restoration action can take place, an in-depth understanding of the drivers, feedback effects and critical thresholds for the shifts is needed, including knowledge of the interaction with predators (such as sea urchins), turf algae and local and global stressors.

3.3.Cystoseira macroalgal beds

Cystoseira macroalgal beds display relatively high reproduction, growth rate and longevity (Ballesteros 1989), with a considerable variation in life history traits at different depths (Capdevila et al. 2016). The shallow beds have, in general (but with exceptions), wide spatial distribution and are dominant habitat-forming species in rocky intertidal and subtidal habitats, while deeper beds are more fragmented. *Cystoseira* beds have a high structural complexity, providing food and shelter to diversified assemblages of understory species. *Cystoseira* beds are vulnerable to various anthropogenic pressures (such as eutrophication, chemical pollution, coastal development, sedimentation) as well as being at risk due to climate change and outbreaks of grazers (Fraschetti et al. 2001, Airoldi et al. 2014). Overgrazing due to sea urchin outbreaks is responsible, along with other local and global stressors, for the loss of *Cystoseira* beds and the subsequent community shifts toward turf-forming algae or barren grounds (Pinnegar et al. 2000, Airoldi et al. 2014).

The high level of fragmentation often found for this habitat and the low connectivity (Thibaut et al. 2016) suggest that restoration actions should be considered over a local scale (metres). Restoration should focus on structural species that provide habitat for associated species. Shallow beds have high growth and fast dynamics (Ballesteros 1989) and may be easier to restore compared to deeper beds (e.g. below 30 m depth). Restoration actions should include large adult organisms. However, in cases where the natural and donor populations are in a critical state, manipulation should be avoided, and restoration must rely on recruitment enhancement and the growth of juveniles (Verdura et al. 2018b, De La Fuente et al. 2019). In these situations, a longer time (possible decades) for restoration must be accepted (Mangialajo et al. 2012, Thibaut et al. 2016, Capdevila et al. 2016). Anthropogenic pressures (such as eutrophication, chemical pollution, coastal development, sedimentation) should be reduced. Restoration practitioners have found that a combination of two approaches (sea urchin eradication to control their impact, and recruitment enhancement techniques) was the best technique to enhance *Cystoseira* forestation from a shallow degraded barren ground (Medrano et al. unpublished data).

3.4.Coralligenous assemblages

Coralligenous assemblages form through the growth of organisms on dead skeletons of previous generations, creating high structural complexity. Most are calcareous algae, sponges, bryozoans, and octocorals, which are relatively slow-growing and long-lived species, with limited recruitment (Coma et al. 1998, Garrabou & Harmelin 2002, Teixidó et al. 2011, Linares et al. 2007). In addition, populations of different coralligenous species, such as the octocorals *Paramuricea clavata* and *Corallium rubrum*, are most likely far apart, and larval supply may be limited (Costantini et al. 2007, Ledoux et al. 2010, Arizmendi-Meija et al. 2015).

Restoration through transplantation would require low initial effort due to high survival of transplants. As coralligenous species are slow-growing and long-lived, with limited recruitment, it takes a long period of time to restore the full complexity of the habitat through transplantation, probably at decadal timescales (Linares et al. 2008, Montero-Serra et al. 2018a). This would be the case for most of the key coralligenous groups, such as sponges (e.g. *Petrosia fisciformis, Spongia lamella, S. officinalis*) and octocorals (e.g. *Paramuricea clavata*, *Corallium rubrum*) (Teixidó et al. 2011, Montero-Serra et al. 2018b). However, there are other groups, such as bryozoans, mainly *Pentapora fascialis*, which can display higher growth rates and recovery of structural complexity could be achieved in a short time scales (5-10 years, Pagés et al. unpublished data). As the habitats are generally fragmented and the population connectivity low, restoration actions need to be performed at very local scales.

Coralligenous assemblages are presently threatened by a combination of nutrient enrichment, invasive species, increase of sedimentation and mechanical impacts, mainly from fishing activities, as well as climate change (Ballesteros 2006, Balata et al. 2007, Garrabou et al. 2009, Piazzi et al. 2012, Cebrian et al. 2012). Reduction of pressures should be a priority before starting restoration actions. The slow population dynamics of coralligenous assemblages make it difficult detect regime shifts, which could be eventually detected after longer time periods exposed to stressors. However, experimental and observational evidences show that extreme warming events can replace a structurally complex habitat with fast-growing and turf-forming species, which can indicate regime shifts (Ponti et al. 2014, Di Camillo & Cerrano 2015, Verdura et al. 2019).

3.5.Cold-water coral habitats

Cold-water coral habitats have among the lowest recovery potential. This is related to coral life-history traits such as slow growth, high longevity and low fecundity, which makes their recovery dynamics extremely slow, particularly for octocorals and black corals. Bypassing sensitive early-life stages, by transplanting adult and reproductive colonies of key coral species, may accelerate the initial recovery of the ecosystem (e.g. Linares et al. 2008, Montero-Serra et al. 2018a). However, the life-history traits of the species will condition the slow recovery of the ecosystem, including its full biodiversity, structure and functioning, which will likely require several decades to centuries. This is because individual native species will regenerate naturally at different time scales and because transplantation may be feasible only for a limited number of species (and if donors are available). Therefore, the appropriate choice of species to transplant may be important, giving priority to species with relatively fast growth rates, so that they can more easily recover and create the three-dimensional structure needed for associated species. The slow population dynamics of the cold-water coral habitats makes it difficult to really know if they are prone to regime shifts, as it would take long-lasting studies.

Cold-water coral habitats are sensitive to a range of human activities, including commercial bottom fisheries, hydrocarbon exploration and extraction, and, if developed, deep-sea mining (Ramirez-Llodra et al. 2011, Ragnarsson et al. 2017). The bottom fisheries are considered to be the major pressure, often resulting in the removal of entire communities, with little evidence of recovery (Clark et al. 2019). An important challenge in the restoration of deep-sea coral habitats is the remoteness of these habitats, which makes restoration actions highly dependent on technological means (e.g. large ships and ROVs) and costly in comparison with shallow-water habitats (van Dover et al. 2014, Da Ros et al. 2019). This may reduce the capacity to restore large areas using coral transplants. Thus, a combination of restoration approaches will likely be necessary, with assisted regeneration at small scales and natural regeneration (through fisheries closures, marine protected areas) at large scales.

4. Conclusion and future perspectives on restoration

Active restoration is required where the impact of human pressures goes beyond a point where no passive (unassisted) recovery may take place or does not proceed at the desired speed. Undertaking active restoration may provide conservation outcomes (Possingham et al. 2015) and should be used in combination with other management practices, such as protected areas (van Dover et al. 2014, Barbier et al. 2014, Da Ros et al. 2019).

Based on the discussions and scoring of the biological and ecological features and their contribution to the successful accomplishment of habitat restoration, the expert group concluded that most of the kelp forests features facilitate successful restoration (high score in Table 3), while the features for the coralligenous assemblages and the cold-water coral habitat did not promote successful restoration (low score). For seagrass meadows and *Cystoseira* macroalgal beds the conclusions were much more variable. Life-history traits of seagrass may lead to restoration failure or success, depending on the species (Table 2), which makes it difficult to score this feature according to its contribution of the successful accomplishment of habitat restoration.

The success of restoration actions depends upon the inherent ecology and biology of the species and habitats being restored. Life history and population connectivity impact restoration success, while structural complexity typically is a feature that will affect the habitat's vulnerability against perturbations (see Table 2). This means that restoration actions should mainly undertake two different activities. The first step should be to protect and maintain structural complexity and diversity, the second should be devoted to enhancing the conditions crucial for those features that make the success uncertain (i.e. life history and population connectivity). The protection and maintenance of structural complexity and diversity may be achieved by coupling the restoration action with management measures to significantly reduce stressors at the restoration site (van Dover et al. 2014). Close proximity of the restoration site to more pristine habitats improves restoration potential as the unaffected populations can provide offspring to support re-colonisation and population connectivity, increasing genotypic diversity, if no other limiting factors (e.g. current directions, topographic barriers) are present.

Based on the experiences from ongoing restoration projects and actions, the expert group suggests that four factors should be considered to obtain the greatest chances of success for restoration:

1) *The choice of the donor and recipient sites* – to ensure that the restoration site has suitable physical conditions and biological characteristics, as similar as possible to that of the donor site
2) *The identification of the best transplantation methodology* – a multitude of transplantation techniques exists for different species and habitats. The choice of the right technique (or combination of techniques) requires reviewing existing literature and outcomes of previous restoration projects.
3) *The influence of positive species interactions* – the presence of species could improve survival by for instance providing habitat or refuge, which may speed up the recovery. Instead of only minimizing competition and predation, restoration actions should also focus on positive, including co-restoration of several habitats.
4) *The potential for regime shifts* – if the habitat is prone to regime shifts, in-depth understanding of the drivers, feedback effects and critical thresholds for the shifts, including the interaction between species (positive and negative) and local and global stressors, is needed.

Point 3 in the list above, which is also relevant for point 4, needs some elaboration. Even though positive interactions between species are highly recognized in ecology, it is not commonly integrated in conservation or restoration efforts. Often, the negative interactions (competition and predations) are easier to identify and is therefore more often included as part of the restoration effort (Silliman et al. 2015). Considering positive interactions are more common in terrestrial (and to a certain degree freshwater) restoration projects. However, Halpern et al. (2007) provide some guidelines on why and when positive interactions should be considered, including for marine habitats. In general, physically or biologically stressful systems benefit more from positive interactions than mild habitats (Halpern et al. 2007, Silliman et al. 2015). It is therefore important that the degree of stress in the system is assessed as part of planning the restoration action. Silliman et al. (2015) shows that doing small adjustments in the restoration design to enhance positive interactions increases the restoration success.

Often, the challenge of marine restoration is that it can require long timescales (from several years to decades) before the success of the restoration methods can be evaluated and it requires substantial funding and high-technology equipment, particularly in deep-sea habitats (Bayraktarov et al. 2016, Verdura et al. 2018b). The cost of restoration is a crucial issue, both in terms of its estimation, for example through the transparent reporting of costs, and also the efficiency of actions (Bayraktarov et al. 2016). Efficiency can be increased by structuring restoration action across several partners (Bodin & Crona 2009) and by thinking creatively, for example using deep-sea corals from fisherman's by-catch in transplantations. In addition, for habitats such as cold-water corals, which recover slowly, short-term monitoring (i.e. a few years) cannot be expected to be a good indication of restoration trajectory or success. In these cases, management measures should be taken to ensure the long-term monitoring of the area under restoration, which may be beyond the typical lifetime of a restoration project. Often (as experienced in kelp forest restoration), maintaining long-term restoration actions is also a prerequisite for success (e.g. continuous sea urchin and turf algae removal).

An additional challenge in marine restoration is that in many cases (at least for the deep sea) we have limited knowledge on key features that support restoration success or can promote resilience. The lack of knowledge of pre-disturbance baselines, which may have shifted along with climate change (Pauly 1995), is also a challenge. Ultimately, this hampers a proper evaluation of the impact of anthropogenic activities, the actual degree of degradation and therefore the choice of the restoration goals.

In conclusion, this work provides an overview of the essential biological and ecological features for a range of marine habitats (ecosystem engineers) that can affect restoration success, highlighting the key factors for a successful restoration. Moreover, we provide some best practice guidelines to improve restoration success. Even though habitat restoration is much more complicated than that which has been discussed here, it is hoped that our discussions and recommendations will be useful when designing and executing future marine restoration.

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Conflict of interest

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

Author contributions

As part of the MERCES WP1 work, an expert group selected the marine habitats and features to be included in this paper. TB, NP and CS lead the focus workshop of experts. TB, CG, CL, NP, CS, TM, DF, KG, SF, CM, EB and EC were all part of this process and earlier analyses. At a later stage, more people were added to the expert group in order to ensure expertise on all habitats and regions, and to support the new analyses. ER, GA, CF and HG were included in the work on the kelp forests, CB on seagrass meadows, MC-S, TM and MB on cold-water coral habitats, CC and SK on the coralligenous assemblages, RD and ER-L on deep-sea habitats and JK and HO on habitat ecology in general. TB, NP, DF, CM, ER, CB, MC-S and CL were responsible for the Table 3 "scoring", but all authors listed have contributed to the discussions and conclusions, and in writing of the manuscript.

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Figure 1. Examples of the selected marine habitats assessed in this paper: (a) Zostera marina seagrass meadow, (b) Laminaria hyperborea kelp forest, (c) Treptacantha elegans macroalgal bed, (d) Mediterranean coralligenous assemblage and (e) Cold-water coral habitat, dominated by the octocorals Callogorgia verticillata, Acanthogorgia sp. and Dentomuricea c.f. meteor in the Azores. Photos by Christoffer Boström (a), Janne K. Gitmark (b), Alba Medrano (c), Cristina Linares (d) and EMEPC, ROV Luso (EMEPC/Luso/ Açores/2009) (e).

Table 1. Description of the key features assessed for the habitats included in this paper and their relevance to the recovery potential.

Key features	**Description**	**Relevance to the recovery potential**	**References**
Life history traits	Reproduction potential, larval biology, age at first maturity, growth rate, longevity, generation length.	Species with low reproductive output, delayed maturity, slow growth, and high longevity take longer to recover from impact.	McMahon et al. (2014), Capdevila et al. (2016). Montero-Serra et al. (2018a)
Population connectivity	Dispersal and gene flow.	Populations with high connectivity / gene flow have higher genetic diversity, which provides resistance to disturbance and high potential for natural recolonization of disturbed areas from nearby sites.	Pascual et al. (2017), Jahnke et al. (2018)
Spatial distribution	Spatial extent, distribution patterns.	Populations in fragmented habitats are more vulnerable to environmental impact and genetic stochasticity, and therefore face a higher risk of local extinction.	Gera et al. 2013, Giakoumi et al. (2013)
Structural complexity	Three-dimensional complexity.	Increased habitat complexity supports higher biodiversity and thus associated food webs, thereby enhancing recovery through various ecosystem processes, including facilitation and positive feedbacks between coexisting species.	Kovalenko et al. (2012)
Regime shift	The potential for regime shift.	Habitats that experience variation in extent, coverage and status, but that don't experience regime shifts, will recover more easily than habitats that show regime shifts	Hughes et al. (2013), Maxwell et al. (2017)

Table 2. The characteristics of the five selected key features for each habitat. Shallow *Cystoseira* macroalgal beds have a different community and different life history traits than deeper ones and are thus treated separately.

Habitat		**Habitat features** Life history	Population connectivity	Spatial distribution	Structural complexity	Regime shifts
Seagrass meadows		Both slow and fast-growing species, both low and high reproductive output	Generally high dispersal and high gene flow, but some populations are clones	Relatively fragmented populations, depending on the species	High 3D complexity	Prone to regime shifts
Kelp forests		High recruitment, growth rate and longevity	High connectivity, number of propagules and dispersal distance	Wide distribution	High 3D complexity	Prone to regime shifts
Cystoseira macroalgal beds	(shallow, i.e. at 0-10 m)	Fast or medium growth and recruitment rate	Medium or poor dispersal ability	Wide distribution, but might occur in patches	High 3D complexity	Prone to regime shifts
	(deeper, i.e. at 10-50 m)	Slow growth and recruitment rate	Poor dispersal ability	Fragmented	High 3D complexity	Prone to regime shifts
Coralligenous assemblages		Slow growth and low recruitment rate, long life span	Low connectivity, disconnected populations and limited larval transport	Fragmented	High 3D complexity	Likely, but unclear
Cold-water coral habitats		Slow growing, long life spans, low reproductive output and low recruitment rate	Low fecundity and larval dispersal	Fragmented	High 3D complexity	Unclear

Table 3. The agreed-on expert scoring of the habitat features according to their contribution to the successful accomplishment of habitat restoration; 1 – low contribution, 5 – high contribution. The habitat features are presented in general in Table 1. Table 2 provides the information used for the agreed-on scoring here. Seagrass meadows are difficult to score when it comes to life history, as the life history of the different seagrass species may lead to both restoration failure and success). Also, some seagrass populations have extremely low connectivity (leading to the score 1 in brackets). Shallow *Cystoseira* macroalgal beds have a different community and different life history traits than deeper beds, and scores are therefore given separately.

Habitat		**Habitat features**				
		Life history	Population connectivity	Spatial distribution	Structural complexity	Regime shifts
Seagrass meadows		1-5	5(1)	2	5	Prone to regime shifts
Kelp forests		5	5	5	5	Prone to regime shifts
Cystoseira macroalgal beds	(shallow, i.e. 0-10 m)	4	3	4	5	Prone to regime shifts
	(deeper, i.e. 10-50 m)	3	2	2	5	Prone to regime shifts
Coralligenous assemblages		2	1	1	5	Likely, but unclear
Cold-water coral habitats		1	1	1	5	Unclear

Figure 1.JPEG

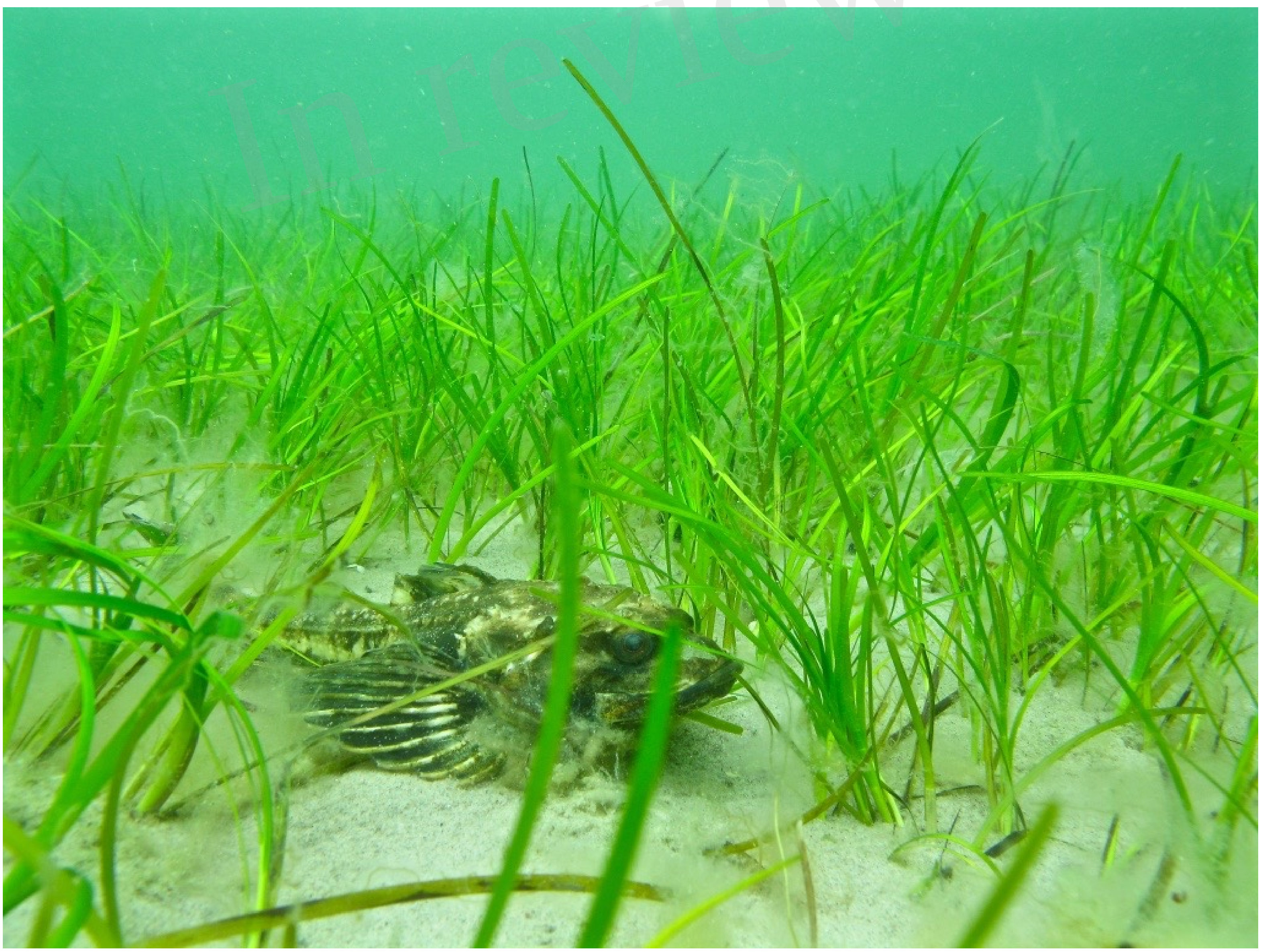

Figure 2.JPEG

Figure 3.JPEG

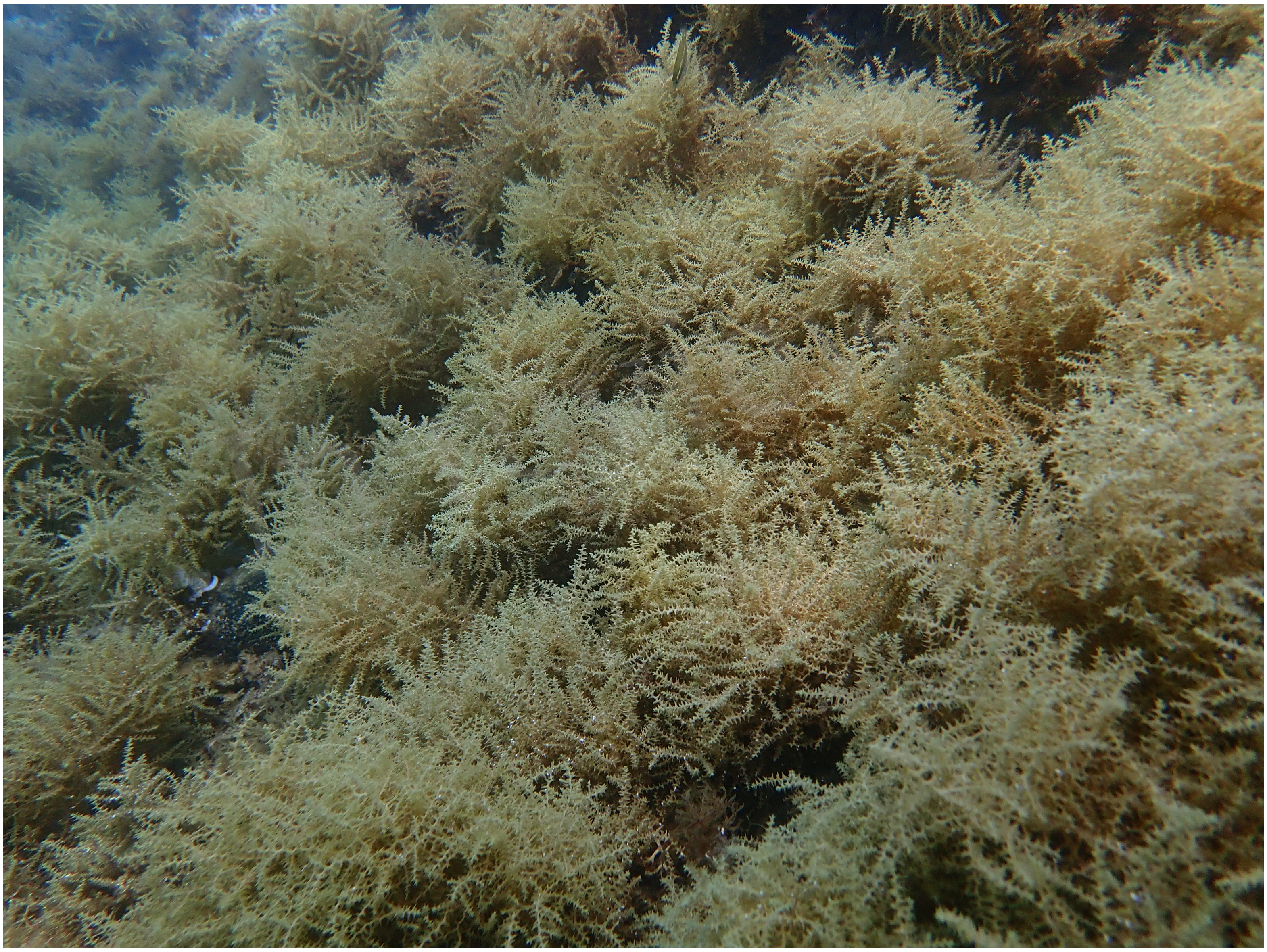

Figure 4.JPEG

Figure 5.TIFF