The world was our oyster: Records reveal the vast historical extent of European oyster reef ecosystems

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Abstract

Anthropogenic activities have impacted marine ecosystems at extraordinary scales. Biogenic reef ecosystems built by the European flat oyster (*Ostrea edulis*) typically declined prior to scientific monitoring. Collating >1,600 records published over 350 years, we created a highly resolved ($10km^2$) map of historical oyster reef presence across its biogeographic range, including documenting abundant reef habitats along the coasts of France, Denmark, Ireland and the United Kingdom. Areal extent data were available from just 26% of locations, yet totalled >1.7 million hectares (median reef size = 30ha, range 0.01 - 1,536,000ha), 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.

Keywords

Biogenic reef, ecosystem collapse, environmental history, historical ecology, shifting baselines, *Ostrea edulis*

Introduction

Human activities have resulted in widespread habitat loss globally (Bunting et al. 2022; Sohl et al. 2012; WWF 2020). Marine systems are no exception, with destructive fishing activities, pollution and reclamation resulting in large-scale habitat degradation and loss (Lotze et al. 2006). European seas are among the most impacted marine environments globally (Halpern et al. 2008; Eigaard et al. 2017; Airoldi and Beck 2007), and there is common agreement on the urgency to conserve and restore habitats to support and recover key ecological functions (Duarte et al. 2020; Waltham et al. 2020; UNEP/FAO 2020). 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 (McAfee et al. 2022; zu Ermgassen et al. 2020a).

Assessments of human impact are commonly restricted by the short time-span of modern scientific data, which is typically limited to recent decades (Halpern 2008; Halpern et al. 2019; Airoldi and Beck 2007). In contrast, activities such as fishing have occurred for centuries (Barrett et al. 2004; Lotze et al. 2006; Knauss 2005). The early, intense and geographically broad exploitation of marine resources in Europe presents a critical challenge for the identification of ecological baselines, and requires significantly deeper time perspectives than those available from scientific monitoring data (Waycott et al. 2009; Fortibuoni et al. 2010; Engelhard et al. 2016; Pogoda 2019). 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 (un)certainty, small sample sizes, and a patchy historical record, among others (Engelhard et al. 2016).

Despite advances in our understanding of historical dynamics in marine environments, studies focusing upon historical changes across a species' biogeographic range remain limited. The European flat oyster (*Ostrea edulis,* Linneaus, 1758 'flat oyster' herein) is a benthic habitat-forming species that was once economically and culturally significant across

Europe. This significance led to its representation in numerous historical sources published in multiple countries (Bennema et al. 2020). 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 vulnerable 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 (Airoldi and Beck 2007). Marine biogenic habitats are formed by assemblages of sessile benthic organisms, which create emergent physical structures distinct from the surrounding seabed (Holt et al. 1998). These habitats are formed by a range of taxa, including bivalves, annelids, corals, sea grasses, and macroalgae (De Clippele et al. 2017; Fariñas-Franco et al. 2017; Gravina et al. 2018; Teagle et al. 2017; Piazzi et al. 2021; Tamburello et al. 2021; Richardson et al. 2022). 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 (Kazanidis et al. 2022; Thomsen et al. 2022). 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 (De'ath et al. 2012; zu Ermgassen et al. 2012; Sunday et al. 2017; Filbee-Dexter and Wernberg 2018; McAfee et al. 2020).

Many species of oyster (e.g. *Ostrea*, *Crassostrea*, *Saccostrea* spp.) create biogenic habitat through gregarious settlement (Kasoar et al. 2015). But centuries of degradation and loss of oyster habitat globally mean that examples of undisturbed reefs are rare (Beck et al. 2011). Thus, our knowledge of the characteristics of oyster reefs (e.g., 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 (Powers et al. 2009; Hemraj et al. 2022).

The flat oyster is a habitat-building oyster native to European seas (OSPAR Commission 2009). Flat oyster exploitation and culture has occurred for thousands of years, with shell remains preserved in kitchen midden deposits from the Mesolithic period (Lewis et al. 2016). Until the early 20th century, European flat oysters were sufficiently abundant to support a significant 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* (Comps 1970; van Banning 1991; Berghahn and Ruth 2005; Bennema et al. 2020). We know of the species' widespread decline (Beck et al. 2011), but not where habitat once existed, the form of the habitat (e.g. density, areal extent) prior to exploitation, or its significance for associated communities.

Today, there is a growing impetus to conserve and restore marine ecosystems at scale (Pogoda et al. 2019; 2020; Waltham et al. 2020; McAfee et al. 2022), furthered by policies such as the Habitats Directive of the EU, the UN Decade on Ecosystem Restoration, the recent adoption of 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” (OSPAR Commission 2013). 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 foundation species (zu Ermgassen et al. 2020a). While there are several modern examples of flat oysters of multiple size classes clustering to form small clumps (Merk et al. 2020; Preston et al. 2020; Smyth et al. 2020; Pouvreau et al. 2021), the majority of known European flat oyster populations are found at average densities of <1 individual m^{-2} (e.g. Bergström et al. 2021; Tully and Clarke 2012; University Marine Biological Station Millport 2007).

Here we collate information from the historical documentary evidence to establish a uniquely highly resolved, ecosystem-wide, robust historical baseline for flat oyster reefs, specifically, i) the historical range and locations of flat oyster reefs; ii) size or extent, and; iii) 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 from >2000 years before present (Andrews 1948) until the 1970s (Todorova et al. 2009).

Flat oyster habitat distribution

Two hundred and twenty-five sources provided 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 $10km^2$ grid cells, with 85% (n = 606 grid cells) assigned a high confidence that biogenic reefs were once present (Fig. 1, Fig. S1, SOM). High confidence of past oyster reef presence was assigned to significant swathes of the coastlines of the UK, France, Ireland, Denmark, Spain, Germany and The Netherlands (for which 205, 109, 75, 38, 37, 30 and 27 grid cells within 12 nm 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). Significant reef habitats were historically reported in the southern North Sea and the English Channel (Bennema et al. 2020), although their locations were not well defined (Fig. 1b, Table 1). The large area of contiguous oyster habitat shown in the Southern North Sea (Fig. 1a,b in blue) likely 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.

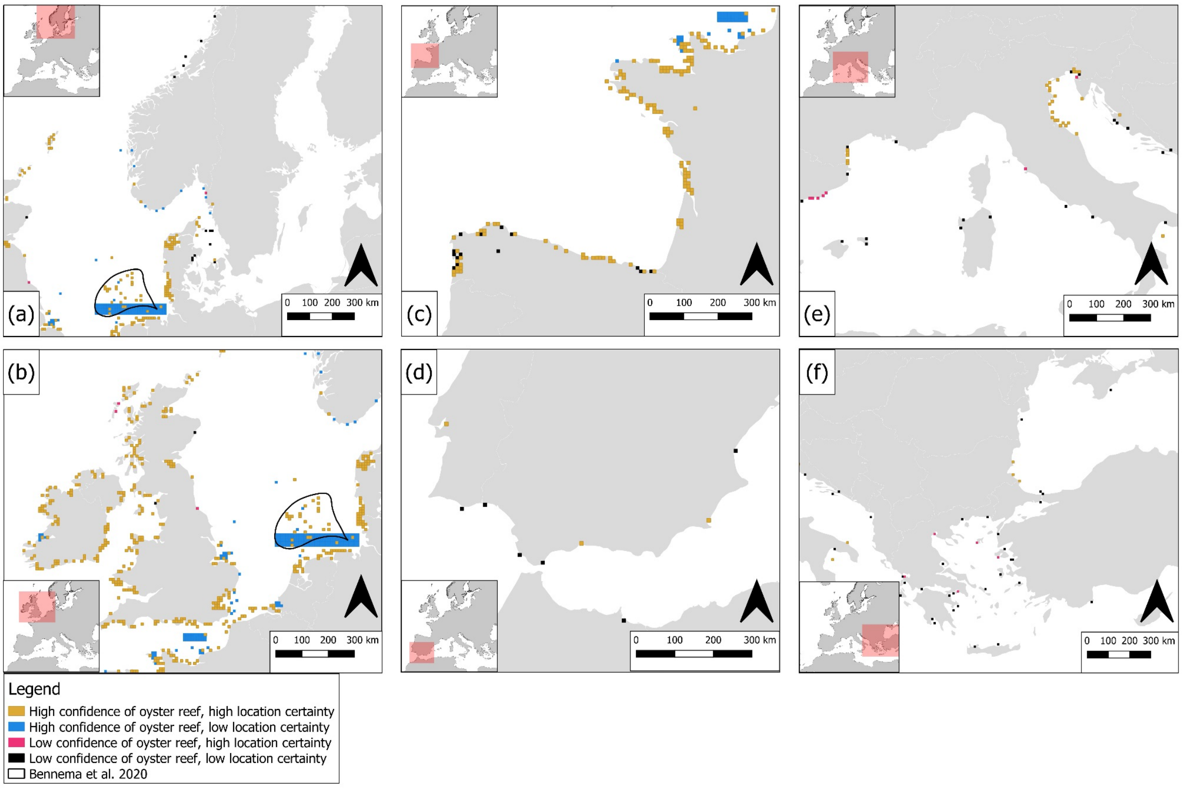

Figure 1a-e. Locations across Europe where oyster reef presence was assigned from historical sources, identified to 10km² grids, with associated confidence levels that biogenic reef habitat was present. For the full map see Figure S1, SOM.

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, Select Committee 1876) and the Atlantic coast of Morocco (85 m, Dollfus 1934). Fishable quantities of oysters were reported at depths > 40 m in the southern North Sea (Buckland 1875; Select Committee 1876), the English Channel (Royal Commission 1866), in the Irish Sea (Isle of Man Times 1874), and occasionally inshore locations such as Belfast Lough (Forbes and Hanley 1853). Quantities of oysters were reported in the intertidal or shallow subtidal zone in Northern Ireland (e.g., Strangford Lough, Harris 1744), the Republic of Ireland (e.g., Sligo River, Went 1962), Wales (e.g., Mumbles, Cliffe 1847), Scotland (e.g., Kirkcudbright, Sinclair 1845), and the northern coast of France (e.g., Cancale, Joubin and Guerin Guanivet 1910) (Fig S3a; Table 1).

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. See Thurstan et al. (2023; In review) for the full list of documentary evidence and locations assigned.

Country	Quote (**attributes bolded**)	Attributes
Ireland	"A very beautiful Peninsula stretches out into '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." (Stoke 1891, 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**." (Harding 1882)	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**." (Fishery Board for Scotland 1887)	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**…" (Olsen 1885)	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**." (Möbius 1877)	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**." (Philpots 1891, 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**.” (Archives du Service Historique de la Défense de Vincennes 1864)	Extent Location 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**....” (Joubin and Guerin Guanivet 1910)	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 [...].” (Dean 1891)	Location Extent Exploitation status
Spain	“In the same **cape of Udra**, the fishermen mark a natural reef and another one at Manrisca, giving the former an **extension of about 800 fathoms long and 400 fathoms wide**. They are **located on rocks** and are difficult to exploit due to this circumstance, which makes it difficult to track, and the depth of the seabed, which does not allow the use of trentones or angazos.” (Paz Graells, 1870)	Location Extent
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** [in Italy]; **on a smaller bank west of Izola**, **near Capo d’Istria** [Koper in Slovenia]; **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 in Croatia]. They occur also near **Sebenico, Stagno** [Šibenik, Mali Ston], & c.; on the Italian coast, **near Brindisi, Ancona, Punto di Maestra and Chioggia**, and near the mouths of the rivers **Po, Adige, and Brenta**.” (Faber 1883)	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 in the same direction where it stops, and then starts opposite Primaro again, ending above Magnavacca.” (Marsili 1715)	Location Depth Extent

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 individual reefs ranged from 0.01 ha to 1,536,000 ha (median = 29.9 ha) and included locations along the coasts of the UK, Ireland, France, Germany, 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 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, Fig. S3b). The length of described reefs ranged from 0.02 to 320 km (median = 4.0 km, n = 45 locations, Fig. S4).

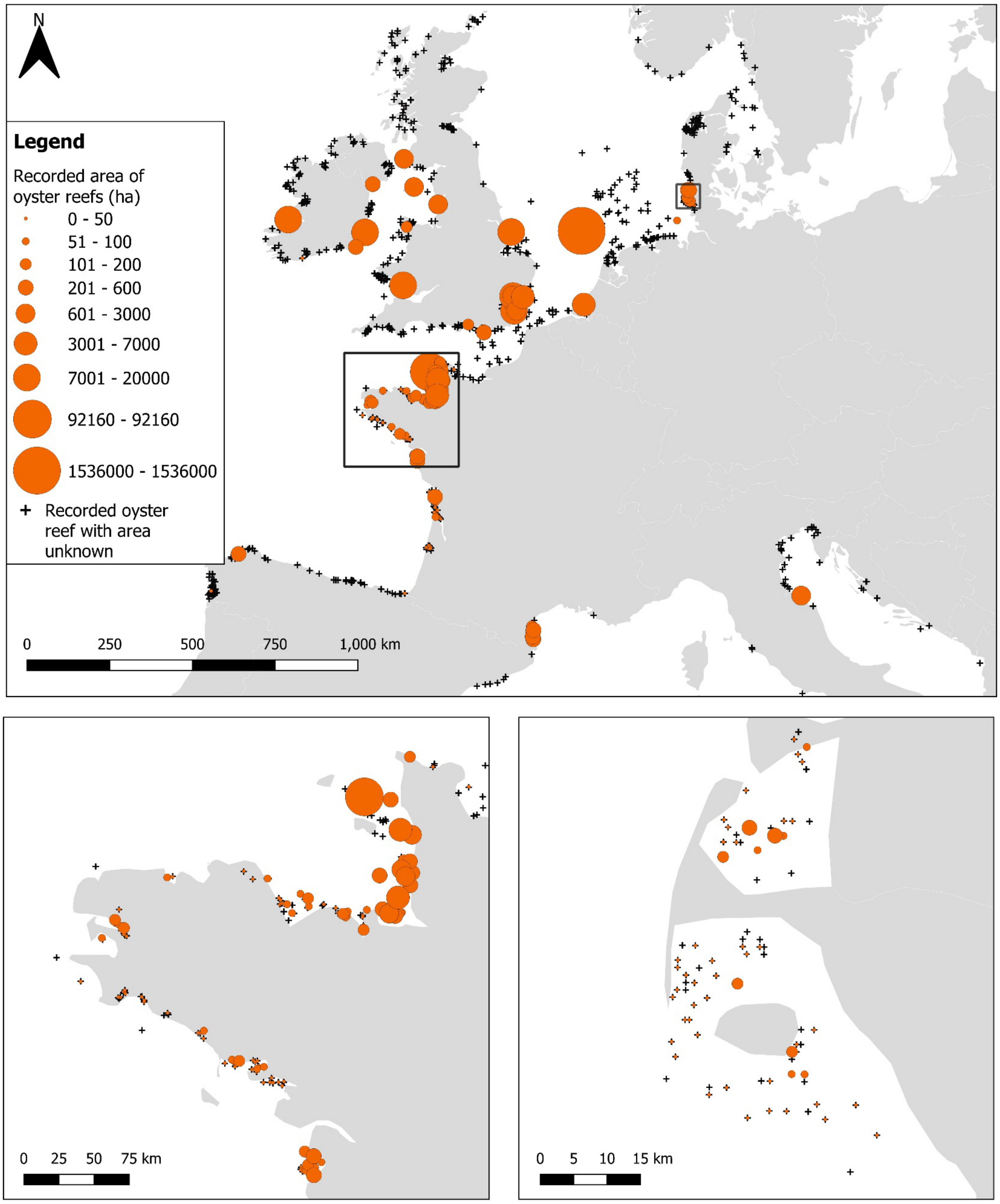

Figure 2. Recorded extent (hectares, orange circles) of oyster reefs. The crosses indicate records of reefs of unknown areal extent. The bottom left panel shows the coast of France in detail, from which data were predominantly extracted from charts published by Joubin and Guerin Guanivet (1910). The bottom right shows the Wadden Sea in detail, with oyster reef extents extracted from Möbius (1877). The location of the bottom panels are shown in the main figure by two open black rectangles.

<u>*Reef form*</u>

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 (Todorova et al. 2009). Within the historical literature, descriptions of reef form - although limited - exist for multiple locations (Table 2). Historical sources described ‘clumps’ of oysters (Buckland and Walpole 1879, Heape 1887, Joubin and Guerin Guanivet 1910), vertical reef formations (Marsili 1715), or an observed increase in seabed depth as reefs were removed by dredges and bottom trawlers (Buckland and Walpole 1879). When newly discovered oyster reefs were described in historical accounts, catches and catch rates indicative of high densities of oysters were recorded (Table 2).

Table 2. Example descriptions of the structure or abundance of exploited oyster reef habitats. For the full list of documentary evidence and locations assigned see Thurstan et al. (2023; In review).

Country	Quote (descriptions of structure bolded)
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"*. (Irish Fisheries 1836)
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**". (Buckland and Walpole 1879)
Ireland	"In Ballycroy Bay, and the Sound of Bullsmouth, **three thousand oysters may be taken in a day, with a dredge**". (Irish Fisheries 1836)
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". (The Cambrian News and Merionethshire Standard 1889)
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". (Olsen 1885)
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**". (Buckland and Walpole 1879)
France	"Until the last fishing season which lasted 6 months & 10 days, this industry (Bay of Brest fishery) came to the aid of **576 fishermen on 144 boats & that 14 million** oysters were sold". (Archives du Service Historique de la Défense de Vincennes 1849)

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**.” (Joubin and Guerin Ganivet 1910)
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"”. (Levasseur 2006)
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.**” (Joubin and Guerin Guanivet 1910)
Italy	“The seafloor is filled with oysters, **almost placed one on top of the other** like stones, **forming a wall**”. (Marsili 1715)

**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 (e.g. Irish Fisheries 1836; Inspector of Sea Fisheries 1890; Holt 1902).*

Associated species

A total of 190 species associated with oyster reef habits were recorded across 13 phyla, representing 7 trophic guilds (Table S1; Figure 3). The distribution of species differed significantly across trophic guilds (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, the 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.*).

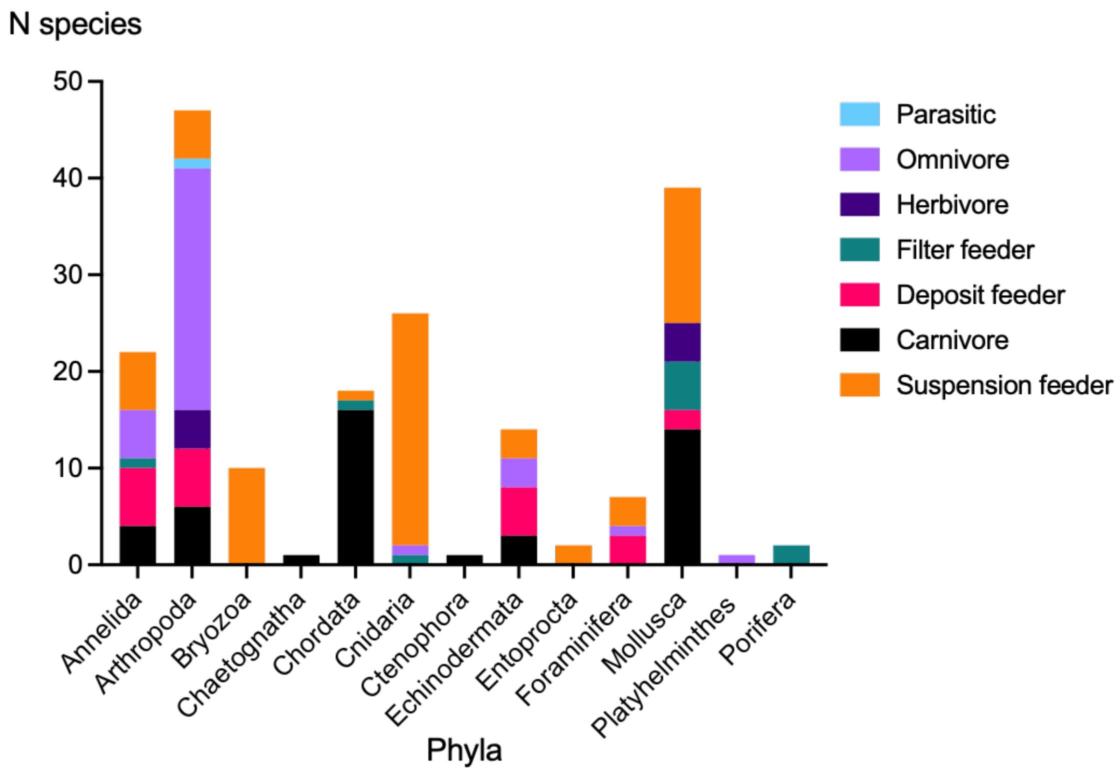

Figure 3. Number of species historically observed in association with historical oyster reef habitats in Northern Europe, assigned to phyla and trophic guild.

Discussion

The results presented here provide the first highly resolved, comprehensive overview of the spatial distribution, areal extent and habitat structure of a benthic marine ecosystem prior to its widespread functional extinction. Centuries of economic, popular and scientific interest in the European flat oyster have produced a record that is likely unique in terms of the longevity and diversity of written sources dedicated to a marine species (Neild 1995; Stott 2004). 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 (Preston et al. 2020). In collating an ecosystem-wide picture, this study indicates a significant and, until now, largely unquantified scale of physical structural transformation in European seabeds prior to the 20th century (Callaway et al. 2007; Frid et al. 2000; Bennema et al. 2020), with corresponding implications for the articulation of conservation and restoration goals.

Transformation of European seafloors

Historically, flat oysters formed enhanced three-dimensional, biogenic reef habitats that could span extents of >10ha, and which supported a diverse associated community (Figs. 1-3, Table 1). Although wild populations of flat oysters persist in some limited locations today, the biogenic habitat that once formed has almost entirely disappeared (Marine Biological Station Millport 2007; Tully and Clarke 2012; Nielsen and Petersen 2019; zu Ermgassen et al., In review). 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 (Thorngren et al., 2019; Tully and Clarke 2012; Pouvreau et al. 2021; Cameron 2022). In contrast, past descriptions identify oysters often clustered together, as highly abundant over extensive areas, and living and dead individuals forming three-dimensional seabed structures at sizes and scales not observed today (Tables 1 and 2; Thurstan et al. 2023, In review). That no known wild native oyster reefs remain at scale of >1 hectare thus signals an unprecedented loss of emergent biogenic structure in European seas, with potentially analogous losses for marine biodiversity (zu Ermgassen et al. In review.).

Oyster habitat historically supported a high taxonomic diversity of associated species (Fig. 3). This diversity was characterised by multiple trophic levels that likely enhanced ecosystem functioning (Fig. 3; Jabiol et al. 2013), such as nutrient cycling through bentho-pelagic coupling, secondary production, and the increased transfer of energy across trophic levels (zu Ermgassen et al. 2020b). Given the large reported extent of the historical habitat it is likely these biogenic reefs played a vital role in supporting European coastal seas trophic webs, potentially 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 the rich biota associated with oyster habitat supports consumers at higher trophic levels (zu Ermgassen et al. 2016; Yeager and Layman 2011). As oyster reefs typically occurred in otherwise soft-bottom habitats, their presence also supported the persistence of a community whose composition differed from surrounding habitats, likely contributing to a higher beta-diversity across the wider system (e.g. Henry et al. 2010; Sea et al. 2022). The complex, three-dimensional structure of reefs may also have impacted local hydrodynamic-regime and sedimentation processes (Lee et al. 2021).

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 (Lõugas et al. 2022). It is less clear if 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 (e.g. Andrews 1948), changing hydrographic flows or sedimentation rates (e.g. Sander et al. 2021), or different environmental conditions for growth meaning reef habitats are less likely to form towards the edge of their range. The situation is made more complex still by the historically uncertain nomenclature of the *Ostrea* species complex in the Mediterranean (González-Wangüemert et al. 2004). Nevertheless, the descriptions which are available indicate that the occurrence of Ostreidae spp., - with the notable exceptions of reef descriptions in the northern Adriatic - were largely patchy in their distribution and associated with rocky habitats throughout the Mediterranean (Thurstan et al. In review).

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 (Royal Commission 1866, Buckland and Walpole 1879). Historical descriptions of these reefs thus cannot be considered pristine (e.g. Möbius 1877; Thomas et al. 2020; Reeder-Myers et al. 2022). While the findings in this study cannot represent an unexploited ecosystem, the evidence still affords robust insights into the past ecological significance 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 (Gaumiga et al. 2007; Hall et al. 2012; Fortibuoni et al. 2010; McAfee et al. 2020). 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 (e.g. Giovio 1524; Cornide 1788) but the frequency and geographic breadth of records proposing overexploitation as the primary cause of decline expanded rapidly in the 19th century (e.g. Anon 1886; Commissioners of Fisheries 1844; Royal Commission 1866; Möbius 1877; Dean 1891; Joubin and Guerin Ganivet 1910), despite attempts to bolster declining populations via translocation and culture (Bromley et al. 2016). 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 (Select Committee 1876), and the influence of changing hydrographic regimes, such as the 19th century expansion of flat oysters into the western Limfjord after storm-induced hydrodynamic and salinity changes (Huxley 1883; Gaardner and Bjerkan 1934; Berghahn and Ruth 2005; Sander et al. 2021). While disease was reported as having significant impacts upon the persistence of oyster populations from the 20th century onwards (e.g. Elston et al. 1986), disease was infrequently mentioned in earlier documents (Giard 1894). 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 (Jackson et al. 2001).

Policy applications

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 (i.e. 0.5-2.0 oyster m^{-2}) defined as habitat for fishery management on a national level (Cameron 2022). 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 significant gains in local biodiversity fostered by their presence (e.g. Guy et al. 2018; Bergström et al. 2021; Lown et al. 2021). Such context is important to ensure existing protections are not removed as baselines are reconsidered. However, policies that rely upon remnant populations alone to define habitat extent and form, or to articulate restoration goals, risk underestimating the past significance and influence of oyster habitat on seabed complexity, biodiversity and species-associated behaviours at an ecosystem scale (Jenkin et al. 2019; Pouvreau et al. 2021). In addition to directly supporting restoration science (e.g. Stechele et al. 2023), a historical evidence base for native oyster will be of considerable importance for encouraging the reconsideration of policy decisions based upon a significantly shifted environmental baseline (European Commission 2022; McAfee et al. 2022).

Conclusions

The restoration of biodiversity is of increasing policy interest at local to international scales (UNEP/FAO 2020; European Commission 2022). The planning and communication of restoration goals requires explicit acknowledgement of past degradation and the construction of a locally-relevant historical reference system (Balaguer et al. 2014; Gann et al. 2019). Given the lack of long-term records for broader benthic ecosystems, our data serve as a rare opportunity to visualise 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 development goals and recent international commitments to restore the 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 specialising in historical ecology, oyster biology, ecology, conservation and restoration (Pogoda et al. 2019; Preston et al. 2020a). 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 focussed 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 use the term ‘reef’ as analogous to oyster biogenic habitat and ‘beds’ or ‘banks’, which we collectively define (*sensu* European Habitats Directive Appendix I) as ‘a biogenic hard bottom which arises from the seafloor and originating 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 location of described fisheries and reef habitats were estimated from descriptions or were identified from charts/mapped areas and assigned to 10 km^2 grid cells. 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, e.g., 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 (e.g. descriptions included people ‘wading’ for oysters or otherwise picking them by hand), but it was unclear if 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) were highlighted but identified as low confidence in location to emphasise the likely but uncertain location of this reported extent of habitat.

The extent (length or area) and depth of described oyster reef habitat were extracted from written records and nautical charts, with a mean value assigned if a range of measurements were described. Reef extents were differentiated from each other using the descriptive locational data, and where overlap was considered likely (i.e. 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 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 (e.g. Jenkin et al. 2019), historical dredge fisheries reported extremely high catch rates when encountering newly discovered oyster grounds (e.g. Irish Fisheries 1836; Buckland and Walpole 1879). 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 (e.g. 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*. 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 (Heral 1989) and was also cultivated in British waters during the 19th century (Philpots 1891). Historical records that differentiated between oyster species (e.g. Joubin and Guerin Guanivet 1910), or which 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 based on the following criteria:

High confidence of reef habitat, high location certainty (HH): record of habitat e.g. a bed or bank of oysters, or record of an active fishery using towed gears with no recorded active intervention, thus indicating an initial high abundance of oysters. We are confident of the location to within 10 km e.g. 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 e.g. 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 reef in this location e.g. 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 visualisation: Digitising and spatial visualisation were completed using QGIS software version 3.24 (QGIS Development Team). European coastline boundaries are derived from the European Environment Agency's open-source Europe coastline shapefile, and European country boundaries are derived from the open-source Eurostat shapefile titled Countries 2020. In cases of historical jurisdictional changes e.g. changes to national borders, present day nation boundaries and waters are 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 Fig. S1 (Supplementary Materials, SOM).

Associated biodiversity: Species associated with oyster reef habitat were extracted from sources published over a period of 150 years, and which predominantly focused on the coasts of Germany, Denmark, Britain, and Sweden (Henke 1743, Ellis 1754, Pennant 1777, Smellie 1790, Beckmann 1800, Wilmsen 1831, Krøyer 1837, Martin 1850, Eyton 1858, Möbius 1877, von Hamm 1881, Möbius 1893). 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 (including phylum, subphylum, class, order where applicable). 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 (Table S1, SOM) to enable both the ecological and trophic functions to be resolved. Statistical analysis was performed using IBM SPSS Statistics v27. Kolmogorov-Smirnov and Shapiro-Wilk tests of normality were used prior to non-parametric (Independent samples Kruskal-Wallis) tests to assess distribution of species across phyla and trophic guilds.

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Supplementary materials

Table S1: Trophic guild classifications and associated definitions as assigned to each species associated with O. edulis *habitat using published descriptions from WoRMs and MarLIN databases.*

Trophic guild	Definition
Primary producer	*Photosynthetic marine plants and algae*
Deposit feeder	*Moves in or on sediment digesting sediment and/or eating food on or in. Includes detritivores (dead bacteria and plants) for this purpose*
Filter feeder	*Suspension feeder that pumps water*
Suspension feeder	*Removes particles from water column via capture (active)*
Parasite	*An organism that obtains food and other requirements from a host organism. The host does not benefit from the association and may be harmed by it*
Herbivore	*Eats plants or algae via grazing or biting*
Omnivore	*Predator/grazer that eats animals and plants or algae (included scavengers-consuming carcases of dead animals) for this purpose)*
Carnivore	*Predator that consumes primarily animals*

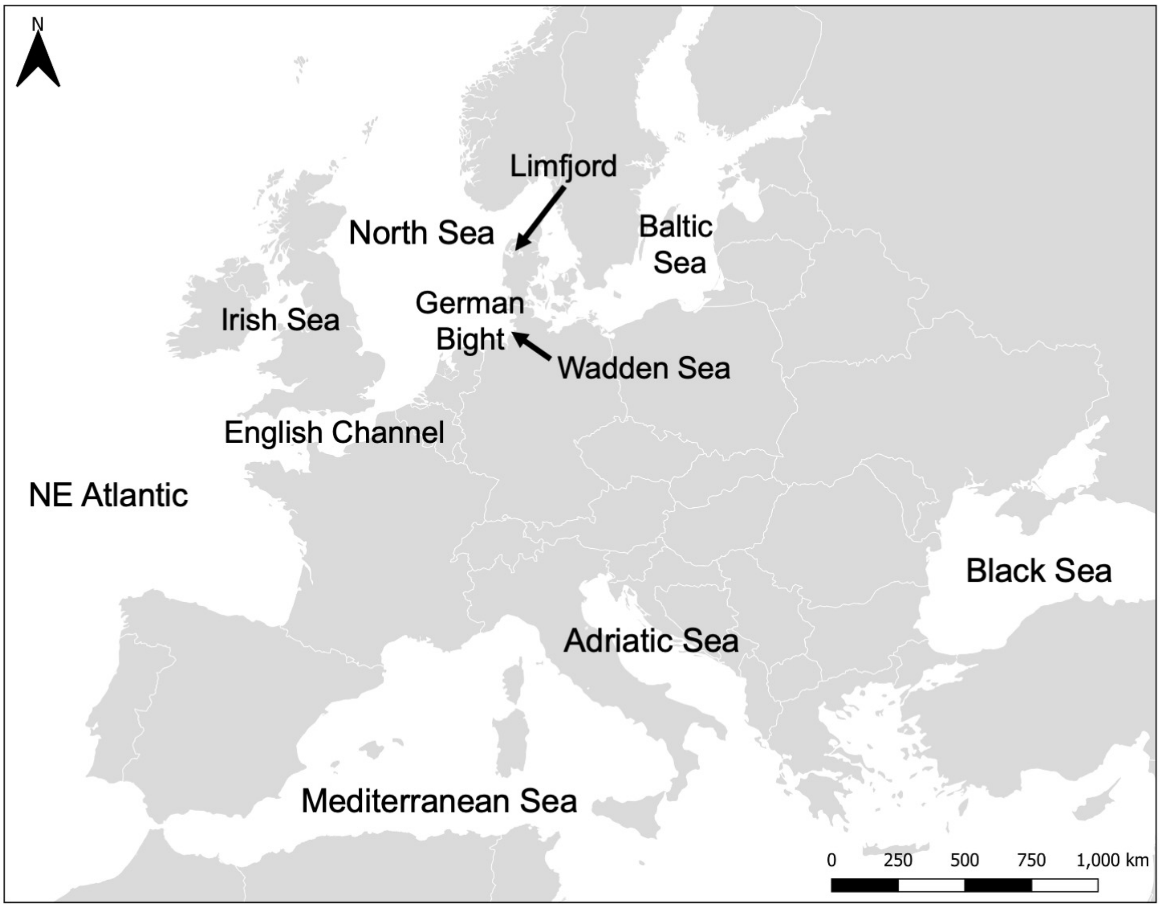

Figure S1. Map showing the locations of seas and sea basins referred to in the manuscript.

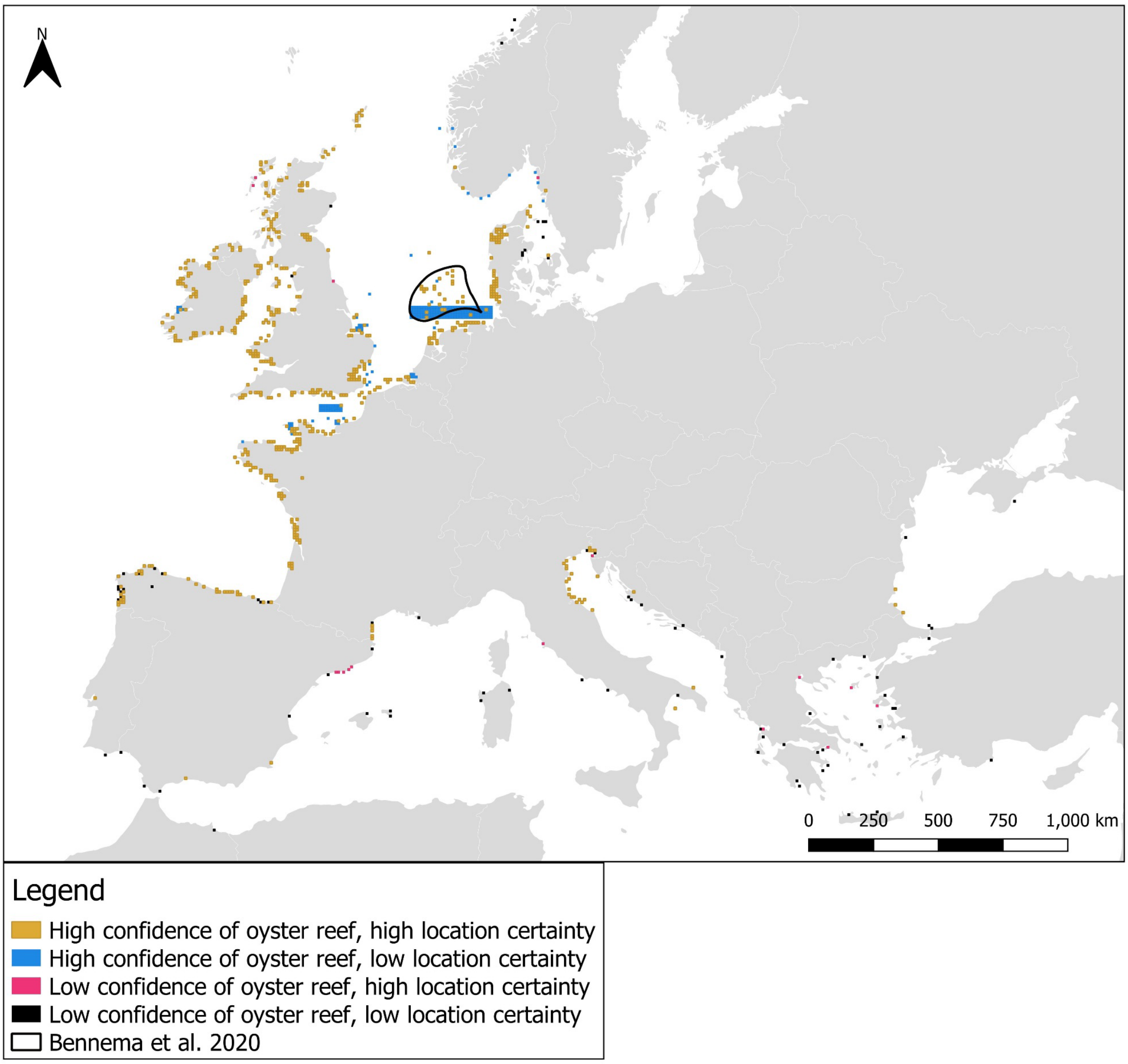

Figure S2: Locations across Europe where oyster reef presence was assigned from historical sources, identified to 10km² grids, with associated confidence levels that biogenic reef habitat once formed.

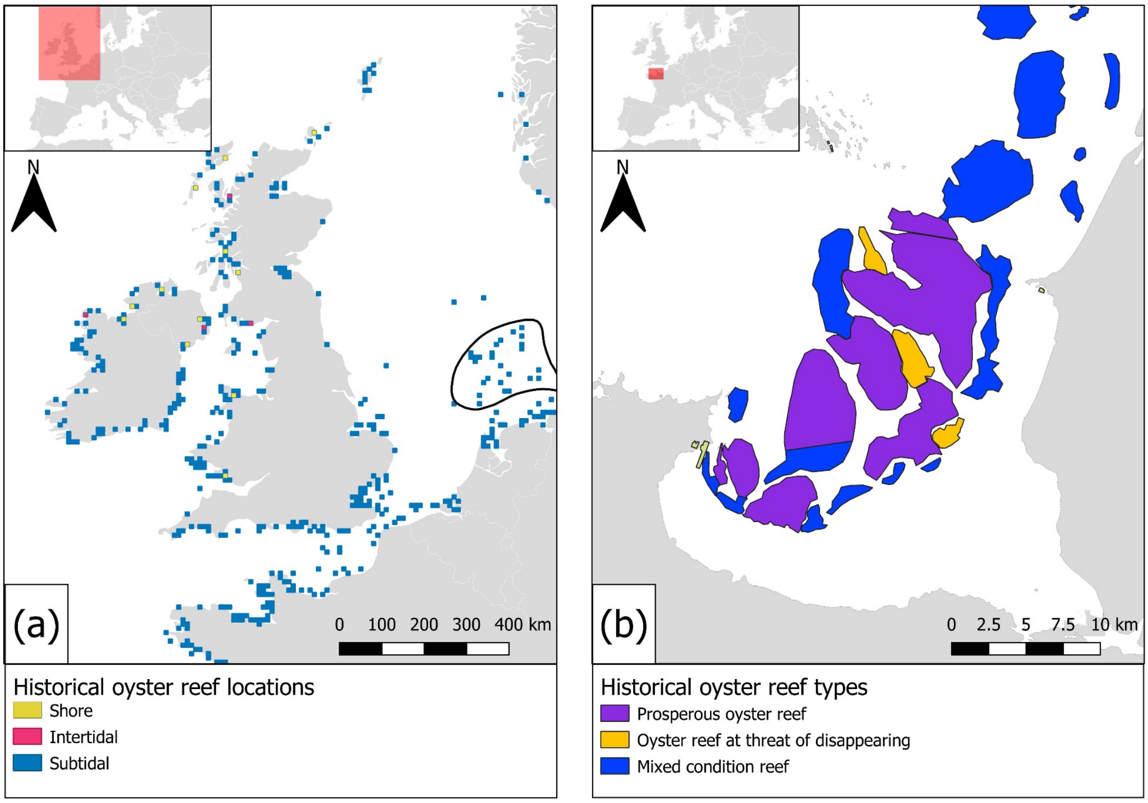

Figure S3. (a) Intertidal, shore and subtidal records of oyster reef habitat. (b) Example of oyster habitat mapped in the Bay of Cancale (Joubin and Guerin Guanivet 1910), detailing the extent and positioning of prosperous, threatened and mixed condition oyster habitat along the coast of France.

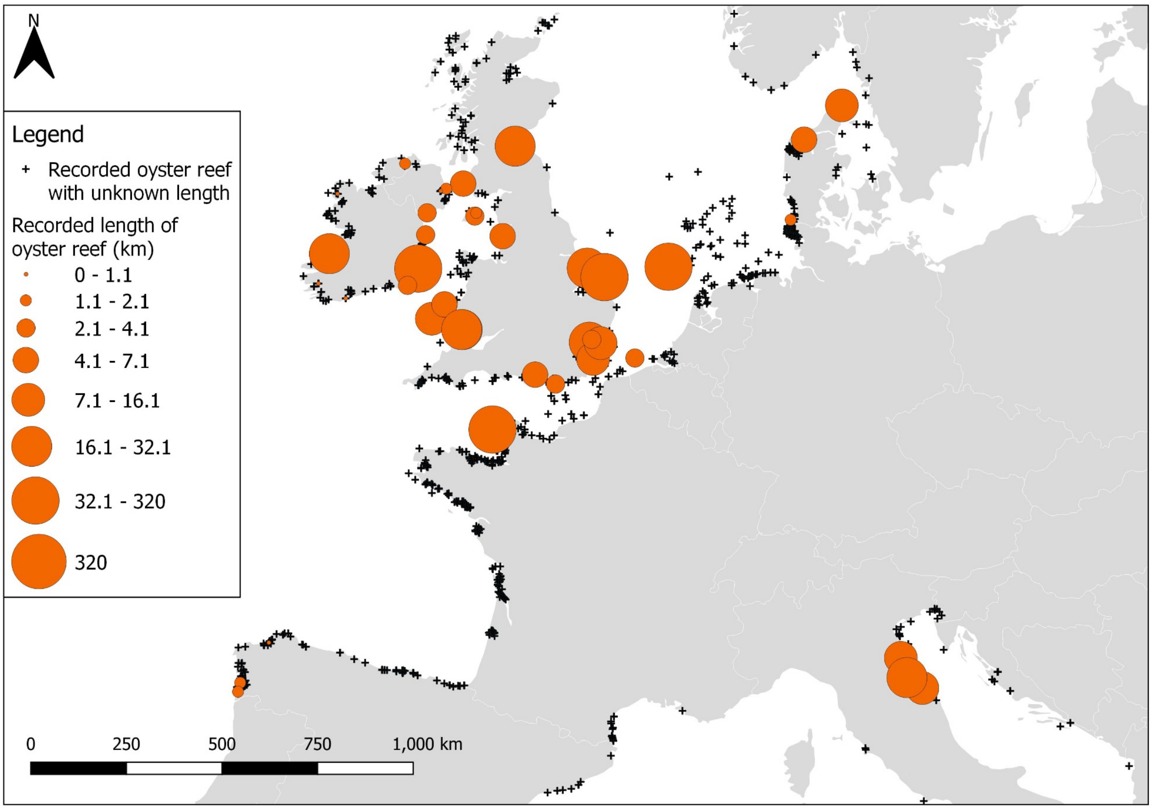

Figure S4. Recorded length (km, orange circles) of described oyster reefs. The crosses indicate records of reefs of unknown length.

References

Airoldi L, Beck MW (2007) Loss, status and trends for coastal marine habitats of Europe. Oceanography and Marine Biology 45, 345-405.

Andrews AC (1948) Oysters as a food in Greece and Rome. The Classical Journal 43, 299-303.

Anon (1886) Fourth annual report of the Fishery Board for Scotland being for the year 1885. HMSO, Edinburgh.

Archives du Service Historique de la Défense de Vincennes (1849) Lettre du Préfet Maritime de Brest au Ministre de la Marine et des Colonies précisant la fermeture du dragage des huîtres plates et leur vente, n°544, 26 avril 1849. CC5/623.

Archives du Service Historique de la Défense de Vincennes (1864) Rapport du capitaine des garde-pêches au Préfet Maritime de Brest sur la pêche des huîtres plates exercée en rade de Brest, 29 décembre 1864. CC5/175.

Barrett JH, Locker AM, Roberts CM (2004) The origins of intensive marine fishing in medieval Europe: the English evidence. Proceedings of the Royal Society B: Biological Sciences, 2417-2421.

Beck MW, Brumbaugh RD, Airoldi L, Carranza A, Coen LD, Crawford C, Defeo O, Edgar GJ, Hancock B, Kay M, Lenihan HS, Luckenbach MW, Toropova CL, Zhang G, Guo X (2011) Oyster reefs at risk and recommendations for conservation, restoration and management. Bioscience 61, 107-116.

Beckmann (1800) Observations respecting oysters, and the places where found. The Philosophical Magazine 6, 97-103.

Bennema FP, Engelhard GH, Lindeboom H (2020) *Ostrea edulis* beds in the central North Sea: delineation, ecology, and restoration. ICES Journal of Marine Science 77, 2694–2705.

Berghahn R, Ruth M (2005) The disappearance of oysters from the Wadden Sea: a cautionary tale for no-take zones. Aquatic Conservation: Marine and Freshwater Ecosystems 15, 91–104.

Bergström P, Thorngren L, Strand Å, Lindegarth M (2021) Identifying high-density areas of oysters using species distribution modeling: Lessons for conservation of the native *Ostrea edulis* and management of the invasive *Magallana (Crassostrea) gigas* in Sweden. Ecology and Evolution 22, 5522-5532.

Bromley C, McGonigle C, Ashton EC, Roberts D (2016) Bad moves: Pros and cons of moving oysters – A case study of global translocations of *Ostrea edulis* Linnaeus, 1758 (Mollusca: Bivalvia). Ocean and Coastal Management 122, 103-115.

Buckland FT (1875) Fisheries (Norfolk): report on the fisheries of Norfolk, especially crabs, lobsters, herrings, and the Broads. [London]: [Her Majesty's Stationery Office].

Buckland FT, Walpole S (1879) Commissioners for Sea Fisheries on the Sea Fisheries of England and Wales. London, HMSO.

Bunting P, Rosenqvist A, Hilarides L, Lucas RM, Thomas N, Tadono T, Worthington TA, Spalding M, Murray NJ, Rebelo L-M (2022) Global Mangrove Extent Change 1996–2020: Global Mangrove Watch Version 3.0. Remote Sensing 14(15): 3657.

Callaway R, Engelhard GH, Dann J, Cotter J, Rumohr H (2007) A century of North Sea epibenthos and trawling: comparison between 1902–1912, 1982–1985 and 2000. Marine Ecology Progress Series 346, 27–43.

Cameron T (2022) Defining oyster beds in the Blackwater Estuary. NECR411. Natural England.

Cliffe CF (1847) The Book of South Wales, the Bristol Channel, Monmouthshire and the Wye ... Illustrated with Maps and Engravings. Hamilton, Adams & Company.

Commissioners of Fisheries (1844) The Second Annual Report of the Commissioners of Fisheries, Ireland. London, HMSO.

Comps M (1970) Observation sur les causes d'une mortalité anormale des huîtres plates dans le bassin de Marennes. Revue des Travaux de l'Institut des Pêches Maritimes 34, 317–326.

Cornide J (1788) Ensayo de una Historia Natural de los peces y otras producciones de la costa de Galicia. Edición facsimilar del Seminario de Estudos Gallegos. Edicións do Castro, 1983.

De Clippele LH, Gafeira J, Robert K, Hennige S, Lavaleye MS, Duineveld CGA, Huvenne VAI, Roberts JM (2017) Using novel acoustic and visual mapping tools to predict the small-scale spatial distribution of live biogenic reef framework in cold-water coral habitats. Coral Reefs 36, 255-268.

Dean B (1891) Report on the European methods of oyster-culture. Bulletin of the United States Fish Commission 11, 357-406.

De'ath G, Fabricius KE, Sweatman H, Puotinen M (2012) The 27–Year decline of coral cover on the Great Barrier Reef and its causes. Proceedings of the National Academy of Sciences 109, 17995–17999.

Dollfus R (1934) Les huîtres comestibles sur la côte atlantique du Maroc: bancs naturels perspectives ostréicoles. Museum National d'Histoire Naturell, Laboratoire des Pêches coloniales. Association française pour l'avancement des sciences, Rabat. Pp. 246-248.

Duarte CM, Agusti S, Barbier E, Britten GL, Castilla JC, Gattuso J-P, Fulweiler RW, Hughes TP, Knowlton N, Lovelock CE, Lotze HK, Predragovic M, Poloczanska E, Roberts C, Worm B (2020) Rebuilding marine life. Nature 580, 39-51.

Eigaard OR, Bastardie F, Hintzen NT, Buhl-Mortensen L, Buhl-Mortensen P et al. (2017) The footprint of bottom trawling in European waters: distribution, intensity, and seabed integrity. ICES Journal of Marine Science 74, 847–865.

Ellis J (1754) A letter from Mr. John Ellis, F.R.S. to Mr. Peter Collinson, F. R. S. concerning the animal life of those coral lines, that look like minute trees, and grown upon oysters and fucus's all around the sea-coast of this Kingdom. Philosophical transactions of the Royal Society 48, 627-633.

Elston RA, Farley CA, Kent ML (1986) Occurrence and significance of bonamiasis in European flat oysters *Ostrea edulis* in North America. Diseases of Aquatic Organisms 2, 49-54.

Engelhard GH, Thurstan RH, MacKenzie BR, Alleway HK, Bannister RCA, Cardinale M, Clarke MW, Currie JC, Fortibuoni T, Holm P, Holt SJ, Mazzoldi C, Pinnegar JK, Raicevich S, Volckaert FAM, Klein ES, Lescrauwaet A-K (2016) ICES meets marine historical ecology: placing the history of fish and fisheries in current policy context. ICES Journal of Marine Science 73, 1386–1403.

European Commission (2022) Proposal for a Regulation of the European Parliament and of the Council on nature restoration, 22 June 2022. COM(2022) 304 final. 2022/0195 (COD), Brussels. Available at: https://environment.ec.europa.eu/system/files/2022-06/Proposal%20for%20a%20Regulation%20on%20nature%20restoration.pdf. Last accessed 6 Mar 2023.

Eyton TC (1858) A history of the oyster and the oyster fisheries. Taylor and Francis, London.

Faber GL (1883) The fisheries of the Adriatic and the fish thereof. A report of the Austro-Hungarian sea fisheries. Bernard Quaritch, London.

Fariñas-Franco JM, Allcock AL, Roberts D (2018) Protection alone may not promote natural recovery of biogenic habitats of high biodiversity damaged by mobile fishing gears. Marine Environmental Research 135, 18-28.

Filbee-Dexter K, Wernberg T (2018) Rise of turfs: A new battlefront for globally declining kelp forests. Bioscience 68, 64–76.

Fishery Board for Scotland (1887) Fifth annual report of the Fishery Board for Scotland being for the year 1886. Edinburgh.

Forbes E, Hanley S (1853) A history of British Mollusca, and their shells. Vol II. John Van Voorst, Paternoster Row, London.

Fortibuoni T, Libralato S, Raicevich S, Giovanardi O, Solidoro C (2010) Coding early naturalists' accounts into long-term fish community changes in the Adriatic Sea (1800–2000). PLoS ONE 5: e15502.

Frid CLJ, Harwood KG, Hall SJ, Hall JA (2000) Long-term changes in the benthic communities on North Sea fishing grounds. ICES J Mar Sci 57:1303–1309.

Gaardner T, Bjerkan P (1934). Østers og Østerskultur i Norge. John Griegs Boktrykkeri, Bergen.

Gann GD, McDonald T, Walder B, Aronson J, Nelson CR, Jonson J, Hallett JG, Eisenberg C, Guariguata MR, Liu J, Hua F, Echeverría C, Gonzales E, Shaw N, Decleer K, Dixon KW (2019) *International principles and standards for the practice of ecological restoration*, Washington, D.C. 20005 U.S.A.: Society for Ecological Restoration.

Gaumiga R, Karlsons G, Uzars D, Ojaveer H (2007) Gulf of Riga (Baltic Sea) fisheries in the late 17th century. Fisheries Research 87, 120–125.

Gercken J, Schmidt A (2014) Current status of the European oyster (Ostrea edulis) and possibilities for restoration in the German North Sea. Bundesamt für Naturschutz.

Giard A (1894) Sur une affection parasitaire de l'huitre (Ostrea edulis L.) connue sous Ie nom de maladie du pied. Comptes Rendus Hebdomadaires des Seances et Memoires de la Societe de Biologie 10(1) (vol. 46), pp. 401-403.

Giovio P (1560) "Libro de'pesci romani", translation by C. Zancaruolo, Venice 1560, pages 188-189. First edition in Latin language was printed in Rome in 1524 and 1527, titled "De piscibus marinis lacustribus fluviatilibus item de testaceis ac salsamentis liber".

González-Wangüemert M, Pérez-Ruzafa A, Rosique MJ, Ortiz A (2004) Genetic differentiation in two cryptic species of Ostreidae, *Ostrea edulis* (Linnaeus, 1758) and *Ostreola stentina* (Payraudeau 1826) in Mar Menor Lagoon, southwestern Mediterranean Sea. The Nautilus 118, 103-111.

Gravina MF, Cardone F, Bonifazi A, Bertrandino MS, Chimienti G, Longo C, Marzano CN, Moretti M, Lisco S, Moretti V, Corriero G, Giangrande A (2018) *Sabellaria spinulosa* (Polychaeta, Annelida) reefs in the Mediterranean Sea: Habitat mapping, dynamics and associated fauna for conservation management. Estuarine, Coastal and Shelf Science 200, 248-257.

Guy C, Blight A, Smyth D, Roberts D (2018) The world is their oyster: Differences in epibiota on sympatric populations of native *Ostrea edulis* and non-native *Crassostrea gigas* (*Magallana gigas*) oysters. Journal of Sea Research 140, 52-58.

Hall CJ, Jordaan A, Frisk MG (2012). Centuries of anadromous forage fish loss: Consequences for ecosystem connectivity and productivity. Bioscience 62, 723–731.

Halpern BS, Frazier M, Afflerbach J, Lowndes JS, Micheli F, O'Hara C, Scarborough C, Selkoe KA (2019) Recent pace of change in human impact on the world's ocean. Scientific Reports 9, 11609.

Halpern BS, Walbridge S, Selkoe KA et al. (2008) A global map of human impact on marine ecosystems. Science 319, 948-952.

Harding CW (1882) Inquiries concerning the propagation of American smelt and shad, and notes on the fisheries of the Wash in England. Bulletin of the United States Fish Commission 1, 428-429.

Harris W (1744) The ancient and present state of the County of Down, containing a chorographical description, with the natural and civil history of the same. Published by E. Ershaw.

Heape W (1887). Notes on the fishing industry of Plymouth. JMBA 1 (1), 45-95.

Hemraj DA, Bishop MJ, Hancock B, Minuti JJ, Thurstan RH, zu Ermgassen PSE, Russell BD (2022) Oyster reef restoration fails to recoup global historic ecosystem losses despite substantial biodiversity gain. Science Advances 8, eabp8747.

Henry LA, Davies AJ, Roberts JM (2010) Beta diversity of cold-water coral reef communities off western Scotland. Coral Reefs 29, 427–436.

Henke D (1743) Fische, die in Austerschalen gefunden worden, von Detlof Henke p.116-117 in Der Königlichen Schwedischen Akademia der Wissenschaften Abhandlungen aus der Naturlehre, Haushaltundkunft und Mechanik, auf das Jahr 1744. Kästner (Ed)

Heral M (1989) Traditional oyster culture in France. In: Barnabe Aquaculture, pp. 342-387. Open Access version: https://archimer.ifremer.fr/doc/00000/3039/.

Holt EWL (1902) The public oyster bed on the coasts of Counties Wicklow and Wexford. Appendix II. Report on the Sea and Inland fisheries of Ireland for 1901, Part II, Scientific Investigations. Department of Agriculture and Technical Instruction for Ireland.

Holt TJ, Rees EI, Hawkins SJ, Seed R (1998) Biogenic Reefs (volume IX). An overview of dynamic and sensitivity characteristics for conservation management of marine SACs. Scottish Association for Marine Science (UK Marine SACs Project), 170p.

Huxley TH (1883) Oysters and the oyster question. The English Illustrated Magazine, London, Vol I, 47-55, continued pp. 110-121.

Irish Fisheries (1836) First Report of the Commissioners of Inquiry into the state of the Irish fisheries; with the minutes of evidence and appendix. HMSO, Dublin.

Isle of Man Times (1874) 'Out to the oyster beds'. Published June 27 1874, p4. Available at British Newspaper Archive, last accessed 21 Feb 2023.

Jabiol J, McKie BG, Bruder A, Bernadet C, Gessner MO, Chauvet E (2013) Trophic complexity enhances ecosystem functioning in an aquatic detritus-based model system. Journal of Animal Ecology 82, 1042-1051.

Jackson JBC, Kirby MX, Berger WH et al. (2001) Historical overfishing and the recent collapse of coastal ecosystems. Science 293, 629-637.

Jenkin A, Trundle C, Owen K, Sturgeon S, Naylor H (2019) Fal Oyster Survey. Cornwall Inshore Fisheries and Conservation Authority (Cornwall IFCA), Hayle.

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

Kasoar T, zu Ermgassen PSE, Carranza A, Hancock B, Spalding M (2015) New opportunities for conservation of a threatened biogenic habitat: a worldwide assessment of knowledge on bivalve-reef representation in marine and coastal Ramsar Sites. Marine and Freshwater Research 66, 981-988.

Kazanidis G, Guido A, Rosso A, Sanfilippo R, Roberts JM, Gerovasileiou V (2022) One on top of the other: exploring the habitat cascades phenomenon in iconic biogenic marine habitats. Diversity 14, 290.

Knauss JM (2005) The growth of British fisheries during the Industrial Revolution. Ocean Development & International Law 36, 1-11.

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

Lee HZ, Davies IM, Baxter JM, Diele K, Sanderson WG (2020) Missing the full story: First estimates of carbon deposition rates for the European flat oyster, *Ostrea edulis*. Aquatic Conservation: Marine and Freshwater Ecosystems 30, 2076-2086.

Levasseur O (2006) Histoire de l'huître en Bretagne. Skol vreizh 58, 83 p.

Lewis JP, Ryves DB, Rasmussen P, Olsen J, Knudsen K-L, Andersen SH, Weckström K, Clarke AL, Andrén E, Juggins S (2016) The shellfish enigma across the Mesolithic-Neolithic transition in southern Scandinavia. Quaternary Science Reviews 151, 315-320.

Lotze HK, Lenihan HS, Bourque BJ, Bradbury RH, Cooke RG, Kay MC, Kidwell SM, Kirby MX, Peterson CH, Jackson JBC (2006) Depletion, degradation, and recovery potential of estuaries and coastal seas. Science 312, 1806-1809.

Lõugas L, Jürjo I, Russow E (2022) European flat oyster (*Ostrea Edulis* L.) in the Eastern Baltic as evidence of long-distance trade in Medieval and Early Modern times. Heritage 5, 813-828.

Lown AE, Hepburn LJ, Heywood JL, Cameron TC (2021) European native oysters and associated species richness in the presence of non-native species in a southern North Sea estuary complex. Conservation Science and Practice 3, e361.

Marsili F (1715) Giornali e memorie per la ricognizione della spiaggie pontificie dell'Adriatico. MS 72 F 4 J, Biblioteca Universitaria di Bologna.

Martin WCL (1850) British fish and fisheries. The Monthly Volume of the Religious Tract Society 49, 1-192.

McAfee D, Alleway HK, Connell SD (2020) Environmental solutions sparked by environmental history. Conservation Biology 34, 386–394.

McAfee D, McLeod IM, Alleway HK, Bishop MJ, Branigan S, Connell SD, Copeland C, Crawford CM, Diggles BK, Fitzsimons JA, Gilby BL, Hamer P, Hancock B, Pearce R, Russell K, Gillies CL (2022) Turning a lost reef ecosystem into a national restoration program. Conservation Biology 36, e13958.

Merk V, Colsoul B, Pogoda B (2020) Return of the native: Survival, growth and condition of European oysters reintroduced to German offshore waters. Aquatic Conservation: Marine and Freshwater Ecosystems 30, 2180-2190.

Möbius KA (1877) Die Auster und die Austernwirthschaft. Wiegandy, Hempel & Parey, Berlin.

Möbius KA (1893) Über die Thiere der schleswig-holsteinischen Austernbänke, ihre physicalischen und biologischen Lebensverhältnisse. p 67-92 in Sitzungsberichte der Königlich Preussischen Akademie der Wissenschaften zu Berlin. Berlin, Verlag der Königlichen Akademie der Wissenschaften.

Neild R (1995) The English, the French and the oyster. Quiller Press, London.

Olsen OT (1885) The fisherman's practical navigator, Second Edition. Imray & Son, London.

OSPAR Commission (2009) Background document for *Ostrea edulis* and *Ostrea edulis* beds. Report number: 428/2009.

OSPAR Commission (2013) Recommendation 2013/4 on furthering the protection and conservation of *Ostrea edulis* in Region II and III1 of the OSPAR maritime area and *Ostrea edulis* beds in Regions II, III and IV of the OSPAR maritime area.

Pauly D (1995) Anecdotes and the shifting baseline syndrome of fisheries. Trends in Ecology and Evolution 10, 430.

Paz Graells M (1870) Exploración científica de las costas del departamento Marítimo del Ferrol verificada de orden del Almirantazgo por el vocal de la Comisión Permanente de Pesca D. Mariano de la Paz Graells en el verano de 1869, Est. Tipográfico de T. Fortanet, Madrid.

Pennant T (1776) British zoology. Printed by William Eyres, for Benjamin White. London, Warrington.

Philpots JR (1891) Oysters and all about them. John Richardson and Co., London.

Piazzi L, Cinti MF, Guala I, Grech D, La Manna G, Pansini A, Pinna F, Stipcich P, Ceccherelli G (2021) Variations in coralligenous assemblages from local to biogeographic spatial scale. Marine Environmental Research 169, 105375.

Pogoda B (2019) Current status of European oyster decline and restoration in Germany. Humanities 8, 1-12.

Pogoda B, Brown J, Hancock B, Preston J, Pouvreau S, Kamermans P, Sanderson W, von Nordheim H (2019) The Native Oyster Restoration Alliance (NORA) and the Berlin Oyster Recommendation: bringing back a key ecosystem engineer by developing and supporting best practice in Europe. Aquatic Living Resources 32, 13.

Pogoda B, Boudry P, Bromley C, Cameron TC, Colsoul B, Donnan D et al. (2020) NORA moving forward: developing an oyster restoration network in Europe to support the Berlin Oyster Recommendation. Aquatic Conservation: Marine and Freshwater Ecosystems 30, 2031-2037.

Pouvreau S, Cochet H, Bargat F, Petton S, Le Roy V, Guillet T, Potet M (2021) Current distribution of the residual flat oysters beds (*Ostrea edulis*) along the west coast of France. SEANOE. https://doi.org/10.17882/79821

Powers SP, Peterson CH, Grabowski JH, Lenihan HS (2009) Success of constructed oyster reefs in no-harvest sanctuaries: implications for restoration. Marine Ecology Progress Series 389, 159-170.

Preston J, Gamble C, Debney A, Helmer L, Hancock B, zu Ermgassen PSE (eds) (2020) *European Native Oyster Habitat Restoration Handbook*. The Zoological Society of London, London, UK.

Reeder-Myers L, Braje TJ, Hofman CA et al. (2022) Indigenous oyster fisheries persisted for millennia and should inform future management. Nature Communications 13, 2383.

Richardson MA, Zhang Y, Connolly RM, Gillies CL, McDougall C (2022) Some like it hot: The ecology, ecosystem benefits and restoration potential of oyster reefs in tropical waters. Frontiers in Marine Science 9, 873768.

Royal Commission (1866) Report of the Commissioners appointed to inquire into the sea fisheries of the United Kingdom, with appendix and minutes of evidence. London: Eyre and Spottiswoode.

Sander L, Hass HC, Michaelis R, Groß C, Hausen T, Pogoda B (2021) The late Holocene demise of a sublittoral oyster bed in the North Sea. PLoS ONE 16(2), e0242208.

Sea MA, Hillman JR, Thrush SF (2022) Enhancing multiple scales of seafloor biodiversity with mussel restoration. Scientific Reports 12, 5027.

Select Committee (1876) Select Committee to inquire into Reasons for Scarcity of Oysters and Effect of Measures adopted after the Report of Royal Commission on Sea Fisheries, 1866. Report, Proceedings, Minutes of Evidence, Appendix, Index.

Sinclair J (1845) The statistical accounts of Scotland (1791-1845), Vol IV. William Creech, Edinburgh.

Smellie W (1790) The Philosophy of Natural History. Edinburgh.

Smyth DM, Horne NS, Ronayne E, Millar RV, Joyce PWS, Hayden-Hughes M, Kregting L (2020) Wild gregarious settlements of *Ostrea edulis* in a semi-enclosed sea lough: a case study for unassisted restoration. Restoration Ecology 28, 645-654.

Sohl T, Sleeter B, Sayler K, Bouchard M, Reker R, Bennett S, Sleeter R, Kanengieter R, Zhu Z (2012) Spatially explicit land-use and land-cover scenarios for the Great Plains of the United States. Agriculture, Ecosystems & Environment 153, 1–15.

Stechele B, Hughes A, Degraer S, Bossier P, Nevejan N (2023) Northern Europe's suitability for offshore European flat oyster (*Ostrea edulis*) habitat restoration: A mechanistic niche modelling approach. Aquatic Conservation: Marine and Freshwater Ecosystems 33, 696-707.

Stoke GT (1891) Pococke's Tour in Ireland in 1752. Hodges, Figgis and Co., Dublin.

Stott R (2004) Oyster. Reaktion Books Ltd, London.

Sunday J, Fabricius K, Kroeker K, Kathryn M. Anderson, Brown NE, Barry JP, Connell SD, Dupont S, Gaylord B, Hall-Spencer JM, Klinger T, Milazzo M, Munday PL, Russell BD, Sanford E, Thiyagarajan V, Vaughan MLH, Widdicombe S, Harley CDG (2017) Ocean acidification can mediate biodiversity shifts by changing biogenic habitat. Nature Climate Change 7, 81–85.

Tamburello L, Chiarore A, Fabbrizzi E, Colletti A, Franzitta G, Grech D, Rindi F, Rizzo L, Savinelli B, Fraschetti S (2022) Can we preserve and restore overlooked macroalgal forests? Science of the Total Environment 806, 150855.

Teagle H, Hawkins SJ, Moore PJ, Smale DA (2017) The role of kelp species as biogenic habitat formers in coastal marine ecosystems. Journal of Experimental Marine Biology and Ecology 492, 81-98.

The Cambrian News and Merionethshire Standard (1889) 'Sea fishing of Cardigan Bay, past and future', 15-March-1889, p8. Available at The National Library of Wales. Last accessed 21 Feb 2023.

Thomas R, Law M, Browning E, Hill A, Small R (2020) The changing exploitation of oysters (*Ostrea edulis* L. 1758) in Late Medieval and Early Modern England: a case study from Dudley Castle, West Midlands. Environmental Archaeology 25, 82-95.

Thomsen MS, Altieri AH, Angelini C, Bishop MJ, Bulleri F, Farhan R, Frühling VMM, Gribben PE, Harrison SB, He Q, Klinghardt M, Langeneck J, Lanham BS, Mondardini L, Mulders Y, Oleksyn S, Ramus AP, Schiel DR, Schneider T, Siciliano A, Silliman BR, Smale DA, South PM, Wernberg T, Zhang S, Zotz G (2022) Heterogeneity within and among co-occurring foundation species increases biodiversity. Nature Communications 13, 581.

Thorngren L, Bergström P, Holthuis TD, Lindegarth M (2019) Assessment of the population of *Ostrea edulis* in Sweden: A marginal population of significance? Ecology and Evolution 19, 13877-13888.

Thurstan RH, McCormick H, Preston J, Ashton EC, Bennema FP, Bratoš Cetinić A, Brown JH, Cameron TC, da Costa F, Donnan D, Ewers C, Fortibuoni T, Galimany E, Giovanardi O, Grancher R, Grech D, Hayden-Hughes M, Helmer L, Jensen KT, Juanes JA, Latchford J, Moore ABM, Moutopoulos DK, Nielsen P, von Nordheim H, Ondiviela B, Peter C, Pogoda B, Poulsen B, Pouvreau S, Scherer C, Smaal AC, Smyth D, Strand Å, Theodorou JA, zu Ermgassen PSE (2023) Historical distribution and habitat characteristics of *Ostrea edulis* reefs in Europe. *figshare* https://doi.org/10.6084/m9.figshare.c.6884167.

Todorova V, Micu D, Klisurov L (2009) Unique oyster reefs discovered in the Bulgarian Black Sea. Hydrobiologie 62, 871-874.

Tully O, Clarke S (2012) The status and management of oyster (Ostrea edulis) in Ireland. Irish Fisheries Investigations No. 24. Marine Institute, Co. Galway. 36pp.

UNEP/FAO (2020) The UN Decade on Ecosystem Restoration 2021-2030. UNEP/FAO Factsheet, June 2020. United Nations Environment Programme and the Food and Agriculture Organisation of the United Nations. Available at: https://wedocs.unep.org/bitstream/handle/20.500.11822/30919/UNDecade.pdf?sequence=11. Last accessed 3 May 2023.

University Marine Biological Station Millport (2007) Conservation of the native oyster Ostrea edulis in Scotland. Scottish Natural Heritage Commissioned Report No. 251 (ROAME No. F02AA408).

van Banning P (1991) Observations on bonamiasis in the stock of the European flat oyster, *Ostrea edulis*, in the Netherlands, with special reference to the recent developments in Lake Grevelingen. Aquaculture 93, 205-211.

von Hamm W (1881) Gesammelte kleine Schriften, Erster Band. Wein, Best, Leipzig, A. Hartlebens Verlag.

Waltham NJ, Elliott M, Lee Shing Y, Lovelock C, Duarte CM, Buelow C, Simenstad C, Nagelkerken I, Claassens L, Wen CK-C, Barletta M, Connolly RM, Gillies C, Mitsch WJ, Ogburn MB, Purandare J, Possingham H, Sheaves M (2020) UN Decade on Ecosystem Restoration 2021–2030—What chance for success in restoring coastal ecosystems? Frontiers in Marine Science 7, https://doi.org/10.3389/fmars.2020.00071.

Waycott M, Duarte CM, Carruthers TJB, Orth RJ, Dennison WC, Olyarnik S, Calladine A, Fourqurean JW, Heck KL Jr, Hughes AR, Kendrick GA, Kenworthy WJ, Short FT, Williams SL (2009) Accelerating loss of seagrasses across the globe threatens coastal ecosystems. Proceedings of the National Academy of Sciences 106, 12377-12381.

Went AEJ (1962) Historical notes on the oyster fisheries of Ireland. Proceedings of the Royal Irish Academy: Archaeology, Culture, History, Literature 62, 195-223.

Wilmsen FP (1831) Handbuch der Naturgeschichte für die Jugend und ihre Lehrer. Zwetier Band. Berlin, Druck und Verlag von C.F. Amelang.

WWF (2020) Living Planet Report 2020 - Bending the curve of biodiversity loss. Almond REA, Grooten M, Petersen T (Eds). WWF, Gland, Switzerland.

Yeager LA, Layman CA (2011) Energy flow to two abundant consumers in a subtropical oyster reef food web. Aquatic Ecology 45, 267–277.

zu Ermgassen PSE, Bonačić K, Boudry P, Bromley CA, Cameron TC, Colsoul B, Coolen JWP, Frankić A, Hancock B, van der Have TM, Holbrook Z, Kamermans P, Laugen AT, Nevejan N, Pogoda B, Pouvreau S, Preston J, Ranger CJ, Sanderson WG, Sas H, Strand Å, Sutherland WJ (2020a) Forty questions of importance to the policy and practice of native oyster reef restoration in Europe. Aquatic Conservation: Marine and Freshwater Ecosystems 30, 2038-2049.

zu Ermgassen PSE, Grabowski JH, Gair JR, Powers SP (2016) Quantifying fish and mobile invertebrate production from a threatened nursery habitat. Journal of Applied Ecology 53, 596-606.

zu Ermgassen PSE, Thurstan RH, Corrales J, Alleway H, Carranza A, Dankers N, DeAngelis B, Hancock B, Kent F, McLeod I, Pogoda B, Liu Q, Sanderson WG (2020b) The benefits of bivalve reef restoration: A global synthesis of underrepresented species. Aquatic Conservation: Marine and Freshwater Ecosystems 30, 2050-2065.

zu Ermgassen PSE, Spalding MD, Blake B, Coen LD, Dumbauld B, Geiger S, Grabowski JH, Grizzle R, Luckenbach M, McGraw KA, Rodney B, Ruesink JL, Powers SP, Brumbaugh RD (2012) Historical ecology with real numbers: Past and present extent and biomass of an imperilled estuarine ecosystem. Proceedings of the Royal Society B 279, 3393-3400.