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PERSPECTIVE NOTE OPEN ACCESS

# Overcoming *Ostrea edulis* seed production limitations to meet ecosystem restoration demands in the UN decade on restoration

Philine S.E. zu Ermgassen[1], Åsa Strand[2], Nienke Bakker[3], Ainhoa Blanco[4], Kruno Bonačić[5], Pierre Boudry[6], Gianni Brundu[7], Tom C. Cameron[8], Iarfhlaith Connellan[9], Fiz da Costa[10], Alison Debney[11], Monica Fabra[12], Anamarija Frankic[13], Celine Gamble[11], Mathew W. Gray[14], Luke Helmer[12,15], Zoë Holbrook[16], Tristan Hugh-Jones[17], Pauline Kamermans[4], Thorolf Magnesen[18], Pernille Nielsen[19], Joanne Preston[12], Christopher J. Ranger[20], Camille Saurel[19], David Smyth[21], Brecht Stechele[22], John A. Theodorou[23] and Bérenger Colsoul[24,*]

1 Changing Oceans Group, School of Geosciences, University of Edinburgh, James Hutton Rd, King's Buildings, Edinburgh EH9 3FE, UK
2 IVL Swedish Environmental Research Institute, Fiskebäckskil, Sweden
3 Roem van Yerseke BV, Yerseke, The Netherlands
4 Wageningen Marine Research, Wageningen University and Research, Yerseke, The Netherlands
5 Department of Applied Ecology, University of Dubrovnik, Dubrovnik, Croatia
6 Département Ressources Biologiques et Environnement, Ifremer, ZI de la pointe du diable, CS 10070, 29280 Plouzané, France
7 International Marine Centre – IMC, Loc. Sa Mardini, 09170 Torre Grande, Italy
8 School of Life Sciences, University of Essex, Colchester, UK
9 Redbank Shellfish, New Quay, Burrin, Co Clare, Ireland
10 AQUACOV, Instituto Español de Oceanografia (IEO, CSIC), Centro Oceanografico de Vigo, Subida a Radio Faro, 50, 36390 Vigo, Spain
11 Conservation & Policy, Zoological Society of London, London, UK
12 Institute of Marine Sciences, School of Biological Sciences, University of Portsmouth, Portsmouth, UK
13 Department of Ecology, Agronomy and Aquaculture, University of Zadar, Zadar, Croatia
14 Horn Point Laboratory, University of Maryland Center for Environmental Science, Cambridge, MD, USA
15 Blue Marine Foundation, London, UK
16 University of Southampton, National Oceanography Centre, Southampton, UK
17 Atlantic Shellfish Ltd, Cork, Ireland
18 Department of Biological Sciences, University of Bergen, Norway
19 Coastal Ecology, Danish Shellfish Centre, National Institute of Aquatic Resources, Technical University of Denmark, Øroddevej 80, 7900 Nykøbing Mors, Denmark
20 Fal Fishery Cooperative CIC - SavingESTER, Mylor, Falmouth, Cornwall, UK
21 School of Ocean Science, Bangor University, Bangor, UK
22 Laboratory of Aquaculture & Artemia Reference Center, Ghent University, Coupure Links 653, 9000 Gent, Belgium
23 Department of Fisheries & Aquaculture, University of Patras, Mesolongi Gr 30200, Greece
24 Biological Institute Helgoland, Alfred-Wegener-Institut Helmholtz-Zentrum für Polar- und Meeresforschung, Helgoland, Germany

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**Abstract –** The European flat oyster, *Ostrea edulis*, is a habitat-forming bivalve which was historically widespread throughout Europe. Following its decline due to overfishing, pollution, sedimentation, invasive species, and disease, *O. edulis* and its beds are now listed as a threatened and/or declining species and habitat by OSPAR. Increasing recognition of the plight of the oyster, alongside rapidly developing restoration techniques and growing interest in marine restoration, has resulted in a recent and rapid growth in habitat restoration efforts. *O. edulis* seed supply is currently a major bottleneck in scaling up habitat restoration efforts in Europe. *O. edulis* has been cultured for centuries, however, research into its culture declined

*Corresponding author: berenger.colsoul@awi.de

following the introduction of the Pacific oyster, *Crassostrea gigas* to Europe in the early 1970 s. Recent efforts to renew both hatchery and pond production of *O. edulis* seed for habitat restoration purposes are hampered by restoration project timelines and funding typically being short, or projects not planning appropriately for the timescales required for investment, research-and-development and delivery of oyster seed by commercial producers. Furthermore, funding for restoration is intermittent, making long-term commitments between producers and restoration practitioners difficult. Long-term, strategic investment in research and production are needed to overcome these bottlenecks and meet current ambitious restoration targets across Europe.

**Keywords:** Ostrea edulis / coastal restoration / aquaculture / hatchery / spatting pond

## 1 Native oyster habitat in Europe

Until the mid-1800 s, European flat oysters, *Ostrea edulis*, formed habitats across expansive areas of Europe's coasts and seas (Olsen, 1883). Multiple generations of oysters lived and grew together to form reefs or beds (Möbius, 1877). These oyster reefs filtered particles from the water and deposited them on the seabed, they formed a habitat in which many other species made their homes (zu Ermgassen et al., 2020), and they were also the basis of large and lucrative fisheries (Thurstan et al., 2013; Hayden-Hughes et al., 2023). Oyster habitats are a mix of living oysters and their dead shells, both of which were removed by dredge fishing. As a result, by the mid-1800 s the habitat they formed was functionally extinct from all but a handful of sites (Beck et al., 2011). Remaining European oyster habitats have been further impacted by increased sedimentation, poor water quality and introduced diseases (Helmer et al., 2019).

Oyster densities in Europe are generally insufficient to support the natural recovery of the habitat, but active restoration in other regions of the world has demonstrated that once oyster populations are at sufficient densities and the underlying substrate is suitable, oyster populations can recover on their own (La Peyre et al., 2014). This potential is supported by evidence of some limited natural recovery in Europe (Smyth et al., 2020). With recovery of the oyster habitats, coastal communities have been shown to benefit from the renewed ecosystem services, such as increased fish production, enhanced nutrient removal, and increased water clarity (Grabowski et al., 2012). This improvement in water clarity may in turn benefit other threatened coastal habitats, such as seagrass meadows (Sharma et al., 2016). In the longer term, healthy oyster populations may also provide "spill over" into areas suitable for recreational or commercial oyster fisheries (Peters et al., 2017). *O. edulis* habitat recovery in coastal systems furthermore has the potential to rekindle historical cultural heritage and community connections to the sea (zu Ermgassen et al., 2013), with many current restoration efforts adopting a strong public engagement focus aimed at reconnecting local communities with this functionally extinct habitat (see Native Oyster Restoration Alliance; NORA, https://noraeurope.eu/category/outreach/for examples).

Ecological restoration is challenging, both because past and ongoing global change mean that conditions for restoration are constantly changing (Jackson and Hobbs, 2009), and because knowledge gaps remain regarding best practice for restoration actions, in particular where reference sites are difficult to identify (Suding, 2011). Yet the need for restoration of degraded or lost habitats remains great and is increasingly included in policy agendas as a key action to mitigate biodiversity loss and increase ecosystem service delivery (Suding et al., 2015). While challenges remain and lessons are still being learnt (zu Ermgassen et al., 2020), the practice *O. edulis* habitat restoration is already established and supported by continued knowledge sharing within the community (Preston et al., 2020).

Native oyster restoration efforts in Europe are expanding rapidly. The number of projects has increased from five (2015) to 33 (2021) within ten countries (Preston et al., 2021). This growth is expected to continue given recent commitments at a governmental level to address the Sustainable Development Goals and the UN Decade on Restoration (https://www.decadeonrestoration.org/), the Department for Environment, Fisheries and Agriculture (Defra, UK) 25 Year Plan for the Environment, and the recent proposal of an Environmental Restoration Law by the European Commission. This proposal sets out a restoration goal of 20% of EU seas to be restored by 2030, and ultimately all ecosystems in need of restoration by 2050 (https://environment.ec.europa.eu/publications/nature-restoration-law_en). If passed into law, this will result in a significant scaling up of current restoration efforts. While huge strides have been made in identifying ways of addressing some of the key barriers to scaling up *O. edulis* habitat restoration (Preston et al., 2020), a significant shortfall in production of *O. edulis* seed that meets the specific needs of ecological restoration remains (Kamermans et al., 2020).

## 2 The current status of *O. edulis* seed production in Europe

European flat oyster seed is currently commercially produced in Europe by one of three methods: 1) spatting ponds; 2) wild sea-based collection; and 3) hatchery reared seed (Colsoul et al., 2021). Pond-based production of oyster spat takes place in land-based ponds which are temporarily closed off from the adjacent open water during oyster spawning to ensure higher densities of oyster recruitment on the supplied substrate within the pond (Strand et al., 2018). Sea-based collectors rely on natural spat settlement in an open water environment. Spat collectors are placed in the water at carefully controlled times relative to spawning and settlement to maximize recruitment. Poorly timed placement can result in reduced oyster recruitment due to competition with biofouling organisms such as mussels, algae, bryozoans, and colonial tunicates or the peak of the reproductive period being missed (van den Brink et al., 2020). Hatchery production involves the conditioning of broodstock in controlled conditions to stimulate spawning, as well as the subsequent care and feeding of larvae until settlement and juvenile recruitment (Helmet al., 2004).

Research effort into *O. edulis* has been limited since the 1970 s, following the introduction and wide scale replacement of this species in aquaculture by the Pacific oyster, *Crassostrea gigas* (Colsoul et al., 2021). *C. gigas*, was introduced to Europe, in response to the decline due to a viral disease (Grizel & Héral, 1991) of the inappropriately named Portuguese oyster (*C. angulata;* which was later discovered to be native to southern Asia; Boudry et al., 1998). Uptake of *C. gigas* in aquaculture increased further following the accidental introduction of the parasite *Bonamia ostreae*, a haplosporidian parasite accidentally introduced into France in the 1970 s (Pichot et al., 1979). Infections by *B. ostreae* develop into the disease 'bonamiosis', which can result in mortalities of 80–90% in affected *O. edulis* populations (Culloty and Mulcahy, 2007). *B. ostreae* is now present throughout much of Europe and must be considered as a factor which requires management when restoring native oyster habitats. Disease research and management is therefore key to scaling up restoration and aquaculture (zu Ermgassen et al., 2020).

The supply of oysters (adults and spat) that fulfil the specific requirements of restoration practices (e.g., certified disease-free, representing local genetic diversity, spat on shell or specific size classes) is a major bottleneck in restoration (Kamermans et al., 2020). This bottleneck is due both to the dearth of productive wild populations, meaning that sea-based collection and pond production are not possible in many locations, and to the challenges of scaling up production within hatcheries. Hatchery production of oyster species is challenging in part due to unexplained mass mortality events of larvae (Gray et al., 2022), while the lack of *O. edulis* specific hatchery protocols and insufficient opportunities for technical training relating to husbandry of this species have also been identified as challenges to the scaling up for hatchery production (zu Ermgassen, Albentosa, Bakker et al., submitted). Substantial advances are, however, being made in addressing research questions relating to the husbandry of *O. edulis* in hatcheries (e.g. Alter et al., 2023; Alter et al., 2023; da Costa et al., 2023).

Existing projects have already purchased and deployed more than half a million oysters over the past five years and have plans to more than double that over the next two years alone (NORA, unpublished data). The projected increase in restoration activities resulting from both an increase in active projects, and the aforementioned international commitments to restore the oceans, represents a dramatic need to scale up *O. edulis* seed production. This is in addition to the ambitious targets for increasing aquaculture production of *O. edulis.* For example, France has recently set the target of increasing aquaculture production of *O. edulis* from <1 000 tons $yr^{-1}$ today to 8 000 tons $yr^{-1}$ by 2030 (Ministère de la mer, 2021).

## 3 How does *O. edulis* seed production for habitat restoration need to develop?

There is currently a fruitful collaboration between existing oyster producers and the native oyster habitat restoration practitioners. Yet, the interannual variability and unpredictable nature of oyster seed production, alongside the need for commercial producers to meet the demands of long-standing customers in the more consistent table market, often leaves producers struggling to meet the increased demand from restoration (Strand et al., 2021). This problem is exacerbated by the current lack of a long term funding model for restoration efforts. While a restoration project may be planned over 10 years, individual elements of the project frequently work with short term funding, meaning that spending cannot be committed more than 1–2 years in advance. The resulting uncertainty in what budget will be available for purchasing oysters for restoration makes it risky for industry to upscale production and divert effort from other parts of their business in order to produce seed that meets the requirements of restoration projects. The lack of ability to commit to spending in the longer term therefore results in higher risk of non-delivery to the restoration projects, resulting in reputational risk for the restoration project managers and a risk of defaulting on commitments to funders. This un-countered risk on both sides makes it challenging to scale up production of oysters and restoration projects without greater and more long-term support.

Moving forward, seed production for restoration efforts can in many cases not rely on current commercial production. Restoration projects have differing and additional requirements to those of the food market for which oyster seed is traditionally produced. For example, restoration projects favour the use of local broodstock, where available, and seek representative genetic diversity in the resulting offspring. Restoration projects also require assurance that the oysters purchased for relaying are *O. edulis* only, and therefore require strict segregation from production of non-native species such as *C. gigas*. Additionally, projects are increasingly interested in receiving their juvenile oysters as "spat on shell" (Kamermans et al., 2020). This is when several oysters are settled together on the same shell. Spat on shell is desirable for habitat restoration projects because it allows oysters to be deployed at a younger age than if they were singles, which can reduce costs and biosecurity risks (Preston et al., 2020). Commercial production from spatting ponds meets many of these requirements and presents a good possible seed source for local restoration demand, where biosecurity concerns can be overcome.

Biosecurity is considered paramount to project success and essential to meeting regulatory guidelines. Biosecurity concerns arise not only from oyster diseases, but also from potential hitchhikers, and particular concern may be raised by the presence of invasive, non-native species. The potential suite of species present at the seed production or grow-on site is considered at several stages of restoration projects prior to deployment (see zu Ermgassen et al., 2020). The application of biosecurity protocols presents a challenge for the movement of small oysters from sources lacking adequate biosecurity measures, as they are typically more sensitive to the physical and chemical cleaning required to reduce the risk of hitchhikers. Spat on shell production in spatting ponds is therefore suitable for meeting local demand, but is not appropriate for meeting demand further afield. Development of hatchery techniques such as spat on shell and remote setting of larvae, which allow for the transport of individuals directly from biosecure hatcheries to grow-out locations is therefore an area which requires further research.

Disease management is a strong focus of many restoration efforts (Pogoda et al., 2019), with the aim of future proofing restoration efforts in the presence and increasing range of *B. ostreae*. While promising genetic selection trials of *O. edulis* for resistance to bonamiosis in hatcheries and spatting ponds exist (Lynch et al., 2014), more research is needed to estimate the heritability and characterize the genomic basis of resistance to *B. ostreae* in the native oyster for restoration purposes. Additionally, implementing aquaculture practices to maintain regional and local genetic diversity, while simultaneously exploring the potential to identify and propagate *B. ostreae* resistant oysters, must be a major focus to protect native oyster restoration efforts from the spread of the disease (Monteiro et al., unpubl. data). Such a focus would also increase opportunities for restorative aquaculture (Overton et al., 2023).

## 4 Moving *O. edulis* seed production forward in the UN decade on ecological restoration

Oyster habitat restoration is a key component of resilient and sustainable coastal systems, as set out in the international objectives of the UN decade on restoration. Large scale investment is needed to support the production of oyster seed for large scale restoration in Europe. An example of how this has been achieved can be found in the USA where in 2009, President Obama signed Executive Order 13508 committing to restoring eastern oyster (*Crassostrea virginica*) habitat in 10 tributaries of the Chesapeake Bay by 2025. To meet this need, the State of Maryland made a major investment ($65 million) to restore oysters in its portion of the Bay (856 acres across 5 sub-estuaries) (Maryland and Virginia Oyster Restoration Interagency Workgroups of the Chesapeake Bay Program's Sustainable Fisheries Goal Implementation Team, 2022). The restoration effort is highly collaborative; the University of Maryland Center for Environmental Science (UMCES) Horn Point Laboratory Oyster Hatchery indirectly receives appropriated federal funds from the National Oceanic and Atmospheric Administration, which is used to condition, spawn, and culture larvae, while a non-profit organisation, Oyster Recovery Partnership (ORP), works with the US Army Corp of Engineers (USACOE) to ensure planting of spat on shell occurs in sanctuaries while not impeding commercial and recreational boating. Sanctuaries are in turn protected from poaching by the Maryland Department of Natural Resources. Total hatchery production and efficiencies have improved over time. Currently more than 11 billion oyster spat have been deployed to the waters of the Chesapeake Bay for restoration purposes since the signing of Executive Order 13508. 'Restored' was defined as a minimum density of 50 animals $m^{-2}$, which is similar to densities recorded 100 years ago (Oyster Metrics Working Group, 2011). If a site does not achieve this goal after the first planting, as determined through underwater surveys, the USACOE will replant until the site is 'restored'. As such, there is also a commitment to monitoring by UMCES and ORP, which stands in stark contrast to earlier efforts of restoration for this species. Since 1995, previous *C. virginica* restoration projects were typically small in scale, funded by both private and public sources, scattered throughout the range of this species (157 separate projects restoring 763 acres across 16 states), and the success of the projects was uncertain since they commonly lacked monitoring or specific ecological goals (Brumbaugh and Coen, 2009).

In Europe, funding has been identified as a key barrier to ecological restoration (Cortina-Segarra et al., 2021). This is also the case for *O. edulis* habitat restoration, where scaling up of restoration cannot be achieved without further investment in the infrastructure of oyster production, including education and training of personnel to manage spatting ponds, hatcheries (zu Ermgassen et al., submitted), and oyster grow-out facilities, as well as consistency in market demand by restoration projects. To ensure that there is sufficient consistency and growth in oyster seed production to enable investment and meet the ever-increasing and specialist demand resulting from international commitments to restore the oceans, greater and more consistent funding is needed.

While it may be anticipated that the proposed restoration law, should it be passed, should result in more direct government funding for restoration activities, to date government investment in oyster habitat restoration has been limited in most European countries. Government investment to meet national and international obligations in ecological restoration remain critical, however, there is also broad interest in developing a wider range of potential funding models. The offshore renewable industry presents one such opportunity, as it increasingly seeks to include habitat restoration and recovery in wind farm designs (Kamermans et al., 2018). For example, in The Netherlands, the assessment of new offshore wind farm licenses consider the mitigation activities for biodiversity proposed within the bids, which may include oyster restoration (ter Hofstede et al., 2023). Another potential avenue whereby regular funding sources may be developed, is through payment for ecosystem services, whereby the services or function an ecosystem or habitat provides of benefit to humans is assigned an economic value and can be traded by the resource owner. The economic value can be estimated by various means, such as replacement costs (cost of providing the service artificially) or avoidance costs (costs that would be incurred due to the absence of the services) (Farber et al., 2002). For example, the benefit of carbon sequestration of a habitat might be bought by a company wishing to offset carbon emissions, through agreed accreditation and credit trading schemes. This approach could be applied to any ecosystem service; in the case of oyster habitat, biodiversity gain or nutrient removal offer potentially significant value (Grabowski et al., 2012; Watson et al., 2020). Finally, restorative aquaculture presents an opportunity to address blue growth and green deal aims simultaneously. By integrating restorative aquaculture and nature management objectives, it may be possible to establish a "win-win" scenario (The Nature Conservancy, 2021), where the wild *O edulis* populations benefit from larval supply from aquaculture, and aquaculture benefits from a greater social licence and recognition of the associated biodiversity benefits during the permitting process. This is possible where aquaculture activities build restoration impacts into their project design from their conception. Aquaculture which does not consider its restorative potential through siting and genetics, has the potential to have negative impacts on restoration efforts (Šegvić-Bubić et al., 2020; Overton et al., 2023).

In Europe, efforts to increase the transferability of industry know-how through protocol development and best practice guidelines have been undertaken for spatting ponds and sea-based seed collection (AquaVitae project H2020). Similarly, many of the commercial and academic hatcheries producing *O. edulis* in Europe are currently cooperating by sharing information on unexpected crashes in larval cultures, and are actively engaging in knowledge exchange, working together to overcome production bottlenecks (zu Ermgassen et al., submitted). The willingness and networks are there; what is now needed is the funding to scale up those efforts.

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