Offshore Wind Evidence + Change Programme

Marine Restoration Potential MaRePo

Report for Natural England and the Crown Estate

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Marine Restoration Potential (MaRePo)

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Authors

Johnson, C.L.E., Axelsson, M., Brown, L., Carrigan, K.H.O., Cordingley, A., Elliot, A. L., Downie, A., Gannon, L., Green, B.C., Jones, J., Marsh, M.K., McNie, F., Mills, S.R.A., Wallace, N.M., Woods, H. J.

Natural England Research Report JP054

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Published September 2023

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Project details

This report should be cited as: C.L.E. Johnson, M. Axelsson, L. Brown, K.H.O. Carrigan, A. Cordingley, A.L. Elliot, A. Downie, L. Gannon, B. Green, J. Jones, M.K. Marsh, F. McNie, S.R.A. Mills, N.M. Wallace, and H.J. Woods (2023) Marine Restoration Potential (MaRePo). Natural England Research Report JP054

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Keywords

Marine recovery, restoration potential, marine restoration, habitat creation

Acknowledgements

We are grateful for our joint funding partners of Natural England and The Crown Estate without which this work would not have been possible.

We would like to thank the project reporting team and specialists within Natural England, Environment Agency, The Joint Nature Conservation Committee and Cefas for their specialist and technical input to this project. We are also grateful to the experts who reviewed and provided comments on the report.

This project was funded by Natural England Strategy and Government Advice and The Crown Estate's Offshore Wind Evidence and Change (OWEC) programme.

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Executive Summary

Marine **Re**storation **Pot**ential (**MaRePo**) project is a proof-of-concept study which explores the habitat restoration potential of some key threatened and declining (subtidal) marine habitats as defined by the OSPAR convention: kelp, maerl, native oysters, horse mussels, and sea pen and burrowing megafauna communities. These habitats were chosen as they occurred within English waters and were known to have some possibility for active or passive restoration interventions. This project uses a spatial analysis approach to investigate the current, historic, and potential future distribution of these habitats in English waters (out to 200 nautical miles (nm) from the shore). Below we outline the main characteristics of each habitat covered in the MaRePo project and summarise our findings on their distribution and restoration potential in English waters.

Kelp species are important bioengineers that modify the environment and resources available to associated species, by providing habitat structure and complexity, altering light, nutrients sediments, and reducing physical scour and water flow. Kelp habitats provide a range of ecosystem services: they support commercial and recreational fisheries through provision of nursery habitat, contribute to nutrient cycling and climate change mitigation. Kelp is also harvested for food, pharmaceutical and fertiliser use.

Kelp habitats are currently under threat from a wide range of pressures, including ecological pressures (such as overgrazing, competition and invasive non-native species) and anthropogenic pressures (e.g. elevated nutrient and sediment inputs, overfishing and abrasion by bottom towed gear). Climate change induced increase in temperature and more frequent and severe storm events may also have an impact on kelp survival and productivity. There are limited examples of successful active kelp habitat restoration, however passive restoration through the removal of pressures (e.g. exclusion of bottom towed gear) has been shown to produce rates of recovery comparable to active restoration in the Sussex kelp restoration project**.**

The two most common habitat-forming kelp species in English waters were included in the MaRePo mapping: *Laminaria hyperborea* and *Saccharina latissima.* The modelled predictions of *L. hyperborea* show significant potential for restoration in English waters, with model highlighting restoration potential areas along the northeast, southern and southwest coasts of England. The modelled predictions of *S. latissima* restoration potential areas in English waters were very limited, with small areas identified in the northeast, southern and southwest of England.

Maerl beds are considered as biodiversity “hotspots” because they form structurally complex habitats important for a wide range of marine species. Maerl ecosystems provide substrate stabilisation, food, and shelter for associated species. Maerl ecosystems have the highest carbonate production of all ecosystems found along European coasts and may thus have an important role in climate change mitigation through carbon capture and storage.

Maerl species form slow-growing habitats that can be found on open coasts and in the tide-swept channels of marine inlets. Although extensive areas of maerl exist in the southwest of Scotland and parts of Europe, maerl habitats are rare in English waters, with few isolated patches present

predominantly in the southwest and northeast of England. Maerl habitats are affected by a range of environmental and ecological factors such as changes in sea water temperature, light availability, currents, and the presence of invasive non-native species including the slipper limpet (*Credipula fornicata*). Maerl is also sensitive to anthropogenic pressures such as commercial fisheries, chemical pollution and industrial extraction. The slow growth and reproductive characteristics of maerl exacerbate their susceptivity to disturbance and therefore hinder the natural recovery potential of impacted maerl populations.

As data on the abiotic factors affecting maerl is lacking and the geographic scope of this study was limited, the predictive habitat models for maerl were developed as a proof-of-concept for the MaRePo project and should therefore not be treated as a finished product. Regardless of these limitations, the draft models show a good alignment to the known distribution of maerl, although the predicted areas of maerl habitat are considerably more extensive than the current known maerl habitat extent. The results of this study identify the presence of potential areas suitable for maerl recovery in English waters; however, as maerl habitats are extremely slow growing, passive restoration through reduction of pressures within existing areas of maerl habitat should be considered as the most feasible option for assisting maerl recovery.

Native oyster (*Ostrea edulis*) is another keystone species that provides a range of ecological functions and ecosystem services, including provision of hard substratum for settlement by other species; biodiversity enhancement; natural protection against shoreline erosion; and potentially, sequestration of carbon. Native oyster habitats are sparsely distributed around the UK, with only a few scattered locations recorded in the southwest and east coasts of England. *O. edulis* beds are highly sensitive to substrate loss, smothering, and introduction of microbial pathogens/parasites and invasive non-native species. The main threat to *O. edulis* beds is overexploitation, as destructive harvesting and overfishing can reduce the extent, vertical relief, complexity and biodiversity of oyster bed habitat. The limited success of restoration efforts in the UK have been attributed to factors such as unregulated harvesting, bonamiosis infection, depletion of donor stocks, biased sex ratio and high mortality.

Here we have produced a restoration potential map to provide a national 'high level' indication of where native oyster beds could potentially be restored in English waters based on three key environmental variables: current speed, presence of subtidal mixed sediment habitat, and depth. Our restoration potential model closely aligns with the current and historic distribution maps, and highlights restoration potential areas for *O. edulis* within all inshore Marine Plan Areas.

Horse mussel (*Modiolus modiolus*) beds play an important role in productivity, habitat complexity and ecosystem functioning. They form physically complex structures which provide favourable feeding environments and important refugia from predation, grazing and physical disturbance for other marine organisms. *M. modiolus* beds also contribute to several ecosystem services including water filtration, nutrient cycling, sediment stabilisation, and potential carbon storage. *M. modiolus* beds are highly sensitive to pressures associated with anthropogenic activities such as bottom towed fishing activities, aggregate extraction, and climate change – induced increase in temperature. Physical pressures are particularly damaging as they can substantially reduce the

extent and complexity of the horse mussel beds or remove them entirely. When combined with the slow growth rates and fragmentation of habitats, the recovery rates of *M. modiolus* beds are thought to be very slow. Restoration of *M. modiolus* beds requires a sufficient larval population and suitable habitat. Case studies have demonstrated the possibility of accelerated recovery of horse mussel beds using translocation and restocking, however long-term studies are lacking.

Sporadic records of horse mussel individuals are common throughout UK waters, particularly in inshore areas. However, the records of *M. modiolus* beds are sparser, with the majority located to the West of the UK, particularly in waters off Scotland and Wales, with just a few in English waters (See page 114 for the definition of *M. modiolus* bed). The habitat suitability model presented here represents the ecological niche occupied by horse mussel beds in the UK, however it has not proven successful in identifying areas for restoration. Our understanding of current population distribution, larval sources/sinks, and dispersal and connectivity dynamics in English waters is still too limited. Further work is needed to develop our understanding in these areas so that appropriate sites for restoration can be determined.

Sea pen and burrowing megafauna habitat occurs on plains of fine mud from the shallow subtidal to the deep sea. These muds are heavily bioturbated by burrowing megafauna species such as decapod crustaceans including *Nephrops norvegicus*, *Calocaris macandreae* or *Callianassa subterranean*, with burrows and mounds typically forming a prominent feature of the sediment surface and may include conspicuous populations of sea pens. This habitat supports a rich fauna of smaller animals and thus forms an important reservoir of biodiversity. The habitat also acts as a source of food and nursery areas for many fish species. The main threats faced by sea pen and burrowing megafauna habitat are physical disturbance and organic pollution. The use of bottom towed gear is the most prominent cause of physical disturbance. Mud habitats are more sensitive to the impact of bottom trawling than sand or gravel habitats and take longer to recover.

Although records of sea pens and burrowing megafauna habitat exist along the south coast of England, the largest known occurrences are in the North Sea and the South West Approaches. Our knowledge of the full habitat distribution is still limited. Our results of distribution models for sea pens show suitable habitat in the northern North Sea and Western Approaches, with *Virgularia mirabilis* extending to muddy habitats in the Celtic and Irish Seas. These areas are thus likely to be the most suitable for restoration of these habitats. Restoration success however depends on the reduction of trawl fishing effort. In some areas of Scotland, Norway and Sweden, protection and restoration efforts have been made by substituting trawl fisheries with creel fisheries.

This report provides the first investigation mapping marine restoration potential in English waters. Although the modelling approaches chosen for the different habitats vary, the restoration potential for some habitats (such as kelp and native oysters) appears more significant than for others such as maerl, horse mussels and sea pens and burrowing megafauna. There is a need for further refinement of the restoration potential models to improve both the confidence of the models and detail the hard constraints to remove areas where restoration would not be possible. There is also a need to future-proof areas of potential restoration by including limitations from climate change. Further opportunities to develop this work to map areas for restoration of blue

carbon habitat as well as developing pilot restoration handbooks and testing the viability of restoration zones with on the ground pilot studies would also be beneficial.

Background

Marine **Re**storation **Pot**ential (**MaRePo**) is a project funded by Natural England and The Crown Estate's Offshore Wind Evidence and Change programme. This proof-of-concept study links intrinsically to the current work being carried out for the cross-Defra, Environment Agency-led Restoring Meadows, Marsh and Reef Initiative (ReMeMaRe), which has developed the initial spatial analyses to explore the restoration potential of intertidal and shallow subtidal habitats including seagrass, saltmarsh, and native oysters. The MaRePo project takes this approach further into the (subtidal) marine environment, by mapping the restoration potential of some of the known threatened and declining marine habitats in English waters (out to 200 nm) as defined by the OSPAR convention. These include kelp, maerl, native oyster, horse mussel, and sea pen and burrowing megafauna habitats.

MaRePo is a partnership project between Natural England (NE), Environment Agency (EA), Joint Nature Conservancy Committee (JNCC) and Centre for Ecology, Fisheries and Aquaculture Science (CEFAS). It will provide evidence needed to set out where Marine Net Gain (MNG) activities could occur and what their benefits may be. The project findings will support both Natural England and Defra's work programmes, primarily within DEFRA's Offshore Wind Enabling Actions (OWEAP) programme, providing information for the strategic compensation work carried out by DEFRA such as COWSC (Collaboration on Offshore Wind Strategic Compensation) and understanding opportunities for MNG. The outputs of MaRePo will also be beneficial to a number of other work areas such as the NE and Defra project proposal 'Using the natural capital approach in practice for place-based decision making at different scales', a project in the application and innovation theme under the Marine Natural Capital and Ecosystem Assessment programme (mNCEA). Furthermore, the outputs will be beneficial to the new cross-government program on marine spatial prioritisation, which aims to create a strategic vision for the future use of the marine environment.

The initial MaRePo project commissioned for 2022/23 is a proof-of-concept study to understand what is possible in determining how best to map the potential restoration of marine habitats. Although the habitats covered in this study (kelp, maerl, native oyster, horse mussels and sea pens and burrowing megafauna) are distinctly different in their current and historic extents and distributions in English waters, these habitats also have some similarities: They all act as ecosystem engineers that provide habitat complexity, structure, and resources for associated marine fauna and flora. These habitats also provide important ecosystem services such as water filtration, sediment stabilisation, habitat provision for commercially important species, and climate change mitigation via flood risk alleviation and/ or carbon storage. However, these habitats tend to be highly sensitive to ecological and environmental factors, anthropogenic impacts, and the effects of changing climate.

This report consists of five habitat-specific sections; one for each habitat included in the MaRePo project (kelp beds, maerl habitats, native oysters, horse mussel beds and sea pen and burrowing megafauna communities). Each habitat-specific section includes a critical literature review on biology and ecological importance, habitat distribution and factors affecting habitat distribution, and the previous restoration approaches trialled for the habitat. The results sections show the collated data on current and historic distribution of each habitat, as well as the proof-of-concept models on habitat restoration potential based on key physical attributes specific to each habitat. The restoration potential maps vary considerably between the habitats included in this study, due to differences in availability and quality of existing abundance and distribution data between the habitats, as well as our understanding on the biotic and abiotic factors and the thresholds for impact on distribution of each habitat.

Kelp

1. Literature review

1.1 Biology and ecological importance

Kelps are species of large brown macroalgae that occur in relatively shallow waters from the low intertidal environments (<1 m above chart datum) to depths greater than 40 m (Smale and Moore, 2017). There are seven confirmed species of kelp found in UK waters; five in the order Laminariales (*Laminaria hyperborea, L. digitata, L. ochroleuca, Saccharina latissima, Alaria esculenta*), one kelp-like brown alga, *Saccorhiza polyschides,* and a recently introduced (first recorded in the Hamble in 1994) non-native species *Undaria pinnatifida* (MarLIN refs), all of which are found along the English coastline (Burrows *et al*., in press). Kelps have two alternating generations: sporophyte (an asexual diploid phase) and microscopic gametophyte (a haploid dioecious phase) (Kain, 1979). Sporophytes consists of a holdfast (root-like structures), a stipe (stem-like structure), and a blade (leaf-like structures), which may comprise many digitate fronds, like with *L. hyperborea*, or a single undivided frond like that of *S. latissima* (Smale et al., 2013). *L. hyperborea, L. digitata, L. ochroleuca, S. latissima,* and *A. esculenta* are long-lived perennials (Burrows et al., 2014, Smale and Moore, 2017, Smale and Vance, 2015, Smale et al., 2015) whereas *S. polyschides* and *U. pinnatifida* are short-lived annuals (Smale and Moore, 2017) . All these habitat-forming species have different environmental requirements (Smale et al., 2013).

A kelp forest consists of a canopy formed by kelp stipes that hold fronds up to several metres above the substratum. Kelps create a multi-dimensional environment which supports understorey and epibiotic communities, which would not persist without the canopy (de Bettignies et al., 2021). Individual kelps provide three primary habitats; the holdfast; the stipe; and the frond. A secondary habitat is provided by epiphytes (which primarily attach to the stipe) (Burrows et al., 2014). Kelps act as ecosystem engineers that modify the environment and resources available to other species, for example through provision of structural habitat and by altering light, nutrients, sediments, physical scour, and water flow conditions (Burrows et al., 2014). Kelp beds provide habitat for a wide range of marine organisms, with over 1,800 species recorded within kelp dominated habitats in the UK (Burrows et al., 2014, Smale et al., 2013). This includes macroalgae (over 40 species), bryozoans (e.g. the 'sea mat' (*Membranipora membranacea*), molluscs (e.g. the blue rayed limpet, *Patella pellucida*), crustaceans (e.g. the European lobster, see Johnson & Hart 2003 (Hart and Scheibling, 1988)), echinoderms (e.g. sea urchins, see Jones & Kain 1967; Kitching & Thain 1983 (Kain, 1979), fish (e.g. Atlantic cod (*Gadus morhua*), pollock (*Pollachius pollachius*), ballan wrasse (*Labrus bergylta*) and goldsinny wrasse (*Ctenolabrus rupestris*), seals and otters (Burrows et al., 2014, Smale et al., 2013).

As *L. hyperborea* and *S. latissima* are the most common habitat-forming species in English waters (Burrows *et al*. in press), they are the focus of this review. Summary information for all seven species is provided in Appendix 1 for comparison.

Laminaria hyperborea is the dominant canopy forming species on most moderately exposed to exposed sublittoral reefs (Smale and Moore, 2017). The distribution of this species is restricted between the Arctic south and northern Portugal (Burrows et al., 2014). *L hyperborea* is found around the English coast although it is sparse on the southeast coast (Tyler-Walters, 2007a). The frond of *L. hyperborea* is smooth, wide, and digitate (divided into five to 20 fingers) (Tyler-Walters, 2007a). The stipe is approximately one to three metres in length and is rigid, holding the fronds above the substratum (Burrows et al., 2014). The age at maturity (when the sporophyte becomes fertile) is two to six years and the species can live for up to 18 to 20 years in the UK (Kain, 1979, Tyler-Walters, 2007a, Burrows et al., 2014).

Saccharina latissima is also distributed from the Arctic to northern Portugal (Burrows et al., 2014) and occurs on all English coasts, usually in sheltered, moderately exposed conditions (White and Marshall, 2007, Burrows et al., 2014). The species typically attaches to semi-stable substrata (such as cobbles and boulders) but can also grow unattached and develop populations in the margins of dense *L. hyperborea* beds (Burrows et al., 2014, White and Marshall, 2007). The species has a short stipe, and a long frond (up to 4m in length) which is undivided with a frilly undulating margin (Burrows et al., 2014). *S. latissima* reaches maturity at 15-20 months and has a life span of two to five years (White and Marshall, 2007). Six Eunis level 4 habitats correspond with kelp habitats (A3.11, A3.12, A3.21, A3.22, A3.31, A3.32), although not all higher-level habitats include kelp. De Bettignies (2021a) identified 25 EUNIS level 5 and level 6 habitats which correspond to kelp forest habitats (Appendix 2).

Kelp forests provide a range of direct and indirect ecosystem services (Hynes et al., 2021) including the harvesting and use of kelp for fertiliser, food, pharmaceuticals and textiles (Smale et al., 2013); and provision of high-quality foraging and nursery habitat for socioeconomically important species such as lobsters and crabs (Bertocci et al., 2015). Kelp forests also contribute to nutrient cycling (Dugan et al., 2011) and act as natural coastal defences (Smale et al., 2013), mitigating the impact of storm surges and reducing coastal erosion (Løvås and Tørum, 2001). Kelp habitats may also play an important role in carbon storage as well as in global carbon cycling (Filbee-Dexter and Wernberg, 2020).

1.2 Habitat distribution

Kelp species dominate shallow rocky habitats, from the low intertidal waters to depths greater than 40 m (Smale and Moore, 2017) in temperate and subpolar regions around the world (Steneck et al., 2002).

In England, suitable rocky reef habitat occurs along much of the coastline, particularly along the wave-exposed south and west coasts (Yesson et al., 2015, Smale and Moore, 2017). Cold water kelps (*L. hyperborea*, *S. latissima* and *A. esculenta*) generally increase with latitude from southern

England to northern Scotland, moving from the southern limit towards the centre of the species' ranges (Burrows et al., 2014).

Laminaria hyperborea is restricted to the northeast Atlantic from the northern coast of Iceland, north to the Russian coast near Murmansk and south to Cape Mondego, mid-Portugal. This species is present in Norway, Faroes, northern France and northern Spain but absent from the Bay of Biscay. *L. hyperborea* occurs on most of the English coasts but is scarce in southeast coastal waters due to lack of suitable substrata (Tyler-Walters, 2007a).

Saccharina latissima occurs on all English coasts and has been recorded from the Atlantic coasts of Europe as far north as Novaya Zemlya, and south to northern Portugal and around Iceland. Also found in Greenland, the Eastern coast of America down to New Jersey, the Pacific coast of America, Bering Straits and Japan (White and Marshall, 2007).

Kelp habitat off the west and north coasts of Scotland is characterised by dense stands of *L. hyperborea* (wave exposed) or *S. latissima* (more sheltered), whereas kelp beds off the south and west coasts of the UK and Ireland are more mixed, with a greater relative abundance of *S. polyschides* and *L. ochroleuca* (Burrows et al., 2014).

Historical distribution information for kelp in England is limited. There has been a lack of targeted research on kelp in the UK resulting in the lack of a robust baseline dataset for both distribution and abundance (Smale and Moore, 2017). Quantitative research on UK kelp forests began during the Second World War following a demand for goods produced using kelp-derived alginates (Parke, 1948, Woodward, 1951, Smale et al., 2013). Detailed surveys carried out in Scotland between 1946 and 1955 were used to map and estimate biomass of kelp in Scotland (Walker and Richardson, 1955, Walker and Richardson, 1956), however no such information has been found for kelp in English waters. The only large-scale assessment of subtidal rocky reef assemblages (including kelp) in the UK was conducted by the Nature Conservancy Council (NCC) (and various successor bodies including the Marine Nature Conservation Review (MNCR)) between 1970 and 2000 (Smale et al., 2013).

1.3 Factors affecting habitat distribution

1.3.1 Environmental factors

The distribution, extent and structure of kelp is influenced by a range of environmental factors, including temperature, light availability, wave exposure, nutrient availability, and grazing pressure (Burrows et al., in press) (Smale and Moore, 2017)). A major driver of geographic distribution is temperature (Burrows et al., 2014, Smale and Moore, 2017), with the optimum range differing between populations and species (Müller et al., 2009, Pang et al., 2007, Smale and Moore, 2017). The upper thermal limit for survival of *L. hyperborea*, *S. latissima* and *L. digitata* is ~ 21 °C (Lüning, 1984) with optimal performance at 10–15 °C (Bolton and Lüning, 1982). The structure and extent of kelp forests has been shown to change along natural gradients of temperature (Smale and Moore, 2017) and cold-water kelps (*L. hyperborea, S. latissima* and *A. esculenta)* generally

increase in relative abundance with latitude from southern England to northern Scotland) (Burrows et al., 2014).

Factors such as habitat type and hydrography can determine local abundance and range edges (Burrows et al., 2014). Smale and Moore (2016) suggest that variability in wave exposure, tidal action and sedimentation rates are important in driving local differences in the abundance and cover of *L. hyperborea*. *L. hyperborea* and *A. esculenta* centred on wave-exposed conditions, *S. polyschides* in less exposed conditions and *S. latissima* predominant in sheltered conditions (Burrows et al*.,* in press). The wave exposure preferences of *L. hyperborea* and *S. latissima* can be clearly seen on the west coast of Scotland (Burrows et al*.,* 2014). Bekkby *et al*. (2009) showed that wave exposure plays an important role in determining the density, morphology and distribution of *L. hyperborea*. Light availability strongly influences the depth distributions of all kelp species (Desmond et al., 2015, Lüning, 1979).

1.3.2 Ecological pressures

Kelp forests are currently under threat from ecological pressures such as overgrazing (Hart and Scheibling, 1988, Leinaas and Christie, 1996), competition between species (Arkema et al., 2009, Hawkins and Harkin, 1985) and the spread of invasive non-native species (Arnold *et al*., 2016, Saunders and Metaxas, 2008). Grazing can be important in determining local distributions of kelp, and overgrazing (generally by sea urchins) can decimate kelp forests (Steneck et al., 2002, Burrows et al., 2014). In England, the extent of deforestation by urchin grazing is generally restricted and patchy, although heavily grazed areas are more common in Scotland. Although listed as "Not relevant" in the MarLIN sensitivity assessments*,* the potential competition between native kelp species and invasive non-native species should be noted for all kelp species other than *L. digitata*.

Urchin population blooms, as a result of predator removal (e.g. through overfishing), has resulted in some of the most significant urchin grazing impacts (Ling et al., 2009) such as widespread destruction of kelp forests and diminished biodiversity (Burrows et al., 2014). Burrows et al. (2014) concluded that there is only a low probability of an urchin population explosion as a result of apex predator removal in the UK as overfishing has occurred for centuries, therefore it could be inferred that the threat of over grazing on kelp is also relatively low. *Undaria pinnatifida* is an invasive non-native species in England, originating in the temperate regions of Japan, China and Korea (Stuart, 2003; (Oakley, 2007). The abundance and distribution of *U. pinnatifida* has increased in UK waters in recent decades (Fletcher and Manfredi, 1995, Burrows et al., 2014) and is now established from the Hamble (Solent), Isle of Wight, Torquay, Plymouth and Jersey (Oakley, 2007, Fletcher and Manfredi, 1995). Epstein and Smale (2018) found that abundance, biomass and morphology of *Undaria* can vary significantly between habitats, and the authors suggest this could greatly alter the species' ecological impacts.

1.3.3 Anthropogenic pressures

Kelp forest habitats are sensitive to human-induced physical and chemical pressures (de Bettignies et al., 2021). Kelp and seaweed communities on sublittoral sediments are considered at high risk from hydraulic dredging for bivalves and at medium risk from otter trawling and scallop dredging;

the substrate abrasion of bottom trawled gear being detrimental to the benthic environment and associated biota (Williams and Davies, 2019).

Pollution (sewage, industrial waste, inorganic fertilizers, and pesticides) in runoff present in rivers affects kelp growth and reproduction, alongside sedimentation leading to smothering (Smale and Moore, 2017). These stressors can cause irreversible shifts from complex, biologically diverse habitats to simple turf dominated 'barrens') (Dayton and Tegner, 1984, Ling et al., 2009, Burrows et al., 2014).

The impacts of large-scale kelp cultivation are poorly known and may be detrimental (Smale and Vance, 2015, Smale et al., 2015). The demand for kelp has grown in recent decades and is likely to continue to increase in the future (Burrows et al., 2014). Currently, kelp is harvested for human consumption, alginate production, medicines, fertiliser and aquaculture feed (Burrows et al., 2014). Kelp harvesting can affect population structure, community dynamics, wider ecosystem functioning, fish abundance and seabird foraging efficiency (Smale et al., 2013). Although a small harvest of kelp could potentially be achieved sustainably, due to the rapid recruitment and growth of kelp, the associated assemblage may take longer to recover (Christie et al., Smale et al., 2013). There is increasing interest in the production of marine biofuels and subtidal large brown kelps of the order Laminariales have been identified as having the greatest potential for bioconversion to energy (Hughes et al., 2013, Singh and Gu, 2010). There is little wild harvest of these species in the British Isles, however, cultivation of *L. hyperborea*, *L. digitata* and *S. polyschides* has been attempted in Ireland and Scotland (Edwards and Watson, 2011). The quantities of kelp required to make a reasonable contribution to the energy market would require large scale cultivation (Burrows et al., 2014).

Appendix 3 provides a summary of the MarLIN sensitivity assessments (Tyler-Walters, 2007a, White and Marshall, 2007, Smirthwaite, 2007, Tyler-Walters, 2008a, White, 2008, Oakley, 2007, Hill, 2008) showing the high and moderate pressures identified for each of the seven kelp species occurring in England. Appendix 4 provides a summary of the (MarLIN) sensitivity assessments for the EUNIS kelp forest habitats (*L. hyperborea* and *S. latissima* kelp forest habitats only) (Jasper, 2015a, Jasper, 2015b, Stamp, 2015a, Stamp, 2015d, Stamp, 2015e, Stamp, 2015c, Stamp, 2015b, Stamp and Hiscock, 2015, Stamp and Tyler-Walters, 2015).

1.3.4 Climate change impacts

Average mean annual UK sea surface temperatures of 3.11°C (±0.98°C) are predicted for the end of the century (Cornes et al., 2023). Such climate change associated increases in sea temperatures have been linked to loss of marginal populations, range contractions and significant reductions in kelp forest extent (Raybaud et al., 2013, Tuya et al., 2012, Wernberg et al., 2016, Smale and Moore, 2017).

Although little is known about the ability and rate at which kelp populations respond to climate change induced changes in temperature (Burrows et al., 2014, Smale et al., 2013), the distribution and relative abundance of kelp species have been shown to change with latitude along the regional-scale temperature gradient on the Northeast Atlantic coast (Smale et al., 2013).

Modelling predicted changes in climate may therefore provide an indication of the future spatial distribution of kelp species. Smale and Moore (2016) found that the distribution-abundance patterns of *L. hyperborea* did not vary predictably with ocean temperature but suggest that species found at the edge of their ranges may undergo distributional shifts. Kelp forest structure in the UK's northernmost regions may therefore become more similar to that currently observed in the southernmost regions. These predicted changes include a poleward range expansion and an increased abundance of more southerly distributed species (e.g. *L. ochroleuca*), and a poleward range contraction and decrease in abundance of more northerly distributed species (e.g. *A. esculenta*) ((Smale and Moore, 2017, Smale and Vance, 2015, Smale et al., 2015).

The distributional changes projected in de Bettignies (2021a) for each kelp species based on intermediate climate change scenarios for 2090 to 2100 are shown in Table 1. Although structurally and functionally similar, little is known about the ecology of *L. ochroleuca* (Smale and Vance, 2015, Smale et al., 2015). The replacement of the cold-temperate *L. hyperborea* with the warm temperate *L. ochroleuca* may have relatively few effects, although even subtle changes in kelp species traits have been shown to influence biodiversity (Blight and Thompson, 2008, Smale et al., 2013).

Table 1. Predicted distributions of kelp species in the UK for 2090-2100 (from de Bettignies, 2021a).

Species	Predicted distribution (UK)
Alaria esculenta	Projected to disappear from some parts of the UK but persist in northern half.
Laminaria digitata	Persistence and expansion of this species was projected for most of UK although the species is also projected to disappear from some parts of the southern coast of the British Isles.
Laminaria hyperborea	UK would continue to be suitable for this species although it may disappear from some parts of the south coast.
Laminaria ochroleuca	Expand northwards to unoccupied parts of the UK
Saccharina latissima	Projected to disappear from some areas of the southern coast of the UK
Saccorhiza polyschides	Projections suggested persistence along most of the coast of UK

The predicted changes in ocean climate may also lead to changes in kelp forest structure and ecosystem functioning (Smale and Moore, 2017). As different kelp species provide structurally different habitats due to their varying morphologies and life histories (Burrows et al., 2014), climate-driven shifts in abundance and distribution of these habitat forming species may have knock-on effects on community structure, ecosystem functioning and associated biodiversity (Jones et al., 1994, Smale et al., 2013, Burrows et al., 2014). However, the wider implications of shifts in the distribution and abundance of different species for kelp productivity, trophic linkages and ecosystem functioning are largely unknown (Burrows et al., 2014).

Burrows et al. (2014) looked at kelp beds further south (Portugal and Spain) as a proxy for the potential future structure of UK kelp beds as a result of ocean warming. The structure of kelp habitats off northern Portugal and Spain is significantly different to those in UK waters; *L. hyperborea* forms 'parks' rather than dense canopies observed in colder conditions and is generally much smaller and lower in abundance. *L. ochroleuca* grows to a larger size and is present in greater abundance. *S. polyschides* is generally more abundant across a wider depth range, and *L. digitata* does not extend further south than France.

Increase in storminess is also likely to negatively impact kelp bed structure and functioning. Intense wave action can damage and remove kelp canopy, alter patch dynamics and lead to ecological phase shifts (Dayton et al., 1999, Burrows et al., 2014, Byrnes et al., 2011, Smale and Vance, 2015).

1.4 Restoration approaches

Restoration is defined as 'the process of assisting the recovery of an ecosystem that has been degraded, damaged or destroyed' (SER, 2004). Active restoration of kelp forests has been attempted by introducing or removing biotic or abiotic materials from the environment. The trialled methods include transplanting, seeding, and installing artificial reefs (Eger et al., 2022a). A fundamental step in any restoration project is to identify the cause(s) of the decline or factors preventing the natural re-establishment (Morris et al., 2020). If kelp reproduction is limited, reproductive individuals are introduced, either by adding spores or gametophytes and/or by transplanting mature plants that act themselves as the spore source. Previously used passive restoration methods include removal of grazers such as urchins (Eger et al., 2022b).

A global meta-analysis by Jones et al. (2018) of seven ecosystem types showed that the cessation of disturbances led to rates of recovery comparable to active restoration and concluded that the first step in a restoration initiative should be determining whether removal of the stressor(s) causing the decline will allow kelp to naturally re-establish. The Sussex Kelp Restoration Project utilises this approach through the implementation of the Sussex Inshore Fisheries and Conservation Authority (IFCA) Nearshore Trawling Byelaw, which makes it illegal to fish with bottom towed gear within a specified area on the Sussex coast. The removal of this pressure may allow kelp to regenerate naturally. The project, which began in 2021 and aims to restore 300 km^2 of kelp in the coastal waters of Sussex, will assess the need for and feasibility of active restoration (Britain Rewilding, 2022). In some cases, where passive restoration may not be successful or may take a very long time, active restoration may be more suitable (Morris et al., 2020). Eger et al. (2022a) completed an extensive global review of active kelp restoration and afforestation and found no recorded projects in the UK. The four main restoration methods used elsewhere in the world to date are:

1. Transplanting – attaching kelp holdfasts (root-like structures) to artificial material and then placing the kelp on the seabed;
2. Seeding kelp populations – dispersing and/or growing the juvenile life stage (i.e. seeds, gametophytes, propagules, zoospores) of the kelp in the ocean;

3. Removing competitors – mechanical or manual removal of kelp competitors from the seafloor;
4. Grazer control – through manual removal or exclusion of nuisance grazers from a restoration area (Eger et al*.,* 2022a).

To date, kelp forest restoration has been expensive and of limited success (Fredriksen et al., 2020). It is important to understand the local ecology to ensure the right restoration methodology is used to increase the success rate of a restoration scheme (Morris et al., 2020). It should be noted that without improving the environment and removing existing pressures to enable kelp to adapt to changing conditions, restoration will be limited or even unfeasible (Morris et al., 2020). New and altered restoration methodologies will be required to keep up with environmental change, such as selecting individuals for restoration that show increased tolerance to warming temperatures (Eger et al*.,* 2022a) (Eger et al., 2022a). For example, Layton and Johnson (2021) are trialling transplanting thermally tolerant kelp (*Macrocystis)* in Tasmania. Fredriksen et al. (2020) recently developed and tested a new approach they have termed "green gravel", this approach uses small rocks which have been seeded with kelp and reared in the laboratory until 2–3 cm, before they are placed on the seabed. The results have shown high survival and growth (over 9 months). This method is cheap and simple, and therefore has potential for application over larger areas and to introduce more resilient kelp populations onto vulnerable populations.

Morris et al. (2020) highlights five important considerations for kelp restoration:

- identifying the causes of kelp decline
- setting appropriate targets, goals, and objectives
- understanding the factors that affect success in re-establishing kelp forests
- developing practical techniques for implementing restoration goals at a scale commensurate with the problem or intended benefits
- monitoring the appropriate variables to evaluate progress toward goals, and to identify if procedures need adjusting.

The strengths and weaknesses of a range of different kelp forest restoration approaches are shown in Table 2 (adapted from: Fredriksen et al*.,* 2020).

Table 2. Strengths of kelp forest restoration approaches (adapted from: Fredriksen et al., 2020).

	Green gravel	Ex situ recruitment enhancement	Direct seeding	transplantation	Local herbivore removals	Artificial reefs	Protected area, fishing gear restrictions and water quality regulations
Overcome substrate limitations	+	+	-	-	-	+	-
Overcomes propagule limitation	+	+	+	+	-	-	-
Effective against top-down drivers (e.g. herbivores)	-	-	-	-	+	-	+
Effective against bottom up drivers (e.g. water quality)	-	-	-	-	-	-	+
Addition of resilient genotypes	+	+	+	+	-	-	-
Propagation of resilient genotypes	+	+	-	-	-	-	-
Scalable to large areas	+	?	-	-	+	-	+

Several studies have developed modelled predictions of the spatial distribution of kelp habitats using both geographic species/habitat records and a range of environmental variables. Four examples are summarised below:

- The potential global distribution of the order Laminariales was modelled by Jayathilake and Costello (2020) using presence only kelp records (from the Global Biodiversity Information Facility (GBIF 2017) and the Ocean Biogeographic Information System (OBIS 2017)) and 13 environment variables (depth, diffuse attenuation coefficient, dissolved oxygen concentration, distance from the land, nitrate concentration, pH, phosphate concentration, photosynthetically active radiation, average sea surface temperature, maximum sea surface temperature, salinity, slope and wave height). As true absence records were not available, the Maximum Entropy (MaxEnt) modelling software was used as it selects random background points as pseudo-absences. This study found that the most important environmental variable for the biome across all species was average sea surface temperature, whereas wave height, distance from the coast and minimum temperature were of most importance for individual species.

- Goldsmit et al. (2021) modelled habitat suitability and cover for four kelp species *(Agarum clathratum, Alaria esculenta, Laminaria solidungula* and *S. latissima*) in the Eastern Canadian Arctic. Ensemble models, which use the average from a set of models rather than results from any single model, were used. Occurrence data of kelp species were compiled from museum data records, diver and drop-down camera transect data, and records from biodiversity databases. Six variables were used for model predictions: maximum surface temperature, mean surface salinity, mean ice thickness, mean bottom iron, mean bottom phosphate, and mean bottom current velocity. Most of the study area was predicted to be suitable for at least one of the species modelled. The area of projected suitable habitat was highest for *L. solidungula* (269,000 km^2) and lowest for *A. esculenta* (183,000 km^2). Habitat suitability was projected to increase for all modelled species except for *L. solidungula*.
- Bekkby and Moy (2011) developed a spatial predictive model of the potential distribution of sugar kelp under natural conditions in the Skagerrak region of Norway. The aim of this study was to integrate information on geophysical factors into a Geographical Information System (GIS), to develop maps on *S. latissima* distribution and identify areas where *S. latissima* no longer occurs. Kelp occurrence data (presence or absence) were recorded from 333 stations and were used to develop the spatial predictive model. The analyses showed that the potential distribution of sugar kelp was best determined by the combined effect of wave exposure, depth, slope and light exposure. Current speed data was not available for the entire study area and therefore excluded from analysis.
- Generalised additive models were used by Gorman et al. (2013) to predict three biologically relevant kelp forest attributes (probability of occurrence, proportional covers and biomass) for *Laminaria* forests within the Bay of Morlaix, France. Data on forest occurrence (presence or absence), proportional covers and biomass were obtained from underwater video surveys and direct diver observations. Forest distribution and proportional covers were predicted using water depth, light availability, wave exposure and sediment dynamics. The biomass models also used seafloor slope and benthic position.

2. Methods for mapping the current, historic and potential distribution

2.1 Current distribution

Kelp data were obtained for *L. hyperborea* and *S. latissima* from the National Biodiversity Network (NBN) Gateway (https://data.nbn.org.uk/) (see Appendix 5 for *L. hyperborea* data sources and Appendix 6 for *S. latissima* data sources) and data for *L. hyperborea* (A3.113; A3.1151; A3.1153; A3.125; A3.2121; A3.2131; A3.2141; A3.2143; A3.222; A3.311 and A3121) and *S. latissima* (A3.122; A3.124; A3.222; A3.3121; A3.3123; A3.3131; A3132 and A5.523) habitats were obtained from Natural England's Marine Evidence Database (NE MEDB).

Only records occurring within English waters (Marine Plan Areas) were included. The data representing "Collection Specimens" and "unverified" records were removed.

The resultant datasets contained 4630 current records for *L. hyperborea* and 17381 current records for *S. latissima*.

To determine current extent, data were then filtered further to select records occurring in 2008 or later. All *L. hyperborea and S. latissima* records were then mapped on ArcGIS to produce maps representing the current extent of these species.

2.2 Historic extent and distribution

Historical distribution information for kelp in England is limited. There has been a lack of targeted research on kelp in the UK resulting in the lack of a robust baseline dataset for both distribution and abundance (Smale and Moore, 2017). Quantitative research on UK kelp forests began during the Second World War following a demand for goods produced using kelp derived alginates (Parke, 1948, Woodward, 1951, Smale et al., 2013). Detailed surveys carried out in Scotland between 1946 and 1955 were used to map and estimate biomass of kelp in Scotland (Walker and Richardson, 1955, Walker and Richardson, 1956), however no such information has been found for kelp in English waters. The only large-scale assessment of subtidal rocky reef assemblages (including kelp) in the UK was conducted by the Nature Conservancy Council (NCC) (and various successor bodies including the Marine Nature Conservation Review (MNCR)) between 1970 and 2000 (Smale et al., 2013).

Kelp data was obtained for *L. hyperborea and S. latissima* from the National Biodiversity Network (NBN) Gateway (https://data.nbn.org.uk/) and data for *L. hyperborea* (A3.113; A3.1151; A3.1153; A3.125; A3.2121; A3.2131; A3.2141; A3.2143; A3.222; A3.311 and A3121) and *S. latissima* (A3.122; A3.124; A3.222; A3.3121; A3.3123; A3.3131; A3132 and A5.523) habitats were obtained from Natural England's Marine Evidence Database.

Only records occurring within English waters (Marine Plan Areas) were included. The data representing "Collection Specimens" and "unverified" records were removed. To determine historic extent data were then filtered further to select records occurring up to and including 2007. This 15-year window reflects the start of an increase in marine evidence gathering since 2007 to support the designation of new special areas of conservation (SACs, e.g. Studland to Portland SAC, Lizard Point SAC), many of which were solely designated for Annex I Reef features to complete England's European Marine Sites network.

The resultant datasets contained c. 2000 historic records for *L. hyperborea* and 1430 historic records for *S. latissima*.

The spatial join tool was then used in ArcGIS to join kelp records to a 10 km^2 hexagonal grid. A series of maps were then produced to represent historic kelp extent, with grid cells where kelp records were present shown in red and grid cells where kelp records were absent shown in blue.

Only historic presence records were mapped, absence was inferred from a lack of records, but this is not necessarily true absence.

The mapped distribution is dependent on survey effort and only provides a general idea of national distribution but does not show local changes in distribution or any possible changes in density or abundance.

2.3 Modelling habitat restoration potential

L. hyperborea and *S. latissima* (Burrows *et al*., in press). Burrows et al. (in press) developed habitat suitability models for kelp around the UK and Ireland. The models used kelp abundance data (recorded on the SACFOR scale from JNCC's Marine Nature Conservation Review (MNCR)), average August sea surface temperature (SST), wave exposure and Chlorophyll *a* concentrations to provide two types of logit-transformed models of habitat suitability for *L. hyperborea* and separately for *S. latissima* (Burrows *et al*., in press). Model 1 integrates available bathymetry information, whilst Model 2 is applied at a 2 m fixed depth contour across English waters, in order to better appreciate the broadscale patterns of habitat suitability and account for any issues with bathymetry data. The models were then further refined to only include areas which overlap with polygons of infralittoral rock (EUNIS habitat code A3) mapped in Natural England's Marine Evidence Database (NE MEDB) as this would reflect where suitable habitat to restore kelp currently exists without requiring habitat modification.

3. Results

3.1 Current distribution

The distribution of current (2008 – 2022) *L. hyperborea* records were predominantly along the northeast, southern and southwest coasts of England, with a few records also occurring on the southeast, east and west coasts (Figure 1). This aligns with the description of *L. hyperborea* distribution provided by Tyler-Walters (2007), which states *L. hyperborea* occurs on most coasts of England but is scarce on southern east coast due to lack of suitable substrate. Appendix 7 shows the number of current records for each Marine Plan Area, with all current *L. hyperborea* records occurring in the inshore Marine Plan Areas and southwest inshore Marine Plan Area had the most records.

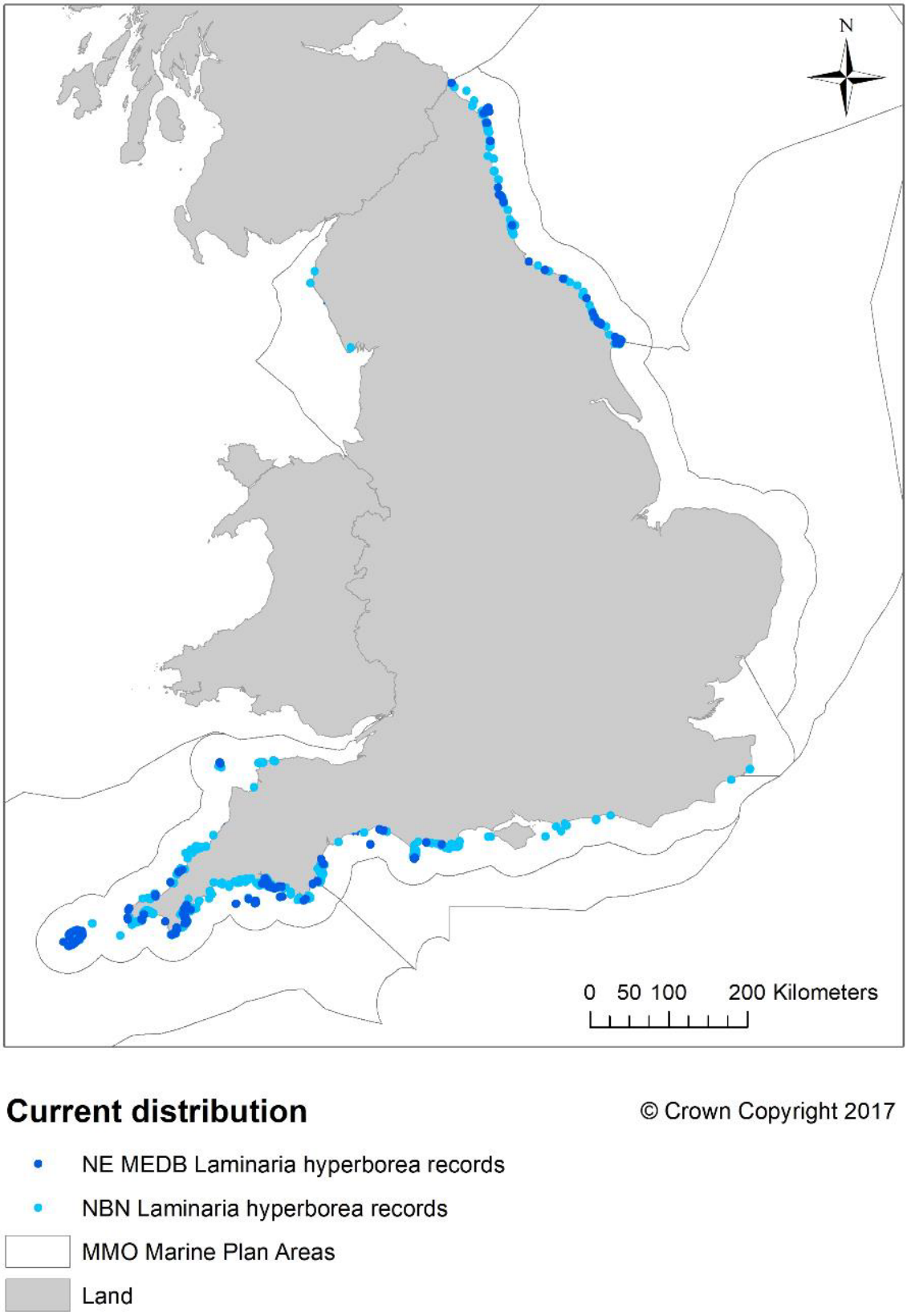


Figure 1. Current distribution of *Laminaria hyperborea* in English waters (2008-2022; point colours indicate data source; NE MEDB = Natural England Marine Evidence Database; NBN = National Biodiversity Network).

Current *S. latissima* records were predominantly distributed along the northeast, southern and southwest coasts of England, with a few records also occurring on the east, southeast and west coasts (Figure 2). This aligns with the description of *S. latissima* distribution provided by White and Marshall (2007), which states *S. latissima* occurs on all English coasts. Appendix 7 shows the number of current records for each Marine Plan Area, with all current *S. latissima* records occurring in the inshore Marine Plan Areas and southwest inshore Marine Plan Area had the most records.

Only current presence has been mapped, absence has been inferred from a lack of records but this is not necessarily true absence.

The mapped distribution is dependent on survey effort and only provides a general idea of national distribution but does not show local changes in distribution or any possible changes in density or abundance.

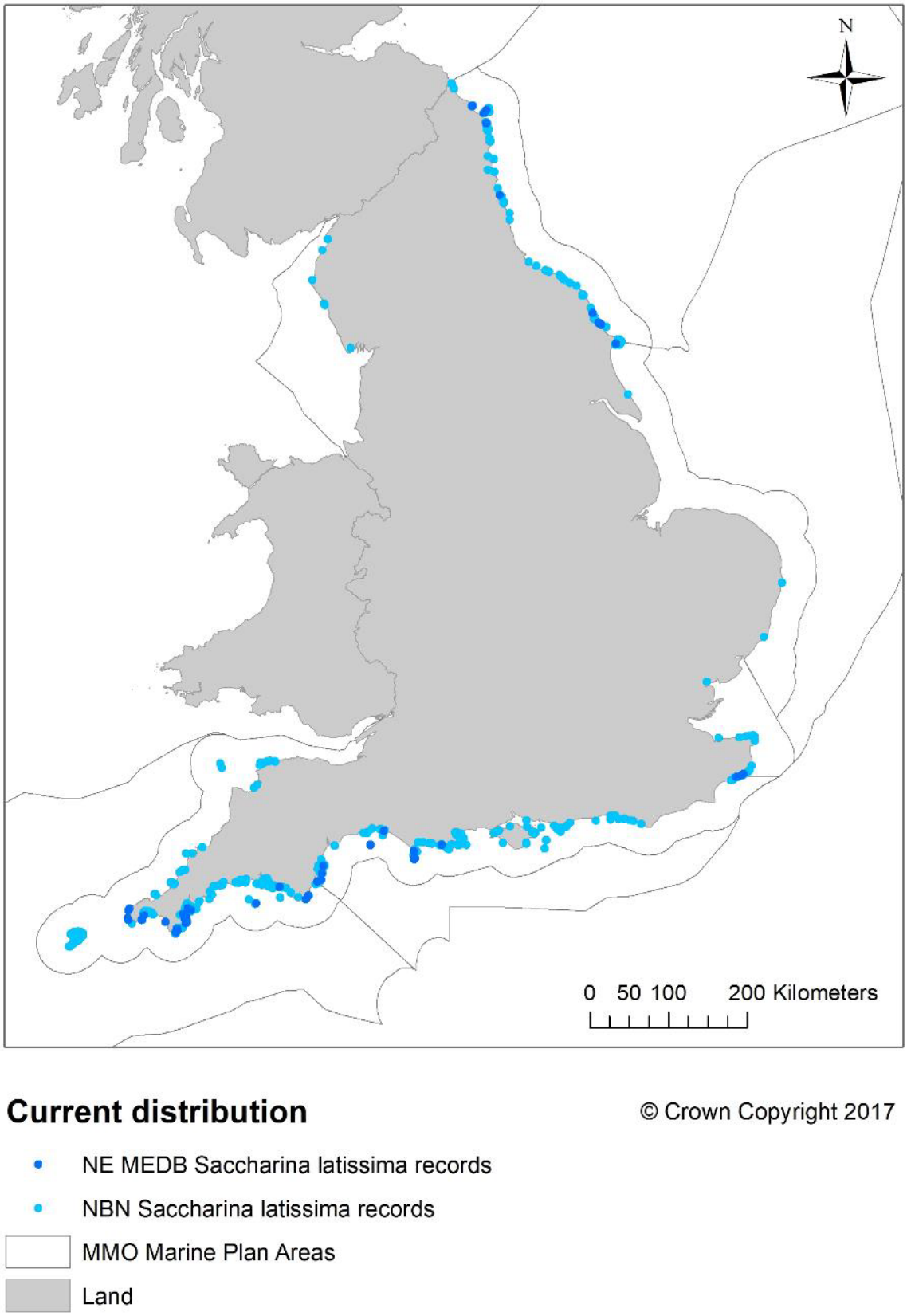
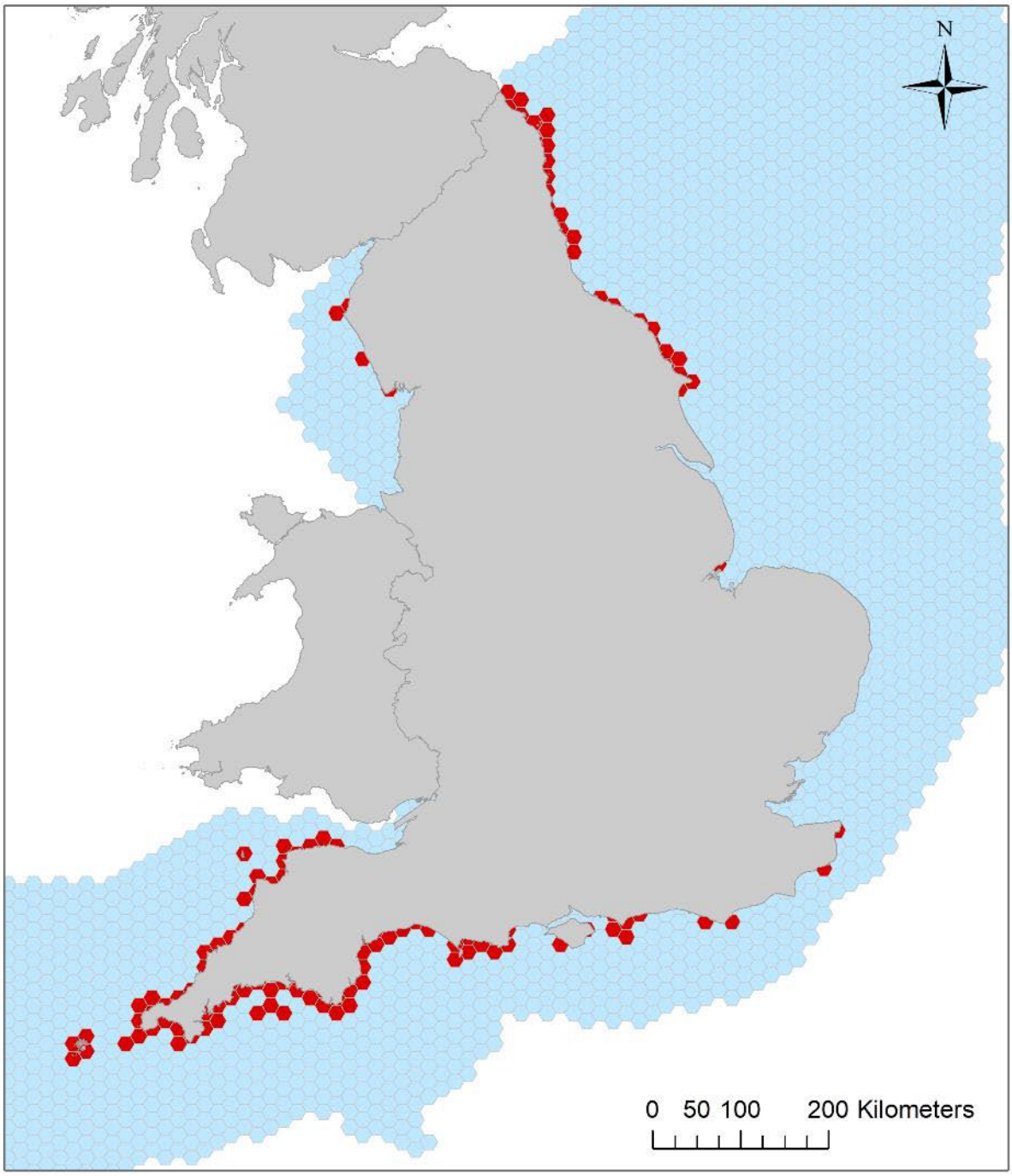


Figure 2. Current distribution of *Saccharina latissima* in English waters. 2008-2022; point colours indicate data source; NE MEDB = Natural England Marine Evidence Database; NBN = National Biodiversity Network).

3.2. Historic distribution

Historic records were limited to the time periods 1973 to 2007 for *L. hyperborea* and 1972 to 2007 for *S. latissima*.

The distribution of historic *L. hyperborea* records was similar to the current distribution, occurring predominantly along the northeast, southern and southwest coasts of England, with a few records also occurring on the southeast, east and west coasts (Figure 3). In total, 2000 historic records for *L. hyperborea* were found. Appendix 7 shows the number of historic records for each Marine Plan Area, with all historic *L. hyperborea* records occurring in the inshore Marine Plan Areas and southwest inshore Marine Plan Area had the most records.



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Historic distribution

Laminaria hyperborea records

Absent

Present

Land

Figure 3. Historic distribution of *Laminaria hyperborea* in English waters.

Historic *S. latissima* records were predominantly distributed along the northeast, southern and southwest coasts of England, with a few records also occurring on the southeast, east and west coasts (Figure 4). This closely aligns with the current S. *latissima* distribution map (Figure 2). In total, 1430 historic records for *L. hyperborea* were found. Appendix 7 shows the number of historic records for each Marine Plan Area, with all historic *S. latissima* records occurring in the inshore Marine Plan Areas and southwest inshore Marine Plan Area had the most records.

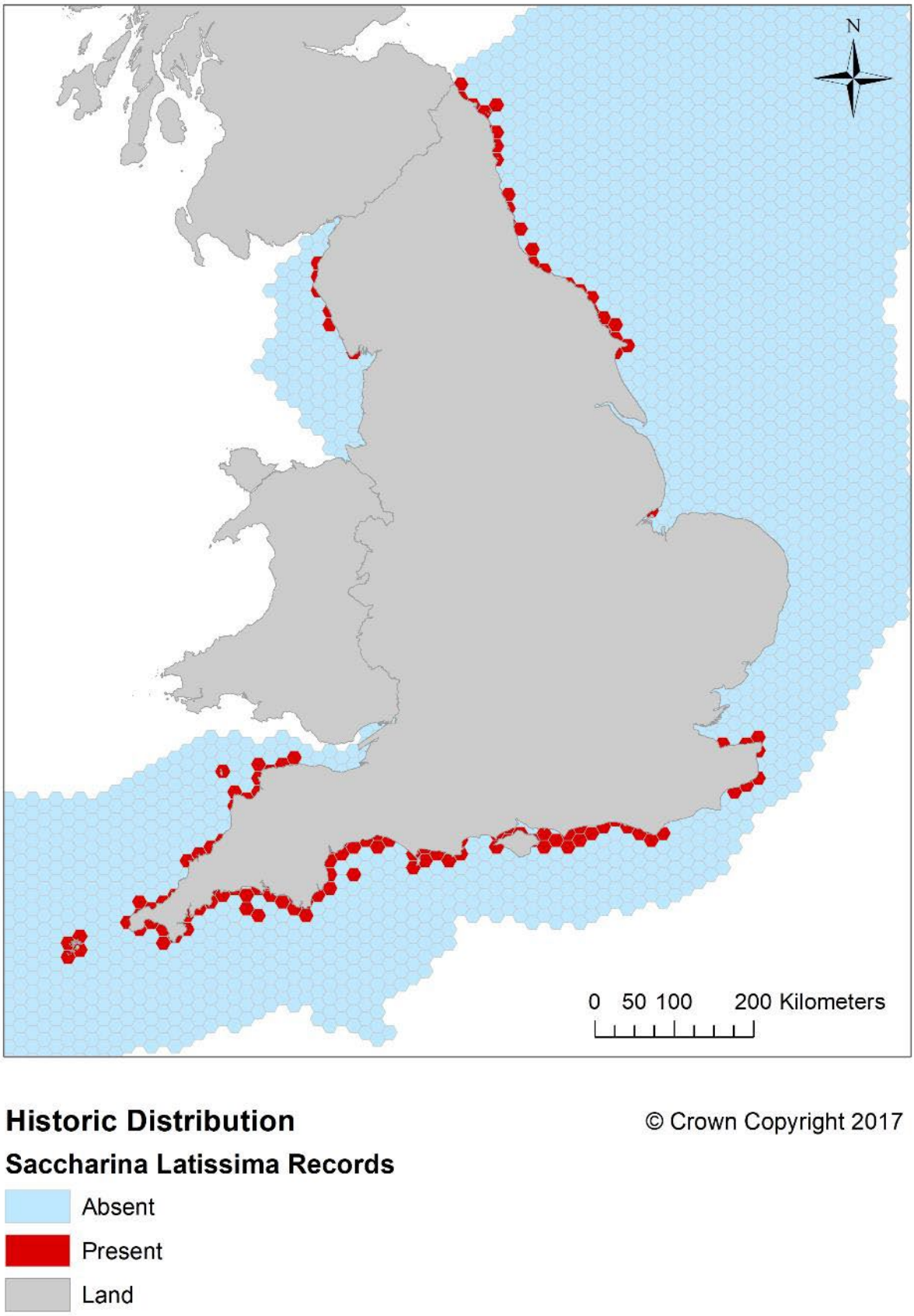


Figure 4. Historic distribution of *Saccharina latissima* in English waters

3.3. Restoration potential

The habitat suitability models of *L. hyperborea* indicate considerable restoration potential across the coastal waters of England. The models highlight restoration potential areas for *L. hyperborea* along the northeast, southern and southwest coasts of England (Figure 5). At a national scale this closely aligns with the current and historic distribution maps of *L. hyperborea* and *L. hyperborea* habitats. Model 1 and model 2 predicted a total potential area for *L. hyperborea* restoration of 84.4 km^2 and 1269.3 km^2 respectively. **.**Table 3 shows the area per Marine Plan Area.

The differences in predicted suitability between model 1 and model 2 can be seen clearly in the close-up restoration potential map for *L. hyperborea* off the North Northumberland coast (Figure 6).

Figures 7 and 8 show the modelled habitat restoration potential areas of *L. hyperborea* in English waters overlaid on the currant and historic distributions respectively.

Table 3. The modelled potential restoration area per Marine Plan Area (km^2). Model 1 used average depth per grid cell whereas model 2 used a standard 2m depth across the entire model domain.

	Laminaria hyperborea		***Saccharina latissima***	
	Model 1	Model 2	Model 1	Model 2
North East inshore	57.53	393.08	0	0.28
North East offshore	0	0	0	0
East inshore	2.16	5.41	0	0
East offshore	0	0	0	0
South East inshore	2.56	0	0	0
South inshore	0	344.59	0.09	0.58
South offshore	0	0	0	0
South West inshore	22.02	524.51	0.04	1.65
South West offshore	0	0	0	0
North West	0	0.12	0	0

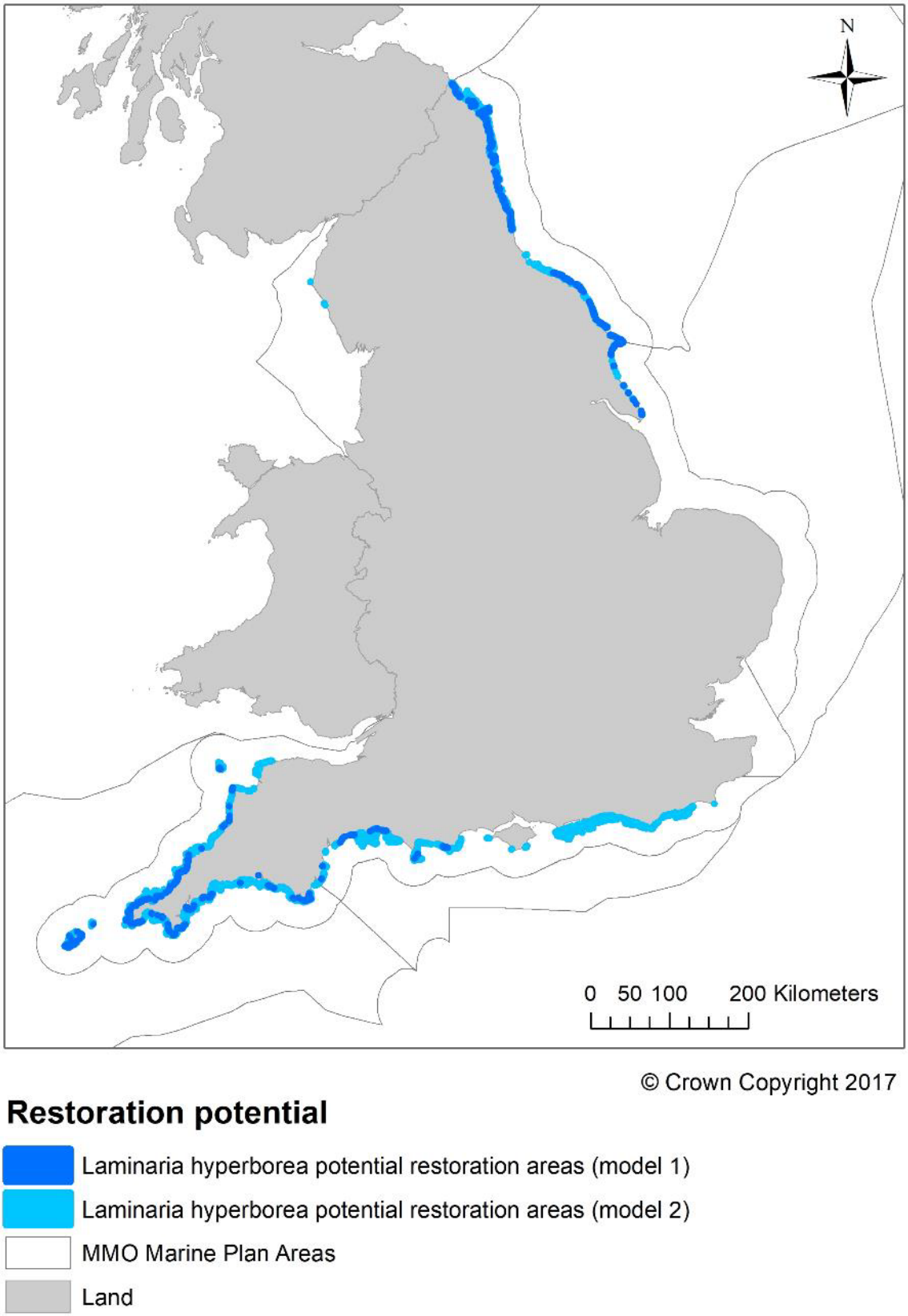


Figure 5. Modelled habitat restoration potential areas of *L. hyperborea* in English waters. Model 1 used average depth per grid cell whereas model 2 used a standard 2m depth across the entire model domain.

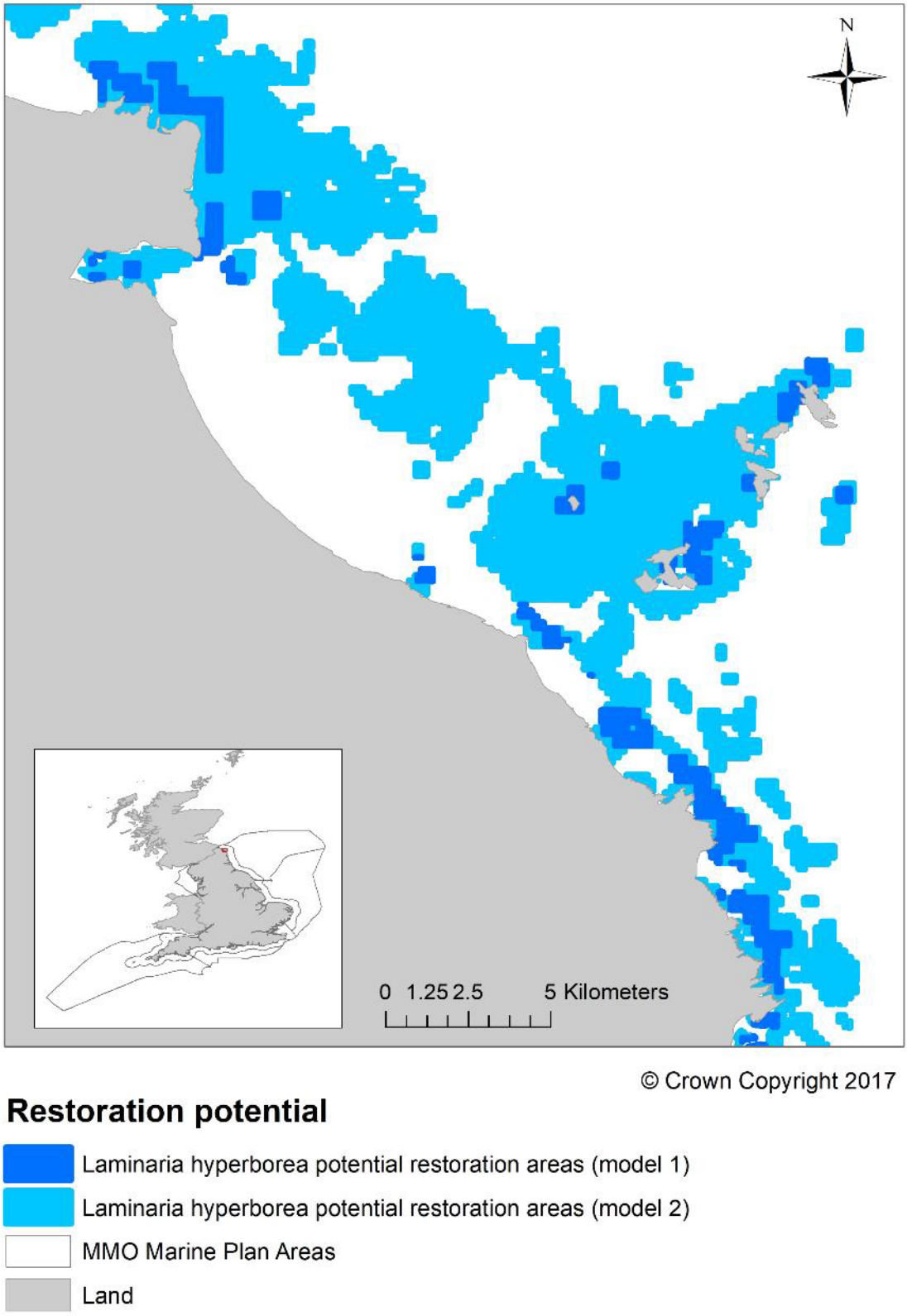
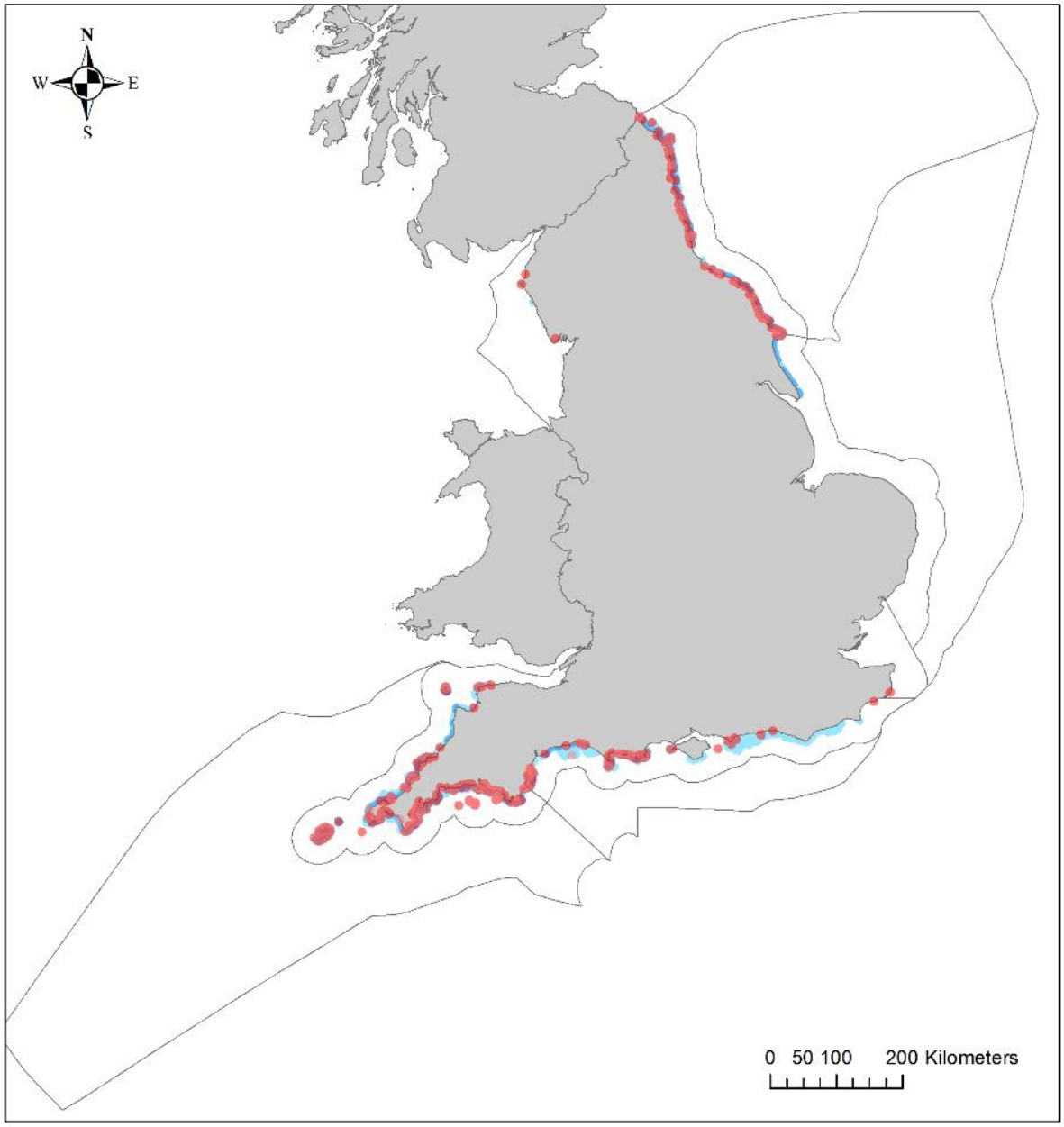


Figure 6. Close-up of the modelled habitat restoration potential areas of *L. hyperborea* along the North Northumberland coast, between Holy Island and Seahouses. Model 1 used average depth per grid cell whereas model 2 used a standard 2m depth across the entire model domain.



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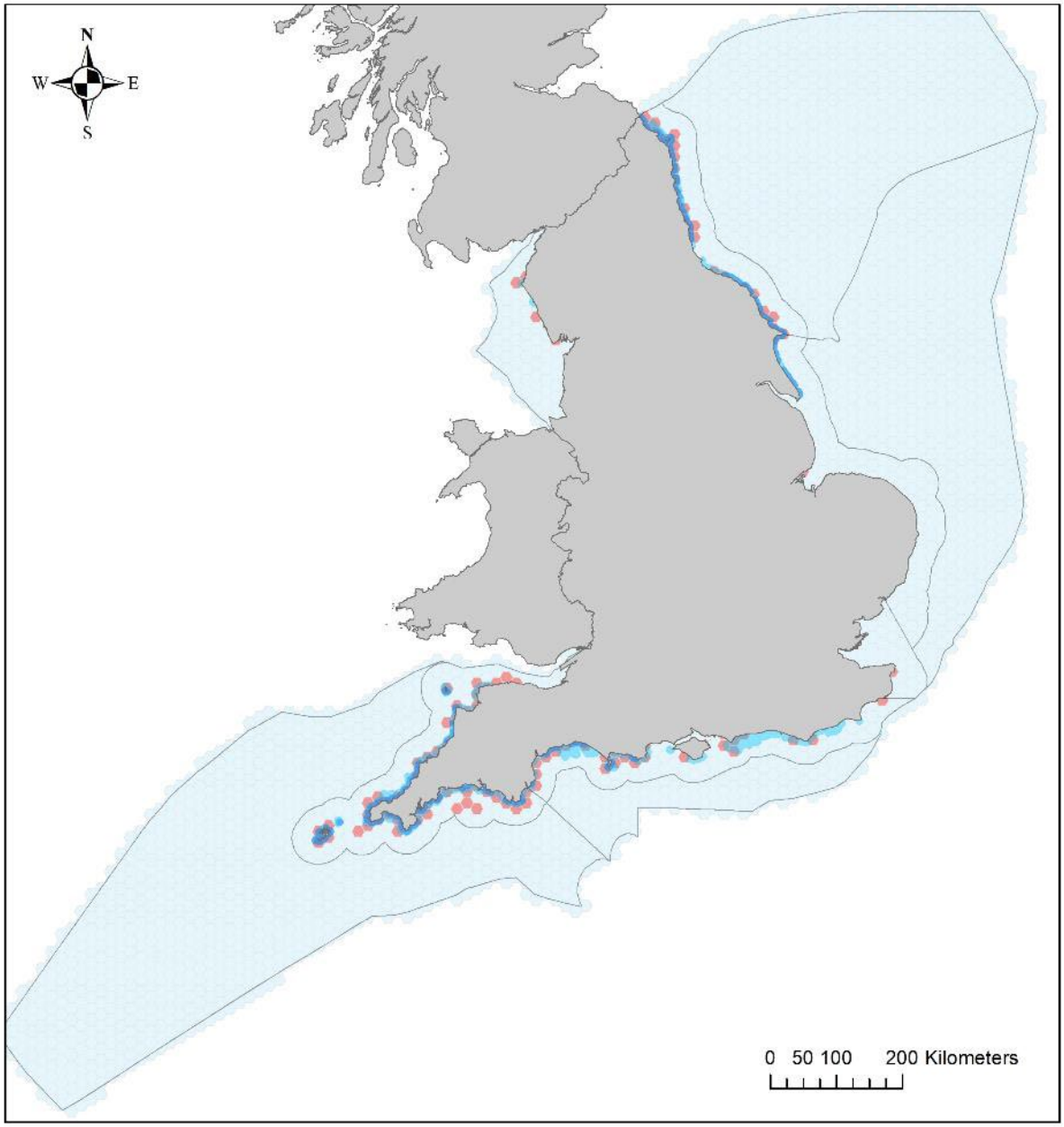
Laminaria hyperborea

- Land
- MMO_Marine_Plan_Areas
- NE MEDB Points - Current
- NE_MEDB Polygons - Current
- NBN - Current
- Laminaria hyperborea potential restoration areas (model 1)
- Laminaria hyperborea potential restoration areas (model 2)

Figure 7. Current distribution of Laminaria hyperborea overlaid on modelled habitat restoration potential areas of *L. hyperborea* in English waters. Model 1 used average depth per grid cell whereas model 2 used a standard 2m depth across the entire model domain.



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Laminaria hyperborea

- Land
- MMO_Marine_Plan_Areas
- Laminaria hyperborea potential restoration areas (model 1)
- Laminaria hyperborea potential restoration areas (model 2)

Historic Distribution

- Absent
- Present

Figure 8. Modelled habitat restoration potential areas of *L. hyperborea* in English waters overlaid on historic distribution of Laminaria hyperborea. Model 1 used average depth per grid cell whereas model 2 used a standard 2m depth across the entire model domain.

The modelled predictions of *S. latissima* restoration potential areas in English waters were limited. Model 1 and model 2 predicted a total potential area for *S. latissima* restoration of 0.1 km^2 and 2.6 km^2 respectively (Figure 9). The majority of areas with current *S. latissima* or *S. latissima* habitat (Figure 2) have not been highlighted by these models as suitable sites for restoration. Table 3 shows the area per Marine Plan Area.

Unlike the predictions for *L. hyperborea* (Figure 6), the restoration potential for *S. latissima* off the North Northumberland coast is very limited (Figure 10). Both model 1 and model 2 predicted restoration potential areas for *S. latissima* in the Plymouth Sound / Tamar area (Figure 11).

Model 1 predicts significantly less restoration potential areas then model 2. This is to be expected as model 2 shows broadscale patterns of suitability, whereas local information was used by model 1 to provide a more localised prediction (Michael Burrows personal communication, 8th August 2022).

Figures 12 and 13 show the modelled habitat restoration potential areas of *S. latissima* in English waters overlaid on the currant and historic distributions respectively.

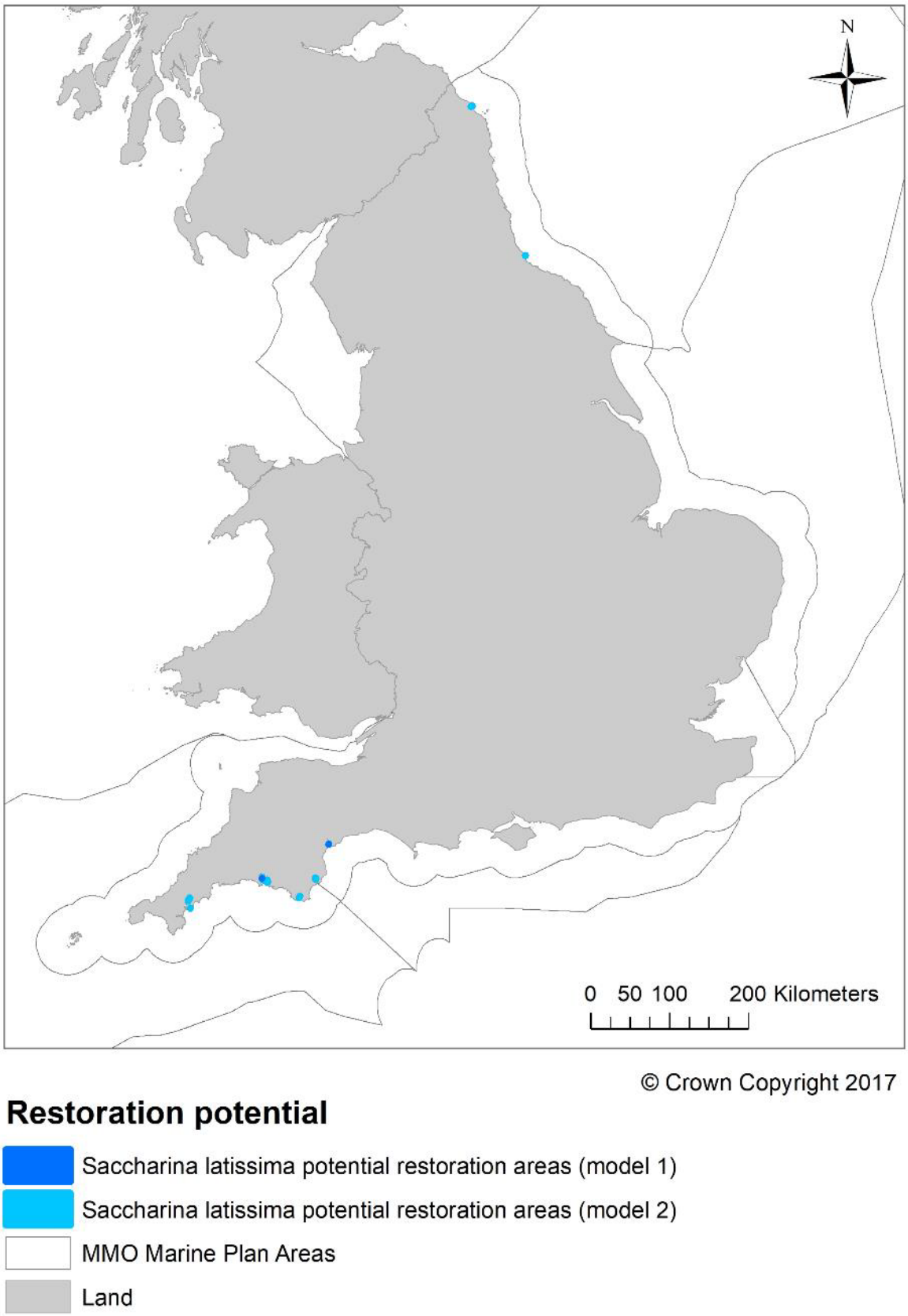


Figure 9. Modelled habitat restoration potential areas of *S. latissima* in English waters. Model 1 used average depth per grid cell whereas model 2 used a standard 2m depth across the entire model domain.

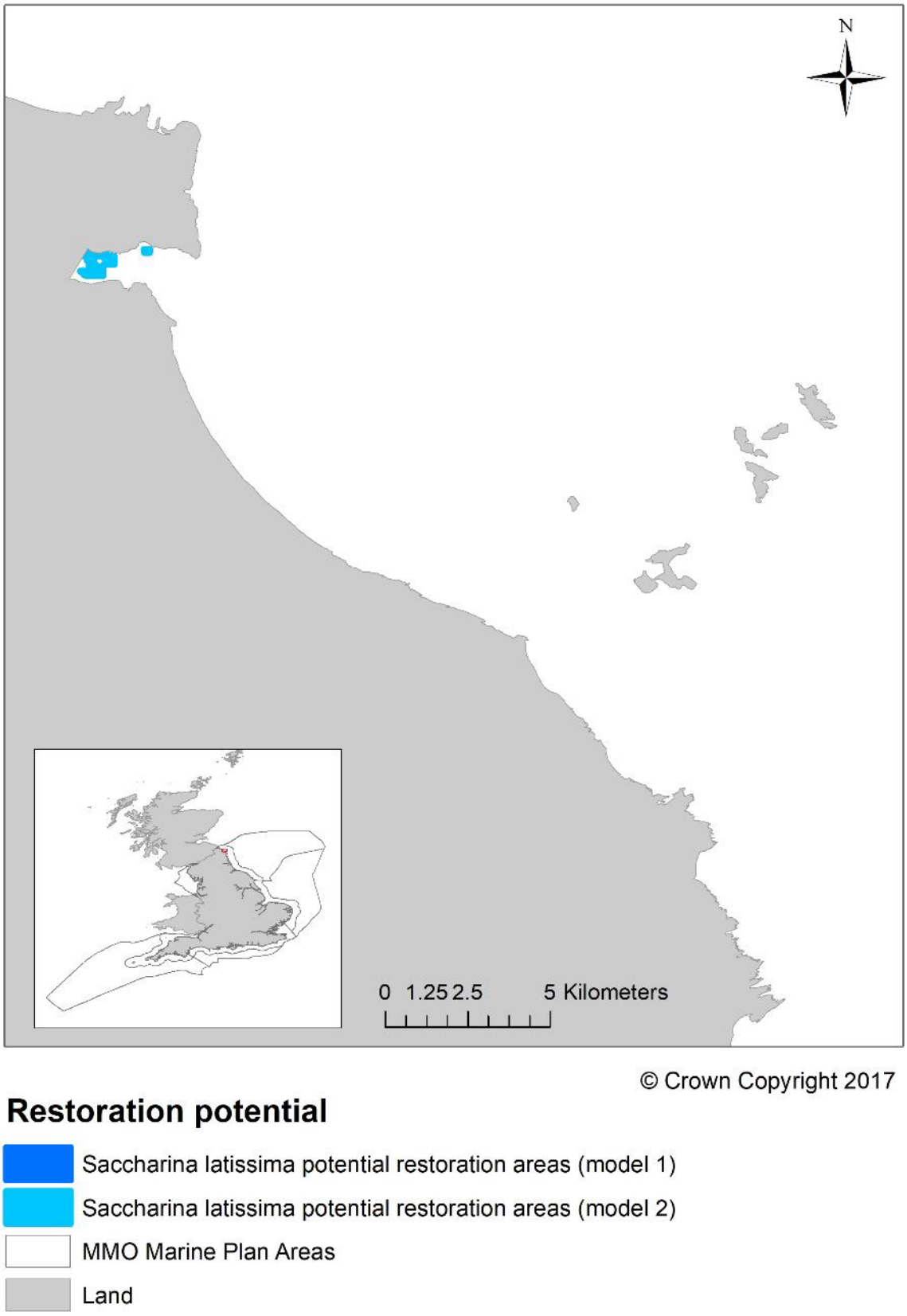


Figure 10. Close-up of the modelled habitat restoration potential areas of *S. latissima* along the North Northumberland coast, between Holy Island and Seahouses. Model 1 used average depth per grid cell whereas model 2 used a standard 2m depth across the entire model domain

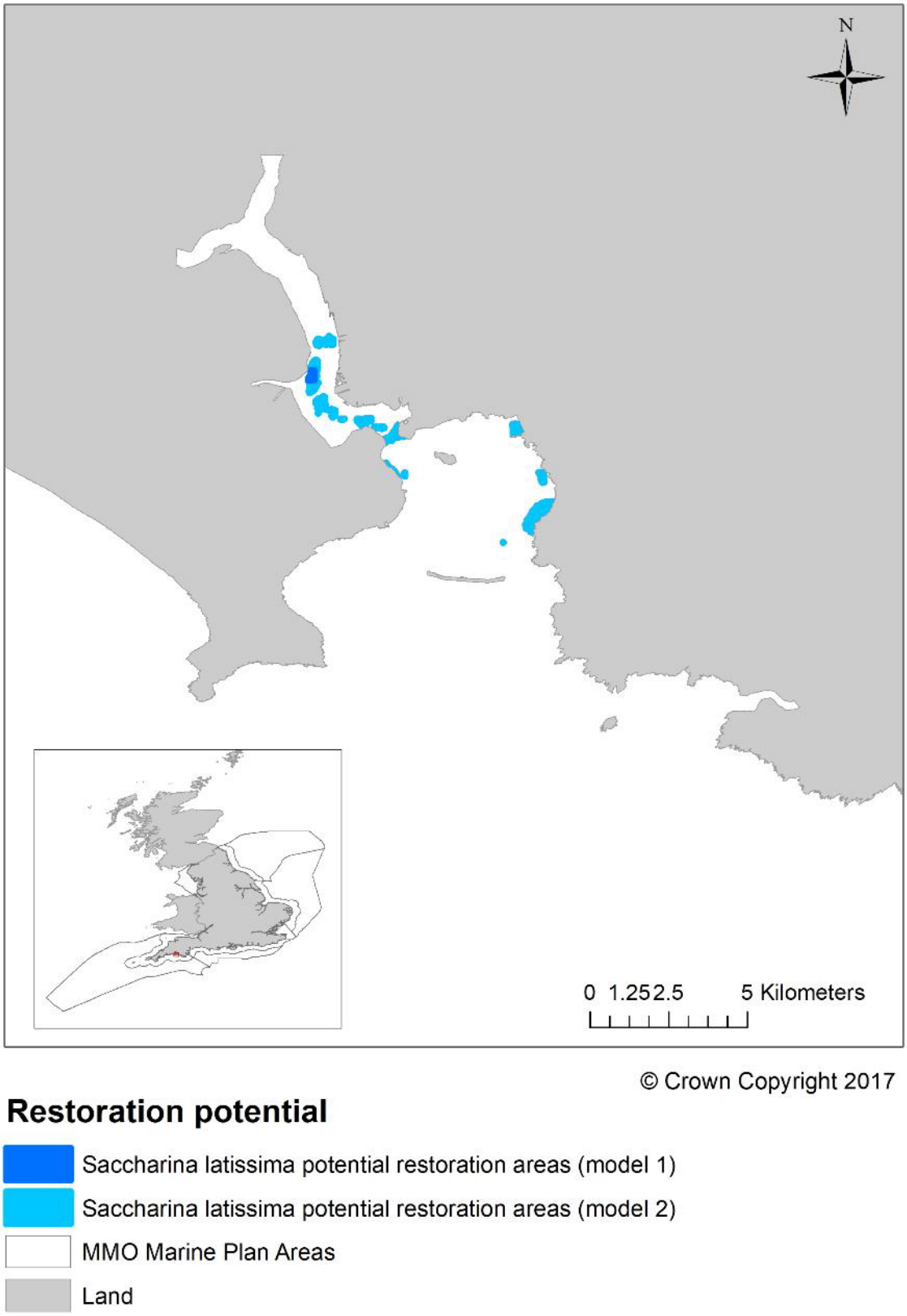
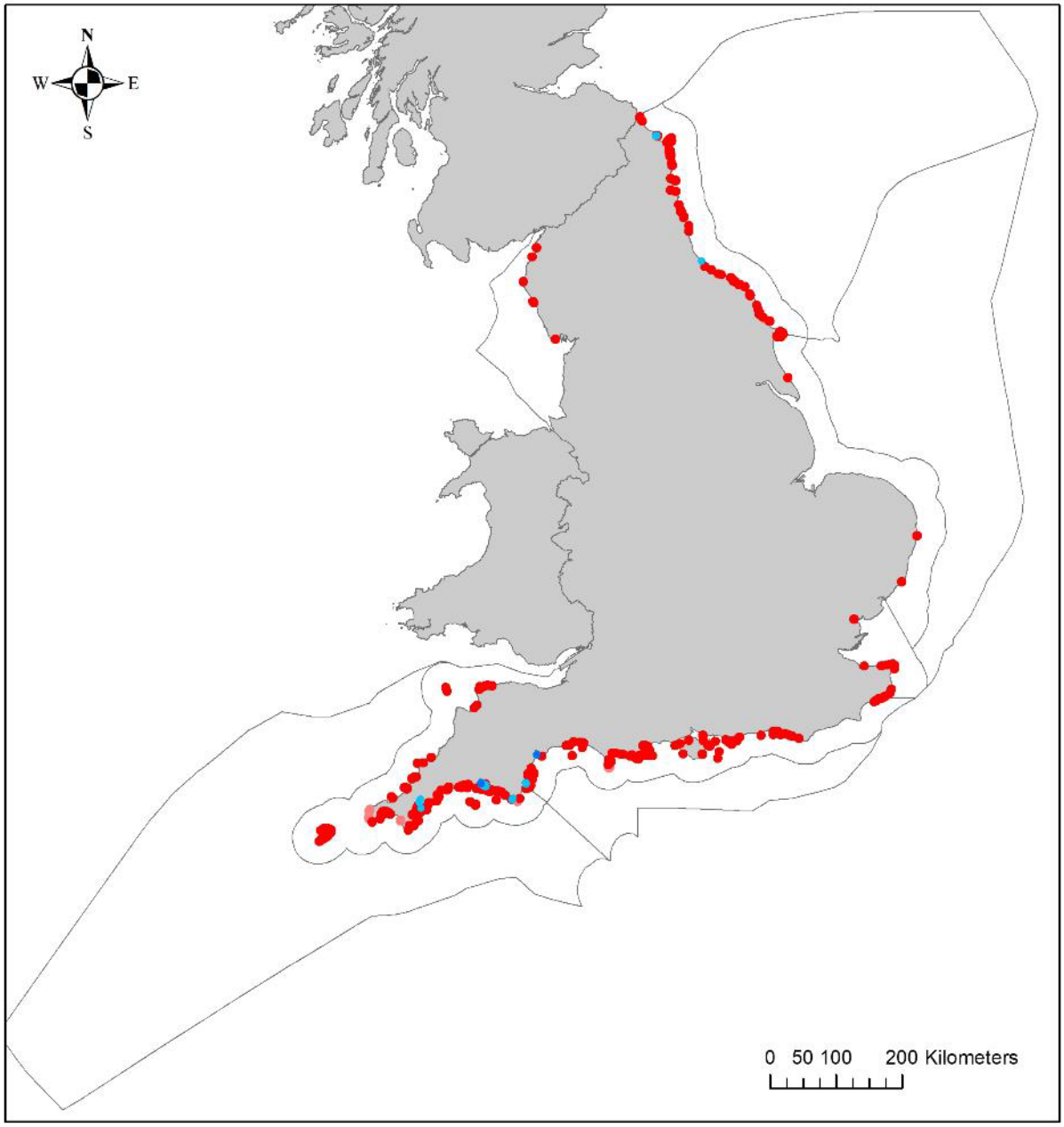


Figure 11. Close-up of the modelled habitat restoration potential areas of *S. latissima* in Plymouth Sound and the Tamar Estuary. Model 1 used average depth per grid cell whereas model 2 used a standard 2m depth across the entire model domain.



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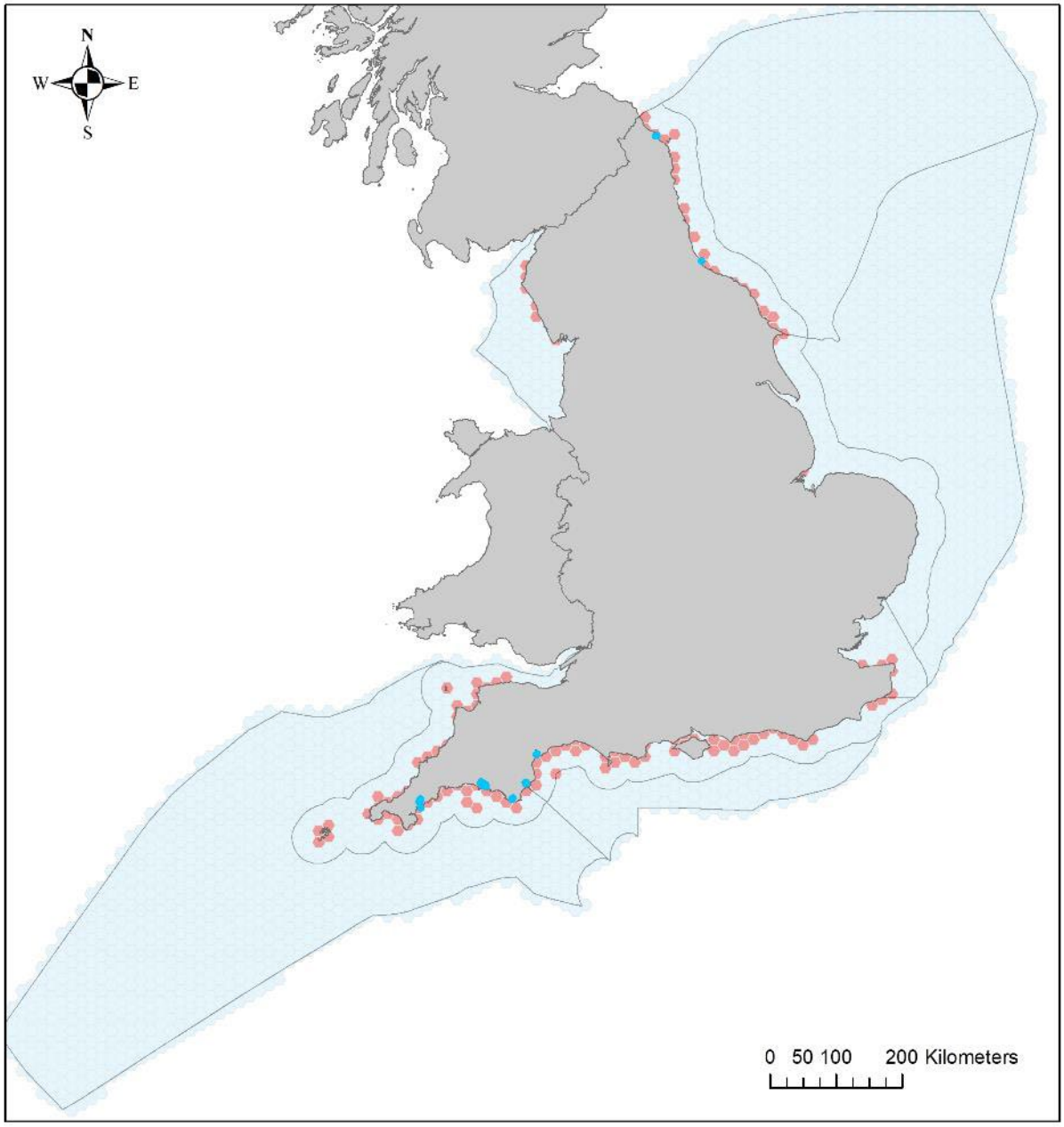
Saccharina latissima

- Saccharina latissima potential restoration areas (model 1)
- Saccharina latissima potential restoration areas (model 2)
- NBN Points - Current
- NE MEDB Points - Current
- NE MEDB Polygons - Current
- Land
- MMO_Marine_Plan_Areas

Figure 12. Current distribution of Saccharina latissima overlaid on modelled habitat restoration potential areas of S. latissima in English waters. Model 1 used average depth per grid cell whereas model 2 used a standard 2m depth across the entire model domain.



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Saccharina latissima

Land

MMO_Marine_Plan_Areas

Saccharina latissima potential restoration areas (model 2)

Saccharina latissima potential restoration areas (model 1)

Historic Distribution

Absent

Present

Figure 13. Modelled habitat restoration potential areas of *L. hyperborea* in English waters overlaid on historic distribution of *S. latissima*. Model 1 used average depth per grid cell whereas model 2 used a standard 2m depth across the entire model domain.

4. Discussion and future recommendations

Research on kelp restoration is still in its infancy. Most of the existing relevant literature focuses on current impacts, previous habitat extents and modelled future habitat distributions, which are then applied to derive theoretical suggestions about potential kelp recovery techniques. Studies have shown both positive and negative interactions with anthropogenic disturbances. For example, benthic trawling increases sea floor scour and reduce kelp forest abundance (Smale et al., 2013), however targeted fisheries have been found to both promote and reduce kelp abundance (Steneck 2013, Tegner 2013). Similarly, increased nutrient inputs have been shown to enhance competition and reduce kelp forest abundance but also to promote kelp growth in some cases (Filbee-Dexter et al., 2016, Filbee-Dexter and Wernberg, 2020). However, these results are formed using correlation between uncontrolled environmental variables, without isolating specific environmental stressors and physiological responses. As a result, applicability of such data to practical kelp habitat restoration is largely unknown.

To date, kelp forest restoration has been expensive and of limited success (Fredriksen et al., 2020). The trialled restoration approaches and attempts worldwide have been covered in detail in section 1.4 above. The only example, to our knowledge, of attempted kelp restoration in the UK is the recent "passive methodology of disturbance exclusion" implemented by the Sussex IFCA. This Sussex Kelp Restoration Project commenced in 2021 and outputs are not yet available. Other studies have suggested that passive restoration through the removal of pressures (e.g. exclusion of bottom towed gear) may promote natural restoration, and should be considered/attempted before active restoration is progressed. This approach is recommended for future kelp restoration in England, however to date there are very few practical examples over a sufficient time period to report results.

Most research on kelp habitat and biodiversity has focussed on *L. hyperborea*, with mixed species kelp restoration remaining untested. Mixed species kelp restoration is particularly relevant in areas such as the UK, where multispecies canopies are present (Morris et al., 2020). As kelp species have different morphologies and life histories and because kelps provide structurally different habitats (Burrows et al., 2014), applying *L. hyperborea* data to varying ecological scenarios may increase unexplained deviation within data. This brings us to question the validity of singular species data when applied to complex and diverse natural communities (Morris et al., 2020).

Further research is needed to understand the impact of climate-driven distribution shifts and the implications on kelp habitat productivity, trophic linkages and ecosystem functioning (Burrows et al., 2014). Smale and Moore (2016) recommend better direct measurements of kelp bed structure, biodiversity, productivity, detritus production and export, and resistance and resilience to perturbation along a regional scale temperature gradient on the north-east Atlantic coastline are needed (Burrows et al., 2014). However, sourcing adequate funding and access to resources and samples over sufficiently long timescales can be challenging for large-scale studies required to fill these evidence gaps.

In this study, we predict habitat restoration potential for *L. hyperborea* and *S. latissima* in a practical and cost-effective manner by adapting model outputs produced by Burrows et al. (in press). The two models presented here only include English waters and areas of infralittoral rock.; Model 1 of this study predicts significantly less restoration potential areas than model 2 for both kelp species, as model 2 predicts broadscale patterns of suitability, whereas model 1 provides a more localised prediction (Michael Burrows personal communication, 8th August 2022). Therefore, model 1 potentially is more applicable to smaller geographical scales, however this is dependent upon the predictor variable data quality and scale. In order to determine which model produced a more accurate output requires further model testing with larger, more extensive data sets.

Model predictions also vary between species. At a national scale, model 2 prediction of *L. hyperborea* habitat suitability closely aligns with the current and historic distributions for this species. Model outputs for *S. latissima* however, are very limited and do not reflect the current or historic distribution. Further work is therefore needed to improve the reliability and accuracy of the *S. latissima* models before they can be used to inform restoration initiatives for this species. The Burrow et al. (in press) models for *S. latissima* align more closely with the species' distribution, suggesting that changes made to these models during the MaRePo project (e.g selecting for only areas of infralittoral rock, or the classification of what model outputs represent suitability) will need to be reassessed.

The models used the "rare" threshold criterion, where Rare was defined as <1 plant per 10 x100m. Although the models were shown by Burrows et al. (in press) to closely align with the kelp observations, using single plant records (rare) as the threshold for the model may result in an over estimation of habitat suitability for kelp forest habitats in which case higher abundance thresholds may be more appropriate. Another limitation of these models is the lack of high-resolution substratum type information (Duarte et al., 2022; Burrows *et al*., in press). Based on the findings of this project, we recommend that further mapping/modelling work will be carried out in the next phase of MaRePo, to exclude areas considered unsuitable for kelp restoration including the location of significant activities (e.g. dredging), marine assets (e.g. submarine cables) and disease control areas. Once factors such as general location, restoration method and scale are determined for future restoration projects, the restoration maps should be used to identify suitable sites and / or exclude unsuitable sites (e.g., areas which are too small).

Maerl

1. Literature review

1.1 Biology and ecological importance

Maerl (*Rhodoliths*) is a collective term used to describe multiple species of non-geniculate Corallinaceae (coralline red algae) which crystallise certain minerals from the water column to form skeletons rich in calcium carbonate, magnesium carbonate, iron, and bio-assimilated elements (Riosmena-Rodríguez, 2017a, Riosmena-Rodríguez, 2017b). Maerl typically grows as unattached nodules which create dense porous biogenic layers known as maerl bed habitats, defined as areas in which more than 30-50% of coralline red algae material is present. A typical maerl bed habitat is composed of varying proportions of living and dead amalgamations of several maerl species growing loosely in fragmented nodules (Bernard et al., 2019, Bosence, Sciberras et al., 2009b, Peña et al., 2014, Hall-Spencer et al., 2010). Maerl grows at an approximate rate of 1-2 mm per year (Adey and McKibbin, 1970, Riosmena-Rodríguez, 2017a, Riosmena-Rodríguez, 2017b). Due to the slow growth rate, maerl bed habitats form over multiple centuries. The morphology of coralline red algae is highly variable and can consist of branching twigs, spheres, nodules and fans that typically range between 1-100 cm in size. Despite such variability, common tropes in shape are found across all maerl species (McCoy and Kamenos, 2015).

Maerl habitats are composed of two families: Corallinaceae and Peyssonneliaceae. The main species found worldwide are *Phymatolithon calcareum, Lithothamnium corallioides, Peyssonnelia rosa-marina, Lithothamnium valens* and *Peyssonnelia crispate*(Hall-Spencer et al., 2010, Cott et al., 2021). Maerl habitats are predominantly found within the photic zone, at depths between 1- 40 m (Hall-Spencer et al., 2010) and often exist in low turbidity, high-energy environments such as on open coastline, tide-swept channels, and in coastal inlets (Foster et al., 2013, Wilson et al., 2004). Depending on topography and abiotic factors such as turbidity, salinity and currents, maerl bed habitats vary in terms of density, number of species present, and ranges in corresponding biotopes (Wilson et al., 2004, Hall-Spencer et al., 2010).

Maerl forms a complex biogenic habitat that provides ecologically and economically valuable ecosystem services including enhanced biodiversity and coastal sediment stability, carbon sinks, and modification of the local environment chemistry (Jones et al., 1994, Burrows et al., 2014). Maerl habitats create three-dimensional structures that provide food and shelter for a diverse range of infaunal, epiphytic, epibenthic, and cryptic species (Sciberras et al., 2009a, and Jackson, 2017, Kamenos et al., 2004b) as well as forming optimal breeding and nursery grounds for many species such as commercially important scallops and infaunal bivalves (Kamenos et al., 2004a, Kamenos et al., 2004b). Due to these qualities, maerl habitats are often considered as keystone species within the temperate and subtropical coastal waters (Smith et al., 2014). Maerl habitats

are considered to be “hotspots” of biodiversity in both marine (species: *P. calcareum*) and lagoonal (species: *L. glaciale*) environments (Perry and Jackson, 2017).

Maerl ecosystems have the highest rate of calcium carbonate and magnesium carbonate production of all ecosystems found along European coasts (Barbera et al., 2003). The high levels of inorganic dissolved carbonate absorbed (to form the coralline skeletal structures) by these organisms may be of importance to help mitigate current trends in climate change (Cott et al., 2021, Trevathan-Tackett et al., 2015). However, these organisms are vulnerable to ocean acidification (Martin and Hall-Spencer, 2017a, Schubert et al., 2021) and benthic disturbance, with recovery rates impeded by slow growth rate (McCoy and Kamenos, 2015), slow maturation and low recruitment (Qui-Minet et al., 2021, Bosence). For this reason, they are considered a “non-renewable resource” (Barbera et al., 2003). Due to the associated high blue carbon budgets (Porter et al., 2020, Burrows et al., 2014) and their ability to host rare and scientifically interesting species, maerl habitats are considered as areas of international conservation interest and are listed as ‘Vulnerable’ on the *European Red List of Habitats* (Hall-Spencer et al., 2010).

1.2 Habitat distribution

Dense concentrations of maerl bed habitat are found across the Mediterranean Sea, Celtic Seas, Greater North Sea, western Europe and Arctic Waters (Maerl Beds (ospar.org) 2019). Within the North Atlantic, maerl habitats are mostly distributed across west coast of Europe and the British Isles. Maerl bed habitats are rare in the eastern and Western English Channel, Irish Sea, North Sea and Baltic Sea (Hall-Spencer, 1998).

Within UK coastal waters, maerl habitat distribution ranges from the southern Dorset coastline, western Celtic and Irish sea, to north of Shetland and the west coast of Scotland. The Hebridean Islands bolster the highest distribution of maerl habitats (Simon-Nutbrown et al., 2020), with isolated patches throughout the English Channel (southern and south-west channel) and the north-east English coastline (Peña et al., 2014). However, further data is required to fully understand the habitat existent of the northeast Atlantic maerl bed habitats, as the current evidence is restricted to grey literature reports (Peña et al., 2014).

Extensive dead maerl beds in Atlantic European waters suggest that environmental conditions may previously have been more suitable for maerl growth (Hall-Spencer, 1998). It has become increasingly evident that maerl habitats have been declining in distribution, overall health and habitat quality over the past 100 years (Hall-Spencer, 1998). Hall-Spencer & Moore (2000) recorded maerl bed decline off the west coast of Scotland and Ireland, related to the expansion of the scallop fishing industry (Hall-Spencer and Moore, 2000). The evaluation of fossilised and living maerl samples have shown that beds have depleted across the Fal estuary in England and a minimum of four maerl beds within Brittany have been destroyed by direct removal by industry (Hall-Spencer, 1998). Maerl beds across Europe are affected by human activities and the only pristine grounds remaining are small compared to the extensive area that maerl beds covered in the 1960s (Grall and Hall-Spencer, 2003). For example, one of the largest maerl beds in Brittany

(Glenan) was covered in living maerl until maerl extraction started during the late 1960s. When surveyed in 1999 live maerl was very rare over most the bank and no macrofauna were observed in grab and core samples in the extraction zone (Grall and Hall-Spencer, 2003), additionally extensive maerl beds have disappeared as a result of physical extraction and sewage discharge (Grall and Glémarec, 1997). Finally, historical data show that the complexity and distribution of maerl habitats have changed extensively across the Firth of Clyde (west coast of Scotland) over the past 100 years (Hall-Spencer et al., 2003, Hall-Spencer and Moore, 2000).

1.3 Factors affecting habitat extent and distribution

1.3.1 Environmental factors

Although evidence is largely lacking on the environmental factors which affect maerl habitats; currents, depth, light, sediment type, water quality, wave action, temperature and salinity are all likely to play an important role in maerl habitat distribution, structure and extent (see Birkett *et al*., 1998). Maerl distribution is primarily controlled by light and temperature (Adey and McKibbin, 1970) with factors such as depth dictating environmental photic conditions (Bosence). Reduced light levels result in impairment of photosynthesis and growth, however, when light and temperature are favourable, the distribution of maerl depends on localised hydrodynamics and the properties of the substratum (Dutertre et al., 2015). Maerl benefits from moderate currents that allow for the slow overturning of the algae as well as for fresh oxygenated water to pass between the nodules (Joshi et al., 2017), thus promoting concentric or radial growth. However, due to their characteristically slow growth rates, maerl require relatively sheltered conditions to reduce unwanted dispersal into unsuitable environments (Hall-Spencer et al., 2010, Hall-Spencer, 1998) and to prevent sedimentary burial (Joshi et al., 2017).

Whilst there is understanding about the ecology and biology of maerl, there are relatively few published papers on previous attempts to model the driving forces of maerl distribution, and there is little understanding of the actual thresholds and limits which refine their distribution.

Results from previous maerl models in other parts of the world (Carvalho, et al., 2020, (Martin et ak, 2014, Simon-Nutbrown, et al., 2020) show consistency in abiotic drivers, but there is inconsistency in thresholds, with significant differences between tropical, temperate and cold-water species thresholds. The abiotic factors which shape a species distribution will vary with location and the interaction with other factors, so where a model is correct in one location, it is not necessarily correct in another. This is most likely to be explained by differences in species or genetic tolerances to local climatic conditions. Topography (e.g. depth) is also an indirect factor, and it may appear to be a driving influence at a local scale (due to its influence on light and temperature), but at larger scales the effect of topography will vary so it can be problematic in models. Recent work looking into the genetic and phenotypic diversity of maerl (Jenkins, et al., 2021), Jenkins et al 2022, in press) highlights significant differences in sub-species across the United Kingdom and Europe, which will need to be considered for the full England-wide model.

1.3.2 Ecological pressures

Maerl bed habitats are threatened by phase shifts due to changes in species composition. This can be a result of the introduction of non-native invasive species, such as the American slipper limpet, *Crepidula fornicata,* that smothers maerl and the surrounding substratum with faeces and pseudofaeces (Barbera et al., 2003). Slipper limpets rapidly colonise the seabed outcompeting maerl for space and reducing species richness and abundance of ecological communities associated with maerl beds (Barbera et al. 2003). Grall and Hall-Spencer (2003) found the number of scallops associated with maerl beds to decrease after the introduction of slipper limpets.

1.3.3 Anthropogenic pressures

Due to high calcium carbonate and magnesium carbonate concentration in the skeletal structures, maerl bed habitats have commonly experienced commercial extraction for cosmetic products (Barbera et al., 2003). Marine aggregate dredging has also negatively impacted maerl bed habitats through the physical removal of sand and gravel as raw material for the UK construction industry (Singleton, 2001).

The growing intensity of fisheries and aquaculture practises over the past 100 years has caused increasing disruption to benthic habitats and their associated communities. Consequently, most European sedimentary benthic systems have been structurally modified to some extent (Bernard et al., 2019, Hall-Spencer et al., 2008). Towed demersal fishing gear destroy the structural complexity and remove biodiversity of maerl bed habitats that can take hundreds of years to form (Hall-Spencer and Moore, 2000). Maerl bed habitats in the northeast Atlantic are considered to have smaller thalli and are of lower abundance than the historic maerl bed habitats sampled in Scotland during the late 1880s. This is thought to be a direct result of scallop dredging (Hall-Spencer et al., 2003, Hall-Spencer, 1998). Although in England, maerl research is limited to the southwest English Channel and Celtic Sea, there has been a long-term cultural and industrial affiliation with towed demersal fishing practises, which have had long-term influence on benthic habitats (Fincham et al., 2020).

Land reclamation, coastal development and dredging directly alter maerl habitats through abrasion, or indirectly through changes in inshore-currents or through the reduction of light availability caused by sediment resuspension (Bernard et al., 2019, Hall-Spencer et al., 2003). Sediment deposition blocks the interstitial spaces between maerl nodules, further reducing refuge for associated fauna (Bernard et al., 2019, Hall-Spencer et al., 2003).

Chemical impacts such as increased organic matter caused by effluent discharge from sewage outlets or aquaculture units may increase sedimentation and nutrification of the habitat (Barbera et al., 2003). These processes typically impact water turbidity and reduce the efficiency of photosynthesis and encourage favourable conditions for competitive fast-growing species of macro-algae (Hall-Spencer et al., 2008, Nelson, 2009).

1.3.4 Climate change impacts

To date, research on climate change effects on marine habitats have largely focused on relatively short-term, single-species experiments, which are difficult to scale up to long-term multispecies and ecosystem-level responses to climate change (Zimmerman 2021). However, even though climate change impacts on coralline algae such as maerl are still relatively poorly understood, there is a growing evidence base on the direct and indirect impacts of changing climatic conditions on maerl health, growth, reproduction and survival (Martin and Hall-Spencer, 2017a). The current and predicted impacts of climate change are likely to intensify when multiple stressors are acting together and although the habitat-specific responses are likely to vary across regions, the resulting degradation of maerl habitats over long term is likely to lead to loss of habitat structure and complexity as well as the associated biodiversity and ecosystem benefits (Martin and Hall-Spencer, 2017a, Russel and Cunningham, 2018).

Warming sea temperatures are predicted to directly affect the growth and recruitment of maerl beds. Small increases in sea temperatures can increase maerl growth, photosynthesis and calcification, however more substantial increases or sudden temperature changes are expected to be detrimental to maerl health (Martin and Hall-Spencer, 2017a, Martin and Hall-Spencer, 2017b). Maerl appears to have species-specific thermal optima over large latitudinal scales (Simon-Nutbrown et al., 2020). Although more evidence is needed, the species distributions may already be changing due to global warming, and they are likely to shift significantly further as sea temperatures continue to rise (Brodie et al., 2014). However, due to the inherent uncertainties in species identification, very few studies have focused on species ranges and their specific environmental requirements (Simon-Nutbrown et al., 2020), and therefore the likely impacts of warming sea temperatures in range shifts alone and in combination with other climate change impacts remain uncertain.

Ocean acidification resulting from sustained CO_2 emissions is likely to have a direct impact on maerl health, growth, recruitment and survival, altering the distribution and extent of maerl habitats in English waters; although ocean acidification could boost maerl growth through the increased availability of inorganic carbon for photosynthesis, the increased metabolic costs of calcification and the corrosive impacts of reduced pH on maerl skeletons are likely to outweigh the potential benefits to productivity (Brodie et al., 2014, Martin and Hall-Spencer, 2017a, Martin and Hall-Spencer, 2017b). Habitats dominated by dead maerl are likely to be most drastically affected and may disappear as the reduced pH dissolves the magnesium-calcite skeletons of dead maerl, whereas the live maerl may degrade more slowly due to its ability to regenerate (Russel and Cunningham, 2018). Field observations have shown that maerl beds mainly form in waters with high carbonate saturation, further confirming the likely negative impact of ocean acidification on maerl (Brodie et al., 2014). As the Arctic waters with low and falling carbonate saturation levels are already expanding southwards (Steinacher et al., 2009), maerl habitats at higher latitudes in the north-east Atlantic are predicted to be particularly vulnerable to ocean acidification due to the significant pH changes projected in this area (Brodie et al., 2014).

Increased storminess and changes in rainfall patterns increase run-off from land resulting in direct physical damage to maerl in the shallow waters where maerl habitats often occur (Russel and Cunningham, 2018). Changes in storminess and weather patterns are also likely to alter physical parameters such as wave exposure, salinity and water quality, all of which are directly linked to the health and extent of maerl habitats. As a result, the trophic interactions and ecosystem feedbacks, fundamental for naturally functioning maerl habitats, may be compromised.

Under conditions of reduced water quality, fast-growing algal species have a competitive advantage over maerl. The presence of these algae impact maerl health, growth and survival via limiting water clarity and thus light availability for photosynthesis, further increasing their vulnerability to climate change impacts. For example, *L. glaciale* and *P. calcareum* are highly intolerant to smothering and have slow recovery (Russel and Cunningham, 2018) and may thus be sensitive to reduced water quality and increased terrestrial run-off due to the climate change driven increases in the frequency of storm events and higher winter rainfall as predicted for the UK (Russel and Cunningham 2018).

Habitat Suitability Models (HSMs) can be used to model climate change impacts on potential species distribution and to identify potential climate change refugia for habitats and species. This approach has recently been applied to investigate likely changes in maerl populations under projected climate change in Scotland (Simon-Nutbrown, et al., 2020).

1.4 Habitat restoration approaches

To our knowledge, active restoration of maerl beds has not yet been attempted in England or elsewhere in the world. However, passive restoration through removal of pressures has been carried out in a maerl bed in Lamlash Bay in Scotland. The Lamlash Bay No Take Zone (NTZ) was established in 2008, after which all fishing within the zone has been prohibited. Although long-term monitoring data are still required to fully assess the success of this protected area and the direct impact of pressure reduction on maerl, initial results (after only four years of protection) have reported more diverse ecological communities within the habitat, structurally more complex habitats have increased and 350% higher juvenile scallop abundance inside the NTZ compared to areas outside (Howarth et al., 2015, Howarth and Stewart, 2014). In the same period, the density and size of adult king scallops have also increased, with average size 25mm larger and 1.6 years older inside the NTZ. The reproductive biomass of king scallops was also reported 185% higher inside the NTZ compared to the fishing areas outside (Howarth and Stewart, 2014). Finally, a European lobster tag and recapture study showed a catch rate 189% higher in the NTZ compared to outside (Howarth and Stewart, 2014, Cunningham et al., 2022).

Experimental relaying of maerl habitat to examine potential for assisted recovery has also been trialled in Falmouth Harbour. The trial demonstrated that removing and replacing (after 12 hours in storage) the top 30 cm of maerl habitat in the same location is technically feasible. There were some differences in the habitat structure following re-laying, associated with loss of fine sediment, this did not seem to affect the habitat quality enough to prevent re-colonisation of infauna. 44 weeks after re-laying the dead maerl matrix, the diversity, abundance and species composition of

infauna was not significantly different between Treatment and Control conditions (Sheehan et al., 2015).

2. Methods for mapping the current, historic and potential distribution

The following general principles were applied in the mapping of both the current and historic distribution of maerl:

- The mapping analysis was carried out using Geographical Information System (GIS) ArcMap 10.2.2 software with data management in file geodatabases.
- All maps displayed throughout the report are in WGS 1984 Web Mercator Auxiliary Sphere Coordinate Reference System.

Data from Natural England's Marine Evidence Base (NE MEB) was used for the current and historic maerl distribution mapping. The NE MEB contains a collation of spatial (point and polygon) data for marine habitats and species from a number of sources. Records are added cumulatively from surveys and Marine Recorder snapshots into the master point data repository, known as Input_Points_WGS84. The records are standardised to EUNIS codes, MCZ feature codes, SAC sub-feature codes, SPA supporting habitat codes and Annex 1 habitat codes. Any records that informed on the presence of maerl (including dead records) were extracted and used for mapping.

2.1 Current distribution

The distinction of current and historic data was assessed on a habitat by habitat basis and was related to the survey effort and age of data. For maerl, the current data was deemed as records from 2009 onwards, and the distribution map therefore included all the actual point data records that were collected from and after 2009. Only records occurring within English waters (Marine Plan Areas) were included.

2.2 Historic distribution

For the historic distribution mapping, a 5 Km hexagonal grid was created in ArcGIS and clipped to English Waters. The ArcGIS intersect analysis tool was run using the historic point data records, this included records that had a date year <= 2008. Any hexagons that intersected with the point data were included as historic presence and coloured red, the remaining hexagons were assumed absences and coloured blue. Only records occurring within English waters (Marine Plan Areas) were included.

2.3 Modelling habitat suitability

The predictive habitat models for maerl were completed by staff in the Data Science Services in Natural England. The models presented in this study were developed as a preliminary proof of concept, and as a result several stages have been scaled down to enable quicker processing within the MaRePo project timelines. This included reducing the area of focus to Dorset and Cornwall, only including a subset of potentially relevant environmental predictors, and not carrying out validation techniques on the model. These models should thus not be treated as a finished product. The models were completed using R v (4.02) (2022) in rStudio and rMarkdown (2022) and ArcGIS Pro (v 2.8.2) under ESRI license for Natural England. More detail on the model parameters and limitations is provided in the discussion section below (Section 4).

The models are based on presence and absence data rather than abundance, with explanatory abiotic environmental predictor layers, to calculate the realised niche of maerl. This reflects the areas with the combination of conditions where the species included in this analysis can maintain a viable population over time, and partially reflects areas excluded by biotic conditions (Guisan et al, 2017, Soberón & Nakamura, 2009, Pulliam, 2000). The impact of anthropogenic pressures is not directly accounted for within the model structure or outputs, though many of the current abiotic conditions included do already reflect years of anthropogenic effects and alteration.

Maerl presence and absence data were sourced from the NE MEB, which is a snapshot from Marine Recorder which contains all NE marine monitoring and other research data. One older survey (Bunker & StP, 2013) and two more recent surveys (EA 2021, Ocean Ecology Ltd, 2023) not yet available in the NE MEB were also sourced. Absence points were collated from targeted maerl surveys where possible. For other areas, background absence data were created from other subtidal EUNIS habitat surveys which are not maerl related biotopes, and where maerl was not listed as a species present. After standard data wrangling and preparation steps, 151 presences and 574 absences remained for Cornwall, and 304 presences and 1108 absences for Dorset.

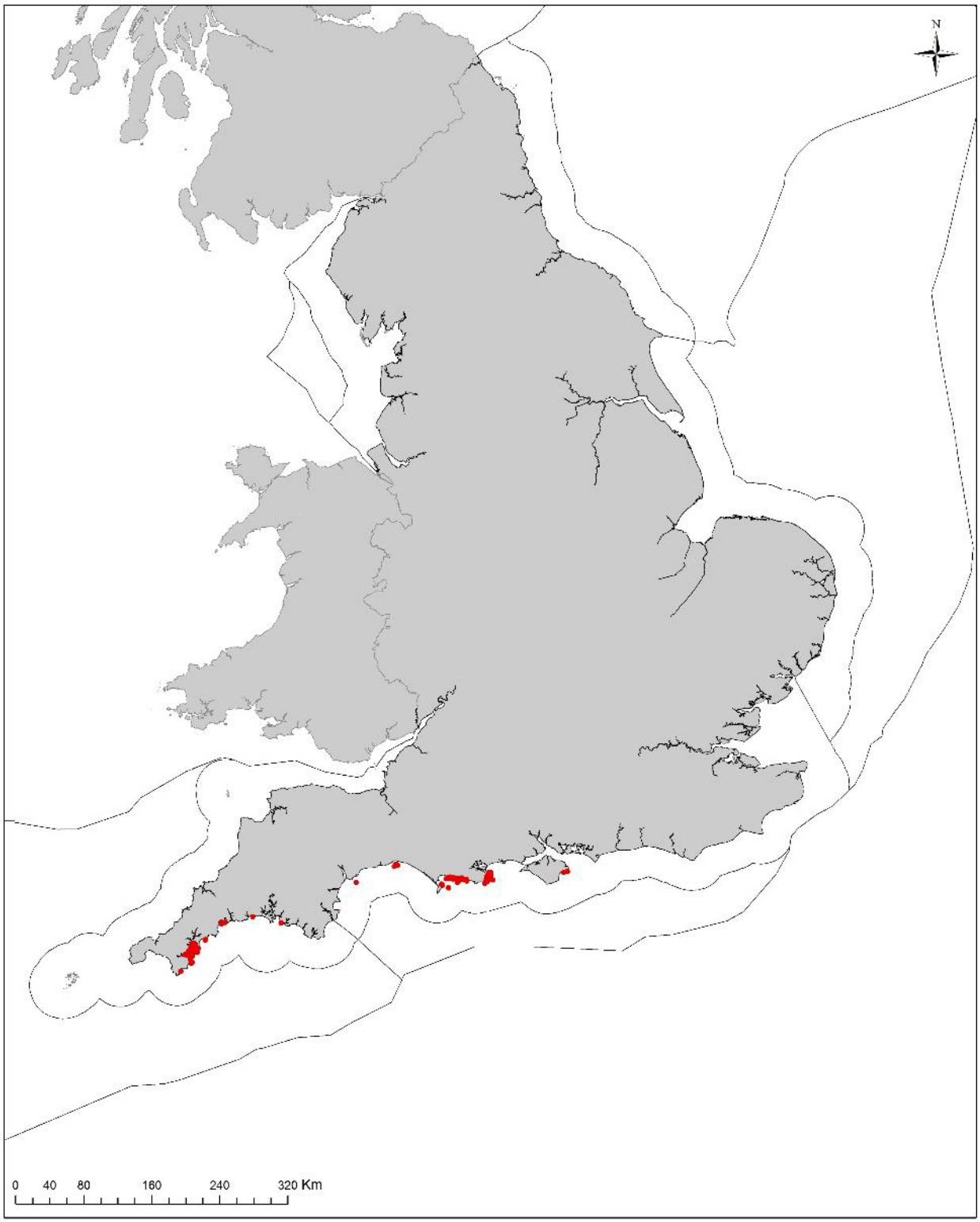
Predictors to explain light, temperature, water quality, depth, substrate, pH, currents, and chemistry were tested in the models (see Appendix 8). Generalised linear modelling (GLM) was used, with a binomial distribution (logit transformed) for presence and absence data. Standard model selection methods were used to find the most parsimonious model.

3. Results

3.1 Current distribution

The current (2009 to 2022) distribution of maerl bed habitats in English waters is from the Lizard Point in Cornwall to the east coast of the Isle of Wight (Figure 14). Maerl has been frequently recorded in the outer Fal and Helford estuaries in Cornwall, with scattered records from St Austell

Bay and along the coast around Plymouth (Figure 15). Maerl has also been recently recorded in Dorset in Lyme Bay, the Purbeck Coast and off Studland Bay (Figure 16).



Current presence of Maerl in English Waters

Current distribution

Maerl presence (2009 to present)

- Presence
- Marine Plan Areas
- Land

Map Reference:
MaRePo_Maerl_Current_Presence_EW

Map produced on 26 January 2023 by
m309458, Natural England

Scale (at A3): 1:4,000,000

Coordinate System: WGS 1984 Web Mercator Auxiliary Sphere
Projection: Mercator Auxiliary Sphere

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Figure 14. Current distribution of maerl habitats in English waters.

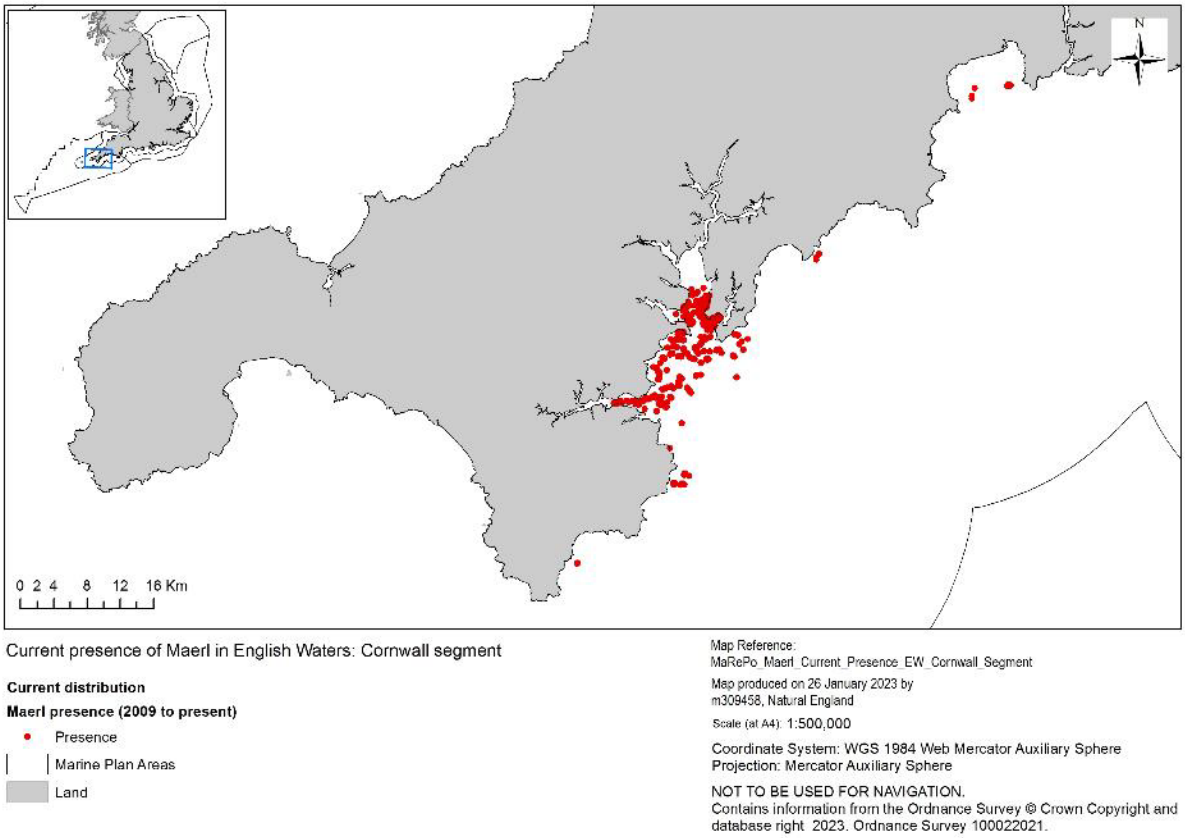


Figure 15. Close-up of current maerl habitat distribution in Cornwall

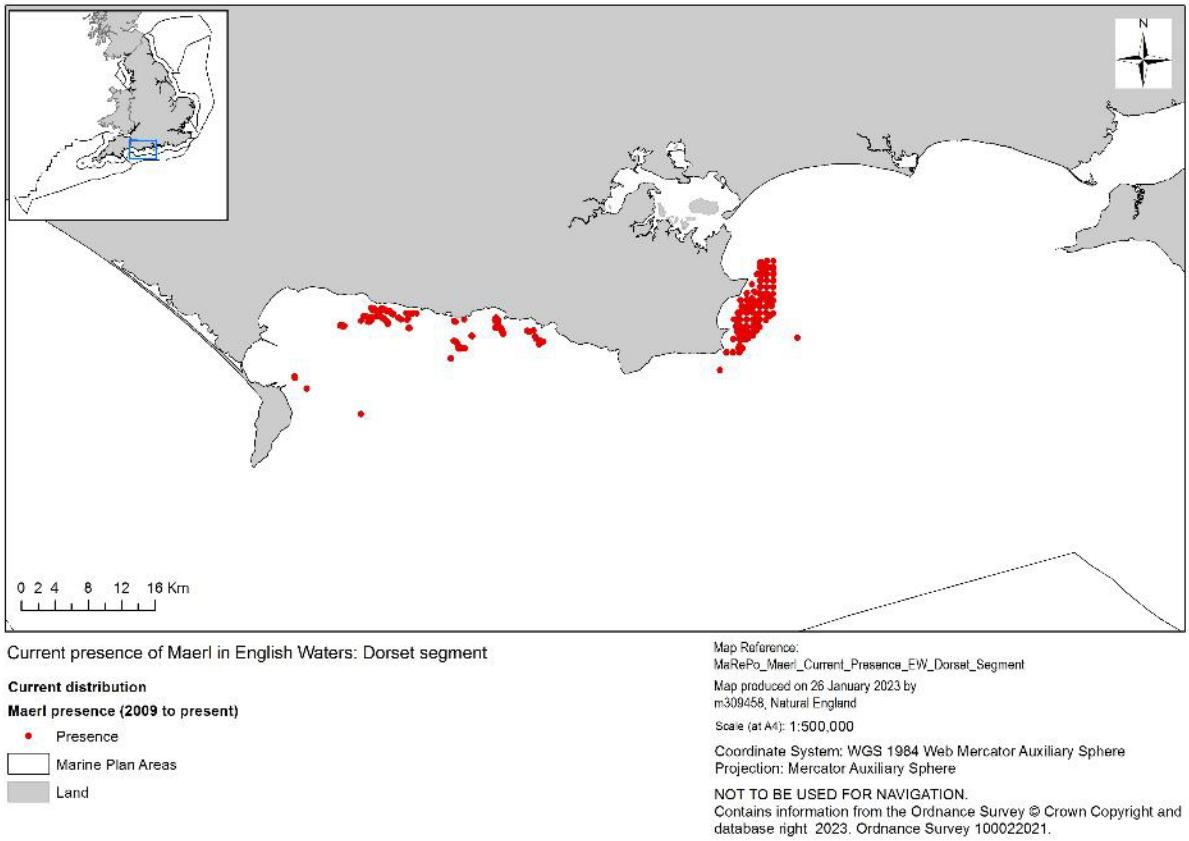
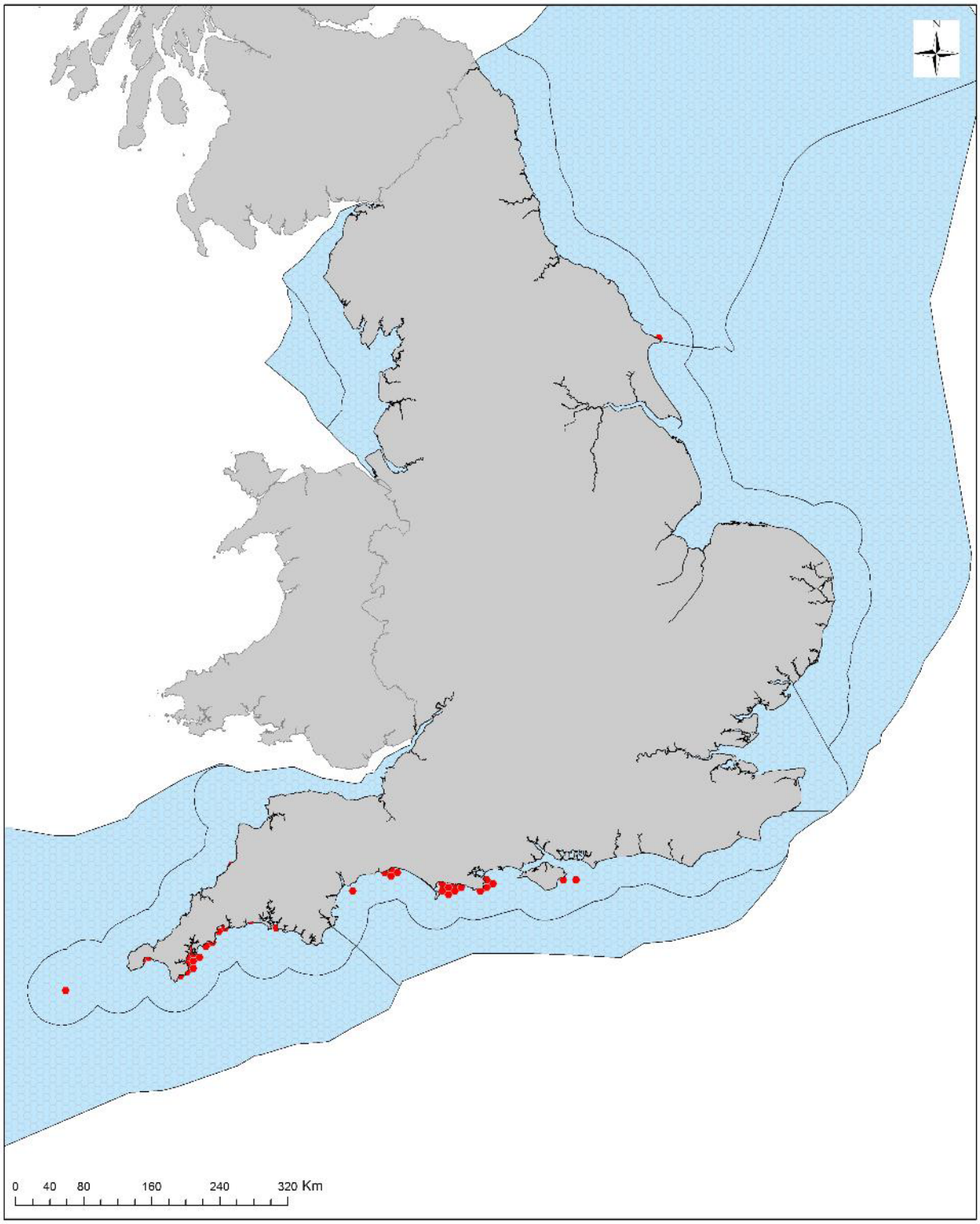


Figure 16. Close-up of the known current distribution of maerl bed habitats in the east coast of Dorset.

3.2. Historic distribution

The historic records for maerl habitats within the English waters are sparse (Figure 17) but the distribution coarsely matches that of the current data (Figure 14). The historic data shows additional data points within the northeast coast, Mounts Bay in Cornwall and the Isles of Scilly. The close-ups of historic maerl distribution in the southwest (Figure 18) and the south coast (Figure 19) suggest larger localised maerl habitat extents compared to current records, however the models require further work as outlined above before any clear conclusions can be drawn.



Historic presence of Maerl in English Waters

Historic distribution

Maerl PA (1885-2008)

- Presence
- Apparent absence
- Marine Plan Areas
- Land

Map Reference:
MaRePo Maerl Historic Presence EW

Map produced on 26 January 2023 by
m309458, Natural England

Scale (at A3): 1:4,000,000

Coordinate System: WGS 1984 Web Mercator Auxiliary Sphere
Projection: Mercator Auxiliary Sphere

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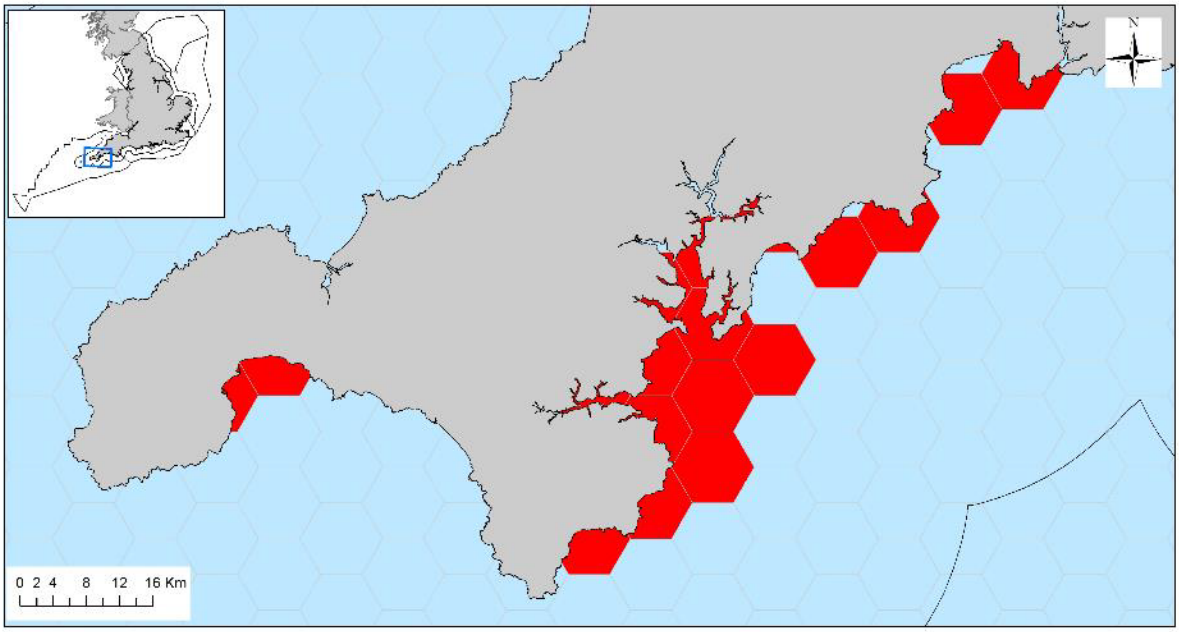
Figure 17. Historic distribution of maerl habitats in English waters.



Historic presence of Maerl in English Waters: Cornwall segment

Historic distribution

Maerl PA (1885-2008)

- Presence
- Apparent absence
- Marine Plan Areas
- Land

Map Reference:
MaRePo_Maerl_Historic_Presence_EW_Cornwall_Segment

Map produced on 26 January 2023 by
m309458, Natural England

Scale (at A4): 1:500,000

Coordinate System: WGS 1984 Web Mercator Auxiliary Sphere
Projection: Mercator Auxiliary Sphere

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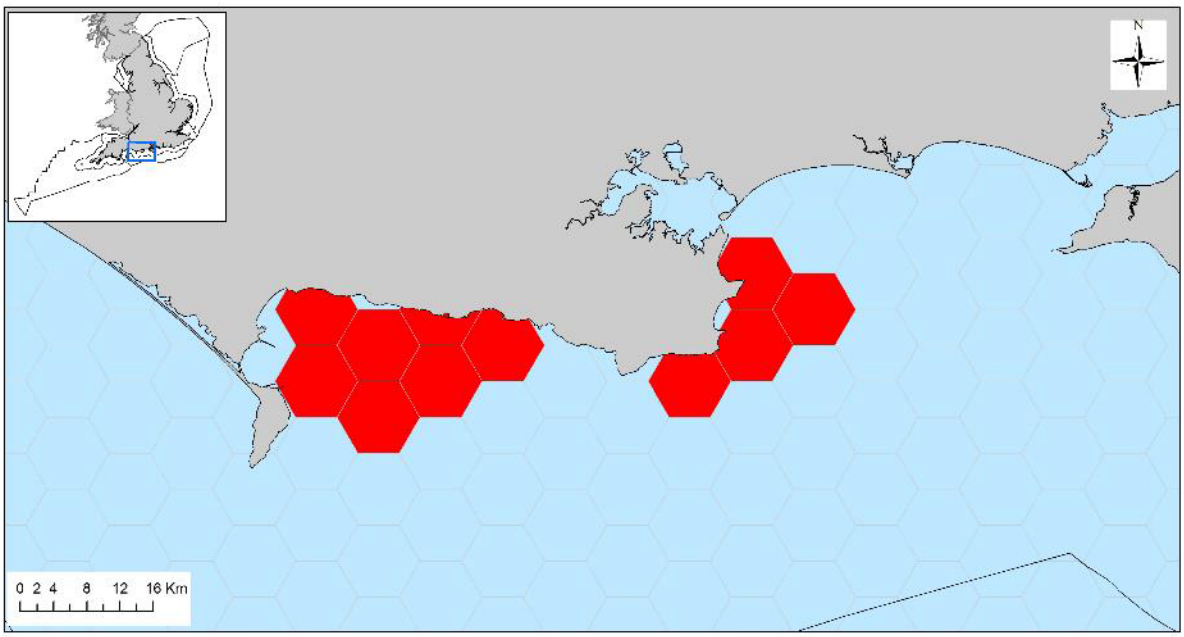
Figure 18. Close-up of the known historic distribution of maerl habitats in Cornwall.



Historic presence of Maerl in English Waters: Dorset segment

Historic distribution

Maerl PA (1885-2008)

- Presence
- Apparent absence
- Marine Plan Areas
- Land

Map Reference:
MaRePo_Maerl_Historic_Presence_EW_Dorset_Segment

Map produced on 26 January 2023 by
m309458, Natural England

Scale (at A4): 1:500,000

Coordinate System: WGS 1984 Web Mercator Auxiliary Sphere
Projection: Mercator Auxiliary Sphere

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Figure 19. Close-up of the historic distribution of maerl habitats in the south coast of England.

3.3. Habitat suitability

Draft maps of the current predicted habitat suitability for maerl on the coasts of England and Cornwall were completed and shown in the Figures 20 and 21. The extent of the model is depicted by colour ranging from zero probability of occurrence (in blue), to the highest probability of occurrence (red). There are several white areas, such as the inner Fal Estuary, where grid cells were excluded from the model due to gaps in the underlying datasets used to calculate probability.

The highest probability areas in Cornwall were on the south coast and strongly aligned with current and historic distributions of maerl. This included the outer Fal and Helford areas, Gerrans Bay and St Austell Bay. Smaller high probability areas included Lantic Bay (east of the Fowey Estuary) and St Ives Bay on the north Cornwall coast. The highest probability areas along the Dorset Coast (from west to east) included areas close to the coast between Ringstead Bay and Lulworth Cove; St Aldelms Head and Durlston Head and Boscombe to Hengistbury Head. An area off Studland Bay was also high probability.

The most parsimonious model for Cornwall included suspended inorganic matter in summer (SPM summer), slope, depth, and suspended inorganic matter in winter (SPM winter). All were significant in the model but SPM summer had the biggest influence, followed by Depth and SPM winter. Slope had a much smaller contribution in the model. Only 45% of the deviance was explained at this stage, as the model is not complete, as explained in paragraph 2.3 (Methods for Modelling habitat suitability for maerl).

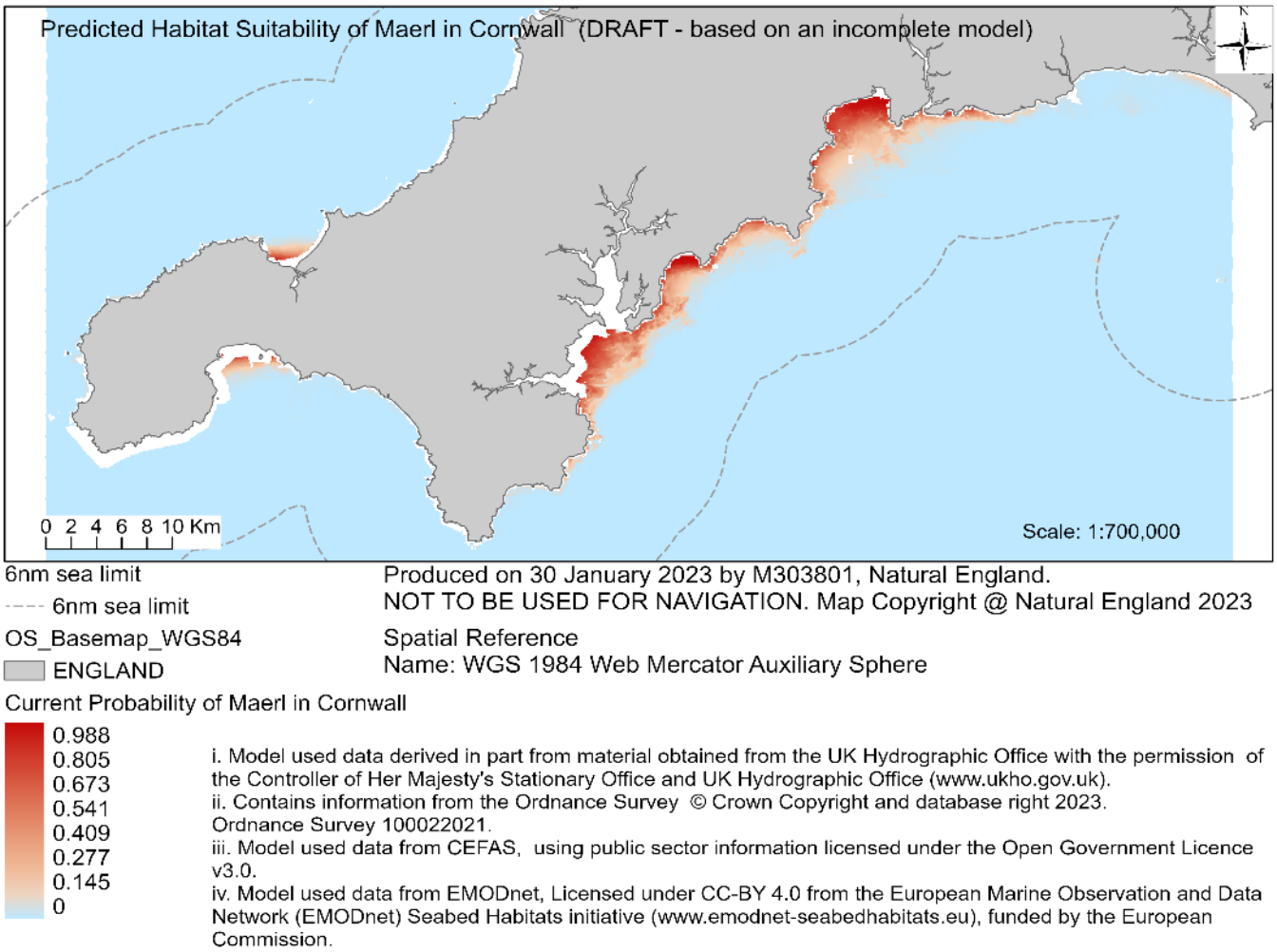

Figure 20. Draft predicted habitat suitability in Cornwall, southwest of England.

The most parsimonious model for Dorset included depth, light at the seabed (PAR), kinetic wave energy at the seabed, suspended inorganic matter in summer (SPM winter) and aspect, though aspect was not significant or influential in the model so should be excluded in a final model. Depth had the biggest influence on the model, followed by PAR, then SPM winter and Kinetic wave energy at the seabed both had much smaller influences in the model. Only 44.97 % of the deviance was explained at this stage, as the model is not complete, as explained in paragraph 2.3 (Methods for Modelling habitat suitability for maerl).

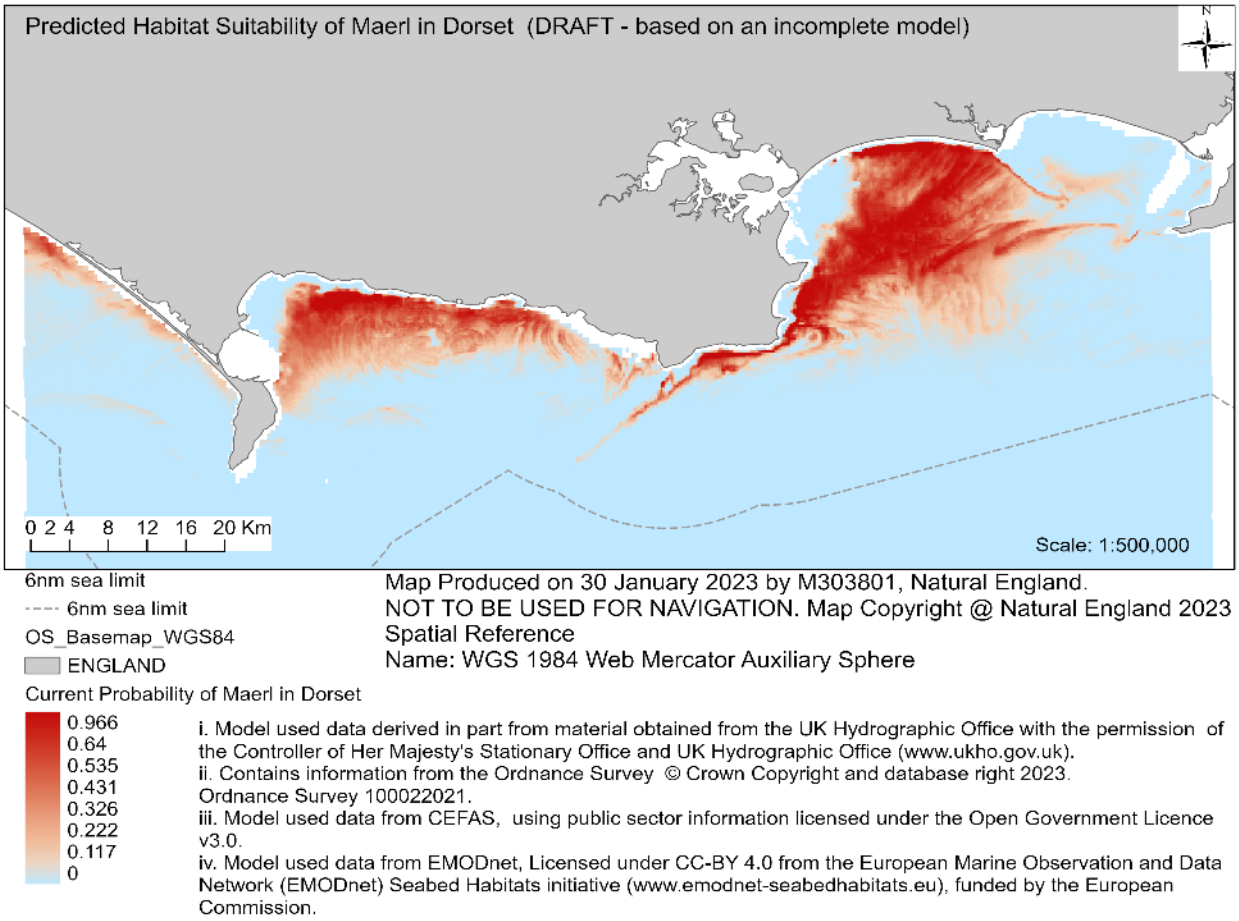

Figure 21. Draft predicted habitat suitability in the south coast of England.

The modelled predictions of maerl in current conditions, in relation to the current and historic maerl presence points can be seen in Figure 22. Only data points which are licenced to be mapped in the report are presented here, which is the majority of them. It should also be noted that due to standard data wrangling modelling requirements, only a subset of the current present points were used in the model. The historic data points were also not used in the model as it was based on the current distribution points, but are presented here for comparison. It is interesting to see where we have historic data in relation to the predictions as it shows that conditions modelled to be suitable, have in the past supported maerl, which may have been lost for various reasons.

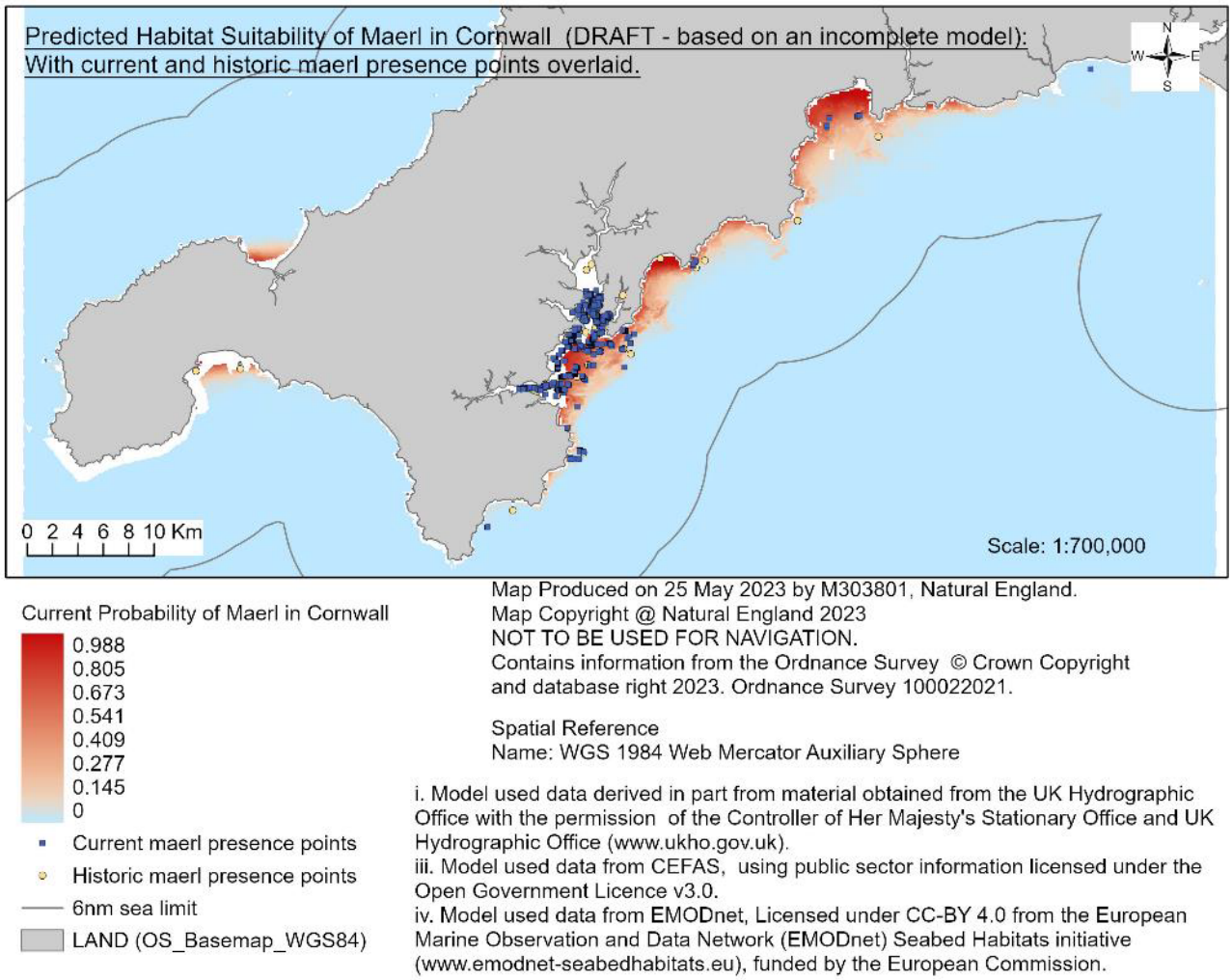

Figure 22. Predicted habitat suitability of maerl in Cornwall (Draft – based on an incomplete model) with current and historic maerl presence points overlaid.

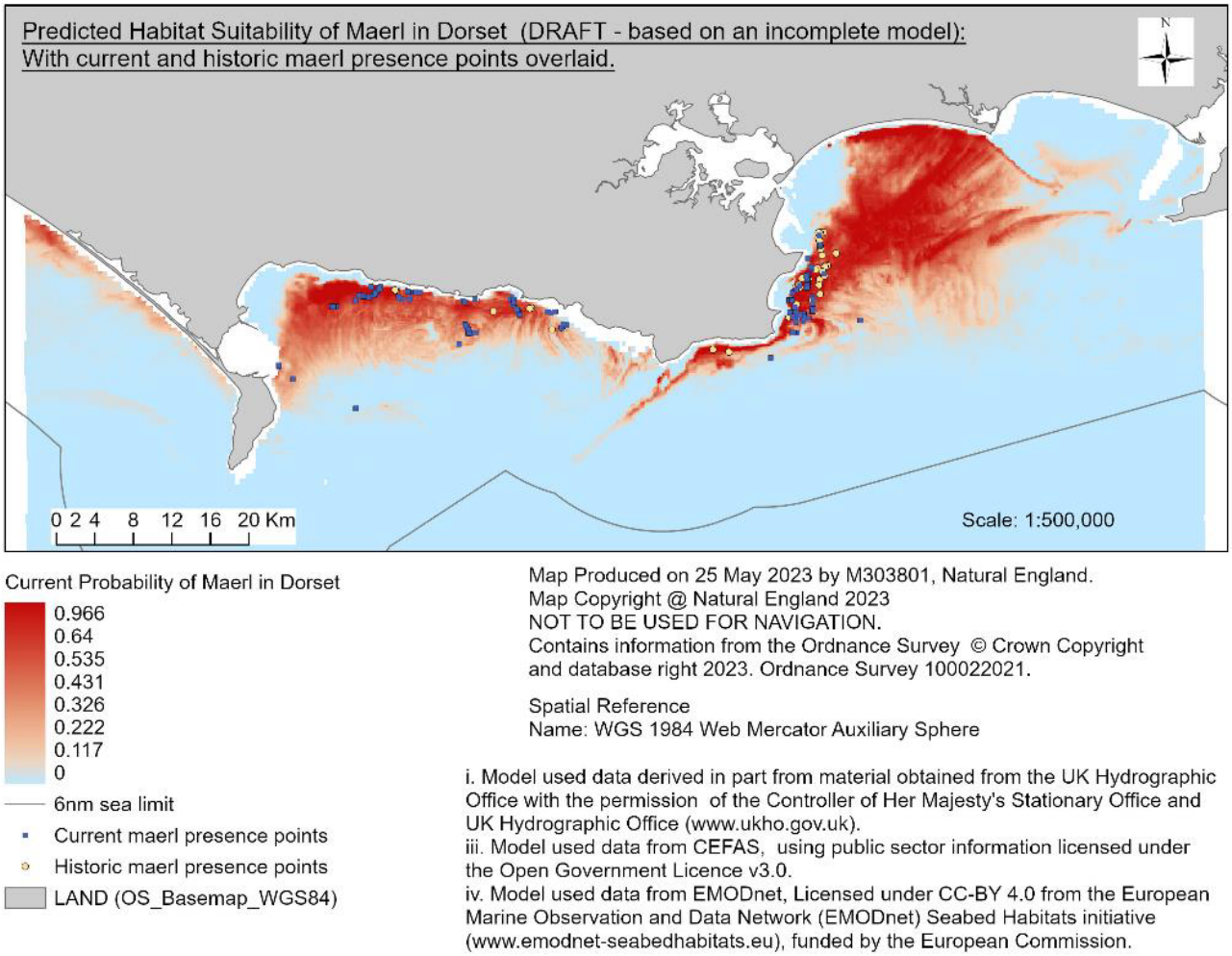

Figure 23. Predicted habitat suitability of maerl in Dorset (Draft – based on an incomplete model) with current and historic maerl presence points overlaid.

4. Discussion and future recommendations

Whilst we have some understanding on how currents, depth, light, sediment type, water quality, wave action, and salinity affect the distribution of maerl habitats and different maerl taxa, little is known about the interactive effects, relative gradients or the thresholds of these factors (Birkett *et al*., 1998). Furthermore, many of the abiotic parameters which could be included in habitat suitability models such as turbidity, light availability, and temperature, are not likely to stay constant over seasonal, annual or decadal time scales. Many of these parameters have been altered by anthropogenic activity during past centuries, for example pollution effects on water quality. Although some conditions may be improving due to interventions implemented such as the Water Environment Regulations, the impacts of climate change are likely to continue to cause significant changes to these variables in the future in different ways. Using these variables in models is therefore challenging.

This project models habitat suitability in English waters using abiotic environmental predictor layers selected on the basis of our understanding on their likely relevance, and the availability of data within the timelines of this pilot study. Habitat suitability models are a primary research tool and can interrogate which environmental factors are important for habitat suitability in a given area and their gradients, as long as all the relevant information is incorporated within the model structure.

As the models presented here are still under development, and some potentially relevant abiotic environmental predictors have not yet been included, caution should be applied when drawing conclusions from the results. The model fit and deviance explained (45 and 44.97 %) could be improved with more environmental data, as this would help explain any remaining uncertainty in the model. In particular, including substrate and sea temperature are likely to refine the model predictions as the explanatory power of both variables have been significant for similar maerl models in other places (Carvalho, et al., 2020, Martin et al, 2014, Simon-Nutbrown, et al., 2020). Incorporating pH into the models may also be important as it is likely to have an increasingly negative effect on maerl distribution due to ocean acidification (Brodie, et al., 2014). .

However, even with missing abiotic information and only recent observation data, the draft models already show an alignment to the known distribution of maerl, even if the area modelled is more extensive than the current distribution (Figures 17 and 19). The realized niche of a species which this model aims to calculate, is often wider than the current distribution. This is potentially where the distribution growth to date has been hindered by barriers limiting access to suitable habitat, or where it has been affected for other reasons temporarily or permanently. However, a realized niche highlights areas where conditions are currently suitable, and this can help to identify new restoration areas. The draft predictive maerl models presented here include recent data only (2009 and beyond), and the environmental predictors represent conditions from the past 20 years. Our model predictions thus reflect the current conditions and distribution of maerl.

In general, it should be noted that many current species and habitat distributions, including maerl, are unlikely to reflect their true native distribution prior to the anthropocene and are likely to be either reduced, or even completely shifted to sub-optimal habitat (Cromsigt et al, 2012, Guisan, et al, 2017). Including historic data in future models can help resolve this, and gives more insight into conditions which supported maerl in the past (Monsarrat et al, 2019). It is also useful to consider where those conditions may exist in the future, and where relevant information is available, model results can be projected into the future. This can be extremely insightful for identifying appropriate restoration areas, as it allows analysis of where the conditions are predicted to remain similar in the future, thus offering potential refugia where restoration efforts are likely to be more successful. It would therefore be beneficial to incorporate additional climate change prediction models into the next phase of the MaRePo project.

Overall, this review demonstrates that based on the current and historic distribution of maerl beds and their modelled habitat suitability, there may be potential to enhance maerl species distribution and abundance to assist with their recovery in English waters. However, even though our knowledge of maerl is increasing, there are several aspects of maerl biology and ecology crucial for restoration

success that remain uncertain or unknown, including species-specific reproduction and biology, distribution of distinct species, and the environmental gradients and thresholds controlling their distribution (see e.g. Birkett *et al*., 1998). Until these significant evidence gaps are filled, restoration of maerl would be extremely difficult and to our knowledge, active restoration of maerl bed habitats has not yet been attempted in England or elsewhere in the world.

Although the sexual and asexual reproduction have been described for *P. calcareum* (Prado et al., 2016), knowledge of these processes remains largely unknown for most maerl species, and other forms of reproduction (e.g. fragmentation) may also be important. Identification of maerl species is notoriously difficult, however novel applications of DNA monitoring have recently provided new evidence on the distribution of different taxa along the European western fringe (Jenkins, 2021) and along the south coast of England (Jenkins *et al*., in prep). As these studies included some 100 samples for DNA analysis collected from relatively few locations, additional research is needed to map the taxa present in all of England, to assess the potential for recovery of these taxa, and to further explore the possibility of endemism and genetic uniqueness of maerl taxa in separate English maerl habitats (Jenkins, 2021). These factors could have wide ranging consequences to any maerl restoration programmes and further studies would be recommended.

Little is also known about ecosystem level feedbacks and interactions within maerl bed habitats, and more extensive research is needed to fully understand the effect of intra-species interactions on maerl distribution and community composition. Although biotic interactions can be positive, they can also alter or limit critical conditions for maerl habitats, such as light levels and sedimentation (Riosmena-Rodriguez 2017a). Greater focus on evaluating the interactions with competitive benthic species and the impact of ecosystem level interactions on maerl distribution is required. Additionally, due to the slow growing characteristics of maerl coupled with the variability in growth forms and morphology, there is little scientific research on the genetic and phenotypic diversity of maerl and the differences in their tolerance thresholds. As there has been comparatively little research into the physiology and reproductive biology of maerl species, it is currently not possible to evaluate how current anthropogenic variables are influencing maerl ecology and furthermore their overall resilience and recovery potential. Filling these evidence gaps will be fundamental for successful restoration of maerl habitats over long term.

Native oysters

1. Literature review

1.1 Biology and ecological importance

The native oyster, *Ostrea edulis,* is a bivalve mollusc of the order Ostreida, characterised by an oval or pear-shaped shell with a rough, scaly surface (Perry et al., 2017) typically with a pale yellow or green colouring and light brown or blue concentric bands (Preston et al.). The left valve is concave and fixed to the substratum, the right valve flat and sitting inside the left (Perry et al., 2017, Perry and Tyler-Walters, 2016).

Ostrea edulis is a suspension feeding invertebrate, using valves to pump water across the gill structures to filter out food particles (phytoplankton, bacteria, particulate detritus and dissolved organic matter) from the surrounding water (Korringa, 1952, Yonge, 1960, Perry et al., 2017, Perry and Tyler-Walters, 2016, Preston et al.). *O. edulis* has slow growth rates and reaches shell heights of up to 15 cm over the typical life span of 5-10 years (although they can live up to 30 years) (Preston et al*.,* 2020).

Ostrea edulis are protandrous hermaphrodites, beginning life as a male and later developing into a female, and then alternating between sexes frequently (Coen et al., 1999, Korringa, 1952). *O. edulis* are larviparous; females draw free swimming sperm, released into the water column by males, into their mantle to fertilise their eggs, and retain them for 7 – 10 days before releasing them as veliger larvae 170-190 µm in size (Korringa, 1952, Walne, 1956, Laing et al., 2006, Woodward, 1951). The larval stage lasts 6-15 days and survival through the pelagic phase to recruitment impacts greatly on population fitness (Korringa, 1952). Recruitment success is influenced by environmental parameters such as temperature, pH, salinity, light, tidal phase, water quality, predation and available substrate (Kennedy and Roberts, 1999, Cole, 1951).

Spawning coincides with spring tides (Korringa, 1952, Yonge, 1960), typically between May and June in the UK (Preston et al.). Hydrographic conditions can result in larvae being dispersed over a large area (Perry et al., 2020). However, settlement can only occur if suitable hard substrates, such as shell and stone, are available (Preston et al., 2020; Rodriquez-Perez et al., 2019). Location is important because the larvae attach to the substrate and metamorphose into immobile adults, becoming reliable on the immediate environment for their survival and the success of the population (Kamermans et al., 2018; Holbrook, 2021b).

Native oysters are gregarious, leading to the formation of biogenic habitat types; oyster beds and oyster beds (Zu Ermgassen *et al*., 2021). OSPAR have defined “oyster beds” as “*Ostrea edulis* occurring at densities of 5 or more per m^2 on shallow mostly sheltered sediments (typically 0–10m depth, but occasionally down to 30m). There may be considerable quantities of dead oyster shell

making up a substantial portion of the substratum." (OSPAR Commission, 2008; Preston *et al*., 2020).

Oyster beds support a diverse fauna consisting of *O. edulis* as well as protozoa, sponges (e.g. *Halichondria bowerbanki, Amphilectus fucorum*), hydroids, the benthic stages of *Aurelia* sp., flatworms, ribbon worms, nematodes, polychaetes (e.g. *Chaetopterus variopedatus, Myxicola infundibulum, Spirobranchus triqueter* and *Sabella pavonina*), amphipods, ostracod crustaceans, decapod crustaceans (*Pagurus bernhardus*, *Carcinus maenas* and *Hyas* Araneus), gastropod molluscs (Seraphsidae, *Ocenebra erinacea* and *Urosalpinx cinerea*), barnacles (e.g. *Balanus balanus* and *Eliminius modestus*), ascidians (e.g. *Aplidium punctum*, *Ascidiella aspersa*, *Ascidiella scabra* and *Dendrodoa grossularia*), bryozoans, starfish (*Asterias rubens*), fish and sea urchins (Korringa, 1951; Yonge, 1960; Perry *et al*., 2020; JNCC, 2022). A turf of seaweeds (e.g., *Plocamium cartilagineum, Nitophyllum punctatum* and *Spyridia filamentosa*) may also be present (Connor *et al*., 2004; Perry *et al*., 2020). In England, oyster beds belong to the EUNIS habitat classification "*Ostrea edulis* beds on shallow sublittoral muddy mixed sediment", the corresponding habitat codes for this biotope are in Table 4. This biotope describes dense native oyster beds from 0 – 20 m on muddy sand and mixed substrate where large amounts of dead oyster shell are often present (Connor et al., 2004, Perry et al., 2020).

Table 4. EUNIS habitat classification for *Ostrea edulis* beds.

	EUNIS code	National Marine Habitat Classification for UK AND Ireland code - JNCC (2004, 2015, 2022)	1997 Biotope
***Ostrea edulis* beds on shallow sublittoral muddy mixed sediment**	A5.435	SS.SMx.IMx.Ost	SS.IMX.Oy.Ost

Ostrea edulis are depositional habitat engineers (Coen *et al*., 1998; OSPAR Commission, 2009) that provide several ecological functions and ecosystem services summarised in Table 5 (Coen et al., 1999). The complexity of the biogenic habitat supports an abundance of fauna and flora (see Appendix 9), a total of 246 species have been recorded within this biotope (Perry et al., 2020). The importance of this species is reflected in the number of conservation designations assigned to it (Preston et al. 2020):

- OSPAR (Convention for the Protection of the Marine Environment of the North-East Atlantic) List of Threatened and/or Declining Species and Habitats. OSPAR agreement 2008-6, (OSPAR Commission 2009), (Region II – Greater North Sea and Region III – Celtic Sea)
- EU Special Area of Conservation (SAC) Features. EU Directive 92/43/EEC on the conservation of natural habitats and of wild flora and fauna also known as the Habitats Directive. Note: There is no specific feature for native oysters, but their habitats might come under subtidal sub features (in England) of 'Reefs' or 'Subtidal Sandbanks', 'Estuaries' or 'Large Shallow Inlets and Bays'. Additionally, in England, it may receive some associated protection under 'A5.4 Subtidal Mixed Sediments' as a 'Supporting Habitat' in some SPAs
- UK Biodiversity Action Priority species. UK Biodiversity Action Plan (1994)

- Species of Conservation Importance (SOCI). Marine and Coastal Access Act 2009
- Feature of Conservation Importance (FOCI). Marine and Coastal Access Act 2009
- Species of principal importance for the purpose of conservation of biodiversity. Natural Environment and Rural Communities Act 2006.

Table 5. Ecological functions and ecosystem services provided by *O. edulis* biogenic habitat.

Ecological function		**Reference**
Hard substrate	Provide settlement substrate, particularly in areas of soft sediment that lack settlement substrate	OSPAR Commission, 2008; Perry et al., 2020
Complex, three-dimensional habitat	Supporting a greater diversity and biomass than surrounding sedimentary seabed	OSPAR Commission, 2008; Preston et al., 2020; Fitzsimmons et al., 2019
	Nursery ground for small and juvenile fish and other species	
Sediment modification	Increasing the amount of shell debris and organically enriching the sediment with faeces and pseudofaeces	Preston et al., 2020; Perry et al., 2020
	Providing a rich food source for infauna, detritivores, deposit feeders, meiofauna (including nematodes and polychaetes) and bacteria	
pelagic-benthic coupling	Transferring phytoplankton primary production and nutrients to benthic secondary production	Dame, 1996; Preston et al., 2020; Perry et al., 2020
Ecosystem service		
Improving water quality and water clarity	Filtration of large quantities (up to 200 l of seawater per day) of water	OSPAR Commission, 2008; Preston et al., 2020
	Removal of nitrogen through denitrification by bacteria in the underlying sediments	
carbon sequestration	Stabilising carbon in sediment	Fitzsimmons et al., 2019; Lee et al., 2020
Reducing shoreline erosion	Stabilising sediments, dissipating wave energy and acting as a breakwater	Fitzsimmons et al., 2019

1.2 Habitat distribution and extent

Ostrea edulis is native to the northeast Atlantic, where the species occurs naturally in intertidal to subtidal shallow waters (OSPAR, 2008) from the Norwegian Sea south to Morocco and is also found in the Mediterranean Sea and Black Sea (Perry et al., 2017, Launey et al., 2002). *O. edulis* is widely distributed around the British Isles but is less common on the east and northeast coasts of

Britain and Ireland. The main stocks are now on the west coast of Scotland, the southeast and the Thames estuary, the Solent, the River Fal, the blackwater (Preston et al., 2020) and Lough Foyle (Tyler-Walters, 2008b, Perry et al., 2017). *O. edulis* has been introduced to many other areas including the United States, Canada and Japan (Korringa, 1952, Wisely, 1978, Launey et al., 2002).

Native oysters once formed vast reefs along the European coastlines, this can be seen in The Piscatorial Atlas, created in 1883, which portrays the known distribution of native oyster beds around the coast of the UK, English Channel and the North Sea (Figure 24), although it is worth noting that the extent of former *O. edulis* beds shown in the Piscatorial Atlas is considered to be an underestimation. Data on the historical distribution of *O. edulis* beds is lacking (OSPAR, 2008) as is evidence on the structure, composition, clustering, density, and the associated fauna and flora that characterise a healthy, natural oyster habitat (Preston *et al*., 2020). This is due to a lack of historical monitoring prior to the habitat being degraded (Zu Ermgassen et al., 2020).

Figure 24. Olsen's Piscatorial Atlas of the North Sea 1883, showing the known distribution of native oysters at the time (taken from Preston et al., 2020).

1.3 Factors affecting habitat extent and distribution

1.3.1 Environmental factors

Ostrea edulis beds typically occur on shallow sublittoral muddy fine sand or sandy mud mixed sediments (JNCC, 2022) at depths of 0 – 20 m (Perry et al., 2020). Historically native oyster beds have been found at depths up to 80 m off the Channel Islands and Grimsby (UK) and the wider North Sea (Perry et al., 2020, Laing et al., 2005). *O. edulis* is euryhaline occurring in estuarine and coastal waters, however the *O. edulis* beds biotope has only been recorded in full salinity (Perry et al*.,* 2020).

Ostrea edulis is found at low energy sites (< 130 Nm^{-2}) in areas with' Very Weak' (negligible), and 'Weak' < 1 knot (<0.5 m/sec.) tidal flows. Increased water flow can cause oysters to be swept away, affect feeding ability, reduce reproductive success, and interfere with spat settlement (Perry et al., 2017). Low current speeds (such as those experienced during neap tides) favour retention of larvae and keep the larvae longer near the oyster bed where the conditions for oysters are favourable for settlement, survival, and growth (Maathuis et al., 2020).

The native distribution of *O. edulis* (and most of the characterising species of this biotope) indicates a tolerance to a wide range of temperatures (Perry et al*.,* 2020). Filtration rate, metabolic rate, assimilation efficiency and growth rates of adult *O. edulis* increase with temperature (Perry et al*.,* 2020). Temperature is also an important factor in the recruitment of *O. edulis,* especially at the northern extremes of its range (Spärck, 1951), with spawning occurring at temperatures above 15-16 °C, (Yonge, 1960). Larval growth rate improves with increasing temperature and the optimal temperature for larval survival is 12.5 - 27.5 °C (Davis and Calabrese, 1969).

1.3.2 Ecological pressures

Assessments of the sensitivity of *O. edulis* and *O. edulis* beds were carried out by Perry et al. (2017) and Perry et al. (2020) respectively (See Appendix 10), *O. edulis* beds are listed as highly sensitive to 12 pressures including the introduction of microbial pathogens and parasites, non-native species, substrate loss, and smothering (Perry et al., 2020).

Of note, is the parasitic protozoan *Bonamia ostreae,* which causes the disease bonamiosis (Preston *et al*., 2020; OSPAR Commission, 2009). Infected populations can experience 90% mortality (Preston et al., 2020). Bonamiosis was first diagnosed in England in 1982 and now occurs in most of the south and east coast oyster producing areas (Laing et al., 2006, Culloty and Mulcahy, 2007). Population crashes caused by bonamiosis have occurred in England as well as the Netherlands, Spain and France (Edwards and Watson, 2011). In the absence of any means to eradicate these pathogens, disease control in Europe is achieved by means of biosecurity, with European Directives (EC Council Directive 2006/88/EC) underpinning national restrictions on the movement of diseased stocks. These restrictions attempt to control the spread of disease through the prohibition of movement of parasite-positive oysters from areas of existing disease into new areas with no oysters, or with oysters that are disease free. Although effective, the recent spread

of *B. ostreae* to New Zealand in the absence of a host introduction (Lane 78 et al., 2016; Lane and Jones, 2020) suggests that efforts to limit the spread of bonamiosis are unlikely to provide absolute and permanent protection.

Aquaculture is a vector for the spread of disease and invasive non-native species (INNS) through both the target fishery species and their hitchhikers. The intentional introduction of Pacific oysters (*Magallana gigas*) into aquaculture has resulted in the proliferation of wild populations establishing in the intertidal zone. Native oysters occur in the lower intertidal and predominantly sub-tidal zone (Preston *et al*., 2020). Although the likelihood is unclear, there is a possibility that the Pacific oyster may take over the niche of the native oyster and therefore limit the opportunities for recolonisation by *O. edulis* (OSPAR Commission, 2009). There is also a direct competition between the species for food (Preston et al 2020).

Shipments of the American oyster (*Crassostrea virginica)* in the 1800's resulted in the introduction of the American slipper limpet (*Crepidula fornicata*) and American oyster drill (also known as the American whelk tingle, *Urosalpinx cinerea*), both of which have negative impacts on the native oyster today (Perry and Tyler-Walters, 2016, Perry et al., 2020).

American slipper limpets compete with native oysters for space and alter the biotope to a *C. fornicata* dominated biotope (e.g., SS.SMx.SMxVS.CreMed) (Walne, 1956, Laing et al., 2006, Connor et al., 2004, Perry et al., 2020); they also compete for food (Walne, 1956, Perry et al., 2020); and smother oysters and the surrounding substratum with faeces and pseudofaeces that prohibit settlement (Blanchard, 1997, Eno et al., 1997, Perry et al., 2020).

The American oyster drill *Urosalpinx cinerea* predates on *O. edulis* spat and is a significant pest to both wild and cultured stocks (Korringa, 1952; Yonge, 1960 in Perry et al*.,* 2020; OSPAR Commission, 2009). *U. cinerea* has previously contributed to the decline of oyster populations; 55 – 58% of the oyster spat settling in 1953 in Essex oyster beds were destroyed by *U. cinerea,* mortality rates decreased to 10% in adult oysters (Hancock, 1954). This non-native species therefore has the potential to hinder *O. edulis* restoration efforts (Laing *et al*. 2006).

1.3.3 Anthropogenic pressures

Excessive harvesting of *O. edulis* beds and the accidental spread of diseases are the two dominant factors that have contributed to a rapid decline in the global population of *O. edulis*, which has so far resulted in over 85% loss of oyster habitat (Jackson et al., 2001; Smith et al., 2006; Smyth et al., 2009; Beck et al., 2011; Grabowski et al., 2012; Gercken and Schmidt, 2014; Long et al., 2017). The UK oyster fishery peaked in the mid-1800s (Preston *et al*., 2020). The overfishing of *O. edulis* beds in the late 1800s and early 1900s was the primary driver of the degradation and decline of this habitat and the biotope faced collapse by the mid-1900s (Preston *et al*., 2020; Zu Ermgassen *et al*., 2021).

The main threat to *O. edulis* and *O. edulis* beds is overexploitation (OSPAR Commission 2009). Destructive harvesting and overfishing can reduce the extent, vertical relief, complexity, and biodiversity of oyster bed habitat (Coen et al., 1999, Beck et al., 2011, Perry et al., 2020). Hall

(2008) found limited evidence of recovery following damage by bottom towed fishing gear. Deposit feeding polychaetes may also colonise *O. edulis* beds which have been severely damaged by trawling, thus limiting recovery (Perry et al*.,* 2020). As well as the impacts of oyster fisheries, bottom towed gear fisheries targeting other species have also caused damage to oyster habitats (OSPAR Commission 2009).

1.3.4 Climate change impacts

The global decline of native oysters has been attributed, in part, to adverse effects of climate change (Beck et al., 2011, Vera et al., 2019), however, no direct climate change associated impacts have been attributed to their distribution and extent in UK waters to date (Mieszkowska et al., 2013). It is important to consider that this species has been heavily impacted by stressor such as overfishing, diseases and competitors, and additional factors such as climate change with rising temperatures and pollution could create cumulative pressure for this species (Holbrook, 2020).

Mortality of adult *O. edulis* is often reported in relation to environmental stressors such as climate fluctuations (Cole, 1951), and temperature has been recognised as an important factor influencing reproductive parameters in many species of bivalves, including *O. edulis* (Korringa, 1952, Wilson et al., 2021, Wilson et al., 2004). Furthermore, larval stages are less tolerant of high temperatures than adult oysters, exasperating the negative impact on recruitment (Perry et al*.,* 2020).

Sea-surface temperatures in the northeast Atlantic and UK coastal waters have been rising since the 1980s by around 0.2-0.9ºC per decade, with further rises predicted for the future (Holliday et al., 2008; Marine Climate Change Impacts Partnership, 2015). *O. edulis* occurs in the Mediterranean, therefore it is expected that it will be able to withstand predicted gradual increases in temperature in UK waters (Perry et al*.,* 2020), however, temperature is likely to impact the behaviour, growth, reproduction, and survival of natural populations (Vera et al., 2019; Joyce et al., 2013).

The effects of ocean acidification on *O. edulis* are unclear; they have been reported to be a robust species to ocean acidification at levels predicted for the end of this century (Prado et al., 2016, Lemasson et al., 2018), unlike other species of oyster, however Sezer *et al*. (2018) observed bleaching and change in micro-community on the shell surface.

There is uncertainty on how sea level rise will affect exposure or tidal energy and how potential changes may affect this biotope (Perry et al*.,* 2020). As a habitat found in low energy areas, it seems likely that increased storminess will have a negative impact.

Interactions between native oysters and invasive species are likely to evolve as a result of climate driven environmental changes; invasive species that originate from warmer climates are likely to proliferate at a greater rate as water temperature increases. INNS, such as the Pacific oyster, will present increased competition for food and space, and predatory INNS will exert greater top-down control on native oyster populations (Mieszkowska *et al*., 2013).

1.4 Restoration approaches

The international standards of ecological restoration are outlined in "Global Restoration Guidelines for Shellfish Reefs" (Fitzsimmons et al., 2019) and Preston *et al*. (2020) provides specific information relating to the restoration of the European native oyster in the UK and Ireland.

Understanding whether an area is recruitment limited (lack of oyster broodstock), substrate limited (lacking reef structure for oysters to attach) or both, will inform decisions on what restoration treatment should be applied (Fitszimmons *et al*., 2019). In a recruitment-limited scenario, adult or juvenile (known as 'seed') oysters will need to be added to the reef. These can be adult animals, but more typically juvenile animals are added. Juvenile shellfish tend to be more readily available in large quantities than adult broodstock; this is particularly true of the quantities required for large-scale restoration (i.e. 0.5 hectares or larger) (Fitszimmons *et al*., 2019).

Oyster supply is a key limiting factor in oyster restoration projects. Sources of native oysters include oyster hatcheries, spatting ponds, on-growing wild spat in ponds and broodstock from wild fisheries (Preston et al*.,* 2020). 'Cultchless' seed (attached to very small pieces of cultch, e.g. a grain of sand) or 'cultched' seed (attached to a larger piece of cultch, e.g. an empty shell) can be produced (Fitszimmons *et al*., 2019). Cultched seed is used most often for restoration as it mimics the natural oyster bed (where larvae attach to shells of previous generations) and may also be less vulnerable to predation than cultchless seed (Fitzsimmons *et al*., 2019). Unset larvae are not currently a viable option for *O. edulis,* as attempts to transport larvae have previously resulted in 100% mortality (Fitszimmons *et al*., 2019). Biosecurity, seasonality and maintaining genetic diversity are important considerations when sourcing oysters (Preston et al*.,* 2020; Fitzsimmons *et al*., 2019) and a very high mortality rate should be anticipated (Fitzsimmons *et al*., 2019).

In a substrate-limited scenario, reef will need to be constructed from an appropriate substrate. Factors to consider when selecting substrate include oyster larvae settlement preferences, wave energy, water depth, purpose of the restoration project, sedimentation, conservation status, fishing activity, material availability and cost (Fitzsimmons *et al*., 2019).

In a both recruitment and substrate limited scenario, restoration efforts will involve constructing reefs first, and then seeding them with oysters (as described above) (Fitszimmons *et al*., 2019). Parameters to consider when selecting a suitable site for oyster restoration include historic presence of the species, suitable water quality (dissolved oxygen, temperature and salinity), water depth and biotic factors (food availability and predators) (Fitzsimmons *et al*., 2019).

To date, restoration of *O.edulis* has been attempted in multiple locations in the UK with varied outcomes. The collection of spat on cultch for seeding suitable areas has been successful in Ireland (Clew Bay, Cork Harbour, Lough Swilly and Lough Foyle) (OSPAR, 2009). Some moderate success was also seen from the addition of shell clutch and adult oysters to the seabed in France (Yonge, 1960). However, attempted restoration of *O. edulis* beds in the Firth of Forth by relaying parental stocks was unsuccessful and resulted in the depletion of the donor stock (Key and Davidson, 1981).

Similarly, the oyster restoration project in the late 1990s in Strangford Lough, Northern Ireland, which included placement of cultch, seed and adult oysters at nine sites, failed to sustain the initially recorded increases in oyster population due to harvesting and bonamiosis infection (Kennedy and Roberts, 1999, Laing et al., 2005, Laing et al., 2006, Smyth et al., 2009). The restoration of native oysters in Chichester Harbour in 2010 has also had limited success: although 2,298kg of broodstock oysters were relayed on the seabed, the population has suffered from a biased sex ratio (male:female of 3:1) and high mortality rates (Vause, 2010, Eagling, 2012, Eagling et al., 2018).

Bonamia has impeded many restoration attempts (Kennedy and Roberts, 1999, Laing et al., 2005, Smyth et al., 2009, Vause, 2010, Eagling, 2012); in order to sustain restored native oyster populations, it has been suggested that the use of parasite-positive, but otherwise healthy, broodstock may increase population resilience (Holbrook et al., 2021). Movement of parasite-positive broodstock is currently restricted (EC Council Directive 2006/88/EC), however, *Bonamia* spp. are now present throughout much of the natural range of *O. edulis* and the recent spread of *B. ostreae* to New Zealand in the absence of a host introduction (Lane et al. 2016; Lane and Jones, 2020) suggests that efforts to limit the spread of bonamiosis are unlikely to provide absolute and permanent protection (Holbrook 2021). Furthermore, since parasite prevalence probably increases with density (Engelsma et al., 2010), the risk of disease incidence may increase through restoration attempts. This should obviously be avoided.

2. Methods for mapping the current, historic and potential distribution

2.1 Current distribution

Although *O. edulis* is widely distributed around the British Isles, native oyster beds are sparsely distributed around the UK and Ireland, and are recorded from Strangford Lough, Lough Foyle and the west coast of Ireland, Loch Ryan in Scotland, Milford Haven in Wales, and from Dawlish Warren, the Dart Estuary and the River Fal in the southwest England, and the River Crouch in east England (Tyler-Walters, 2008a, Perry et al., 2020).

O. edulis beds are tolerant of a wide range of temperatures and occur in full salinity waters (Perry et al., 2020). Perry et al. (2020) states *O. edulis* beds are highly sensitive to 12 pressures including substrate loss, smothering, introduction of microbial pathogens/parasites and introduction of non-native species.

Native oyster data from Natural England's Marine Evidence Database and data previously compiled as part of the Marine Management Agency project MMO1135 (which carried out an

OBIS database search (MMO, 2019)) were mapped in ESRI ArcGIS. Data sources are listed in Appendix 11.

To determine current extent, data were then filtered to select records occurring in 2010 or after. Only records occurring within English waters (Marine Plan Areas) were included. The resultant datasets contained 120 “current” records for *O. edulis*. A map of current (post 2010) extent of *O. edulis* was produced in ArcGIS. Data sources can be viewed in Appendix 11.

2.2 Historic distribution

Ostrea edulis beds were historically a dominant feature of European coastal and offshore waters (Zu Ermgassen *et al*., 2021). The UK oyster fishery peaked in the mid-1800s (Preston *et al*., 2020). The overfishing of *O. edulis* beds in the late 1800s and early 1900s was the primary driver of the degradation and decline of this habitat (Zu Ermgassen *et al*., 2021). The biotope faced collapse by the mid-1900s due to overfishing, habitat loss, poor water quality/pollution, disease, and the introduction of invasive species (Preston *et al*., 2020; Zu Ermgassen *et al*., 2021).

Native oyster data from Natural England’s Marine Evidence Database and data previous compiled as part of the Marine Management Agency project MMO1135 (OBIS database search (MMO, 2019)) and Environment Agency project WP4 (which searched government archives, scientific and public libraries for written resources for evidence of past native oyster fisheries/habitats (Environment Agency, 2022)) were mapped in ESRI ArcGIS. Data sources are listed in Appendix 11. To determine historic extent, data were then filtered to select records occurring up to and including 2009.

Only records occurring within English waters (Marine Plan Areas) were included. The resultant datasets contained 717 “historic” records for *O. edulis*.

The spatial join tool was then used in ArcGIS to join oyster records to a 10km^2 hexagonal grid. A series of maps were then produced to represent historic oyster distribution, with grid cells where native oyster records were present shown in red and grid cells where native oyster records were absent shown in blue. An overall map of historic (pre-2010) extent and historic extent maps for the periods "pre-1850”; “1850-1899”; “1900-1949” and “1950-2009” have been produced. Data sources can be viewed in Appendix 11.

2.3 Modelling habitat restoration potential

Parameters used to inform restoration site selection should meet both the biological needs of *O. edulis* and human uses (Fitzsimmons et al*.,* 2019). Parameters include:

- Historic presence of *O. edulis;*
- Water quality e.g. suitable dissolved oxygen, temperature and salinity to support *O. edulis*;
- Water depth;
- Biotic factors e.g. predation issues and food availability;

- Overall feasibility e.g. reef material availability, logistics, public acceptance, regulatory framework, fisheries and user group conflicts (Fitzsimmons et al., 2019).

Previously, the Environment Agency developed a GIS layer depicting the native oyster bed potential for English waters out to 1 nautical mile from the coast, providing a national indication of where native oyster beds could potentially be restored but may not be accurate at a local level. This project has built on the Environment Agency model, to produce a national 'high level' indication of where native oyster beds could potentially be restored was created for *O. edulis* in English waters based on three key environmental variables: current speed (Low Energy sites, < 130 Nm^{-2}, mean of annual 90th percentile values over six years), broadscale habitat type (Subtidal mixed sediments; EUNIS Level 3 = A5.4), and depth (only subtidal areas to a maximum depth of 30 m were included).

Expert judgement was used to exclude some further areas considered unsuitable for native oyster bed restoration. This includes sites close to major ports, but does not include the location of significant activities (e.g. dredging), marine assets (e.g. submarine cables) and disease control areas.

3. Results

3.1 Current distribution

The current distribution of *O. edulis* in English waters has been inferred from the distribution of *O. edulis* records (Figure 25). Recent records are very limited and the most current records of *O. edulis* are predominantly for the south coast, with a few records for the southwest. This does not include areas of recent native oyster restoration and reintroduction, e.g., the Essex Native Oyster Restoration Initiative in the Blackwater Estuary. Appendix 12 shows the number of records per Marine Plan Area.

Only current presence records were mapped, absence was inferred from a lack of records, but this is not necessarily true absence.

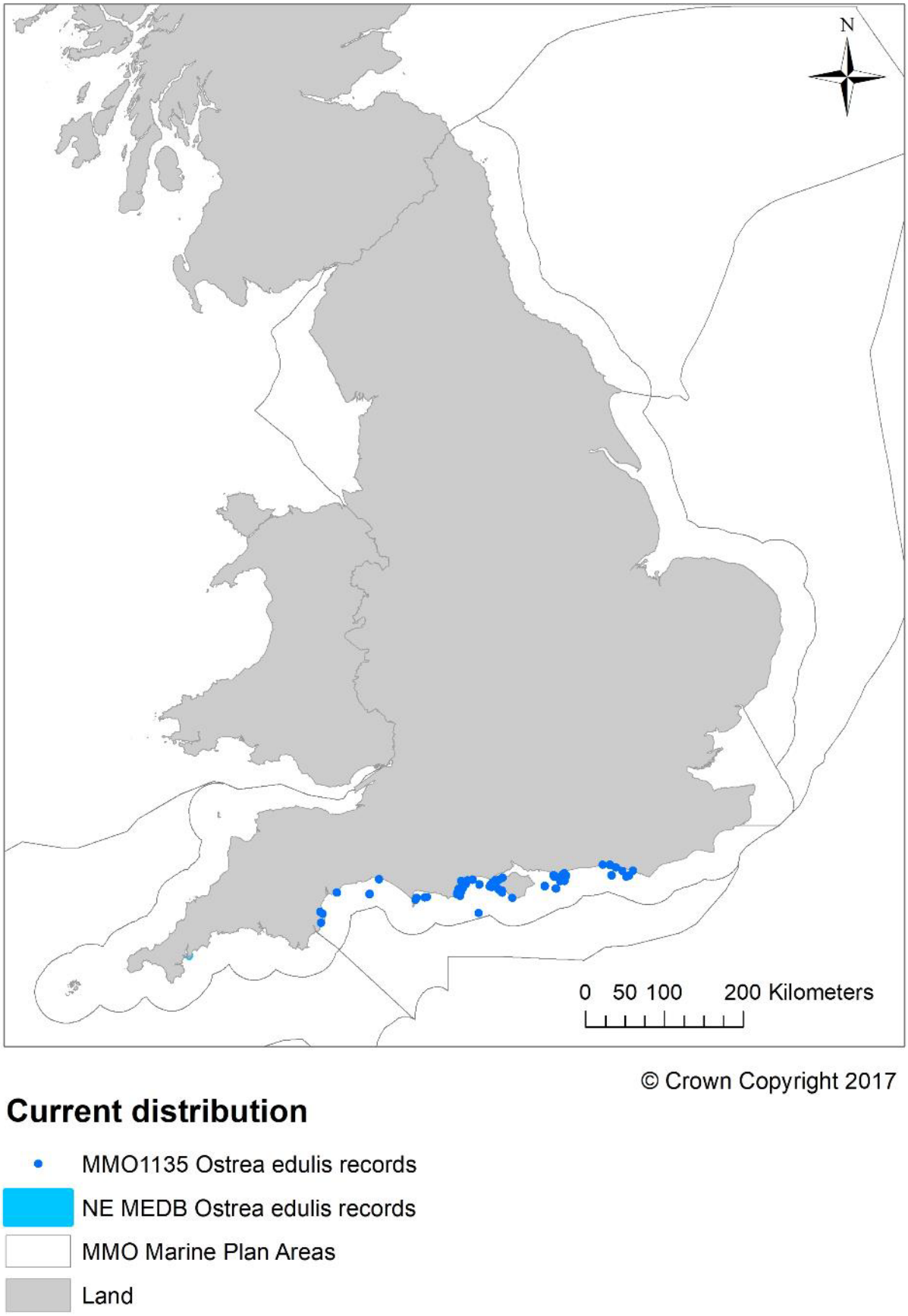

Figure 25. Current (2010 - 2022) distribution of *Ostrea edulis* records in English waters.

3.2 Historic distribution

Historic *O. edulis* records were mapped for the time period 1154 to 2009 (Figure 26 and Figure 27). Records were present for all Marine Plan Areas except southwest offshore. Appendix 12 shows the number of historic records for each Marine Plan Area.

Figure 26 shows the historic distribution of native oysters in English waters over time, divided here into 50-year time periods.

The overall map of historic (pre-2010) extent (Figure 26) shows that the distribution of historic records was predominantly within the South Inshore Marine Plan Area.

Commercial exploitation of oysters in Great Britain dates back to at least the Roman occupation, with a boom in oyster production occurring in the 1830s due to factors such as transport improvements (railway), population growth and poverty. A fall in production occurred between the 1860s and the 1890s (Humphreys et al*.,* 2014). These events were not reflected in the historic records, likely due to the low number of records (Figure 26).

The 1950 to 2009 records (Figure 26) closely matched the overall historic records (Figure 27). The Solent, which falls within the south Marine Plan Area was once home to one of Europe's largest oyster beds, the oyster population crashed in 2007 (Harrison *et al*., 2022).

Only historic presence records were mapped, absence was inferred from a lack of records, this is not necessarily true absence.

The mapped distribution is dependent of survey effort and only provides a general idea of national distribution but does not show local changes in distribution or any possible changes in density or abundance.

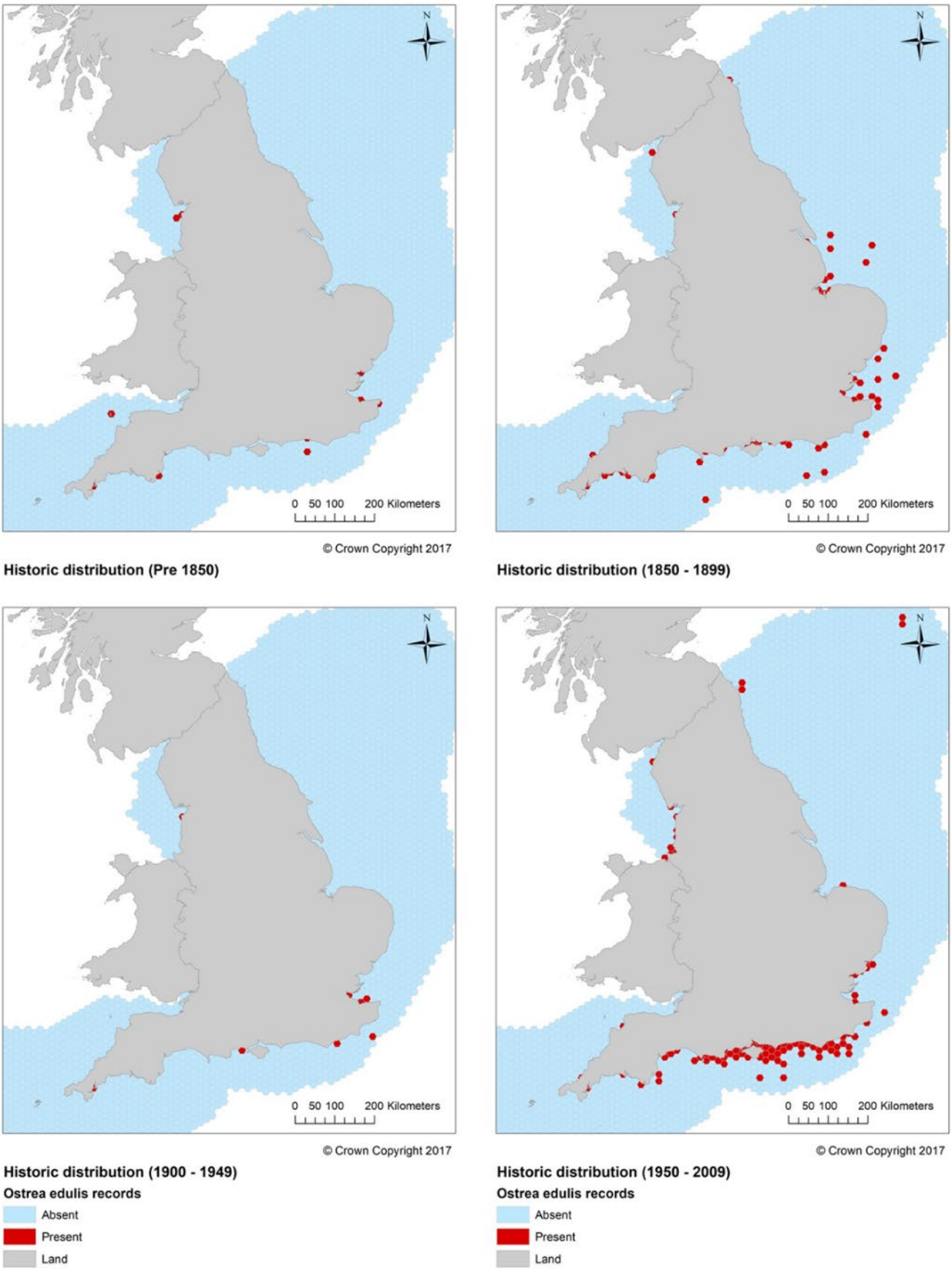

Figure 26. Historic distribution of *O. edulis* records in English waters. The historic data periods are divided into pre- 1850; 1850-1899; 1900-1949; and 1950-2009.

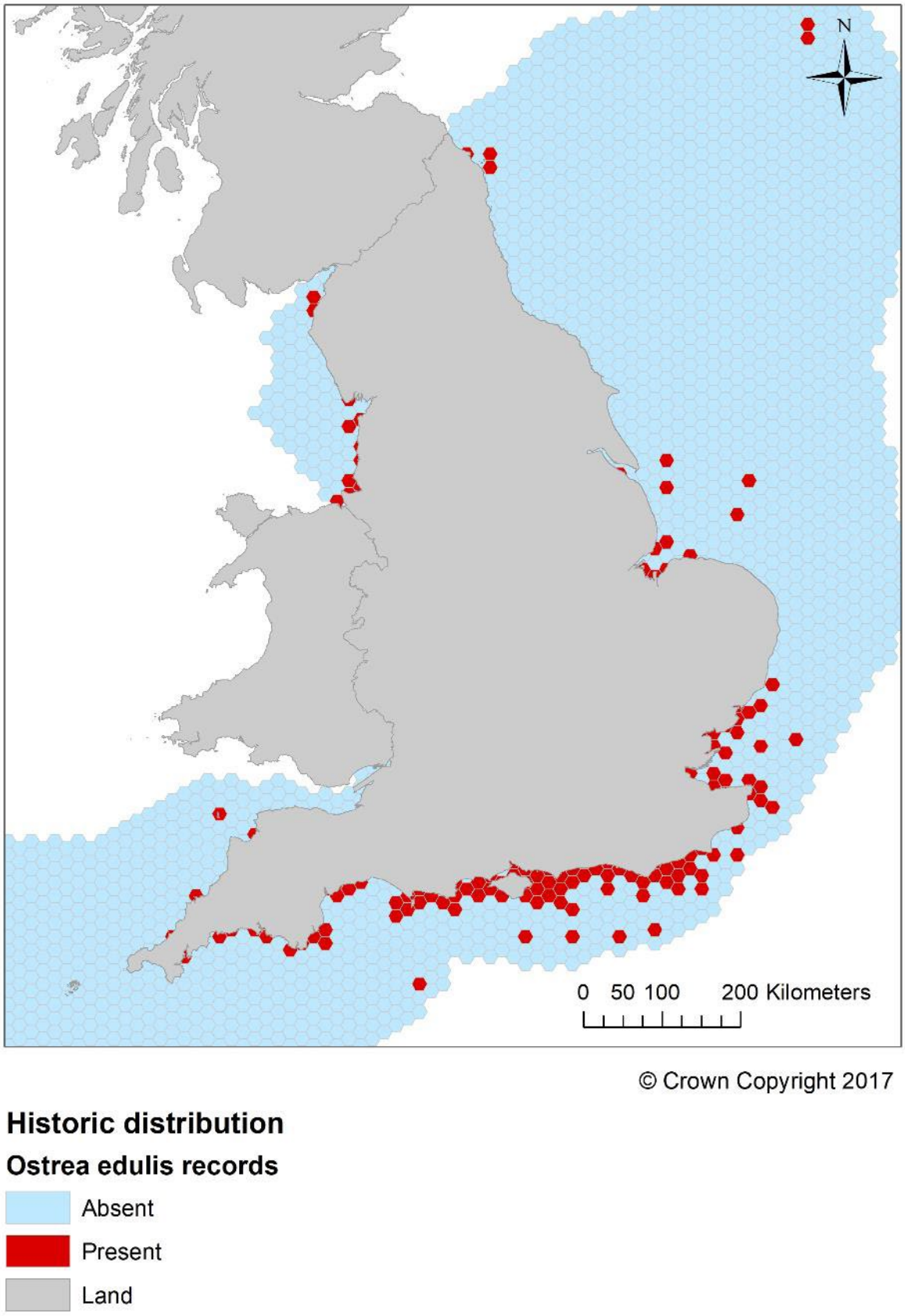

Figure 27. Historic (1154 – 2009) distribution of *Ostrea edulis* records in English waters.

3.3 Restoration potential

The model highlighted restoration potential areas for *O. edulis* along all coastlines, and predominately within 12 nm of the coast, also within all the inshore Marine Plan Areas (Figure 28), with notable large areas in Lyme Bay (Dorset/Devon), Kent and the Northumberland Coast (Figure 28). A small area of oyster restoration was also possible outside of 12 nm in two areas: within the Dogger Bank SAC in the East Offshore Marine Plan Area, and within the West of Copeland MCZ in the offshore North West Marine Plan Area. At a national scale this closely aligns with the current and overall historic distribution maps of *O. edulis* (Figure 25 and Figure 26). A total potential area for *O. edulis* restoration was calculated as 1958.7 km^2. Table 6 shows the area per Marine Plan Area and Figure 29 shows a close-up of the restoration potential areas for the North Northumberland coast.

Figure 30 and Figure 31 show the modelled habitat restoration potential areas of *Ostrea edulis* in English waters with current and historic records overlaid respectively.

Further work is needed to exclude areas considered unsuitable for native oyster bed restoration, including the location of significant activities (e.g. dredging), marine assets (e.g. submarine cables) and disease control areas.

Once factors such as general location, restoration method and scale are determined for future restoration projects, the restoration maps should be used to identify suitable sites. Table 6. Restoration potential area for *Ostrea edulis* per Marine Plan Area (km^2).

Marine Plan Area	Potential (km^2)
North East inshore	382.92
North East offshore	0
East inshore	104.06
East offshore	9.56
South East inshore	193.19
South inshore	1092.91
South offshore	0
South West inshore	72.53
South West offshore	0
North West	100.33

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Restoration potential

Oyster potential restoration areas

MMO Marine Plan Areas

Land

Figure 28. Modelled habitat restoration potential areas of *Ostrea edulis* in English waters.

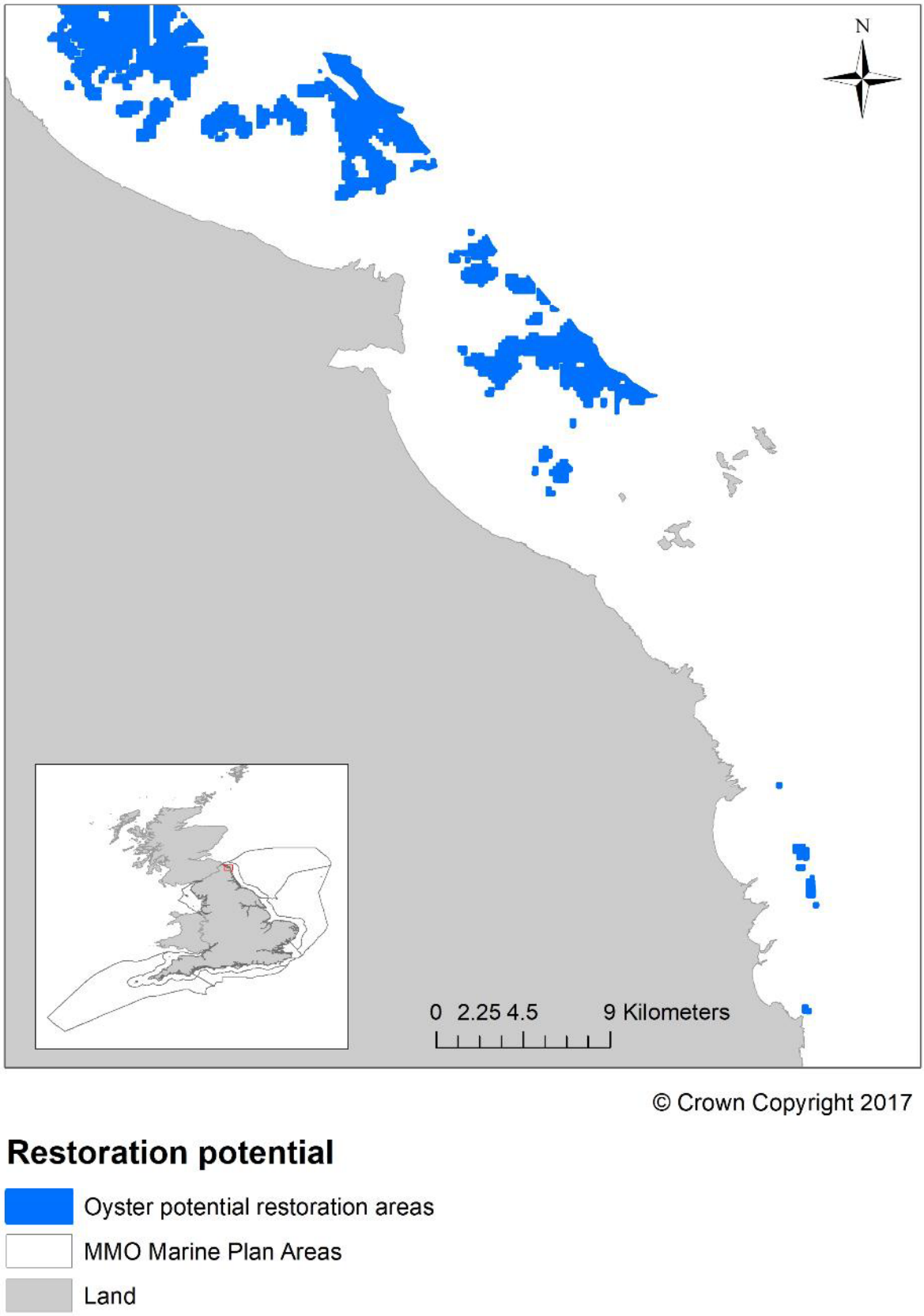
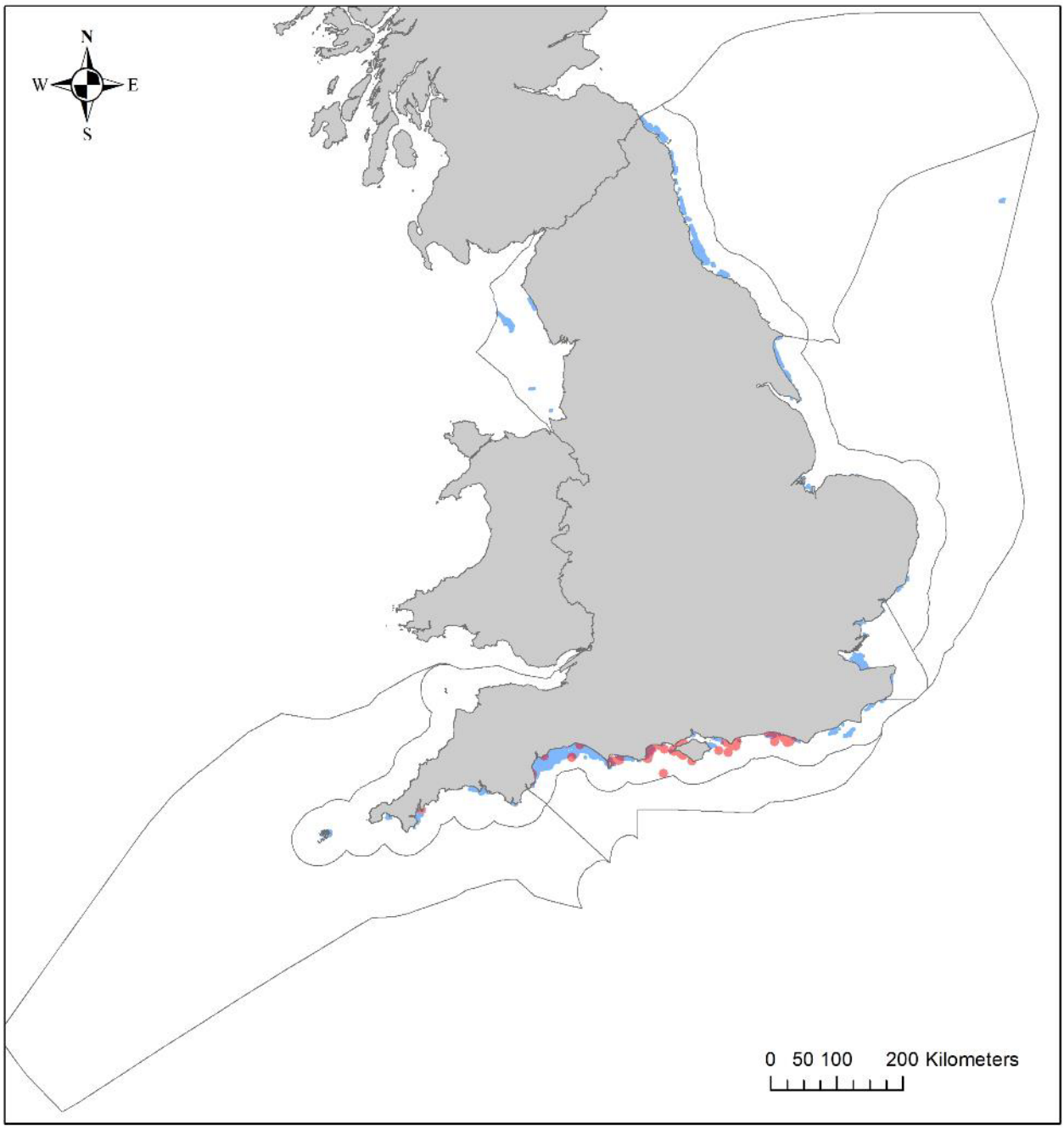


Figure 29. A close up of modelled habitat restoration potential areas of *Ostrea edulis* on the Northumbrian coast



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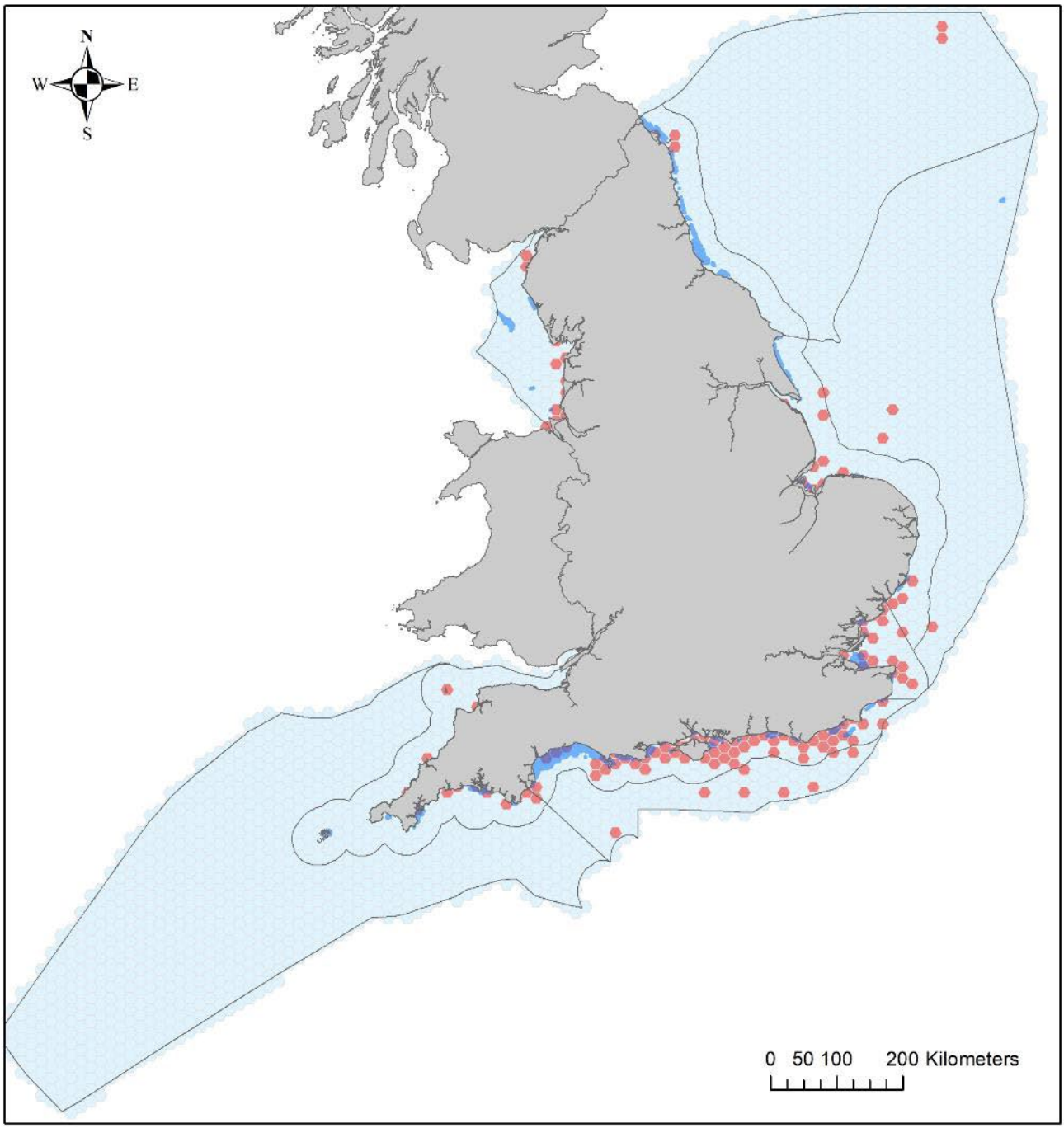
Oyster

- Land
- MMO_Marine_Plan_Areas
- MMO1135 Ostrea edulis records - Current
- NE MEDB Ostrea edulis records - Current
- Oyster potential restoration areas

Figure 30. Modelled habitat restoration potential areas of *Ostrea edulis* in English waters with current records overlaid.



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Oyster

- MMO_Marine_Plan_Areas
- Land
- Oyster potential restoration areas

Historic distribution

- Absent
- Present

Figure 31. Modelled habitat restoration potential areas of *Ostrea edulis* in English waters with historic records overlaid.

4. Discussion and future recommendations

This new updated native oyster restoration potential map expands on the existing layer produced by the Environment Agency and Restoring Meadows, Marsh and Reef (ReMeMaRe) Initiative that extended out to 1nm from shore. This new map demonstrates there is 1956 km^2 of seabed potentially suitable for native oyster restoration. As with the ReMeMaRe maps, these native oyster restoration potential maps should not be considered definitive. Once factors such as general location, restoration method and scale are determined for future restoration projects, users should always undertake more localised modelling to refine the site selection before any active oyster restoration work takes place.

Outside of 1 nm and marine protected areas, many areas of seabed are only mapped using European Marine Observation and Data Network (EMODnet) modelled habitats, with limited groundtruthing. The native oyster restoration potential map relies on extents of 'A5.4 Subtidal mixed sediment' habitat a key defining parameter of oyster distribution; therefore, areas of modelled seabed habitats may underrepresent the potential area where native oysters could be restored. Therefore, this map should be updated as more sediment samples are collected over time and seabed habitat maps improve in confidence.

The models used to create the maps focused on abiotic factors (current speed, sediment type, depth) that determine native oyster distribution, but when identifying sites at a finer scale, biotic factors should also be considered. Larval connectivity and retention are biotic factors that have been identified as key for the success of a restoration site (Preston et al., 2020). This is because the native oyster is functionally extinct in many European locations, therefore larval supply is limited unless a restoration site happens to be close to a relict population or a population in an adjacent basin. If larvae were transported out of the restoration site within the planktonic period of the larvae, the site would not develop to a self-sustaining population. Therefore, techniques such as dispersal modelling and baseline surveys to assess existing native oyster density should be carried out as part of the site selection work.

Further work is needed to exclude areas considered unsuitable for native oyster bed restoration, including the location of significant activities (e.g., maintenance dredge sites), marine assets (e.g. submarine cables) and existing fishing activities using bottom towed gear. Bonamiosis disease control areas should also be considered; there are three designated by the government in English waters that extend out to 12 nm from shore (Essex and Kent; Dorset & Hampshire; South Devon & Cornwall) that restrict movement of oysters in and out of the area. These areas do not prevent restoration; there are many examples of oyster restoration taking place within (e.g., the Essex Native Oyster Restoration Initiative), however, such projects require lower stocking densities to keep bonamiosis prevalence low and sustain restored oyster beds.

Horse mussels

1. Literature review

1.1 Biology and ecological importance

Horse mussels (*Modiolus modiolus*) are suspension feeding bivalve molluscs known to aggregate into dense "beds" by attaching to a variety of substratum; including cobbles, muddy gravel and to each other using byssal threads (OSPAR, 2009). *M. modiolus* is a large, long-lived species, with adult shells typically growing to c. 35-40mm in length and the life span reaching 20-100 years. *M. modiolus* beds can build up as biogenic reefs through the accumulation of shell and faecal deposits (Lindenbaum et al., 2008); Holt et al. (1998) defined these reefs as: "Solid, massive structures created by accumulations of organisms" which "clearly form a substantial, discrete community or habitat which is very different from the surrounding seabed" (Holt, 1998). *M. modiolus* growth and development is variable but they typically reach adulthood and sexual maturity at 4-8 years (Brash et al., 2018, Tillin and Tyler-Walters, 2018, Gormley et al., 2013, Anwar et al., 1990, Dinesen and Morton, 2014, Mackenzie et al., 2022).

OSPAR (2009) indicates that patches of *M. modiolus* extending over 10m^2 with more than 30% cover should be classified as "beds". However, mosaics also occur where frequent smaller clumps of mussels influence ecosystem functioning, so that for conservation and management purposes lower thresholds can be accepted for defining beds (OSPAR, 2009). Scattered populations of isolated full-grown individuals or of spat at quite high densities are not classified here as "beds" (OSPAR, 2009).

Modiolus modiolus beds form on a range of coarse substrata as well as bedrock and anthropogenic offshore developments (Anwar et al., 1990). *M. modiolus* beds tend to occur in the moderately tide swept lower intertidal on gentle slopes, mostly in fully saline areas (Dinesen & Morton 2014, OSPAR, 2009), however dense populations have been recorded in sheltered bays, fjords, or lochs (OSPAR, 2009), with variable temperature and salinity regimes (MacKenzie et al., 2022). *M. modiolus* beds are currently found to extend over only a few square kilometres, and several semi-discrete beds may occur within a limited area (OSPAR 2009).

Modiolus modiolus beds typically form at depths up to 70m but have been found below 100m (Tyler-Walters, 2007a), although individuals have been found at even greater depths (Dinesen and Morton, 2014). *M. modiolus* accumulations can be very variable in size and shape, ranging from mosaics of isolated clumps to ribbon like biogenic reefs and sheets (OSPAR, 2009) with densities of up to 400 individuals/m^2 (Tillin et al., 2020).

Horse mussels reproduce by dispersing planktotrophic larvae into the water column (Dinesen & Morton 2014). The timing and duration of spawning events is highly variable between populations (Dinesen & Morton 2014, Tillin et al., 2020) and the degree to which populations self-recruit has

important consequences for a population's structure, functioning and resilience (MacKenzie et al.2022). Models indicate that connectivity of *M. modiolus* beds between 150 km (Tillin et al., 2020) and 500km (MacKenzie et al., 2022) is possible.

Compared to other bivalves, horse mussels have low success rates of spawning and settlement of larvae (Strong and Moore). They do, however, have a relatively long planktonic phase of approximately 50 days (Ockelmann, De Schweinitz and Lutz, 1976, Roberts et al., 2011). This extended retention in the plankton allows maximum dispersal and connectivity between populations (Brown, 1984).

Horse mussel aggregates form complex biogenic reefs, which provide favourable feeding environments and important refugia from predation and physical disturbance for many marine communities (Witman, 1984, Dinesen and Morton, 2014, Fariñas-Franco et al., 2013, Gormley et al., 2013, Hutchison et al., 2016, Ragnarsson and Burgos, 2012, Rees et al., 2008, Strong and Moore). *M. modiolus* beds play an important role in productivity, habitat complexity and ecosystem functioning (Gormley et al., 2013, Ragnarsson and Burgos, 2012). Consequently, *M. modiolus* beds are hotspots for biodiversity, with studies frequently reporting 100-200 associated macrofaunal taxa (Fariñas-Franco et al.2013, Strong et al.2016, Tillin et al., 2020). Such communities often include hydroids, red seaweeds, solitary ascidians and bivalves (OSPAR 2009). *M. modiolus* reefs are also thought to contribute to several ecosystem services including water filtration, sediment stabilisation, habitat provision for commercially important species and potential carbon storage (Mackenzie et al., 2022).

1.2 Habitat distribution and extent

Modiolus modiolus is an Arctic-Boreal species with a range that includes the Northeast Pacific, Arctic and North Atlantic Oceans and which extends as far south as the Bay of Biscay (OSPAR 2009). Although horse mussels are a widespread and common species *M. modiolus* beds are much more limited in their distribution (OSPAR, 2009). The habitat is considered threatened and/or declining under the OSPAR Convention for the Protection of the Marine Environment of the North-East Atlantic 1992 and a Habitat of Principal Importance across the UK.

Within UK waters, *M. modiolus* settlement occurs between the shallow intertidal zone down to depths of 280 m on a range of hard substrates (Tyler-Walters, 2007b). Sporadic horse mussel records are common throughout the UK, however records of *M. modiolus* beds are sparser, with the majority located to the west of the UK, particularly in Scottish and Welsh waters. On the west coast of the UK, isolated reefs extend from the Pen Llŷn to Shetland and on the east, from Shetland to the Humber (Holt, 1998). *M. modiolus* is not known to form beds south of the North Sea and in the southern Irish Sea (OSPAR, 2009).

Reports on the current state of *M. modiolus* beds in UK waters are relatively sparse. The magnitude of declines has often been difficult to accurately assess due to the varied methods used to study and record horse mussel beds and the absence of compiled historical data maps of distribution (Strong et al. 2016). Furthermore, very few *M. modiolus* beds have been surveyed for

long enough time periods to see evidence of change, which makes it difficult to determine the scale of any anthropogenic impacts (OSPAR, 2009).

1.3 Factors affecting habitat distribution

Several *M. modiolus* beds in UK waters have experienced substantial declines in extent and density, including the horse mussel beds in Strangford Lough (Elsäßer et al., 2013, Fariñas-Franco and Roberts, 2023, Strong and Moore), the Isle of Man (Cook, 2016), and North Anglesey (Cook et al., 2013). Despite an overall decline in *M. modiolus* bed extents between 1950 and 1990, the long lifespan of *M. modiolus* individuals might make the detection of disturbance difficult, therefore introducing a time lag between impacts occurring and detection of decline (Gormley et al., 2013).

1.3.1 Environmental pressures

Horse mussel bed habitat distribution is influenced by several environmental parameters which have a direct impact on the fitness, survival, and recruitment of *M. modiolus*. Temperature is known to influence the growth rate of bivalves and therefore the age at which they reach sexual maturity (Brash et al., 2018). *M. modiolus* beds grow more slowly at the northern range in the UK in comparison to the south because the seabed temperatures are 3-4 C° lower on average. Lower temperatures have also resulted in later maturation occurring in larger individuals (Brash et al 2018). *M. modiolus* beds at the southern extent of the UK range experience reduced reproductive output and larval survival as a result of higher sea temperatures (Dinesen and Morton, 2014).

Current speeds may be an important factor in determining where *M. modiolus* beds occur (Strong and Moore), as they have the potential to impact on growth rates, mortality, larval settlement and dispersal (Brash et al., 2018, Dinesen and Morton, 2014, Tillin and Tyler-Walters, 2018). Horse mussel communities that experience fast water currents typically express elevated growth rates, due to higher associated food availability and improved connectivity between the beds (Brash et al., 2018). However, population growth is reduced at flow rates that exceed approximately 16 cm/s due to the associated energetic cost of byssal thread production (Brash et al., 2018, Dinesen & Morton 2014). There is, however, disagreement about whether *M. modiolus* prefer non-mobile substrates in the absence of excessive currents (Wildish et al., 1998) or tidally swept regions where currents can reach 10 cms-1 (Wilson et al., 2021). Mortality rate and settlement potential of larvae are also highly variable between *M. modiolus* beds, potentially due to differences in larval supply density influenced by surrounding hydro-dynamic conditions (Dinesen & Morton 2014; Tillin et al., 2020; Brash et al., 2017).

Salinity is thought to impact the subtidal distribution of *M. modiolus* (Dinesen & Morton 2014, Tillin et al., 2020). *M. modiolus* is an osmoconformer; a marine organism that maintains an internal environment which is isotonic to their external environment, and is consequently highly sensitive to salinity changes (Bakhmet et al., 2012, Dinesen and Morton, 2014). The tolerance ranges of *M. modiolus* vary by location, but in the UK *M. modiolus* beds have only been found in locations with a salinity level of 30-40 ppt (Tillin and Tyler-Walters, 2018). Populations show resilience to short term fluctuations in salinity, but longer-term increases are likely to increase

mortality rates (Dinesen & Morton 2014, Tillin et al., 2018). Salinity changes are associated with activities such as energy generation and waste management, particularly discharge events (Robson et al. 2018) . Although this literature review found no reported examples of *M. modiolus* declines linked directly to salinity changes, this pressure still has the potential to impact on *M. modiolus* as an osmoconformer.

Elsäßer et al. (2013) found that substratum type was a key predictor of distribution of *M. modiolus* beds indicating that changes in seabed types are likely to alter the habitat suitability which may impact on bed fitness and recruitment. Changing the sediment/seabed type has been shown to impact the fitness and survival rates of horse mussels, particularly as older individuals may be adapted to a particular environment (Tillin et al., 2018). Other environmental variables known to impact on horse mussels are, depth, slope and seabed morphology (Brash et al 2017, Elsäßer et al. 2013 Gormley et al 2013, Strong et al 2016, Tillin et al., 2018).

1.3.2 Ecological pressures

The existing density of horse mussels within a *M. modiolus* bed has a significant impact on recruitment rates, regardless of larval density or geographical dispersal area (Tillin et al., 2018). Larvae receive settlement cues from adult specimens, and existing aggregations improve survival rates by protecting juveniles from predation, with spat survival being highest in the crevices amongst the byssal threads of the mature clumps (Brash et al., 2018, Elsäßer et al., 2013, Tillin and Tyler-Walters, 2018). Consequently, as *M. modiolus* bed densities decline, larval settlement rates are predicted to decline at a higher rate, reducing recruitment even further (Dinesen and Morton, 2014).

1.3.3 Anthropogenic pressures

M. modiolus beds are considered sensitive to several human-induced physical pressures because of the sessile nature of this biogenic habitat (Tillin et al. 2018). Evidence of long-term damage to horse mussel bed density and the associated epifauna have been reported in areas with high benthic abrasion and sub-surface penetration pressures (Tillin et al., 2018). The impact of benthic trawling, dredging and other direct anthropogenic activities is difficult to quantify, but is likely to depend on spatial scales and levels of activity. These pressures are considered a particular threat as they can flatten, dislodge, break and remove individuals and clumps of horse mussels (Tillin et al., 2018). Studies looking into the impact of disturbance activities report very low levels of post-event recovery and suggest that repeated disturbance may result in the complete loss of *M. modiolus* beds (Tillin et al., 2018).

Although horse mussels have previously been targeted for human consumption in the British Isles (Mackenzie et al., 2022, Dinesen and Morton, 2014), *M. modiolus* fishery does not currently exist in the UK. However, horse mussel beds are highly sensitive to the removal of non-target species, because *M. modiolus* beds can be physically altered/removed as by-catch (Tillin et al., 2018). Scallop dredging has been highlighted as a key cause of decline in *M. modiolus* habitat extent and distribution in the UK and across Europe (Dinesen & Morton 2014 and references therein, MacKenzie et al., 2022, OSPAR, 2009, Strong et al., 2016). Furthermore, Cook et al. (2013) found

that 90% of all epifaunal organisms were removed following the single pass of a trawl within a *M. modiolus* bed. With increases in anthropogenic disturbance activities and historic trends in slow bed recovery rates further declines are predicted over the next 100 years (MacKenzie et al., 2022).

M. modiolus beds are also thought to be highly sensitive to sediment extraction as individuals/beds are removed along with the sediment (Tillin et al. 2018). Recovery is possible via larval recolonisation but is dependent on the scale of the disturbance and the removal of adults is likely to reduce the chances of successful settlement (Tillin et al. 2018).

Hutchinson et al. (2016) found the *M. modiolus* beds were capable of surviving short term (<16 day) sediment burial, but mortality increases with duration of burial, particularly with finer grained sediments (Hutchison et al., 2016). Site-specific hydrodynamics will influence the mobility of deposited sediments which could mediate the pressure, but if smothering/siltation rates are very heavy the deposits are likely to persist for some time before removal, increasing the risk (Tillin et al., 2018). Sedimentation can occur naturally during storms and floods but is increasingly the result of human activities. Marine industries that result in sedimentation include, aggregate extraction, dredging, and installation of offshore energy developments (Hutchinson et al 2016). These developments can also cause habitat loss or degradation through physical damage (OSPAR, 2009). The more recent development of the marine renewable sector is likely to increase these pressures in future years.

Anthropogenic impacts can lead to fragmentation of *M. modiolus* beds, which reduces connectivity between subpopulations, limiting the available larval sources and subsequent recruitment and regeneration that takes place (Elsäßer et al. 2013). Natural regeneration of biogenic reefs will depend on the length of time without disturbance, proximity of larval sources, hydrodynamic influences on larval dispersal and availability of suitable habitat for settlement and growth (Elsäßer et al. 2013). The sensitivity assessment undertaken by Tillin et al., 2018 indicates that juvenile recruitment of *M. modiolus* in cleared areas can be rapid if there is a good supply of larvae and the area is free of predators. However, they clearly state that this does not guarantee the development and establishment of horse mussel beds. Post impact recovery times are thought to be long and depend on wider population status as recovery is unlikely if recruitment is adversely affected (Tillin et al., 2018). Whilst some populations are self-sustaining, Tillin et al., 2018 states that if populations are reduced in extent or abundance, it will take many years to recover to a mature bed. Furthermore, populations that are destroyed will require a very long time to re-establish and recover as recovery from significant impacts could be inhibited by the lack of adults to provide settlement cues and protection to larvae and juveniles.

1.3.4 Climate change impacts

Climate induced changes in environmental conditions are predicted to impact the distribution, health, productivity and ecosystem functionality of *M. modiolus* habitats. Although the reproductive cycle of *M. modiolus* is highly variable, spawning seems to commence within a reasonably small range of temperatures (7-10°C) and the upper sea temperature limit for long-term survival has been reported as 23°C (Tillin et al., 2018). The elevated average summer sea

temperatures predicted for the UK may therefore reduce the reproductive output, fitness and survival rates of *M. modiolus* larvae (Dinesen & Morton 2014). This may be particularly relevant to populations in the UK as this is the southernmost limit of the horse mussel range and populations may respond by shifting Northwards (Brash et al., 2017).

Under current emission scenarios, sea temperatures are predicted to rise by 3 - 4°C by the end of this century 2081-2100 (Tillin et al., 2018). Furthermore, winter temperatures are expected to rise to 9-10°C in Scotland, further reducing the window for recruitment, whereas in the rest of the UK the temperature window for recruitment would be wholly exceeded (Tillin et al., 2018). Modelling habitat suitability of *M. modiolus* beds under baseline and increased ocean temperature scenarios have also suggested that *M. modiolus* beds in the UK are increasingly vulnerable to rising sea temperatures (Gormley et al., 2013). Established horse mussel beds may be less impacted by increases in temperature in the short term, although their long-term abundance may decline due to reduced reproductive outputs (Gormley et al., 2013). Increases in sea temperatures may also lead to increased predation pressures and decreases in food availability (Dinesen & Morton, 2014). Evidence is lacking on whether *M. modiolus* will be able to withstand changes to future ocean carbonate conditions with acidification. Although many bivalves seem to be tolerant of ocean acidification, different species show variation in their response to CO_2 (Tillin et al., 2018). *M. modiolus* is known to occur in intertidal rockpools, where pH can vary by as much as 3 pH units throughout the year suggesting some level of resistance to acidification changes (Tillin et al., 2018).

Overall, it is expected that changing climatic conditions will lead to a gradual loss of *M. modiolus* beds in the UK, compounding the issue of low recruitment in beds that are unable to tolerate the impacts of anthropogenic activities

1.4 Habitat restoration approaches

The recovery of *M. modiolus* beds and their associated communities after disturbance to pre-impacted states can take decades (Holt, 1998, Fariñas-Franco et al., 2013). Active restoration approaches are therefore likely to take a significant amount of time, and passive restoration should be considered as the crucial first step in a restoration project (Cook et al., 2013, Cook, 2016, Fariñas-Franco and Roberts, 2023). The *M. modiolus* spawning season and its associated drivers are still poorly understood (Brash et al., 2018), which makes it difficult to predict successful spawning and subsequent settlement. Many of the studies considered in this literature review indicate highly variable responses between populations and the authors of this report are not aware of any studies specific to English waters.

Cook (2016) looked to develop restoration techniques to accelerate the recovery of biogenic reefs including *M. modiolus* beds, finding that the addition of hard substrate, and in particular, substrates providing structural complexity such as crushed shells proved a reliable restoration technique for *M. modiolus*. Other restoration techniques, such as stock enhancement and substrate stabilisation were found to be less effective. Despite this information, most examples to date, involve restocking (Elsäßer et al., 2013; Fariñas-Franco et al., 2013).

Elsäßer et al. (2013) discussed restoration approaches involving adult restocking to increase larval recruitment. They indicated that the best approach to accelerate restoration of *M. modiolus* beds in Strangford Lough would be to provide protection to all remaining larval sources and establish additional patches of *M. modiolus* in areas with high modelled larval release density. Hydrodynamic and habitat suitability modelling was considered vital for species such as *M. modiolus*, to ensure that restoration sites are located where recovery has the highest likelihood of success. However, the establishment of new larval sources alone is not sufficient to restore areas with no remaining Modiolus beds (Elsäßer et al., 2013). Fariñas-Franco et al. (2013) conducted a trial to regenerate damaged *M. modiolus* reefs in Strangford Lough using translocated mussel clumps. They showed that translocation of *M. modiolus* clumps had a positive effect, significantly enhancing the recruitment of juvenile horse mussels and stimulating re-colonization by a faunal assemblage similar to natural communities. This was only a short term (1 year) study and further work is needed to determine if the positive impacts are retained longer term. The construction of artificial reefs has been proposed as a particularly useful restoration approach when impacted communities are unlikely to recover naturally from anthropogenic stress without intervention (Fariñas-Franco et al., 2013).

Over the years several attempts have been made to generate habitat suitability models for *M. modiolus* beds to identify areas in need of restoration and candidate areas for reintroduction programs. Gormley et al. (2013) used Species Distribution Models (SDM) to create modelled habitat maps of *M. modiolus* extent under different ocean temperature scenarios (Gormley et al., 2013). Under the 2080 ocean temperature scenario, they found that all of the “most suitable” habitat areas would be lost. This would mean that maintaining populations of habitats such as *M. modiolus* beds would require management of the decline and migration rather than maintenance of present extent (Gormley et al., 2013). Strong et al. (2016) used habitat suitability models to refine presence/absence maps for *M. modiolus* and modelled change through time. They found that the models reflected niche theory giving a distribution of known environmental preference rather than one that reflected current distribution maps. Elsäßer et al. (2013) studied Strangford Lough and used a series of hydrodynamic and particle dispersal models to identify if dispersing larvae could reach suitable bed habitats and determine if translocated horse mussels would reseed themselves or act as sources for other nearby beds. They found that *M. modiolus* populations were largely self-recruiting with little connectivity between them. Larvae settlement tended to be near the larval source with any movement largely dependent on the tides rather than by wind or waves (Elsäßer et al., 2013).

2. Methods for mapping the current, historic and potential distribution

2.1 Current distribution

For the development of current horse mussel bed distribution maps, the current habitat data were defined as *M. modiolus* records collected from 2010 onwards. This approach was selected due to the increased survey effort in the recent years. *M. modiolus* bed point data were obtained from the Marine Recorder public UK snapshot (v52 - 20220124) and only data records with a "EUNIS2007" entry of A5.621, A5.622, A5.623 or A5.624 were included. Once filtered by date, the data points were clipped in ArcGIS to English waters using the MMO Marine Plan Areas. Initially the data were filtered to remove any uncertain data points ("qualifier" IN ('Certain match; part record' 'Certain match; whole record')), however this resulted in zero returned data points, so this filter was relaxed to allow uncertain data records.

The following additional data sources were also checked for *M. modiolus* bed habitat points:

- Natural England's Marine Evidence Database (June 2021) – point layer. Filtered to include data post 2009 with a HAB_TYPE field of A5.621, A5.622, A5.623 OR A5.624 or a "FOCI_name" of 'Horse mussel (*Modiolus modiolus*) beds' OR 'Horse mussel beds' and a "Survey_quality" of 2 or 3.
- OSPAR Habitats in the North-East Atlantic Ocean (2020) point and polygon layers. Filtered to show only data in English waters, post 2009 with a "HabType" of '*Modiolus modiolus* horse mussel beds', a "HabStatus" of 'Present' and a "Certainty" of 'Certain'.

Any overlaps/ duplicate data points between these datasets and the Marine Recorder were discounted. No extra data points were found in either of the additional sources even when the confidence/certainty restraint was removed.

Due to the limited number of *M. modiolus* bed habitat data points (n=1), species occurrence data were also obtained from the following sources:

- Marine Recorder public UK snapshot (v52 - 20220124). Filtered to show only data with a "SpeciesName" of '*Modiolus modiolus'* only and a "Date" post 2009. Only live organism records were included i.e. excluding dead and shell only records.

- NBN Atlas. Accepted '*Modiolus modiolus'* occurrence data post 2009 and excluding any dead or shell only records.

- The archive for marine species and habitats data (DASSH). *Modiolus Modiolus species* data (aphia id: 140467) post 2009, excluding any dead or shell only records.

As with the habitat point data, all datasets were clipped to English waters and duplicated data points between the sources were excluded.

All current *M. modiolus* beds and species records were then mapped in ArcGIS to produce maps representing the current extent.

2.2 Historic distribution

For the development of historic distribution maps, historic data were defined as *M. modiolus* records collected prior to 2010. *M. modiolus* bed historic data were obtained from the Marine Recorder public UK snapshot (v52 - 20220124). Only data records with a "EUNIS2007" entry of A5.621, A5.622, A5.623 or A5.624 and a "Date" pre 2010 were included. Once filtered the data points were clipped in ArcGIS to English waters using the MMO Marine Plan Areas

The following additional data sources were also checked for *M. modiolus* bed habitat data points:

- Natural England's Marine Evidence Database (June 2021) – point layer. Filtered to include data pre 2010 with a HAB_TYPE field of A5.621, A5.622, A5.623 OR A5.624 or a "FOCI_name" of 'Horse mussel (*Modiolus modiolus*) beds' OR 'Horse mussel beds' and a "Survey_quality" of 2 or 3.
- OSPAR Habitats in the North-East Atlantic Ocean (2020) point and polygon layers. Filtered to show only data in English waters, pre 2010 with a "HabType" of '*Modiolus modiolus* horse mussel beds', a "HabStatus" of 'Present' and a "Certainty" of 'Certain'.

Any overlaps/ duplicate data points between these datasets and Marine Recorder were discounted. No extra data points were found in either of the additional sources even when the confidence/certainty restraint was removed. Due to a very limited number of data points for *M. modiolus* bed habitats, species occurrence data were also obtained from the following sources:

- Marine Recorder public UK snapshot (v52 - 20220124). Filtered to show only data with a "SpeciesName" of '*Modiolus modiolus'* only and a "Date" pre 2010 including live organism records were and excluding any dead and shell only records.

- NBN Atlas. Accepted '*Modiolus modiolus'* occurrence data pre 2010 and excluding any dead or shell only records.

- The archive for marine species and habitats data (DASSH). *M. modiolus* data occurrence data pre 2010 and excluding any dead or shell only records.

As with the habitat point data, all species occurrence datasets were clipped to English waters and any duplicated data points between the sources excluded to ensure each data point was only included once.

The historic data were then grouped into 50- year time periods to allow any changes through time to be visualised. For individual *M. modiolus* species occurrence records, the following historic time periods were used: 1860-1909, 1910 – 1959 and 1960 – 2009. For the *M. modiolus* bed habitat points, all data fell within the most recent historic period. Data from each time period was then

aggregated using a 10km hexagonal grid and mapped on ArcGIS to produce maps representing the historic extent.

2.3 Modelling habitat restoration potential

JNCC has developed a habitat suitability model for *M. modiolus* beds in UK waters based on Species Distribution Modelling (SDM) framework (Castle et al., 2020). It models the areas suitable for the establishment of *M. modiolus* beds based on key environmental variables and records of presence of the habitat. Creation of this model involved the following steps:

1. A literature review to determine ecological characteristics known to influence habitat distribution for inclusion in the model.

2. Sourcing of suitable environmental variable data based on step 1. Each dataset was transformed into a common coordinate system and resampled to a common raster grid with a resolution of 300 m before being fed into the model.

3. Restrictions were then applied to the model extent based on existing depth limits of the habitat. For the *M. modiolus* beds model the extent was restricted to a depth range between 0 m and 242 m, which is the known depth range from which horse mussels beds have been recorded in UK waters.

4. Species occurrence data was selected. The model utilised data from the Natural England Evidence base, the OSPAR Threatened and/or declining habitats database 2018, and Marine Recorder Database 2019. Habitat suitability models require two types of occurrence data (also known as response data): presence data and absence data. As true absences are particularly scarce in survey data, presence of other habitats was used as a proxy for absences instead; this is referred to as pseudo-absence data.

5. Due to the nature of surveying, the presence and pseudo-absence observations tended to be clustered so that several data points often occurred within a single 300 m raster grid cell. Reductions were made to both presence and absence data to reduce this clustering within every grid cell within the environmental raster stack.

6. For each model run, 25% of the response data were held back for testing the model performance, the remaining 75% were used to train the model.

7. To predict habitat suitability, the JNCC Species Distribution Modelling (SDM) Framework (JNCC, 2019) was used and a Random Forest algorithm chosen as the final model algorithm based on a higher mean Area Under the Curve (AUC) statistic. For full details of the model please see Castle et al (2020).

The intention for mapping restoration potential in this project was to use JNCCs *M. modiolus* habitat suitability model for the UK (Castle et al., 2020), re-run it using updated data inputs and overlay the current and historic extent data to identify possible areas suitable for restoration.

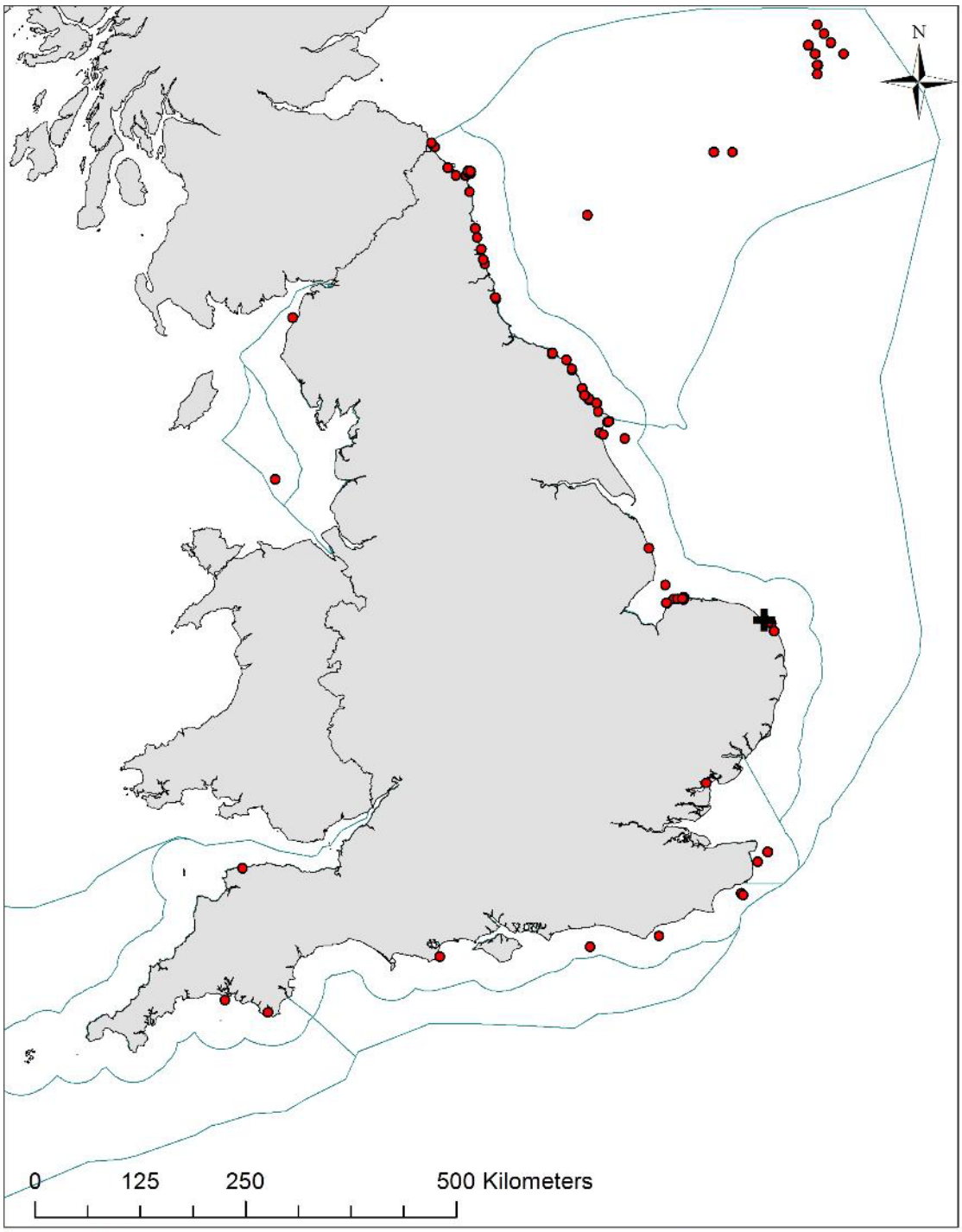
Unfortunately, there was very little new *M. modiolus* bed habitat data at the UK scale and no new points in English waters. Therefore, the existing model was utilised to test whether it would be possible to identify suitable restoration potential areas.

The next step was to overlay the outputs from current and historic mapping exercise to see if there were overlaps with areas of potentially suitable habitat.

3. Results

3.1 Current distribution

There was only a single uncertain *M. modiolus* bed habitat data point off the coast of Norfolk representing the current distribution of *M. modiolus* beds in English waters. However, the current distribution of *M. modiolus* individuals based on the species occurrence data points is much more widespread (Figure 32). The majority of the 141 species occurrence data points are confined to inshore areas. Sporadic records are shown throughout English inshore waters with greater densities of records occurring along the northeast coast. There are also 31 records in an offshore area of the northeast of the North Sea. Notable is the presence of species records in the Norfolk area where the single *M. modiolus* bed habitat data point was also located.



Current distribution

- *M. modiolus* bed record
- *M. modiolus* record
- Land
- Marine Plan Areas

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Map projection: Web Mercator (EPSG:3857)

Figure 32. Current distribution of *M. modiolus* in English waters, based of species occurrence data. Only one single data point was identified for *M. modiolus* bed habitats this is also shown using an alternate symbology.

3.2 Historic distribution

There were very few data points (n=7) representing *M. modiolus* bed habitats in English waters. Only two hexagonal grids in the coastal waters of the Northern North Sea region show the presence of *M. modiolus* bed habitats in recent history (1960-2009) (Figure 35).

More records of historic *M. modiolus* species occurrence (n=571) were found compared to data on horse mussel bed habitats. Sparse distribution of *M. modiolus* was found during the earlier time periods of 1860-1911 and 1910-1959 as shown in Figure 33 and Figure 34 respectively, with only a few inshore areas showing species presence. *M. modiolus* was found in the southeast and northeast regions throughout this time period, In the most recent historic time period (1960-2009) the species records are more widespread (Figure 35).

The existing data on current or historic *M. modiolus* bed habitats were insufficient to determine any changes in distribution, however, the most recent historic species occurrence map (Figure 31) shows more frequent and widespread records of *M. modiolus* than the current map of *M. modiolus* species occurrence (Figure 26). The current distribution of *M. modiolus* in the northeast is consistent with the recent historic records of species occurrence distribution, however other geographical areas (such as the Southern North Sea and the southwest coastal waters) show declines in species presence. It is not clear whether these apparent declines are true changes in distribution or a result of reduced sampling effort in some areas.

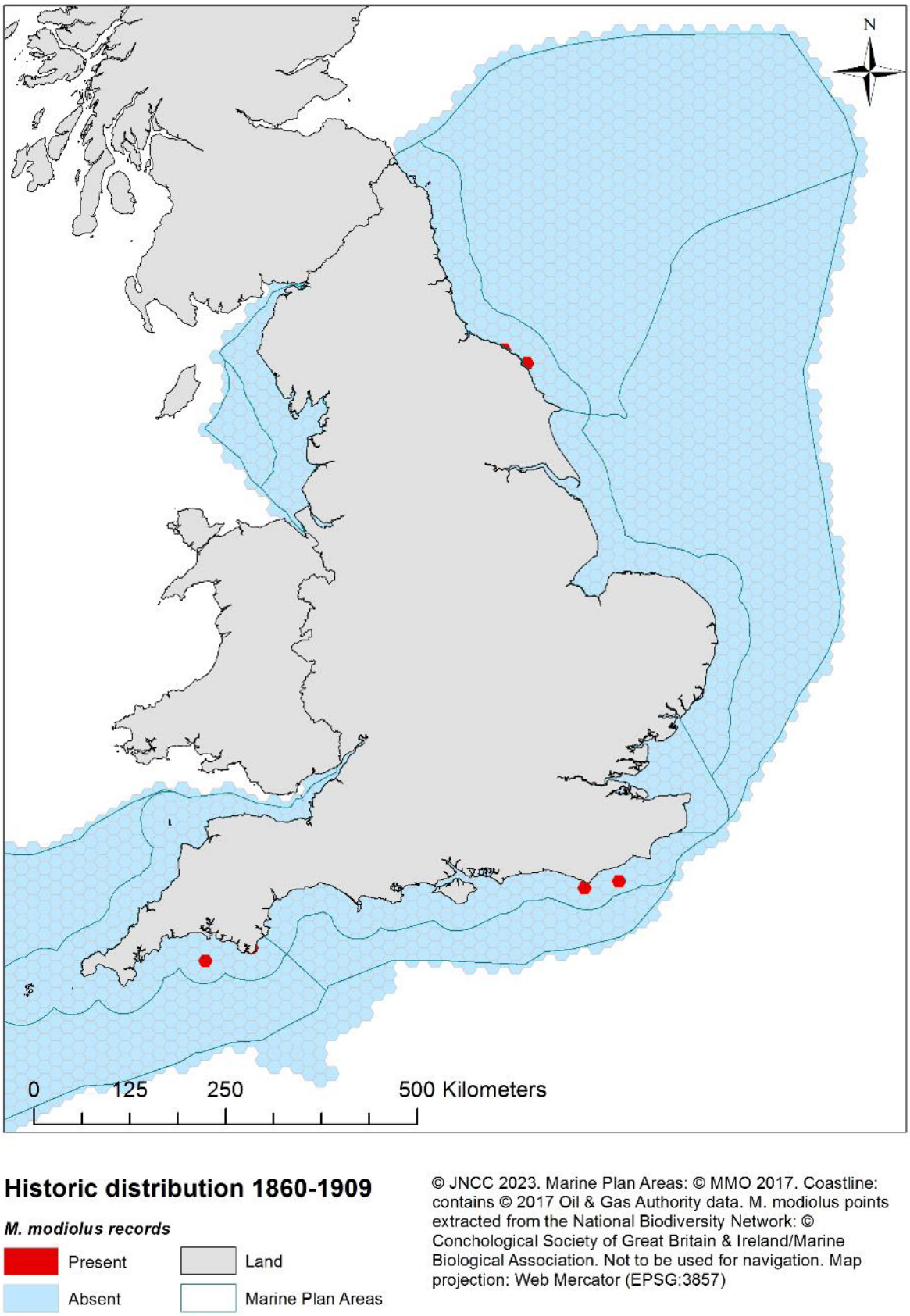
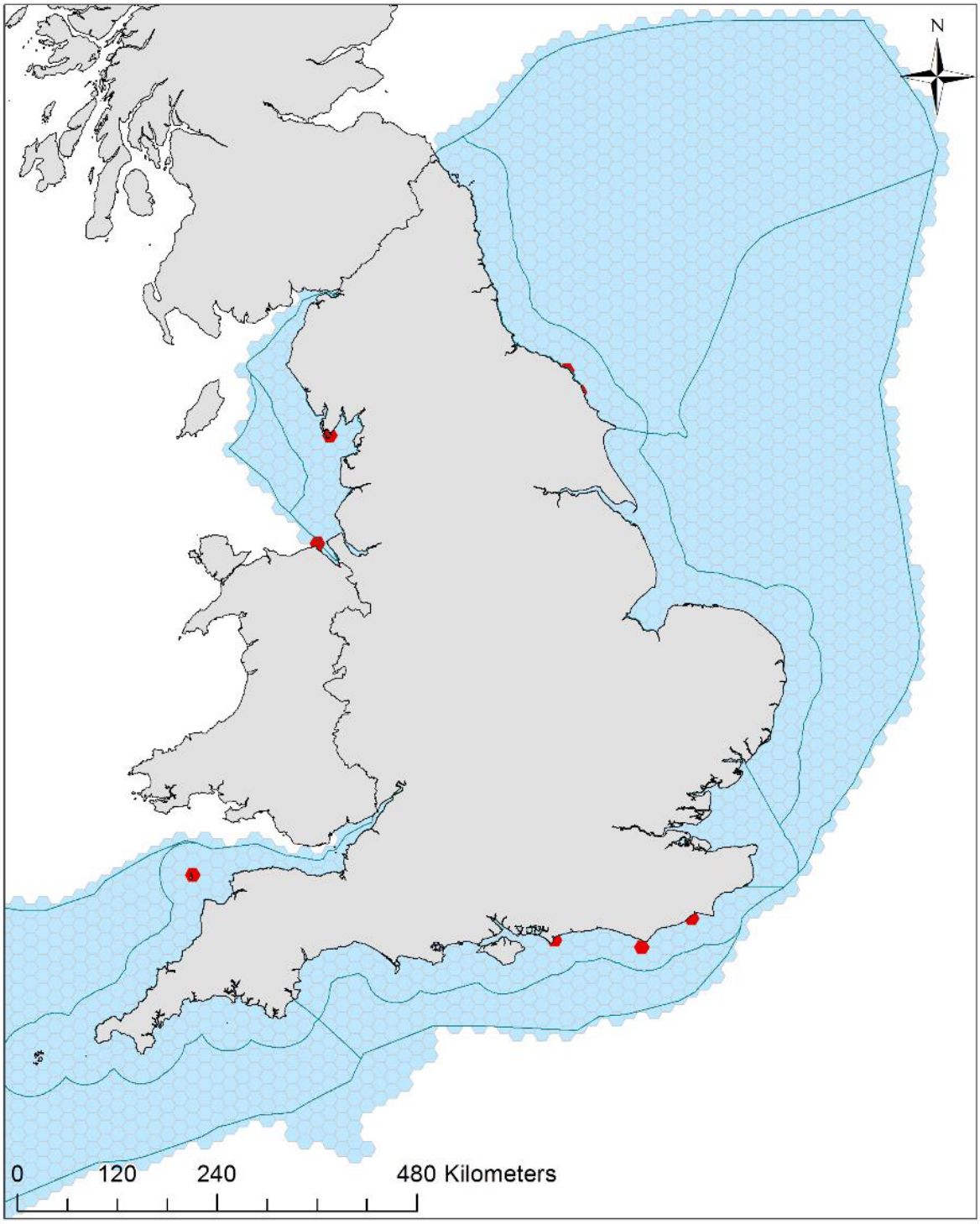


Figure 33. Historic (1860 – 1909) distribution of *M. modiolus* in English waters, based on species occurrence data.



Historic distribution 1910-1959

***M. modiolus* records**

Present

Absent

Land

Marine Plan Areas

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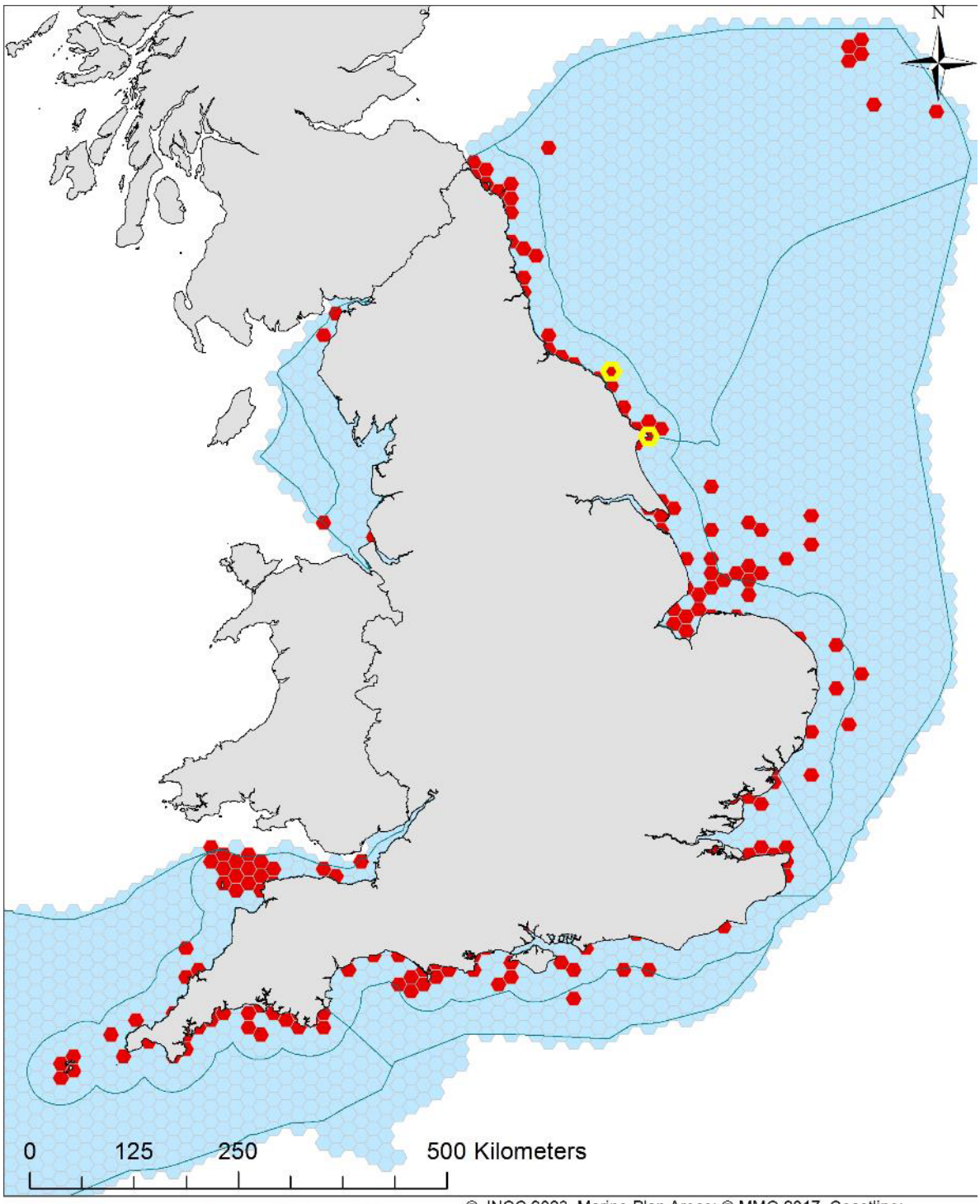
Figure 34. Historic (1910- 1959) distribution of *M. modiolus* in English waters, based on species occurrence data.



Historic distribution 1960-2009

***M. modiolus* records**

Present

Absent

bed habitat also present

Land

Marine Plan Areas

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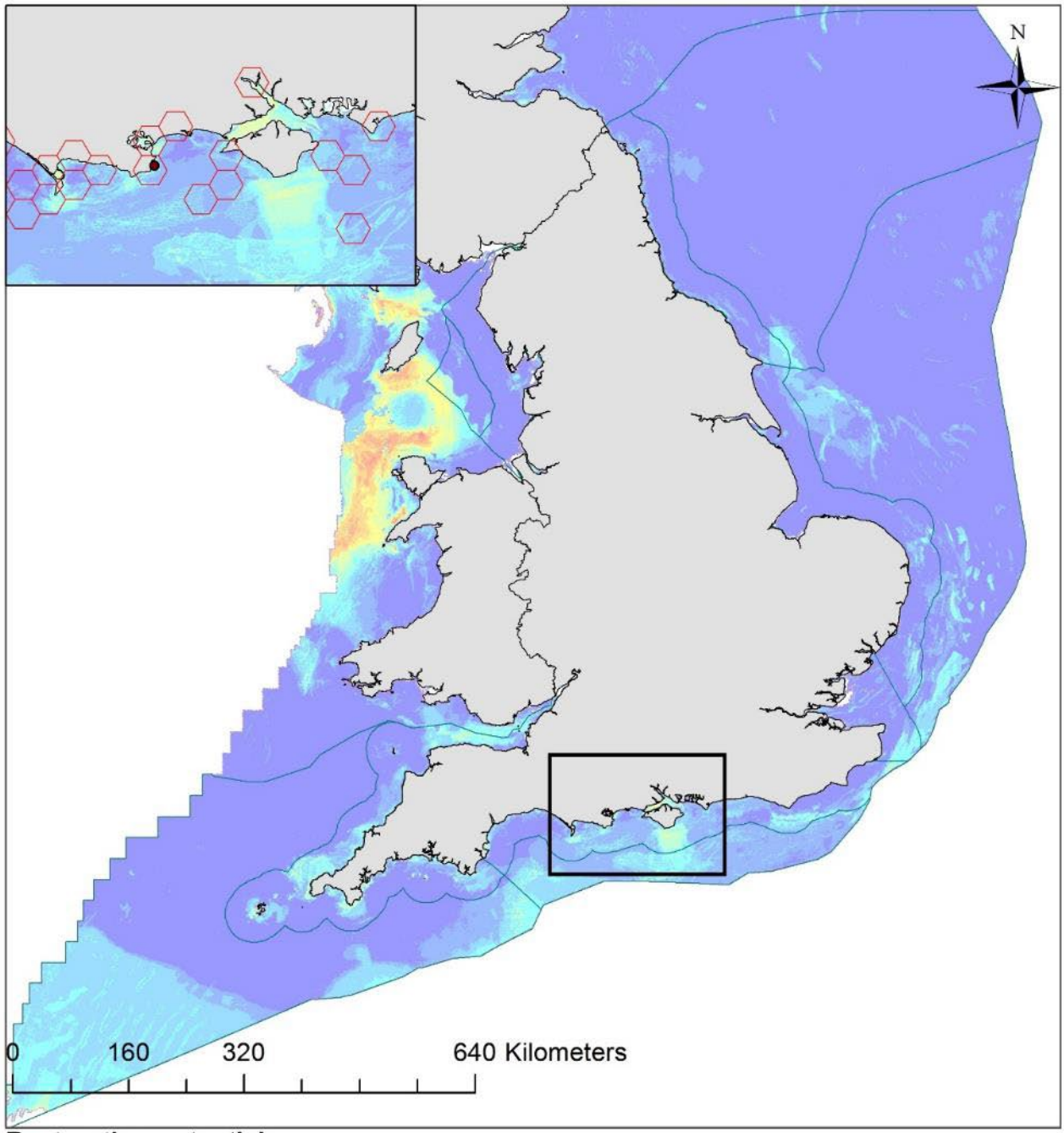
Figure 35. Historic (1960 – 2009) distribution of *M. modiolus* in English waters, based on species occurrence data. The grids which also contained historic horse mussel bed data are highlighted.

3.3. Restoration potential

The key parameters affecting the suitability of habitat for *M. modiolus* beds in the model were, in order of importance: minimum salinity at seabed, current energy at seabed, mean temperature at seabed, depth, wave energy at seabed, slope and finally substrate. In general, the variables identified as being important match those discussed in the literature review section above.

Model outputs (Figure 36) indicate that the probability of the habitat being suitable for *M. modiolus* beds is relatively low (<0.5) for most of English waters. The model was created at the UK scale and the vast majority of presence data points were from Scottish and Welsh waters, with English waters containing mostly pseudo-absences. Most of the areas of high probability occur off the North and West coastlines of Scotland, and in the Irish sea, particularly in Welsh waters and around the Isle of Man. There is a small area in the English northwest offshore region that has a high probability for suitable habitat, but none of the current or historic *M. modiolus* species occurrence or habitat data fall within these areas (Figure 37 and Figure 38). Whilst this could mean *M. modiolus* is truly absent it could equally be caused by a lack of survey effort and data collection in this area. There are some areas around the Isle of Wight and Cornwall which the model output suggest are more suitable, with probabilities of between 0.5 and 0.7. The more recent historic species data (1860 – 2009) does indicate that *M. modiolus* could be found in these areas but there are no current habitat and only a single species data record to verify the model output. When the current and historic *M. modiolus* bed habitat records were overlaid onto the model output they were all located in areas of very low probability for suitable habitat. It is difficult to accurately determine the reasons for this due to the very limited number of data points (n=8) available. It is possible that the model isn't a good match for the English data distribution due to low data availability. It is also possible that these areas aren't particularly suitable and it would be worth investigating if the historic beds are still present to help verify the model.



Restoration potential

Land

Marine Plan Areas

***M. modiolus* species data**

Historical (1960 - 2009) presence

Current records

Probability of suitable habitat

0 - 0.1
0.1 - 0.2
0.2 - 0.3
0.3 - 0.4
0.4 - 0.5
0.5 - 0.6
0.6 - 0.7
0.7 - 0.8
0.8 - 0.9
0.9 - 1

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Figure 36. Modelled habitat suitability areas of *M. modiolus* beds in UK waters.

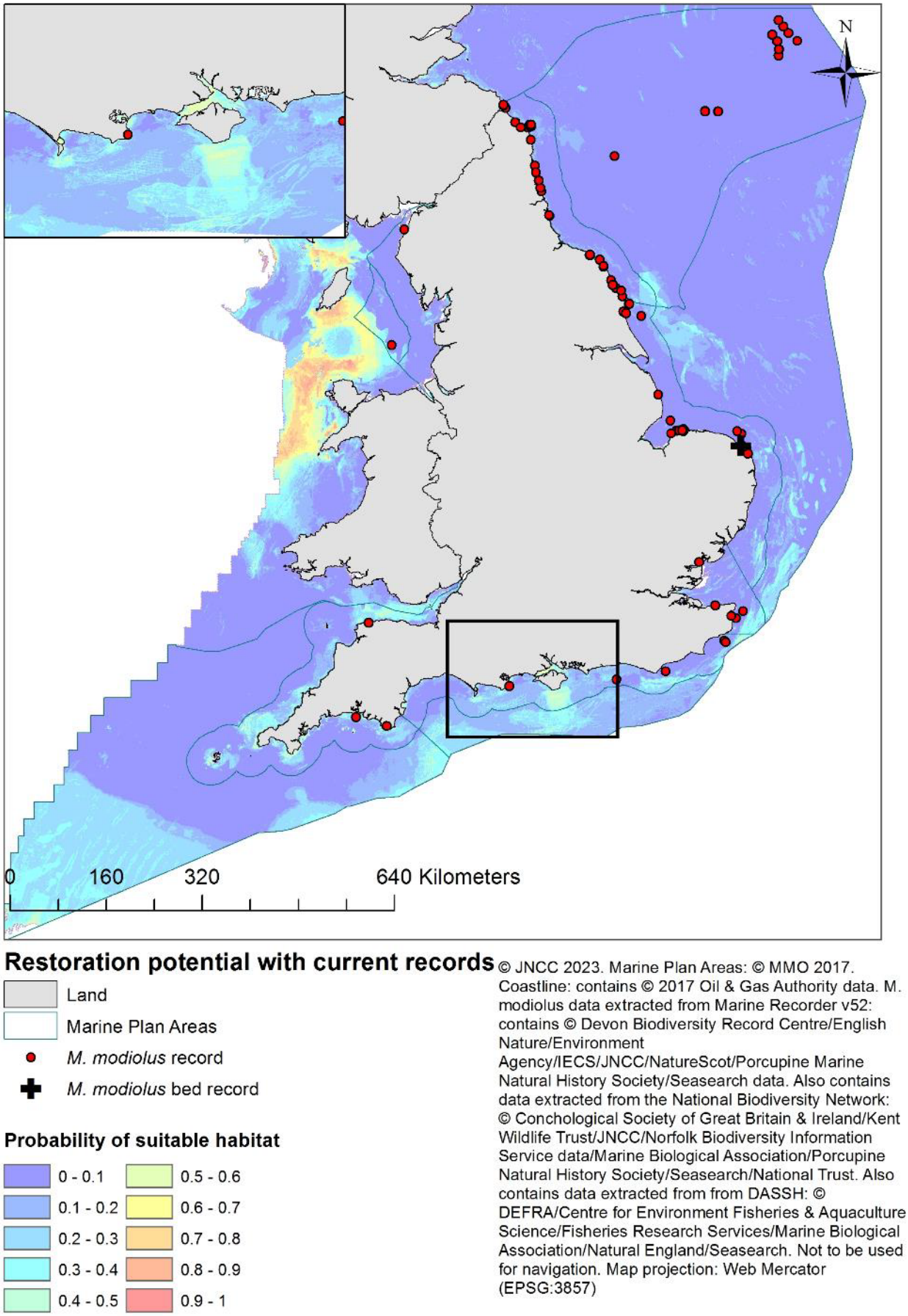
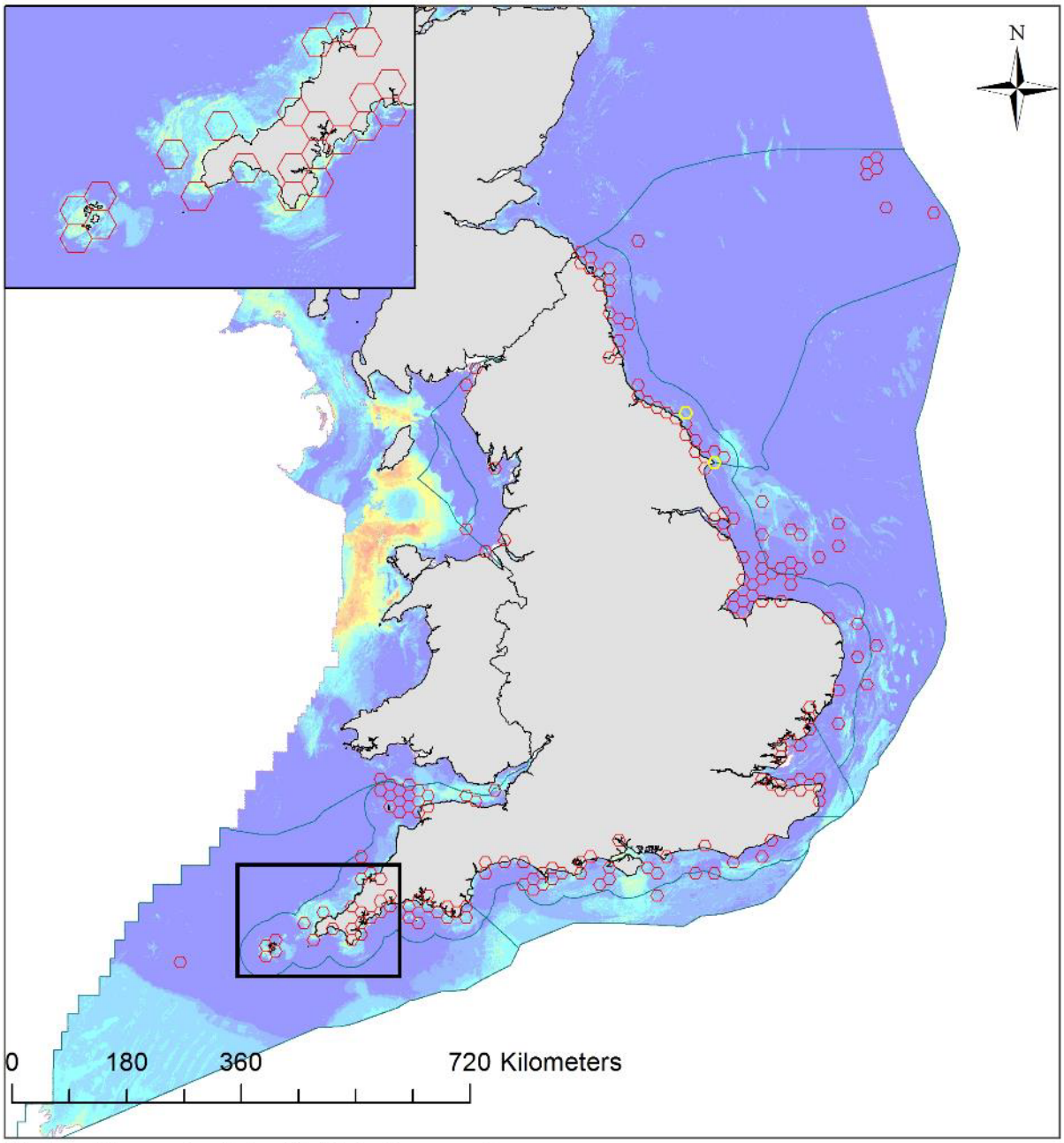


Figure 37. Modelled habitat suitability areas of M. modiolus beds in UK waters with current records overlaid.



Restoration potential with historic records

- Land
- Marine Plan Areas

***M. modiolus* historic records**

- Present
- bed habitat also present

Probability of suitable habitat

0 - 0.1	0.5 - 0.6
0.1 - 0.2	0.6 - 0.7
0.2 - 0.3	0.7 - 0.8
0.3 - 0.4	0.8 - 0.9
0.4 - 0.5	0.9 - 1

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Figure 38. Modelled habitat suitability areas of M. modiolus beds in UK waters with historic records overlaid.

4. Discussion and future recommendations

The distribution of the current records of *M. modiolus* matches the reported literature, showing that whilst horse mussels are widespread and common, *M. modiolus* bed habitats are much more limited in their distribution (OSPAR, 2009). The presence of horse mussel individuals is not enough to classify bed habitats; however, it does give an indication of larval availability and recruitment.

Whilst it is possible that horse mussel beds have a very limited distribution, given the number of species records of *M. modiolus* across the UK and the coverage of suitable habitat, it is unlikely that there is actually only a single horse mussel bed in English waters. The authors believe it is more likely that the lack of records of *M. modiolus* bed habitats is due to insufficient survey coverage and effort to enable their detection.

A possible reason for the lack of *M. modiolus* bed habitat records is the difficulties associated with classifying a *M. modiolus* "bed". OSPAR (2009) suggests that patches extending over $10m^2$ with more than 30% cover by mussels should be classified as a "bed". However, mosaics also occur where frequent smaller clumps of horse mussels influence ecosystem functioning, and thus lower thresholds can be accepted for defining *M. modiolus* beds for conservation and management purposes (OSPAR, 2009). Morris (2015) outlines several difficulties in classifying *M. modiolus* beds:

1. Defining areas $>10m^2$ particularly when *M. modiolus* are patchy in distribution or appear to mostly consist of dead shell.
2. Establishing the presence of live reef amongst dead shell.
3. Establishing the difference between beds lightly covered by sediment and infrequent patches of *M. modiolus.*

These challenges are further exacerbated in deeper waters where remote survey techniques must be used because in-situ survey by divers is impractical or impossible, (Morris 2015).

The changes in the distribution of *M. modiolus* over time, illustrated by the differences between the historic and current species occurrence data, could be linked to increased anthropogenic activity and associated pressures. The magnitude of declines has often been difficult to accurately assess due to the varied methods used to study and record horse mussel beds and the absence of compiled historical data maps of distribution (Strong and Moore et al., 2016). Furthermore, very few *M. modiolus* beds have been surveyed for long enough time periods to see evidence of change, which makes it difficult to determine the scale of any anthropogenic impacts (OSPAR, 2009). An in-depth analysis of anthropogenic pressures is not within the scope of this report, and additional research and monitoring are needed to determine if the changes in species occurrence detected in this project area is a true pattern or an artefact of changes in sampling effort. Considerable evidence gaps remain regarding the biology, ecology, reproductive success and ecosystem level interactions of *M. modiolus* bed habitats, which complicate restoration effort

measures. For example, *M. modiolus* spawning season and the associated drivers are still poorly understood (Brash et al., 2017), which makes it difficult to predict successful spawning and subsequent settlement. Many of the studies considered in this literature review indicate highly variable responses between populations and the authors of this report are not aware of any studies specific to English waters.

Similarly, there are several pressures where evidence is currently lacking including *M. modiolus* sensitivity to chemical contaminants such as heavy metals (Dinesen & Morton 2014), pathogens and litter (Tillin et al., 2018). Dinesen & Morton (2014) also reported that it is difficult to determine the long-term causal effects of activities such as fishing due to difficulties distinguishing them from other anthropogenic activities with similar pressures. A lack of long-term studies on the impacts of pressures on *M. modiolus* and their recovery also makes protecting this habitat and promoting its recovery difficult. For example, salinity and ocean acidification both have the potential to impact on horse mussels but long-term studies specific to *M. modiolus* are lacking (Tillin et al., 2018). We also do not currently have information on cumulative impacts.

The habitat suitability model identified some small areas with a higher probability of suitable habitat, such as around the Isle of Wight (see inset map of Figure 30). These areas overlap with locations with both historic *M. modiolus* presence and a single individual record. Research suggests that *M. modiolus* larvae can disperse over relatively long distances (Tillin et al., 2018), but an existing adult population is required to provide a sufficient larval source, and larval settlement of *M. modiolus* is positively influenced by the presence of adults (Tillin et al., 2018). The presence of species records in the areas of restoration potential identified by the habitat suitability model could indicate the presence of larval sources. To further investigate the restoration potential of these areas, targeted monitoring is required to determine the larval density of *M. modiolus* in the areas where the modelled habitat suitability overlaps with current and/or historic species occurrence data.

However, larval source alone is not sufficient to ensure restoration success in areas where *M. modiolus* habitat have been lost (Elsäßer et al., 2013). Fariñas-Franco et al. (2013) inferred that successful restoration of *M. modiolus* involves addressing the loss of habitat and removing any causes of decline as well as restocking, hypothesising that habitat recovery is possible when strict protective ecological restoration measures are put in place, even when the *M. modiolus* bed habitat has become severely impacted. (Fariñas-Franco & Roberts 2023). For bivalves, such restorative approaches might include protection and translocation, deployment of cultch to enhance natural recruitment, and hatchery production of spat or juveniles to reseed damaged populations and habitats (Zu Ermgassen et al., 2020).

Table 7. Key limitations and suggested improvements to the MaRePo habitat suitability models for *M. modiolus*.

Model area	Limitations	Potential improvements
Environmental data	The 300 m resolution of the predictor variables will not capture any small-scale variability in physical conditions, which could impact habitat suitability or patchiness at a much finer scale.	Trialling the modelling method on a case study with higher resolution environmental raster data would provide informative outputs on local variability of the habitats.
Environmental data	High sedimentation rates result in high mortality rates among *M modiolus* individuals (Hutchinson et al., 2016). Data on this variable could not be sourced.	Authors are not aware of any suitable UK scale datasets, but if a more local scale dataset could be sourced it could be used as a case study.
Environmental data	The depth range applied reflects the existing depth limits of the habitat. Whilst it is theoretically possible for *M. modiolus* to occur in this range it may not be truly representative, particularly at the min/max depths.	If this model were developed with restoration in mind the depth included should be refined to a more typical depth range and to a range whether restoration is possible in practise e.g. <50m.
Presence/Absence data	Low numbers of presence data points used within the model. Imbalanced presence/absence data levels.	The use of true absence data, as opposed to pseudo-absences, is likely to provide a more accurate prediction; however, the existence of such data is very limited. A more careful choice of pseudo-absences and balanced number with presences will be tested in future modelling efforts.

The habitat suitability model appears to identify an appropriate ecological niche of *M. modiolus* beds rather than potentially suitable areas for restoration. The current model has several limitations (see Table 7) and the model outputs could be improved by refining the model to a smaller geographical scale. Without sufficient data on the current distribution of *M. modiolus* bed habitats in English waters it is extremely difficult to determine both the scale of the restoration potential and any areas suitable for restoration via modelling. To ensure suitable sites for potential habitat restoration are chosen more model development is needed to consider factors influencing *M. modiolus* habitat distribution, such as, larval sources, sinks and dispersal, and population connectivity. Consequently, identification of suitable areas for restoration of *M. modiolus* bed habitats is not possible based on the current habitat suitability model, and more data are required to improve the model outputs.

The following work is necessary when considering future habitat restoration projects relating to *M. modiolu*s beds.

1. Model other important factors that would influence the success of *M. modiolus* bed establishment and longevity including climate change and larval dispersal and connectivity. An understanding of these aspects is crucial for the selection of suitable areas for restoration.

2. Improve our understanding of the current extent of *M. modiolus* beds in English waters to feed into modelling work.

    - Work to refine what is and isn't considered a bed.

    - Consider species records in light of definition to see if additional beds can be identified.

    - Targeted sampling to identify beds.

3. A revised habitat suitability model including the improvements listed in Table 7.

    - Could look to refine it to English waters if enough data were available or choose a small case study area to refine the model.

4. Investigation of anthropogenic activities that may impact on the success of any areas considered for restoration.

Sea pens and burrowing megafauna

1. Literature review

1.1 Biology and ecological importance

Sea pens and burrowing megafauna communities are recognised as a priority habitat of conservation importance in the UK and internationally. The habitat is included in the UK Biodiversity Action Plan (BAP)(BRIG, 2007), the list of Habitat Features of Conservation Importance in the Marine Conservation Zone (MCZ) network and the OSPAR List of threatened and/or declining species and habitats (OSPAR agreement 2008-6). OSPAR (2010) is the most current and widely accepted definition of the habitat: 'Plains of fine mud, at water depths ranging from 15-200m or more, which are heavily bioturbated by burrowing megafauna with burrows and mounds typically forming a prominent feature of the sediment surface. The habitat may include conspicuous populations of sea pens, typically *Virgularia mirabilis* and *Pennatula phosphorea*. The burrowing crustaceans present may include *Nephrops norvegicus*, *Calocaris macandreae* or *Callianassa subterranea*. In the deeper fjordic lochs which are protected by an entrance sill, the tall seapen *Funiculina quadrangularis* may also be present. The burrowing activity of megafauna creates a complex habitat, providing deep oxygen penetration. This habitat occurs extensively in sheltered basins of fjords, sea lochs, voes and in deeper offshore waters such as the North Sea and Irish Sea basins.'

There is a presence of burrowing megafauna that consists of an assemblage of taxa, which construct large, often long-lasting burrows across all example habitats. Common taxa of these habitats found in UK shelf waters include the burrowing crustaceans *C. subterranea*, *C. macandreae, Goneplax rhomboides* and *N. norvegicus*, worms such as *Maxmuelleria lankesteri,* brittlestarts of the genus *Amphiura* and fish such as *Cepola rubescens*, *Lesueurigobius friesii* (Hughes et al., 1996, Hill and Tyler-Walters, 2018, BRIG, 2007). Recent observations of the habitat have added to our understanding of the role of sea pens in the habitat. For example, the OSPAR definition states that sea pen, *F. quadrangularis,* occurs in fjordic lochs which are protected by an entrance sill. However, *F. quadrangularis* has since been recorded as deep as 2000 m and is considered to be a cosmopolitan species (e.g. (De Clippele et al., 2015, Lauria et al., 2017, Bastari et al., 2018), and can be considered to represent a bathyal species which 'intrudes' into sea lochs and fjords (BRIG, 2007). In the UK, *F. quadrangularis* is mostly present in lochs on the west coast of Scotland. Additionally, *F. quadrangularis* has been observed in the deep circalittoral in the Northern North Sea, mainly the Fladen Ground (Eggleton et al., 2017), and in English waters, fields of *F. quadrangularis* have been observed in the interfluves area of the Canyons Marine Conservation Zone (MCZ), on the shelf edge in the South West Approaches (Davies et al., 2008). Elsewhere in the Nort East Atlantic *F. quadrangularis* is mainly found in deeper bathyal waters (Ruiz-Pico et al., 2017, Ross et al., 2021). Other deeper water sea pen species included in the UK

definition comprise *Kophobelemnon stelliferum* and *Umbellula encrinus*, which are only known to occur in the deep waters below the shelf break (JNCC, 2014).

The burrowing megafauna and the sea pens share a habitat preference and often coexist in circalittoral and deep mud and sand. They are, however, functionally and ecologically dissimilar in most other respects (Hughes, 1998). This nature of the habitat, with two components that, whilst both considered part of the habitat, are not consistently associated with each other (JNCC, 2014, Hughes, 1998) makes identification of the habitat more complicated. In its 2014 clarification of the habitat description, JNCC state that the defining feature of the habitat are the burrowing megafauna, whether or not sea pens are present (JNCC, 2014). Furthermore, there is evidence suggesting reduced populations of sea pens and some burrowing species in conditions impacted by seafloor abrasion (Hiddink et al., 2006, OSPAR, 2010, Downie et al., 2021, Downie et al., 2022, Sköld et al., 2018, Sköld et al., 2021), which can make the identification of this habitat in impacted areas difficult. On the other hand, dense fields of sea pens can occur in sandier sediments without the larger burrowing megafauna, which are currently considered the defining feature of the habitat. The "sea pens and burrowing megafauna" classification should therefore be used with the understanding that in practice the habitat should be divided into more appropriate smaller groupings where scientific questions or conservation actions so require (Ross et al., 2021). With the expanding understanding of the distribution of sea pens in deep offshore sediments, further work is required to establish their role in the "sea pens and burrowing megafauna" habitat and other sediment habitats.

Other taxa associated with the habitat include epibenthic scavengers such as the common starfish *Asterias rubens*, hermit crabs (Paguridae) and swimming crabs such as *Liocarcinus depurator* (BRIG, 2007). The infauna can contain populations of polychaetes and bivalves. Another species that occurs in the habitat, albeit with a limited distribution, is the fireworks anemone *Pachycerianthus multiplicatus* (Hughes, 1998). The habitat supports a rich fauna of smaller animals and so forms an important reservoir of biodiversity. The burrows of macrofauna house other invertebrates and some fish (Hughes, 1998). Miatta and Snelgrove (2022) found sea pen density to be one of the primary drivers of community composition with higher infauna density and taxonomic diversity in sea pen fields in the Gulf of Lawrence. *N. norwegicus* and *Funiculina quadrangularis* also both support commensal species (Hill et al., 2018, Hughes, 1998). The effects of burrowing and other bioturbation activity influence the structure and chemistry of the sediments (Hughes, 1998). The habitat is also known to act as nursery areas for a number of fish, including hake (*Merluccius merluccius*;(OSPAR, 2010)).

1.2 Habitat distribution

The sea pens and burrowing megafauna habitat occurs from shallow coastal bays to the deep sea. The majority of reported distribution in the UK occurs in Scottish waters (e.g. (Greathead et al., 2015, Greathead et al., 2005). In English waters, the greatest distributions are in the North Sea and the South West Approaches, although the habitat is also present along the south coast. In the OSPAR definition the two most common sea pens in UK waters, *V. mirabilis* and *P. phosphorea,* are

described as occurring together. This seems to be the case on the west coast of Scotland and at the Fladen Ground (Greathead et al., 2015, Greathead et al., 2005). However, observations from the Farne Deeps basin off the coast of Northumberland show distributions that clearly reflect an inshore-offshore distinction between the two species (Downie et al., 2022). Ross et al (2021) similarly found the two species rarely co-occur in Norway.

Our knowledge of the full distribution of the habitat is limited due to the difficulty in identifying the habitat. Burrowing species can be observed in grab samples in sufficient numbers (at least 'frequent' on the SACFOR scale; (JNCC, 2014)) to attribute the habitat type, however video or stills imagery is ideally required to verify the presence of large burrows and/or mounds. Imagery is also the appropriate sampling method to detect the presence and investigate the abundance of sea pens. Particle Size Analysis (PSA) samples can further be used to confirm the mud habitat (JNCC, 2014). Video and still imagery collected for the marine protected areas Programme for verification and monitoring of marine protected areas, and video collected for *Nephrops* stock assessments have increased our understanding of the distribution of this habitat, and especially the distribution of sea pens, over the last decade but many gaps in the spatial coverage of appropriate sampling remain.

1.3 Factors affecting habitat distribution

1.3.1 Environmental factors

The sea pens and burrowing megafauna habitat covers muddy and muddy sand substrata at a range of depths from the shallow subtidal (< 10 m) to the deep sea. The major environmental variable driving the distribution of the habitat is grain size, and correlated to it, sediment organic content, which is typically higher in finer sediments (Hughes, 1998). Some burrowing megafauna are strongly associated with organic-rich muddy substrata but others have a tolerance of a wider range of sediment types. Whilst habitats with clear evidence of the relevant biological assemblages can be classified as 'Sea pen and burrowing megafauna communities' regardless of the grain size composition of the sediment (JNCC, 2014), coarse sands and gravels generally lack burrowing megafauna.

The burrowing megafauna, which live and in many cases feed from the sediments, have a more obvious link to particular sediment conditions. Sea pens, however, although anchored within the sediment, do not depend on it for food (Hughes, 1998) and occur over a wider range of sediments. Of the three sea pen species *V. mirabilis* has the broadest sediment tolerances (Downie et al., 2021, Greathead et al., 2015, Greathead et al., 2005, Ross et al., 2021), occurring in sediment ranging from extremely fine inner sea loch muds to much sandier substrata and is still recorded at 50% gravel content (Greathead et al., 2015). *P. phosphorea* and *F. quadrangularis* seem less tolerant of gravel and Greathead (2015) found a requirement of >10 % mud content with habitat suitability increasing to its highest at 100 % mud in populations off the west coast of Scotland. Eggleton et al. (2017), however, found the highest density of *F. quadrangularis* at the Fladen Ground in the North Sea in sand with only 6 % mud content. *F. quadrangularis* on the shelf edge in

the South West Approaches was found in sediments with approximately 90:10, 60:40 and 45:55 sand/mud ratios, with a range from 0 to 3 % gravel [No ref for this yet as unpublished data]. Ross et al. (2021) also found that in Norwegian waters *F. quadrangularis* was most common on sandy substrata, ideally with 50:50 sand/mud and *Pennatulidae* spp., likewise, seemed to be found in lower mud contents, always with some proportion of sand.

In distribution models utilising all available presence and absence observations on the UK shelf, Downie et al. (2021) found that instead of depth and substrate, the most important variables driving the distribution of the three sea pen species were mean bottom temperature, wave and current velocities and the concentration of suspended particulate matter in the water column. The temperature ranges of all species, based on a modelled temperature layer, were similar at ~7−12 °C, although in the North Sea *F. quadrangularis* was most likely to occur between 8 and 9 °C. All species were also more likely to occur in low current and wave velocities, with low concentration of suspended matter. *F. quadrangularis* and *P. phosphorea* were found to have the highest likelihood of occurrence in current and wave velocities up to 0.3 and 0.5 m^{s-1}, respectively. *V. mirabilis* was found to tolerate higher wave velocities up to 1.1 m^{s-1}. Ross et al (2021) found both *Pennatulidae* spp. and *F. quadrangularis* to favour areas with currents of ∼0.07 m^{s-1} with maximum current speeds observed at 0.2 m^{s-1} for *Pennatulidae* and 0.28 m^{s-1} for *F. quadrangularis*. Downie et al. (2021) also found 95 % of *F. quadrangularis* and *P. phosphorea* occurrences in areas with suspended matter at less than 2 g^{m-3}, whilst *V. mirabilis* tolerated suspended matter loads of up to 5.5 g^{m-3}. Colony density models for *P. phosphorea* and *V. mirabilis* by Downie et al. (2022) support the importance of suspended particulate matter over other environmental variables, finding *P. phosphorea* only to be present at low particulate matter concentrations and *V. mirabilis* to be abundant in the more turbid waters, regardless of depth.

Each of the three sea pen species has differing depth distributions. *F. quadrangularis* has the deepest distribution with optimal depths reported between 95-650 m depth in the North Atlantic (Ruiz-Pico et al., 2017, Ross et al., 2021, Greathead et al., 2007, Grinyó et al., 2022), and *V. mirabilis* has the shallowest distribution at around 20 m of depth in the UK (e.g. (Downie et al., 2022, Greathead et al., 2015)). *V. mirabilis* is however, found down to 1700 m in Norwegian waters with optimal depths at 400 and 700 m (Ross et al., 2021). Ross et al. (2021) points out that there may be issues with misidentification between *V. mirabilis* and other members of the Virgulariidae family (*Virgularia tuberculata*, *Virgularia glacialis* and *Stylatula elongata*) present in the region. *P. phosphorea* has a depth range on the west coast of Scotland from 15 to 100 m (Greathead et al., 2007) and in the southern Bay of Biscay from 95 to 179 m (Ruiz-Pico et al., 2017), this species was found on the shelf, being replaced by *Pennatula aculeata* in deeper waters (Ruiz-Pico et al., 2017). Depth is, however, more likely to be proxy for differing temperature and water clarity requirements of the sea pens, with response possibly modified by their tolerance to physical disturbance.

1.3.2 Ecological pressures

There is still a dearth of information on how biological interactions structure sea pen and burrowing megafauna communities and their effect on natural long-term variability in this habitat.

Studies focusing on soft sediment communities in general have found both enhancing and inhibitory effects between species. Mesocosm experiments on subtidal macrobenthic assemblages suggest that the identity, density and distribution of large bioturbating organisms are important drivers of the structure and diversity of benthic communities (Widdicombe 1999). However, no single member of macrofaunal assemblages in mud habitats is known to be a 'keystone' species essential to determining the community structure (Hughes 1998, Widdicombe 2000).

Burrowers and deposit feeders both alter the structure of marine soft sediments, changing the sediment water content and oxygenation (Hughes, 1998, Widdicombe et al. 2000). Sediment oxygenation and added surface area from burrowing activity is generally seen as positive for other fauna. The changes in sediment structure may, however, also have negative effects on other taxa. Brenchley (1982) found that tube-mats formed by polychaetes and small crustaceans caused significant reductions in the mobility of a variety of other burrowing taxa. Nes et al. (2007) observed a change from a community dominated by the burrowing ophiuroid *Amphiura filiformis* to a *Callianassa subterranea* dominated community with an associated change in sediment stability and suggest that the interaction between sediment compaction and the benthic community can lead to irreversible changes in community composition.

Other potential negative effects of burrowing megafauna on other species include dislodgement, burial and increased turbidity from displaced sediment. There may also be competition for burrow space and food resources as well as direct predation (Hughes, 1998, Johnson et al. 2013). *Nephrops* has been observed to prey on e.g. *Goneplax rhomboides* and *Calocaris macandreae*, and is likely to feed on any of other thalassinidean species encountered (Johnson et al. 2013). Hughes (1998) also suggests that sea pens may conceivably be adversely affected by high levels of megafaunal bioturbation for example through reducing the survival of small, newly settled colonies, but no studies have been done on the interaction between them.

1.3.3 Anthropogenic factors

Fishing activities disturb the seafloor impacting on the density of *P. phosphorea*, and the occurrence of *F. quadrangularis.* Studies by both Murray et al. (2016) in the Fladen Ground and Downie et al. (2022) at the Farne Deeps, found a negative relationship between increasing abrasive pressure and the density of *P. phosphorea,* with no impact on *V. mirabilis*. *F. quadrangularis* inhabiting creel *Nephrops* fishing areas in sea lochs of the west coast of Scotland were found to occupy a different niche to those inhabiting a similar habitat in the extensively trawled area of the North Sea. However, Downie et al. (2022) found no links between the predicted distributions of *V. mirabilis* and *P. phosphorea* and the intensity of demersal fishing.

1.3.4 Climate change impacts

Changes in temperature, acidification and salinity in many shelf sea regions resulting from climate change can influence mortality and reproduction in benthic macrofauna. Specific to burrowing megafauna, temperature, pH and salinity modulate both host susceptibility and pathogen growth rates. For example, at temperatures above 13–14◦C bacteria-induced muscle and cholinolytic necrosis of the cuticle is observed in *N. norwegicus*, (Hernroth et al., 2012). The changes to

surrounding ocean chemistry are projected to result in increased susceptibility of crustaceans to pathogens and the emergence of many more pathogens over the next century (Shields, 2019). Temperature and ocean acidification also affect the developmental rate and physiology of *N. norvegicus*, including changes to larval release that can be attributed to warming (Hernroth et al., 2012).

Wider studies in climate effects for benthic macrofauna by e.g., Birchenough et al (2015), Hiddink et al. (2015) and Göransson (2017), show evidence for shifts in distributions in response to increase in the temperature of the bottom water observed in the last decades across the North-East Atlantic, the North Sea and the Kattegat, respectively. Changes included an observed reduction in the total number species in the Kattegat(Göransson, 2017), North-westerly range shifts with reductions in the ranges of species with a northern range and increases in species with a southern range;(Birchenough et al., 2015, Göransson, 2017) along with deepening of ranges (Hiddink et al., 2015). Hiddink et al. (2015) suggest that many species have not been able to follow the changing geographical range of their thermal niches over the study's time period and are consequently already partly occupying habitat with suboptimal thermal conditions. Birchenough et al. (2015) indicate that the observed changes in ranges were particularly clear around the UK and northern France, where species of Lusitanian origin overlap with species from Boreal origin.

Gormley et al. (2015) modelled the distribution and extent of 'Sea pens and burrowing megafauna habitats' as part of a group of "Priority Marine Habitats" (PMHs) in the North-East Atlantic under future scenarios of climate-induced environmental change. Under a temperature scenario of a 4°C increase by 2100 they report a 2% loss of overall area as suitable for 'Sea pens and burrowing megafauna habitats' in the Greater North Sea ecoregion and no change in the Celtic Seas ecoregion. Weinert et al. (2016), in turn, modelled the distribution of 75 species to assess the response of benthic species in the North Sea to expected changes in temperature and salinity. Species included in the study with relevance to 'Sea pens and burrowing megafauna habitats' consist of the sea pen *Pennatula phosphorea*, the tubeworm *Chaetopterus variopedatus* and the burrowing crustacean *Callianassa subterranea*. *P. phosphorea* was predicted to respond with a southeast extension of range amounting to a 34% increase in area of suitable habitat, whilst a predicted southeastern shift in the distribution of *C. subterranea* led to a 31% loss in area of suitable habitat, and a northwestern shift in *C. variopedatus* saw a 96% loss in area of suitable habitat. In a further study investigating predicted gains and losses in North Sea MPAs, Weinert et al 2021 found a more or less stable or even increasing distribution area in the MPAs between 2001 and 2050 for most species but in some MPAs by 2099. For *C. subterranea* a decline of the distribution area was projected for the Dogger Bank (from 55% to 28%) and Klaverbank (from 100% to 20%) by 2099, but an increase (from 49% to 86%) for MPAs in the southeastern North Sea. Overall, the trend in area suitable for *C. subterranea* showed a substantial decline within the protected areas by 2099. The burrowing crustacean *Upogebia deltaura* was projected to move in an easterly direction with losses (from 32% to 16% suitable habitat) in MPAs along the coast of England and gains from (0% to 85% suitable area) in MPAs on the west coast of Germany and Denmark. Much less is known about the potential effects of climate change on sea pens.

1.4 Restoration approaches

Potential for successful restoration and recovery of sea pen and burrowing megafauna habitats is dependent on our ability to restore the natural structure of the soft sediment and ensure its colonisation by burrowing fauna and sea pens. Recovery generally depends on the type and duration of impact along with environmental factors and supply of larvae for recruitment (Mazik et al., 2015). The timescale for recovery will be determined by whether recovery of the physical habitat is required before natural communities can be re-established or whether community and habitat recovery can occur at the same time (Mazik et al., 2015).

There are no studies on targeted restoration of sea pen and burrowing megafauna habitats. There are, however, MPAs set up throughout the Northeast Atlantic with management measures including closure of bottom contacting fisheries to protect this habitat. Incentives have also been introduced in Norway and Sweden to switch from trawl to creel fisheries for *Nephrops* (OSPAR Status Assessment 2022). The results of these can give us an idea of suitable restoration approaches. Studies conducted on Swedish *Nephrops* fisheries in the Skagerrak and Kattegat have shown creeling offers a substantial reduction of fishing mortality of both undersized *Nephrops* and fish (Hornborg et al., 2017). Although proportionally more females carrying roe are caught by creels than trawls (Ziegler and 2006) the effects of a switch to creeling on the *Nephrops* population are positive overall, including considerable increases in biomass and egg (Eichert et al., 2018). Creeling has also been shown to increase economic and environmental benefits with an overall increase in profits and a greatly lower impact on the seafloor per landed tonne of *Nephrops* (Hornborg et al., 2017, Ziegler and 2006, Hammarlund et al., 2021). The area of seafloor impacted per tonne of landed *Nephrops* by creeling is 0.003–1.3 km^2 in comparison to the 40 km^2 impacted by mixed trawling (Hornborg et al., 2017). The reduced physical impact leads to a change towards a more stable structuring of the sediments as well as an increase in the general biodiversity at all levels (Eichert et al., 2018) and in the total abundance of epifauna (Sköld et al., 2021). There is also evidence showing that the tall sea pen (*F. quadrangularis* and its commensal ophiuroid *A. loveni*), rarely present in trawled areas, are present in areas with creel fisheries (Adey, 2007, Downie et al., 2021, Greathead et al., 2005, Sköld et al., 2021).

In the UK management measures prohibiting the use of bottom towed fishing gear have recently been implemented within multiple MPAs and the possibility of a change to creel fisheries has been investigated at the West of Walney MCZ (Tabrizi, 2019). The measures have not been in place for long enough to see recovery but will be a source of knowledge going forwards.

2. Methods for mapping the current, historic and potential extent and distribution

2.1 Current extent and distribution

Several data sources (Appendix 13) including Marine Recorder, OneBenthic, OBIS, the Cefas fisheries surveys database (FSS) and other survey data from towed camera surveys under the Marine Protected Areas Programme and from *Nephrops* UWTV surveys (provide by Cefas and Marine Institute), were used to identify all possible observations of sea pen species (*P. phosphorea*, *V. mirabilis* and *F. quadrangulris*) and species associated with "burrowing megafauna" communities (Appendix 14). For each species, presence observations were extracted from each data source and compiled into a single dataset, where duplicate records were then removed. This dataset was then used to create point shapefiles for each of the sea pen species and the burrowing megafauna which were then clipped to Marine Plan Areas in ArcMap (Version 10.5).

For each species, observations collected between 2000 and present (inclusive) were selected from the shapefile and extracted and considered as the current extent. These data representing the current extent for each species/feature have been represented as individual point observations.

The data used in this study to represent the extent of each of the species is in the format of presence only data, meaning that absence cannot be inferred. Areas with no recorded presence may equally likely be due to lack of survey effort as absence. In addition, as presence only data has been used there is no indication on the density or biomass of the species of interest within a given area.

2.2 Historic distribution

Observations for the historic extent were extracted from the point data file (method on its production and data used outlined in the previous section). For each species, point observations were selected for the years 1950 – 1999 (inclusive) and were considered to represent their historic extent.

Historic observations for each species were represented by a 10 km hexagonal grid, where a single cell was assigned as a "presence" or "apparent absence" depending on whether a single observation of the species of interest fell within it or not. This was achieved using the "Spatial join" tool in ArcMap (version 10.5).

2.3 Restoration potential

With the incomplete knowledge of the current and historic distribution of the sea pen and burrowing megafauna habitat, the best approach to identify areas for potential restoration is

through habitat suitability modelling. Modelling can identify areas with suitable environmental conditions for each sea pen species, burrowing taxa and burrow density, as well as the habitat itself. The nature of the sea pens and burrowing megafauna habitat makes it less likely for human impact to cause a reduction in the habitat extent, than to effect loss in habitat quality and health. Restoration in this case would entail removing pressure(s), to return the burrowing and associated epifaunal community to a relatively undisturbed state. Habitat suitability model outputs combined with the current distribution of fishing pressure and an assessment of the potential success of transitioning from a trawl to a creel fishery could be used to indicate locations with restoration potential.

The sea pen and burrowing megafauna habitat has previously been modelled at a coarse scale covering the OSPAR region (North-East Atlantic) by Gormley et al. (2015). The model was based on the OSPAR database of "Priority Marine Habitats" (PMHs), which at the time was not representative for English waters. Sea pen distribution has recently been modelled for the whole UK shelf by Downie et al. (2021). As no current and accurate model output exists for the whole habitat (i.e. inclusive of the burrowing megafauna), the results of the distribution modelling for sea pens have been used to illustrate habitat suitability across England.

Restoration potential areas were identified based on the outputs from distribution models for the three sea pen species occurring on the UK shelf (*P. phosphorea*, *V. mirabilis* and *F. quadrangularis*) described in Downie et al. (2021). In the case of *F. quadrangularis*, Downie et al. (2021) concluded it covered different environmental ranges between the ecoregions and posited that the Greater North Sea ecoregion showed potential range modification due to bottom contact fishing activity. Consequently, a second map is provided for *F. quadrangularis* based of the predicted distribution from the model trained using data from the Celtic Seas ecoregion only. The second map represents potential suitable habitat without the suggested range modification. The maps were created using a 10 km hexagonal grid, where a single cell was assigned as a "presence" or "apparent absence" depending on whether ≥ 6 out of the 10 repeated run outputs of the model predicted a presence of the sea pen species.

3. Results

3.1 Current distribution

The current distribution (available observations collected between 2001 and 2022) of *P. phosphorea* (Figure 37) is predominantly clustered in the North East Inshore and Offshore Marine Plan Areas, with 96% of the observations falling within these areas. Of the observations which fall within the North East Marine Plan Areas, 75% fall within three existing marine conservations zones (MCZs; Farnes East, North East of Farnes Deep and Swallow Sand). There are also a considerable number of observations which fall to the South of the Farnes East MCZ, co-occurring with the

Farne Deeps *Nephrops* fishing ground. The remaining observations fall within the East Offshore, South Inshore and South West Inshore and Offshore Marine Plan Areas.

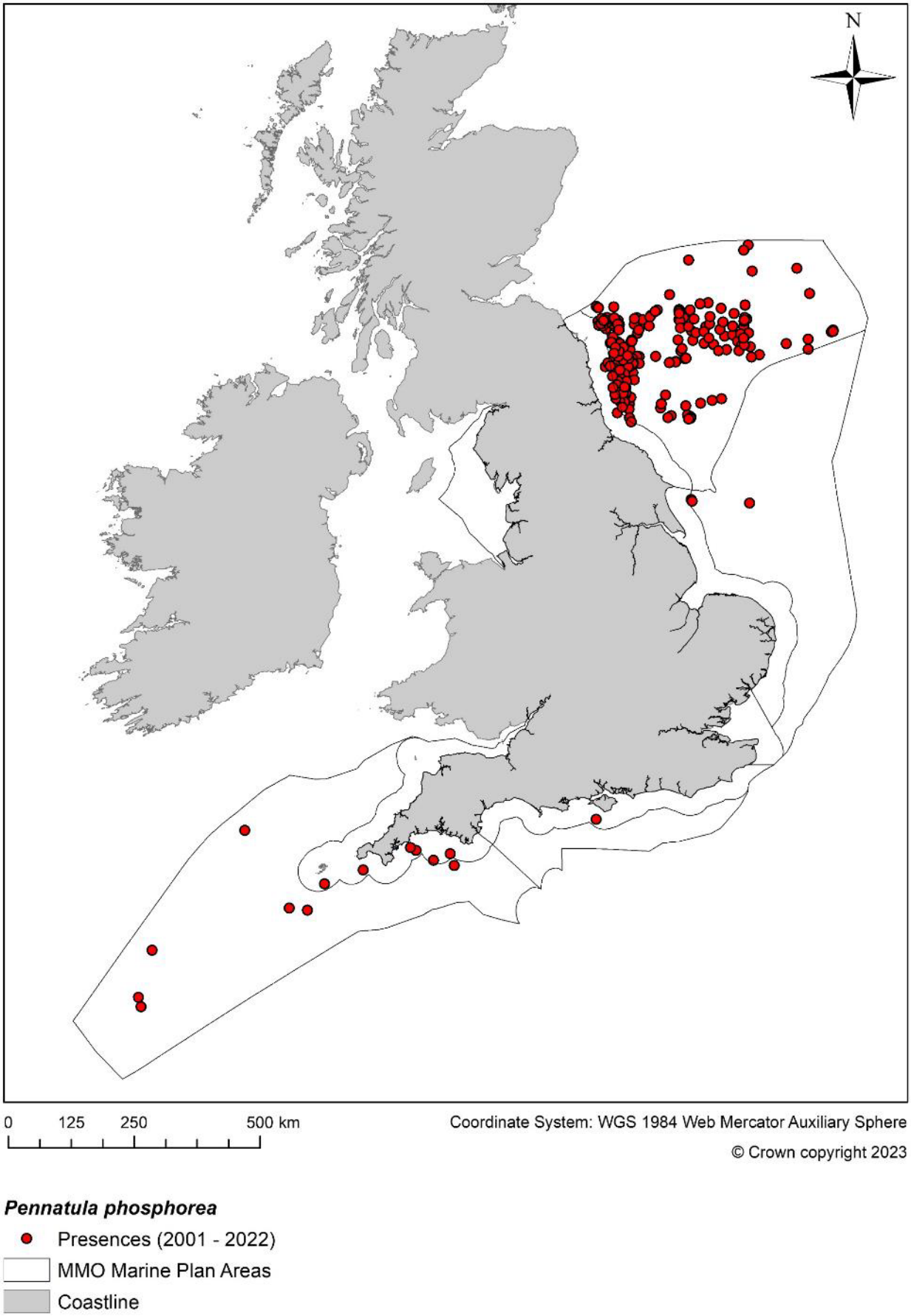

Figure 39. Current known distribution of *Pennatula phosphorea* from 2001-2022.

The current distribution (available observations collected between 2001 and 2022) of *V. mirabilis* (Figure 38) is predominantly clustered within the North East Inshore and Offshore and the South West Offshore Marine Plan Areas. In the south-west the majority of presences fall outside of existing MCZ boundaries, except for those which fall within North-West of Jones Bank MCZ and The Canyons MCZs. Almost all the observations found in the North East Inshore and Offshore Marine Plan Areas are located outside of existing MCZs.

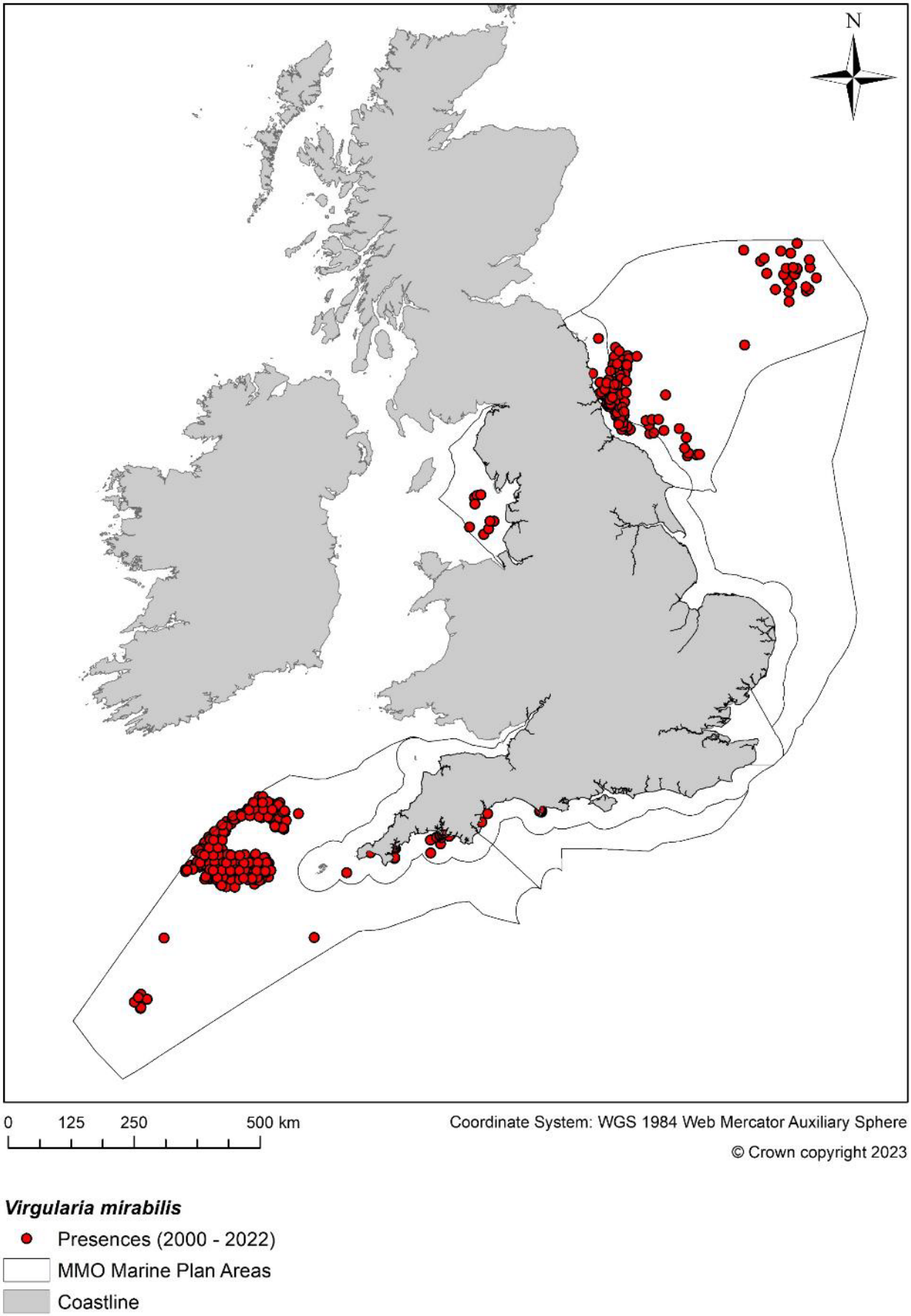

Figure 40. Current known distribution of Virgularia mirabilis from 2001-2022.

There were very few observations of *F. quadrangularis* within English waters (Figure 39). For the current distribution of the species, only 14 observations were identified from the available datasets collected between 2004 and 2020. Half of the presences (7 observations) were found in the South West Offshore Marine Plan Area, inside the Canyons MCZ. Four presences were observed within existing MCZs (Fulmar and Swallow Sand) within the North East Offshore Marine Plan Area. One observation fell within the North West Inshore Marine Plan Area, one within the East Inshore Marine Plan Area and one within the South Inshore Marine Plan Area. The two singular observations in the Southern North Sea and the Eastern Channel were recorded in groundfish trawl surveys where identification has been made by a non-benthic expert. The observations are outside the confirmed known extent of *F. quadrangularis* in UK waters and the possibility of mistaken identification cannot be ruled out as no photograph or physical sample was retained.

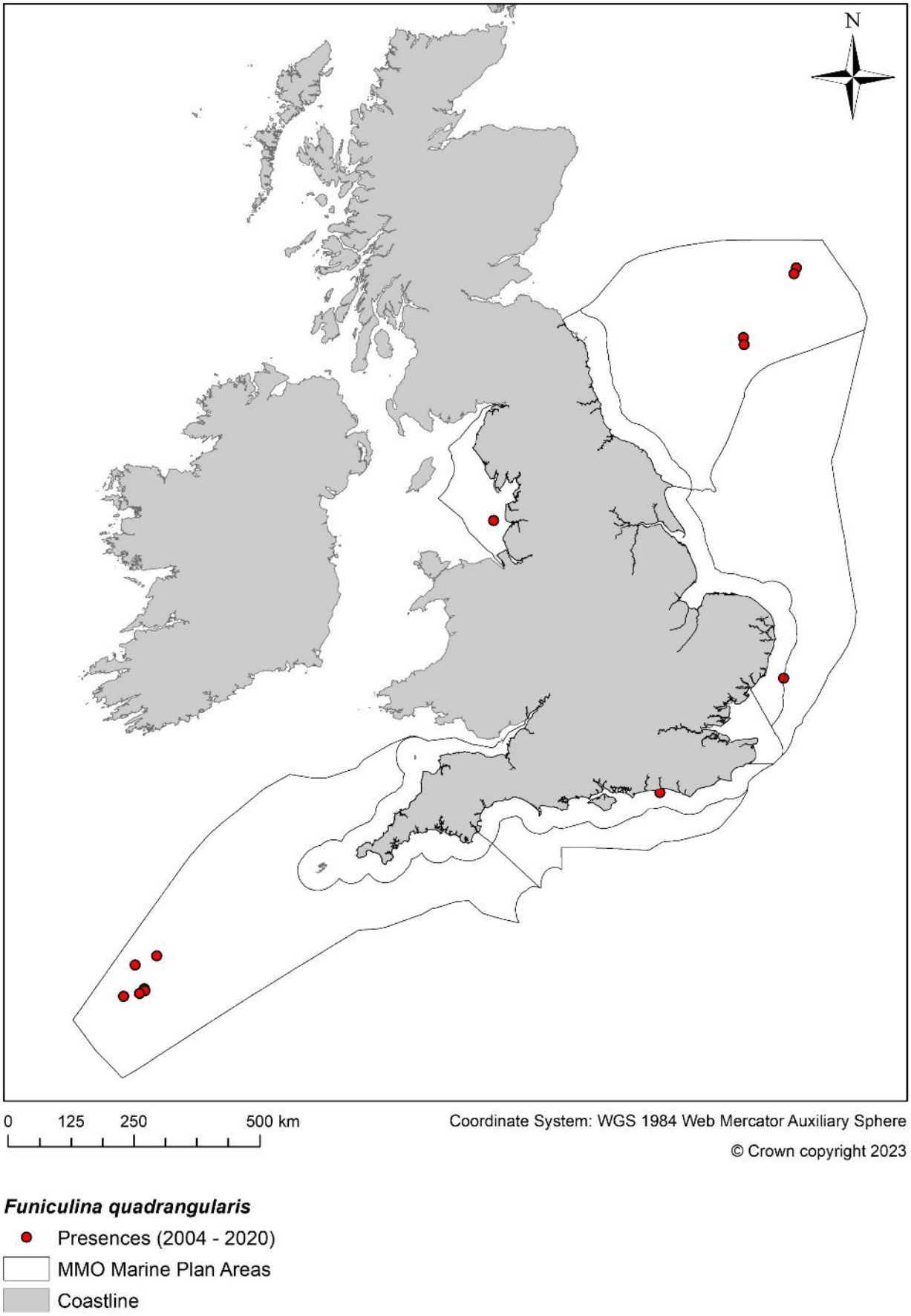

Figure 41. Current known distribution of *Funiculina quadrangularis* from 2001-2022.

The current distribution of burrowing megafauna species (Figure 40) indicates that species associated with “Burrowing megafauna communities” can be found across English waters. There are observations within all five Offshore Marine Plan Areas and all six Inshore Marine Plan Areas. The presented distribution map should, however, be viewed with caution. The point locations shown are for presence of taxa known to be associated with burrowing megafauna communities. Many of them are not exclusively observed in mud and observations may fall in areas with coarser substrata. For the sea pen species also, but especially in the case of burrowing megafauna, an understanding of the density and/or biomass of species of interest within the different Marine Plan Areas is necessary to accurately assign the habitat ‘Sea pens and burrowing megafauna’. The JNCC (2014) clarification of the habitat description states that, regardless of the presence of sea pens, the defining feature of the habitat are the burrowing megafauna, which must be at least ‘Frequent’ on the SACFOR scale (see Hiscock, 1996). The abundance requirement can be met either by density of the burrowing megafauna in grab samples or the density of individual or visible burrow entrances or mounds in imagery. Only a subset of existing data can be used to infer density, or has already been assigned a ’Sea pens and burrowing megafauna’ habitat. In future, data burrow density or the abundance or biomass of burrowing taxa could be used to model the spatial distribution of the habitat to get a more accurate and generalised map.

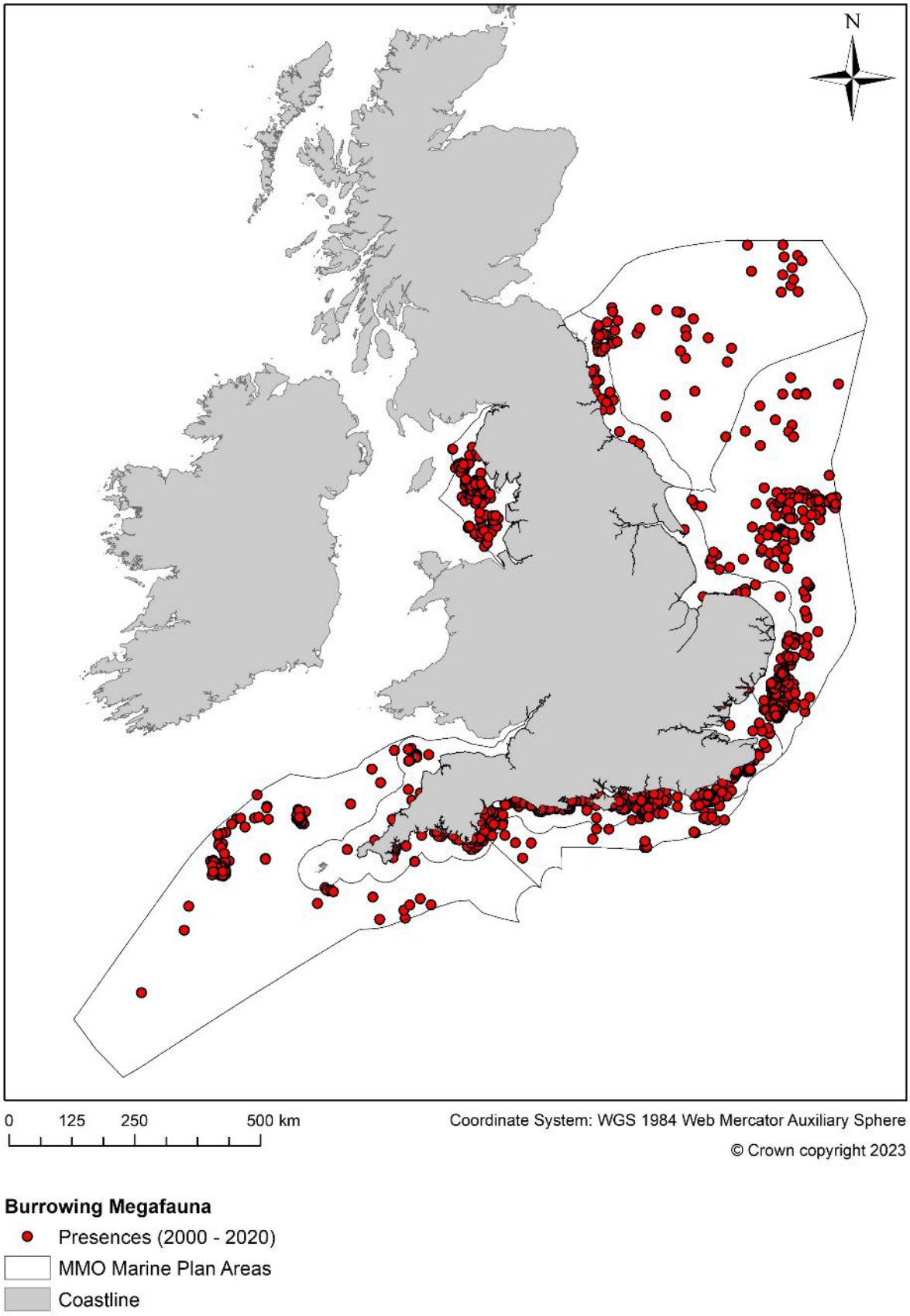

Figure 42. Current known distribution of burrowing megafauna species from 2001-2022. The full list of species included in "burrowing megafauna" communities for the purposes of this figure is available in Appendix 14.

3.2 Historic distribution

The distribution of historic records (records available between 1974 and 1999) for *P. phosphorea* was much smaller in comparison to the current distribution, with presences only falling within 16 grid cells (Figure 41). Historic records were all observed in the North East (Inshore & Offshore) Marine Plan Areas.

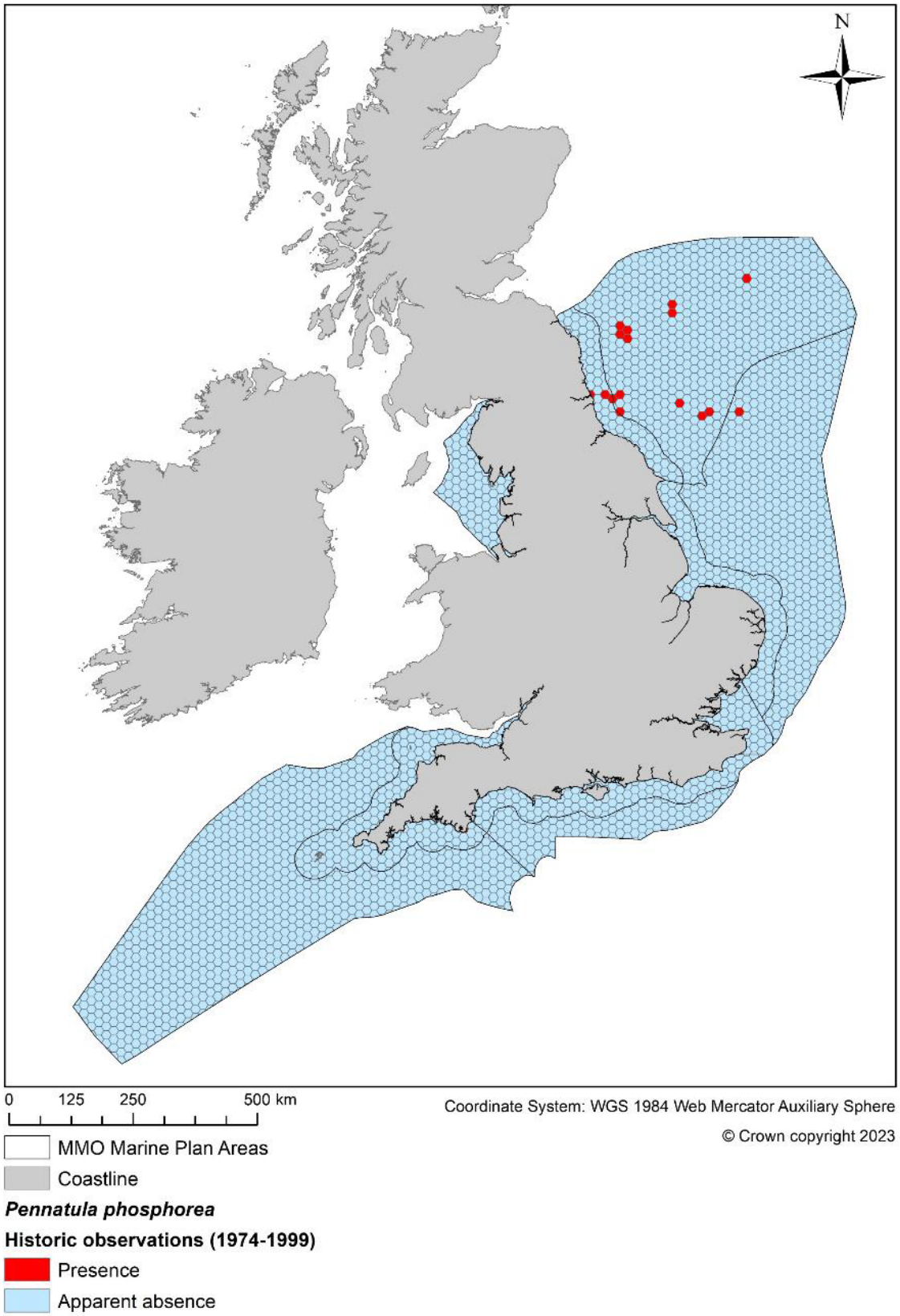

Figure 43. Historically known distribution of *Pennatula phosphorea* from 1974-1999.

The historic distribution of *V. mirabilis* (records available between 1953 and 1999) appears to be much smaller compared to the current distribution, with records falling within just 13 hexagonal grid cells (Figure 42), which are predominantly located nearer the coastline. Historic observations

of this species fall within the North East (Inshore & Offshore), South (Inshore) and the North West Marine Plan Areas.

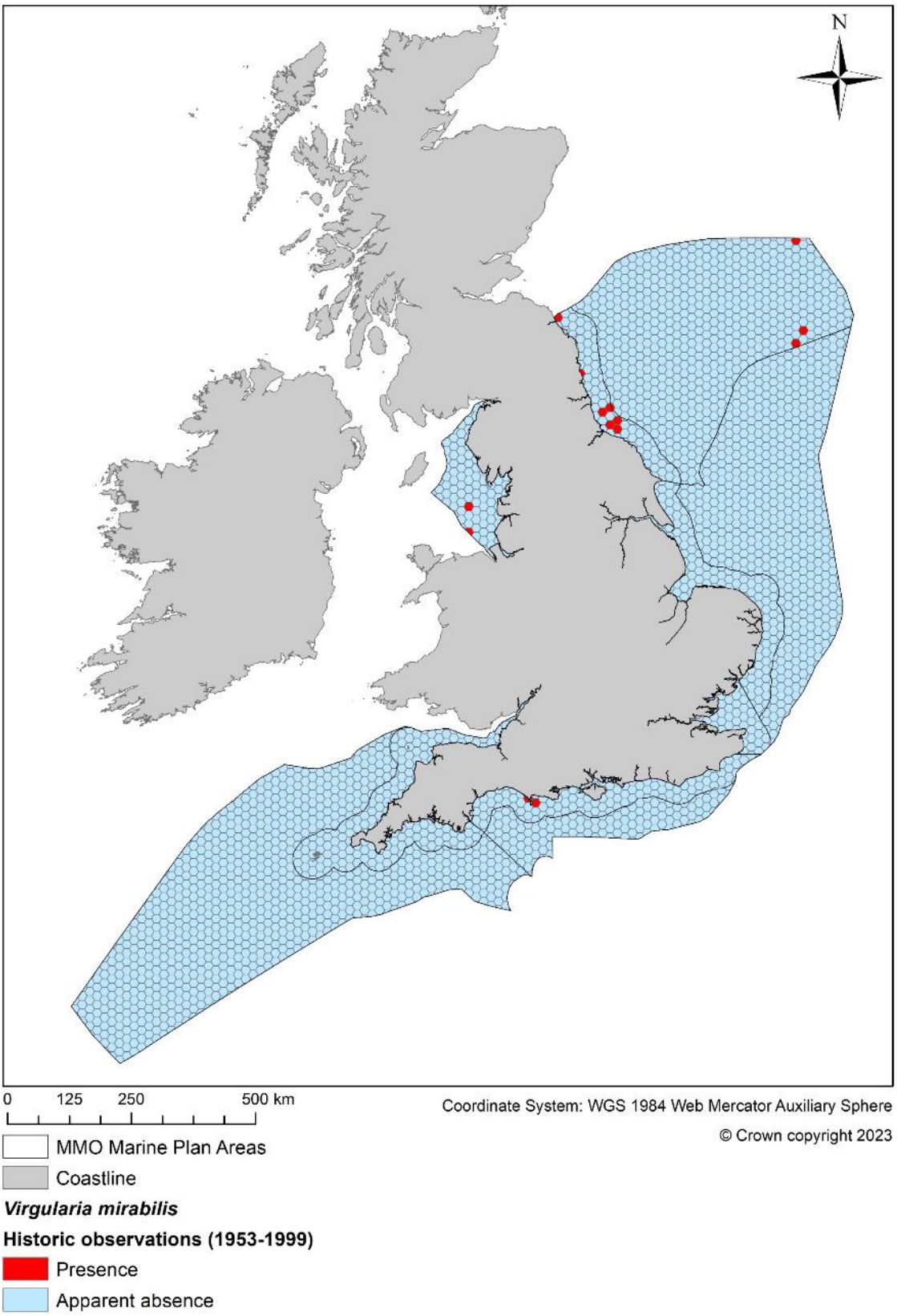

Figure 44. Historically known distribution of *Virgularia mirabilis* from 1974-1999.

Only one hexagonal grid cell with an observation of *F. quadrangularis* was identified using the available datasets (Figure 43). The observation was made in 1996 and occurs within the Swallow Sand MCZ, which falls within the North East Offshore Marine Plan Area.

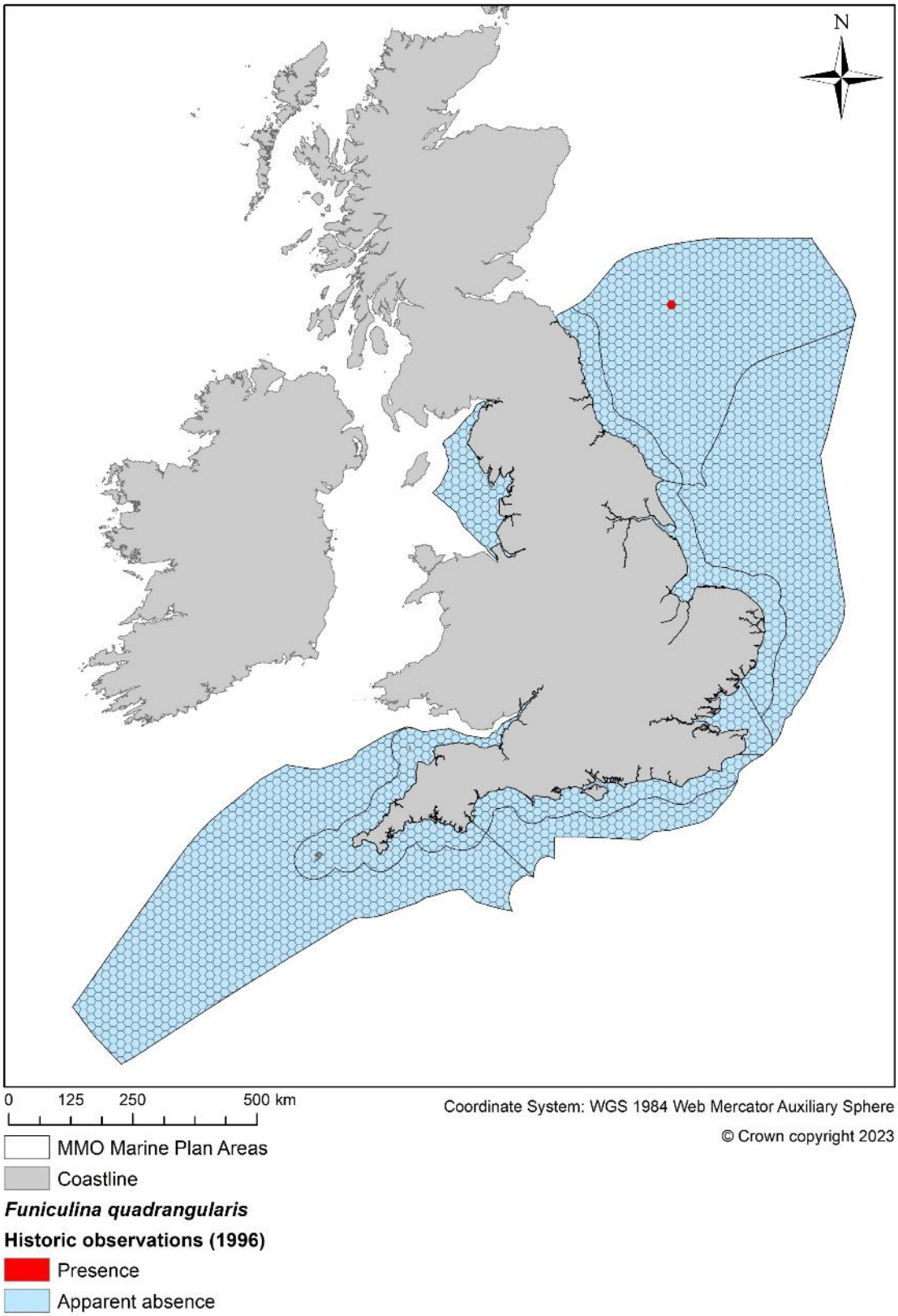

Figure 45. Historically known distribution of *Funiculina quadrangularis* from pre-2000.

The historic extent of burrowing megafauna (Figure 44) appears to be much smaller in comparison to the current extent. In addition to the apparent smaller extent for these species, most of the historic observations are located nearer to the coastline. There are observations within all six inshore Marine Plan Areas and within the North East Offshore Marine Plan Area.

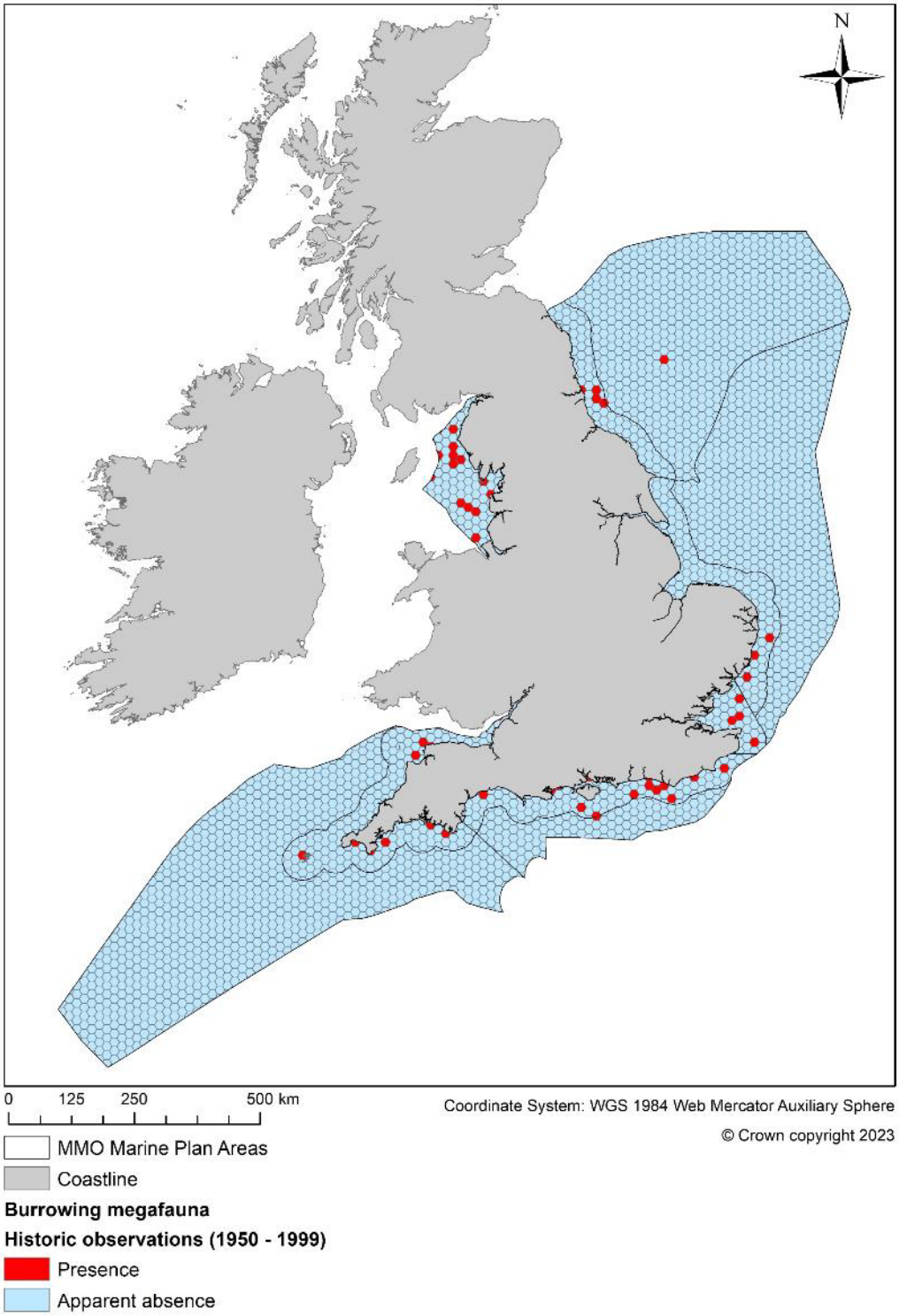

Figure 46. Historically known distribution of burrowing megafauna species from 1950-1999. The full list of species included in "burrowing megafauna" communities for the purposes of this figure is available in Appendix 14.

The historic distributions for all three species of sea pen and the burrowing megafauna species appear to have a smaller extent when compared to their current distribution. However, this does not mean that extent of the sea pens and burrowing megafauna habitat was smaller in English waters historically. The smaller historic extent mapped in Figures to 35 - 38 reflects the significantly lower survey effort in the past compared to today, and consequently an even poorer understanding of the habitat's distribution than we have today (which still remains incomplete). The effect is especially pronounced offshore, as the survey effort of the historic data appears to be more concentrated nearer the shore. Accordingly, it is not truly possible to map the historic extent of sea pen and burrowing megafauna habitats with the data available. *F. quadrangularis* provides a good example of the gaps in our understanding of offshore distributions. Prior to 2000, only one observation of *F. quadrangularis* is recorded, located in the Northern North Sea. Multiple research surveys starting from 2014, visiting the Explorer and Dangaard canyons in the Western Approaches found previously unknown fields of *F. quadrangularis* in the canyon interfluves. The full extent of the distribution of *F. quadrangularis* in the southwest is still unknown.

3.3 Restoration potential

The maps showing areas with restoration potential for sea pens are based on models developed by Downie et al. (2021). They found the most important variables predicting the distribution of all three sea pen species included mean bottom temperature, wave and current velocities, and the concentration of suspended particulate matter in the water column in winter. All three species are more likely to occur in low current and wave velocities and with low concentration of suspended matter, although *V. mirabilis* occurs in higher suspended matter concentrations than the other two. *P. phosphorea* and *V. mirabilis* were found to consistently occur in areas with sheltered concave topography, increasingly enclosed by higher ground. Whilst *F. quadrangularis* was found to follow this trend in the Celtic Seas Ecoregion (mainly western Scottish waters), in the North Sea it occurred almost exclusively offshore and on flat or slightly elevated ground. The models all had good predictive power (≥ 0.9 Sensitivity and Specificity scores, ≥ 0.5 Kappa and ≥ 0.8 True Skill Statistic, Downie et al., 2021).

Downie et al. (2021) suggest the discrepancy in occupied habitat between the Celtic Seas and Greater North Sea Ecoregions may be driven by different primary modes of fishing (creeling vs. trawling) in the enclosed mud habitats. Consequently, the area for potential recovery for F. quadrangularis is presented both based the habitat suitability derived from the Greater North Sea distribution model, and as a combination of suitable habitat from both ecoregions. The maps presented show areas that are suitable habitat for *P. phosphorea* (Figure 45), *V. mirabilis* (Figure 47), *F. quadrangularis* (ecoregion-specific,Figure 49), and *F. quadrangularis* (less impacted conditions, Figure 50).).

The predicted suitable habitat extent with overlaid historic and current presences has also been mapped for *P. phosphorea* (Figure 46), *V. mirabilis* (Figure 48), and *F. quadrangularis* (Figure 51).

The percent of area predicted to be suitable for the three sea pen species present on the UK shelf by MMO Marine Plan Area is given in Table 7. The results reflect the known distributions well. The offshore regions are more suitable than the inshore regions and the North West is only predicted suitable for *V. mirabilis*. The North East Offshore Marine Plan Area is predicted to be almost entirely suitable for all sea pen taxa along with large part (30-72%) of the North East Inshore Marine Plan Area. The Northern boundary of the East Offshore Marine Plan Area is also suitable for all sea pen species along with a narrow east-west oriented strip further south adding up to 11-17% of the total area. The suitable proportion (6-16%) of the South West offshore region is underestimated, with 38% of the area outside of the model extent, due to the limited extent of the environmental predictor layers used by Downie et al. (2021). The distribution of *F. quadrangularis* is known to extend further towards the shelf edge.

Table 8. Percent of area predicted to be suitable for the three sea pen species present on the UK shelf by MMO Marine Plan Area. Two values are given for F. quadrangularis, one for the ecoregion-specific model and one including area predicted suitable by the Celtic Seas model, which is representative of less impacted conditions. The model does not cover the whole area of interest, so the percent of area outside the model extent is also given.

Marine Plan Area	*Pennatula phosphorea*	*Virgularia mirabilis*	*Funiculina quadrangularis* (ecoregion specific)	*Funiculina quadrangularis* (combined)	Outside model extent
East inshore	3%	6%	0%	1%	24%
East offshore	17%	16%	6%	11%	0%
North East inshore	51%	72%	0%	30%	10%
North East offshore	99%	99%	73%	92%	0%
North West	0%	30%	2%	2%	16%
South inshore	0%	4%	0%	1%	12%
South offshore	0%	0%	0%	0%	10%
South East inshore	0%	0%	0%	0%	36%
South West inshore	9%	9%	2%	3%	10%
South West offshore	15%	16%	6%	6%	38%

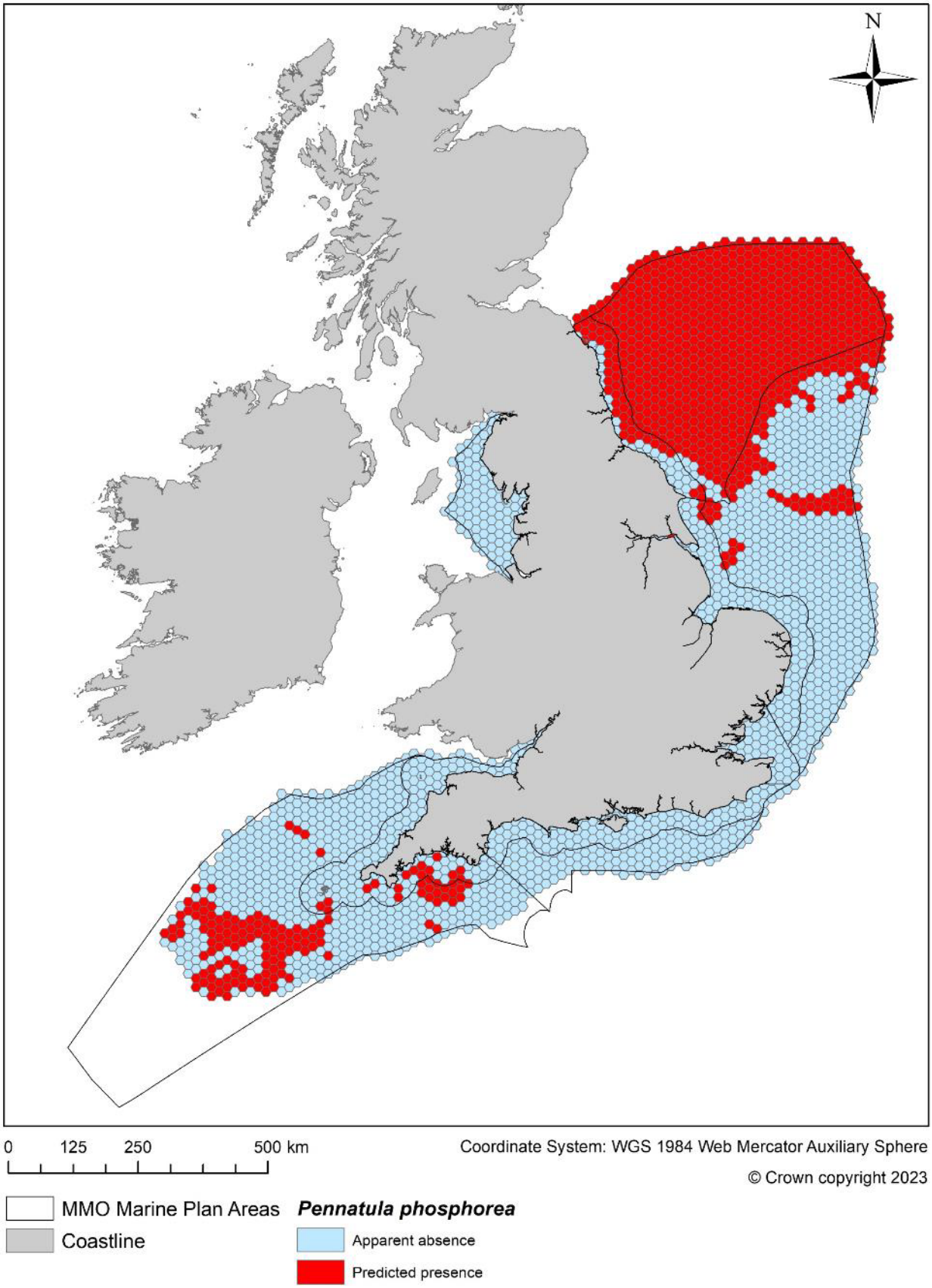

Figure 47. Predicted suitable habitat extent for *P. phosphorea*.

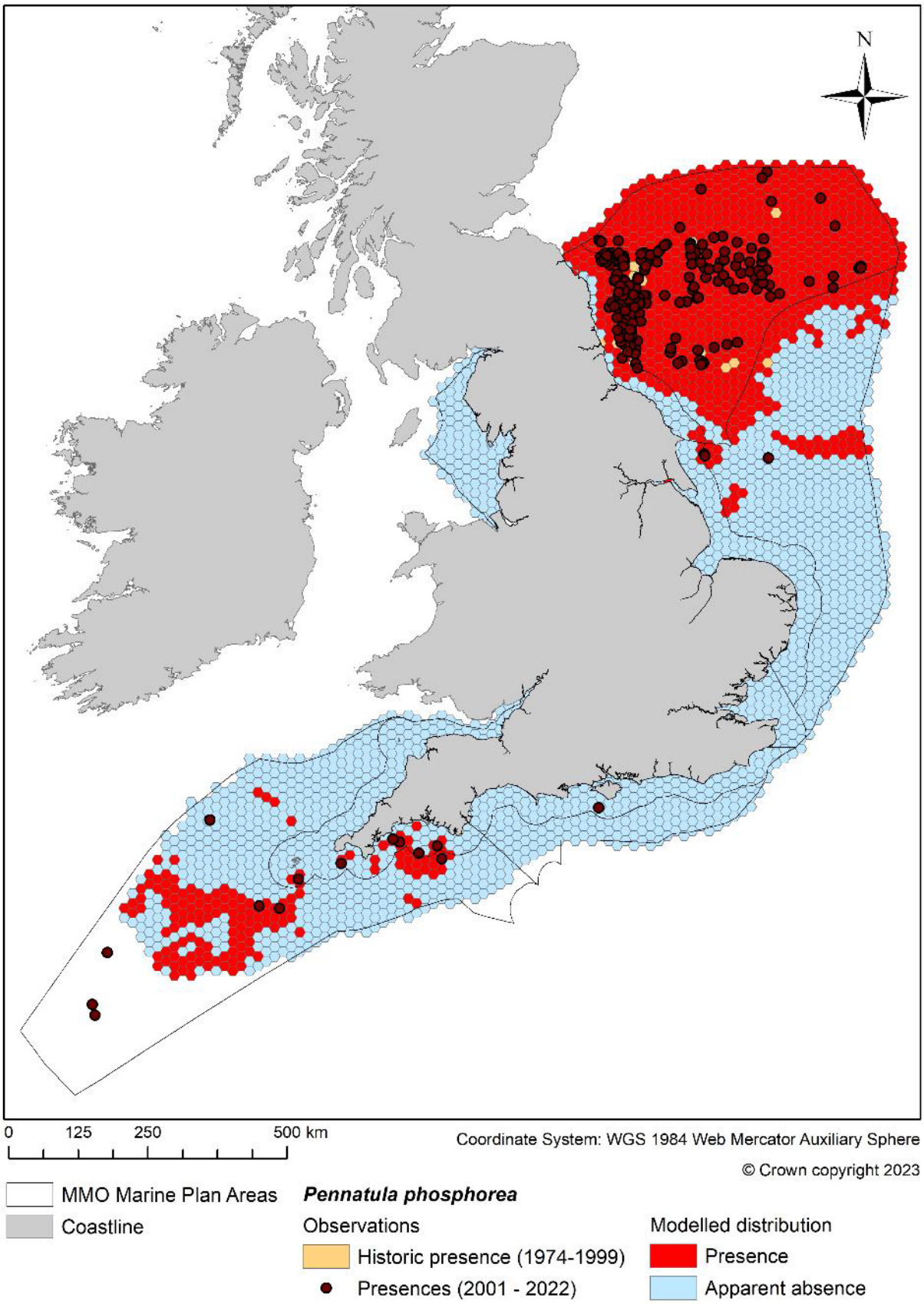

Figure 48. Predicted suitable habitat extent for *P. phosphorea*, overlaid with historic and current presences.

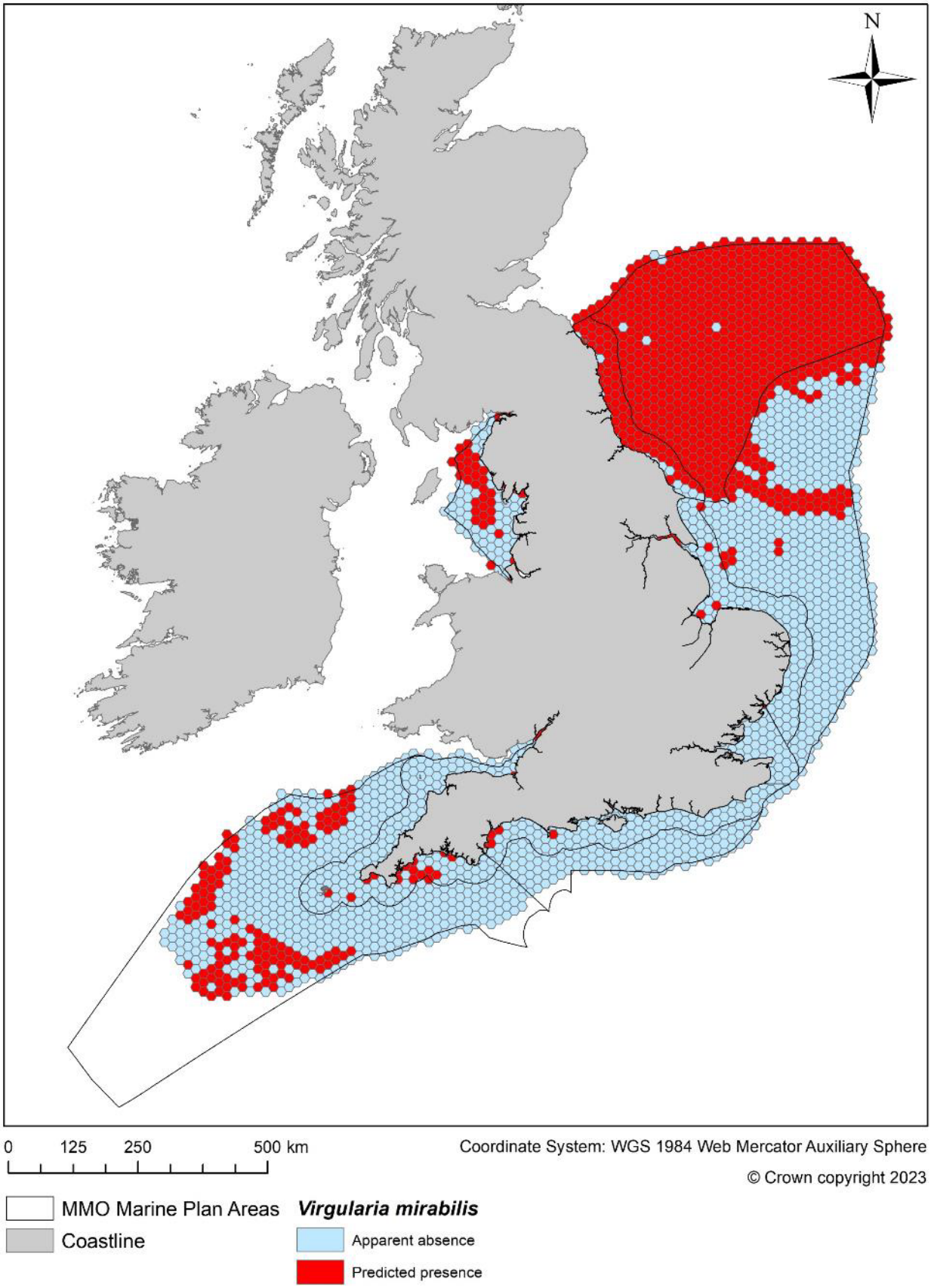

Figure 49. Predicted suitable habitat extent for *V. mirabilis*.

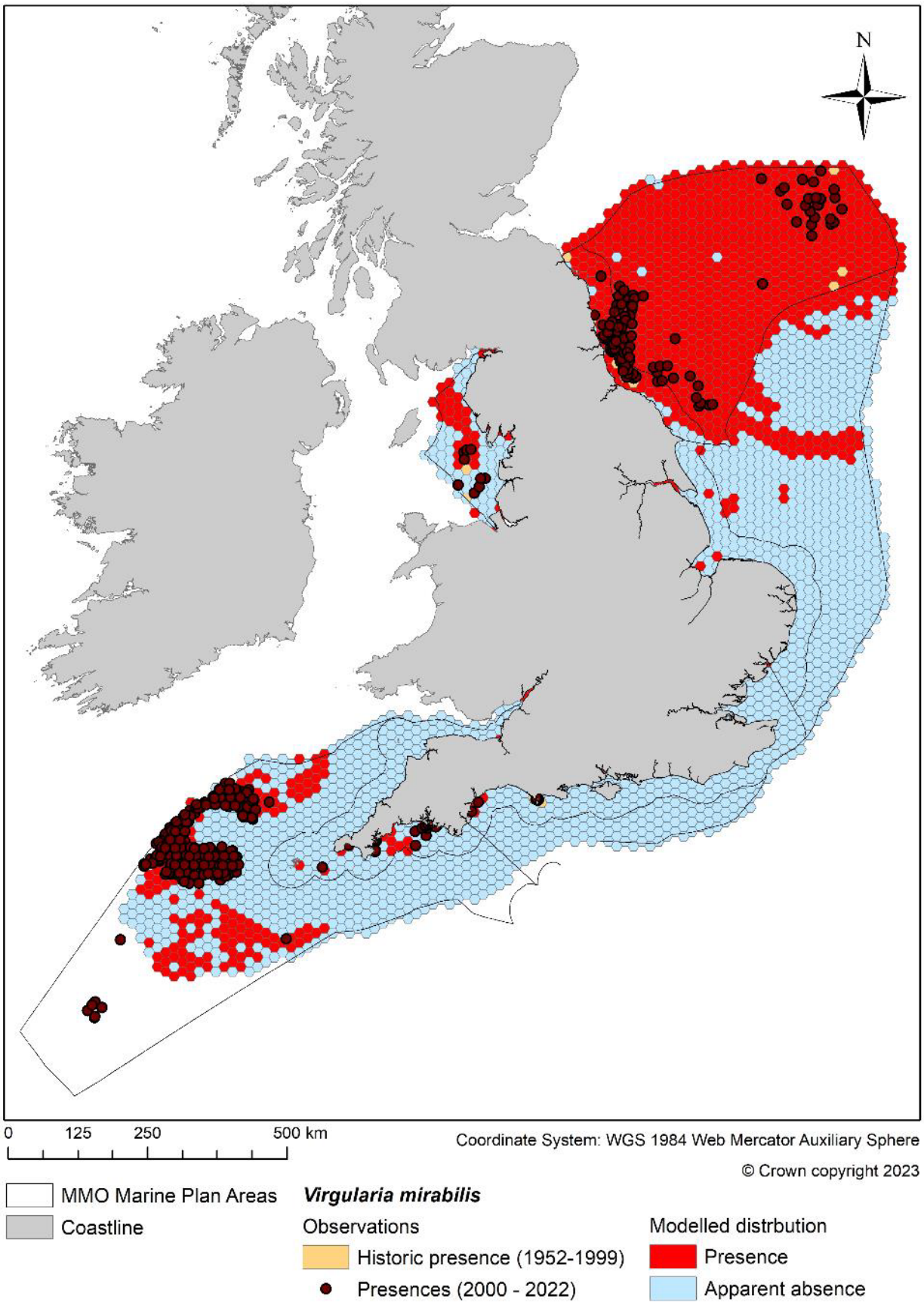

Figure 50. Predicted suitable habitat extent for *V. mirabilis*, overlaid with historic and current presences.

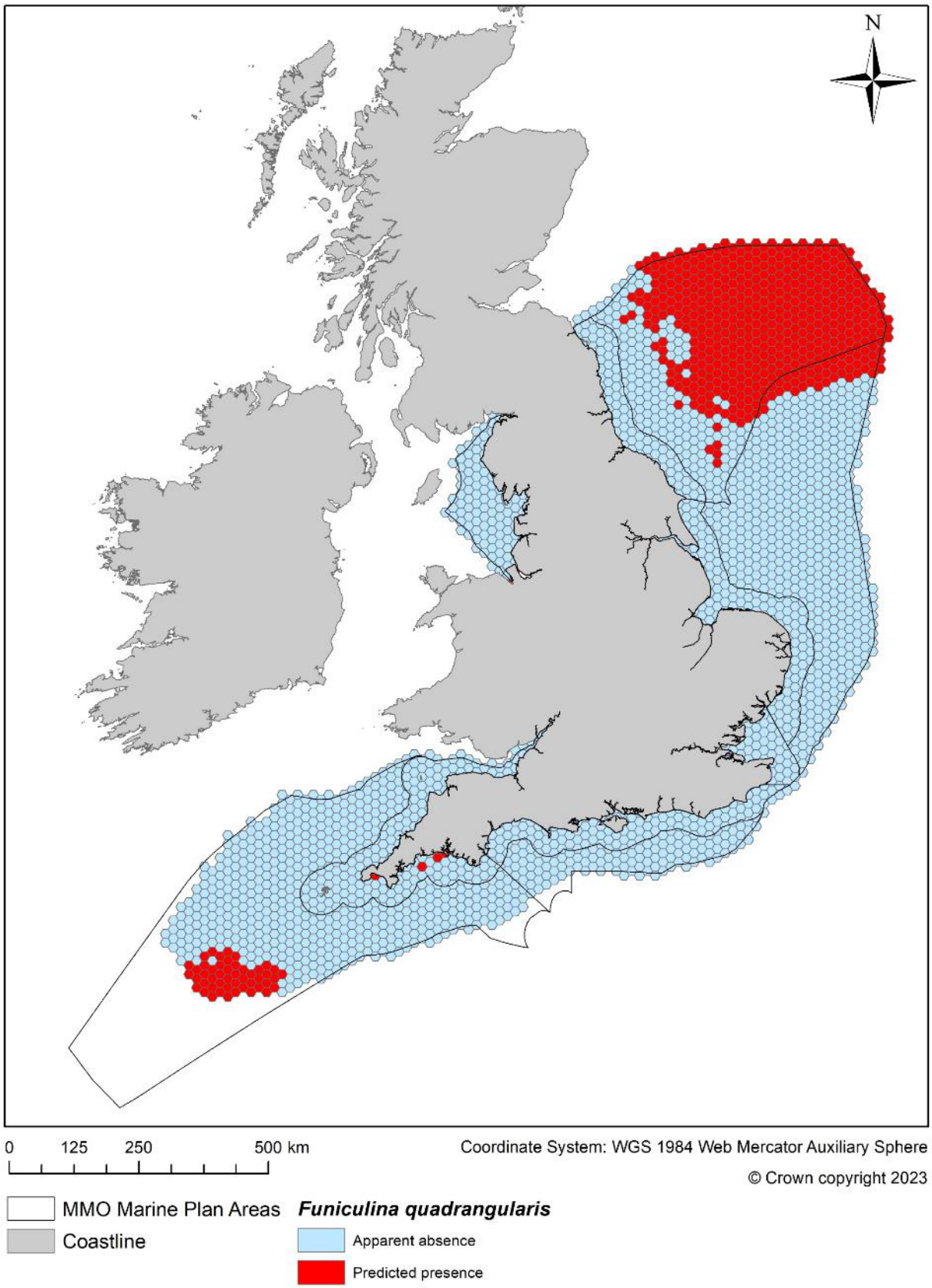

Figure 51. Predicted suitable habitat extent for *F. quadrangularis* based on known on ecoregion-specific conditions.

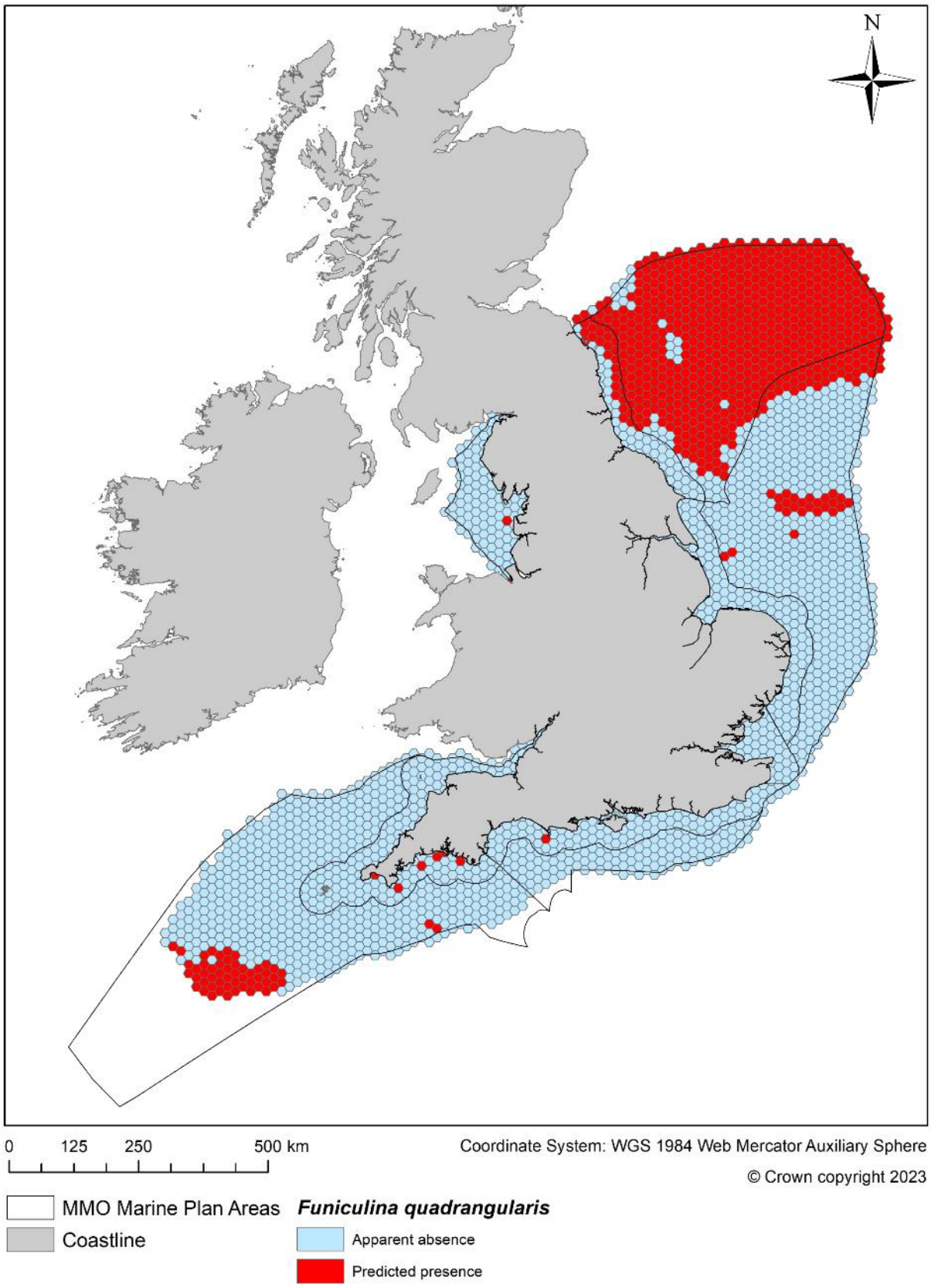

Figure 52. Predicted suitable habitat extent for *F. quadrangularis* extending the suitable habitat to include conditions where the species is present on the less impacted Scottish West Coast.

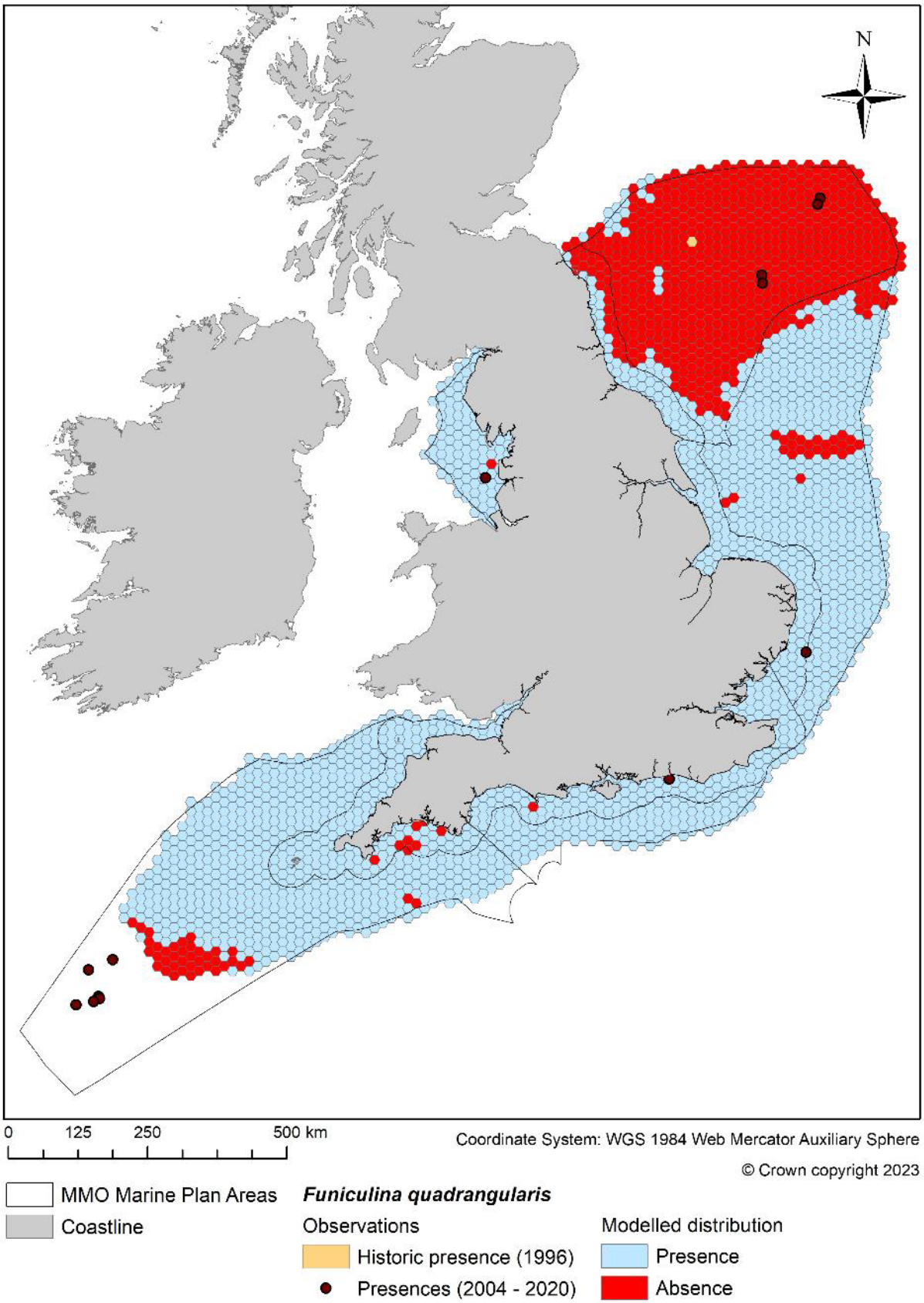

Figure 53. Predicted suitable habitat extent for *F. quadrangularis*, overlaid with historic and current presences.

4. Discussion and future recommendations

Although our knowledge of the distribution of both sea pens and burrowing megafauna has increased over the last decade through habitat mapping efforts, the sea pens and burrowing megafauna habitat is still not fully mapped over the UK shelf.

The restoration potential models presented here have identified areas of suitability for *P. phosphorea*, *V. mirabilis*, and *F. quadrangularis* to cohabit. Offshore regions have lower water temperatures and lower loads of suspended matter in the water column and are consequently more suitable than the inshore regions. The largely sand and muddy seabed of the North East offshore Marine Plan Area is predicted to be almost entirely suitable for all sea pen taxa, along with large part (30-72%) of the North East Inshore Marine Plan Area. The distributions of *P. phosphorea* and *F. quadrangularis* especially, are restricted by the suspended matter loads in the water column in the East, South and South East Inshore and North West Marine Plan Areas, as well as the South West Inshore and Offshore Marine Plan Areas north of Lands End. The gravellier substrata in the South Offshore Marine Plan Area make it unsuitable for all three sea pen species. Although all three sea pen species occur in mud habitats, it must be noted that they are also present on sandy bottoms. On the other hand, sea pens, other than *V. mirabilis* tend to be absent from mud habitats with high suspended matter loads. Consequently, the habitat suitability of sea pens cannot be directly equated with the distribution of the sea pens and burrowing megafauna habitat, nor should the three sea pen species be treated as one for purposes of mapping or management of their habitat. It was not possible to model areas with restoration potential for burrowing megafauna within the scope of the project, due to time limitations. In future work, estimates of restoration potential could be improved by multiple mapping and modelling approaches appropriate for the different subsets of data describing aspects of the habitat collated during this project.

The recommended approach is a multi-pronged one. A coarse approximation (at the scale of 30 min latitude and 1 degree longitude ICES statistical rectangles) could be derived from landing statistics for *Nephrops*. Existing model outputs of the mud content of substrata (% mud) combined with seabed topography could be utilised to identify potential mud basins. These two approaches do not, however, entirely account for the communities of sea pens and burrowing megafauna. The already existing distribution models for sea pens can be updated to extend over the whole area of interest, using environmental data layers covering the entire UK shelf, and including the new data on burrowing species and *F. quadrangularis* collected in the Canyons MCZ (along with any other new sea pen observation data collected). The data collated for this study can be further augmented and subset into separate datasets of 1) locations that have been determined to fulfil the description of 'sea pens and burrowing megafauna' habitat based on observed burrow density or the density of burrowing taxa, 2) the density of burrowing taxa based on seabed sampling such as grabs, and 3) the density of burrows based on video footage. Model outputs from a simple presence-absence distribution model of the habitat and both types of density model will each add to the information base for narrowing down areas suitable for restoration.

Selection of areas of physically suitable habitat as candidates for restoration will in practise face both ecological and socio-economic limitations. Restoration potential is affected by the availability of sources of larvae. When considering locations that may be suitable for restoration, information is required on the connectivity of populations between suitable habitat patches. An analysis identifying potential source and sink populations, especially for species with short dispersal distances or restricted extant distribution is useful for determining the practicality of restoration efforts across the suitable habitat. Dispersal of the sea pen *F. quadrangularis,* which occurs in small patches in two areas (Northern North Sea and the shelf edge in the Western Approaches) separated by large areas of unsuitable habitat, for example may be limited by local and broader current patterns. Sea pen and burrowing megafauna habitats are generally also important fishing grounds. Whilst distribution and density models, supported with connectivity analysis, can indicate the optimal areas for habitat recovery, areas most suitable for restoration in practice are also dependent on the viability of change from more to less destructive forms of fishing. Further research into viability studies for less destructive fishing practises, such as replacing trawl fisheries with creeling, can help identify areas with practical restoration potential. Little is known about temporal trends and responses of the communities to natural variability, as well as the population dynamics and connectivity of discreet populations of sea pens and burrowing megafauna. This makes assessment of impact from pressures and the recovery potential of the habitat difficult. Whilst we know that the burrowing megafauna habitat occurs without sea pens and that sea pens also occur in sandier sediments without burrowing megafauna, we have very little knowledge on the role of the sea pens in structure and health of the habitat.

Discussion

The Marine Restoration Potential (MaRePo) study has demonstrated the potential for habitat creation and restoration around English waters out to 200 nautical miles from the shore for five vulnerable and declining marine habitats. Habitats such as kelp and native oyster offer potentially thousands of hectares of restoration opportunities across England, which can link into potential habitat compensation and Marine Net Gain opportunities in the future.

This study has also illustrated the change and/or decline in habitat distribution over the last 100-200 years, reinforcing why restoration, passive or active, is one tool required to protect our marine and coastal environments and achieve the targets set out in the Defra 25 Year Environment Plan.

There are opportunities for active and passive restoration across all eleven Marine Plan Areas (Table 9 for inshore, Table 10 for offshore). Overall, the South West and North East Inshore Marine Plan Areas had potential for the largest number of different habitats to be restored, whilst the South East Marine Plan Area had the least. Having a large number of habitats to be restored in a Marine Plan Area opens the opportunity for restoration across a seascape scale, especially when considered with the additional inshore and coastal habitat restoration potential maps (e.g., for seagrass and saltmarsh) identified by the Restoring Meadows, Marsh and Reef (ReMeMaRe) initiative.

Individual habitats vary in their suitability for restoration. Kelp (Figures 5 and 6) and native oysters (Figure 28 and 29) both show significant potential for restoration, with large areas of suitable habitat in English inshore waters. Both habitats have national and international research programmes looking at active interventions to support their recovery. Unlike native oysters, *Modiolus* beds have a smaller area of habitat suitability (Figure 36), and far less research into their active restoration. Maerl is a slow-growing inshore habitat with a more limited potential (Figure 22 and Figure 23), and the immediate focus should be on supporting and recovering its current distribution.

Conversely, there are vast areas of the seabed suitable for at least one species of sea pen (Figures 45 - 51). Sea pens show suitable habitat in the northern North Sea and Western Approaches, with *V. mirabilis* extending to muddy habitats in the Celtic and Irish Seas. Sea pen and burrowing megafauna community restoration would be through passive means, such as areas closed to abrasion pressures from trawl fisheries, but the recovery of sea pens would indicate relatively undisturbed communities which would bring additional biodiversity benefits.

Next steps

There is significant scope for further refinement of the models in order to improve the confidence of the outputs. The next step for most of the habitats in this study would be an assessment of hard

constraints; areas where restoration would never be possible. This includes areas of existing infrastructure and installations, and areas of impacted seabed such as maintenance dredge sites.

Additionally, areas of soft constraints should also be added to future iterations of the restoration potential models. These are areas where existing pressures could be managed in a way that would not preclude restoration taking place, e.g., MPAs, areas of existing fisheries management, anchorages or recreational vessel uses.

Furthermore, as highlighted individually in some of the chapters, the impacts of climate change should be more closely modelled in order to better understand how sea level rise, changes in wave energy, storm frequency and sea temperature may impact the natural distribution and restoration potential of these habitats in future. Both active and passive restoration of these habitats could require considerable investment, and therefore confidence is needed that any implemented measures will, at best, be buffered from climate change impacts, or at worst, be able to confidently assess the climate risks to habitat recovery.

Finally, in parallel with further model refinement as outlined above, the next steps should include using the best available evidence together with expert knowledge and judgement to trial marine habitat restoration in suitable locations. As the amount of empirical data being collected in the UK is generally decreasing, spatial models often tend to present the same, aging data in different ways.

The most important step for restoration of marine habitats will be to trial and test real life examples on the ground at sea. This feasibility testing will enable real-life testing of proposed approaches and techniques. It is equally important that whilst trailing restoration activities that data is collected to evaluate, improve and refine marine habitat recovery.

Table 9. Summary of different habitat suitabilities for each inshore Marine Plan Area. Suitabilities are reported as potential extents (km^2 for kelp, oysters; for kelp the model with the highest extent is reported for each Marine Plan Area, see kelp section 3.3), % of Marine Plan Area (for sea pens) and overall assessment (for maerl and *M. modiolus*).

	Marine Plan Area (inshore)		**North East**	**East**	**South East**	**South**	**South West**	**North West**
Habitat	**Kelp** (Km^2)	*Laminaria hyperborea*	393	5	3	345	525	<1
		Saccharina latissima	<1	0	0	<1	2	0
	Maerl (General habitat suitability)		N/A	N/A	N/A	some potential	some potential	N/A
	Native oyster (km^2)		383	104	193	1093	73	100
	Modiolus beds (General habitat suitability)		Low	Low	Low	some potential	Low	Low
	Sea pens & burrowing megafauna (% of marine area plan)	*Pennatula phosphorea*	51	3	0	0	9	0
		Virgularia mirabilis	72	6	0	4	9	30
		Funiculina quadrangularis (combined)	30	1	0	0	3	2

Table 10 Summary of different habitat suitabilities for each offshore Marine Plan Area. Suitabilities are reported as potential extents (km2 for kelp, oysters; for kelp the model with the highest extent is reported for each Marine Plan Area, see kelp section 3.3), % of Marine Plan Area (for sea pens) and overall assessment (for maerl and *M. modiolus*).

	Marine Plan Area (offshore)		**North East**	**East**	**South East**	**South**	**South West**	**North West**
Habitat	**Kelp** (Km^2)	*Laminaria hyperborea*	0	0	-	0	0	0
		Saccharina latissima	0	0	-	0	0	0
	Maerl (General habitat suitability)		N/A	N/A	-	N/A	N/A	N/A
	Native oyster (km^2)		0	10	-	0	0	100
	Modiolus beds (General habitat suitability)		Low	Low	-	Low	Low	some potential
	Sea pens & burrowing megafauna (% of marine area plan)	*Pennatula phosphorea*	99	17	-	0	15	0
		Virgularia mirabilis	99	15	-	0	15	30
		Funiculina quadrangularis (combined)	92	11	-	0	6	0

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