Title: **European native oyster reef ecosystems are universally Collapsed**

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Keywords

Ostrea edulis, shellfish reef, threats, IUCN Ecosystem Red List, habitat restoration, historical ecology, shifted baseline

Abstract

Oyster reefs are often referred to as the temperate functional equivalent of coral reefs. Yet evidence for this analogy is lacking for the European native species *Ostrea edulis* and its biogenic habitat. Recently assembled historical data provide a unique opportunity to develop a robust definition for this ecosystem type, confirm that *O. edulis* are biogenic reef builders, and assess its current conservation status. Today, *O. edulis* typically occur as scattered individuals or, in a few locations, as dense clumps over a few m^2, however, historically *O. edulis* reef ecosystems persisted at large scales. A key finding is that *O. edulis* reef ecosystems should therefore be assessed at the >ha scale.

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 assessed as data deficient and Criterion E (quantitative risk analysis) was not completed as the ecosystem was already deemed collapsed.

Our assessment has far reaching implications for conservation policy and action, and shows that the scale of current restoration efforts fall far short of what is necessary for ecosystem recovery.

Introduction

Oyster reef ecosystems were once a widely distributed ecosystem type in temperate coastal seas and estuaries globally (Beck et al., 2011; Gillies et al., 2020; zu Ermgassen et al., 2012, Williams et al. in press, Thurstan et al. in review a, b). In historical accounts, oyster reefs were described as the temperate equivalent of coral reefs (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 (Hinke, 1916, Dumain 1832). 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 (Szabó & Amesbury 2011, Rick et al. 2016, Fariñas-Franco et al. 2018, Thurstan et al., 2020, Astrup et al. 2021). Dramatic declines in the extent of oyster reefs were documented globally following European colonisation and the industrial revolution (Alleway & Connell, 2015; Beck et al., 2011; Thurstan et al., 2013; zu Ermgassen et al., 2012, Thurstan et al., 2020). Although pollution, harsh winters and changes to hydrological conditions were noted in historical texts to have caused localised extinctions (Krøyer 1837, Royal Commission 1866, Holmes 1927), the primary driver of loss of oyster reef ecosystems has been extraction by fishing (Went 1961, Thurstan et al. in review a).

Today, ecosystem-forming oyster species including those in the genus of *Saccostrea, Crassostrea* and *Ostrea species* still form high relief, complex reef structures in many temperate estuaries across the globe (Bahr & Lanier, 1981; Hedgpeth, 1954; Gillies et al. 2017, Norgard et al. 2018), albeit over significantly smaller areas, and with a substantially reduced habitat complexity relative to historical records (zu Ermgassen et al. 2012; Gillies et al. 2018). 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} (Thorngren et al. 2019; Allison et al. 2020; Pouvreau et al, 2023). Recognition of the degraded status of *O. edulis* populations and the reef ecosystems they form is reflected in their many conservation designations, with *O. edulis* and its habitat recognised as threatened and/or declining in Region II and Region III (Greater North Sea and Celtic Sea respectively) under the OSPAR convention (OSPAR Commission 2009), its recognition by some member states under the “Reefs” feature of the Habitats Directive (European Council 1992), and its inclusion in some Biodiversity Action Plans (e.g. UKBAP 1999). These designations are critically important for the protection of *O. edulis* habitats and ecosystems.

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. 2021; 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 (United Nations General Assembly, 2020, EU Commission 2022). An improved description of the ecosystem’s main physical and biological attributes prior to significant disturbance is thus 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. (in review a,b) documented the historical locations, ecosystem characteristics and extents of *O. edulis* reef ecosystems in Europe. The broad spatial scale and highly resolved nature of the data presents a unique historical record for marine ecosystems, which provides a novel opportunity to visualise the form and extent of *O. edulis* reef ecosystems prior to its widespread degradation. Thurstan et al. (in review a) 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). Additionally, they identified sources describing the rich benthic community associated with this complex structured habitat. These descriptions all serve to elucidate the historical extent and physical and biological characteristics of oyster reef ecosystems throughout Europe, based primarily on a 1800-1930 baseline (Thurstan et al. in review b).

Here, we follow the IUCN Red List of Ecosystems Framework (Bland et al. 2017) to assess the current status of the European native oyster reef ecosystem. Ecosystem red lists are one of the headline indicators in the monitoring framework for 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 much needed 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, prioritise and monitor restoration action, inform resource management, and to raise public awareness to support management and protection policy.

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 clearly 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 criterion (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 (Bland et al. 2017).

Development of ecosystem and ecosystem Collapse definitions

Following the IUCN Red List of Ecosystems Framework (Bland et al. 2017), we developed a comprehensive definition of the European native oyster ecosystem type created by *O. edulis*, and the associated threshold of collapse. While definitions of oyster habitats exist (e.g. OSPAR Commission 2009), comparison of modern definitions with historical sources illustrate clearly that modern definitions describe a habitat in a degraded state, as opposed to an ecosystem type (Table S1a-e, Figure S1). Modern definitions based on small habitat patches, fail to adequately describe the full physical and biological attributes and key processes of the ecosystem and are therefore ill equipped to be applied as ecological baselines against which ecosystem condition can be assessed.

We reviewed existing definitions of shellfish ecosystems globally to identify important ecosystem attributes representative of shellfish ecosystems irrespective of ecosystem-forming species, including the IUCN Global Ecosystem Typology (Keith et al. 2020) and "biogenic reef habitat" *sensu* Brown et al. (1997) (Table S2a-c). These 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). Historical evidence of past *O. edulis* reef structure, spatial scale, and functions were assessed (Table S2b-d). Oyster density is a key attribute of oyster reef condition (zu Ermgassen et al. 2021; Pouvreau et al. 2021), but quantitative assessments of densities were not available from the baseline period of assessment. Furthermore, habitat descriptions from the principle period of documentary evidence (1800-1930) often described reefs which were known to be overexploited (Möbius 1877, Krøyer 1837, Table S1a-c, Figure S1). Our threshold densities for ecosystem assessment were therefore based on cumulative evidence from descriptions of the ecosystem, catch rate information, and quantitative information from related species in other geographies, as well as the current understanding of *O. edulis* reef formation (Pouvreau et al. 2021, Table S2d-e).

Our definition of the collapsed European native oyster reef ecosystem and the threshold of collapse was derived from relevant literature and expert knowledge on the pathways to collapse.

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 Rodriguez et al. (2015) and Bland et al. (2017). Significant declines in *O. edulis* reefs were observed in the 1800s (Thurstan et al. 2013, Royal Commission 1866), or earlier (Went 1961, Giovio 1524, Levasseur, 2006). In contrast, data from the past 50 years is 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. Tully and Clarke 2012, Thorngren et al. 2019, Jenkin et al. 2023, The Marine Institute and Bord Iascaigh Mhara 2023). 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 in Thurstan et al. (in review a).

Thurstan et al. (in review a, b) extracted historical data on the presence, condition and function of *O. edulis* reefs from targeted searches of government records, nautical charts, popular media, and scientific journals. Identified locations 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. These data were primarily recorded between 1800-1930 (Thurstan et al. (in review b), yet we consider them representative of a c. 1750s baseline for oyster reef presence. It is recognised that, following exploitation, oyster reef ecosystem quality declines before reef locations are extirpated (zu Ermgassen et al. 2012, Table S1a). Locations recorded as oyster reefs between 1800-1930 therefore likely represent reefs that were extant in 1750, even if their condition at the time of recording was degraded. Furthermore, historical sources described discovering new oyster grounds until the late 19th century, highlighting that some *O. edulis* reef habitats remained unexploited until this time period (Thurstan et al. in review a). Only historical locations assigned a high confidence that *O. edulis* were once present at densities at which they formed reefs were included in our assessment. Areas in the southern Mediterranean with historical records of *O. edulis* were therefore excluded from the analysis, as there is low confidence in the historical documentary evidence that these populations were reef building, although it is not known whether this lack of evidence is the result of an already shifted baseline, or the natural ecological condition of *O. edulis* populations in the region (Thurstan et al. in review a).

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 using the terms "oyster, *Ostrea*, COUNTRY" for each country known to fall within the historical distribution of the European native oyster (based on Thurstan et al. in review b). The searches were undertaken between September 2022 and June 2023. Where recent surveys were not identified for a country, or where data were inconclusive, data was requested from local experts.

Application of Red List criteria

The collated historical and recent data were used to assess the risk of collapse in Criterion A (reduction in geographic distribution), under sub criterion 3 (relative to a 1750 baseline) and Criterion B (restricted geographic range), under sub criterion 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 Criteria 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. in review a and b). To determine the Extent of Occurrence (Criterion B1), point locations of all high confidence historical *O. edulis* reef occurrences (Thurstan et al. in review a,b), were used to draw a minimum convex polygon using the Minimum Bounding Geometry tool in QGIS 3.24. To determine the Area of Occupancy (Criterion B2), a grid layer of 10x10km squares was then overlaid, and all grid squares that contained at least one historical oyster reef point were identified (Coordinate Reference System used is ETRS89-extended / LAEA Europe).

Criterion C (environmental degradation) was assessed using shell substrate as a defining non-living feature of oyster reefs, the loss of which “reduces the capacity of the ecosystem to sustain its characteristic biota” (Bland et al. 2017). We sought to identify data from the literature, suitable for assessing the current distribution and extent of shell substrate. Criterion D assessed the risk of disruption of biotic processes, relative to a 1750 baseline (sub criterion 3; Bland et al. 2017). Evidence for the ecological functions associated with *O. edulis* reefs historically and recently were examined. Criteria E (quantitative risk analysis), and Criteria B (subcriterion 1 and 2) require a thorough understanding of the existing and future threats (pathways to collapse) facing the ecosystem being assessed. Expert opinion and literature review were used to assess whether identified threats still impact, or have the potential to impact, *O. edulis* reef condition.

Results

Definition of the European native oyster reef ecosystem type

European native oyster reefs are found from 20-42 ppt salinity, 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). While populations of *O. edulis* persist as non-native species on the eastern coast of North America, it native range is restricted to Europe from Norway to the African coast of the Mediterranean and into the Black Sea (Thurstan et al. in review a).

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). The ecosystem contains patches with high oyster density, often forming clumps of oysters and creating a complex three-dimensional structure (Bodvin et al. 2011, Kennon et al. 2023, Thurstan et al. in review a, b, 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*. These 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 & Bord Iascaigh Mhara 2023).

The European native oyster ecosystem is biogenic, with previous generations forming the underlying substrate on which the reef is built (Thurstan et al. in review a, Table S2b-d, Table 1). While accurate mapping of *O. edulis* reefs historically is rare, the spatial scale at which reefs historically persisted is best visualised through mapping undertaken on the French oyster beds in the early 1900's (Joubin & Guérin-Ganivet 2009, Thustan et al. b, Figure 2). While individual reefs within the ecosystem may predominantly form on the scale of hectares (Figure 2a), multiple reefs persist within a wider ecosystem (Figure 2b). 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 across a km^2 scale.

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 oysters in the local population, gregarious settlement leading to clumps are absent, and oysters do not contribute to biogenic formation of three-dimensional structure at the hectare scale, assessed at the km^2 scale (Table 1, Figure 1c). 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 (>ha patches within km^2 extents of European native oyster ecosystem). The collapsed European native oyster ecosystem does not deliver ecosystem functions such as water filtration, nutrient cycling, enhanced biodiversity, sediment stabilisation or shell production at significant scales.

Pathways to collapse

Oyster reef ecosystems are particularly sensitive to collapse, as oysters and their shells are the preferred settlement substrate for oyster larvae (Rodriguez-Perez et al. 2019, Colsoul et al. 2020). 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). Additionally, 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 2020a) and disease (Virvilis & Angelidis 2006, Culloty and Mulcahy 2007) 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 salinity regime have also historically played a role in the local extirpation (Krøyer 1837) or establishment (Collin 1884) of native oyster populations.

Applying the IUCN Ecosystem Red Listing criteria

Ecosystem Red listing Criterion A - reduction in distribution

Criterion A considers the change in extent of the ecosystem type over time (Bland et al. 2017). No recent records of *O. edulis* persisting at higher densities over areas > ha were identified throughout the native range of the European native oyster. 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 spatial extent of oyster reef ecosystems was only documented from 317 of 1197 recorded historical locations, those locations encompassed a known reef area of >1.7 million ha (Thurstan et al. in review a, b). There are no records of reef extent meeting the ecosystem criteria of > ha (Table 1) in the present day (Table S4) and the European native oyster reef ecosystem type is therefore deemed to be Collapsed under category A3.

Ecosystem Red listing Criterion B - restricted distribution

Criterion B considers the current range of the ecosystem type (Bland et al. 2017). 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) . No current records of *O. edulis* persisting at higher densities over areas > ha scales were identified (Table S4), which qualifies the ecosystem type as Collapsed under sub criterion B1 and B2. Furthermore, numerous threats were identified as still driving declines in *O. edulis* populations (Table S3).

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 (Bland et al. 2017). The shell substrate underlying oyster reefs is a key abiotic attribute of the system. While removal of living oysters by its nature removes the shell which would otherwise be contributed to building the primary physical attribute of the ecosystem (Solinger et al. 2022), shell material can persist in the marine environment for millenia (Fariñas-Franco et al. 2018, Sanders et al. 2021). This makes it challenging to assess the extent and condition of areas of shell dominated substrate currently present in European seas and estuaries.

Although it can be unequivocally stated that the extent and condition of shell dominated substrate has declined significantly over the past centuries as a result of destructive fishing practices and increased sedimentation (Helmer et al. 2019, Sanders et al. 2021), it was not possible to identify independent records of the extent and condition of oyster shell and shell of species associated with oyster reef community (e.g. *Mytilus edulis*, Möbius 1877) deposited on the seabed. While there are known locations where oyster and associated bivalve shells are the dominant feature of the substrates (e.g. Todorova et al. 2009), there is insufficient data reported to assess their extent and condition. This assessment therefore deemed European native oyster reef ecosystem type to be data deficient under Criterion C.

Ecosystem Red listing Criteria D - disruption of biotic processes

Criterion D considers the degree to which biotic processes and interactions change within the extent of the ecosystem. Oysters are both allogenic and autogenic ecosystem engineers, substantially altering biotic processes and interactions both through their feeding activity and their physical structure (Smyth and Roberts 2010, Kennon et al. 2023, Lee et al 2020, 2023). That *O. edulis* reef ecosystems have a distinct associated community is well established (Krøyer 1837, Möbius 1877, summarised in Thurstan et al. in review a). While a distinct associated community has also been recorded in remnant areas (Kennon et al. 2023), the loss of living oysters and their reef-associated community from the seafloor and large-scale shift from structured reefs to sediments, has resulted in substantial changes to the biotic community and biotic interactions (Reise 1982). The loss of trophic interactions is perhaps most strikingly evidenced by the loss of oyster reefs as a key foraging ground for shorebirds such as 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). Today, mussels, clams and worms dominate the diet of *H. ostralegus* in Europe (Pol et al. 2009). *O. edulis* reefs historically supported a range of ecological functions, however, modern data to quantify those functions is lacking (zu Ermgassen et al. 2020). Overall, this assessment deemed the European native oyster reef ecosystem type to be Collapsed under Criterion D.

Ecosystem Red listing Criterion E - quantitative assessment of risk

Criterion E considers the probability of future ecosystem collapse. Threats to the existing oyster populations in Europe were identified from the established pathways to collapse (summarised in Figure 3, Table S3). It was, however, not possible to assess the probability of future collapse, as the ecosystem type is already deemed collapsed (Criteria A, B and D). As such, this assessment deemed Criterion E to be "Not Applicable" to the European native oyster reef ecosystem type.

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

Discussion

That European native oyster reef ecosystems were assessed as Collapsed (Table 2) is a stark finding, and should promote wider conversations about how much (or little) we know about the status of our marine environments, and the subsequent implications of these knowledge gaps for ocean policy and management. European native oyster reef ecosystems historically covered millions of hectares of the European seafloor at a range of depths (Thurstan et al. in review a,b), 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, Table S2b-d). These ecosystems would have provided important ecosystem functions such as larval output, enhanced biodiversity, water filtration, nutrient cycling, sediment stabilisation and enhanced productivity at multiple trophic levels (Lippold 1801, Christianen et al. 2018, zu Ermgassen et al. 2020, Lee et al. 2020, 2023, Kennon et al. 2023). 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 framework provides a deeper time dimension than existing assessments which classify European native oyster habitats based on more recent data, 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. in review a, Table S1a,b, 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, 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 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 illustrated that there was substantial historical evidence that criteria for being considered a “biogenic reef habitat” *sensu* Brown et al. (1997), were met by oyster reefs historically (Table S2b). Our ecosystem type definition can also serve to inform an understanding of *O. edulis* reef “reference ecosystem” attributes (Gann et al 2019), the minimum population size, area or density needed for the ecosystem to recover, all of which have been been identified as a critical knowledge gap (Preston et al. 2020b, zu Ermgassen et al. 2020, McAfee et al. 2021). While the definition developed here does not provide a quantitative answer to this important question, it does 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). While 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 et al. 2020b, 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 was possible because of the large scale, variable depth range and high abundance at which oysters were found (Thurstan et al. in review a). 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).

Despite the 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 in locations 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 to support a diverse epibiotic community and distinct associated community (Smyth and Roberts 2010, Kennon et al. 2023). Smaller scale habitat restoration efforts are a key stepping stone to larger scale ecosystem restoration (zu Ermgassen et al. 2016), ultimately leading to a tipping point where recovery is self-sustaining.

That the European native oyster reef ecosystem type is Collapsed is an important indicator of the intensely degraded status of European marine benthic ecosystems, not only due to the scale of loss of ecosystem function that their decline represents, but also because they may 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.

Acknowledgements

This work was funded by the Flotilla Foundation. RHT was funded by the Convex Seascape Survey, and the COST Action MAF-WORLD CA20102, supported by COST (European Cooperation in Science and Technology), www.cost.eu. Figure 1 was produced by Maria Eggertsen, funded by the European Research Council (ERC) under the European Union's Horizon 2020 research and innovation programme (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, and Prof Aydin and Dr Yildiz for their local knowledge.

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Figures

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. in review a. Panel A illustrates high density and relief oyster reef, which may on a larger scale be interspersed with patches or lower complexity habitat (Panel B). Panel C illustrates the degraded habitat structure now representative of oyster habitats. Artist: Maria Eggertsen.

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, digitised from *Joubin and Guérin-Ganivet 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.

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. in review a,b as having high confidence that oyster reef was historically present.
Coordinate Reference System: ETRS89-extended / LAEA Europe.

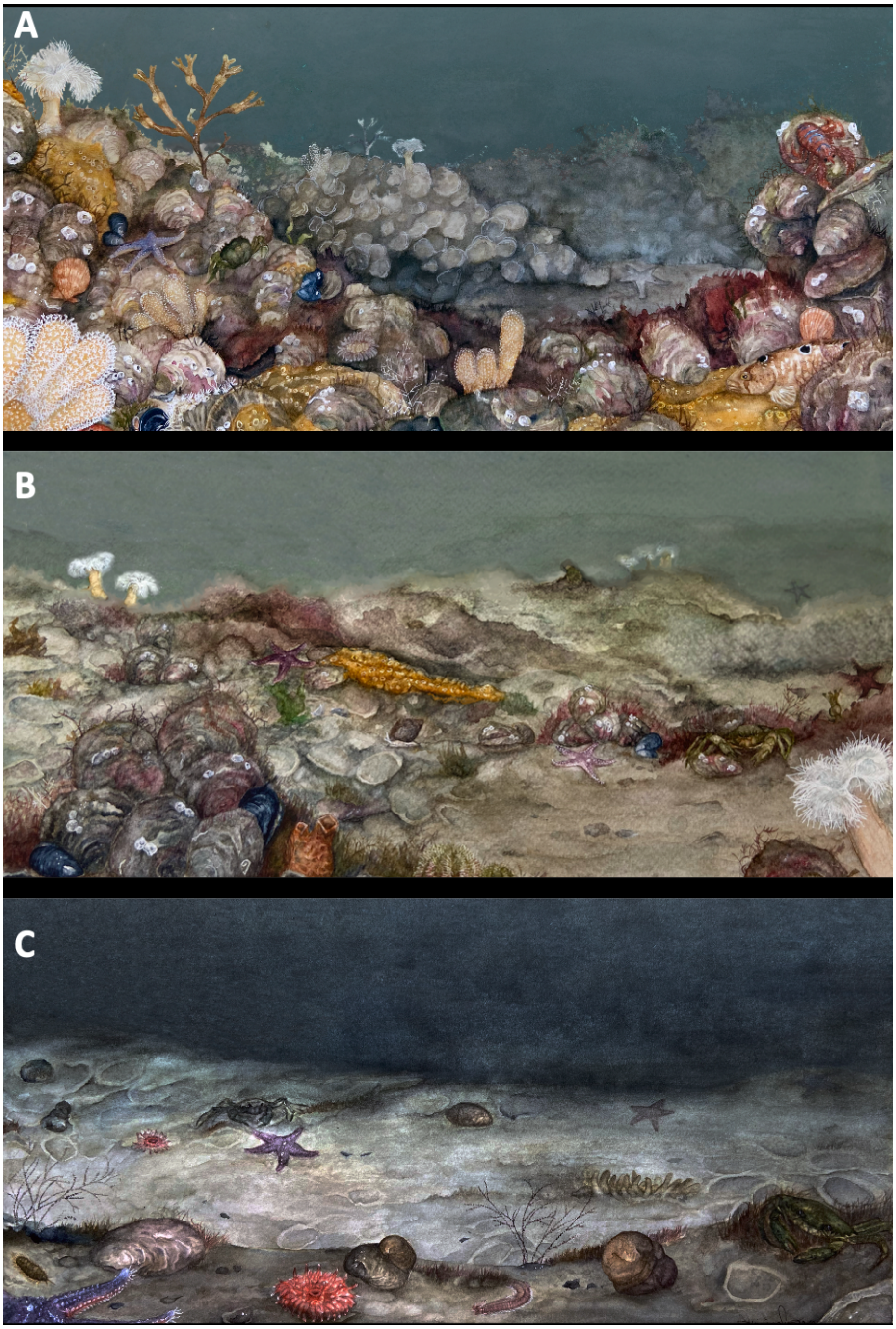
Supporting Material

Supporting materials S1: Summary of evidence of an early (<1800) shifted baseline in *Ostrea edulis* reef condition.

Supporting materials S2 Summary of the evidence underpinning the definition of the European native oyster reef ecosystem.

Supporting materials S3. Summary of evidence of ongoing threats to *Ostrea edulis* populations in Europe. Threats listed relate to those illustrated in Figure 3 within the main manuscript.

Supporting materials S4 Summary of literature relating to the current presence of *Ostrea edulis* reef ecosystems in coastal nations within the native range of the species.



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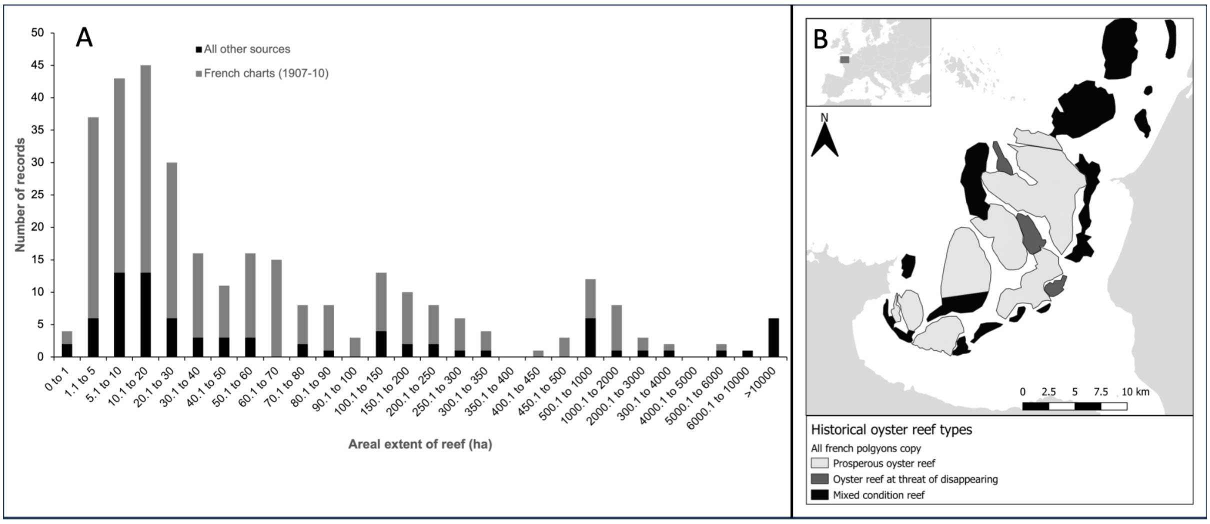

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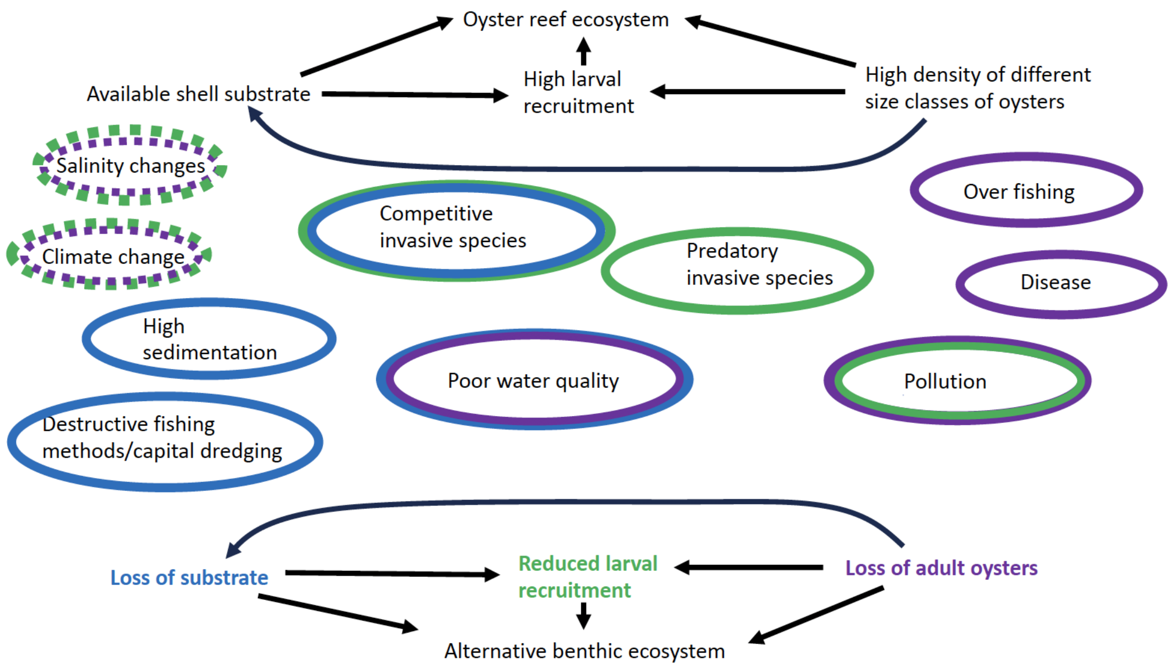

Figure 3. Pathways to collapse as identified by literature review and expert opinion. Colours indicate which component of the pathway to collapse is affected by each driver listed. Blue indicates that the driver results in loss of substrate, green indicates that the driver results in reduced larval survival 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).

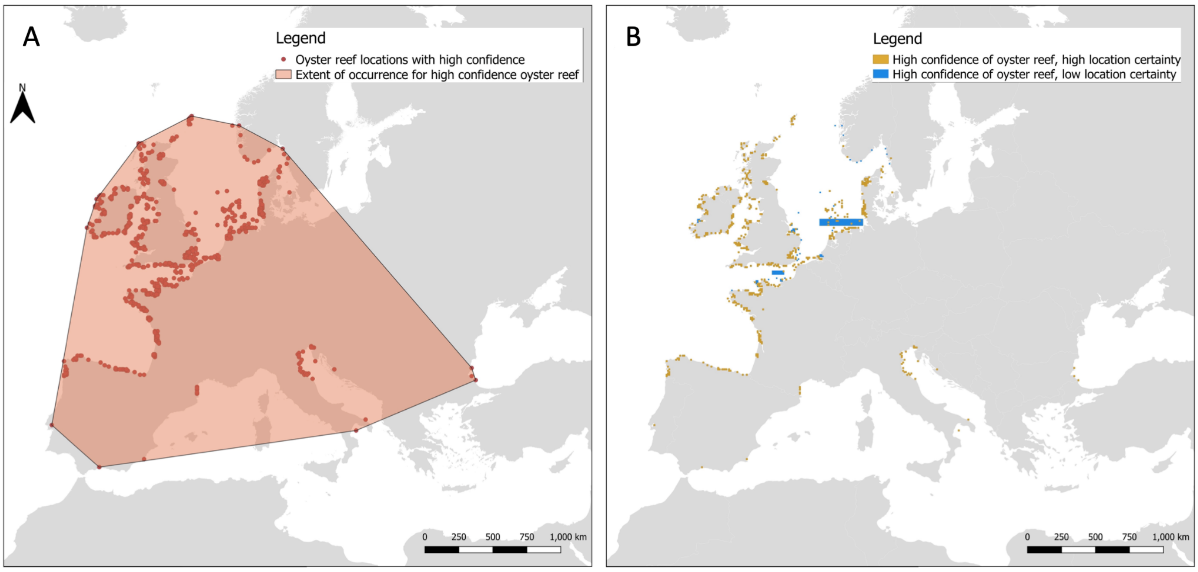

Figure 4. Past (c.1750) Extent of Occurrence (A) and Area of Occupancy (B) of the European native oyster (*Ostrea edulis*) reef ecosystem, based on locations identified by Thurstan et al. in review a,b as having high confidence that oyster reef was historically present. Coordinate Reference System: ETRS89-extended / LAEA Europe.

Tables

Table 1 Proposed reef attributes (physical form and functional features) of the European native oyster reef ecosystem. Adapted from Gillies et al. (2020) to represent habitats built by *O. edulis.* This table aims to aid the delineation of reef ecosystems versus alternative ecosystems with oyster populations.

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 (> $5m^2$), which may be separated by a few m to cover an area > 1h	Multiple patches of reef (> $5m^2$), which may be separated by a few m to cover an area < 1h	Few or no patches of oyster reef	Krøyer 1837, Joubin and Guérin-Ganivet 2009

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*	B: Restricted geographic distribution §	C: Environmental degradation* 0	D: Disruption of biotic processes	E: Quantitative analysis±	Overall threat ranking
1	DD	CO	DD	DD	NA	CO
2	NA	CO	NA	NA	NA	
3	CO	CO	DD	DD	NA	

Sub-criteria: *1= Past 50 years, 2= Next 50 years, 3=Since 1750; §1= Extent of Occurrence, 2= Area of Occupancy, 3= # threat locations; ±1= ≤50% in 50 years, 2= ≤20% in 50 years, 3= ≤10% within 100 years.

Supplementary online materials

Title: European native oyster reef ecosystems are universally Collapsed

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Supporting materials S1 Summary of evidence of an early (<1800) shifted baseline in *Ostrea edulis* reef condition.

Table S1a: Summary of evidence that data on *Ostrea edulis* habitat form and function from the mid-1800s-early 1900s represents a shifted baseline relative to pristine or fully functioning *Ostrea edulis* reef ecosystems, i.e. that the condition of described beds, in particular those which provide insight into form and function, such as Möbius 1877 and Krøyer 1837, are describing oyster reefs which have been overfished and impacted for over a century.

Year of observation	**Quotation**	**Location**	**Reference**
1703	"The tenant who, at the beginning of the last century, was in possession of the banks, petitioned (1700) to either be released from the lease or to receive a reduction in the expense. When, however, on further investigation of the matter, the conclusion was reached that he had destroyed the banks by fishing them too hard, he was deprived of them (1703), to let them rest until the expiry of the lease term (1706); but equally to pay the stipulated lease fee."	Wadden Sea	Krøyer (1837)
1769	"They are then 10 to 12 fathoms of water in the open sea, with the scrapers provided for the purpose, under full sail, cut up, taken out of the shoals, or put into the bath, whereupon the shoals are again lowered into the sea, or are then carried away until they have had as much as they desire. In such a boat, 3 or 4 scrapers can be towed, or if a dozen boat are set out, they can, in a hurry, scrape up 20 or 40,000 oysters. But as this oyster bed never rests, or is always abused in summer and winter, and also in the unused months, in a bad or disorderly manner, even by farmers far away and other strangers, it is already very ruined, and will soon be destroyed, unless it is put under proper inspection, that nothing is harvested for 2 or 3 years, and then only at certain times. which protection could best be put into effect, if the inhabitants of Skagen alone became entitled to this oyster catch." "On the Slesvig banks in 12 hrs in good conditions, 3-4000 oysters, or Aalbaekkerne which use bigger boats 5-5600 oysters in one day." In contrast Kroyer (1837): "It is generally believed that the banks have improved since the Peace. In the first years after the war a boat could at most scrape a few hundred oysters a day; now, however, more than double that."	Skagen, Denmark	Pontoppidian (1769)
~1830	"In the Wash, about fifty years ago, were enormous oyster beds; one extending nearly the whole length of the Wash and continuing outside about 50 miles. One bed in particular, which was discovered about forty years ago, being (as the fishermen state) a fathom and a half deep, with	The Wash, England	Harding (1882)

	nothing but oysters. Now everything is changed; the oysters on these beds are nearly exhausted, there not having been a fall of spat for a great number of years..."		
1849	"The oysters, when he was a boy, were as deep as the Town Hall is high. The bank was two miles long by half a mile wide" … "Attributes the failure to the French working eight or ten miles to the southward of Brighton. This is the ground where there was a great oyster bed which has been dredged out. The oysters fell off first and the French tore away the oysters and made a trawl ground of it. It is 30 years since the oysters were torn away."	Brighton / English Channel	Buckland & Walpole (1879)
1870	“In the year 1870 a small oyster bed was discovered at the mouth of the Thames, north east from Whitstable. It was about 18 metres long by 6 metres broad. Forty-eight hours later 75 boats were there, close alongside of one another, fishing up the oysters.... Upon every old oyster which was taken were found only from nine to ten young ones of different ages. This bed had never been previously disturbed, and the oysters were accordingly found in their natural condition.”	Margate Sands, England	Möbius (1883)
1871	“I remember when the boats could go out and dredge at Milford Haven, round by the Stack Rock, and each boat would get from 1000 to 1200 oysters in three or four hours. The last catch I took, I took 16 boats catch for a week; they had moderately fine weather during the week, and the largest catch was 600 oysters each, there were three men to a boat, and all of them did not bring in 5,000 in the gross, and that was starvation to the men.”	Milford Haven, Wales	Anon (1876)
1874	"OUT TO THE OYSTER BEDS. We were, on Thursday last, one of a party of about a dozen persons who went out to the Oyster beds recently discovered off Douglas Bay. The swift sailing yacht Lizzie was at our disposal, and, with the fair wind which prevailed, she, in considerably under an hour, took us out to the scene of the destructive operations of the thirty boats which we found playing havoc with the bivalves. Anyone looking at these vessels from the shore would almost fancy that they were anchored in line, head on to the land, but we found that this was a delusion to which the distance lent a semblance of reality. The vessels were crossing and re-crossing the paths of each other in every possible way, and the men appeared to work with a degree of vigour which lent strength to the assertion made by one of them to us, that in a fortnight hence there would not be an oyster left on the bank. That they are already getting scarce is apparent from the fact that in the dredges large quantities of stones are now brought up, indicating that already the bed has been broken up to the bottom. Each boat has out, so far as we could see, four dredges, so that in all there were about 120 of these destructive engines at work on the bank. The dredges are lifted and emptied about every fifteen or twenty minutes. Say that this operation is performed three times an hour, it follows that there are 300 hauls per hour, or 3,000 in a working day of ten hours, made from the bank. Of course	Douglas, Isle of Man	Isle of Man Times (1874)

	we have no means of knowing the exact extent of the oyster bed, but it is very evident that, no matter how extensive it may be, if these boats are permitted to " rag at it"' (as the local phrase is) without intermission, in season and out of season, the total destruction of the bank is only a question of a very limited time. The operations of the boats extended over a space of about a mile and a-half to two miles in length, and about half a mile or so in width; so that we may presume that the bank is about that in dimensions. The vessels engaged are cutter-rigged, and appeared to be handy, smart boats, for, notwithstanding the deterring influence of the dredges out on the weather side, they went through the water at a good speed. The depth of water at the bank is from 30 to 35 fathoms. Out of the thirty boats engaged in the fishery, there was only one Manx boat (a Ramsey smack) that we saw...."		
<1875	“I will read a very short extract from my report to the Board of Trade [on an inquiry at Poole]… It is dated the 19 of June 1875: ‘Some years ago the fishery was very productive. I had witnesses before me who agreed in stating that they had taken 2000 or 3000, or even 5000 oysters a day. The witnesses before me were also agreed that 500 or 600 oysters a day constituted now a good catch; that this number could only be taken at the very commencement of the season, and that the take rapidly fell off…. There is no reason to suppose that the small stock of oysters is attributable to any failure of spat. On the contrary, it is clear, from the age of the few oysters found, that a certain amount of spat must have fallen in each of the two last years. The fishermen themselves admit that the oysters are over-dredged; and I have no doubt whatever that the gradual failure of the oyster fishery in Poole Harbour is due to over-dredging.”	Poole Harbour, England	Anon (1876)
<1872	“It took 20 boats seven years to dredge away these oysters. There is a fathom more water on the bed now than when they began to dredge. The oysters were thick on that bed and they used to spat. There is no dredging on it now as there are no more oysters to dredge. One boat has got 30,000 oysters a week…”	Ramsey, Isle of Man	Buckland & Walpole (1879)
1879	“There are oysters, in patches, in the bay. They are in lumps, 8 or 10 together. They would be 4 to 6 inches long. Nobody fishes for them here. There has been trawling for many years here by strange boats. The local trawling has increased of late years. The inshore ground has only recently been worked…”	Aberystwyth Bay, Wales	Buckland & Walpole (1879)
<1906	“It is certain that in the past, in each river of the Bay of Quiberon, the oyster bed was continuous and that in the past it was linked to the large natural bed of the open sea […]. The oysters, in the most favourable conditions, rest on a hard soil, formed of old shells which, when packed and mixed with mud, form a solid ground. The oysters are sometimes isolated, sometimes attached to each other to form more or less large clumps.”	Bay of Quiberon	Joubin (1907)

Table S1b. Descriptions by the natural historian Karl Möbius are frequently referred to as a historical baseline, however, descriptions by Möbius (1883) and even by Krøyer (1837), who write some decades earlier, provide a description of impacted and long exploited oyster reefs off the coast of Denmark and Germany.

Year of observation	**Quotation**	**Location**	**Reference**
1877	“In no place upon the seaflats do oysters grow upon rocky bottom. They grow best where there is a substratum of old oyster and other shells. The most of them lie singly, and they are seldom found growing together in clumps of masses. The wide-spread notion that they are found growing firmly attached to the sea-bottom, and piled upon one another, layer upon layer, is accordingly false. Upon the best of the Schleswig-Holstein beds the dredge must drag over a surface of from 1 to 3 square metres, and often over a greater distance, in order to secure a single full grown oyster.”	Schleswig-Holstein, Germany	Möbius (1883)
1877	“The living oysters do not lie in thick masses, stuck to and on one another on the banks, rather mostly more than one meter from one another apart, so that on a meter square of bank area mostly less than one adult oyster will be caught. And yet smaller is the count of half grown oysters. On the largest and most fruitful Bank Huntje, were in ten surveys undertaken between 1730-1852 on average for every 1000 grown oyster only 484 half grown caught, and on most other banks relatively fewer half grown.”	Wadden Sea	Möbius (1883)

1837	“If the sea-bed consists of solid rock, or of loose stones, some oysters are attached to the projections of the rock, or to the individual stones, but many also lie loose on the bottom. Where this consists of clay, sand, or silt, all the oysters must naturally lie loose, except where some are grouped in irregular clusters of three, four, or five individuals. More than five to six I have never seen united; and it is also evident that, if the oysters lay in many layers one above another, and, as a natural consequence, grew together in great masses, the underlings would be hindered not only in their development, but also in opening their shells, and consequently die in a shorter or longer time. The easternmost banks are so far from forming outcrops on the sea-bed that they usually lie in or on the edge of the deeper trenches in the sea-bed.”	Wadden Sea	Krøyer (1837)

Figure S1. Oysters caught during semi-quantitative dredge surveys of known oyster banks in the Wadden Sea from 1709-1830, illustrating that fisheries had overexploited oyster reefs in the region prior to published descriptions of the ecology of oyster reefs (published by Krøyer 1837 and Möbius 1877). Krøyer

(1837) provided an in depth review of the status of the Wadden sea oyster banks in the 1830s, drawing on survey data and reports from 1700 onwards. While “oyster banks” continued to be discovered during this time period, nine of the 44 banks known in 1730 were already considered “fished to nothing”.

Supporting materials S2 Summary of the evidence underpinning the definition of the European native oyster reef ecosystem.

Table S2a: Examples of current definitions of habitats with mention of *O. edulis*. It is worth noting that *O. edulis* is listed as a feature of "Atlantic littoral *Mytilus edulis* beds on mixed substrata", "Assemblages of Mediterranean euryhaline and/or eurythermal lagoon biocenosis on sand", and "Assemblages of the euryhaline and/or eurythermal lagoon biocenosis on mud" (EUNIS, 2022). *O. edulis* not among the species listed for "Bivalve reefs in the Atlantic circalittoral zone" or "Bivalve reefs in the Atlantic littoral zone" (EUNIS, 2022). *O. edulis* not explicitly mentioned nor excluded from: "Infralittoral biogenic habitat", "Black Sea infralittoral biogenic habitat" (EUNIS, 2022).

Related policy or framework	**Attribute defined**	**Description**	**Reference**
OSPAR	Oyster beds	"*Ostrea edulis* occurring at densities of 5 or more per m^2 on shallow mostly sheltered sediments (typically 0–10m depth, but occasionally down to 30m). There may be considerable quantities of dead oyster shell making up a substantial portion of the substratum."	OSPAR Commission (2009)
Ramsar	Bivalve reef	"Bivalve reef consists of large areas of biogenic habitat, dominated by living bivalves where the complex structure of hard shells supports a distinct community that is persistent through time. Expanding on this general definition: 'large areas' typically consist of multiple patches, at least some of which are larger than 5 m^2; 'dominated' means at least 25% cover of live shell matter across that space – non-living shell (cultch) may further add to habitat structure and to continuity over time, but without new growth they are unlikely to persist; a 'distinct community' is one that supports species and interactions that are rare or absent in surrounding communities; and 'persistent through time' describes communities that are likely to remain over decadal timescales or longer."	Koasar et al. (2015)
EUNIS	Bivalve reefs in the Atlantic infralittoral zone	Infralittoral reefs in the Atlantic formed by bivalves such as *Limaria hians* and *Ostrea edulis*	EUNIS (2022)
EUNIS	*Ostrea edulis* beds on Atlantic infralittoral muddy mixed sediment	Dense beds of the oyster *Ostrea edulis* can occur on muddy fine sand or sandy mud mixed sediments. There may be considerable quantities of dead oyster shell making up a substantial portion of the substratum. The clumps of dead shells and oysters can support large numbers of *Ascidiella aspersa* and *Ascidiella scabra*. Sponges such as *Halichondria bowerbanki* may also be present. Several conspicuously large polychaetes, such as *Chaetopterus variopedatus* and terebellids, as well as additional suspension-feeding polychaetes such as *Myxicola infundibulum* and *Sabella pavonina* may be important in distinguishing this biotope, whilst the *Opisthobranch Philine*	EUNIS (2022)

		aperta may also be frequent in some areas. A turf of seaweeds such as *Plocamium cartilagineum*, *Nitophyllum punctatum* and *Spyridia filamentosa* may also be present. This biotope description may need expansion to account for oyster beds in England.	
EUNIS	Polychaete worm reefs in the Black sea infralittoral zone	Biogenic circalittoral reefs formed by a variety of polychaete worms. In more sheltered and freshwater-influenced environments the non-native serpulid tubeworm *Ficopomatus enigmaticus* is the most common reef building species. In moderately exposed environments reefs formed by the serpulid *Vermiliopsis infundibulum* are present. Finally, on lower infralittoral rock serpulids form massive reefs in collaboration with bivalves (i.e. *Ostrea edulis, Mytilus galloprovincialis*). These reefs are an important component of the Black Sea ecosystem and are characterised by high biodiversity.	EUNIS (2022)

Table S2b. Based on the current status of *O. edulis* habitats in Europe, it has previously been called into doubt whether *O. edulis* is capable of forming biogenic habitat. For example, *O. edulis* reefs were explicitly not considered as biogenic reefs during the UK marine SACs Project (Holt et al. 1998), because in their current highly impacted state, and the remaining habitats left, it was “doubtful if natural beds would qualify as reefs”. Here we provide a summary of the historical evidence that *O. edulis* reefs fulfilled the attributes of “biogenic reef habitat” *sensu* Brown et al. (1997), prior to their widespread degradation by human activities.

Biogenic reef habitat attributes	**Evidence from *O. edulis* reef**	**Reference**
Biogenic reef must “create a substratum which is **reasonably discrete and substantially different to the underlying or surrounding substratum**” (Brown et al. 1997)	“The oyster banks of Wicklow have become hard like a rock, as is generally believed for want of dredging. The more the banks are dredged, the more oysters breed. It would do the banks great good to be broken up by a heavy dredge worked from a large smack.”	Irish Fisheries (1836)
	“These great oyster banks are situated on patches in the North Sea, especially off the Dutch coast. The trawlers carefully avoid these beds as the heavy clumps tear the nets."	Buckland and Walpole (1879)
	"The trawlers avoid this “rough ground” as they call it, as much as possible; but when they do by accident get on to it, the oysters are so numerous that they fill up the trawl net and nearly bring up the vessel" … “The dredgermen who go out fishing in the North Sea (as I found out in my inquiries at Yarmouth) come across every now and then an	Buckland (1875)

	enormous tract of oyster ground, which tears their nets all away to pieces, and for that reason they get away from it.”	
	“It is certain that in the past, in each river of the Bay of Quiberon, the oyster bed was continuous and that in the past it was linked to the large natural bed of the open sea […]. The oysters, in the most favourable conditions, rest on a hard soil, formed of old shells which, when packed and mixed with mud, form a solid ground. The oysters are sometimes isolated, sometimes attached to each other to form more or less large clumps.”	Joubin (1907)
	“It was reported that large oyster beds had been discovered off New Quay, but strong dredges would be required to open them.”	The Aberystwith Observer (1897)
	[In Bay of Saint Brieuc, North Brittany] “The Parliament of Brittany issued a decree on 16 October 1784, because the Saint Brieuc bed was almost completely exhausted: "In many places where it was formerly composed of several layers, only mud is currently being removed"”.	Levasseur (2006)
Biogenic reef “unit should be … **somewhat raised**” (Brown et al. 1997)	The seafloor is filled with oysters, almost placed one on top of the other like stones, forming a wall.”	Marsili (1715)
	“In no place upon the seaflats do oysters grow upon rocky bottom. They grow best where there is a substratum of old oyster and other shells.	Möbius (1883)
	"The oysters, when he was a boy, were as deep as the Town Hall is high. The bank was two miles long by half a mile wide"	Buckland and Walpole (1879)
	The oyster reefs found by us are constructed mainly of *Ostrea edulis* shells, with calcareous tubes of serpulid polychaetes also present as cementing material. They represent erect biogenic structures with a distinguishing irregular, branching or netted shape with serrated margins attaining 7 m height, 30–50 m length and 10 m width	Todorova et al. (2009)
Biogenic reef “unit should be **substantial in size** (generally of the order of a metre or two across as a minimum)” (Brown et al. 1997)	“Trawlers have lately found oyster beds in the North Sea. The huge ‘Skelling Bank’ off Heligoland consists of numerous patches of oysters; other great oyster beds have been found off the Dutch coast by trawlers. A trawl has a beam which spreads about 40 feet, and especially in very deep water, where dredges will not work nicely, it picks up a great many oysters…”	Philpots (1891)

	In the year 1870 a small oyster bed was discovered at the mouth of the Thames, north east from Whitstable. It was about 18 metres long by 6 metres broad. Forty-eight hours later 75 boats were there, close alongside of one another, fishing up the oysters.... Upon every old oyster which was taken were found only from nine to ten young ones of different ages. This bed had never been previously disturbed, and the oysters were accordingly found in their natural condition.	
	“Over the Schleswig-Holstein seaflats there exist 50 oyster beds of very different sizes. The largest is not far from 2 km long, but the greater number are shorter than this. Their breadth is much less than their length, which is in the same direction as the channels along the slopes of which they lie.... “	Möbius (1883)
	Each boat has out, so far as we could see, four dredges, so that in all there were about 120 of these destructive engines at work on the bank. The dredges are lifted and emptied about every fifteen or twenty minutes. Say that this operation is performed three times an hour, it follows that there are 300 hauls per hour, or 3,000 in a working day of ten hours, made from the bank. Of course we have no means of knowing the exact extent of the oyster bed, but it is very evident that, no matter how extensive it may be, if these boats are permitted to " rag at it"' (as the local phrase is) without intermission, in season and out of season, the total destruction of the bank is only a question of a very limited time. The operations of the boats extended over a space of about a mile and a-half to two miles in length, and about half a mile or so in width; so that we may presume that the bank is about that in dimensions.	Isle of Man Times (1874)

Table S2c. The IUCN Ecosystem Red Listing process requires that the developed ecosystem definition is cross-referenced to relevant ecological classifications such as the IUCN Global Ecosystem Typology (Keith et al. 2020). Here we provide a summary of evidence that *O. edulis* reefs historically fulfilled the ecological trait criteria of forming “Shellfish beds and reefs”, as defined by the IUCN Global Ecosystem Typology (Keith et al. 2020).

Ecological trait	**Evidence from *O. edulis* reefs**	**Reference**
High productivity and moderate diversity, heterotrophic energy.	The oysters, which, as we have seen above, is itself so worthless, and consequently peaceful, animal, is given at the price of a great many	Krøyer (1837)

	enemies. It is this circumstance which makes the oyster-banks so interesting to a zoologist; one can probably always be sure … of drawing from the sea between the oysters a host of other animals, whose amusement is undoubtedly largely derived from the oyster. Such animals are various species of crabs, starfish, snails, worms, &c. Although the oyster by its shell should appear to be amply protected against these enemies, it will be evident from what follows that even the adult oyster does not always find a reassuring shelter in the armour with which nature has equipped it; still less can this be the case with the very infant. So great is the fertility of the oyster, that I alone find on our banks a long greater number of young oysters. When the full-grown oyster is drawn up from the depths, its shell is generally found lined with calcareous or membranous tubes, which serve as a dwelling-place for various worms (serpulare or worm-tubes, &c.); with balans, anomia, chitonians, ascidians, and similar immobile or unwieldy animals. The more of these there are, the more loopholes are formed (and especially if two or three oysters are together) for numerous small crabs (*Porcellana longicornis* and *Galachea strigosa*) of size from that of a grain of manure to that of a large pea, for polynids, ophids, &c. ; oyster young, however, are comparatively rarely seen; I suppose because they are for the most part devoured by these many small but very large predators.”	
Structural complexity from shell aggregations.	In the year 1870 a small oyster bed was discovered at the mouth of the Thames, north east from Whitstable. It was about 18 metres long by 6 metres broad. Forty-eight hours later 75 boats were there, close alongside of one another, fishing up the oysters.... Upon every old oyster which was taken were found only from nine to ten young ones of different ages. This bed had never been previously disturbed, and the oysters were accordingly found in their natural condition.	
	“There are oysters, in patches, in the bay. They are in lumps, 8 or 10 together.	Buckland and Walpole (1879)
	“The seed is like a viscus or glue, which immediately attaches itself to trees and stones and, in the absence of these, often to the oysters themselves, so that three or four can still be attached to an oyster.”	Oedmann (1743)

	“In June, when oysters are most scarce, they reproduce on the bottom of the sea, by leaving out their eggs or spawn, which looks like a drop of glue, and attaches itself to everything in the sea, often to oysters themselves.”	Wilmsen (1831)
Dominated by sessile filer-feeders, secondary deposit-feeders.	“Generally the [oyster] net is allowed to drag from five to ten minutes… and the entire contents of the bag emptied upon the deck. This mass consists of old oyster shells, mussels of various kinds, living oysters, snails, crabs, worms, starfish, sea-urchins, polyps, sponges, and sea-weeds, which are generally mixed up with sand and mud... Despite these manifold cleansings [by fishermen for market] many oysters when they are exposed for sale are covered with dead and living animals, and the peculiar odour which oysters have when carried into the interior arises from the death and decay of the organic materials upon the outside of the shells...”	Möbius (1883)
	Even the shells of the living oysters are inhabited. Barnacles (*Balanus crenatus*) [...] often cover the entire surface of one of the valves. Frequently the shells are bedecked with yellowish tassels a span or more in length, each of which is a community of thousands of small gelatinous bryozoa (*Alcyonidium gelatinosum*), or they are overgrown by a yellowish sponge (*Halichondria panicea*) [...] Upon many beds the oysters are covered with thick clumps of sand which are composed of the tubes of small worms (*Sabellaria anglica*). These tubes, called 'sand-rolls' resemble organ-pipes, and are formed from grains of sand cemented into shape by means of slime from the skin of the worm [...]. Upon certain beds near the south point of the island of Sylt [...] there lives upon the oyster shells a species of tube-worm (*Pomatoceros triqueter*) [...] The shells of many oysters upon these beds also carry what are called 'sea hands' (*Alcyonium digitatum*) which are white or yellow communities of polyps of the size and shape of a clumsy glove. Often the oyster shells are also covered over with a brownish, clod-like mass, which consists of branched polyps (*Eudendrium rameum* and *Sertularia pumila*) or they may be covered with tassels of yellow stems which are nearly a finger long and have at their distal ends reddish polyp-heads	Möbius (1883)

	(*Tubularia indivisa*). Among these polyps, and extending out beyond them, are longer stems, which bear light yellow or brown polyp-cups (*Sertularia argentea*) [...]. I once took off and counted, one by one, all the animals living upon two oysters. Upon one I found 104 and upon the other 221 animals of three different species [...]. Soles [...] stone-picks, and stingrays [...] are abundant upon the oyster banks.	
	in addition to the “fern” (*Sertularia abietina*), which is not disfiguring, there are a good many soft worm tubes (*Terehella*, or the like), sea-squirts (*Ciona intestinalis*), and small shell-fish (*Crenella diseors*) to be cleaned off.	Holt (1902)
	“These shells are very often covered with productions of the coral kind: they are frequently loaded also with small muscles and multitudes of worms, but only on the convex side, which appears to be the upper one, so that the animal rests on the flat side. It frequently happens that both shells are quite pierced through, and gnawed by worms in the same manner as old wood.”	Beckmann (1800)
	Very often one finds corellanic plants on the oyster shells; often they are also covered with mussels and other plants.	Lippold and Funke (1810)

Table S2d. Summary of relevant historical catch rates and habitat descriptions, depicting the reef-building nature and high densities of *O. edulis* encountered in *O. edulis* reef ecosystems historically. For further analysis, see Thurstan et al. in review a,b.

Evidence from *O. edulis* reef	**Reference**
Fishermen from Holland and Germany dredge for oysters here, especially during the months of August, September, and October, and often catch, at a single drag of the dredge, as many as 1,000 oysters. Sometimes great bunches of oysters growing attached to one another are gathered into the net.	Möbius (1883)
“In Ballycroy Bay, and the Sound of Bullsmouth, three thousand oysters may be taken in a day, with a dredge. They are often sold for 3d per hundred…. There are several natural oyster beds in Broadhaven and Blacksod bays, and in Achil Sound; they are open to the public and dredged.”	Irish Fisheries (1836)
“I remember when the boats could go out and dredge at Milford Haven, round by the Stack Rock, and each boat would get from 1000 to 1200 oysters in three or four hours. The last catch I took, I took 16 boats catch for a week; they had moderately fine weather during the week, and the largest catch was 600 oysters each, there	Anon (1876)

were three men to a boat, and all of them did not bring in 5,000 in the gross, and that was starvation to the men.”	
“I will read a very short extract from my report to the Board of Trade [on an inquiry at Poole]… It is dated the 19 of June 1875: ‘Some years ago the fishery was very productive. I had witnesses before me who agreed in stating that they had taken 2000 or 3000, or even 5000 oysters a day. The witnesses before me were also agreed that 500 or 600 oysters a day constituted now a good catch; that this number could only be taken at the very commencement of the season, and that the take rapidly fell off…. There is no reason to suppose that the small stock of oysters is attributable to any failure of spat. On the contrary, it is clear, from the age of the few oysters found, that a certain amount of spat must have fallen in each of the two last years. The fishermen themselves admit that the oysters are over-dredged; and I have no doubt whatever that the gradual failure of the oyster fishery in Poole Harbour is due to over-dredging.”	Anon (1876)
“Clew Bay abounds with oysters, where they are taken in large quantities, (considering the wretched small dredges with which they are fished for,) out of an open boat, rowed by two men, and a third holding the dredge rope. They seldom catch more than a thousand a day, as they find it difficult to dispose of them, even at a moderate price... the expense of sending them up [to Dublin] by carriers runs away with any profit that the fishermen would derive from a good market, and they now seldom fish for them unless they are bespoke."	Brabazon (1848)
“It took 20 boats seven years to dredge away these oysters. There is a fathom more water on the bed now than when they began to dredge. The oysters were thick on that bed and they used to spat. There is no dredging on it now as there are no more oysters to dredge. One boat has got 30,000 oysters a week…”	Buckland and Walpole (1876)
“Helligsø - 'one of the oldest banks in the whole Limfjord. It was initially extremely rich, so that even in one day, about 14,000 oysters were fished of a single boat despite the fishermen's inferior exercise scraping… The bank decreased year by year in fullness, but was still in the spring of 1868 so rich that a single boat in one day scraped about 5000 stkr. Now it gives so little that the scraping can't pay off... has been abandoned."	Collin (1871)
From the locality the bed extends not less than 60 miles in the North-West direction, where they lie very thick; 1200 have been caught here in the space of four hours by the trawl net. Towing by steam power, the whole space of ground appears almost inexhaustible, at all events it will take a great number of years to exhaust it. The water being deep, improved dredges are required, and steam winches to heave them up with. If enterprising gentlemen were to form a company, and have a few steamers of about 70 tons built, with wells in them, and fitted with steam winches, it is highly probably it would pay well… The vessels, I should estimate, would bring from 35 to 50 thousand [oysters] per week, and that ought to pay well. Already small sailing vessels have been getting 20 thousand per week, without the aid of steam power. … Grimsby has now twenty oyster vessels.”	Olsen (1885)

“The period of the Cancale Fishery is known as "la Caravane" [...]. The 1909 "Caravane" involved 6 trips of 360 boats each, manned by 2500 men. From 10 April to 24 April, fishing took place for 38 hours and 45 minutes. The number of oysters caught was 16 million.”	Joubin (1910)
“In Auray River (near the bay of Quiberon), in 1885, 150 boats, manned by 1648 men, have dredged 4.2 million oysters within 4 days…”	Joubin (1907)
There were then very few boats in the Bay, from six to seven thousand oysters were often got in one day with only one dredge, but when larger boats from Jersey with superior tackle came this became a small haul.	The Cambrian News and Merionethshire Standard (1889)
“Until the last fishing season which lasted 6 months & 10 days, this industry (Bay of Brest fishery) came to the aid of 576 fishermen on 144 boats & that 14 million oysters were sold.”	Archives du Service Historique de la Défense de Vincennes (1849)
“It is by far the best stocked bed on the coast, and may, I think, be considered in a satisfactory condition, since the catch comprised oysters of all ages	Holt (1902)
“An old oyster often has twenty small ones attached to it”	Beckmann (1800)

Table S2e. Reported densities of reef building oysters from geographies outside or Europe. *Ostrea* spp. densities reflect densities in current exploited and protected areas. Reported *Crassostrea virginica* densities are provided for context. *C. virginica* are known reef builders, yet as a result of over-exploitation, mean densities recorded in the 1880s in Virginia, USA were similar to those reported in degraded *O. edulis* habitats today.

Species	**Location**	**Mean density range (Ind m^{-2})**	**Reference**
Ostrea angasi (exploited)	Australia	17-67	Jones and Gardener 2016
Ostrea lurida (protected)	British Columbia	21-507 (across the 9 of 14 sites sampled, with a mean density of >20 Ind m^{-2})	Norgard et al. 2018
Crassostrea virginica (exploited)	Texas	24-67	Moore and Danglade 1917
Crassostrea virginica (over exploited)	Virginia	0.07-0.57	Winslow 1881

Table S3. Summary of evidence of ongoing threats to *Ostrea edulis* populations in Europe. Threats listed relate to those illustrated in Figure 3 within the main manuscript.

Threat	**Summary of evidence for current trend/future threat**
Over harvesting	Over harvesting is the leading cause for the decline in *O. edulis* historically. There are very few wild fisheries still active in Europe, as most stocks were fished to economic extinction by the 1930s (Thurstan et al. 2013). Many of the remaining fisheries are suffering from poor recruitment and declining catches (Southern IFCA 2019, Kent and Essex IFCA 2022, Marine Institute & Bord Iascaigh Mhara 2023). Although the reasons for these recent declines are diverse and include, for example, the introduction of invasive species and disease, fishing remains a pressure on these declining populations, as reflected by fisheries restrictions to aid in the recovery of the population (Southern IFCA 2019, Kent and Essex IFCA 2022, Marine Institute & Bord Iascaigh Mhara 2023). Illegal and unregulated harvesting is also an ongoing threat to native oyster populations and their recovery. *O. edulis* stocks in Strangford Lough, Northern Ireland recovered to >1 million individuals in 2007 but declined to 650,000 by 2005 (Smyth et al. 2009). This decline was linked to illegal and unregulated harvesting (Smyth et al. 2009), which is supported by the continued observation that *O. edulis* populations remain suppressed in areas which are not policed. In contrast, well protected areas are maintaining their population (Smyth et al. 2023).
Poor water quality (Eutrophication)	The *O.edulis* population in the Mar Menor, Spain, was estimated at ~135 million in 1989 (Garcia Garcia et al 1989), but has declined to levels at which there is no evidence of recruitment (Ruiz et al. 2020).
Pollution (TBT)	TBT impacted *O. edulis* populations (Thain and Waldock 1986), but this threat has been declining since the banning of TBT in the 1980s (Crouch estuary, UK; Rees et al. 2001).
Climate change	Temperatures above 28°C are detrimental to *O. edulis,* and temperatures above 36°C are fatal (Eymann et al. 2020), this may have implications for part of the species range, in particular in the eastern Mediterranean, under a warming climate (Sakalli 2017) as well as lagoonal areas. For example, water temperatures in the Mar Menor (Spain) reached 31C in July 2023 (McGeer 2023). At lower temperatures, populations may be impacted by a temperature-mediated skewed sex ratio, with a study on two UK populations finding that higher temperatures resulted in a male-skewed sex ratio, which may impact population viability (Eagling et al. 2018). Furthermore, there may be interactions between climate change and other threats, such as invasive species. For example, rising temperatures will differentially affect *C. gigas* and *O. edulis*, and it is as yet unknown what its impact will be on the balance in population growth between the two species (Stechele et al. 2022).
Invasive species (*Crassostrea gigas*)	There are many examples of *C. gigas* and *O. edulis* coexisting, either within the same water body, but at differing depths (Staglicic et al. 2020), or within mixed reefs (Christianen et al. 2018, Thorngren et al. 2019). Given the currently limited presence of *O. edulis* in European coasts and seas, it is challenging to draw conclusions on whether interactions between these two species are positive for *O. edulis*, or negative. In areas of substrate limitation, *C.*

	gigas has been observed to provide an important source of substrate (Christianen et al. 2018), however, *C. gigas* has also been observed to consume the larvae of *O. edulis*, as well as having a high overlap in feeding traits, which could indicate that competitive interactions will become more important when *O. edulis* numbers increase (Ezgeta-Balic et al. 2020). In marine management policies, the precautionary principle is therefore applied and further introduction of *C. gigas* is not recommended (Ezgeta-Balic et al. 2020). *C. gigas* is expanding its range across Europe and will therefore impact increasing numbers of sites where *O. edulis* was historically present (Anglès d'Auriac et al. 2017).
Invasive species (*Rapana venosa*)	Introduced to the Black Sea in the 1940s, the predatory gastropod *Rapana venosa*, had consumed almost all oysters on the large Gudauta oyster bank by the 1950s (Zolotarev & Terentyev 2012). This species continues to present a significant issue to the recovery of shellfish populations, with impacts on shellfish species throughout the Black Sea (Janssen et al. 2014) and in the northern Adriatic, where it was first recorded in 1973 (Savini & Occhipinti-Ambrogi 2006).
Invasive species (*Crepidula fornicata*)	*C. fornicata* can dominate substrates it invades and change the nature of the substrate to one of anoxic mud and making it less suitable for *O. edulis* settlement. This is especially problematic as their niches strongly overlap (Blanchard et al 2008). There are also direct interactions with *O. edulis*. Where substrate is limiting *C. fornicata* may outcompete *O. edulis* for settlement substrate (Preston et al. 2020). Furthermore, *C. fornicata* larvae may outcompete *O. edulis* larvae for food (Blanchard et al. 2008, Preston 2020). Finally, also of relevance to the ecosystem red listing, where *C. fornicata* is abundant, it can result in reduced biodiversity associated with *O. edulis* habitats, relative to when *C. fornicata* is absent (Lown et al. 2021).
Disease (*Martelia refringens*)	*Marteilia refringens* was first recorded in Europe in 1968, where it caused high mortality (Grizel et al. 1974). *Martelia* spp. was implicated in the extinction of *O. edulis* from Gulf of Thessaloniki, Greece (Virvilis and Anglidis 2006)
Disease (*Bonamia ostreae*)	*Bonamia ostreae* is an invasive haplosporidan parasite that has been a leading cause of mortality in populations of *O. edulis*, since its introduction into Europe in the late 1970s (Grizel et al. 1985), causing over 90% mortality in 4+ ages oysters in naïve populations (Culloty & Mulcahy 2006). The disease caused by *B. ostreae* has subsequently been implicated in the decline and economic extinction of numerous remnant *O. edulis* populations, and the disease is considered a potentially limiting factor to restoration efforts in some locations (Laing et al. 2005). Recently, genetic markers which may indicate resistance or tolerance to *B. ostreae* have been identified (Sambade et al. 2022), and many restoration efforts are now seeking to work with resistant or tolerant individuals in their active restoration efforts (Kamermans et al. 2023). The effectiveness of the markers in response to a *B. ostreae* challenge have yet to be tested, but there is evidence that populations with a longer exposure history to *B. ostreae* or slow-growth life histories have better survival in the presence of the parasite (Culloty et al. 2008; Egerton et al. 2020).

Salinity changes	*O. edulis* is found in European waters with salinities ranging from c.20 ppt to 42ppt (Davis & Ansell 1962, Ruiz et al. 2020). Historically there are examples of increases in salinity resulting in the establishment and growth of *O. edulis* populations in the Limfjord, Denmark (Collin 1884). Similarly, within the Roskilde fjord and along the central eastern coast of Jutland (around Horsensfjord), oysters were previously recorded in areas where salinities are now too low for viable populations (Krøyer 1837, Rasmussen et al. 2007).
High sedimentation	Avoiding high sedimentation rates is a critical factor in site selection for *O. edulis* restoration efforts (Hughes et al. 2022, Kamermans et al. 2022). Fishers in some locations have traditionally sought to combat the effects of sedimentation through the practice of "harrowing", during which gear is towed over oyster habitats to remove sediment prior to larval settlement (Bromley et al. 2016). While increased sedimentation was not a reported driver of decline in the documentary historical literature (Thurstan et al. in review b), it has been implicated as a potential driver of decline in late Holocene reefs (Sander et al. 2021). It is widely accepted that deforestation during numerous periods from the 1000 onwards resulted in increased siltation of European coastal ecosystems (Poirier et al. 2011). With improved land use management, river sediment load in Europe may decrease in the future (Bakker et al. 2008).
Destructive fishing methods/capital dredging	Bottom towed gears have been recognized as a threat to *O. edulis* populations since the early 1800s (e.g. Krøyer 1837 and references within Table S3). Towed gears disturb the habitat, flatten the structure, and re-suspend sediments (Watling and Norse 1998, Oberle et al. 2016). As a result, bottom towed gears are known to reduce the diversity and complexity of seabed habitats (Hiddink et al. 2019, Pitcher et al. 2022). Much of the European shallow seas is trawled 1-10 times a year, and many inshore waterways are dredged (Eigaard et al. 2017). There are, however, areas where bottom towed gears are banned (e.g. Milford Haven, Wales; Sweden, Norway in waters <60 m depth), and where recovery of *O. edulis* habitat is not precluded.

Table S4

Summary of literature relating to the current presence of *Ostrea edulis* reef ecosystems in coastal nations within the native range of the species.

Country	Any m^2 areas with >20 oysters m^{-2}?	Any > 1 ha areas with >20 oysters m^{-2}	Details
Albania	no	no	*O. edulis* and *O. stentina* present in species checklist. (Dhora 2009) No further mentions identified.
Algeria	no	no	*O. edulis* present, but not "strong presence" in north-western Algeria (Hussein and Talet 2019).
Belgium	no	no	No *O. edulis* collected from the scuba operated video footage on the Westhinder sandbank (Houziaux et al. 2007).
Bosnia and Herzegovina	no	no	Neum Bay, individuals of *O. edulis* also encountered when collecting mussels (Trozic-Borovac et al. 2022).
Croatia	no	no	*O. edulis* common, but not dominating locally (Zavodnik and Kovavic 2000). Max densities from survey <2 oysters m^{-2}. Coexistence with *C. gigas* (Staglicic et al. 2020). Listed as present in Novigrad and Karin Seas, but no further mention (Kruschel et al. 2011).
Cyprus	no	no	*O. edulis* present in species list (Fischer 1997).
Denmark	no	no	No recent records of *O. edulis* from the Wadden Sea. Max *O. edulis* biomass in the Limfjord is given as >0.25kg m^{-2} over small area, with most areas 0.01-0.05kg m^{-2} (Fomsgaard and Petersen 2015).
Egypt	no	no	*O. edulis* present in Nile lagoons, but not a dominant species (Bernaschoni and Stanley 1994). Few *O. edulis* individuals (28-30 total) found at two sites within Burullus Lagoon (Orabi et al. 2018).
England	no	no	Some areas within the oyster beds have *O. edulis* at >5 m^{-2}, but average in Blackwater c. 3m^{-2} (Allison 2018); Fal catch rates c. 1-5kg hr^{-1} (Sturgeon et al. 2022). In Solent:, *Ostrea edulis* stock assessment (Southern Inshore Fisheries and Conservation Authority 2019) only 33% of tows were positive (contained an oyster). Of these positive tows, the average CPUE (kg/m/hr/>70mm) was 3.29 with a range of 1.27 - 5.18. The *Ostrea edulis* population had declined by 96% in the last two decades (1999-2019; Helmer et al 2019). The threshold CPUE to reinstate a fishery is 15 oysters m^{-2} hr^{-1}.

France	yes	no	Patches with *O. edulis* at >20 m^{-2}, but not over extended area (< 1000 m^{2}). Many places in Brittany were density is less than 1 oyster m^{-2}. See database on Pouvreau et al. (2021) https://www.seanoe.org/data/00686/79821/
Georgia	no	no	Large bank of *O. edulis* extirpated by *Rapana venosa* in the 1950s (Zolotarev and Terentyev 2012).
Germany	no	no	*O. edulis* extirpated in Germany (Gerken and Schmidt 2014)
Greece	no	no	*O. edulis* beds in the Gulf of Thessaloniki extinct due to *Martelia* (Virvilis and Angelidid 2006).
Ireland and Northern Ireland	yes	no	Lough Foyle- *O. edulis* densities <4 m^{-2} even in the best areas (Loughs Agency 2020). Area of beds in Inner Tralee Bay 4km^{2}, *O. edulis* density range 0-50 m^{-2}, but most areas <1 m^{-2} . In other sites in Ireland (Kilkieran Bay) densities did not exceed 5 m^{-2}(Tully and Clarke 2012, Marine Institute & Bord Iascaigh Mhara, 2021). In Strangford Lough, in 2004 some areas settled with >30 m^{-2} (Smyth et al. 2009), but there was subsequent decline to low numbers (Smyth et al. 2020).
Israel	no	no	*O. edulis* reared from introduced spat (Shpigel 1989); Present in species list (Fischer 1997).
Italy	no	no	*O. edulis* on 90 % of shells of *Pinna nobilis*, but *Pinna nobilis* at c. 0.1 m^{-2} in Sardinian estuaries (Addis et al. 2009). *O. edulis* on species check list for all areas barr the southern and middle Adriatic (Renda et al. 2022).
Lebanon	no	no	Listed as present after 1950, but not in records prior to 1950 (Crocetta et al. 2013).
Libya	no	no	Single shell from beach (Hera and Haris 2015). Oysters listed as present (Bek-Benghazi et al. 2020). Eleven *O. edulis* found at two sites in Regata (Abushaala et al. 2014).
Malta	no	no	No wild *O. edulis* populations known (Agius et L. 1978).
Montenegro	no	no	No survey of wild *O. edulis*, but *O. edulis* imported from Mali Ston (Croatia) for growth trials (Joksimovic et al. 2011 and Cataudella et al. 2005); *O. edulis* mentioned in check list as found on hard substrate (Petovic 2018).
Morocco	no	no	Only few oysters sampled from Morocco. All were *O. stentina* (Lapegue et al. 2006).
Norway	yes	no	Several *O. edulis* habitat areas along the Norwegian coast with patches with >50 m^{-2} (Bodvin 2011; AT Laugen et al, unpublished data). Quantitative data on extent are lacking but known patches are generally small (Mortensen et al 2023; Ane Timenes Laugen Pers Comm).
Scotland	yes	no	Scattered individual *O. edulis* found around Shetland (Shelmerdine and Leslie 2009) and several areas around the Scottish west coast (Sanderson unpubl. data). Three

			areas with high density (>5 m^{-2}) and populations measurable in the thousands, but are limited in extent to 10s m^{2} (Sanderson unpubl. data). Loch Ryan is the only known remnant population measurable in millions and where densities are often >5 m^{-2} (Ramday et al. 2024). In Loch Ryan densities can reach c. 20 oysters m^{-2} in limited areas (10s m^{2}, Sanderson unpubl. data).
Slovenia	no	no	Present as epifauna on *Cladocora caespitosa* reefs (Piacco et al. 2014). Listed as a fouling species in the harbour of Piran (Ferrario et al. 2018).
Spain	no	no	Live *O. edulis* in 4% of samples from the river mouth (Rio Ulla) and no other sites. Not habitat forming (Cadee 1968). Population of 300,000 *O. edulis* found in natural bed in San Cibran, but no habitat description given (Ruiz et al. 1992). No samples in extensive species list from Bay of Algeciras (van Aartsen et al. 1984); *O. edulis* beds >1 km in length but max *O. edulis* density <3 m^{-2} and at A Caleira (Ortigueira) *O. edulis* bed c. 300m in length with some patches with oysters <5 m^{-2} (Iglesias et al. 2013). Mar Manor population too low for natural recovery (Ruiz et al. 2020)
Sweden	yes	no	Numerous oyster beds near Resö, with the largest covering 26,000 m^{-2}. The beds are mixed with *C. gigas*. Mean native oyster density ranges from 0.4-12.9 m^{-2}, although patches with c. 20 oysters m^{-2} exist (Holthuis 2022).
Syria	no	no	No recent evidence available in the literature or OBIS.
The Netherlands	no	no	Mixed shellfish reef in the Dutch Voordelta, *O. edulis* 6.8 +-0.6 m^{-2} in patches within the reef. *C. gigas* and *Mytilus edulis* more abundant. (Christianen et al. 2018)
Tunisia	no	no	*O. edulis* rare in south eastern Tunisia (Ktari-Chakron and Azouz 1971). *O edulis* listed as very common at one site, but "Oysters (*Ostrea edulis* var. tarentina) never form exploitable beds." (Lubet and Azouz 1969). 68 oysters from Bizert Lagoon and the Gulf of Hammamet in northern Tunisia- mix of *C. gigas* and *O. stentina* (Dridi et al. 2008). Six *O. edulis* and seven *O. stentia* specimens found across 28 locations in Skhira Bay (Boudaya et al. 2019)
Turkey	no	no	31 tonnes *O. edulis* harvested from the wild nationally in 2006. (Yildiz et al. 2011); Oysters present in the Marmara Sea (Sütcuoglu and Korun 2011); *O. edulis* almost disappeared from Gemlik Bay. The Istanbul Strait, a hard-bottom fauna has been replaced by a soft bottom fauna of polychaetes (öztürk and öztürk 1996). *O. edulis* not habitat forming in Turkish waters (Pers. comm. Dr. Aydin 2021)

Wales	no	no	Milford Haven intertidal density mean 0.03 +-0.01s.e. oysters m^{-2}, with a max of 0.2 oysters m^{-2} (zu Ermgassen 2017). Subtidal density at various sites ranged from 0.05-0.17 m^{-2} (Lock 2017).

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