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Records reveal the vast historical extent of European oyster reef ecosystems

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Anthropogenic activities have impacted marine ecosystems at extraordinary scales. Biogenic reef ecosystems built by the European flat oyster (*Ostrea edulis*) typically declined before scientific monitoring. The past form and extent of these habitats thus remains unknown, with such information potentially providing valuable perspectives for current management and policy. Collating >1,600 records published over 350 years, we created a map of historical oyster reef presence at the resolution of 10 km^2 across its biogeographic range, including documenting abundant reef habitats along the coasts of France, Denmark, Ireland and the United Kingdom. Spatial extent data were available from just 26% of locations yet totalled >1.7 million hectares (median reef size = 29.9 ha, range 0.01–1,536,000 ha), with 190 associated macrofauna species from 13 phyla described. Our analysis demonstrates that oyster reefs were once a dominant three-dimensional feature of European coastlines, with their loss pointing to a fundamental restructuring and 'flattening' of coastal and shallow-shelf seafloors. This unique empirical record demonstrates the highly degraded nature of European seas and provides key baseline context for international restoration commitments.

Destructive fishing activities, pollution and reclamation have resulted in large-scale marine and coastal habitat degradation and loss globally[1]. European seas are among the most impacted marine environments[2], and there is common agreement on the urgency to conserve and restore habitats to support and recover key ecological functions[3,4]. However, without an understanding of the full extent of ecological changes resulting from human influence, the setting of policy goals can be impeded or contested[5].

Assessments of human impact are commonly restricted by the short time span of modern scientific data, which is typically limited to recent decades[2]. In contrast, activities such as fishing and coastal harvesting have occurred for centuries to millennia[1,6]. The early, intense and geographically broad exploitation of marine resources in Europe presents a critical challenge for the identification of ecological baselines and requires substantially deeper time perspectives than those available from scientific monitoring data[7].

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Yet there remains a lack of integration of historical perspectives into management and policy due to challenges such as resolving differences in spatial resolution of historical versus modern data, issues with data certainty, small sample sizes and a patchy historical record, among others[7].

Despite advances in our understanding of historical dynamics in marine environments, studies focusing on historical changes across a species' biogeographic range remain limited. The European flat oyster (*Ostrea edulis*, Linneaus, 1758 'flat oyster' hereafter) is a benthic habitat-forming species that was once of economic and cultural importance across Europe. This led to its representation in numerous historical sources published in multiple countries[8]. Interrogation of the historical record for this species thus presents a unique opportunity to understand the historical distribution and characteristics of a biogenic marine habitat, one that is functionally extinct due to human activity, across its full biogeographic range, and subsequently acts as a signal of the scale of change in shallow European shelf seas over the course of centuries.

Seabed habitat-forming species are particularly vulnerable to widespread and persistent human impacts such as trawling and dredging[1,2]. Marine biogenic habitats are formed by assemblages of sessile benthic organisms, which create emergent physical structures distinct from the surrounding seabed[9]. These habitats are formed by a range of taxa, including bivalves, annelids, corals, sea grasses and macroalgae[10–14]. They support multiple ecosystem services, high levels of biodiversity and influence ecosystem functioning by creating a complex, three-dimensional surface that other species adhere to, shelter within or feed upon[15,16]. Their vulnerability to human-induced pressures means many have deteriorated in quality, declined in extent or vertical relief, or been rendered functionally extinct by fishing, coastal development, eutrophication and pollution, disease and the effects of climate change[17–20].

Many species of oyster (for example, *Ostrea*, *Crassostrea*, *Saccostrea* spp.) create biogenic habitat through gregarious settlement. But centuries of degradation and loss of oyster habitat globally mean that examples of undisturbed reefs are rare[21]. Thus, our knowledge of the characteristics of oyster reefs (for example, extent, vertical relief, density of oysters, species composition) is variable across genera and locations, and is mostly derived from locations where extant, remnant reefs exist or have been actively restored[22].

The flat oyster is a habitat-building oyster native to European seas[23]. Flat oyster exploitation has occurred for thousands of years, with shell remains preserved in kitchen midden deposits from the Mesolithic period[24]. Until the early twentieth century, European flat oysters were sufficiently abundant to support a major commercial fishery across multiple European countries; however, overexploitation led to the widespread removal and decline of oyster reefs, with population collapse exacerbated by decreasing water quality, sedimentation and the introduction in the 1970s of the disease-causing haplosporidian, *Bonamia ostreae* and the protozoan *Marteilia refringens*[8,25]. We know of the species' widespread decline[21], but not where habitat once existed, the form of the habitat (for example, density, areal extent) before exploitation, or its importance for associated communities.

Today, there is a growing impetus to conserve and restore marine ecosystems at scale[26], furthered by policies such as the Habitats Directive of the EU, the UN Decade on Ecosystem Restoration, the EU's Nature Restoration Law and, in the case of the European flat oyster, its recognition by OSPAR as a 'Threatened or declining species'[27]. Developing a robust and evidenced historical baseline, both in terms of extent and condition of flat oyster habitats, is of critical importance for guiding restoration efforts and for informing policy relating to the conservation of this formerly widespread species[5]. While there are several modern examples of flat oysters of multiple size classes clustering to form small clumps[28–31], the majority of known European flat oyster populations are found at average densities of <1 individual m^{-2} (for example, refs. 32–34).

Here we collate information from the historical documentary evidence to establish a uniquely resolved, ecosystem-wide, robust historical baseline for flat oyster reefs. Specifically, we identify evidence for (1) the historical range and locations of flat oyster reefs, (2) size or extent and (3) characteristics of these reefs and their associated communities in European seas.

Results

Documentary evidence was sourced from popular books, scholarly papers, government reports, customs accounts, oyster licensing records, travelogues, naturalists' accounts, newspaper articles, nautical charts and scientific surveys. Records included reports of oyster fisheries and habitat presence recorded >2,000 years before present until the 1970s[35,36].

Flat oyster habitat distribution

Two hundred and twenty-five sources provided 1,667 records of oyster fisheries, presence or habitat, published between 1524 and 2022 (Supplementary Fig. 1 and Supplementary Information). These were mapped to 1,196 locations across Europe and North Africa where fishable quantities of flat oysters and/or oyster biogenic reef habitats were historically described. This translated to oyster presence being assigned to 713 10 km² grid cells, with 85% (n = 606 grid cells) assigned a high confidence that biogenic reefs were once present (that is, where sources indicated the presence of oysters was high enough to support a towed-gear fishery with substantial landings, or bank/reef features were mentioned; Fig. 1 and Supplementary Fig. 2). High confidence of past oyster reef presence was assigned to broad swathes of the coastlines of the United Kingdom, France, Ireland, Denmark, Spain, Germany and the Netherlands, for which 205, 109, 75, 38, 37, 30 and 27 grid cells within 12 nautical miles of the coast were recorded as high confidence, respectively (Fig. 1a–c). High confidence of historical reef presence was also assigned to sections of the coastline around Italy (22 grid cells), most notably the Northern Adriatic (Fig. 1e). Substantial areas of reef habitat were historically reported in the southern North Sea and the English Channel[8], although their locations were not able to be defined within a 10 km² area and hence were marked as low locational certainty (Fig. 1b and Table 1). The large area of contiguous oyster habitat shown in the Southern North Sea (Fig. 1a,b in blue) probably reflects several very extensive oyster reef systems (Tables 1 and 2). Historical documentary records were not found for parts of the southern and central Mediterranean or the Baltic Sea.

Oysters were reported in fishable quantities at depths spanning the intertidal zone to >80 m (n records reporting depth = 103). The deepest locations reported were in the English Channel (84 m) and the Atlantic coast of Morocco (85 m)[35]. Fishable quantities of oysters were reported at depths >40 m in the southern North Sea, the English Channel, the Irish Sea and occasionally inshore locations such as Belfast Lough[35]. Quantities of oysters were reported in the intertidal or shallow subtidal zone in Northern Ireland (Strangford Lough), the Republic of Ireland (Sligo River), Wales (Mumbles), Scotland (Kirkcudbright) and the northern coast of France (Cancale)[35] (Supplementary Fig. 3a and Table 1).

Areal extent

Habitat extent (area or length) was reported in 52 sources published between 1715 and 1910. Despite finding only 317 quantitative descriptions of habitat extent, the area assigned high confidence of reef presence totalled 1,758,077 hectares. Descriptions of areal extent of individual reefs ranged from 0.01 ha to 1,536,000 ha (median = 29.9 ha) and included locations along the coasts of the United Kingdom, Ireland, France, Germany and Denmark, the Netherlands, the northern coast of Spain and the north-east coast of Italy, as well as the southern North Sea and the English Channel (Fig. 2). The largest of these were reported

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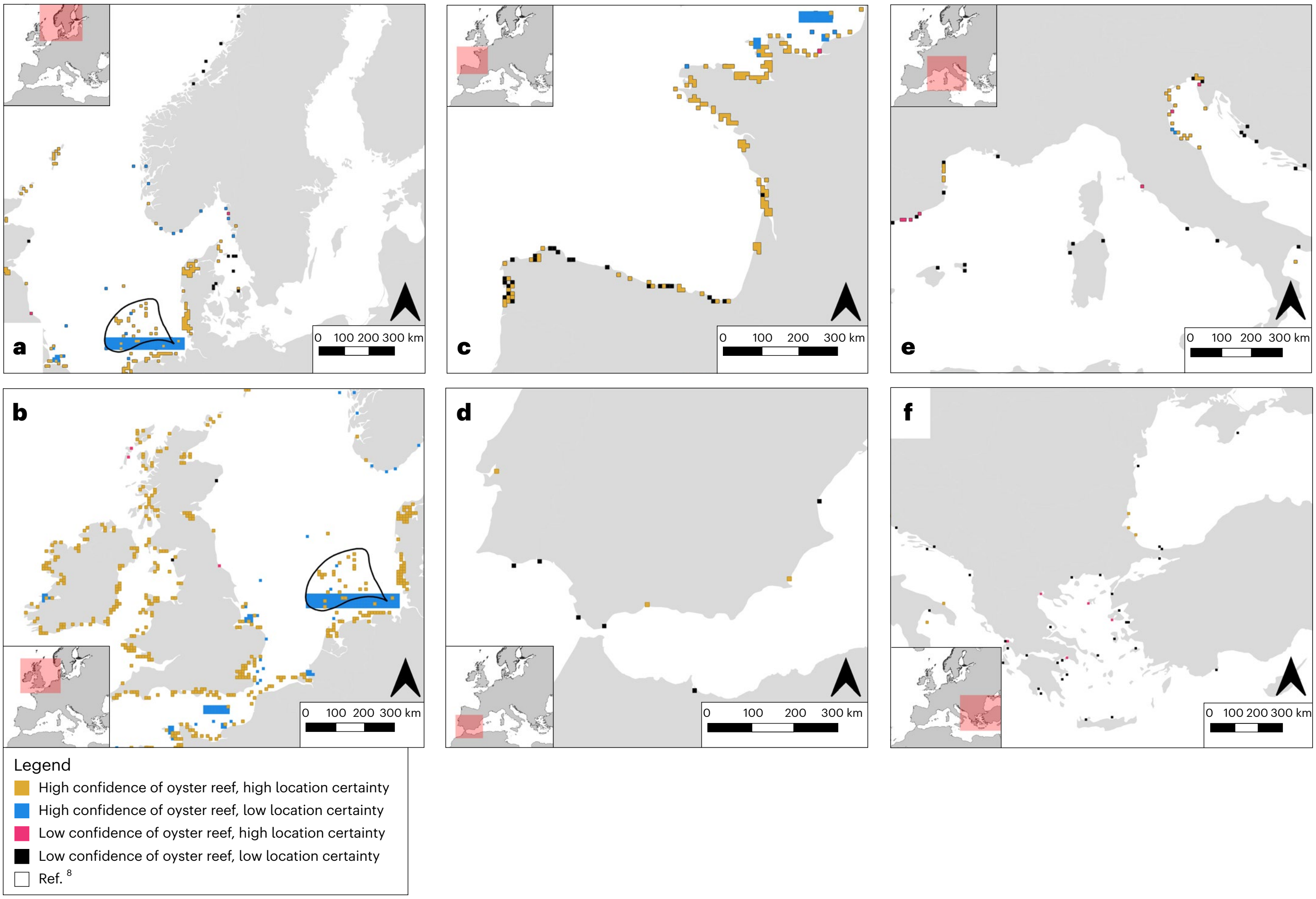

Fig. 1 | Historical oyster reef presence across Europe. a–f, Locations across Europe where oyster reef presence was assigned from historical sources, identified to 10 km^2 grids, with associated confidence levels that biogenic reef habitat was present. Base map source, ref. 82. For the full map, see Supplementary Fig. 1.

from the southern North Sea/German Bight region, at 1.5 million ha, with substantial extents also described around the Channel Islands, southeast coast of England, south coast of Wales, and the east and west coasts of Ireland. Highly resolved oyster habitats were sourced from the coasts of France and the Wadden Sea (Fig. 2 and Supplementary Fig. 3b). The length of described reefs ranged from 0.02 to 320 km (median = 4.0 km, n = 45 locations; Supplementary Fig. 4).

Reef form

Descriptions of reef height and structure typically referred to exploited reef habitats, with few historical descriptions of unexploited reefs found. As recently as 2008, the remains of flat oyster reefs at heights of up to 7 m were described in the Black Sea[37]. Within the historical literature, descriptions of reef form, although limited, exist for multiple locations (Table 2). Historical sources described 'clumps' of oysters in exploited areas, vertical reef formations, or an observed increase in seabed depth as reefs were removed by dredges and bottom trawlers[35]. When newly discovered oyster locations were described in historical accounts, catches and catch rates indicative of high densities of oysters were recorded (Table 2).

Associated species

A total of 190 species associated with oyster reef habitats were recorded across 13 phyla, representing 7 trophic guilds (Supplementary Table 1 and Fig. 3). The distribution of species differed significantly across trophic guilds (Kruskal–Wallis $H(6) = 17.718$, $P = 0.007$) and phylum classifications ($H(9) = 19.494$, $P = 0.021$). The trophic guilds were dominated by active suspension feeders (n species = 68, 36% of species observed), carnivores (n spp. = 45, 24%) and omnivores (n spp. = 36, 19%). Significantly more species were observed within the suspension feeding trophic guild (dominated by cnidarian, molluscan and bryozoan species), than most of the other phyla groupings (parasitic $H = 31.45$, $P = 0.001$; herbivorous $H = 26.6$, $P = 0.001$; filter feeders $H = 20.3$, $P = 0.01$; omnivores $H = 17.1$, $P = 0.04$). Across the 13 phyla, Arthropoda (n spp. = 47, 25%), Mollusca (n spp. = 39, 20%) and Cnidaria (n spp. = 26, 13%) contributed almost two-thirds of the species observed. The Arthropoda included species across six trophic guilds, the majority from the subphylum Crustacea. The Mollusca contained 39 species from five trophic guilds and included other suspension feeding bivalves. The 26 Cnidaria species were mostly suspension feeders. Apex predators were also observed, including thornback ray (*Raja clavata*), common stingray (*Dasyatis pastinaca*), short-snouted seahorse (*Hippocampus hippocampus*) and the now critically endangered European sturgeon (*Acipenser* sp.) (see Supplementary Table 1 for further IUCN Species Redlist Classifications and population trends of assessed species).

Discussion

The results presented here provide presumably the first highly resolved, comprehensive overview of the spatial distribution, areal extent and habitat structure of a benthic marine ecosystem in Europe, before its widespread functional extinction. Centuries of economic, popular

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Table 1 | Example descriptions from historical sources and recorded attributes that contributed to the mapping and understanding of oyster reefs, including location, depth, areal extent and exploitation status

Country	Quote (attributes in bold) and year of publication	Attributes
Ireland	"'Blacksod' Bay, joined to the eastern land by a long narrow Isthmus. They have a **bed of small oysters here**, which **at spring tides is left by the sea**, and the people go and pick 'em up, pickle 'em and send them to Dublin." (1891[83], originally described 1752)	Location Depth Exploitation status
England	"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**." (1882[84])	Location Extent Exploitation status
Scotland	"Oysters are got in the **Bay of Firth**.... A few years ago fishing for them paid well, but now it is only with **low spring ebbs** that **a few hundreds are occasionally got**." (1887[85])	Location Depth Exploitation status
Southern North Sea	"...yet all this time there have been **extensive tracts** of oyster grounds existing in the North Sea, but **known only to a few fishermen comparatively**. This bed or ground is of enormous dimensions compared with other oyster grounds; its length Easterly and Westerly is nearly **200 miles**, and varying in breadth from **30 to 70 miles**..." (1885[86])	Location Extent Start of exploitation
Southern North Sea/ German Bight	"Over the Schleswig-Holstein [Germany] sea flats there exist **50 oyster beds** of very different sizes. The largest is not far from **2 kilometers 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. The greater number of the beds have a **depth of water of at least 2 meters above them when the ebb-tide has left the neighbouring flats dry**." (1877[66])	Location Extent Depth
English Channel	"**New oyster ground** lately discovered in the British Channel; **lies off Guernsey and Jersey**; **extends 40 miles in length and 9 miles in breadth**." (1891[81], quoting a description published in 1849)	Location Extent Start of exploitation
France	"Thus, I estimate that an oyster bed in a flourishing state is capable of supplying **10 adult oysters per square metre**, that is to say 100,000 oysters per hectare and 1 million per 10 hectares. This year, in fact, the "Bon Repos" oyster bed, which covers an **area of about 20 hectares, provided 2 million oysters**; the "Capelan bed", which covers **an area of 90 hectares, provided nearly 9 million**." (1864[87])	Location Extent Exploitation status
France	"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**...." (1910[68])	Location Exploitation status
Spain	"...**San Nicolas de Neda** was recorded in 1870 as having an **extent of 2 square miles**, or that of San Martin de Noya, 50 miles from Coruña, smaller, but exceedingly rich. These have been little protected by legislative measures and have been **ruthlessly dredged**, even by those who should have been their guardians [...]" (1891[67])	Location Extent Exploitation status
Italy, Croatia and Slovenia	"Oysters are found mostly on rocky shores in **2-5 fathoms**; on a bank to the **south-west of Grado, near the estuary of the river Isonzo**; **on a smaller bank west of Izola, near Capo d'Istria**; **near Pula and Novigrad, east of Zadar**; **along the coast of San Cassano** [Sukošan], and on the **Scogli Ostia and Galisniac** [islets Oštarije and Galešnjak]. They occur also near **Sebenico, Stagno** [Šibenik, Mali Ston], & c. [...], **near Brindisi, Ancona, Punto di Maestra and Chioggia**, and near the mouths of the rivers **Po, Adige, and Brenta**." (1883[88])	Location Depth
Italy	"There is another bank in front of **Fano** and far from the beach **four miles**. In this place, it is **twelve steps deep and four hundred long and extends towards the northwest as far as Pesaro**. It begins again in Rimini continuing up to Cesenatico [...], and then starts opposite Primaro again, ending above Magnavacca." (1715[89])	Location Depth Extent

See refs. 35,36 for additional evidence and locations assigned.

and scientific interest in the European flat oyster have produced a record that is probably unique in terms of the longevity and diversity of written sources dedicated to a marine species[38,39]. Despite this extensive historical record, the past distribution of the European flat oyster, its habitat structure and contributions to ecosystem functioning remain unknown and contested[29]. In collating an ecosystem-wide picture, this study indicates a substantial and, until now, largely unquantified scale of physical structural transformation in European seabeds before the twentieth century, with corresponding implications for the articulation of conservation and restoration goals.

Transformation of European seafloors

Historically, flat oysters formed complex three-dimensional, biogenic reef habitats that could span extents of >10 ha, and which supported a diverse associated community (Figs. 1–3 and Table 1). Although wild populations of flat oysters persist in some limited locations today, the biogenic habitat that once formed has almost entirely disappeared[33,34,40,41]. Extant flat oyster populations are universally described as patchy, with small areas of higher densities sometimes found within a broader landscape of sparsely distributed oysters[31,33,42,43]. In contrast, past descriptions identify oysters often clustered together, as highly abundant over extensive areas, and living and dead individuals forming raised three-dimensional seabed structures at sizes and scales not observed today[36] (Tables 1 and 2). That no known wild native oyster reefs remain at a scale of >1 ha thus signals an unprecedented loss of emergent biogenic structure in European seas, with potentially analogous losses for marine biodiversity[41].

Oyster habitat historically supported a high taxonomic diversity of associated species (Fig. 3). This diversity was characterized by multiple trophic levels that likely enhanced ecosystem functioning[44] (Fig. 3), such as nutrient cycling through bentho-pelagic coupling, secondary production and the increased transfer of energy across trophic levels[45]. Given the large reported extent of the historical habitat, it is likely that these biogenic reefs played a vital role in supporting European coastal seas trophic webs, driving bentho-pelagic coupling of seston-derived nutrients and creating complex habitats that provided refuge or food sources for benthic and pelagic fish populations. This is supported by findings from extant remnant oyster reefs in other biogeographic regions, showing that the reef structure and rich biota associated with oyster habitat support consumers at higher trophic levels[46] and function as nursery grounds, therefore enhancing fisheries production (for example, Eastern USA and northern Gulf of Mexico[47]). Although such inference is beyond the scope of our data, we show that commercially targeted species were historically recorded at oyster reefs (for example, *Homarus gammarus*, *Cancer pagurus*, *Pleuronectes platessa*). As oyster reefs typically increase the structural complexity of the underlying substrate, their presence also supported the persistence of a community whose composition differed from that of surrounding habitats, probably contributing to a higher beta-diversity across the wider system, as observed in other systems[48,49]. The complex, three-dimensional structure of reefs and biodeposition of organic matter is also likely to have influenced local hydrodynamic-regime and sedimentation processes[50]. The impacts of these extensive reef structures upon nearshore ecosystem functioning remain unknown, but evidence from extant

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Table 2 | Example descriptions of the structure or abundance of exploited oyster reef habitats

Country	Quote (descriptions of structure and abundance in bold) and year of publication
Ireland	"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."* (1836[90]) *Some accounts expressed a belief that dredging was required to facilitate settlement and growth of oysters by removing predator and competing species, and enhancing growth to marketable sizes and shapes.
Isle of Man	"There was a great oyster bed in [Ramsey] Bay three miles from the pier. 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**... One boat has got **30,000 oysters in a week**." (1879[58])
Ireland	"In Ballycroy Bay, and the Sound of Bullsmouth, **three thousand oysters may be taken in a day, with a dredge**." (1836[90])
Wales	"About sixty years ago there was a fine bed of oysters near the end of St. Patrick's Causeway at Mochras. **Nine hundred have been got in one day by a rowing boat** starting from Barmouth, but many more were got by sailing craft [...]. 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." (1889[91])
Southern North Sea	"**1000 oysters have been caught in four hours** in 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 [...]. Already small sailing vessels have been getting **20 thousand per week**, without the aid of steam power." (1885[86])
Southern North Sea	"These great oyster banks are situated in **patches** in the North Sea, especially off the Dutch coast. The trawlers carefully avoid these beds as the **heavy 'clumps' tear the nets**." (1879[58])
France	"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**." (1910[68])
France	[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." (2006[92])
France	"[In the Bay of Quiberon]... 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**." (1910[68])
Italy	"The seafloor is filled with oysters, **almost placed one on top of the other** like stones, **forming a wall**." (1715[89])

For additional evidence and locations assigned, see refs. 35,36.

and restored systems within and outside of Europe suggests that reef presence can enhance carbon burial and accumulation rates[51], reduce erosion and improve water quality[52].

Evidence of reef-forming habitat was particularly extensive for the southern North Sea, Irish Sea, English Channel and surrounding coastlines, and the western coasts of the Adriatic and Black Seas (Fig. 1). We found no descriptions of oyster reef habitat in the Baltic Sea, with shell remains in the region potentially linked to trade and/or failed efforts to transplant oysters[53]. It is less clear whether our findings represent a fair reflection of the distribution and form of oyster reefs in the Mediterranean. Low confidence of reef-forming habitat in this region could be reflective of sources remaining hidden, earlier losses of oyster habitat driven by exploitation (for example, ref. 54), changing hydrographic flows or sedimentation rates (for example, ref. 55), or different environmental conditions for growth meaning that reef habitats are less likely to form towards the edge of their range. The situation is made even more complex by the historically uncertain nomenclature of the *Ostrea* species complex in the Mediterranean[56]. Nevertheless, the available descriptions indicate that the occurrence of Ostreidae spp., with the notable exception of reef descriptions in the northern Adriatic, were largely patchy in their distribution and associated with rocky habitats throughout the Mediterranean[36].

Despite the striking magnitude of oyster reefs described historically in this study, the historical accounts commonly describe oyster populations 'after' the commencement of wide-scale exploitation[57,58]. The majority of written records used in this study were published during the nineteenth century (Supplementary Fig. 1), but occasional accounts before this period described localized declines or losses of oyster habitat as a result of fishing pressure (for example, refs. 59,60). Moreover, harvested flat oyster shell remains dating from the Mesolithic period have been found in archaeological deposits across Atlantic Europe, demonstrating that coastal flat oyster populations have been exploited for thousands of years[61,62]. Written historical descriptions of these reefs thus cannot be considered pristine. While the findings in this study cannot represent an unexploited ecosystem, the evidence still affords robust insights into the past ecological importance and extent of oyster reef habitats across the species' historical distribution.

Drivers of change

Historical sources are increasingly used to reveal the scale and drivers of ecological changes through time[1,7]. Proposed drivers of change were commonly observed in written records, including reports of the rapid loss of reef habitat when heavily exploited (Table 2). Overexploitation was mentioned in some earlier written records as being responsible for the decline and loss of oyster reefs (for example, refs. 63,64), but the frequency and geographic breadth of records proposing overexploitation as the primary cause of decline expanded rapidly in the nineteenth century (for example, refs. 57,65–68), despite attempts to bolster declining populations via translocation and culture[69]. Glimpses of wider environmental changes and their impacts upon oyster reef persistence are also observed. These include reports of oyster mortalities under very cold winter conditions, which frequently affected shallow-water oyster layings[70], and the influence of changing hydrographic regimes, such as the nineteenth century expansion of flat oysters into the western Limfjord after storm-induced hydrodynamic and salinity changes[71]. While disease was reported as having serious impacts on the persistence of oyster populations from the twentieth century onwards (for example, ref. 72), disease was infrequently mentioned in earlier documents[73]. The almost complete removal of oyster habitat from European coastal waters started by widespread fishing and mechanical extraction, was thus compounded by a cascade of degradation, with pollution, introduced species, disease and climate change contributing to further declines from the late 1800s.

Policy applications

The restoration of biodiversity is of increasing policy interest at local to international scales[4,74,75]. In practice, relatively small patches of higher oyster density (a few m^2 in extent) are often defined as oyster habitat in conservation advice, or larger areas of very low oyster density (that is, 0.5–2.0 oyster m^{-2}) defined as habitat for fishery management on a national level[43]. Such definitions reflect the current rather than historical status of this habitat. These remaining patches of oyster habitat are of high conservation value given their rarity and the gains in local biodiversity fostered by their presence[76,77]. Recognition of the value of these remnant habitats is important to ensure existing protections are

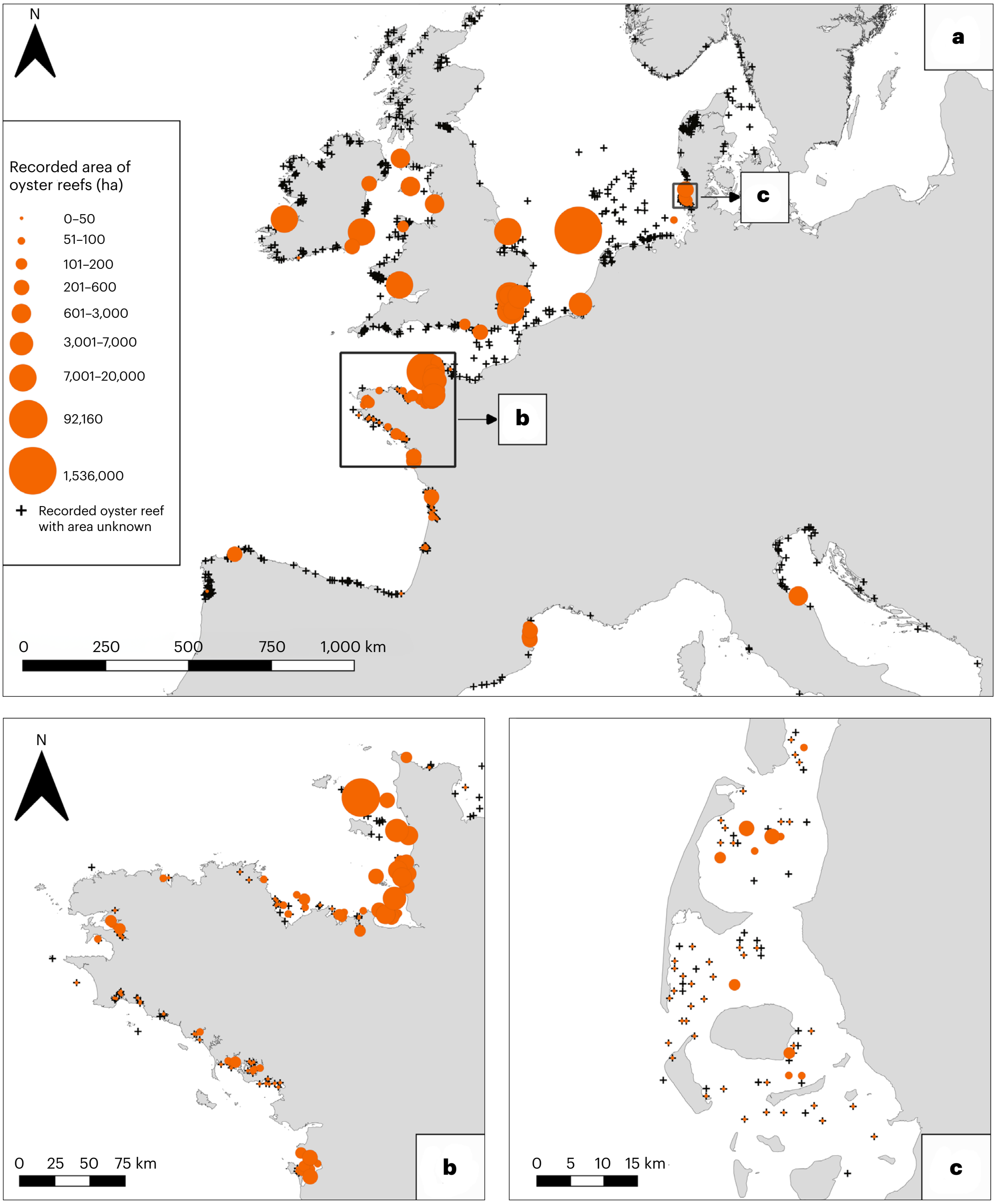

Fig. 2 | Extent of past oyster reefs. **a**, Recorded extent (hectares, orange circles) of oyster reefs. The crosses indicate records of reefs of unknown areal extent. **b**, The coast of France, from which data were predominantly extracted from charts published in ref. 68. **c**, The Wadden Sea, with oyster reef extents extracted from ref. 66. Circle sizes remain consistent across panels. Base map source, ref. 82.

not removed as baselines are reconsidered. However, policies that rely on remnant populations alone to define habitat extent and form, or to articulate restoration goals, risk underestimating the past importance and influence of oyster habitat on seabed complexity, biodiversity and species-associated behaviours at an ecosystem scale[31,78]. In addition to directly supporting restoration science (for example, ref. 79), a historical evidence base for native oyster is of considerable importance for encouraging the reconsideration of policy decisions based on a notably shifted environmental baseline[75]. Our findings demonstrate that restoring even a fraction of these past habitats requires both ambitious policy agreements and a step-change in our understanding of the long-term nature of human-induced ecosystem degradation and the scales of historical loss in marine ecosystems.

Given the lack of long-term records for broader benthic ecosystems, our data further serve as a rare opportunity to visualize the fundamental restructuring of coastal and shallow-shelf seafloors resulting from centuries of human impact. The expansive historical documentary record for the flat oyster provides a unique empirical record that acts as a broader signal of the highly degraded current status of European seas. Studies such as this are critical for understanding the present-day degraded status of habitat-forming species in marine coastal waters and provide key context to global sustainable

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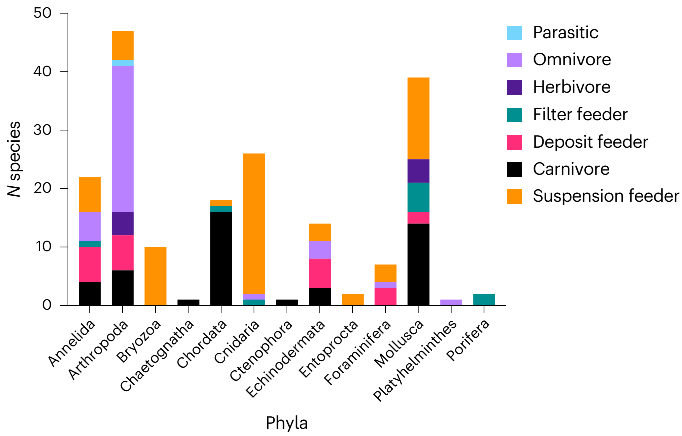

Fig. 3 | Species recorded in the presence of oyster reefs. Number of species historically observed in association with historical oyster reef habitats in Northern Europe, assigned to phyla and trophic guild. Sources are provided in Supplementary Information.

development goals and recent international commitments to restore the seas. In addition to informing restoration targets, our findings present a sobering reminder of the scale of work to be achieved if we are to restore even a small fraction of what has been lost from our seas.

Methods

Team development

Initial collaborators were identified via self-selected membership of the Native Oyster Restoration Alliance, a pan-European network of researchers and practitioners specializing in historical ecology, oyster biology, ecology, conservation and restoration[26,29]. Calls for collaboration were also advertised at related workshops and conferences. Additional collaborators were approached individually when a specific knowledge gap was identified during the data collation phase. These experts were identified by the lead authors through targeted literature searches or by asking in-country researchers already known to the group.

Sources and search terms

National library and museum collections were searched for references to historical oyster habitat and fisheries, including government records, nautical charts, naturalists' accounts, fishery reports, customs accounts, popular media and scientific journals. In addition to 'oyster' and '*Ostrea edulis*', search terms included regional and local name variations, such as 'flat oyster', 'native oyster', 'mud oyster', 'edible oyster', 'Pandores' (Scotland), 'huîtres plates', 'belons' and 'huîtrière' (France), 'østers' (Denmark), 'Auster' (Germany), 'zeeuwse platte', 'zeeuwse bolle' (Belgium/the Netherlands), 'ostra plana' (Spain) and 'ostrica piatta' (Italy). Mapping the locations of past oyster habitat as data were submitted enabled the identification of gaps and precipitated further targeted searches. While archaeological records provide extensive and useful information about pre-industrial fisheries, it is challenging to reconstruct historical habitat extent or habitat characteristics, which were the focus of this study, hence data collection primarily focused on the written record.

Biogenic oyster habitat is referred to as both 'reefs' and 'beds' across Europe, while much historical literature referred to high densities of oysters as a 'bed' or 'bank'. For consistency, we used the term 'reef' as analogous to oyster biogenic habitat and 'beds' or 'banks', which we collectively defined (sensu European Habitats Directive Appendix I) as 'a biogenic hard bottom that arises from the seafloor and originates from dead or living oysters and associated species, which supply habitats for epibiotic species'.

Data extraction

Locations of oyster fisheries or oyster reefs were extracted from historical written sources. The locations of described fisheries and reef habitats were estimated from descriptions or identified from charts/mapped areas and assigned to 10 km^2 grid cells. In instances where historical place names were no longer in use or where nautical locations (for example, names of fishing grounds) were mentioned, we identified locations by cross-checking with historical nautical charts or maps. Contextual descriptions within historical sources were also used to identify the likely area referred to, which was then cross-checked using historical charts. For reefs marked on nautical charts or mapped in more recent publications, areas were traced using the polygon tool in ArcGIS and the centroids of each polygon were converted into point data (latitude and longitude). In written descriptions, oyster grounds could be named after the local town and/or a cursory description of the location provided, for example, the number of miles from shore. In other cases, oyster presence might be described as occurring within a harbour or bay. As such, 10 km^2 was deemed a reasonable level of precision for most locations, although some occurrences could be reasonably identified to a higher resolution. Locations where oysters were reported within the intertidal zone or shoreline were noted. 'Shore' was assigned when oysters were mentioned as present at very shallow depths (for example, descriptions included people 'wading' for oysters or otherwise picking them by hand), but it was unclear whether this included the intertidal zone. Descriptions of oyster reefs that were far larger than 10 km^2 were allocated a grid point within the estimated central part of the range, and the relevant additional number of grids (related to the described size) was highlighted but identified as low confidence in location to emphasize the likely but uncertain location of this reported extent of habitat.

The extent (length or area) and depth of described oyster reef habitats were extracted from written records and nautical charts, with a mean value assigned if a range of measurements was described. Reef extents were differentiated from each other using the descriptive locational data, and where overlap was considered likely (that is, descriptions of the location of a reef were vague, such as occurred for records describing the vast extent of oyster reef habitat in the southern North Sea), suspected duplicates were removed. When using nautical charts, because some of the polygon boundaries were difficult to differentiate, areas of oysters were considered independent reefs if separated by more than 200 m.

Descriptions of habitat characteristics were also recorded, such as the depth at which oyster habitat was found, extent, habitat structure and associated species. While flat oysters form biogenic habitat in suitable environmental conditions, they also occur singly. Historical sources were commonly concerned with recording oyster extraction rather than describing the characteristics of the habitat directly, with exploited habitats commonly termed 'beds' or 'banks'. For regions where descriptions of oyster reefs existed and where dredge or trawl gear were primarily used to exploit oysters, we interpreted the presence of fisheries with notable landings as high confidence that oyster reefs were once present in an area. Although today's dredge oyster fisheries will exploit oyster populations at low densities (for example, refs. 78), historical dredge fisheries often reported high catch rates when encountering newly discovered oyster grounds[35]. Conversely, in regions where written descriptions of reefs were not found and/or where fisheries indicated extraction by diving and handpicking, as opposed to extracting high volumes by dredge, low confidence of reef habitat was assumed.

Survey data that identified the presence of an individual or very low numbers of oysters were excluded, as were archaeological or museum records where the abundance or original location of past oysters was unclear. Locations (for example, oyster ponds) that were clearly created for oyster culture were discarded. Records were also excluded if it was deemed likely that the species of oyster referred to was not *O. edulis*.

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Non-native species of oysters were introduced as flat oyster abundance declined; for example, the Portuguese oyster (*Crassostrea angulata*, also known as *Magallana angulata*) was introduced along the French Atlantic coast from 1860 and spread rapidly[80], and was also cultivated in British waters during the nineteenth century[81]. Historical records that differentiated between oyster species (for example, refs. 68), or that clearly referred to flat oysters were thus preferentially sourced. Written historical records were used wherever possible, but where such records could not be identified and contemporary or material records were available, these were consulted in place of written descriptions.

Levels of confidence that historical sources were referring to biogenic oyster reef habitats, as opposed to scattered oysters, and confidence of location accuracy were assigned on the basis of the following criteria:

High confidence of reef habitat, high location certainty (HH): record of habitat, for example, a bed or bank of oysters, or record of an active fishery using towed gears with notable landings and no recorded active intervention, thus indicating an initial high abundance of oysters. We are confident of the location to within 10 km, for example, oyster presence within a bay or harbour.

High confidence of reef habitat, low location certainty (HL): we were confident a habitat existed, but the location is uncertain to >10 km, for example, named open-water locations without positioning detail.

Low confidence of reef habitat, high location certainty (LH): we know oysters were fished but the descriptions (or corresponding descriptions) do not provide evidence that the species formed biogenic reefs in this location, for example, individuals were described as attached to rocks. We are confident of the location to within 10 km.

Low confidence of reef habitat, low location certainty (LL): we know oysters were fished, but the descriptions (or corresponding descriptions) do not provide evidence that the species formed biogenic reefs in this location. The location is uncertain to >10 km.

Data visualization

Digitizing and spatial visualization were completed using QGIS software v.3.24 (QGIS Development Team). European coastline boundaries were derived from the European Environment Agency's open-source Europe coastline shapefile, and European country boundaries were derived from the open-source Eurostat shapefile titled Countries 2020[82]. In cases of historical jurisdictional changes (for example, changes to national borders), present-day nation boundaries and waters were applied. The Coordinate Reference System (CRS) used is ETRS89-extended/LAEA Europe. The locations of major seas and sea basins as described in the manuscript are shown in Supplementary Fig. 5.

Associated biodiversity

Species associated with oyster reef habitat were extracted from 12 sources published over a period of 150 years and which predominantly focused on the coasts of Germany, Denmark, Britain and Sweden (Supplementary Table 1)[35]. Species identified were corrected to currently accepted species names as listed in the world register of marine species (WoRMS; https://www.marinespecies.org/) and taxonomic classification was assigned to each species from kingdom to genus levels (including phylum, subphylum, class and order where applicable). IUCN Redlist Classifications and population trends were listed for assessed species (https://www.iucnredlist.org). Each species was assigned a trophic guild using published descriptions listed in WoRMs or the Marine Life Information Network (MarLIN; https://www.marlin.ac.uk/) databases. The trophic guilds combined types of feeding and trophic level (Supplementary Table 2) to enable both the ecological and trophic functions to be resolved. Statistical analysis was performed using IBM SPSS Statistics v.27. Kolmogorov–Smirnov and Shapiro–Wilk tests of normality were used before non-parametric (independent-samples Kruskal–Wallis) tests to assess distribution of species across phyla and trophic guilds.

Reporting summary

Further information on research design is available in the Nature Portfolio Reporting Summary linked to this article.

Data availability

The data that support the findings of this study are available in figshare at https://doi.org/10.6084/m9.figshare.c.6884167.v1 (ref. 35). The world register of marine species (WoRMS; https://www.marinespecies.org/) and Marine Life Information Network (MarLIN; https://www.marlin.ac.uk/) databases are publicly available. For the purpose of open access, the author has applied a Creative Commons Attribution (CC BY) licence to any author-accepted manuscript version arising from this submission.

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Author contributions

R.H.T. and P.S.E.z.E. conceptualized the project, developed the methodology, contributed and curated data, and wrote the original draft. H.M. conducted formal analysis and wrote the original draft. J.P. contributed data, conducted formal analysis and wrote the original draft. E.C.A., F.P.B., A.B.C., J.H.B., T.C.C., F.d.C., D.W.D., C.E., T.F., E.G., O.G., R.G., D.G., M.H.-H., L.H., K.T.J., J.A.J., J.L., A.B.M.M., D.K.M., P.N., H.v.N., B.O., C.P., B. Pogoda, B. Poulsen, S.P., C.S., A.C.S., D.S., A.S. and J.A.T. contributed data, and reviewed and edited the manuscript. C.M.R. reviewed and edited the manuscript.

Competing interests

The authors declare no competing interests.

Additional information

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Our web collection on statistics for biologists contains articles on many of the points above.

Software and code

Policy information about availability of computer code

Data collection	No computer code software was used
Data analysis	Statistical analysis was performed using IBM SPSS Statistics v27; Digitising and spatial visualisation were completed using QGIS software version 3.24.

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The data that support the findings of this study are available in Figshare with the identifier https://doi.org/10.6084/m9.figshare.c.6884167.v1. The world register of marine species (WoRMS: https://www.marinespecies.org/) and Marine Life Information Network (MarLIN https://www.marlin.ac.uk/) databases are publicly available. 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 (EEA 2017).

Human research participants

Policy information about studies involving human research participants and Sex and Gender in Research.

Reporting on sex and gender	Not applicable to this study - this information has not been collected
Population characteristics	Not applicable to this study
Recruitment	Not applicable to this study
Ethics oversight	Not applicable to this study

Note that full information on the approval of the study protocol must also be provided in the manuscript.

Field-specific reporting

Please select the one below that is the best fit for your research. If you are not sure, read the appropriate sections before making your selection.

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Ecological, evolutionary & environmental sciences study design

All studies must disclose on these points even when the disclosure is negative.

Study description	Use of archival records to document historical oyster (Ostrea edulis) reef presence across its biogeographic range, its form and extent and associated species present. We used qualitative data (descriptions, presence of species) to identify locations of and characteristics of a past ecosystem
Research sample	Locations of oyster fisheries or oyster reefs were extracted from historical written sources extracted from public libraries and other archives (e.g. government, university archives). Sources were identified via searches of library or archive catalogues for 'oyster' and 'Ostrea edulis', with search terms also including regional and local name variations across European countries.
Sampling strategy	Sampling strategy was dependent on historical sources existing in archival collections and being able to be found via keyword searches described above. Mapping the locations of past oyster habitat as data were submitted enabled the identification of gaps and precipitated further targeted searches.
Data collection	Authors collated data for their country or region of expertise, with data further collated and checked by Thurstan and zu Ermgassen (lead authors)
Timing and spatial scale	Sampling of archival collections took place between June 2020 and June 2023. The earliest publication used in our sample was published in 1524 and the latest in 2022. The sampling of archival data encompasses the biogeographic (native) range of the flat oyster.
Data exclusions	Due to our focus on mapping historical reef systems, 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. These exclusion criteria were pre-established based on author knowledge of historical records and aimed at increasing the confidence of our findings for locations where reef habitat was historically present.
Reproducibility	All data records will be made publicly available as will the original source references.
Randomization	Not relevant due to archival/qualitative nature of data
Blinding	Blinding was not possible as cross-referencing of historical sources is key to interpreting their meaning and understanding potential biases of the source and hence our prescribed level of confidence in historical recordings

Did the study involve field work? ☐ Yes ☒ No

Reporting for specific materials, systems and methods

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Materials & experimental systems

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☒	☐ Eukaryotic cell lines
☒	☐ Palaeontology and archaeology
☒	☐ Animals and other organisms
☒	☐ Clinical data
☒	☐ Dual use research of concern

Methods

n/a	Involved in the study
☒	☐ ChIP-seq
☒	☐ Flow cytometry
☒	☐ MRI-based neuroimaging