Conservation Letters

WILEY

Conservation Letters
A journal of the Society for Conservation Biology
Open Access

REVIEW OPEN ACCESS

European Native Oyster Reef Ecosystems Are Universally Collapsed

Philine S. E. zu Ermgassen[1] | Hannah McCormick[2] | Alison Debney[2] | José M. Fariñas-Franco[3] | Celine Gamble[2] | Chris Gillies[4] | Boze Hancock[5] | Ane T. Laugen[6] | Stéphane Pouvreau[7] | Joanne Preston[8] | William G. Sanderson[9] | Åsa Strand[10] | Ruth H. Thurstan[11]

[1]Changing Oceans Group, School of Geosciences, University of Edinburgh, Edinburgh, UK | [2]Zoological Society of London, ZSL London Zoo, London, UK | [3]Marine and Freshwater Research Centre and Department of Natural Resources and the Environment. School of Science and Computing, Atlantic Technological University, Galway, Ireland | [4]SeaGen Aquaculture, Newhaven, Victoria, Australia | [5]Global Oceans Team, The Nature Conservancy, University of Rhode Island, Kingston, Rhode Island, USA | [6]Department of Natural Sciences, Centre for Coastal Research, University of Agder, Kristiansand, Norway | [7]Ifremer, LEMAR, Argenton en Landunvez, Bretagne, France | [8]Institute of Marine Sciences, School of Environment and Life Sciences, University of Portsmouth, Portsmouth, UK | [9]Institute of Life and Earth Sciences, EGIS, Heriot-Watt University, Edinburgh, Scotland, UK | [10]Department of Environmental Intelligence, IVL Swedish Environmental Research Institute, Fiskebäckskil, Sweden | [11]Centre for Ecology and Conservation, University of Exeter, Cornwall, UK

Correspondence: Philine S. E. zu Ermgassen (philine.zu.ermgassen@ed.ac.uk)

Received: 21 December 2023 | **Revised:** 19 October 2024 | **Accepted:** 22 October 2024

Funding: This work was funded by the Flotilla Foundation. RHT was funded by the Convex Seascape Survey, the European Research Council (ERC) under the European Union's Horizon 2020 research and innovation program (grant agreement No 856488 – ERC Synergy project "SEACHANGE: Quantifying the impact of major cultural transitions on marine ecosystem functioning and biodiversity"), and the COST Action MAF-WORLD CA20102, supported by COST (European Cooperation in Science and Technology), www.cost.eu. WGS was funded by the Dornoch Environmental Enhancement Project, funded by The Glenmorangie Company. Figure 1 was produced by Maria Eggertsen, funded by the European Research Council (ERC) under the European Union's Horizon 2020 research and innovation program (grant agreement No 856488 – ERC Synergy project "SEACHANGE: Quantifying the impact of major cultural transitions on marine ecosystem functioning and biodiversity").

Keywords: habitat restoration | historical ecology | IUCN Ecosystem Red List | *Ostrea edulis* | shellfish reef | threats | shifted baseline

ABSTRACT

Oyster reefs are often referred to as the temperate functional equivalent of coral reefs. Yet evidence for this analogy was lacking for the European native species *Ostrea edulis*. Historical data provide a unique opportunity to develop a robust definition for this ecosystem type, confirm that *O. edulis* are large-scale biogenic reef builders, and assess its current conservation status. Today, *O. edulis* occur as scattered individuals or, rarely, as dense clumps over a few m^2. Yet historically, *O. edulis* reef ecosystems persisted at large scales (several km^2), with individual reefs within the ecosystems present at the scale of several hectares. Using the IUCN Red List of Ecosystems Framework, we conclude the European native oyster reef ecosystem type is collapsed under three of five criteria (A: reduction in geographic distribution, B: restricted geographic range, and D: disruption of biotic processes and interactions). Criterion C (environmental degradation) was data deficient, and Criterion E (quantitative risk analysis) was not completed as the ecosystem was already deemed collapsed. Our assessment has important implications for conservation policy and action, highlighting that the habitat definitions on which conservation policies are currently based reflect a highly shifted baseline, and that the scale of current restoration efforts falls far short of what is necessary for ecosystem recovery.

1 | Introduction

Oyster reef ecosystems were once a globally distributed ecosystem type in temperate coastal seas and estuaries (Beck et al. 2011; Gillies et al. 2020; Thurstan et al., 2024a, 2024b; zu Ermgassen et al. 2012). In historical accounts, oyster reefs were described as the temperate equivalent of coral reefs (Ritter von Hamm 1881), forming elevated three-dimensional structures over large areas (Williams 1837; zu Ermgassen et al. 2012). In parts of the world, these reefs were so massive they represented a navigational hazard (Dumain 1832; Hinke 1916). Reef-building oyster species have a long history of human exploitation, with evidence of extensive collection and consumption of oysters from middens across Europe, Asia, Australia, and the Americas illustrating that oysters have been an important food and cultural resource in coastal communities for thousands of years (Astrup et al. 2021; Rick et al. 2016; Szabó and Amesbury 2011; Thurstan et al. 2020). Dramatic declines in the extent of oyster reefs were documented globally following European colonization and the industrial revolution (Alleway and Connell 2015; Beck et al. 2011; Thurstan et al. 2013; Thurstan et al. 2020; zu Ermgassen et al. 2012). Although pollution, harsh winters, and changes to hydrological conditions were noted in historical texts to have caused localized extinctions (Krøyer 1837; Holmes 1927; Royal Commission 1866), the primary driver of loss of oyster reef ecosystems has been extraction by fishing (Krøyer 1837; Thurstan et al. 2024a; Went 1961).

Today, ecosystem-forming oyster species including those in the genus of *Saccostrea*, *Crassostrea*, and *Ostrea* still form high-relief, complex reef structures in many temperate estuaries across the globe (Bahr and Lanier 1981; Gillies et al. 2017; Norgard et al. 2018), albeit over significantly smaller areas, and with a substantially reduced habitat complexity relative to historical records (Gillies et al. 2018; zu Ermgassen et al. 2012). This is, however, not the case in Europe, where (with the exception of a few locations) the native oyster, *Ostrea edulis*, predominantly exists as scattered individuals, occurring at densities rarely greater than 1 individual m^{-2} (Allison et al. 2020; Pouvreau et al. 2023; Thorngren et al. 2019). Recognition of the degraded status of *O. edulis* populations and the reef ecosystems they form is reflected in their many conservation designations. *O. edulis* and its habitat are recognized as threatened and/or declining in Region II and Region III (Greater North Sea and Celtic Sea, respectively) under the Convention for the Protection of the Marine Environment of the North-East Atlantic (the OSPAR convention; OSPAR Commission 2009), and are recognized by some member states under the "Reefs" feature of the Habitats Directive (European Council 1992) and in some Biodiversity Action Plans (e.g., UKBAP 1999). These designations are critically important for the protection of *O. edulis*; however, they are focused largely on the species or on the habitat at a small scale (OPSAR Commission 2009). It is likely that this consideration of the habitat at a small spatial scale has consequences for its ecological recovery, as it is widely recognized that metapopulation dynamics are key to the recovery of habitat-building oyster species (e.g., Schulte et al. 2009). Current habitat definitions are therefore ill equipped as ecological baselines against which ecosystem condition can be assessed.

The growing recognition of the degraded and yet ecologically important status of *O. edulis* oyster reef ecosystems has resulted in increasing efforts to restore the habitat at numerous locations across its native range (Preston et al. 2020; Pouvreau et al. 2023). Restoration activities are set to increase both in scope and scale as the focus on restoration of degraded terrestrial and marine habitats gains momentum at a national and international level (EU Commission 2022; United Nations General Assembly 2020). An improved description of the ecosystem's physical and biological attributes prior to significant disturbance is essential for developing a historical baseline against which current and future recovery efforts can establish targets, assess progress, and determine the efficacy of conservation interventions, including for the application of the EU Restoration Law.

Recent work by Thurstan et al. (2024a, 2024b) documented the historical locations, ecosystem characteristics, and extents of *O. edulis* reef ecosystems in Europe. The broad spatial coverage and habitat descriptions compiled provide a novel opportunity to visualize the form and extent of *O. edulis* reef ecosystems prior to their widespread degradation. Thurstan et al. (2024a) found that *O. edulis* reefs were historically widely distributed throughout coastal waters of Europe and North Africa, as well as in the southern North Sea, to 80 m depth. They gathered numerous descriptions of reefs extending over many ha or even km^2 and forming complex structures with vertical relief "composed of several layers" (Levasseur 2006), with "oysters, almost placed one on top of the other like stones, forming a wall" (Marsili 1715). In addition, they identified sources describing the rich benthic community associated with this structurally complex habitat. These descriptions all serve to elucidate the historical extent and physical and biological characteristics of oyster reef ecosystems throughout Europe, based primarily on an 1800–1930 baseline (Thurstan et al. 2024b).

Here, we follow the IUCN Red List of Ecosystems Framework (Keith et al. 2013) to assess the current status of the European native oyster reef ecosystem. The Red List of Ecosystems is a tool for assessing the risk of ecosystem collapse, much in the same way as the Red List of Threatened Species assesses the risk of species extinction. Ecosystem red lists are one of the headline indicators in the monitoring framework of the post-2020 Global Biodiversity Framework (Kunming-Montreal Global Biodiversity Framework), and therefore play a critical role in providing structured evidence to support policy development and decision-making. We develop a definition of the European native oyster reef ecosystem type based on historical descriptions of *O. edulis* reefs and analogous shellfish ecosystems formed by *Ostrea* species in other regions. Our definition and Red List Assessment can be used to guide national and Europe-wide conservation strategies, prioritize and monitor restoration action, inform resource management, and raise public awareness to support management and protection policy.

2 | Methods

Applying the IUCN Red List of Ecosystems assessment framework to an ecosystem requires that the ecosystem in its functional and collapsed states are clearly defined, and that the pathways to collapse (drivers of decline) are identified. Once the definitions are clear, the current status of the ecosystem can be assessed by applying those definitions to current data. Assessment is undertaken by applying each of five criteria (A: reduction in distribution, B: restricted distribution, C: environmental degradation, D: disruption of biotic processes, and E: quantitative assessment of risk), with the final classification equal to the highest threat level identified (Keith et al. 2013).

2.1 | Development of Ecosystem and Ecosystem Collapse Definitions

Following the IUCN Red List of Ecosystems Framework (Keith et al. 2013), we developed a comprehensive definition of the European native oyster ecosystem type created by *O. edulis*, and the associated threshold of collapse. This ecosystem definition relates to hierarchical Level 5 (global ecosystem type), as defined by the IUCN Global Ecosystem Typology (Keith et al. 2020).

European native oyster reefs are found both intertidally and down to 80 m depth (Thurstan et al. 2024a), from 20 to 42 ppt salinity and where the underlying sediment is not overly mobile and current speeds are typically 0.05–0.45 m s^{-1} (Pogoda et al. 2023). European native oyster reefs have a rich, diverse, and distinct associated community, supporting a higher species richness and abundance of species than surrounding unstructured habitats (Kennon et al. 2023). Although populations of *O. edulis* persist as non-native species on the eastern coast of North America, its native range is restricted to Europe from Norway to the African coast of the Mediterranean and into the Black Sea (Thurstan et al. 2024a).

We reviewed existing definitions of shellfish ecosystems globally to identify important ecosystem attributes representative of shellfish ecosystems irrespective of ecosystem-forming species, including the Ecosystem Functional Group (M1.4) "Shellfish beds and reefs" from the IUCN Global Ecosystem Typology (Keith et al. 2020) and "biogenic reef habitat" *sensu* Brown et al. (1997) (Table S2a–c). Consistently identified attributes included the structure and form of reefs, the formation of biogenic structure created by oysters when occurring in high densities, the contribution of dead shells to maintain a positive shell budget (Hemeon et al. 2020; Solinger et al. 2022), and the spatial scale at which these ecosystems historically functioned (Table S2a–c). We then determined collapse threshold values for identified attributes including *O. edulis* reef structure (oyster density, reef complexity, and reef height), spatial scale, and functions (associated community) by reviewing descriptions from historical texts collated by Thurstan et al. (2024a; relevant data extracted and presented in Table S2b–d), as well as evidence from related oyster species in other geographies (Table S2e). The geographical location of oyster reefs and their spatial extent were extracted from Thurstan et al. (2024a).

Oyster density is a key attribute of oyster reef condition (Pouvreau et al. 2021; zu Ermgassen et al. 2021), but quantitative assessments of densities were not available from the baseline period of assessment. Furthermore, habitat descriptions from the principal period of documentary evidence (1800–1930) typically described reefs, which were known to be overexploited (Krøyer 1837; Möbius 1877; Table S1a–c; Figure S1). Our threshold densities for ecosystem assessment were therefore based on cumulative evidence from descriptions of the ecosystem (Table S2b,c), catch rate information (Table S2d), and quantitative information from related species in other geographies (Table S2e), as well as the current understanding of *O. edulis* reef formation (Pouvreau et al. 2021; Table S2d,e).

Ecosystem collapse is when an ecosystem loses its defining attributes (Keith et al. 2013). Threshold values for those important attributes allow for the ecosystem state to be assessed. Our definition of the collapsed European native oyster reef ecosystem and the threshold of collapse was derived from relevant literature on reef-building attributes observed today (Pouvreau et al. 2021) and on the pathways to collapse.

2.2 | Collating Baseline and Current Ecosystem Data

The risk of collapse of the European native oyster reef ecosystems was assessed using the IUCN Red List of Ecosystems guidelines set out in Keith et al. (2013) and Bland et al. (2017). Significant declines in *O. edulis* reefs were observed in the 1800s (Royal Commission 1866; Thurstan et al. 2013) or earlier (Giovio 1524; Krøyer 1837; Levasseur 2006; Went 1961). In contrast, data from the past 50 years are limited to biological records of species occurrence (e.g., through the Global Biodiversity Information Facility), which may represent shell remains as opposed to live individuals, catch data, which are often challenging to disaggregate from aquaculture production (e.g., FAO), or stock assessments from a few geographically limited locations (e.g. Jenkin et al. 2023; The Marine Institute and Bord Iascaigh Mhara 2023; Thorngren et al. 2019). Due to this lack of more recent data, the IUCN Ecosystem Red Listing risk assessment was undertaken relative to a c. 1750 baseline using the historical data presented by Thurstan et al. (2024a).

Thurstan et al. (2024a, 2024b) extracted historical data on the presence of *O. edulis* reefs from targeted searches of government records, nautical charts, popular media, and scientific journals. Identified records were further assessed for whether there was high or low confidence that oysters were present in sufficient abundance to be reef-forming based on descriptions, landings data, and catch per unit effort information. Data were primarily recorded between 1800 and 1930 (Thurstan et al. 2024b), yet, as undisturbed bivalve reefs may persist for millennia at the spatial scale at which this dataset was compiled (10 km^2) (Manoutsoglou et al. 2024), likely represent reefs that were extant in 1750. The later date associated with the records is a product of both the increase in government and scientific publications in the 1800s relative to the 1700s and due to new oyster reefs being discovered as the fishery expanded its footprint (Bennema et al. 2020). Most records from the 1800s described fisheries that were already exploited, and it was rare for sources to recall information more than a few decades old (Table S1a,b). The one resource that did draw on quantitative records from across the Wadden Sea from 1709 noted that some "oyster banks" could no longer be located already by the 1740s (Krøyer 1837). As such, it is possible that the baseline extent represented here is an underestimate of the extent in 1750. It is also worthy of note that by using the IUCN Ecosystem Red Listing risk assessment baseline of c. 1750 and restricting our assessment to records with a high confidence that the reef was formed, we are excluding the southern Mediterranean from the analysis. It is not known whether the lack of evidence for reef building in this region is the result of overexploitation prior to the written records that formed the basis of the quantitative database or the natural ecological condition of *O. edulis* populations in the region. Written records from Xenocrates (4th century BCE) describe the River Nile and the Libyan Gulf, among other sites, as the source of some of the finest oysters (Andrews 1948), yet written records indicating high confidence of reef building are restricted to the northern Mediterranean. It is therefore possible that a 1750 baseline is inadequate for assessing the impact of human overexploitation in the southern Mediterranean.

To identify locations where *O. edulis* reef currently meets our ecosystem definition, data describing the location and ecosystem attributes of remaining oyster habitats were identified by using the Google search engine with the terms "oyster OR *Ostrea* AND COUNTRY" for each country known to fall within the historical distribution of the European native oyster (based on Thurstan et al. 2024b). The searches were undertaken between September 2022 and June 2023. Data were extracted from 56 publications (Table S4). Where recent surveys were not identified for a country, or where data were inconclusive, data were requested from local experts.

2.3 | Application of Red List Criteria

The collated historical and recent data were used to assess the risk of collapse through Criterion A (reduction in geographic distribution), under subcriterion 3 (relative to a 1750 baseline), and Criterion B (restricted geographic range), under subcriteria 1 and 2 (area of occupancy, extent of occurrence). Spatial data representing the location of sites (historical and current) meeting the *O. edulis* reef ecosystem definition were processed using QGIS software version 3.24 (QGIS Development Team). For Criterion A, the change in the extent was assessed both by comparing the number of locations, where *O. edulis* reef was recorded historically and presently, and by comparing the described extents of *O. edulis* reef, where such data were available historically (Thurstan et al., 2024a, 2024b). For Criterion B1, the extent of occurrence was determined by drawing a minimum convex polygon using the Minimum Bounding Geometry tool in QGIS 3.24, while for Criterion B2, the area of occupancy was determined by overlaying a grid layer of 10×10 km^2 overall grid squares that contained at least one oyster reef point today (the coordinate reference system used is ETRS89-extended/LAEA Europe). Criterion B (subcriteria 1 and 2) requires a thorough understanding of the existing and future threats (pathways to collapse) facing the ecosystem being assessed. Threats that currently impact, or have the potential to impact, *O. edulis* reef conditions were identified by Hughes et al. (2023), and subsequent evidence for each threat was sought from the literature (Table S3).

Criterion C (environmental degradation) was not assessed due to data deficiency. Although climate change, sedimentation, and changes in coastal salinity were identified as key abiotic factors impacting the expansion or recovery of *O. edulis* reefs (Table S3), we were unable to identify suitable long-term datasets within the timeframe of *Ostrea edulis* decline to assess the risk of collapse due to these environmental drivers.

Criterion D assessed the risk of disruption of biotic processes relative to a 1750 baseline (subcriterion 3; Keith et al. 2013). Three biotic factors were considered: (1) abundance of key species, (2) structural complexity, and (3) trophic diversity. Oysters are both allogenic and autogenic ecosystem engineers, substantially altering biotic processes and interactions both through their feeding activity and their physical structure (Kennon et al. 2023; Lee et al. 2023; Smyth and Roberts 2010). Their presence and abundance underpin these ecosystem engineering properties and associated biotic processes, as recognized in the Red List of Ecosystems assessment of the related Australian oyster species, *Ostrea angasi* (Gillies et al. 2020). Sustained recruitment of oysters at high densities contributes significant structural complexity to the sea floor (Pouvreau et al. 2021), while both their allogenic and autogenic ecosystem engineering properties likely contribute to the distinct associated community recorded on European native oyster reefs historically (Krøyer 1837; Möbius 1877; summarized in Thurstan et al. 2024a). Evidence that European native oyster reefs historically supported higher level trophic interactions is evident from observations of the natural history and feeding of the oystercatcher (*Haematopus ostralegus*), which was described in 1801 as follows: "*Oystercatcher, oyster thief, oyster collector.… The oystercatcher also swims but is more likely to be seen walking along the beach. At low tide, it seems to be particularly cheerful; then it runs around with a hooting sound, looking for its food, which consists mainly of oysters. The bird knows how to break open the shells very skillfully without hurting its beak on the sharp edges. If they are closed too tightly, it hits them against a rock so that they crack. If it can't find oysters, it will eat mussels, snails, and other worms, even dead animals*" (Lippold 1801, translated from German). Similarly, there is evidence that the loss of oyster reefs contributed to a reduced and altered trophic diversity in the Waddensea when samples from the late 1800s and early 1900s were compared with samples from the 1970s (Reise 1982).

Criterion E (quantitative risk analysis) was not assessed.

3 | Results

3.1 | Definition of the European Native Oyster Reef Ecosystem Type

European native oyster reefs can be defined as areas with high densities of multiple size classes of *Ostrea* spp. on a shell-dominated substrate (Table 1). Oysters within the reefs often form clumps and create a complex three-dimensional structure (Bodvin et al. 2011; Kennon et al. 2023; Thurstan et al., 2024a, 2024b; Table S2b–d; Figure 1). Associated bivalve species, such as *O. stentina* (in the Mediterranean) and *Mytilus edulis*, also contribute to the reef structure (Möbius 1877), but the primary ecosystem engineer is *O. edulis*. High-density patches may be interspersed with areas of low structural complexity (Figure 1B) or other habitats, such as eelgrass beds or maerl beds (Abancourt 1842; Marine Institute and Bord Iascaigh Mhara 2023).

The European native oyster reef ecosystem is a self-sustaining network of reefs. Oyster reefs are biogenic; for oyster reefs to persist or grow, oysters must be present at high enough densities to contribute shell to the underlying substrate at a rate greater than that lost through dissolution, biodegradation, or burial

TABLE 1 | Proposed reef attributes (physical form and functional features) of the European native oyster reef ecosystem.

Attribute	Fully functional reef ecosystems	Partially functional reef ecosystems	Oyster populations within alternate ecosystems	References
1. Oyster density and size frequency	> 20 live oysters m^{-2} representing multiple size classes	5–20 oysters m^{-2} representing multiple size classes	< 5 oysters m^{-2} multiple size classes may not be represented	Pouvreau et al. (2021)
2. Shell cover	> 25% cover		< 25%cover	Kasoar et al. (2015), Kennon et al. (2023)
3. Shell budget and reef height	Increasing or stable spatial extent and/or height.		Little or no evidence of shell substrate	Hemeon et al. (2020), Solinger et al. (2022)
4. Patch size and number	Multiple patches of reef (> 5 m^2), which may be separated by a few m to cover an area > 1 ha	Multiple patches of reef (> 5 m^2), which may be separated by a few m to cover an area < 1 ha	Few or no patches of oyster reef	Krøyer (1837), Joubin and Guérin-Ganivet (2009)

Note: Adapted from Gillies et al. (2020) to represent habitats built by *O. edulis*. This table aims to aid the delineation of reef ecosystems vs. alternative ecosystems with oyster populations by identifying threshold values for each attribute.

(Solinger et al. 2022). Based on historical evidence and congeneric reef-forming species, we propose a threshold density of 20 oysters m^{-2} for reef areas (Thurstan et al. 2024a; Tables S2b–d and 1). Accurate mapping of *O. edulis* reefs historically is rare, with mapping undertaken on the French oyster beds in the early 1900s providing the clearest insight into the spatial scale at which reefs historically persisted (Joubin and Guérin-Ganivet 2009; Thurstan et al. 2024a; Figure 2). Although individual reefs within the ecosystem predominantly formed on the scale of hectares (> 1 ha) (Figure 2A), multiple reefs persisted within a wider ecosystem (Figure 2B). This is a common feature of bivalve reef ecosystems (e.g., Baggett et al. 2014). A resilient ecosystem persists on a broader biogeographical scale, or metapopulation, even when individual reefs within it are smothered or negatively impacted (e.g., Krøyer 1837). The European native oyster reef ecosystem should therefore be assessed at the km^2 scale.

3.2 | Definition of European Native Oyster Reef Ecosystem Collapse

The European native oyster reef ecosystem is considered collapsed at the point at which there are no longer multiple size classes of *O. edulis* in the local population, and gregarious settlements leading to clumps are rare or absent, meaning that *O. edulis* do not contribute significantly to biogenic formation of three-dimensional structure. This results in a change from shell-dominated substrate to sand, mud, or subtidal mixed sediment without significant (> 25%) shell cover (Kasoar et al. 2015). The associated community is therefore representative of the alternative underlying substrate, which may be soft-bottomed, low-complexity habitat, cobble, or subtidal mixed sediments, depending on the location. Where invasive species have moved in to occupy the niche previously held by *O. edulis*, the associated community may instead reflect this shift. A collapsed European native oyster ecosystem does not span the expected depth range of the species nor the necessary spatial extent to classify as an ecosystem (individual reefs formed at the scale of hectares and reef systems functioning at the km^2 scale) (Table 1 and Figure 1C). The collapsed European native oyster ecosystem does not deliver ecosystem functions such as water filtration, nutrient cycling, enhanced biodiversity, sediment stabilization, or shell production at significant scales.

3.3 | Pathways to Collapse

Oyster reef ecosystems are particularly sensitive to collapse, as oysters and their shells are the preferred settlement substrate for oyster larvae (Colsoul et al. 2020; Rodriguez-Perez et al. 2019). The removal of the biogenic habitat therefore disrupts or interrupts the life cycle of the primary ecosystem engineer, *O. edulis*, and can tip the ecosystem into a state of negative feedback (Figure 3). The loss of oysters or reduction in larval recruitment has primarily occurred through the removal of oysters (i.e., fishing) (Thurstan et al. 2013). In addition, habitat disturbance from bottom-towed gears (Ezgeta-Balić et al. 2021), sedimentation (Sander et al. 2021), pollution (Helmer et al. 2019), invasive species (Drapkin 1963; Preston, Fabra et al. 2020), and disease (Culloty and Mulcahy 2007; Virvilis and Angelidis 2006) all play a role in the reduction or loss of oyster reefs in some locations (Helmer et al. 2019; Pouvreau et al. 2023; Table S3). Finally, changes in the salinity regime have also historically played a role in the local extirpation (Krøyer 1837) or establishment (Collin 1884) of *O. edulis* populations.

4 | Applying the IUCN Ecosystem Red Listing Criteria

4.1 | Ecosystem Red Listing Criterion A—Reduction in Distribution

Criterion A considers the change in extent of the ecosystem type over time (Keith et al. 2013). No recent records of *O. edulis* persisting at densities > 20 ind m^{-2} over areas > 1 ha (Table 1) were

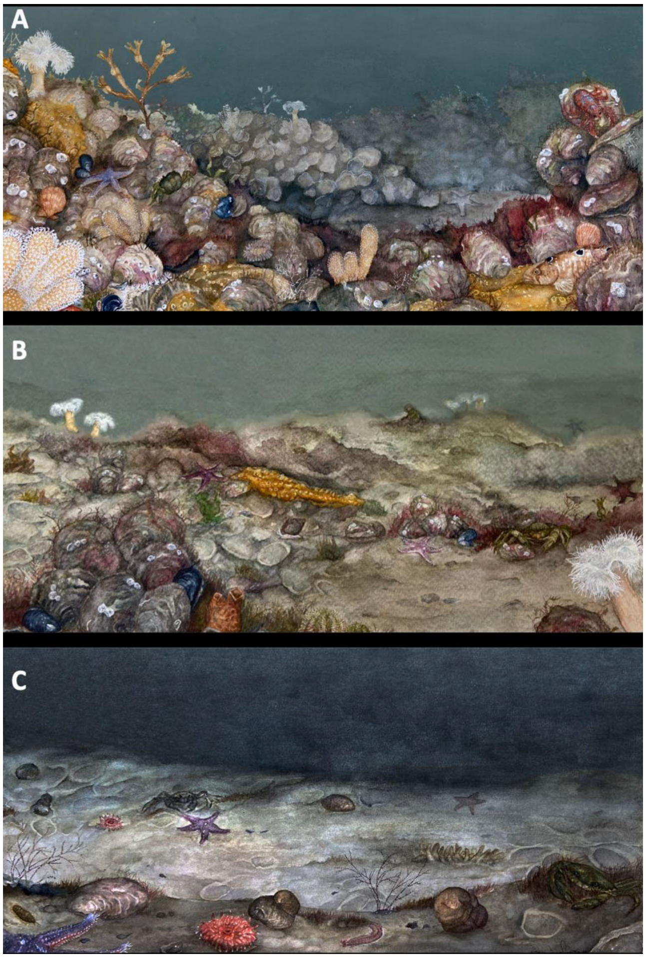

FIGURE 1 | Artist's impression of a European native oyster reef ecosystem, based on historical descriptions of associated species and habitat forms from Thurstan et al. (2024a). Panel A illustrates high-density and relief oyster reefs, which may, on a larger scale, be interspersed with patches or lower-complexity habitats (Panel B). Panel C illustrates the degraded habitat structure now representative of oyster habitats. Artist: Maria Eggertsen.

identified throughout the native range of the European native oyster (Table S4). As such, the extent of the European native oyster reef ecosystem was deemed to have declined from being present in 606 (10 km^2) grid cells in c. 1750 (Figure 4B) to zero in the present day (Table S4). In addition, while the historical spatial extent of oyster reef ecosystems was only documented from 317 of 1197 recorded locations, those locations encompassed a known reef area of > 1.7 million ha (Thurstan et al., 2024a, 2024b). The European native oyster reef ecosystem type is therefore deemed to be collapsed under category A3.

4.2 | Ecosystem Red Listing Criterion B—Restricted Distribution

Criterion B considers the current range of the ecosystem type (Keith et al. 2013). No current records of *O. edulis* persisting at densities > 20 ind m^{-2} over areas > 1 ha were identified (Table S4), which qualifies the ecosystem type as collapsed under subcriteria B1 and B2. In order to put this finding into context, the historical extent of occurrence and area of occupancy were also calculated based on point locations of all high-confidence historical *O. edulis* reef occurrences (Thurstan et al., 2024a, 2024b). The historical extent of occurrence was found to be 7,718,991 km^2 and the historical area of occupancy was found to be 606 (10 km^2) grid squares (Figure 4). Furthermore, numerous threats including poor water quality, invasive species, disease, and over-exploitation are still driving declines in *O. edulis* populations across its range (Table S3).

4.3 | Ecosystem Red Listing Criterion C—Environmental Degradation

Criterion C considers the condition of abiotic attributes of the ecosystem which have a defining role in ecological processes and/or the distribution of an ecosystem type (Keith et al. 2013). This assessment deemed the European native oyster reef ecosystem type to be data deficient under Criterion C.

4.4 | Ecosystem Red Listing Criterion D—Disruption of Biotic Processes

Criterion D considers the degree to which biotic processes and interactions change within the extent of the ecosystem. Three biotic factors were considered: (1) abundance of key species, (2) structural complexity, and (3) trophic diversity. Oyster reefs today are restricted to small habitat patches and are generally found at densities below 1 m^{-2} (Table S4). Although there are several modern records of oysters forming clumps and three-dimensional structures (Bodvin et al. 2011; Smyth et al. 2020; Pouvreau et al. 2023), the spatial extent of these areas of increased structural complexity is in the order of m^2. The reduced abundance of oysters currently precludes the building of reefs at an ecosystem scale, as populations at low densities do not contribute sufficient shells to the substrate to build reefs at large scales.

The loss of living oysters and their reef-associated community and the large-scale shift from structured reefs to sediments has resulted in substantial changes to the biotic community and biotic interactions (Reise 1982). Given that most reefs were extinct before the advent of modern marine science, there are few quantitative assessments of the biodiversity impact of the loss of oyster reef ecosystems. The Waddensea provides among the oldest observations of the associated community, albeit based on an already heavily impacted, nearly extirpated ecosystem (Möbius 1877). Early records (1869–1936) were compared by Reise (1982) with benthic samples taken between 1976 and 1980. Reise (1982) found that eight species associated with oyster reefs historically were notable for their rarity or absence in modern samples. Of the species that were recorded to have increased over time, polychaetes were disproportionately well represented, with Reise (1982) noting that the loss of oyster reefs, alongside declines in *Sabellaria* reefs and seagrass meadows, has ultimately led to a shift in the associated community across the whole Waddensea system. The decline of oysters as a key habitat-building species in intertidal areas appears also to have had implications for the associated food web, with *H. ostralegus* in Europe now predominantly feeding on mussels, clams, and worms (Pol et al. 2009), as opposed to oysters (Lippold and Funke 1801). The weight

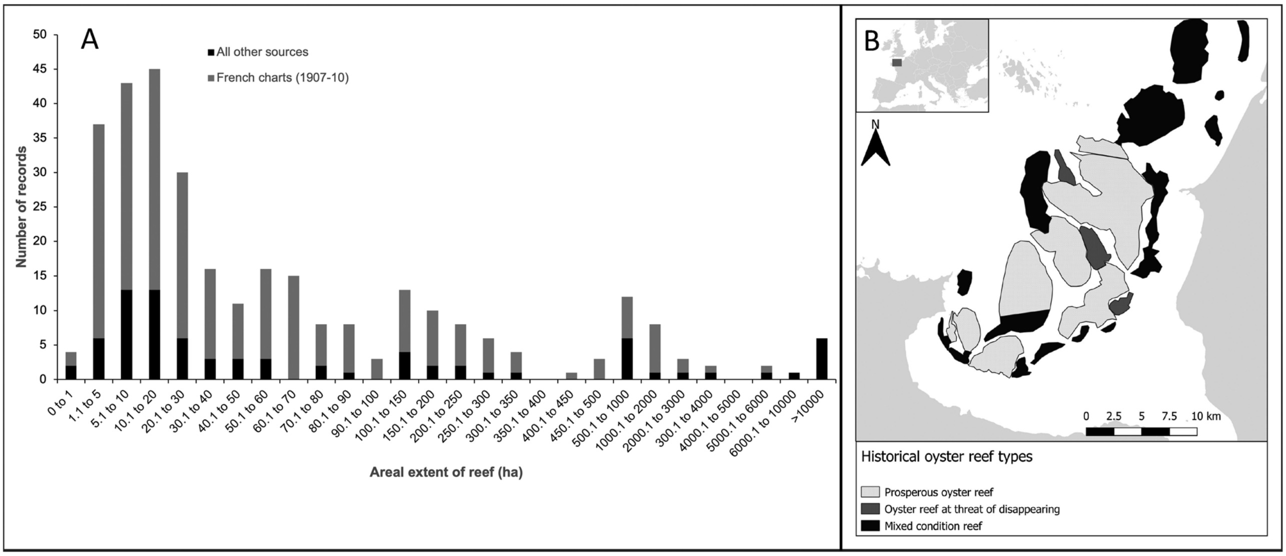

FIGURE 2 | (A) Histogram of reported sizes of oyster reefs from the historical (< 1910) literature. (B) An example map illustrating one of the French charts from which oyster reef extent was extracted, digitized from Joubin (1910). The chart illustrates how reefs in the Bay of Cancale at various stages of degradation due to overfishing were mapped at the > ha scale but were distributed over many km^2 of the bay.

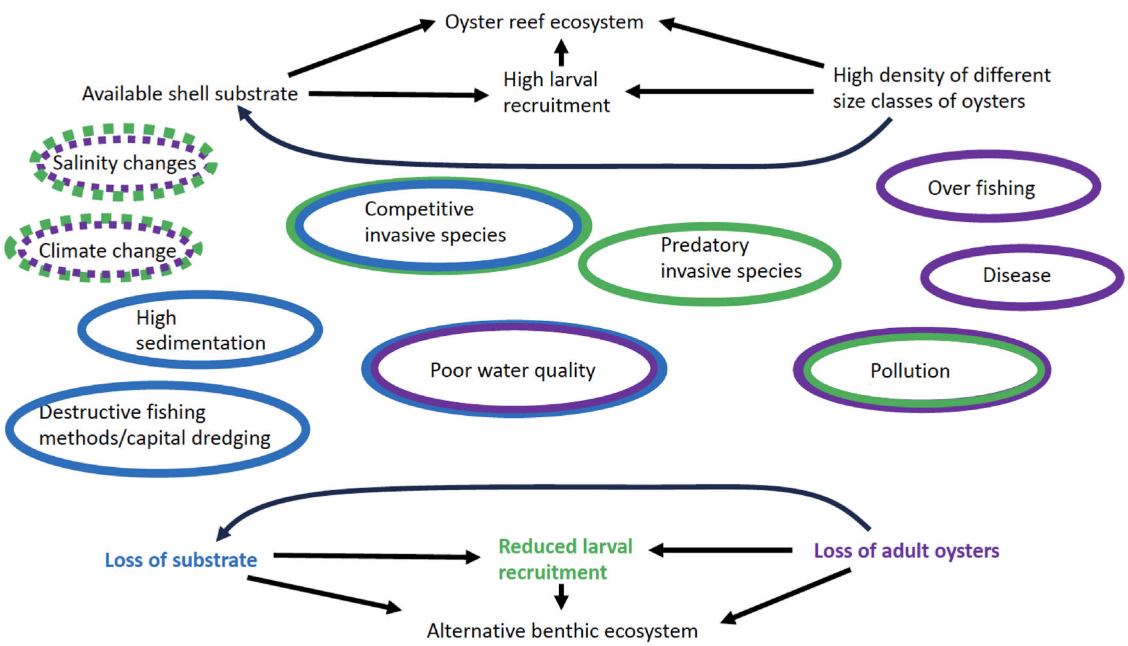

FIGURE 3 | Pathways to collapse as identified by literature review and expert opinion. Colors indicate which component of the pathway to collapse is affected by each driver listed. Blue indicates that the driver results in loss of substrate, green indicates that the driver results in reduced larval survival, and purple indicates the driver results in loss of adult oysters. Solid circles indicate a unidirectional negative impact, whereas dashed circles indicate that the effect may be positive or negative (see Table S3 for examples).

of evidence points to the European native oyster reef ecosystem type to be collapsed under Criterion D.

4.5 | Ecosystem Red Listing Criterion E—Quantitative Assessment of Risk

Criterion E considers the probability of future ecosystem collapse. This assessment deemed Criterion E to be “Not Applicable” to the European native oyster reef ecosystem type, as the ecosystem is already deemed collapsed (Criteria A, B, and D).

5 | IUCN Ecosystem Red Listing Assessment Outcome

The overall threat ranking in the IUCN Ecosystem red listing assessment reflects the highest risk ranking. In the case of the

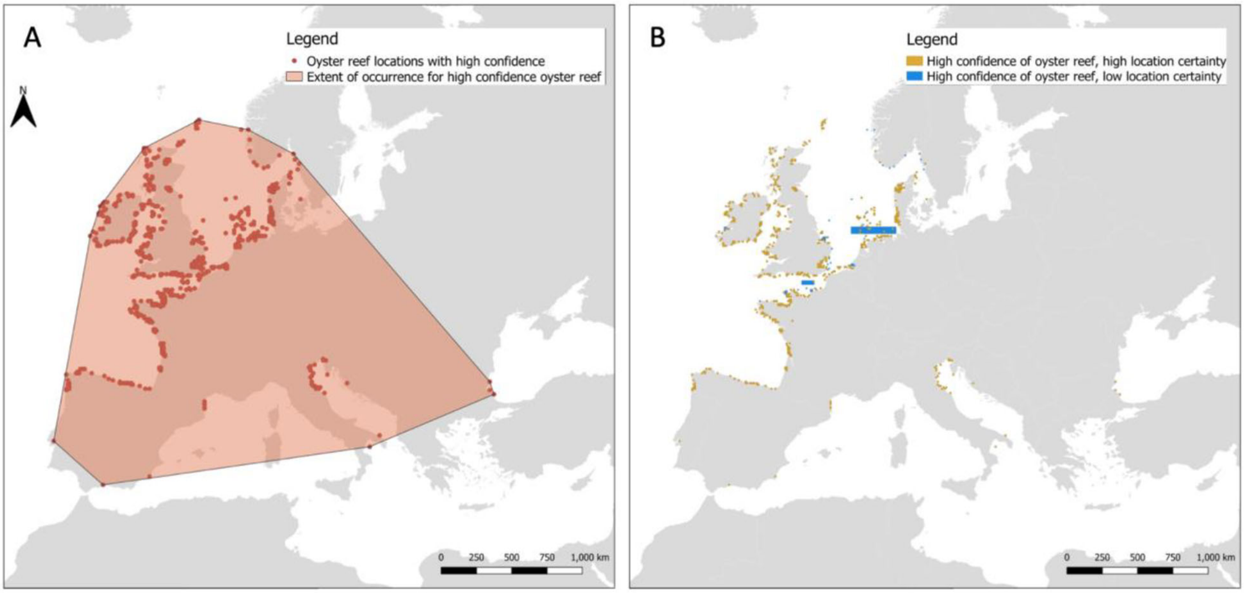

FIGURE 4 | Past (c.1750) extent of occurrence (A) and area of occupancy (B) of the European native oyster (*Ostrea edulis*) reef ecosystem, based on locations identified by Thurstan et al. (2024a, 2024b) as having high confidence that oyster reef was historically present. Coordinate Reference System: ETRS89-extended/LAEA Europe.

TABLE 2 | IUCN Ecosystem Red Listing Assessment Outcomes, where CO = collapsed, DD = data deficient, and NA = not applicable. The overall threat ranking is based on the highest risk ranking.

Criterion	A: Reduction in extent[a]	B: Restricted geographic distribution[b]	C: Environmental degradation[a]	D: Disruption of biotic processesa	E: Quantitative analysis[c]	Overall threat ranking
1	DD	CO	DD	DD	NA	CO
2	NA	CO	NA	NA	NA	
3	CO	CO	DD	CO	NA	

[a]1 = past 50 years, 2 = next 50 years, 3 = since 1750.
[b]1 = extent of occurrence, 2 = area of occupancy, 3 = # locations.
[c]Probability of collapse wit the next 50-100 years.

European native oyster reef ecosystem type, this threat ranking is Collapsed (Table 2).

6 | Discussion

That European native oyster reef ecosystems were assessed as collapsed (Table 2) is a stark finding that should promote wider conversations about how much (or little) we know about the status of our marine environments, and the subsequent implications of the resulting shifted baseline for ocean policy and management. European native oyster reef ecosystems historically covered > 1.7 million hectares of the European seafloor at a range of depths (Thurstan et al., 2024a, 2024b), across which their reef structures, created by living and dead shells, formed vertical relief and interstitial spaces that supported highly diverse, distinct associated communities (Figure 1 and Table S2b–d). These ecosystems would have provided important ecosystem functions such as larval output, enhanced biodiversity, water filtration, nutrient cycling, sediment stabilization, and enhanced productivity at multiple trophic levels (Lippold 1801; Christianen et al. 2018; Kennon et al. 2023; Lee et al. 2023; zu Ermgassen et al. 2020), in addition to cultural and economic value (Bertram 1865; Young Walser 2015). They formed reef systems, where individual reefs could be many ha in size, with numerous reefs occurring across the system at the scale of several km^2 (Figure 2). In contrast, today there are no known locations where reefs with high densities of *O. edulis* are found at the scale of more than 0.1 ha in extent (Table S4).

Our assessment of the European native oyster reef ecosystem relative to a c. 1750 baseline using the IUCN Red List of Ecosystems framework provides a longer time dimension than existing assessments. Based on more recent data, European native oyster habitats are classified as being threatened and/or declining throughout much of their range (OSPAR Commission 2009), endangered (Mediterranean infralittoral oyster beds, European Environment Agency 2022), or critically endangered (*Ostrea edulis* beds on Atlantic shallow sublittoral muddy mixed sediments, EU Red List of habitats, Gubbay et al. 2016). In general, current definitions of *O. edulis* habitats (e.g., OSPAR Commission

2009; Cameron 2022) reflect a significantly degraded ecological state, a "shifted baseline," relative to the historically described ecosystem (Thurstan et al. 2024a; Tables S1a,b and S2a). This is because declines in the condition of *O. edulis* reef ecosystems were already being documented by the early 1700s (Pontoppidan 1769; Krøyer 1837; Brehm 1872; Levasseur 2006; Table S1a and Figure S1), prior to scientific monitoring or commonly accepted historical baselines (e.g., Möbius 1877; Krøyer 1837; Table S1b). This shifted baseline presents a challenge for oyster restoration both in policy and in practice. For example, *O. edulis* reefs were not included as biogenic reefs during the process of developing UK marine Special Areas of Conservation (SACs), as it was not believed they were capable of forming reefs (Holt et al. 1998). In developing the definition of the *O. edulis* reef ecosystem type, however, we have illustrated that there was substantial historical evidence for them being considered a "biogenic reef habitat" *sensu* (Brown et al. 1997; Table S2b). Our definition of oyster reef ecosystems, grounded on the historical evidence and on evidence from species within the same genus, is therefore essential to ensure that future policy and goals to restore the ecological integrity of European seas reflect this and not the existing shifted baseline. Our findings illustrate that restoration projects will have to be vastly scaled-up for ecosystem scale recovery to be achieved.

Our assessment was undertaken at a time when governments and NGOs are seeking to address the important issue of scaling up ecological restoration efforts (as exemplified by the UN Decade on Ecosystem Restoration and EU Nature Restoration Law). Although European native oyster reef restoration efforts have been pilot-scale to date, there are increasing efforts to scale up, both in the nearshore and offshore (Preston, Gamble, et al. 2020; zu Ermgassen et al. 2021). Our findings and the developed ecosystem definition highlight how critical these efforts are. In the past, high levels of ecosystem resilience to disturbances such as harsh winters, sedimentation, and predation were evidenced, likely because of the large scale, variable depth range and high abundance at which oysters were found (Thurstan et al. 2024a). European native oyster ecosystems no longer exist at a scale capable of providing ecosystem resilience or function (Table S4), with each of these drivers of decline now considered to be a significant threat at individual locations (Pouvreau et al. 2023; Helmer et al. 2019; Table S3). To assist in restoration planning and ultimately overcome these threats, our ecosystem type definition can serve to inform an understanding of *O. edulis* reef "reference ecosystem" attributes (Gann et al 2019), such as the minimum population size, area or density of oysters needed for the ecosystem to recover; all of which have been identified as critical knowledge gaps (McAfee et al. 2021; Preston, Gamble, et al. 2020; zu Ermgassen et al. 2020).

Despite the current collapsed status of the European native oyster reef ecosystem, the benefits associated with the recovery of shellfish reefs, even at a smaller spatial scale, should not be understated. In particular, where oyster populations are protected from harvest, remnant *O. edulis* populations can build three-dimensional complex habitats (Bodvin et al. 2011; Smyth et al. 2020; Pouvreau et al. 2023), and support a diverse epibiotic community and distinct associated community (Kennon et al. 2023; Smyth and Roberts 2010). Smaller scale habitat restoration efforts are a key stepping stone to larger scale ecosystem restoration (zu Ermgassen et al. 2016), which can ultimately lead to a tipping point where recovery is self-sustaining.

Case studies from Australia present an analogous system to consider the feasibility and benefit of large-scale *O. edulis* reef restoration, following ecosystem collapse. *Ostrea angasi* was classified as functionally extinct in Australia (Beck et al. 2011), but recognition and understanding of the socio-economic benefits of shellfish restoration and how it aligned with public interests, enabled Australia's largest marine restoration initiative "Reef Builder" (McAfee 2022). Integral to this process was the use of historical ecology data to engage public and political interest via compelling storytelling and reimagining of past ecosystems. To justify investment in restoration, restoration communicators utilized data on the social benefits arising from large-scale restoration in the USA (increased fisheries production, enhanced biodiversity, job creation, recreational benefits, e.g., Grabowski et al. 2012). Following large-scale oyster reef restoration, similar recovery and benefits have been documented in Australia (McAfee et al. 2024) and may be anticipated from bivalve habitat restoration in Europe (zu Ermgassen et al. 2015).

That the European native oyster reef ecosystem type is collapsed is an important indicator of the intensely degraded status of European marine benthic ecosystems. Their decline represents a huge loss of ecosystem function, but may also be a proxy for other sensitive, less commercially important and therefore less well historically documented ecosystems. The current collapsed state of the European native oyster reef ecosystem is therefore a powerful warning that the state of the European seas is more dire than commonly acknowledged when limiting our assessments to more recent baselines. This evidence should be taken into consideration when planning the long-term recovery of these highly impacted waters, for example, when developing or applying the EU Restoration Law.

Acknowledgments

This work was funded by the Flotilla Foundation. RHT was funded by the Convex Seascape Survey, the European Research Council (ERC) under the European Union's Horizon 2020 research and innovation program (grant agreement No 856488 – ERC Synergy project "SEACHANGE: Quantifying the impact of major cultural transitions on marine ecosystem functioning and biodiversity"), and the COST Action MAF-WORLD CA20102, supported by COST (European Cooperation in Science and Technology), https://www.cost.eu. WGS was funded by the Dornoch Environmental Enhancement Project, funded by The Glenmorangie Company. Figure 1 was produced by Maria Eggertsen, funded by the European Research Council (ERC) under the European Union's Horizon 2020 research and innovation program (grant agreement No 856488 – ERC Synergy project "SEACHANGE: Quantifying the impact of major cultural transitions on marine ecosystem functioning and biodiversity"). The authors would like to thank the Native Oyster Restoration Alliance Historical Ecology working group, who's earlier work identifying historical locations of oyster reefs helped lay the foundations for this assessment, Gösta Fredriksson who shared recent data about oyster populations in Sweden, and Prof Aydin and Dr Yildiz for their local knowledge.

Data Availability Statement

Data openly available in a public repository that issues datasets with DOIs.

References

Abancourt. 1842. "Archives du SHD de Vincennes, MAR/CC5/623, Pêche des huîtres, mémoires et documents divers, Rapport d'Abancourt au préfet maritime." .

Alleway, H. K., and S. D. Connell. 2015. "Loss of an Ecological Baseline Through the Eradication of Oyster Reefs From Coastal Ecosystems and Human Memory." *Conservation Biology* 29: 795–804. https://doi.org/10.1111/cobi.12452.

Allison, S., M. Hardy, K. Hayward, T. C. Cameron, and G. J. C. Underwood. 2020. "Strongholds of *Ostrea edulis* Populations in Estuaries in Essex, SE England and Their Association With Traditional Oyster Aquaculture: Evidence to Support a MPA Designation." *Journal of the Marine Biological Association of the United Kingdom* 100: 27–36.

Andrews, A. C. 1948. "Oysters as a Food in Greece and Rome." *Classical Journal* 43, no. 5: 299–303.

Astrup, P. M., J. Benjamin, F. Stankiewicz, et al. 2021. "A Drowned Mesolithic Shell Midden Complex at Hjarnø Vesterhoved, Denmark and Its Wider Significance." *Quaternary Science Reviews* 258: 106854.

Baggett L. P., S. P. Powers, R. Brumbaugh, et al. 2014. *Oyster Habitat Restoration Monitoring and Assessment Handbook*. Arlington, VA: The Nature Conservancy.

Bahr, L. M., and W. P. Lanier. 1981. "*The Ecology of Intertidal Oyster Reefs of the South Atlantic Coast: A Community Profile*." Washington, D.C.: U.S Department of the Interior.

Beck, M. W., R. D. Brumbaugh, L. Airoldi, et al. 2011. "Oyster Reefs at Risk and Recommendations for Conservation, Restoration and Management." *Bioscience* 61, no. 2: 107–116.

Bennema, F. P., G. H. Engelhard, and H. Lindeboom. 2020. "*Ostrea edulis* Beds in the Central North Sea: Delineation, Ecology, and Restoration." *ICES Journal of Marine Science* 77, no. 7–8: 2694–2705.

Bertram, J. G. 1865. *The Harvest of the Sea*. London, UK: John Murray. pp. 519.

Bland, L. M., D. Keith, R. M. Miller, N. J. Murray, and J. P. Rodríguez. 2017. "Guidelines for the Application of IUCN Red List of Ecosystems Categories and Criteria." https://www.iucn.org/resources/publication/guidelines-application-iucn-red-list-ecosystems-categories-and-criteria.

Bodvin, T., S. Mortensen, A. Jelmert, Ø. Strand, and E. G. Grefsrud. 2011. "Utredning av europeisk flatøsters *Ostrea edulis* L.—Kunnskapsoversikt med forslag til handlingsplan. DN-utredning 10–2011." http://www.miljodirektoratet.no/old/dirnat/attachment/2857/DN-utredning-10-2011.pdf.

Brehm, A. 1872. *Illustriertes Tierleben für Volk und Schule, bearbeitet von Freidrich Schrödler*. Hildburghaufen. Verlag des Bibliographischen Instituts. pp. 945.

Brown A. E., A. J. Burn, J. J. Hopkins, S. F. Way. 1997. *The Habitats Directive: Selection of Special Areas of Conservation in the UK*. JNCC Report 270. Peterborough, UK: Joint Nature Conservative Community.

Cameron, T., R. Smart, A. Lown, A. Baker, and R. Korda. 2022. "Defining Oyster Beds in the Blackwater Estuary." *Aquatic Living Resources* 36, no. 2023: 28. NECR411. https://doi.org/10.1051/alr/2023021.

Christianen, M. J. A., W., Lengkeek, J. H., Bergsma, J. W. P., Coolen, K., Didderen, M., Dorenbosch, F. M. F., Driessen, P., Kamermans, E., Reuchlin-Hugenholtz, H., Sas, A., Smaal, van den K. A., Wijngaard, and van der T. M., Have 2018. Return of the native facilitated by the invasive? Population composition, substrate preferences and epibenthic species richness of a recently discovered shellfish reef with native European flat oysters (*Ostrea edulis*) in the North Sea. *Marine Biology Research*, 14(6), 590–597. https://doi.org/10.1080/17451000.2018.1498520.

Collin, J. S. 1884. *Om Limfjordens tidligere og nuværende marine fauna, med særligt hensyn til bløddyraunaen. Danmark Ministeriet for kirke- og undervisningsvæsenet*. Copenhagen, Denmark: Gyldendal.

Colsoul, B., S. Pouvreau, C. Di Poi, et al. 2020. "Addressing Critical Limitations of Oyster (*Ostrea edulis*) Restoration: Identification of Nature-Based Substrates for Hatchery Production and Recruitment in the Field." *Aquatic Conservation: Marine and Freshwater Ecosystems* 30: 2101–2115.

Culloty, S. C. and M. F. Mulcahy. 2007. Bonamia ostreae in the Native Oyster Ostrea edulis. A Review. Marine Environment and Health Series No. 29. Galway, Ireland: Marine Institute.

Drapkin, E. I. 1963. "Effect of *Rapana bezear* Linne on the Black Sea Fauna." *Doklady Akademiia Nauk SSSR 151 700–703 Translation Biological Science Section* 151: 964–966.

Dumain, L. 1832. "Survey of the Coast of Louisiana [1806-1807, Communicated to the Senate 1811]. Class IV, Commerce and Navigation." In Document No. 158 in the American State Papers*,* Vol. 7, edited by W. Lowrie and M. S. Clair Clarke, 839–842. Washington, DC: Gales and Seaton.

EU Commission. 2022. "Proposal for a Regulation of the European Parliament and of the Council on Nature Restoration." https://www.europarl.europa.eu/legislative-train/theme-a-european-green-deal/file-restoration-of-healthy-ecosystems.

European Council Directive. 1992. "Council Directive 92/43/EEC." http://data.europa.eu/eli/dir/1992/43/2013-07-01.

European Environment Agency. 2022. "European Red List of Habitats—Enhanced by EEA." https://www.eea.europa.eu/en/datahub/datahubitem-view/de2276d8-e295-4cd7-89c9-88812065db87.

Ezgeta-Balić, D., N. Vrgoč, I. Isajlović, et al. 2021. "Comparison of Beam Trawl Catch, by-Catch and Discard in Fishing and Non-Fishing Areas—A Case Study From the Northern Adriatic Sea." *Mediterranean Marine Science* 22: 108–120.

Gann, G. D., T. McDonald, B. Walder, et al. 2019. "International Principles and Standards for the Practice of Ecological Restoration." *Restoration Ecology* 27: S1–S46.

Gillies, C. L., S. Castine, H. K. Alleway, et al. 2020. "Conservation Status of Oyster Reef Ecosystem of Southern and Eastern Australia." *Global Ecology and Conservation* e00988. https://doi.org/10.1016/j.gecco.2020.e00988.

Gillies, C. L., I. M. McLeod, H. K. Alleway, et al. 2018. "Australian Shellfish Ecosystems: Past Distribution, Current Status and Future Direction." *PLoS ONE* 13, no. 2: p.e0190914.

Gillies, C. L., C., Crawford, and B., Hancock 2017. Restoring Angasi oyster reefs: What is the endpoint ecosystem we are aiming for and how do we get there? *Ecological Management & Restoration*, 18(3), 214–222. Portico. https://doi.org/10.1111/emr.12278.

Giovio P. 1524. Libro de'pesci romani. Translated by C. Zancaruolo. De piscibus marinis lacustribus fluviatilibus item de testaceis ac salsamentis liber. Venice.

Grabowski, J. H., R. D. Brumbaugh, R. F. Conrad, et al. 2012. "Economic Valuation of Ecosystem Services Provided by Oyster Reefs." *Bioscience* 62, no. 10: 900–909.

Gubbay, S., N., Sanders, T., Haynes, J. A. M., Janssen, J. R., Rodwell, A., Nieto, M. G., Criado, S., Beal and J., Borg 2016. European red list of habitats. Part 1: Marine habitats. European Union. Luxembourg: Publications Office of the European Union.

Helmer, L., P., Farrell, I., Hendy, S., Harding, M., Robertson, and J., Preston 2019. Active management is required to turn the tide for depleted Ostrea *edulis* joubin stocks from the effects of overfishing, disease and invasive species. *PeerJ*, 7, e6431. https://doi.org/10.7717/peerj.6431.

Hemeon, K. M., K. A. Ashton-Alcox, E. N. Powell, et al. 2020. "Novel Shell Stock–Recruitment Models for *Crassostrea virginica* as a Function of Regional Shell Effective Surface Area, a Missing Link for Sustainable Management." *Journal of Shellfish Research* 39: 633–654.

Hinke, W. J. 1916. "Report of the Journey of Francis Louis Michel From Berne, Switzerland, to Virginia, October 2, 1701-December 1, 1702." *Part II. Virginia Magazine of History and Biography* 24: 113–141.

Holmes, H. B. 1927. *An Investigation of Saw Dust Pollution in Relation to Oysters in Yaqunia Bay*. California: Department of Commerce, Bureau of Fisheries.

Holt, T. J., E. I., Rees, S. J., Hawkins, R., Seed 1998. Biogenic Reefs (volumeIX). An overview of dynamic and sensitivity characteristics for conservationmanagement of marine SACs. Scottish Association for Marine Science (UK MarineSACs Project). 170 Pages.

Hughes, A., K. Bonačić, T. Cameron, et al. 2023. "Site Selection for European Native Oyster (*Ostrea edulis*) Habitat Restoration Projects: An Expert-Derived Consensus." *Aquatic Conservation: Marine and Freshwater Ecosystems* 33, no. 7: 721–736.

Jenkin, A., C. Trundle, C. Daniels, S. Sturgeon, and K. Street. 2023. Fal *Oyster Survey Summary Report* 2023. Hayle, UK: Cornwall Inshore Fisheries and Conservation Authority.

Joubin, L., and J. Guérin-Ganivet. 2009. *Cartes des gisements de coquilles comestibles des côtes de France*. Ifremer. https://doi.org/10.12770/c502ed30-0d7d-11de-a4b1-000086f6a603.

Joubin, L. 1910. Études sur les Guisements de Mollusques comestibles des Côtes de France. La baie de Cancale (avec deux cartes). Bulletin de L'Institut Océanographique. No. 174. pp.32.

Kasoar, T., P. S. E. zu Ermgassen, A. Carranza, B. Hancock, and M. Spalding. 2015. "New Opportunities for Conservation of a Threatened Biogenic Habitat: A Worldwide Assessment of Knowledge on Bivalve-Reef Representation in Marine and Coastal Ramsar Sites." *Marine and Freshwater Research* 66: 981–988.

Keith, D. A., J. R. Ferrer-Paris, E. Nicholson, and R. T. Kingsford, eds. 2020. *The IUCN Global Ecosystem Typology 2.0: Descriptive Profiles for Biomes and Ecosystem Functional Groups*. Gland, Switzerland: IUCN.

Keith, D. A., J. P. Rodríguez, K. M. Rodríguez-Clark, et al. 2013. "Scientific Foundations for an IUCN Red List of Ecosystems." *PLoS ONE* 8, no. 5: e62111.

Kennon, N. A., A. Robertson-Jones, S. Jemmett, T. Hugh-Jones, M. C. Bell, and W. G. Sanderson. 2023. "Rotational Fishing Enables Biodiversity Recovery and Provides a Model for Oyster (*Ostrea edulis*) Habitat Restoration." *PLoS ONE* 18, no. 3: e0283345.

Krøyer, H. 1837. De danske østersbanker - et bidrag til kundskab om Danmarks Fiskerier. København.

Lee, H. Z., I. M. Davies, J. M. Baxter, K. Diele, and W. G. Sanderson. 2023. "A Blue Carbon Model for the European Flat Oyster (*Ostrea edulis*) and Its Application in Environmental Restoration." *Aquatic Conservation: Marine and Freshwater Ecosystems*. 34, no. 1: e4030.

Levasseur, O. 2006. *Histoire de l'huître en Bretagne, Skol Vreizh*. Coop breizh. Morlaix, France.

Lippold, G. H. C. 1801. *Neues Natur- und Kunstlexicon enthaltend die wichtigsten und gemeinnützigsten Gegenstände aus der Naturgeschichte, Naturlehre, Chemie und Technologie*. Charleston: Nabu Press.

Manoutsoglou, E., T. Hasiotis, and A. F. Velegrakis. 2024. "Holocene Records of Oyster Reefs in a Shallow Semi-Enclosed Island Embayment of the Aegean Sea." *Estuarine, Coastal and Shelf Science* 302: 108781.

Marine Institute and Bord Iascaigh Mhara. 2023. *Shellfish Stocks and Fisheries Review 2022: An Assessment of Selected Stocks*. Galway, Ireland: Marine Institute.

Marsili, F. 1715. Giornali e memorie per la ricognizione dellaspiaggie pontificie dell'Adriatico (Biblioteca Univ. di Bologna).

McAfee, D., R. Costanza, and S. D. Connell. 2021. "Valuing Marine Restoration Beyond the 'Too Small and Too Expensive.'" *Trends in Ecology & Evolution* 36: 968–971.

McAfee, D., I. M. McLeod, H. K. Alleway, et al. 2022. "Turning a Lost Reef Ecosystem Into a National Restoration Program." *Conservation Biology* 36, no. 6: e13958.

McAfee, D., L. D. McLeod, S. Carruthers, and S. D. Connell. 2024. "Reversing Functional Extinction: Successful Restoration of Eradicated Oyster Reefs." *Restoration Ecology* 32: e14169.

Möbius, K. A. 1877. *Die Auster und die Austernwirthschaft*. Berlin, Germany: Wiegandy, Hempel & Parey.

Norgard, T. C., M. I. Bigg, S. E. M. MacConnachie, J. L. Finney, and G. E. Gillespie.2018. *Index Site Surveys for Olympia Oysters (Ostrea lurida Carpenter, 1864) in British Columbia –2009 to 2017. Canadian Technical Report of Fisheries and Aquatic Sciences 3153*. Nanaimo, Canada: Fisheries and Oceans Canada.

OSPAR Commission. 2009. Background document for *Ostrea edulis* and *Ostrea edulis* beds.

Pogoda, B., T. Hausen, M. Rothe, et al. 2023. "Come, Tell Me How You Live: Habitat Suitability Analysis for *Ostrea edulis* Restoration." *Aquatic Conservation: Marine and Freshwater Ecosystems* 33, no. 7: 678–695. https://doi.org/10.1002/aqc.3928.

Pol, M., B. J. Ens, K. Oosterbeek, et al. 2009. "Oystercatchers' Bill Shapes as a Proxy for Diet Specialization: More Differentiation Than Meets the Eye." *Ardea* 97: 335–347.

Pontoppidan E. 1769. *Den Danske Atlas*. Copenhagen, Denmark: Rosenkilde and Bagger.

Pouvreau, S., H. Cochet, F. Bargat, et al. 2021. "Current Distribution of the Residual Flat Oysters Beds (*Ostrea edulis*) Along the West Coast of France." *SEANOE* https://doi.org/10.17882/79821.

Pouvreau S., S. Lapègue, I. Arzul, and P. Boudry. 2023. "Fifty Years of Research to Counter the Decline of the European Flat Oyster (*Ostrea edulis*): A Review of French Achievements and Prospects for the Restoration of Remaining Beds and Revival of Aquaculture Production." *Aquatic Living Resources* 36: 13. https://doi.org/10.1051/alr/2023006.

Preston J., M. Fabra, E. Johnson, L. Helmer, I. Hendy. 2020. "Interactions of Larval Dynamics and Substrate Preference Have Ecological Significance for Benthic Biodiversity and *Ostrea edulis* Linnaeus, 1758 in the ~Presence of *Crepidula fornicata*." *Journal of Aquatic Conservation: Marine and Freshwater Ecosystems*. 30: 2133–2149. https://doi.org/10.1002/aqc.3446.

Preston J., C. Gamble, A. Debney, L. Helmer, B. Hancock, and P. S. E. zu Ermgassen, eds. 2020. *European Native Oyster Habitat Restoration Handbook*. London, UK: The Zoological Society of London.

Reise, K. 1982. "Long-Term Changes in the Macrobenthic Invertebrate Fauna of the Wadden Sea: Are Polychaetes About to Take Over?" *Netherlands Journal of Sea Research* 16: 29–36.

Rick, T. C., L. A. Reeder-Myers, C. A. Hofman, et al. 2016. "Millennial-Scale Sustainability of the Chesapeake Bay Native American Oyster Fishery." *Proceedings of the National Academy of Sciences of the United States of America* 113: 6568–6573.

Ritter von Hamm, W. 1881. *Gesammelte kleine Schriften von Dr*. Ritter von Hamm. Wein, Pest, Leipzig. A. Hartleben's Verlag. pp. 352.

Rodriguez-Perez, A., M. James, D. W. Donnan, T. B. Henry, L. F. Møller, and W. G. Sanderson. 2019. "Conservation and Restoration of a Keystone Species: Understanding the Settlement Preferences of the European Oyster (*Ostrea edulis*)." *Marine Pollution Bulletin* 138: 312–321.

Royal Commission. 1866. *Report of the Commissioners Appointed to Inquire Into the Sea Fisheries of the United Kingdom, With Appendix and Minutes of Evidence*. London, UK: Eyre and Spottiswoode.

Sander, L., H. C. Hass, R. Michaelis, C. Groß, T. Hausen, and B. Pogoda. 2021. "The Late Holocene Demise of a Sublittoral Oyster Bed in the North Sea." *PLoS ONE* 16: e0242208.

Schulte, D. M., R. P., Burke, and R. N., Lipcius 2009. Unprecedented Restoration of a Native Oyster Metapopulation. *Science*, 325(5944), 1124–1128. https://doi.org/10.1126/science.1176516.

Smyth, D., and D. Roberts. 2010. "The European Oyster (*Ostrea edulis*) and Its Epibiotic Succession." *Hydrobiologia* 655: 25–36.

Smyth, D. M., N. S., Horne, E., Ronayne, R. V., Millar, P. W. S., Joyce, M., Hayden-Hughes, and L., Kregting 2020. Wild gregarious settlements of *Ostrea edulis* in a semi-enclosed sea lough: a case study for unassisted restoration. *Restoration Ecology*, 28: 645–654. Portico. https://doi.org/10.1111/rec.13124.

Solinger, L. K., K. A. Ashton-Alcox, E. N. Powell, et al. 2022. "Oysters Beget Shell and Vice Versa: Generating Management Goals for Live Oysters and the Associated Reef to Promote Maximum Sustainable Yield of *Crassostrea virginica*." *Canadian Journal of Fisheries and Aquatic Sciences* 79: 1241–1254.

Szabó, K., and J. R. Amesbury. 2011. "Molluscs in a World of Islands: The Use of Shellfish as a Food Resource in the Tropical Island Asia-Pacific Region." *Quaternary International* 239: 8–18. https://www.sciencedirect.com/science/article/pii/S1040618211001285.

Thorngren, L., P. Bergström, T. D. Holthuis, and M. Lindegarth. 2019. "Assessment of the Population of *Ostrea edulis* in Sweden: A Marginal Population of Significance?" *Ecology and Evolution* 9: 13877–13888.

Thurstan, R. H., B. K. Diggles, C. L. Gillies, et al. 2020. "Charting Two Centuries of Transformation in a Coastal Social-Ecological System: A Mixed Methods Approach." *Global Environmental Change* 61: 102058. https://doi.org/10.1016/j.gloenvcha.2020.102058.

Thurstan, R. H., J. P. Hawkins, L. Raby, and C. M. Roberts. 2013. "Oyster (*Ostrea edulis*) Extirpation and Ecosystem Transformation in the Firth of Forth, Scotland." *Journal for Nature Conservation* 21, no. 5: 253–261. https://doi.org/10.1016/j.jnc.2013.01.004.

Thurstan, R. H., H. McCormick, J. Preston, et al. 2024a. "Records Reveal the Vast Historical Extent of European Oyster Reef Ecosystems." *Nature Sustainability* https://doi.org/10.1038/s41893-024-01441-4.

Thurstan, R. H., H. McCormick, J. Preston, E. C. Ashton, F. P. Bennema, A. Bratoš Cetinić, J. H. Brown, T. C. Cameron, F. da Costa, D. W. Donnan, C. Ewers, T. Fortibuoni, E. Galimany, O. Giovanardi, R. Grancher, D. Grech, M. Hayden-Hughes, L. Helmer, K. T. Jensen, and P. S. E. zu Ermgassen 2024b. Historical dataset details the distribution, extent and form of lost Ostrea edulis reef ecosystems. *Scientific Data*, 11: 1198. https://doi.org/10.1038/s41597-024-04048-8.

UKBAP. 1999. Native oyster (*Ostrea edulis*). Species Action Plan. In *Tranche 2 Action Plans. Vol. V. Maritime Species and Habitats*, edited by UK Biodiversity Group. Peterborough, UK: English Nature for the UK Biodiversity Group. p. 67–69.

United Nations General Assembly. 2020. "Decade on Ecosystem Restoration." https://www.decadeonrestoration.org.

Virvilis, C. and P. Angelidis. 2006. "Presence of the Parasite *Marteilia* sp. in the Flat Oyster (*Ostrea edulis* L) in Greece." *Aquaculture* 259: 1–5.

Went, A. E. J. 1961. "Historical Notes on the Oyster Fisheries of Ireland." *Proceedings of the Royal Irish Academy. Section C: Archaeology, Celtic Studies, History, Linguistics, Literature* 62: 195–223. http://www.jstor.org/stable/25505107.

Williams, J. L. 1837. *The Territory of Florida: Or Sketches of the Topography, Civil and Natural History, of the Country, the Climate, and the Indian Tribes, From the First Discovery to the Present Time*. New York: A. T. Goodrich.

Young Walser, R. 2015. "Dreg Songs Lost… and Found." *Folk Life* 53, no. 1: 19–35.

zu Ermgassen, P. S. E., O. Bos, A. Debney, et al. eds. 2021. *European Native Oyster Habitat Restoration Monitoring Handbook*. London, UK: The Zoological Society of London.

zu Ermgassen, P. S. E., M. D. Spalding, B. Blake, et al. 2012. "Historical Ecology With Real Numbers: Past and Present Extent and Biomass of an Imperilled Estuarine Ecosystem." *Proceedings of the Royal Society B* 279: 3393–3400. https://doi.org/10.1098/rspb.2012.0313.

zu Ermgassen, P. S. E., R. H. Thurstan, J. Corrales, et al. 2020. "The Benefits of Bivalve Reef Restoration: A Global Synthesis of Underrepresented Species." *Aquatic Conservation: Marine and Freshwater Ecosystems* 30: 2050–2065.

zu Ermgassen, P., B. Hancock, B. DeAngelis, et al. 2016. *Setting Objectives for Oyster Habitat Restoration Using Ecosystem Services: A Manager's Guide*. Arlington, VA: The Nature Conservancy.

Supporting Information

Additional supporting information can be found online in the Supporting Information section.