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DATA DESCRIPTOR

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

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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 or at what scales this ecosystem once existed, or its past form, remains. The described datasets present qualitative and quantitative extracts from written records published between 1524 and 2022. These show: (1) locations of past flat 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 flat oyster 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<sup>1,2</sup>. Efforts to counteract marine ecosystem degradation and loss include increased policy efforts to conserve and restore threatened marine nature, ecosystems, and their associated biodiversity<sup>3,4</sup>. Knowledge of where these systems occurred, their extent, form, and function prior to significant human influence is required to inform such policy efforts<sup>5</sup>. The fields of historical ecology and environmental history have repeatedly demonstrated the potential for recovering data from historical sources<sup>6</sup> to expand our understanding of past marine ecosystems and human impacts<sup>7,8</sup>.

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<sup>9</sup>. The early and widespread nature of these activities means some of the most dramatic changes to populations or habitats were not scientifically observed<sup>10</sup>. 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<sup>11,12</sup>. 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. They also influence their surrounding environment through their filter feeding 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 a target for fisheries<sup>13,14</sup>. Their high vulnerability to towed gears, direct exploitation, and a lack of historical monitoring, means the full impact of human activities on these seabed habitats remain underestimated if we rely on recent monitoring data alone<sup>15,16</sup>.

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<sup>17–19</sup>. Their long-standing economic and cultural significance means these species maintain a presence in the historical record, including government documents and the popular media<sup>20,21</sup>. These sources present opportunities to fill knowledge gaps of past distribution, seabed structure and ecological conditions, as well as draw conclusions on the spread of influence of early human activity upon seafloors.

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The European flat oyster (*Ostrea edulis*) is a biogenic reef builder, once widely distributed across European coastal seas<sup>11</sup>. From the 19th century onwards, and possibly before this, industrial fishing and habitat degradation led to the collapse of wild flat oyster populations. This was further amplified by declines in water quality, introductions of pest species, and disease<sup>22,23</sup>. The known biodiversity and wider benefits of bivalve reefs means the restoration and conservation of the European flat oyster is of high scientific and policy interest<sup>24,25</sup>. However, the long 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 widely spread historical records existing in public and private archives. It is a collation 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)<sup>25</sup> in early 2020 presented a unique opportunity to coalesce interdisciplinary expertise and resources from multiple European countries. 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 the focus on collating historical written records from archives across Europe, researchers were instructed to conduct searches of archives for accounts of historical oyster fisheries and/or reef ecosystems.

**Data generated.** The data generated includes descriptions and locations of historically reported reefs and oyster fisheries. 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

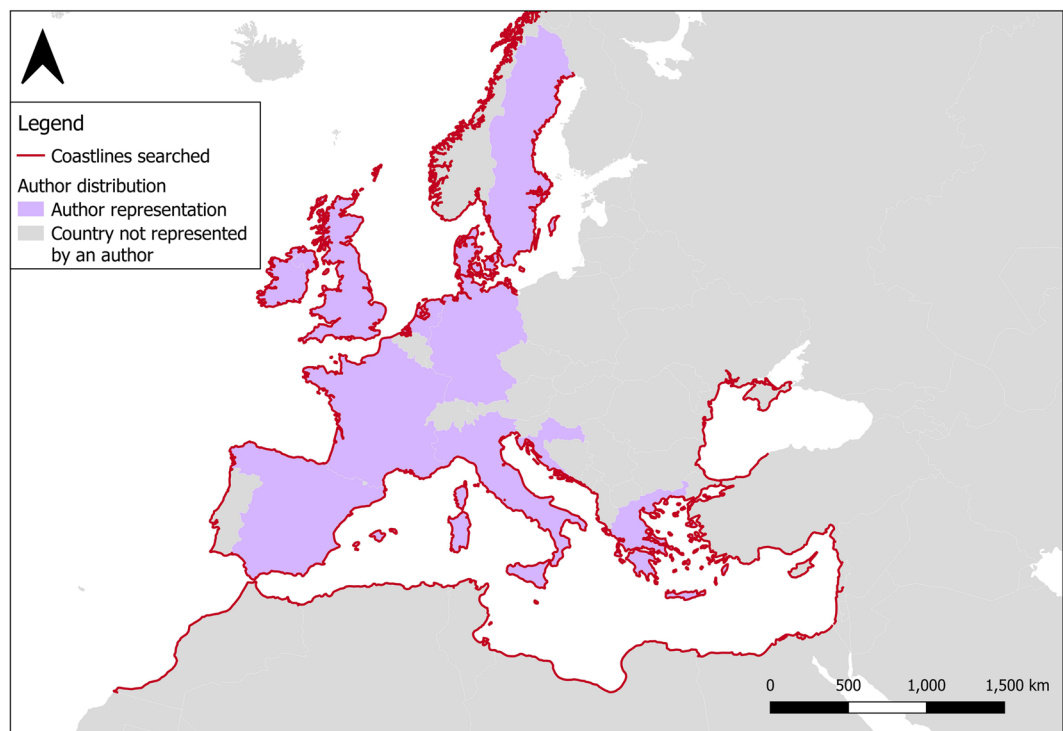
**Data search and literature review.** Experts conducted searches of online repositories, libraries, and museum collections for references to historical oyster habitats and fisheries. They were asked to extract qualitative and quantitative information that identified the locations, extent, depth and/or characteristics of oyster fisheries and/or reef ecosystems prior to or during their exploitation. The nature of searches differed from country to country due to the availability and accessibility of written archives, and the knowledge of in-country experts. Relevant information was extracted from key primary sources of oyster descriptions known to experts or identified from the keyword searches (below), e.g., Paz Graells<sup>26</sup> (Spain), Royal Commission<sup>27</sup> (Great Britain and Ireland), Collin<sup>28</sup> (Denmark), Joubin and Guérin-Ganivet<sup>29</sup> (France), Marsili<sup>30</sup> (Italy), Krøyer<sup>31</sup> (Denmark), and Möbius<sup>32</sup> (Germany). Data were also extracted from identified secondary sources e.g., Went<sup>33</sup> (Ireland), de Nicolò<sup>34,35</sup> (Italy), Gercken and Schmidt<sup>36</sup> (Germany), Houziaux *et al.*<sup>37</sup> (Belgium). From these, (1) locations of past oyster fisheries or habitat descriptions were mapped as data were submitted and an iterative approach was subsequently followed, whereby for regions with data gaps the lead collaborators either (2) conducted their own search of online archives (predominantly focused on archives in English, French, German or Danish) or (3) contacted further local experts identified from the published literature with a request to search available historical sources. Where archive catalogues were searched, search terms included common, scientific, and regional and local name variations relevant to the region, such as 'oyster', 'Ostrea edulis', 'flat oyster', 'native oyster', 'mud oyster', 'edible oyster', 'Pandores', 'huîtres plates', 'Belons', 'huître', 'osters', 'Auster', 'Zeeuwse platte', 'Zeeuwse bolle', 'ostrea plana' and 'ostrea piatta'.

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).

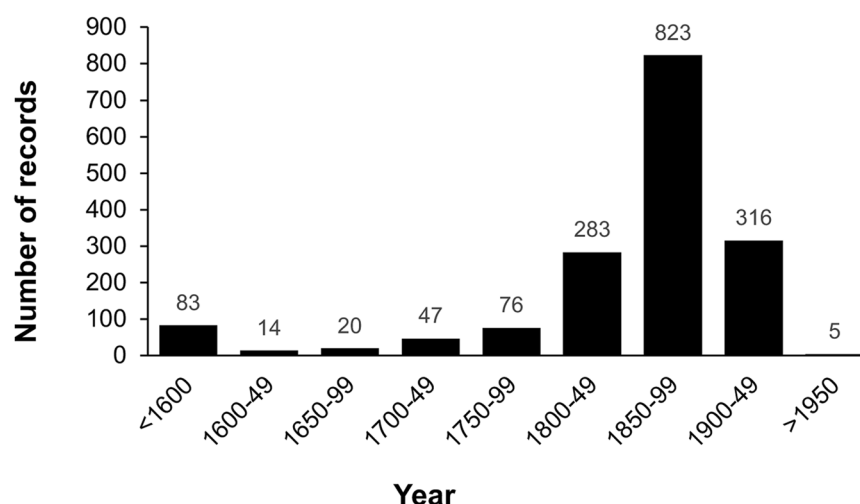
**Data extraction.** Records were sourced from scientific, popular media, government, and archaeological publications and collections published between 1524 and 2022. These provided 1,667 records of oyster fisheries, habitat structure or presence, dating from 200 BC to 2008, with the majority of records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

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). Where boundaries of oyster reefs were marked on nautical charts (e.g.<sup>29</sup>), areas were traced using the polygon tool in ArcGIS or QGIS software version 3.24 (QGIS Development Team) (Fig. 3), and the centroids of each polygon converted into latitude and longitude.

Data points were assigned to 10 km<sup>2</sup> grid cells (Fig. 4), the centroids for which are provided in the final dataset (Table 1)<sup>38</sup>. Descriptions of the extent (length or area) and depth of oyster reef habitat were extracted. Descriptions of oyster reefs larger than 10 km<sup>2</sup> 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,



**Fig. 1** Countries represented by co-authors (purple block colour) and coastline where additional targeted searches were undertaken (red outline colour). Grey areas with no outline indicates countries that were not searched.

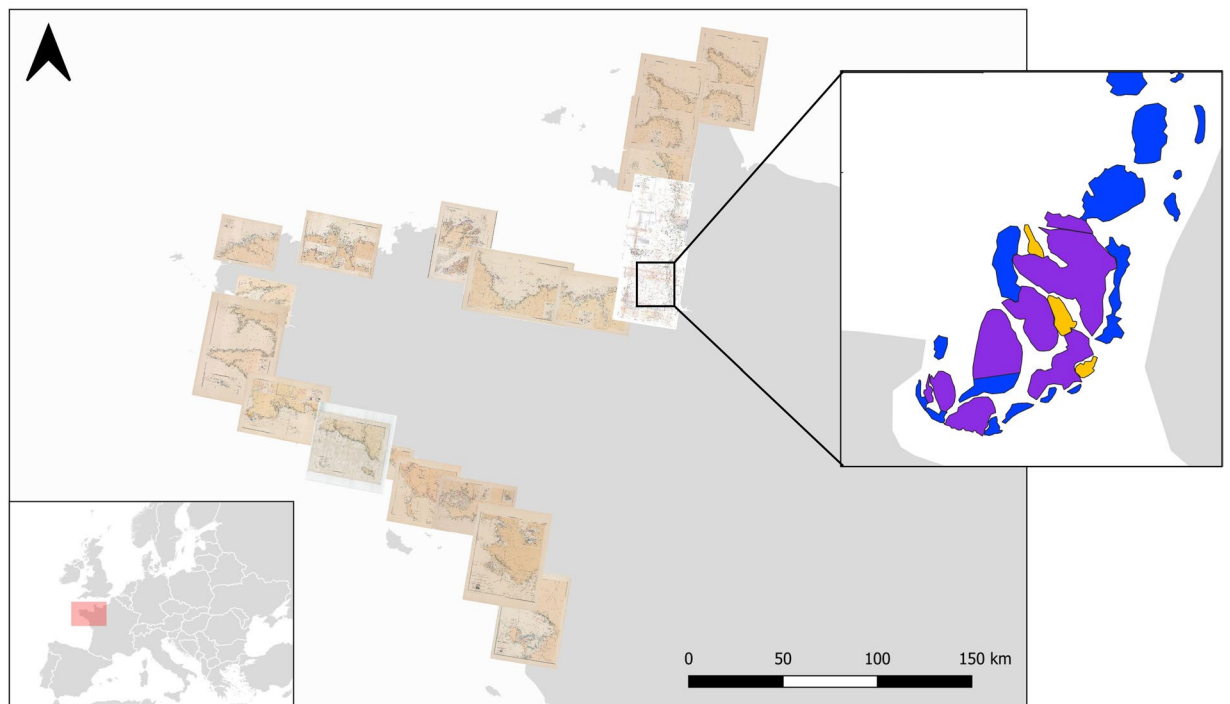


**Fig. 2** Frequency of records reporting on the presence of oyster fisheries or reef habitat, assigned to 50-year periods.

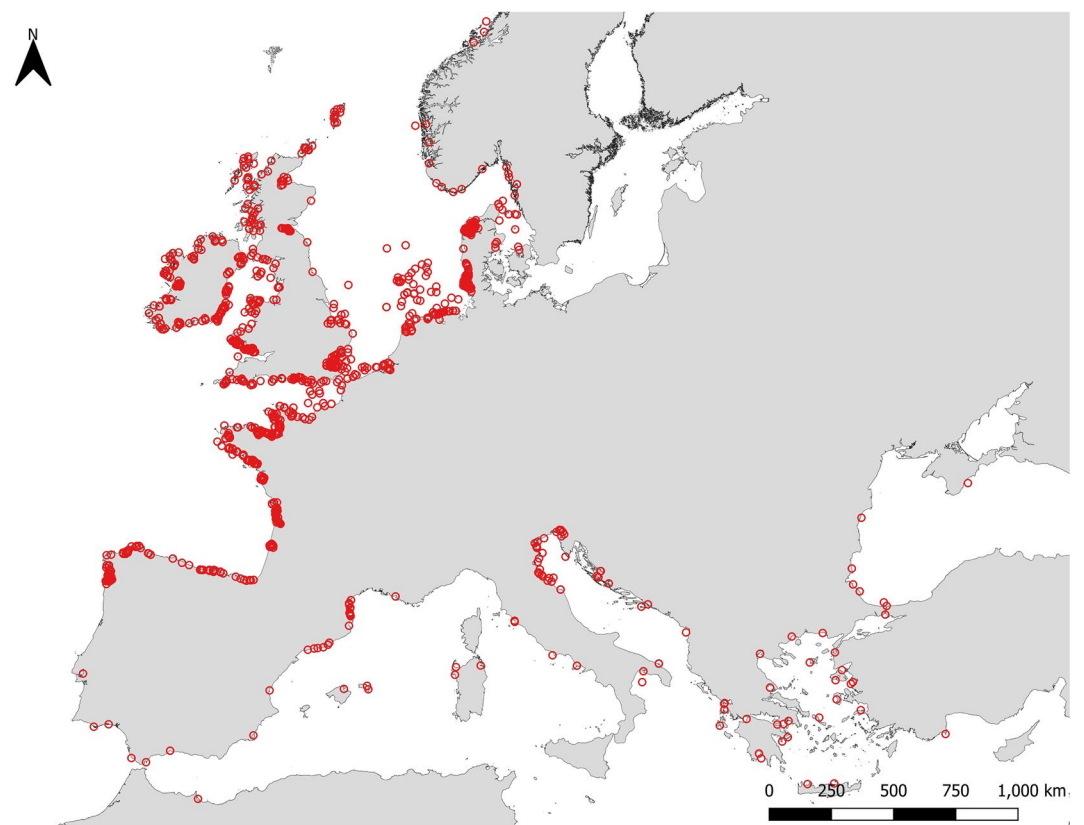
oyster locations were considered independent if separated by  $>200$  m. Where descriptions allowed or when oyster locations were described in nautical charts or maps, locations that could feasibly be resolved to  $1 \text{ km}^2$  were noted. Descriptions of habitat structure and associated species were also collated<sup>38</sup>.

Records that identified individual oysters were excluded from analysis. Locations or structures that clearly indicated oyster culture were discarded. Records were excluded if the species of oyster was deemed by local co-authors from the physical or environmental description as unlikely to be *O. edulis*.

**Data visualisation.** ArcGIS and QGIS software version 3.24 (QGIS Development Team) was used to 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. We used point (raster) data, with



**Fig. 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 source<sup>29</sup> further provided an indication of the condition of oyster reef habitats (inset) whereby the colours depict varying conditions, such as prosperous reef (purple, inset), reef under threat of disappearance (yellow, inset) and mixed condition reef (blue, inset).



**Fig. 4** Locations of oyster reefs mapped from historical sources.

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 <sup>29</sup> .	.shp, .shx

**Table 1.** Attributes of data files stored in the online database<sup>38</sup>. File types as follows: Excel spreadsheet = .xlsx, table in Word document = .docx, GIS shapefiles = .shp and .shx.

each datum allocated to a 10 km<sup>2</sup> grid, to visualise all known reef locations. For the French coastline, highly resolved spatial extent data were available from historical surveys. Given the significance and uniqueness of these data, and their utility for present-day restoration activities, we included these locations as point data and provide them as a separate polygon data layer (see Data Records section).

**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<sup>38</sup>.

Data Records

Six datasets are available in the database *figshare* [6884167.v1]<sup>38</sup>. 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).

Technical Validation

Due to the nature of the source data, which was extracted from multiple types of historical references (e.g. academic, scientific, popular, and government sources), we cannot always be certain of the accuracy of any individual record. By applying the criteria described below to our decision making, and assigning levels of confidence to reports of habitat and location, we aimed to explicitly acknowledge uncertainties to aid future applications of these data.

**Reef definition.** We defined 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 (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<sup>2</sup> grid cell. Where locations could be feasibly estimated to within 1 km<sup>2</sup> (i.e. oyster habitat was marked on nautical or hand-drawn charts) this is noted in a separate column in spreadsheet 1 (Table 1). It was rare that sources would contradict each other, but in the few instances where sources from multiple time periods described the same oyster reef differently, the earlier source was used to assign 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. For regions 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 10 km, 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<sup>1</sup>. The deeper time perspective that this dataset provides therefore has diverse applications. Firstly, as a spatial and an ecosystem condition baseline, as these records provide robust evidence that the habitat was once widely spread across European coastlines and shallow seas, highly abundant, and was recorded in some locations as occurring over large (>1 ha) extents. These data thus have the potential to provide an indicator of the degree to which marine benthic systems have been impacted over the past ~200 years. Secondly, this dataset, which includes not only descriptions of the habitat but also 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<sup>39</sup>. Thirdly, the data can inform ongoing or future restoration practice, such as site selection, defining reference models, and goal setting. While the 10 km<sup>2</sup> scale used in this study may be too broad a resolution for local restoration efforts, for some locations the written sources provide qualitative descriptions of a higher spatial resolution. Where it is indicated in the spreadsheet that location data may provide a higher spatial (<= 1 km) resolution, note that the latitude-longitude provided as the centroid of the 10 km<sup>2</sup> grid cell may therefore not be within 1 km of the more highly resolved location, and that there may be several oyster reefs indicated within the 10 km<sup>2</sup> grid cell. Higher resolution locational data may be sought from the primary references in these cases, or may be used as a starting point for sourcing more spatially refined information from local archives. Whether data of the required resolution exists or not, historical location data should be used with caution given the likelihood of altered environmental conditions over time, and in combination with current known suitability requirements for successful oyster growth and reproduction<sup>40</sup>. Alternatively, the data may inform larger scale site selection processes, such as illustrated in northern Europe<sup>41</sup> and in England in the recent “Marine Restoration Potential” report<sup>42</sup>. Fourthly, given the well documented contribution of oyster reefs to a variety of ecosystem functions and services<sup>14</sup>, 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. 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.

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<sup>15</sup>. Past records of oyster habitat, therefore, are unlikely to provide a ‘pristine ecological baseline’ for this species (see Thurstan *et al.*<sup>43</sup> for further discussion). Furthermore, due to a patchy historical record, locations where oyster fisheries or reefs were *not* recorded does not mean we can rule out that oyster habitat once existed in that location. By presenting the locations of searches undertaken by in-country researchers, where searches of online databases alone were undertaken, and the countries that were not investigated (Fig. 1), we aim to aid clarification of the investigation effort for managers. We also 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.

### Code availability

No custom code was used to generate or process the data described in the manuscript.

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### Competing interests

The authors declare no competing interests.

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