Title

Historical dataset details the distribution, extent and form of lost *Ostrea edulis* reef ecosystems.

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Abstract

Ocean ecosystems have been subjected to anthropogenic influences for centuries, but the scale of past ecosystem changes is often unknown. For centuries, the European flat oyster (*Ostrea edulis*), an ecosystem engineer providing biogenic reef habitats, was a culturally and economically significant source of food and trade. These reef habitats are now functionally extinct, and almost no memory of where this ecosystem once existed, at what scales, or its past form and functioning, remains. The described datasets present qualitative and quantitative extracts from written records published between 1524 and 2022, which show: (1) locations of past oyster fisheries and/or oyster reef habitat described across its biogeographical range, with associated levels of confidence; (2) reported extent of past oyster reef habitats, and; (3) species associated with these habitats. These datasets will be of use to inform accelerating restoration activities, to establish reference models for anchoring adaptive management of restoration action, and in contributing to global efforts to recover records on the hidden history of anthropogenic-driven ocean ecosystem degradation.

Background & Summary

Accelerating pressure on marine ecosystems since mediaeval times has led to their degradation globally[1,2]. Efforts to counteract marine ecosystem degradation and loss include increased policy efforts to conserve and restore threatened marine nature, ecosystems, and their associated biodiversity[3,4]. Knowledge of where these systems occurred, their extent, form, and function prior to significant human influence is required to inform such policy goals, but this is often hampered by the long-term origin and nature of anthropogenic impacts compared to the shorter periods over which ecological monitoring data are available[5]. In response to this knowledge gap, the fields of historical ecology and environmental history have repeatedly demonstrated the potential for recovering data from historical sources that expand our temporal depth of understanding of past marine ecosystems and human impacts[6, 7, 8].

Bottom trawling and dredging activities have occurred for centuries, but the use of these fishing gears expanded and intensified with the onset of the Industrial Revolution[9]. The early and widespread nature of these activities means some of the most dramatic changes to populations or habitats were not scientifically observed[10,8]. Biogenic reef ecosystems, where individuals of one or multiple species aggregate to form emergent structures on the seabed, are particularly vulnerable to the physical impacts generated by bottom-towed gears[11,12]. Reef-building species demonstrate three-dimensional structural complexity, vertical relief, and a gregarious nature, and include bivalves, annelids and corals, among other taxa. These biogenic structures typically support a plethora of other life as well as influencing their surrounding environment by filtration and the presence of a solid, raised habitat that provides shelter and food for other species. Some of these species, such as oysters or mussels, are also a target for fisheries[13,14]. This high vulnerability to towed gears, direct exploitation, and a lack of historical monitoring, means the full impact of human activities on these seabed habitats, and the resultant changes to marine ecosystems are destined to remain underestimated if we rely on recent scientific monitoring data alone[15,16].

While we lack early scientific data on these habitats, some biogenic habitat-forming species, such as oysters, have been exploited for millennia and cultured and widely traded for centuries[17,18,19]. Their long-standing economic and cultural significance means these species maintain a presence in the historical record, including government documents and the popular media[20,21]. These sources present opportunities to fill knowledge gaps of past distribution and seabed structure, as well as draw conclusions on the spread of influence of early human activity upon seafloors more broadly.

The European flat oyster (*Ostrea edulis*) is a biogenic reef builder, and was once widely distributed across European coastal seas[11]. From the 19th century onwards, and possibly before this, industrial fishing and habitat degradation led to the collapse of wild flat oyster populations, further amplified by declines in water quality, introductions of pest species, and disease[22,23]. The known biodiversity and wider benefits of bivalve reef presence means the restoration and conservation of the European flat oyster is of high scientific and policy interest[24,25]. However, the long time period over which flat oysters have been exploited means we have almost no extant examples of healthy and natural biogenic reef ecosystems for this species. This creates difficulties for the evidence-based setting of restoration and conservation goals.

Broader goals: This dataset assembles previously untapped, widely spread, historical records existing in public and private archives. Taken together, these data contribute to the building of a knowledge base of the historical distribution, extent, and biogenic formations of flat oyster ecosystems prior to and during the intensification of bottom fishing activities. To identify and recover such information requires significant resources and expertise. The establishment of a Historical Ecology Working Group under the umbrella of the Native Oyster Restoration Alliance (NORA)[25] in early 2020 presented a unique opportunity to coalesce interdisciplinary expertise and resources from multiple European countries to collate and interrogate historical data sources. To date, this is the only known dataset that evidences the past distribution, extent and characteristics of this seabed ecosystem across its full biogeographic range.

Study design: Researchers and practitioners from multiple disciplinary backgrounds (e.g. marine biology, restoration ecology, environmental history, historical ecology, conservation, management) self-selected or were approached to map the past distribution and characteristics of the European flat oyster, with a focus on collating historical written records from archives across Europe. Researchers were instructed to conduct searches of within-country archives for accounts of historical oyster fisheries and/or reef ecosystems, and to collate qualitative and quantitative information to identify the locations, extent, depth and/or characteristics of these ecosystems prior to or during their exploitation.

Data generated: The data generated includes a list of reported reef locations, estimated reef sizes, depth of occurrence, habitat form and associated species descriptions, for past oyster reef habitats described in the historical literature. Locations, depths and extents were assigned spatial coordinates and a year of observation. Each location record has an assigned confidence level (high or low), which refers to the level of confidence that biogenic oyster habitat once existed (as opposed to non-gregarious settlement e.g. oysters attached individually to rocks) and the accuracy of the location.

Methods

Data search: Experts were self-selected or identified by the lead authors using existing networks (including NORA) and literature searches. They conducted searches of online repositories, libraries, and museum collections for references to historical oyster habitats and fisheries. Search terms included ‘oyster’, ‘Ostrea edulis’, and regional and local name variations, such as ‘flat oyster’, ‘native oyster’, ‘mud oyster’, ‘edible oyster’, ‘Pandores’, ‘huîtres plates’, ‘Belons’, ‘huîtrière’, ‘østers’, ‘Auster’, ‘Zeeuwse platte’, ‘Zeeuwse bolle’, ‘ostra plana’ and ‘ostrica piatta’ (Thurstan et al. In review). The nature of searches differed from country to country due to the availability and accessibility of written archives, hence an iterative approach was followed: 1) The locations of past oyster fisheries or habitat descriptions were mapped as data were submitted; 2) for regions with data gaps the lead collaborators then either conducted their own search of online archives (predominantly focused on archives in English, French, German or Danish) or contacted local experts identified from the published literature with a request to search available historical sources.

Data collection primarily focussed on the written record as archaeological and museum data rarely allow for conclusions to be drawn on historical habitat extent or habitat characteristics. However, for locations where written records could not be identified, archaeological or museum sources were used to identify past oyster presence. The final dataset contains data collated from authors based in 15 countries, with additional oyster presence confirmed for the Atlantic, Mediterranean, and Black Sea coasts (Fig. 1).

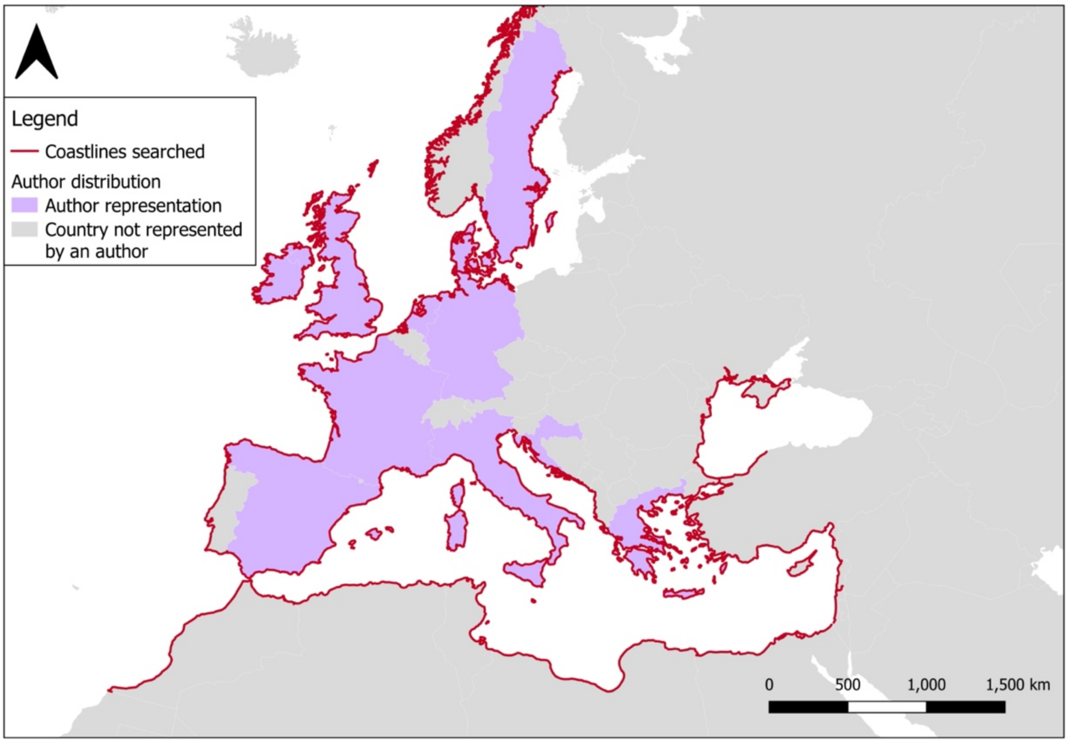

Figure 1. Countries represented by co-authors (purple block colour) and coastline where additional targeted searches were undertaken (red outline colour).

Data extraction: Records were sourced from scientific, popular media, government, and archaeological publications and collections published between 1524 and 2022. These provided 1,667 records of oyster fisheries, habitat structure or presence, dating from 200 BC to 2008, with the majority of records (n=823) referring to observations recorded between 1850 and 1899 (Fig. 2).

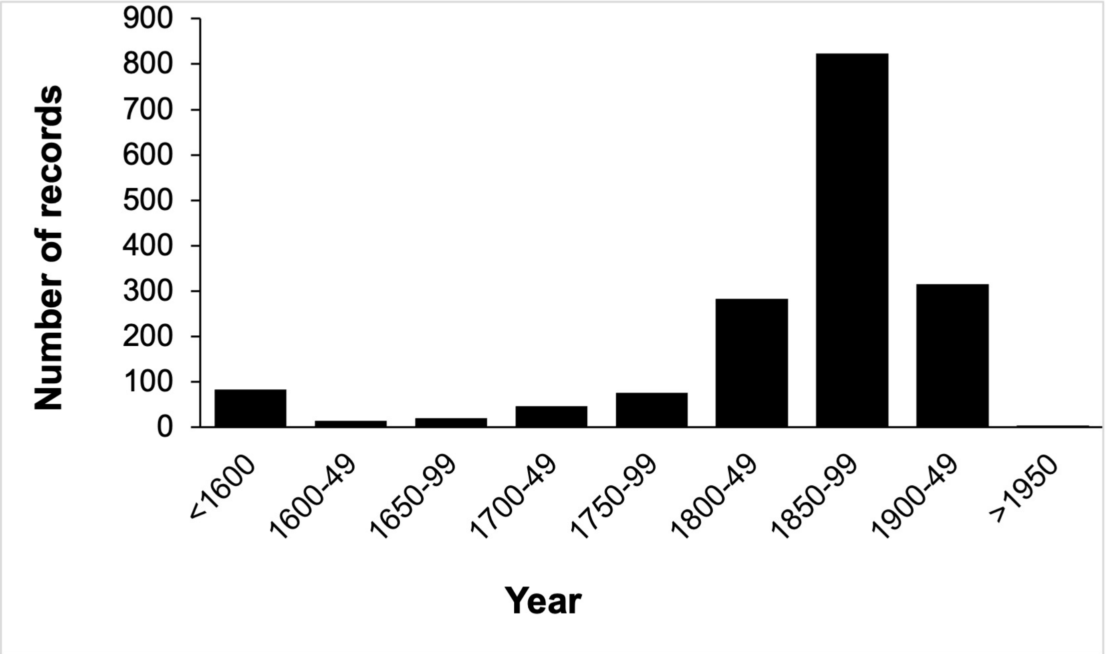

Figure 2. Frequency of records reporting on the presence of oyster fisheries or reef habitat, assigned to 50-year periods.

The location of described fisheries and reef habitats were estimated from written descriptions or identified from nautical charts and assigned latitude and longitude in decimal degrees to a precision of two decimal places (an approx. resolution of 0.5-1.0 km dependent on latitude). For oyster reefs marked on nautical charts (e.g.[26]), areas were traced using the polygon tool in ArcGIS (Fig. 3), and the centroids of each polygon were converted into latitude and longitude.

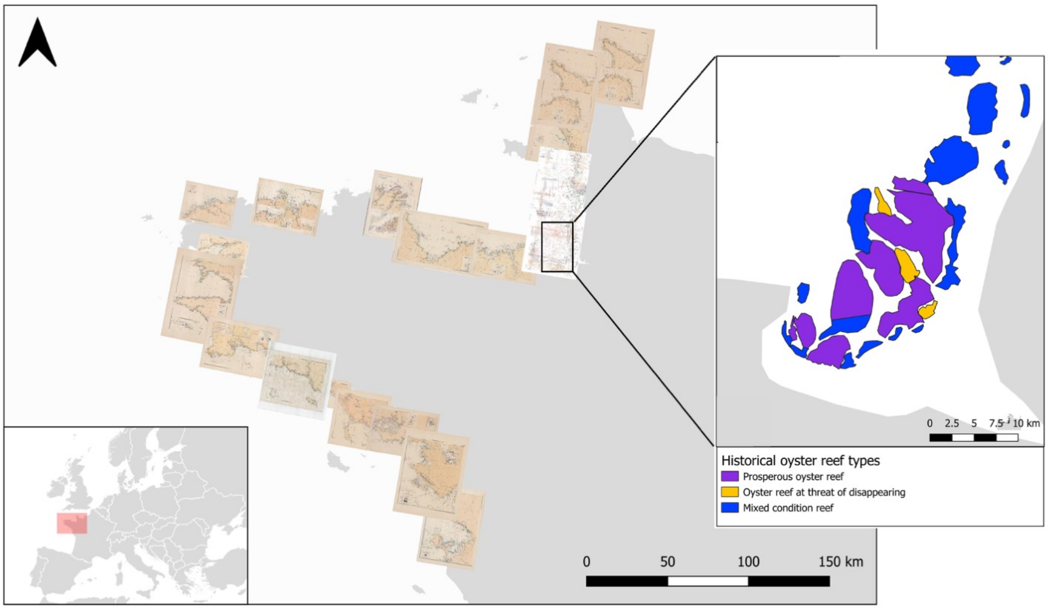

Figure 3. An example of historical charts showing the presence of oyster reef habitat, positioned as per their alignment to the Atlantic coastline of France. This particular source[26] further provided an indication of the condition of oyster reef habitats (inset) whereby the colours depict varying conditions, from prosperous to under threat of disappearance.

Data points were assigned to 10 km^2 grid cells (Fig. 4), the centroids for which are provided in the final dataset (Table 1)[27]. Descriptions of the extent (length or area) and depth of oyster reef habitat were extracted. Descriptions of oyster reefs larger than 10 km^2 were allocated multiple grid points reflecting the described size, with location confidence labelled as high in the centre grid and low in outer grids. When using nautical charts, oyster locations were considered independent if separated by >200 m. Descriptions of habitat structure and associated species were also collated[27].

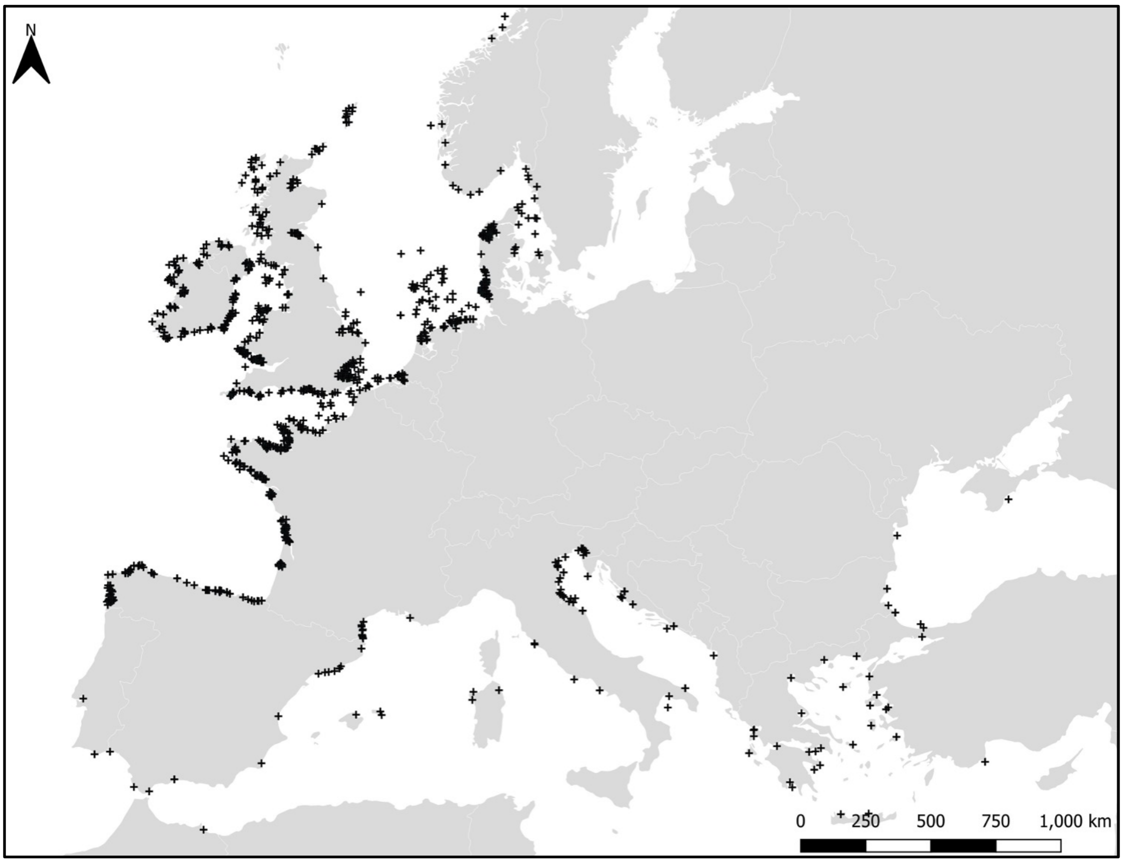

Figure 4. Locations of historical oyster reefs mapped from historical sources.

Records that identified individual or very low numbers of oysters were excluded from analysis, as were records where the abundance or original location of past oysters was unclear. Locations or structures built to facilitate oyster culture were discarded. Records were excluded if the species of oyster was unlikely to be *O. edulis*.

Data visualisation: QGIS software version 3.24 (QGIS Development Team) was used to digitise and visualise spatial data. The European Environment Agency's 'Europe coastline' shapefile was used to derive European coastline boundaries. The Eurostat shapefile 'Countries 2020' was used to derive European country boundaries. The Coordinate Reference System (CRS) is ETRS89-extended/LAEA Europe.

Associated biodiversity: Listed species recorded as historically associated with oyster reefs were corrected to currently accepted species names using WoRMS (https://www.marinespecies.org/) and taxonomic classification and trophic guild were assigned using WoRMs or MarLIN (https://www.marlin.ac.uk/) databases[27].

Data Records

Six datasets are available in the database *figshare*[27]. These data records are freely available to use with appropriate citation under Creative Commons Attribution 4.0 International Public

License. The datasets consist of Microsoft Excel spreadsheets, Microsoft Word documents, and GIS shapefiles (Table 1).

Table 1: Attributes of data files stored in the online database[27]. File types as follows: Excel spreadsheet = .xlsx, table in Word document = .docx, GIS shapefiles = .shp and .shx.

No.	File_name	Dataset descriptor	File format
1	1_Oyster_habitat_location_with centroids	Contains the estimated locations of historical oyster reef habitats, details of their depth and assigned certainty of the record, alongside relevant quotations extracted from the historical sources. This file contains a mixture of spatial point data, quantitative and qualitative data.	.xlsx
2	2_Oyster_habitat_extent	Contains the described extent (area, ha, or length, km) of historical oyster reef habitats, and their approximate location. This file contains a mixture of spatial point data, quantitative and qualitative data.	.xlsx
3	3_Oyster_habitat_descriptions.	Provides qualitative descriptions of habitat, the estimated year, and the location referred to.	.xlsx
4	4_Oyster_reference_list	Lists the references from which oyster reef/fishery descriptions were sourced and the assigned number used for cross-referencing across Datasets 1-4.	.docx
5	5_Oyster_historical_species_list	Provides a list of the species recorded as historically present in the vicinity of historical oyster reefs and their associated taxonomic description. References are provided within the document. This is a presence-only species list.	.docx
6	6_Georeferenced_data_files	GIS package with polygon shape files of oyster reef habitats, as mapped from French charts showing the extent and condition of oysters and other shellfish beds[26].	.shp, .shx

Technical Validation

Technical validation methods were applied to ensure consistency in how information extracted from historical sources was interpreted. We note that, due to the nature of the written historical information, which is sourced from multiple origins (e.g. academic, scientific, popular, and government sources), we can never be absolutely certain of the accuracy of any individual record. By applying (1) consistent criteria to our decision making, (2) being cautious in our application of spatial resolution, and (3) assigning levels of confidence to reports of habitat and location, we aimed to explicitly acknowledge these uncertainties to aid future applications of these data.

We further define oyster 'reef' as '*a biogenic, three-dimensional hard bottom which arises from the seafloor and originating from dead shell material, living oysters and associated* *species, which supply habitats for epibiotic species and refugia for mobile species*' (*sensu* European Habitats Directive Appendix I).

Spatial data records: In historical written descriptions, the precise locations of oyster grounds were rarely described, with a cursory description (of e.g. local town, distance from shore) provided. As such, we estimated coordinates to a resolution of 0.01 degrees, and in the data layer each record was assigned to a 10 km^2 grid cell. If sources from multiple time periods described the same oyster reef differently, the earlier source was chosen for assigning spatial coordinates. Where it was considered likely that multiple sources were referring to the same reef system (such as occurred for a few records describing oyster reef habitat in the southern North Sea), suspected duplicates were removed. In these cases, the sources were read by three authors (Thurstan, zu Ermgassen, McCormick) and discussed to minimise the likelihood of misinterpretation, with final locations mutually agreed.

Confidence assigned: Historical records - despite their deep temporal perspective - commonly referred to locations that were already impacted by fisheries and typically described extractive activities rather than the habitat. Where descriptions of oyster reefs existed and/or where mobile bottom fishing gears were primarily used to exploit oysters (e.g. dredge, trawl), we assumed 'high confidence' that oyster reef habitat was once present. Where written descriptions of reefs could not be found, oysters were described as predominately attached to rocks, and/or where fisheries were extracted by diving and handpicking, we assumed 'low confidence' of reef habitat.

Where the location of oyster reefs could be identified close to a town or within a bay or estuary, or other descriptions were provided that helped us to pinpoint the location to within 10km, we assumed 'high confidence' in location. Where oyster reefs occurred in open water or were noted without positioning detail, we assumed 'low confidence' in location. Larger areas of reef that were identified across multiple grid cells were highlighted as 'low confidence' to emphasise the uncertain location of this reported extent of habitat.

Levels of confidence were thus assigned one of four codes (LL, LH, HL, HH):

HH - High confidence of oyster reef habitat, high location certainty: record of habitat or an active fishery using towed gears with no recorded active intervention. Confident of the location to within 10 km.

HL - High confidence of oyster reef habitat, low location certainty: record of habitat or an active fishery using towed gears with no recorded active intervention. Location is uncertain to > 10 km.

LH - Low confidence of oyster reef habitat, high location certainty: records of oyster extraction, but descriptions do not provide evidence that the species formed a biogenic reef. Confident of the location to within 10 km.

LL - Low confidence of oyster reef habitat, low location certainty: records of oyster extraction, but descriptions do not provide evidence that the species formed a biogenic reef. Location is uncertain to > 10 km.

Usage Notes

There is a significant dearth of information relating to European marine benthic ecosystems prior to 1900, with existing records often piecemeal and local[1]. The deeper time perspective that this dataset provides therefore has diverse applications: 1) as a spatial and a condition baseline; 2) in developing a definition of this largely functionally extinct ecosystem, and; 3) in informing various aspects of ongoing or future restoration practice, such as site selection, defining reference models, and goal setting.

In applying this dataset, users should be mindful of the fact that historical records typically exist because exploitation was already occurring in an area, often for an unknown time span[15]. Past records of oyster habitat, therefore, are unlikely to provide a 'pristine ecological baseline' for this species (see Thurstan et al. In review, for further discussion). What these records do provide is robust evidence that a habitat we know to be functionally extinct today (zu Ermgassen et al. In review), was once widely spread across European coastlines and shallow seas, was highly abundant, and was recorded in some locations as occurring over large (> 1 ha) extents.

These data represent, for the first time, a pan-European baseline of the historical extent and condition of European oyster reef ecosystems. Given the well documented contribution of oyster reefs to a variety of ecosystem functions and services[14], these data could also serve to understand or even model the likely keystone function these large reefs had prior to their degradation and decline and, hence, the degree to which ecosystem services have been lost, or trophic relationships have altered over time.

Significantly, these large-scale baseline data represent historical records of a sensitive marine benthic habitat, dating back more than two centuries. Such a complex record is unique in the European context, with other benthic habitat mapping generally limited to shallow areas at the local scale[1]. These data have the potential to serve as a proxy habitat, providing an indicator of the degree to which marine benthic systems have been impacted by (largely) human activities over the past ~200 years (but see [[28]], which shows some oyster habitat declines occurred far earlier and were not due to fishing pressure).

European native oyster reefs are now largely functionally extinct, with oysters commonly persisting as scattered individuals. Reference ecosystems, which can be referred to when developing restoration goals, monitoring or adaptive management plans are therefore lacking[29]. This dataset, which includes not only descriptions of the habitat structure, location and extent, but also historical records of the associated community, can serve to inform future definitions of reference ecosystems, as well as definitions of the ecosystem itself, which can have utility in assessing the current status of the ecosystem (zu Ermgassen et al. In review).

A further use for this dataset is in informing site selection for future local or larger scale restoration of native oyster habitats. To date, the lack of a comprehensive map of the historical extent of oyster reef ecosystems in Europe meant that data had to be exclusively collected on a local scale to establish whether native oysters were historically present. This larger scale overview of the historical distribution of native oyster reef ecosystems can now inform larger scale site selection processes, such as illustrated in northern Europe[30] and in England in the recent "Marine Restoration Potential" report[31]. Despite these promising applications, we caution that the impact of land-use changes and changing conditions in former oyster reef habitats, in terms of hydrology, on current flows, salinity, sediment composition and sediment loading, among other factors, means the historical presence of oysters does not promise suitable conditions for oyster restoration success in the present day. Hence, historical location data should be used in combination with current known suitability requirements for successful oyster growth and reproduction[32].

Finally, these data can be used to instruct an appropriate scale of ambition and the timely implementation for nature-based solution-oriented policy, such as the recent EU Restoration Law, which is needed to achieve climate and biodiversity mitigation over the coming decades.

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Competing interests

The authors declare no known conflicts of interest.

Figures

Within manuscript.

Figure Legends

Within manuscript.

Tables

Within manuscript.

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