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Forty questions of importance to the policy and practice of native oyster reef restoration in Europe

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Abstract

1. Oyster reefs are among the most threatened marine habitats globally. In Europe, oyster reefs have been extirpated from most locations within their historical range. Active restoration of the native oyster (*Ostrea edulis*) in Europe has grown substantially in recent years. In sharing experiences between oyster restoration projects in Europe at the Native Oyster Restoration Alliance conference, NORA2, in Edinburgh in May 2019, it became apparent that a number of similar barriers are experienced.
2. This study identified the top 40 questions, which, if answered, would have the greatest influence on the policy and practice of oyster restoration in Europe. Initially 71 people were consulted across 28 institutions and 11 European countries to generate 194 questions. An established process of one round of pre-workshop voting followed by a one-day online workshop and two post-workshop rounds of voting resulted in the final 40 questions.
3. Questions were broadly grouped into the following 10 themes: baselines, site selection, restoration methods, quantifying benefits, disease management, biosecurity, genetic diversity and population differentiation, policy and management, novel technologies, and current and future threats.
4. We anticipate that this list will provide a starting point for developing collaborative projects across the NORA network, as well as assisting policy makers and funders with identifying key areas that need to be addressed in order to overcome existing barriers to scaling up oyster restoration in Europe.

KEYWORDS
alien species, estuary, fishing, invertebrates, pollution, restoration, subtidal

1 | INTRODUCTION

Oyster reefs are among the most threatened marine habitats globally, having suffered losses of over 85% (Beck et al., 2011). In Europe, the native oyster *Ostrea edulis* is locally extirpated throughout much of its historical range (Fariñas-Franco et al., 2018; Gercken & Schmidt, 2014; Pogoda, 2019; Smaal, Kamermans, van der Have, Engelsma, & Sas, 2015; Thurstan, Hawkins, Raby, & Roberts, 2013). In recent years, there has been growing interest in restoring this key habitat in many places across Europe. Oyster habitat restoration was first undertaken in the USA around 50 years ago (Hernandez et al., 2018), and restoration of the eastern oyster *Crassostrea virginica* in particular is now widely practised. As a result, there is a large body of experimental and practical knowledge, primarily from the USA, that guides restoration management and policy interactions (see Fitzsimons, Branigan, Brumbaugh, McDonald, & zu Ermgassen, 2019). Oyster restoration in Europe, in contrast, is a new but fast-growing field (Pogoda et al., 2019, 2020). While much can be learnt from the existing knowledge base of restoration of other oyster species, including *Ostrea angasi* (Gillies et al., 2015; Gillies, Crawford, & Hancock, 2017) in Australia, *O. chilensis* (Michael, 2019) in New Zealand and *O. lurida* in USA (Brumbaugh & Coen, 2009), the species-specific traits of *O. edulis* also require location- and species-specific empirical results in order to develop effective and adaptive restoration practices (e.g. Helmer et al., 2019). Novel disease challenges, differences in coastal settings where these species are found and restored and the complex cross-border issues present in Europe represent specific challenges that have to be addressed in order to ensure efficient progress in oyster restoration. Furthermore, the reproductive strategy of *O. edulis* means that the management of genetic diversity of restored populations is of prime importance to avoid inbreeding and ensure long-term adaptability (Lallias, Boudry, Lapègue, King, & Beaumont, 2010).

Oyster restoration and conservation is a key biodiversity issue in the European context. *Ostrea edulis* is identified as a threatened and/or declining habitat in all OSPAR regions where it occurs (OSPAR Commission, 2009), as well as being listed as a Critically Endangered Species by the EU 28 (EUNIS, 2016) and as a wetland habitat type under Ramsar (Kasoar, zu Ermgassen, Carranza, Hancock, & Spalding, 2015). On a national level, *O. edulis* and its habitat have been identified as a Scottish Priority Marine Feature, as well as a special feature in a number of English Marine Conservation Zones, while in France the species now appears in action plans for the preservation and restoration of certain regional marine parks and is listed among 'Special coastal habitats of high or major importance' by the French Biodiversity Agency. The EU Habitats Directive (Council Directive 92/43/EEC) also affords *O. edulis* habitats protection in some countries indirectly through their inclusion under the category 'reefs' or as a key structural species in 'estuaries' and 'large shallow inlets and bays'. For example, the designated management plans for Natura 2000 sites in the German Economic Exclusive Zone include the restoration of biogenic reefs, namely native oyster reefs, to support the achievement of a Good Environmental Status according to the EU Marine Strategy Framework Directive (2008/56/EC). Belgium has also included a positive trend in frequency of occurrence of the adult *O. edulis* as one of the indicators for good environmental status within this directive, resulting in the exclusion of bottom-contacting fisheries in gravel bed areas and gravel bed restoration as measures that could be beneficial for oyster restoration (De Mesel et al., 2018). As a result of this wide-ranging legislative recognition, efforts are underway across Europe (the Southern North Sea, the Channel, the Skagerrak and the Atlantic Ocean) with the aim of protecting and restoring the native oyster.

While not as expensive as many other forms of marine habitat restoration, oyster restoration is still costly (Bayraktarov et al., 2016), and in the European context still in its infancy with most projects currently focusing on pilot studies and relying heavily on partnerships between conservation, ecology and aquaculture practitioners. In order to best progress the practice of oyster restoration in Europe, the Native Oyster Restoration Alliance (NORA) was established in 2017 as a network of people seeking to exchange knowledge on restoring the native oyster and native oyster habitat in European waters. Within NORA, which includes experts in various aspects of oyster restoration and management across 13 countries, it is clear that many projects face similar challenges and are seeking to overcome similar barriers. At the first NORA conference in Berlin, key themes of universal interest were identified as oyster production, site selection, disease management and monitoring (Pogoda, Brown, Hancock, & von Nordheim, 2017). Now we seek to identify the key research questions within these identified themes and identify further themes and questions that can address current barriers to oyster restoration in Europe.

Here we present the results of a priority-setting exercise used to identify the top 40 questions that if answered will have the greatest influence on the policy and practice of oyster restoration in Europe. Given the focus of the NORA network, these questions were focused on addressing specific barriers to restoration of native oyster habitats, rather than oyster aquaculture. We anticipate that this list of questions will provide a focus for researchers and policy makers, as well as assisting funders and programme managers in allocating funds and planning projects to address the gaps identified and hence improve the implementation of oyster habitat restoration in Europe.

2 | METHODS

To identify the top questions, we used the Priority Setting Exercise method outlined in Sutherland et al. (2009) and Ockendon et al. (2018). This approach uses a multistage, collaborative and transparent approach to filter a long list of candidate questions down to a focused, democratically agreed list of priority questions. In order to ensure that the candidate questions were pulled from the full diversity of expertise available regarding oyster restoration in Europe, the NORA Secretariat made an open call in September 2019 to all NORA 2 participants and their networks (including the Native Oyster Network UK and Ireland) requesting that participants submit the top questions that, if answered, will have the greatest influence on the policy and practice of oyster restoration in Europe. Submissions were requested to be specific and answerable through scientific research within the near term (i.e. within 5–10 years). Seventy-one participants from 28 organizations and 11 European countries (plus one US-based NORA member) submitted a total of 194 questions. Where necessary the submissions were moderately rephrased to meet the requirements listed above and returned to the submitting organization to ensure that the questions' meaning remained as intended. The questions were then grouped into six broad themes. All contributing organizations were asked whether a representative would be able to participate in the process of assessing the proposed questions. Participation was limited to one set of votes per organization to avoid bias in the selection of questions resulting from a particular organization's primary focus of research. Representatives from 16 organizations participated in the workshop, with areas of expertise self-identified as genetics (25%), ecology (88%), aquaculture (56%) and policy (31%). All those who participated in the assessment and selection of the final questions are included as co-authors. The 16 participating experts (hereafter referred to as 'experts') were requested to identify questions that were similar or identical and to identify their top 10% of questions in each theme. Each theme addressed had to be assessed in its entirety. If a theme fell outside of the expertise of the lead representative from an organization, they were encouraged to seek input from colleagues.

At the end of the first round of assessment, the number of votes for each question was tallied. Thirty-eight questions were identified as being similar to/the same as existing questions. These questions were shared with the experts and they were given the opportunity to object to them not being taken forward to the workshop. There were no objections. An additional four questions were also proposed at this stage and added to the list. A summary detailing the results of the voting for the remaining 160 questions was recirculated to experts in advance of the workshop.

The workshop itself was conducted online by video conference on 11th November 2019 with all experts invited to an initial plenary session in which the structure and aims of the workshop were clarified. Three subgroups of five or six experts each examined the questions from two themes. Within the subgroups experts were first asked to identify whether they wanted to take forward any questions that had failed to attract any votes in round 1. Identified questions, along with all those receiving one or more votes in round 1, were then discussed within the subgroup. Once all questions had been discussed, experts were asked to vote on their top 20% questions within each theme through an anonymous online poll. These votes were compiled and returned to the subgroups, where experts were given the opportunity to review whether any key issues were missing from the questions that had received votes. All 63 questions that had received at least one vote were taken to the plenary; of these, 46 had received two or more votes. The 17 questions that had received just one vote in the subgroups were reviewed by all experts, who were given the opportunity to 'rescue' these questions through to the next round of voting. Six questions were taken forward and the remaining 11 questions were discarded. The questions were also reviewed in their entirety to identify whether the resulting set of questions failed to cover general themes identified during the workshop as important in overcoming existing barriers in the practice or policy of oyster restoration in Europe. Six questions addressing the identified gaps were drafted and taken forward to the next round, resulting in 58 questions in total.

The resulting list of 58 questions was shared with the experts for a further round of anonymous voting after the workshop, in which they were asked to identify their top 40 questions. Thirteen questions received votes from no more than 50% of voters. Experts were given the opportunity to 'rescue' any low scoring questions and provide information explaining their proposal. Three questions were identified and taken forward, resulting in 10 questions being eliminated at this stage. The remaining 48 questions were taken forward to the final vote. Experts were once again asked to identify the top 40 questions, but were not obliged to use all 40 votes. Thirty-seven questions received votes from at least 75% of experts. Six votes were tied with 11 (69%) votes each. The six questions were examined for overlap with existing questions and consensus was reached regarding the three questions to include in the final top 40 questions. The final 40 questions were split into 10 broad themes; the order of the questions does not reflect rank or importance. The experts were then asked to independently rank the questions within each theme and identify questions as either limiting to oyster restoration or addressing the optimization of native oyster restoration.

3 | RESULTS

Questions that over 70% of experts identified as being either limiting or optimizing were considered to fall within those categories. Consensus of categorization was reached for only 14 of the 40 questions, with three of the 40 questions identified as limiting oyster restoration (questions 10, 11 and 16) and 11 questions identified by the majority as pertaining to optimization of oyster restoration (1, 5, 8, 9, 12, 22, 26–30). No consensus was reached for 26 of the 40 questions.

3.1 | Baselines

Establishing a baseline is a critical first element in undertaking ecological restoration, because a baseline provides context from which to assess the progress of restoration efforts (Gann et al., 2019). In the case of *O. edulis* in Europe, reference sites that may provide a baseline for assessing the progress of restoration efforts are absent from much of the range. Moreover, sites that still contain populations are generally modified as a result of a history of oyster production, dredging and other fishing activities, or modified via shifts in the dominant biotic community (Allison, Hardy, Hayward, Cameron, & Underwood, 2019; Helmer et al., 2019; Preston et al., 2020). As such, establishing reasonable baselines to inform adaptive management of restoration efforts where *O. edulis* habitats are currently absent is a key priority. On a larger scale, baselines regarding the current and historical extent of *O. edulis* reefs provide critical background for determining eligible sites for oyster restoration, which should be used in combination with habitat suitability (Shelmerdine & Leslie, 2009) and site connectivity mapping (Gormley et al., 2015) to ensure that restoration sites across Europe are optimally co-located. Finally, understanding the current and historical extent of oyster reefs in Europe is also important for communication and outreach (Fitzsimons et al., 2019). Communicating the scale of the loss and re-forging cultural connections with this widely extirpated keystone habitat will facilitate stakeholder engagement in restoration efforts.

1. Using data from contemporary studies and historical data from other shellfish systems, what does a reference model system for *O. edulis* look like?
2. What is the current distribution and abundance of *O. edulis* in Europe?
3. What is the historical ecology of *O. edulis* across its full range?

3.2 | Restoration methods

Numerous guidelines for undertaking oyster restoration exist, especially from the USA (e.g. Brumbaugh, Beck, Coen, Craig, & Hicks, 2006) and globally (e.g. Fitzsimons et al., 2019). Much of this guidance is universally applicable and has proven itself invaluable in the early stages of oyster restoration in Europe, for example in identifying suitable cultch material. European experts, however, identified a number of species- or landscape-setting-specific challenges on which the global guidance does not, as yet, provide suitability detailed guidance. These relate to addressing substrate limitation (surface texture, timing of deployment, height of placement) and overcoming recruitment limitation (production bottlenecks, best practice in translocating stock, natural recruitment enhancement), both of which are themes that are identified at a higher level in existing guidance. In the case of substrate limitation, the relaying of settlement substrate is a traditional method of oyster mariculture in Europe, which relies on ensuring that appropriate material for spat settlement is available and attractive at the key moment when oyster larvae are looking to settle out of the water column. However, as most potential restoration sites in Europe are both recruitment and substrate limited, there is heightened interest in ensuring that settlement material is as attractive as possible, so as to increase the settlement of the limited numbers of larvae in the water column. While it is known that the presence of conspecifics and of a biofilm is important in encouraging settlement (Rodriguez-Perez et al., 2019), translating this from the laboratory to the field across the geographic range of the *O. edulis* will require further investigation.

4. What methods (e.g. timing, handling, substrate) can be applied to maximize the cost effectiveness of relaying spat?
5. What are the most cost effective and validated monitoring indicators that can provide widespread evidence of the success of restoration projects and therefore market confidence?
6. What role does the timing of deployment of new substrate play in settlement success or recruitment?
7. How does population density affect reproductive success in *O. edulis*?
8. To what extent is oyster recruitment and survival related to the height of the restored oyster reef?

3.3 | Site selection

Ensuring the sustainability of oyster reefs is key to restoration success. One key element of ensuring sustainability is to select a location that supports the settlement, growth and survival of oysters and hence the growth of the biogenic habitat itself (Beseres Pollack, Cleveland, Palmer, Reisinger, & Montagna, 2012; Kamermans et al., 2018). A positive shell budget, where the oysters are contributing enough shell material to the habitat to offset the loss of shell through burial, movement and erosion, would be indicative of a sustainable biogenic reef system (Jordan-Cooley, Lipcius, Shaw, Shen, & Shi, 2011; Soniat et al., 2012). Selecting a site where oysters not only grow well, but also promote the recruitment of spat is key to sustaining shell inputs over time. Given the life history of the species, with its relatively long lifespan and intermittent local spawning success, it is likely that in many locations such sustainability must be viewed at a larger scale, with restoration projects ideally considering not only local site conditions, but also the role of the site as a source or sink of larvae relative to other locations. Such source–sink dynamics across populations are well recognized in other oyster species (Dumbauld, Kauffman, Trimble, & Ruesink, 2011; Michael, 2019). While some of the abiotic requirements of *O. edulis* are already well understood (Korringa, 1957; Orton, 1937), the natural setting of oyster restoration, coupled with the goal of habitat sustainability, places a starkly different emphasis on the existing knowledge and reveals significant gaps. For example, a recent study in Essex, UK found little explanatory power of abiotic variables such as temperature and pH in explaining the occurrence of *O. edulis*. Occurrence and abundance were instead predominantly determined by the presence of shell (Allison et al., 2019). Given that *O. edulis* is largely extirpated from much of its range, there is a significant role to be played by habitat suitability models in identifying suitable locations if appropriate input data can be improved (see Gormley, Porter, Bell, Hull, & Sanderson, 2013). It was also noted that species distribution models could seek to account for distributions of known associated species, to assist with identifying potential suitable sites in the absence of more *O. edulis*-specific data.

9. How can a map of the connectivity potential of restoration sites (accounting for current populations) be developed?
10. What is the minimum oyster population size, density or area in order for an oyster reef to successfully regenerate?
11. Which biotic and abiotic factors determine and limit flat oyster recruitment, with recruitment defined as settlement, growth and survival to age two years.
12. Can the success of restoration efforts be increased by using species distribution modelling to identify suitable oyster habitats/areas for restoration?

3.4 | Biosecurity

Disease and invasive species were highlighted as major barriers to progressing native oyster restoration in Europe. Large-scale movements of oysters and other shellfish have historically introduced non-native species such as *Crepidula fornicata* and pathogens such as *Marteilia refringens*, *Bonamia ostreae* and *B. exitiosa* to European waters (Culloty & Mulcahy, 2007; Wolff & Reise, 2002). Pathogens and non-native species represent a significant threat to the remaining *O. edulis* populations. While there was agreement among experts that in areas where diseases are present it is necessary to work *with* the disease in undertaking restoration efforts, there was also a strong emphasis on maintaining a disease-free status where possible. Strong biosecurity measures, underpinned by scientific understanding of the vectors of disease and invasive species, which can be incorporated at both the project planning (in particular site selection) and the project implementation stages, are key to conserving existing disease and invasive species-free populations. Whilst there has been a large body of work related to oyster pathogens, there is still a need for better understanding of the vectors and the life cycle for bonamiosis and other diseases (Lynch, Armitage, Coughlan, Mulcahy, & Culloty, 2007).

13. How can the biosecurity risk associated with translocating oysters and cultch best be minimized?
14. How can the biosecurity risk associated with moving oysters through a hatchery supply chain best be minimized?
15. What are the pathways and risk in establishing connectivity between *Bonamia* affected areas and those currently disease free?

3.5 | Disease management

Eradication of diseases or invasive species is generally not possible in the open marine environment (Thresher & Kuris, 2004). The management of oyster restoration therefore needs to account for this reality where diseases or invasive species are found. In the case of *O. edulis*, the primary disease threat throughout much of its range is *B. ostreae* (Carnegie, Arzul, & Bushek, 2016). While interactions between stressors and disease prevalence and mortality in oyster production have been described (van Banning, 1991), there remains uncertainty regarding the impacts of the disease under natural conditions, such as those that restoration projects aim to achieve. Understanding interactions between the oyster and its disease in the wild, the ecology and the life cycle of the parasite, and the development of either resistance or tolerance to the disease remain critical data-gaps (Sas et al., 2020). Experts agreed that, as new diseases are encountered or expand their range, they may similarly need to be investigated.

16. How can *Bonamia*-challenged and *Bonamia*-free *O. edulis* spat be produced and upscaled (with mandatory European declaration)?
17. What are the mechanisms behind *Bonamia* 'resistance' and 'tolerance'?
18. What stressors affect the susceptibility to and rate of mortality associated with *Bonamia* infection?
19. How does oyster density relate to disease prevalence of *Bonamia*? Are there interactions with temperature or food availability?
20. How does *O. edulis* population size relate to resilience and disease prevalence within a population?

3.6 | Genetic diversity and population differentiation

Maintaining genetic diversity and understanding the evolutionary forces that shaped the observed existing genetic structure in *O. edulis* populations (Diaz-Almela, Boudry, Launey, Bonhomme, & Lapègue, 2004; Vera et al., 2016) were identified as key themes in the process. This is unsurprising given the heavy reliance that reintroduction and restoration projects with limited recruitment are required to have on hatchery-reared or translocated stocks. Understanding of whether potential source populations for restoration are not only genetically distinct owing to neutral evolutionary forces, but also adapted to their local environment is needed to avoid the introduction of individuals that would result in low fitness and therefore poor return on investment. The call for examining the implications of geographic variability in *O. edulis* genetics, with regards to environmental tolerance, is not new (Rödström & Jonsson, 2000), and yet the issue remains poorly resolved not least because of an increased rate of discovery of emerging, re-emerging or rediscovered populations that have not yet been phenotypically or genetically characterized. Whether there is a genetic basis for any phenotypic variability in *O. edulis* populations will be an important question to resolve to support oyster restoration now and in the future as environments throughout its range are changing in response to climate, disease and anthropogenic stressors. In order to facilitate progress in understanding the genetic diversity and population structure of *O. edulis* across Europe, it was emphasized that a common language, in the form of a reference set of genetic markers, would greatly speed up the rate at which a pan-European knowledge base is acquired. This will facilitate genome-wide studies of the genetic structure and local adaptation of European flat oysters and help to identify factors shaping their differentiation, as was recently undertaken for *Crassostrea gigas* (Vendrami et al., 2018) and *Pecten maximus* (Vendrami et al., 2019).

21. To what degree are native oysters adapted to local conditions and how does this affect their response to environmental change?
22. Which reference set of genetic markers (preferably SNPs) should be used in order to monitor genetic diversity as part of a restoration programme?
23. What are the best protocols for maintaining genetic diversity while optimizing hatchery production of *O. edulis* for restoration projects.
24. What are the implications of relaying hatchery seed on population genetic diversity?

3.7 | Novel technologies

Experts identified a series of outstanding questions where it is possible that new and emerging technologies may assist in addressing these significant challenges. Oysters and their habitats are often difficult to sample. The remnant reefs are often found in deep or turbid environments and can even be challenging to identify owing to their low population densities in many locations. The traditionally used method for sampling oyster populations is oyster dredging; however, the destructive nature of this gear means that extreme caution must be applied in a habitat restoration scenario. Furthermore, the use of dredges is restricted in many of the protected areas where oyster restoration is taking place. Other options include acoustic methods, foreshore sampling at low tide and diving campaigns, but the former is unsuitable for many of the metrics that restoration projects need to monitor (such as oyster size and density), while the latter is restricted by both depth and conditions at sea, which limits its utility in many situations. It is therefore critical that novel submarine technologies and monitoring methods are explored; indeed some are already in the process of development (Thorngren, Dunér Holthuis, Lindegarth, & Lindegarth, 2017). A further monitoring challenge is presented by the low concentration of the larvae of this species which makes it difficult to identify its presence in the water column. In the case of *Bonamia* disease monitoring, traditional methods require pathology to be established using histological screening methods and *in situ* hybridization, with polymerase chain reaction assays to distinguish between the morphologically similar parasites species (OIE, 2016). To establish the prevalence of disease a minimum sample size of 30 individuals is routinely used (Flannery et al., 2014). Given the low abundance of oysters in many locations, reaching this sample size can present a challenge in itself. eDNA analysis represents a potential opportunity to overcome these difficulties in sampling (Holman, Hollenbeck, Ashton, & Johnston, 2019; Mérou, Lecadet, Pouvreau, & Arzul, 2020). In a hatchery setting, production of *O. edulis* spat is an ongoing challenge (Lapègue, Beaumont, Boudry, & Goulletquer, 2007). Problems at various stages in the production cycle are well recognized within the industry, e.g. health and biosecurity management (pathogens, parasites), reliable spawning induction, prediction of the swarming phase and the management of larval mortality through metamorphosis. The development of protocols and affordable monitoring techniques within hatcheries which are sensitive enough to inform an adaptive process of production could considerably reduce mortalities at critical bottlenecks in the spat production of *O. edulis*.

25. What technologies can be introduced or improved to make hatchery and pond production more reliable?
26. How can remote monitoring methods be adapted to provide an accurate and cost-effective measure of the density and size distribution of *O. edulis* and their associated communities?
27. How can eDNA techniques be used effectively to assess the onset of spawning and the presence and abundance of larvae in the water column?
28. How can eDNA techniques be used effectively to assess biosecurity risks associated with disease and invasive species?

3.8 | Quantifying benefits

It is widely accepted that many of the benefits associated with extant or recovered reefs of other oyster species, such as increased biodiversity (Christianen et al., 2018), enhanced fish and shellfish production (zu Ermgassen, Grabowski, Gair, & Powers, 2016), improved water quality (Grizzle, Rasmussen, Martignette, Ward, & Coen, 2018; Kellogg et al., 2014), carbon storage (Lee, Davies, Baxter, Diele, & Sanderson, 2020) and sediment stabilization (Kent, Last, Harries, & Sanderson, 2017), are provided by *O. edulis*. This is probably because these benefits are predominantly a direct result of the ecosystem engineering properties of shellfish (zu Ermgassen et al., 2020). What is missing is understanding of the degree to which these benefits are provided (Lown, 2018; zu Ermgassen et al., 2020). Quantification of the benefits of restoration can play a critical role in stakeholder engagement, as well as site selection and restoration design (Gilby et al., 2018). Understanding and communicating the benefits can also open up new funding sources (Goldman & Tallis, 2009) and inform restoration goal setting (zu Ermgassen, Spalding, & Brumbaugh, 2014), which may be especially useful where historical baselines are absent or present an unrealistic restoration goal. Understanding the degree to which benefits are provided by restoration can be especially critical in areas of multiple use, where there may be tradeoffs between the provision of ecological services (White, Halpern, & Kappel, 2012).

29. How does ecosystem service delivery scale with oyster density?
30. What is the quantitative and qualitative relationship between oyster habitat quality (density, size distribution) and the biodiversity of the reef?
31. What is the relationship between oyster spawning biomass and potential spillover effect?

3.9 | Policy and management

Oyster restoration is a relatively new field in Europe compared with, for example, the USA, and policy and management measures may need to be adapted to develop an appropriate best practice and policy framework that better reflects the needs of oyster reef restoration projects. This applies to all aspects of restoration from initial site licensing to introducing oysters and cultch and to the protection of the oysters once they are established. Most of these policy and legislative aspects will need to be addressed on an individual country basis. Clear communication with permitting organizations and policy makers is key in supporting the development of decision-making frameworks to support native oyster restoration and in overcoming existing barriers (Fitzsimons et al., 2019).

There are three particular restoration settings which in particular require greater research to overcome barriers to oyster restoration: co-management of oyster fisheries, coordinating confidence in demand for spat and restoration in marine protected areas. Private ownership of existing fisheries has had a role to play in preserving some native oyster populations, as illustrated in Ireland, where privately owned fishing rights prevented overexploitation (Eagling, Ashton, & Eagle, 2015), and Sweden, where most of the *O. edulis* habitats have been privately owned for at least three centuries and oysters cannot be collected without permission from the landowner (Thorngren, Bergström, Holthuis, & Lindegarth, 2019). The potential for the fishery to positively interact with oyster restoration aims should not be underestimated, with fishers representing a fount of local ecological knowledge and in some cases safeguarding remaining populations (OSPAR Commission, 2009). The extractive nature of the fishery, however, means that careful co-management needs to be developed to ensure that the needs of the fishery and the restoration of oysters to densities representing oyster habitats (defined as >5 oysters m^{-2} by OSPAR, 2009) are both achieved (Lown, Hepburn, Dyer, & Cameron, 2020). This could include the potential to develop industry-led funding initiatives if a higher market price could be secured for fished oyster populations with restoration aims. Fisheries management based on annual stock assessments of fluctuating stocks, closed areas with brood stock and dynamic annual total allowable catch may ensure the persistence of endangered populations and support a local sustainable fishery, as in the Danish Limfjorden (Nielsen & Petersen, 2019). The lack of spat available for restoration is a major barrier to scaling up restoration in Europe (Pogoda et al., 2017). This current deficit in oyster spat for purchase results in part from a mismatch between the timeframes over which project funding becomes available and has to be implemented and the lead time hatcheries require to produce the spat. Furthermore, the fact that the current demand is unreliable makes the process of shifting to *O. edulis* cultivation a risky economic commitment for hatcheries. Determining how this uncertainty in price and demand can be resolved, through either policy or project coordination, would greatly assist the planned scaling up of restoration efforts in Europe.

In the case of restoration in marine protected areas, the primary issue identified was how to plan for oyster restoration alongside other protected features. As oysters were largely extirpated before the establishment of marine protected areas in Europe, the shifted baseline on oyster reef extent presents some challenges in meeting obligations to maintain or improve other associated habitats, which could be addressed by better understanding the impact of oyster reef restoration on such features. Managing areas outside of protected areas to allow for oyster restoration and protection, for example through the restriction of towed gears in areas known to be suitable for *O. edulis*, was also highlighted.

32. How do we best communicate research findings to impact policy and support the reintroduction of *O. edulis*?
33. What is the best practice for fisheries management of oyster populations with restoration aims?
34. How can the current challenges regarding the mismatch in funding and hatchery supply timelines be best overcome? For example, can a mechanism for guaranteeing spat purchase be formulated?
35. How could new, appropriate approaches to marine licensing and legislation best be developed in relation to native oyster restoration programmes?
36. How can the trade-offs between the benefits of restoring oyster habitat and impacts on other marine features of importance best be balanced?

3.10 | Current and future threats

The first step in any restoration project is to assess the level of threat and to mitigate them before restoration is undertaken. At larger temporal and spatial scales, understanding the key drivers of decline, how they are changing and if they can be mitigated can play an important role in site selection (Pogoda et al., 2020). In the case of *O. edulis* a number of threats which have the potential to change in severity or spatial distribution have been identified, including climate change, sedimentation, pollution, invasive species, predator dynamics and disease. A clearer understanding of the severity of the threats, their likely interactions and their geographic distribution were all identified as key questions which could inform site selection and management into the future. The benefits of having a pan-European network examining these threats was also highlighted, as complementary experiments and knowledge exchange across different parts of the *O. edulis* range can play a key role in understanding the identified threats.

37. How do aquatic levels of emerging chemicals and pollutants prevent the recovery of flat oysters?
38. How great a risk does sedimentation and burial pose to the survival of this species, and will this risk change with sea-level rise?
39. What are the major pressures on *O. edulis* populations around Europe today and do they vary in type or intensity geographically? How can they be or are they mitigated differently across Europe?
40. How does the presence of *C. gigas* affect the demographic development, growth and survival of *O. edulis*?

4 | DISCUSSION

Ecological restoration and its scientific study through restoration ecology is a growing field aimed at reducing biodiversity loss and recovering lost habitats (Gann et al., 2019). It is also a bridge between the social and natural sciences and society. This field of research is especially relevant in the intensively managed, farmed, urbanized and industrialized landscapes common in Europe, and in the marine context, restoration is still in the early stages of development (Ockendon et al., 2018). Oyster reef restoration is increasingly embedded in European marine management practice, owing to established legal frameworks (OSPAR, EUNIS, Ramsar, MSFD, EU Habitats Directive) and growing enthusiasm from NGOs, government agencies and businesses. The questions presented in this paper identify where research could usefully be focused to progress the implementation of oyster restoration in Europe. These include questions that address barriers such as those presented by partial knowledge of its ecology and diseases, limited supply of oysters for restoration, limited understanding of the role and function of oyster reefs by stakeholders, funders and the public, changing threats to oysters and practical advice. The need to widen current participation in native oyster restoration in Europe to include the aquaculture industry and decision makers was a key issue running through many of the themes. While there appears to be a bias toward ecological and practically focused questions, many questions pertain to improving the understanding of native oyster restoration by widening participation (questions 29–36) or removing barriers which currently prohibit the aquaculture industry and policy makers from becoming more actively engaged (questions 13, 14, 23 and 34). For example, question 34 highlights the need to overcome the mismatch in funding streams in restoration projects and oyster production timelines, in order that existing hatcheries are better able to supply the native oyster restoration market without taking on unacceptable levels of risk.

It is striking that, despite the long history of oyster culture in Europe (Buestel, Ropert, Prou, & Goulletquer, 2009; Gunther, 1897), there are still many unanswered questions relating to the biology and ecology of the species. This is probably the result of the near disappearance of the species from European waters for more than 50 years, following the successful introduction of *C. gigas* in aquaculture. As a result, it has been the subject of few recent studies, compared with *C. gigas* or *Mytilus edulis*. In consequence, much of the extensive existing body of science on *O. edulis* was undertaken in laboratory conditions (e.g. Tritar, Prieur, & Weiner, 1992; Wilson, 1980) or relates to topics of importance to aquaculture (e.g. González-Araya & Robert, 2018; Labarta, Fernández-Reiriz, & Pérez-Camacho, 1999; Mesías-Gansbiller et al., 2013), which may differ from those of oyster reef restoration. For example, the disease and invasive non-native species issues of taking oysters from aquaculture to the table market are very different from those of taking oysters from aquaculture and placing them back into the marine environment elsewhere. As a consequence, many of the identified knowledge gaps require field studies that can be addressed through pilot restoration efforts, as opposed to laboratory work, enabling restoration progress despite the many identified questions. This is also reflective of the fact that few of the questions (three of 40) were identified by >70% the experts as being truly limiting.

The 'natural' setting of oyster reefs in Europe was another key identified knowledge gap. The lack of an established baseline, with regard to either the historical extent and habitat attributes or a current-day reference state, presents challenges for oyster restoration in Europe today. The fact that the historical losses in extent and habitat quality largely occurred prior to the 1900s has resulted in a collective, intergenerational amnesia (Alleway & Connell, 2015), which presents challenges for stakeholder engagement and communication as well as with acceptance by policy and permitting agencies.

While restoration in Europe is currently restricted to relatively small-scale projects at individual sites, a number of questions highlighted the need for recognition of the larger-scale geographical linkages at the project planning stage. This was with regards to both the location of restoration efforts to maximize the benefits of overspill of larvae from restoration sites and consideration of the possible risks of connectivity between diseased and naive populations. Understanding the connectivity of populations also has implications for the effective population size, and correspondingly the potential for the population to respond to new stressors as they arise.

By necessity, the questions were scoped to meet the immediate needs of the oyster restoration community in Europe (identifying questions that can be answered within 5–10 years); however, a number of questions clearly have implications for oyster restoration into the future, in particular with regards to the potential interactions between threats which may themselves change spatially or in severity over time. The fact that these questions are drawn from across Europe greatly increases their relevance into the future. With the reality of environmental change, information from across the full range of the species is likely to be pertinent in the future, and collaborative large-scale efforts are likely to yield greater benefits than isolated projects.

Oyster reef restoration in Europe may be in its infancy, but there is currently rapid growth in interest and funding for projects. It is intended that the questions posed here will encourage research and focus efforts on resolving the key issues that are currently barriers to the expansion and scaling up of oyster restoration in Europe. A coordinated approach to answering these questions will allow for a cost-effective and efficient scaling up of oyster restoration, and we hope that researchers, funders and policymakers will take note.

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