## Report No.413



# The Diversity and Resilience of Kelp Ecosystems in Ireland

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#### **EPA RESEARCH PROGRAMME 2021–2030**

## The Diversity and Resilience of Kelp Ecosystems in Ireland

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### **Executive Summary**

Kelp forests can be found along rocky shorelines in temperate to Arctic coastlines on six continents. In Ireland, kelp dominates rocky substrata along moderately exposed coastline (approximately 3010 km of 7524 km of national shoreline). These ecosystems potentially provide a range of ecosystem services (ESs), including important primary and secondary production (including for commercial fisheries such as edible crab - Cancer pagurus) in local or adjacent habitats, carbon fixation and sequestration, and protection of coastal habitats via physical attenuation of wave action. However, there is still little known about them in this geographical range. Subtidal kelp ecosystems are dominated by cuvie (Laminaria hyperborea) and can produce up to 19.5kg wet weight m<sup>-2</sup> of this kelp, making them an important cultural, ecological and economic resource, as well as a target for conservation across the country.

Despite major knowledge gaps in understanding kelp ecosystems, anthropogenic stressors are predicted to affect Irish kelp populations. These include but are not limited to warming oceans, overgrazing due to fished-down food webs, eutrophication, sedimentation and wild harvesting. The ability to recover from threats can be defined using the term "resilience", which is defined as the ability of an ecosystem to recover and maintain normal ecological function after a disturbance event. The concept of resilience has slightly different meanings in ecological and evolutionary contexts, and we have examined the resilience of subtidal cuvie forests in Ireland using both evolutionary and ecological metrics. This research also aimed to define the past and present distribution of kelp in Ireland, along with the tools needed to monitor future kelp ecosystems via citizen science efforts and remote-sensing tools.

Using microsatellite loci to evaluate evolutionary resilience, *L. hyperborea* populations were found to exhibit isolation by distance, suggesting limited gene flow along the coast of Ireland, and pockets of high genetic diversity were identified, including on the southern coast of Ireland (a putative glacial refugium). Recruitment probably occurs on a very local scale. To maintain genetic diversity and effectively manage wild resources, legislative bodies require a priori knowledge of where diversity is highest; this requires the use of population genetics tools. The patterns of genetic structure uncovered in the KelpRes project are an important first step in managing kelp ecosystems in Ireland and creating an adaptive management plan for regions facing threats ranging from changing ocean temperature and storminess to harvesting.

Investigations on the presence of banks of microscopic kelp forms (either the gametophyte or undeveloped sporophyte) were carried out to evaluate ecological resilience in kelp ecosystems. Using a combination of aquarium- and molecular-based techniques, microscopic kelps were found in the benthic biofilm. Heterogeneity in the presence of microscopic kelp forms across space and time, even within a kelp forest, was observed. Experiments within natural kelp canopies defined unique recruitment periods for kelp species and banking in experimental communities, and detected the presence of microscopic stages of non-native kelp species, despite the absence of the macroscopic sporophyte stage. Multiple kelp species were often amplified with brown algae-specific primers using a barcoding approach; therefore, metabarcoding should be used to resolve kelp identification in the future.

Knowledge gaps remain in our understanding of kelp forests in Ireland including species-specific interactions in L. hyperborea food webs, the scope of kelp distribution along Ireland's coastline, the regional variation in species and biomass, and the carbon capture and storage potential of these ecosystems. Filling these gaps would provide important information for calculating Ireland's "blue carbon" mitigation strategies for meeting Paris Agreement targets and truly defining the ESs provided by kelp, including how they add to nature's contributions to people. The indicators and the satellite remote-sensing tool piloted in this report should be used for future management of kelp on the Irish coast under the Habitats Directive and these ecosystems should be specifically identified in both the Marine Strategy Framework Directive and the Water Framework Directive as monitoring targets for good environmental or ecosystem status.

### **1** Introduction

Historically, Ireland has maintained a special relationship with seaweed in its food and culture, but research on subtidal algal communities, such as on their ecology, physiology, distribution or abundance, has been quite limited. This research project, "The Diversity and Resilience of Kelp Ecosystems in Ireland", focused on kelp ecosystems dominated by Laminaria hyperborea (commonly called cuvie or mayweed), which is a common cold-water kelp species in Europe that structures nearshore subtidal communities on Ireland's rocky coastlines. Key objectives in the KelpRes project (identified as "project aims" throughout this report) were to create a record of the distribution of historical to present-day L. hyperborea ecosystems, define evolutionary and ecological metrics for kelp ecosystem resilience, and develop monitoring tools to track future changes in kelp distribution and ecosystem health. Historical records of kelp ecosystems are highly dispersed across herbariums and other data repositories, and in records from the few research efforts over the past century (e.g. BioMar or MarClim). Existing records were collected in a single open-access resource (section 1.3) to provide a basis for future recording efforts. Evolutionary resilience within L. hyperborea communities was defined using a population genetics approach with microsatellite loci (Chapter 2). Ecological resilience was examined by investigating the existence of "banks" of microscopic kelp stages. This was carried out using a combination of field and laboratory experiments with molecular identification tools and microscopy (Chapter 3). Future monitoring of kelp ecosystems was promoted through multiple workshops delivering key information on kelp ecosystem function, diversity and productivity alongside a dive slate that can be used by citizen scientists (section 4.1). Furthermore, a pilot study using satellite and bathymetry data created a method for estimating coverage of kelp ecosystems remotely (section 4.2). These resources can be used to integrate ecosystem services (ESs) into the management of water and coastal resources through various suggested monitoring applications (section 5.2).

#### 1.1 Kelp Ecosystems Worldwide

Kelps are large brown seaweeds within the order Laminariales (some Tilopteridales are referred to as kelps as well) that contribute to understorey and overstorey canopies in intertidal and subtidal habitats worldwide. Globally, kelp occupies 22% of coastlines, meaning that kelp ecosystems account for the second most abundant marine biome (after seagrasses) and have a greater global coverage than coral or mangrove ecosystems (Jayathilake and Costello, 2020). Light, sea surface temperature (SST) and the presence of bedrock are major predictors of kelp presence and distribution (Yesson et al., 2015a; Jayathilake and Costello, 2020). Kelp is generally found in nearshore waters, although deep kelp reefs have been identified worldwide (Santelices, 2007). Kelp species are often referred to as ecosystem engineers because they structure marine habitats physically (see Jones et al., 1994), but they also provide other services, such as primary production and organic carbon, and foster biodiversity, making them valuable from an ESs perspective (Kain, 1979; Dayton, 1985; Connolly et al., 2001; Steneck et al., 2002). They are susceptible to anthropogenic disturbances and climate change, making the investigation of kelp's potential resilience pertinent for the protection of this natural resource. Here, resilience in natural ecosystems is defined as the capacity to recover from a disturbance and to maintain normal ecological patterns.

Threats faced by kelp species include ocean warming and marine heat waves (MHWs), defined as periods when daily SSTs exceed a local seasonal threshold for at least 5 consecutive days (see Hobday *et al.*, 2016), overgrazing by herbivores (often via fishing down predators in food webs) (Harrold and Reed, 1985; Hagen, 1995; Steneck *et al.*, 2004; Sivertsen, 2006; Blamey *et al.*, 2010; Foster and Schiel, 2010; Ling *et al.*, 2015), eutrophication and sedimentation (Airoldi, 2003; Russell and Connell, 2009; Filbee-Dexter and Wernberg, 2018), wild harvesting of kelp forests (Valero *et al.*, 2017; Greenhill *et al.*, 2021) and increased storm activity (Norderhaug *et al.*, 2020). The impacts of one or multiple stressors have already caused shifts in the distribution of modern kelp ecosystems (Krumhansl et al., 2016) and, without international mitigation efforts, are projected to have ongoing negative impacts on these systems. Australia and northern California provide the most drastic examples of kelp ecosystem collapse: the combined effects of decades of gradual warming, MHWs and the tropicalisation of reef fish assemblages have prevented kelp recovery on temperate Australian coastlines (Wernberg et al., 2016), while an MHW combined with a decline in predators has caused urchin barrens to proliferate on northern Californian reefs (Rogers-Bennett and Catton, 2019). Management efforts for Californian reefs include the commercial harvesting of urchins, the captive breeding of the native urchin predator Pycnopodia helianthoides and the creation of a "bank" of genetic stock for native kelp species (see Gleason et al., 2021), while Australian efforts focus on restoring kelp ecosystems by out-planting juvenile kelp (Morris et al., 2020).

Of great concern is the fact that some of these changes seem irreversible (e.g. kelp forests have not recovered in parts of Australia; Wernberg et al., 2016) and in many locations the biodiversity or productivity of local kelp ecosystems and their potential resilience to climate change have yet to be described. Research has often neglected the full life cycle of the Laminariales when describing kelp ecosystem loss, as noted by North (1971): "The ecology of the Macrocystis gametophyte is very poorly understood, as is the entire field of microbiology of kelp beds". Most in situ and in vitro studies focus on kelps at the macroscopic sporophyte stage (diploid, 2N; Figure 1.1) because they are easier to survey, measure and collect in the field. Kelp microscopic stages include the zoospores released from sorus material on the sporophyte blade, gametophytes (haploid, 1N) and juvenile sporophytes, which live on benthic structures and within biofilms in the marine environment (Figure 1.1). Few studies have been done in vitro on gametophyte tolerance to different light regimes (e.g. Lüning, 1980), tolerance of climate change in juvenile sporophytes (e.g. Muth et al., 2019; Ng and Micheli, 2020) or gametophytes (Oppliger et al., 2012; Mabin et al., 2019). Recent evidence from multiple studies suggests that microscopic stages may persist in habitats without apparent sporophyte stages, potentially dormant until a trigger pushes them to sexually recombine or grow to macroscopic



Figure 1.1. The life cycle of Laminariales (*Laminaria hyperborea* pictured). The diploid sporophyte (2N) is the stage well known for structuring ecosystems. Zoospores are born on the lamina of the sporophyte, produced through meiosis, and they typically settle within 24 h of release (Fredriksen *et al.*, 1995) and develop into male and female haploid gametophytes (1N) on the benthos. Gametes are produced via mitosis and male gametes fertilise the female ovum (guided by pheromones from the female structures) and produce juvenile sporophytes which then develop into large kelp sporophytes when space and light become available (reviewed in Bartsch *et al.*, 2008).

sizes (e.g. Santelices *et al.*, 1995, 2002; Carney *et al.*, 2013; Robuchon *et al.*, 2014a; Akita *et al.*, 2019, 2020; Schoenrock *et al.*, 2021a). Although microscopic stages may aid ecosystem recovery after disturbances, these have rarely been investigated; therefore, quantifying these stages in Irish kelp forests formed one of the objectives in the KelpRes project.

As threats are continually identified, innovative solutions are being developed, or recycled (see North, 1976, 1978), to assist in kelp forest restoration and conservation (Fredriksen *et al.*, 2020; Layton and Johnson, 2021). Of emerging importance is the genetic composition of natural forests, which is probably directly linked to the environmental tolerance of individuals and populations [see the high variation in phenotypes of *Ulva* spp. strains in Fort *et al.* (2019)]. Kelp species seem to show regional phenotypic variation, as exhibited along the coastline of Chile (Camus *et al.*, 2018), which will affect not only their ESs and response to climate change, but also their performance in kelp aquaculture (Valero *et al.*, 2017) or valorisation post harvest. Therefore, it is critical to better understand the genetic diversity, connectivity across populations and distribution of genetic resources within a species before working to preserve or capitalise on a resource. For this reason, an objective of KelpRes was to define the population genetics of the major canopy-forming kelp species in Ireland, *L. hyperborea*.

One of the important ESs provided by kelp habitats is their potential to be a carbon sink. Although kelp is generally consumed by herbivores or exported to adjacent habitats (ranging from the deep sea to the shoreline), burial of kelp carbon is possible in sediments (Queirós et al., 2019), which may ultimately sequester and store carbon, known as "blue carbon" (Krause-Jensen et al., 2018). Wild and farmed kelps both have this potential, although further research on the fate of kelp biomass is required. Legal requirements such as the EU framework directives requiring good environmental status (GES) to be maintained in marine and coastal waters have also led to a focus on nearshore ecosystems including kelp forests (Burrows et al., 2014a; Smale et al., 2016), which historically have been harvested in Europe and are a potential candidate in fisheries' diversification (Greenhill et al., 2021).

## 1.2 Status of Kelp Ecosystems in Ireland

#### 1.2.1 Ecology

In Ireland, there are five species of kelp that are common in the intertidal and subtidal zone: *Laminaria digitata*, *L. hyperborea*, *Saccharina latissima* (formerly *L. saccharina*), *Saccorhiza polyschides* and *Alaria esculenta* (Figure 1.2). There is regional variation in kelp composition along the coastline (Schoenrock *et al.*, 2020a), probably driven by wave-exposure gradients (Burrows *et al.*, 2014b). Open coasts are more suitable for *L. hyperborea*-dominated forests, where they can occur down to ~40 m [e.g. Aran Islands, County Galway; C.A. Maggs (NUI Galway), M.D. Guiry (NUI Galway) and M.J. Dring (Belfast University), 1988, unpublished data], whereas fjord-like, sediment-rich habitats are more suitable for *S. latissima*-dominated forests or kelp "parks" (Schoenrock *et al.*, 2020a; Figure 1.2).

L. hyperborea can live for up to 18 years (Norway; Sjøtun et al., 1993); the oldest individual found in Ireland to date was aged at 15 years [K.M. Schoenrock (NUI Galway), J.A. Adams (Aberystwyth University, UK), J.B. Schram (University of Oregon, OR), N. Thompson (University of Oregon, OR), A. Galloway (University of Oregon, OR), J.J. Ratcliff (NUI Galway) and D.B. Stengel (NUI Galway), unpublished data]. In contrast, the other European kelps live for 1-5 years (L. digitata or Laminaria ochroleuca). Past reviews have generally aligned the ecology of these habitats with other European kelp forests, citing work from France, the UK and Norway as relevant to the Irish coastline (Kelly, 2005). Unfortunately, there is small-scale regional variation across sites (maybe environmentally or biologically driven), which changes the composition of species assemblages within kelp forests in Ireland (Schoenrock et al., 2021b), making it impossible to draw conclusions from overseas research on large- and small-scale processes affecting Irish kelp forests without a national ecological baseline.

"Healthy" kelp forests dominated by L. hyperborea in the west of Ireland are characterised by the presence of two-spotted gobies (Gobiusculus flavescens), top shells (Steromphala spp.), an abundance of echinoderms such as the common starfish (Asterias *rubens*, generally < 10 cm diameter), common urchin (Echinus esculentus) and cotton spinner (Holothuria forskali) (Schoenrock et al., 2021b). It is important to note that, although echinoderms (grazing urchins) pose a threat to kelp forests globally, the detrimental species do not seem to be abundant in Ireland (Schoenrock et al., 2021b). L. hyperborea not only structures the habitat that these organisms live in, but is also a surface for colonisation by multiple invertebrate and algal species numbering in the thousands on larger, older thalli (Edwards, 1980; Schoenrock et al., 2021b). Furthermore, juveniles of multiple commercially and ecologically important species recruit to kelp habitats, especially in spring (Schoenrock et al., 2021b). Seasonally, crab and lobster pots are frequently placed in kelp forests, as they are locally known as a good habitat for capturing these species.



Figure 1.2. Images depicting common kelp species from locations around Ireland give an idea of the exposure gradients of each species. Native species: (a) *A. esculenta* in an *Laminaria hyperborea* forest (Hook Head, Wexford), (b) *Saccharina latissima* (Cill Chiaráin, Galway), (c) *Saccorhiza polyschides* (Lough Hyne, Cork), (e) *Laminaria hyperborea* forest (Árainn Mhór Island, Donegal) and (f) *Laminaria digitata* (Cill Chiaráin, Galway). Non-native species: (d) *Laminaria ochroleuca* (Béal an Mhuirthead, Mayo) and (g) *Undaria pinnatifida* (Greystones, Wicklow). Photo credit: Kenan Chan.

Recovery of kelp habitats, or succession after a disturbance event, occurs quickly in these communities; generally, new sporophytes replace the kelp canopy within 6 months of clearance (K.M. Schoenrock *et al.*, unpublished data). Artificial substrata take over a year to develop kelp communities as an annual reproductive event and the presence of a robust biofilm is required to seed these habitats (Schoenrock *et al.*, 2021a). *L. hyperborea* produces sori during late autumn and winter, releasing zoospores in higher density later in winter than in autumn. This is the only native kelp species that produces sori at this time of year, although *U. pinnatifida* can produce sporophylls yearround in its colder, invaded ranges (reviewed in Chan *et al.*, 2021). Other *Laminaria* spp., *S. latissima* and

S. polyschides, form sori in summer and autumn (Bartsch et al., 2008; Olischläger et al., 2012), theoretically "seeding" intertidal and subtidal benthic communities at different times of the year, which may isolate them from hybridisation with L. hyperborea propagules if they are short-lived. After sori are spent, the blade of L. hyperborea begins its new growth and the laminae are discarded, washing up on shorelines (which is where cuvie gets its other common name, "mayweed") or moving into adjacent habitats such as maërl beds or the deep sea (Ramirez-llodra et al., 2020; Schoenrock et al., 2021b). Spring is also when juvenile kelps peak in abundance in the subtidal zone (all juvenile sporophytes and gametophytes within the Laminariales look alike); however, they can be present year-round after a canopy clearance event (e.g. storms), which may indicate the presence of microscopic kelp stages in a form of a "bank" akin to terrestrial seed banks (Schoenrock et al., 2021a,b).

Despite the large amount of research on kelp forest ecology worldwide, very little is known about Irish kelp habitats, although some monitoring started in the west of Ireland in 2016 (Schoenrock *et al.*, 2021b). More information is needed to create ecological baselines for these habitats in Ireland to measure and track change in these communities, to better estimate the ESs they provide and how they add to nature's contribution to people, and to understand how these natural resources respond to disturbance.

#### 1.2.2 Productivity

The productivity of kelp forests can be measured in multiple ways, from standing stock of biomass to oxygen production and carbon sequestration. Multiple environmental parameters (e.g. light, depth and exposure) feed into how productive an ecosystem is, making extrapolation across a coastline incredibly difficult. Biomass of L. hyperborea is linearly related to age (K.M. Schoenrock et al., unpublished data), as the stipe of individuals grows incrementally over the years with the seasonal regrowth of the new year's lamina (Kain and Jones, 1964) (see Table 1.1). To date, the largest wet weight biomass collection in Ireland was 19.72 kg m<sup>-2</sup> (wet weight), but productivity can also be measured in terms of carbon (C) (ash-free dry weight), which ranges from 1 to 4.8 kg m<sup>-2</sup> in Ireland (Werner and Kraan, 2004; Kelly, 2005). Gundersen et al. (2021) recently reported an even higher maximum standing

#### Table 1.1. *Laminaria hyperborea* biomass (wet weight, kg m<sup>-2</sup>) and average age of individuals (per m<sup>-2</sup>) within kelp forests on the west coast of Ireland in autumn, winter, spring and summer

Measurement	Autumn	Winter	Spring	Summer
Wet weight (kg m <sup>-2</sup> )	8.58	2.51	6.32	9.11
Age (years)	3.04	1.1	2.61	3.35

biomass of 15.8-27.2 kg m<sup>-2</sup> for *L. hyperborea* along the coast of Norway, indicating that this cold-adapted species is more productive in its northern ranges.

Biomass measurements and population estimates will be sensitive to season, as natural phenology and environmental conditions shift the scope of these communities. On average, kelp biomass peaks in summer and autumn when the kelp blade is largest. Older individuals are found in kelp collections (haphazard guadrat collections; K.M. Schoenrock et al., unpublished data) and this heterogeneity in age structure within the community is likely to be driven by storm events. The new blade growth rate increases from February to April, reaching 2.2 cm day-1, and is greatest in 3-year-old individuals (K.M. Schoenrock et al., unpublished data). Oxygen production of L. hyperborea also peaks with growth in winter and spring, and total annual kelp production of dissolved organic carbon (via exudate) has been estimated at 1129-4129 g C m<sup>-2</sup> (26% of fixed carbon; Abdullah and Fredriksen, 2004). This, as a potential food source, has considerable implications for marine food webs, affecting organisms from the microbiome within the diffusion boundary layer (DBL) of an individual kelp to apex predators within the food web (Fredriksen, 2003; Norderhaug et al., 2003, 2005).

## 1.2.3 Invasive species, industry exploitation and conservation

Invasive and non-native species in the marine environment can be introduced through a variety of vectors, including deliberate or accidental human-mediated transport (e.g. recreational craft or aquaculture). Invasive species are generally recognised as having negative effects on biodiversity and related ESs within their new environment, while non-native species do not exhibit invasive tendencies or associated negative effects. Nonnative marine macroalgae in Ireland include the red algae Asparagopsis armata (de Valera, 1942), Bonnemaisonia hamifera (Holmes, 1897), Heterosiphonia japonica (Sjøtun et al., 2008) and Gracilaria vermiculophylla (Krueger-Hadfield et al., 2017), and the brown algae Sargassum muticum (Minchin, 2007; Salvaterra et al., 2013), Colpomenia peregrina (Minchin, 2007) and Rugulopterix okamurae (the invasion potential of which is summarised in Casal-Porras et al., 2021). U. pinnatifida is an invasive kelp now found in Ireland [reviewed in Chan et al., 2021; see also K.M. Schoenrock (National University of Ireland Galway), K.M. Chan (National University of Ireland Galway), S.A. Krueger-Hadfield (University of Alabama at Birmingham), unpublished microsatellite data; Figure 1.2g]. U. pinnatifida was first observed in Northern Ireland in 2012 (Minchin and Nunn, 2014) and has been recorded occasionally in Ireland since (six site records), most recently in Greystones Harbour, where it forms a forest on bedrock, rather than just growing on pontoons (Chan et al., 2021).

Although not considered invasive, *L. ochroleuca* is a warm-water kelp that has expanded its distribution range northwards in Europe and has been recorded only once in Ireland, in 2018, at Scotch Port in Béal an Mhuirthead, County Mayo (Schoenrock *et al.*, 2019; Figure 1.2d), where *S. latissima, L. digitata* and *S. polyschides* can also be found. This species has repeatedly been documented in 2019, 2020 and 2021 at Scotch Port and habitat suitability models (HSMs) indicate that the westward islands of Ireland could also be suitable for this southern European species (Yesson *et al.*, 2015a). Monitoring the distribution of these species is important moving forwards as we try to better understand their impacts on the ecology of native kelp ecosystems in Ireland.

Ireland's most profitable seaweed harvest is of the intertidal rockweed *Ascophyllum nodosum*, which is hand-harvested using rakes from boats at high tide (29,500 ty<sup>-1</sup>; Mac Monagail and Morrison, 2020). Harvesting of kelp, specifically *L. hyperborea* (also known as slataí mara or budógaí), dates back over 100 years to when it was economically profitable to carry it up from the beach to create alkali or potash in the west and north-west (Mac Monagail and Morrison, 2020). Despite the considerable advances in aquaculture, harvesting from wild sources contributed 68% of production in Europe (in 11 countries, 85% of producers practise hand-harvesting; Mac Monagail *et al.*, 2017; Araújo *et al.*, 2021). Of the seven kelp species in Ireland, only L. hyperborea and L. ochroleuca life cycles have not yet been optimised for aquaculture in Europe (Edwards and Watson, 2011) (note that U. pinnatifida and L. ochroleuca were not brought to Ireland for aquaculture). In Europe, *L. hyperborea* and *L. digitata*, together with a small amount of L. ochroleuca, are important targets of mechanical wild harvesting, especially in Norway, which is the largest seaweed producer in Europe in terms of biomass (Araújo et al., 2021). Mechanical harvesting is performed using "modified dredges" (Norway) or "scoubidous" (France), which either cut or pull the kelp from depth, removing most of the existing sporophyte population. Few data exist on how each mechanism influences recovery of the kelp habitat, but it can take over 5 years for kelp ecosystems to recover from trawling in Norwegian forests (Christie et al., 1998; Greenhill et al., 2021).

To conserve wild resources, quotas on biomass and vessel numbers (tracked by vessel monitoring systems) within harvest areas are applied to L. digitata and L. hyperborea during harvesting seasons in France (Bajjouk et al., 2015). L. hyperborea harvesting takes place from the beginning of September to mid-May, while L. digitata harvesting occurs from May to September and a "crop rotation" system is applied to let ecosystems recover over 3 years (Araújo et al., 2021). In Norway, the kelp harvesting industry uses a 5-year rotation cycle which permits 130,000-180,000 ty<sup>-1</sup> to be collected across harvest sites (Vea and Ask, 2011), but this is not a long enough recovery period (Greenhill et al., 2021). Recommendations for the harvest of Scottish kelp forests are based on French and Norwegian data, including the 5-year rotation of harvesting locations, continual monitoring of environmental impacts, biodiversity and standing stock of kelp (Burrows et al., 2018), although no harvesting licences have been granted to date. There are prospects for using beach-cast seaweeds in biofuel or other industries, but this has been predicted to cause major effects in trophic cascades, particularly in bird populations which depend on the species assemblages within beach wrack (Orr, 2013).

Kelp ecosystems are an important habitat not only for commercial species of interest (Schoenrock *et al.*, 2021b) but also for seabirds and other vertebrates (Lorentsen *et al.*, 2010), which brings these ecosystems under the auspices of the EU Birds and Habitats Directives. Gaps remain on the structure and function of kelp forests across Europe, including the extent of these ecosystems along coastlines, baseline biodiversity and productivity assessments, and ecological or evolutionary mechanisms of resilience to stressors, such as climate change or habitat degradation. Climate change, especially ocean warming, is believed to be a major threat to marine forests worldwide (Krumhansl *et al.*, 2016; Wernberg *et al.*, 2019), including those in Europe (Araújo *et al.*, 2016), where we already see a contracting southern distribution range for cold-water species (Simkanin *et al.*, 2005; Assis *et al.*, 2016) and expanding northern ranges for warm-water species (Assis *et al.*, 2018; Schoenrock *et al.*, 2019).

#### 1.2.4 Defining resilience in marine ecosystems, particularly kelp forests

Building the resilience of marine ecosystems may be achieved via ecological means (e.g. ecosystems with multiple stable states; Filbee-Dexter and Scheibling, 2014) or engineered aspects of the habitat (i.e. the speed of recovery in an ecosystem because of life cycle characteristics in ecosystem engineers; Pelletier et al., 2020). Evolutionary (genetic) and ecological drivers of resilience in kelp ecosystems are integral to their response to future climate shifts, including ocean warming (or cooling of the subpolar North Atlantic; Sgubin et al., 2017), increased storminess, MHWs and overharvesting/fishing. More practically, these could be conceptualised as mechanisms facilitating the replacement of lost individuals on short timescales and retaining good genetic diversity on long timescales. The salient point is the need to obtain a baseline for normal ecological patterns, as well as metrics that can be used to measure ecosystem recovery.

#### 1.3 Distribution of Kelp Ecosystems in Ireland

**Project aims.** To assess the historical distribution of kelp ecosystems, data from multiple surveys in Ireland were cleaned and combined with insight from project partner Seasearch Ireland. Historical datasets are a useful baseline but need to be compiled and presented in a publicly accessible format. Compiling multiple datasets into an accessible, historical time series and species distribution map should create a platform to support future monitoring (e.g. by indicating which

sites have historically been suitable for kelps) and help to track ecosystem loss or stability over time.

#### 1.3.1 Historical records of kelp forests in Ireland, specifically Laminaria hyperborea

A previous assessment of kelp ecosystem distribution along the west coast of Ireland estimated that kelp occurs along 56% of the coastline (Hession et al., 1998), and broader projections from HSMs indicate similar or greater coverage on northern and southern coastlines as well (Yesson et al., 2015a). Compared with intertidal seaweeds, kelps are more difficult to survey and assess because they are predominantly found below the lowest astronomical tide (LAT) level (in subtidal zones). Expert assessment on kelp ecosystem status across Europe by Araújo et al. (2016) returned "do not know" answers to questions about trends in kelp forest "extension and density" in Ireland. Few subtidal surveys have taken place on a national scale in Ireland (e.g. BioMar; Picton and Morrow, 2006), including records for kelp species. Therefore, gaps remain in knowledge of the coverage and biomass of kelp on the Irish coastline and changes in its status over time.

Historical records of L. hyperborea presence (distribution) and status were drawn from international and national datasets (herbaria, old texts and online data repositories) to create a chronological timeline and measure the effort taken to record these critical ecosystems (Schoenrock et al., 2020a). Prior to the 20th century, few people recorded subtidal habitats or species unless individuals were pulled up on anchors or washed ashore in storms [but see Jung (2021) for examples of subtidal science dating back to 300 BC]. However, historical accounts mention how important kelp was for cultural (e.g. material for religious artefacts) and agricultural/commercial purposes in Ireland (Mac Monagail and Morrison, 2020; Schoenrock et al., 2020a). The first records of L. hyperborea in Ireland began in 1913 (Hook Head, County Wexford; Figure 1.3). The records do not denote the presence of a kelp forest, as there are generally very few metadata attached to georeferenced data points in online repositories such as the Global Biodiversity Information Facility (GBIF) and the Ocean Biodiversity Information System (OBIS)



Figure 1.3. Record of recording period for presence of *Laminaria hyperborea*, either on shorelines or *in situ*. Reproduced from Schoenrock *et al*. (2020a); licensed under CC BY 4.0 (https://creativecommons. org/licenses/by/4.0/).

(Schoenrock *et al.*, 2020a); however, they do paint a picture of recording effort that reflects advances in technology, such as scuba equipment and the development of citizen science monitoring efforts in recent years (Schoenrock *et al.*, 2020a; Figures 1.3 and 1.4).

## 1.3.2 Current understanding of Laminaria hyperborea distribution

Schoenrock *et al.* (2020a) showed that kelp forest sightings are prevalent along southern, western and northern coastlines in Ireland but not along the eastern shores, which tend to have high sedimentation rates

Figure 1.4. Record of repeated *Laminaria hyperborea* records from 1913 onwards, either on shorelines or *in situ*. Few sightings of this kelp have been reported over multiple years, which may or may not indicate the absence of a kelp ecosystem. Reproduced from Schoenrock *et al.* (2020a); licensed under CC BY 4.0 (https:// creativecommons.org/licenses/by/4.0/).

(see Figures 1.3 and 1.4). This aligns with previous HSMs that predict the present and future distribution of all kelp species across the British Isles (Yesson *et al.*, 2015a,b). The best predictors of the distribution of kelp in Ireland seem to be bedrock, water depth and light availability (Yesson *et al.*, 2015a), and habitat wave-exposure gradients are also important for *L. hyperborea* (Burrows, 2012). Moreover, van Son *et al.* (2020) stress the importance of bottom wave exposure in HSMs for kelp abundance; therefore, future HSMs in Ireland should utilise this suite of factors if repeating this work in a more focused study.

### 2 Genetic Connectivity between Kelp Populations along Ireland's Coastline

**Project aims.** "Seascape genetics" were evaluated at the national level and then EU-wide (including data from Brittany and Iberia), to determine how important the genetic diversity of Irish populations is within the context of EU *L. hyperborea* populations. These data will help us to understand population connectivity and novel alleles in Irish kelp habitats that may contribute to genetic resilience in subtidal ecosystems and ultimately could help us to understand evolutionary processes and inform management decisions for stakeholders.

#### 2.1 *Laminaria hyperborea* Reproductive Systems

The reproductive system of a population encompasses traits that determine the balance between sexual and asexual reproduction and the relevant amounts of outcrossing versus self-fertilisation (Barrett, 2010). The prevailing reproductive mode governs the transmission of genes between generations, affecting the partitioning of genetic diversity within and among populations (Hamrick and Godt, 1996) and the evolutionary response to environmental change (Eckert et al., 2010). Historically, more work has focused on the axis of variation from outcrossing (gametes produced by different individuals) to selffertilisation (gametes produced by the same individual) in angiosperms than in other eukaryotes; however, across eukaryotes, general forces are likely to be shaping reproductive system evolution, with important consequences for gene flow range size (Barrett, 2002). Outcrossing is associated with greater genetic diversity, whereas self-fertilisation is associated with lower genetic diversity and increased homozygosity. Thus, self-fertilisation often leads to inbreeding depression in which there are declines in offspring fitness with serious demographic and evolutionary consequences (Charlesworth and Charlesworth, 1987). In angiosperms and animals, separate sexes are often used as proxies for outcrossing. However, in haploid-diploid taxa, such as L. hyperborea, separate sexes do not prevent self-fertilisation. If fertilisation occurs between two gametophytes that

share the same sporophytic parent, this is wholly analogous to self-fertilisation in a plant or animal (Klekowski, 1969). For many marine macroalgae, it is therefore critical to assess reproductive systems using population genetics (see, for example, Krueger-Hadfield *et al.*, 2015; Krueger-Hadfield, 2020). Yet, few studies have explicitly described reproductive system variation in marine macroalgae, including kelps (Valero *et al.*, 2001; Olsen *et al.*, 2020), and none of these has investigated patterns of genetic diversity in gametophytes (Krueger-Hadfield *et al.*, 2021). As the reproductive system partitions genetic diversity, it is a critical missing piece of information for appropriate management strategies.

L. hyperborea has a complex life cycle that effectively separates two of the critical steps in sexual reproduction: (1) meiosis occurs on the sporophyte where zoospores are created within sori (not all will be genetically identical and this may be a source of genetic variation within a population) and (2) fertilisation of male and female gametes produced by gametophytes (see Figure 1.1). The ratio of male and female gametophytes is thought to be 50:50 within L. hyperborea (Kain and Jones, 1964) and the male gametophytes use chemolocation to sense pheromones of the female ovum (Maier, 1987). Instances of self-fertilisation have been documented in the Laminariales (Camus et al., 2021), as well as in populations that are partially clonal, i.e. undergoing asexual reproduction (Oppliger et al., 2014; Revnes et al., 2021). Although laboratory studies have suggested that hybridisation does not occur between Laminaria spp. in the North Atlantic (tom Dieck, 1992), there are currently few examples of this occurring.

#### 2.2 Patterns of Genetic Diversity in *Laminaria hyperborea* across Europe

Dispersal varies across kelp species. In some species, such as the giant kelp (*Macrocystis pyrifera*), sporophylls – where sori are produced – are at the base of the sporophyte, theoretically limiting dispersal to the subcanopy region of the kelp forest; however, pneumatocysts along the thallus of this species make it buoyant, permitting rafting in individuals if they become dislodged and enhancing dispersal potential in reproductive individuals (Macaya et al., 2005). Stipitate kelps, such as *L. hyperborea*, produce sori on their lamina within the canopy (or subcanopy), which may give the zoospores access to currents that disperse them further than their own mobility allows; however, these species are often negatively buoyant and cannot raft. Using nine microsatellite loci [four developed for L. digitata (Billot et al., 1998) and five developed for L. ochroleuca (Coehlo et al., 2014)], Schoenrock et al. (2020b) observed patterns of isolation by distance between populations in Counties Cork, Clare, Galway and Donegal (Figure 2.1), which was also shown in French and Norwegian populations (Robuchon et al., 2014b; Evankow et al., 2019). Furthermore, using a calibration across laboratory platforms for microsatellite loci, Irish kelp forests were shown to be very distinct from those in Brittany, France (Figure 2.1), and they also show stronger patterns of genetic structure (i.e. greater differentiation over shorter distances). It is important to compare studies of





Irish populations with more studies from other regions of Europe (see Evankow *et al.*, 2019), but it is crucial to first calibrate allele calling in microsatellite data to ensure that allelic richness is not overestimated (Schoenrock *et al.*, 2020b; S.A. Krueger-Hadfield (University of Alabama at Birmingham), S. Mauger (Station Biologique de Roscoff, SBR), M. Valero (SBR), J. Neiva, E. Serrao (Centro de Ciênces do Mar, CCMAR) and K.M. Schoenrock (NUI Galway), unpublished data).



Figure 2.2. Map of *Laminaria hyperborea* populations showing where samples were collected from 12 counties. Sites from Schoenrock *et al.* (2020b) are shown in yellow and collections from 2019 to 2020 are shown in blue. Kelp collections at most sites occurred every metre along a 30-m transect within the forest, except for two sites where a 300-m transect was used with varying distances between collections (black). Other sites were sampled over multiple years to assess the stability of the genetic stock within populations (red).

## 2.3 Genetic Diversity of *Laminaria hyperborea* in Ireland

## 2.3.1 Patterns of genetic structure in Laminaria hyperborea populations

In total, the KelpRes project sampled 48 sites from 12 counties (Figure 2.2), amplifying nine microsatellite loci following Schoenrock *et al.* (2020b). Data were hand calibrated with the allele calls used in Robuchon *et al.* (2014b) so that they can be compared with future European datasets (Schoenrock *et al.* 2020b; Krueger-Hadfield *et al.*, unpublished data). We analysed these data as previously described for a subset of populations by Schoenrock *et al.* (2020b) and uncovered similar patterns of genetic diversity, with the greatest diversity detected in the southern part of Ireland, a known glacial refugium (Assis *et al.*, 2016). Using GenAIEx 6.5 (Peakall and Smouse, 2006, 2012), we generated summary statistics and present these in Table 2.1 with populations assigned to different geographical regions (west, north-west, northeast, east, south-east and south-west). High genetic diversity (as unbiased expected heterozygosity) was found in the south, but also in the east and north-western regions of Ireland. We are currently exploring patterns of reproductive system variation using spatially explicit sampling to determine if the positive fixation index ( $F_{IS}$ ) values are due to spatial substructuring or if they suggest patterns of self-fertilisation (see Krueger-Hadfield *et al.*, 2013).

#### 2.3.2 Connectivity

Previously, strong isolation by distance was shown in *L. hyperborea* populations along the Irish coastline (Schoenrock *et al.*, 2020b; Figure 2.3). Increasing the number of populations (though these are not uniformly spread across the coastline) and including nested regions of collections (Hook Head and Árainn Mhór

#### Table 2.1. Summary statistics for 48 populations of Laminaria hyperborea

	Statistic							
Region	N	N <sub>e</sub>	H <sub>o</sub>	μH <sub>e</sub>	F <sub>is</sub>			
West	489	1.918	0.333	0.389	0.131			
North-west	155	2.238	0.420	0.46	0.094			
North-east	19	1.907	0.329	0.399	0.123			
East	22	2.118	0.334	0.461	0.354			
South-east	150	2.256	0.379	0.456	0.121			
South-west	210	2.05	0.371	0.419	0.091			

 $F_{is}$ , fixation index;  $H_o$ , observed heterozygosity;  $\mu H_e$ , unbiased expected heterozygosity; *N*, number of individuals;  $N_e$ , number of effective alleles.



Figure 2.3. Isolation by distance of populations of *Laminaria hyperborea* in four counties (Cork, Clare, Galway and Donegal). Pairwise genetic differentiation was regressed against pairwise geographical distance (log km, calculated on Google Earth). Reproduced from Schoenrock *et al.* (2020b), with permission.



Figure 2.4. Discriminant analysis of principal component plots highlighting the relationship between *Laminaria hyperborea* microsatellite genotypes within populations subdivided by regions north-east, north-west, west, south-west, south-east and east along different principal component axes. North-east: Co. Antrim; northwest: Cos Donegal, Sligo and Mayo; west: Cos. Galway, Clare and Kerry; south-west: Co. Cork; south-east: Cos. Waterford and Wexford; east: Cos. Wicklow and Dublin.

Island; Figure 2.2) showed similar patterns of strong regional genetic structure (Figure 2.4). Dispersal is likely to be limited along the coastline, leading to local retention of propagules. We are currently investigating patterns on smaller spatial scales within regions, as well as within sites, to address patterns of gene flow on various spatial scales.

## 2.3.3 Hybridisation or phenotypic plasticity in Laminaria species

The initial study by Schoenrock et al. (2020b) indicated that the highest genetic diversity was found in County Cork, in the south-west of Ireland, which was predicted to be a region exempt from glaciation during the Little Ice Age (LIA) and potentially a refuge for high genetic diversity in L. hyperborea (Assis et al., 2016). As part of an allele calibration with the SBR in France and the CCMAR in Portugal (Krueger-Hadfield et al., unpublished data), many of the L. hyperborea samples in County Cork had allele sizes similar to those found in L. digitata in previous work (Robuchon et al., 2014b). This was noticeable in many samples from Lough Hyne, suggesting misidentification of the species (L. hyperborea) due to phenotypic plasticity or potentially hybridisation of Laminaria spp. This is under investigation in collaboration with SBR to determine the extent of hybridisation in L. hyperborea and L. digitata in Lough Hyne, as well as at other sites across Ireland.

#### 2.4 "Evolutionary Resilience" in Kelp Ecosystems

The presence of high genetic diversity in the southern region of Ireland (Table 2.1) supports the concept of glacial refugia in this area, as suggested by Assis et al. (2016). High genetic diversity was also found in the two populations in eastern Ireland, as well as in populations in the north-west (Table 2.1). Understanding the historical and contemporary forces shaping patterns of genetic diversity is critical to effectively protecting species of kelp against the threats that they face. Our data are among the finest scale available for kelp, covering the entire distribution within a subregion (i.e. Ireland and Northern Ireland). These fine-scale data are necessary for describing patterns of diversity on various spatial scales and understanding population connectivity, both of which underpin the resilience of kelp species.

### **3** Microscopic Banks of Kelp Propagules

**Project aims.** It has long been hypothesised that there is a bank of microscopic algal stages in marine communities analogous to terrestrial seed banks (summarised in Schoenrock *et al.*, 2021a), but this is very difficult to assess in natural communities. A multifaceted approach was used to quantify the microscopic banks of kelp stages (including settled zoospores, gametophytes or undeveloped juvenile sporophytes; see Figure 1.1) in Irish kelp ecosystems through seasonal sampling of the benthic and experimental biofilm communities. Microscopy and cell stains targeting brown algae were used alongside aquarium and molecular identification methods to assess the abundance of microscopic propagules in these microscopic banks.

#### 3.1 The Role of the Life Cycle in the Ecology of *Laminaria hyperborea* Ecosystems

The life cycle of any organism is an incredibly important aspect of the ecology and potential resilience of ecosystems. The heteromorphic variation in macroscopic sporophyte and microscopic gametophyte morphologies in the Laminariales (Figure 1.1) enables ecosystem structuring in the former and potentially refuge from environmental disturbance in the latter. Few studies have targeted banks of microscopic forms in the benthic DBL of kelp ecosystems (reviewed in Schoenrock et al., 2021b), possibly because this is difficult to evaluate in situ. Previous observations of juvenile kelp growth throughout the year after a canopy clearance event indicate either that annual production of gametophytes (from all kelp species) is seeding new kelp forests or that there is a bank of vegetative gametophytes or dormant juvenile sporophytes within the DBL waiting for light cues to grow (Lüning and Neushul, 1978). If L. hyperborea gametophytes and sporophytes were to form a bank in the benthic DBL, they would be present year-round despite this species' seasonal phenology, namely zoospore production in late autumn and winter and gametophyte development and sporophyte production from winter to spring

(Kain, 1979). KelpRes tested this using a threepronged approach:

- Settlement plates (microscope slides; Figure 3.1) were used at two monitoring locations (Figure 3.2) to quantify zoospore settlement and gametophyte development throughout the year across depths and canopy cover levels.
- Genetic barcoding techniques were used to evaluate the same settlement slides and quantify which kelp species settle at each site, depth and canopy cover level.
- An aquarium system (Figure 3.3) was used to cultivate microscopic forms present on bedrock at each site and season across canopy cover levels; the different canopy cover levels were studied to determine whether or not "banks" of kelp forms will grow when removed from canopy shading.



Figure 3.1. *In situ* settlement experiment blocks were organised to hold two racks of five microscope slides (one for microscopy and the other for barcoding techniques) for both seasonal and annual collections within kelp forest monitoring sites (see Figure 3.2). On one transect at each site, Hobo pendant loggers were placed on an eyebolt to measure irradiance and temperature.



#### Figure 3.2. Map of Ireland indicating the two monitoring locations where settlement experiments were set up, An Cheathrú Rua and Doire-Fhíonain (yellow), and the locations of summer bedrock collections across Ireland (blue).

KelpRes also used a barcoding approach to assess the presence of microscopic kelp forms on bedrock collected across Ireland in summers 2019 and 2020 (a season when juvenile sporophytes of *L. hyperborea* theoretically are already growing unless dormant). Before doing this, it was important to assess the fecundity of sporophytes at each site to determine reproductive potential of kelps at monitoring locations and whether or not gametophytes could grow and become reproductive *in vitro* as a proof of concept for the aquarium experiment.

#### 3.1.1 Fecundity of sporophytes and settlement and survival of zoospores in vitro

Kelp blades with sori were collected in late autumn and winter, 2019/20, from Doire-Fhíonain and An Cheathrú Rua (Figure 3.2) and brought back to the laboratory to stimulate zoospore release *in vitro* following the methods of Redmond *et al.* (2014) in the aquarium (Figure 3.3).

Zoospore release was noted as a change in water turbidity in 500-ml beakers, and microscope slides were removed from the bottom of beakers after 24 h and then every 7 days to monitor settlement of zoospores and development into gametophytes. In An Cheathrú Rua, zoospore abundance was found to be greater in winter, with 27.9 zoospores cm<sup>-2</sup> of sori found on slides, than in autumn, with 4.6 zoospores cm<sup>-2</sup> of sori recorded. After zoospores were released, they migrated to the bottom of beakers, but remained somewhat motile for 27 days (no flagellar movement but not settled; Table 3.1).

## 3.1.2 Gametophyte development and reproduction in vitro

Some gametophytes developed within 7 days of zoospore release *in vitro*, and over 50% of the zoospores developed into gametophytes within 62 days of release. Survival of these waned over time, as the number of gametophytes and presence of "dead" gametophytes increased (unpigmented multicellular structures; Table 3.1). No gametophytes developed ova or gametangia *in vitro*. Whether this is a product of the conditions or a rare process could not be determined for these *L. hyperborea* populations, and this monitoring ended with the onset of the COVID-19 pandemic.

#### 3.2 Seasonal and Annual Patterns of Kelp Propagule Abundance in the Benthic Kelp Forest Habitat

#### 3.2.1 Microscopy-based examination of presence/absence of propagules across kelp forests, canopy cover levels and seasons

Microscope slides were fixed and embedded in resin so that they could be surveyed for the presence of Laminariales zoospores and gametophytes. The numbers of single, double, triple and quadruple cell stages (size of gametophyte) were quantified across 40 random plots on each slide, for each site, season, depth and canopy level. There were significant differences in these microscopic communities across sites, seasons and depths, but canopy cover level had



Figure 3.3. The set-up for aquarium incubations at the National University of Ireland Galway. The conditions reflected those of the ambient ocean, following light period and intensity, as well as seawater temperature across seasons. All rock collections were placed in labelled 500-ml beakers within water tables and sterilised seawater was recirculated from a sump to the beakers with a fluence rate of 4 ml s<sup>-1</sup>. When kelp growth was found, individuals were removed and preserved in silica for barcoding, and rocks were placed back in the aquarium.

Days	Unicellular zoospore	Settled zoospore	Gametophytes	Reproductive gametophyte	Dead gametophyte
13	0.92	0.01	0.07	0	0
21	0.46	0.10	0.21	0	0
27	0.21	0.05	0.41	0	0
62	0	0	0.56	0	0.11
70	0	0	0.26	0	0.18

Table 3.1. *In vitro* settlement of zoospores, development into gametophytes and then senescent individuals as a fraction of the original zoospore community

no effect on the abundance of zoospores or different sizes of gametophyte, indicating that shading has no relevance to their persistence in the DBL. Patterns indicated that the number of zoospores in the DBL was greatest in shallow depths, potentially close to zones where *L. digitata* and other kelps are most abundant, and all stages were least abundant at depth (Figure 3.4b). Slides collected in autumn had the greatest abundance of all stages and slides kept in place year-round had levels of abundance equal to winter, spring and summer (Figure 3.4a). If we extrapolate these data, the DBL within kelp forests



Figure 3.4. Total number of zoospores (purple) and gametophytes of two (red), three (brown) and four (green) cells in size (a) across seasons including those kept *in situ* for 1 year (annual) and (b) across depths within coastal kelp forests (deep= $\sim$ 5–6m, middle=4–5m and shallow=2–3m). Note that kelp forests can be found at greater depths on islands or other regions with better water clarity [C.A. Maggs, M.D. Guiry (NUI Galway) and M.J. Dring (Belfast University), 1988, unpublished data].

might retain a maximum of 0.08 zoospores cm<sup>-2</sup> benthos and 0.045 developed gametophytes cm<sup>-2</sup> benthos on average. These kelp forms were not as dense as might be assumed from *in vitro* data and were variable at all levels examined in the experiment. Molecular methods were required to identify these microscopic forms at the species level.

#### 3.2.2 Molecular-based examination of presence/absence across kelp forests, canopy cover levels and seasons: barcoding with atp8 and trnWI primers

To genetically identify the Laminariales that were quantified in microscopy data, swabs were obtained of the biofilm (including kelp stages) from microscope slides in experiments. Extracts were taken from all slides collected across sites, seasons, depths and canopy cover levels, and DNA was amplified using the brown algae-specific primers atp8 and trnWI (Engel et al., 2008). The trnWl primer set was more successful than atp8 at amplifying DNA, and, when sequence results were compared with sequences sourced from the GenBank database (most accession numbers correspond to data from Table 4 in Engel et al., 2008), many samples produced chromatograms that suggested multiple brown algal species were present in the sample (Table 3.2). The results indicated seasonal recruitment of L. hyperborea (winter and, to a lesser extent, spring) and L. digitata (autumn),

as well as the presence of *U. pinnatifida* (which was not visible as a sporophyte at the site) in microscopic form at An Cheathrú Rua. Annual slides were also found with juvenile kelp growing on them from both An Cheathrú Rua and Doire-Fhíonain, all of which were removed and identified as *L. hyperborea* (and one *S. polyschides*) with the *trnWI* barcoding primers.

#### 3.2.3 Growth of kelp in aquarium incubations

Few kelps grew in aquarium conditions, even though they mirrored in situ conditions (Hobo pendant loggers from the sites and the aquarium were used to compare the conditions). The low numbers of developing sporophytes could have been due to spatial patchiness in the settlement of kelp zoospores and development of gametophytes on the selected bedrock samples. This could also have been associated with the artificial aguarium habitat including nutrient concentrations, salinity or pH. Nevertheless, some bedrock samples from An Cheathrú Rua and Doire-Fhíonain did produce juvenile Laminariales in spring and autumn (regardless of canopy cover level or depth). In spring, 66% of kelps were L. hyperborea, 11% L. digitata and 11% S. polyschides, while 11% were mixed kelps that could not be identified with the trnWI barcoding primers. In autumn, 50% of kelps were L. hyperborea and 50% were L. digitata. Spring collections align with the recruitment window of L. hyperborea and S. polyschides, and autumn collections align with

Table 3.2. Presence of kelp species in microscope slide collections (n=1-5 slides) from Doire-Fhíonain
and An Cheathrú Rua across seasons (including those left for 1 year, annual), depths and canopy
cover levels

Site	Depth	Canopy	Spring	Summer	Autumn	Winter	All
An Cheathrú	Deep	Outer	Up, mk	Up, mk	Ld	Lh	mk
Rua		Middle	Lh	Up, mk	Ld	Lh	mk
		Inner	Lh	Ld, Up, mk	Ld	Lh	Sp, mk
	Middle	Outer	Sp, Lh		Ld	Lh	
		Middle	Lh		Ld	Lh	Up, Ld
		Inner					Up, mk
	Shallow	Outer			Ld	Lh	
		Middle	Lh	mk		Lh	mk
		Inner	Ae, Ld, mk	mk	Ld	Lh	mk
Doire-	Deep	Outer					
Fhíonain		Middle					
		Inner					
	Middle	Outer		mk	Ld		
		Middle	mk				
		Inner			Ld		
	Shallow	Outer					
		Middle	mk	mk	mk, Sp		mk
		Inner	mk		Ld, mk		

Note: some slides were lost during the study, including all those from the "deep" experiments from Doire-Fhíonain. Ae, *A. esculenta*; Ld, *L. digitata*; Lh, *L. hyperborea*; Lo, *L. ochroleuca*; mk, mixed kelp; Sl, *S. latissima*; Sp, *S. polyschides*; Up, *U. pinnatifida*.

*L. digitata* recruitment, so this evidence suggests that some kelp forms may persist outside their recruitment and growth window.

#### 3.3 Barcoding Examination of Kelp Propagule Banks in Summer Bedrock Collections (2019–2020) from Kelp Ecosystems across Ireland

Bedrock collections from kelp forests across the country (Figure 3.2) were sampled for the presence of *L. hyperborea* in the summer, which potentially indicates the presence of banks of microscopic kelp forms. DNA sequences from most of these samples indicated that there were likely to be multiple brown algae species present within the samples, though a few samples had clean *L. hyperborea*, *L. digitata* 

and *U. pinnatifida* sequences (the last not only in Greystones, where the sporophyte is abundant, but also in Scotch Port, where no sporophytes have been identified (Table 3.3). In some samples, no kelp was found (despite being taken from kelp forests), which indicates high spatial variability in kelp propagule settlement or a possible detection limit of the barcoding methodology (i.e. more gametophyte/ sporophyte material might have been required than was present).

#### 3.4 "Ecological Resilience" in Kelp Ecosystems

These experiments are the first step to better understanding the potential for microscopic kelp stages to exist as a "bank" within the DBL on benthic substrata in kelp forests. There is no easy way to test Table 3.3. Presence of kelp species in bedrock collections. Rock samples were scrubbed in sterile seawater, filtered and DNA extracted; samples were amplified with primers targeting the Laminariales. Two monitoring sites (An Cheathrú Rua, ACR, and Doire-Fhíonain, DYN) were sampled across four seasons and all canopy cover levels. Most samples that were sequenced (between 3 and 6, depending on the site) contained sequence from more than one kelp species, making the results indecipherable

Site	County	L. hyperborea	L. digitata	L. ochroleuca	S. latissima	S. polyschides	U. pinnatifida	A. esculenta	Mixed kelps
SKR	Dublin								×
GRY	Wicklow						×		×
GTP	Cork								
BCT	Waterford								
CRB	Wexford								
TMP	Waterford								×
IRLH	Cork								
ORLH	Cork								
EOH	Cork								×
GTI	Cork								
TPA	Donegal								
STP 2019	Mayo								
STP 2020	Mayo						×		×
PNB	Donegal								×
KLH	Donegal								×
KEM	Mayo								
GIA	Donegal	×							×
COA	Kerry								
BCA	Donegal								×
PTC	Мауо								×
ACR	Galway	×	×						×
DYN	Kerry		×						×

BCA, Béal an Chraois; BCT, Ballinacourty; COA, Coonana; CRB, Carne Beach; EOH, East Old Head; GIA, Illanaran; GRY, Greystones; GTI, Ceann Ardoginna; GTP, Gortnakilla Pier; IRLH and ORLH, the Rapids, Lough Hyne; KLH, Cionn Caslach; PNB, Port na Bláiche; PTC, Port an Chlóidh; SKR, Skerries; STP, Scotch Port (sampled twice); TMP, Tramore Pier; TPA, Tor an Éidigh.

for these functional communities in vitro; however, the presence of multiple kelp species on microscope slides that were left in situ for 1 year (compared with seasonal slides that had mono-specific results) indicates that there is no seasonal turnover in these "banks", but a build-up of species richness over time (see the sole presence of L. hyperborea and L. digitata on seasonal slides; Table 3.2). Furthermore, the growth of predominantly L. hyperborea juvenile sporophytes on annual slides confirms that, despite the presence of other kelp species within the biofilm, this species has a competitive advantage in this subtidal habitat. The facts that kelp grew in few aguarium experiments and that samples from bedrock collections often returned no kelp DNA highlight the spatial heterogeneity in the distribution of these banks of microscopic kelp forms, even within kelp forests.

Although evidence suggests that these microscopic banks exist, they may not be evenly distributed in these ecosystems. Spatial distribution may be affected by other factors, including grazers or abiotic factors unique to a habitat. The brown algae-specific primers also identified non-native species within these microscopic communities, similar to environmental DNA (eDNA) studies that used water samples to detect non-indigenous species (Fernandez et al., 2021). Thus, biofilm samples can provide an insight into the presence of these species in the benthos. To conclude, banks of kelp forms probably lend resilience to kelp ecosystems and the techniques used in this study could translate into tools for monitoring these populations across Ireland, potentially at the nonprofessional level through citizen science (Larson et al., 2020).

### 4 Continued Monitoring of Kelp Ecosystems

Project aims. Indicator species have been defined in previous kelp forest ecology monitoring programmes (Schoenrock et al., 2020b, 2021b) to equip citizen science scuba divers or recreational dive clubs with a dive slate that will help to evaluate the presence and health of kelp ecosystems. Simple notes on the presence or absence of key species in these systems, along with species abundance estimates, can help to track the health of kelp ecosystems across Ireland. Furthermore, an effective and inexpensive remotesensing tool was tested for monitoring kelp forest distribution in Ireland using satellite imagery. Lastly, a data pipeline for citizen science or institutional data records was sought, and workshops and outreach activities promoting the recording of kelp in marine habitats continue.

#### 4.1 Using Citizen Science in Continued Monitoring of Kelp Habitats along Ireland's Coastlines

Citizen science, or community science, is the practice of recruiting the non-specialist public to collaborate in scientific research, expanding the scope of research projects while increasing scientific literacy around certain subjects. There are a few citizen science initiatives on the island of Ireland that focus on subtidal marine habitats; the most prominent of these are Seasearch Ireland and Seasearch Northern Ireland. Observing subtidal habitats requires specific training in skin or scuba diving, which presents a unique hurdle to obtaining subtidal datasets. The development of Seasearch Ireland programmes has directly influenced the number of subtidal records of kelp forests submitted to the National Biodiversity Data Centre (NBDC) in Ireland (Schoenrock et al., 2020a, Figure 1.4), and has boosted our understanding of the natural history of nearshore ecosystems countrywide.

Kelp forests and seaweeds in general suffer from a lack of interest because of the difficulty in species identification for the non-specialist public. Unlike decapod crustaceans and fish, distinctive characteristics in the morphology of seaweeds can be challenging for citizen scientists, even for the few kelp species present in the North Atlantic (see section 2.3.3). Therefore, along with Seasearch, KelpRes has provided a series of workshops on seaweed identification and kelp forest ecosystems to broaden interest in and understanding of these systems for recreational divers and dive clubs. This has led to a better understanding of species morphology and the discovery of new site records for invasive species, including U. pinnatifida (at Greystones; Chan et al., 2021) and L. ochroleuca (at Béal an Mhuirthead; Schoenrock et al., 2019). The next step is mobilising this knowledge to maintain and grow species records for kelp ecosystems. KelpRes developed a dive slate using the indicator species defined in Schoenrock et al. (2020a; Table 4.1); this is available online via KelpRes websites hosted by Explore Your Shore! (https://exploreyourshore.ie/ marine-biodiversity-surveys/kelpres/) and NUI Galway (http://www.nuigalway.ie/zoology/research/kelpres/), and through a QR code widely distributed on KelpRes business cards (Figure 4.1). There have been 313 taxa observed within Irish kelp forests across sites and seasons (Schoenrock et al., 2021a), and this dive slate is intended to provide the impetus to enhance records of national kelp ecosystems.

For non-divers, information on collecting intertidal algal sightings, including kelp and invasive macroalgae species in intertidal habitats, can be accessed on the Explore Your Shore! website (https://exploreyourshore. ie/shore-surveys/). A separate citizen science project, the "Valorisation of invasive seaweeds", asks citizen scientists to also report sightings of invasive species that may have an impact on kelp in the future, e.g. *U. pinnatifida* (https://exploreyourshore.ie/ valorisation-potential-of-invasive-seaweed-species-inireland/).

#### 4.2 Remote Sensing to Examine Kelp Forest Distribution along Ireland's Coastline

Remote sensing enables the detection and monitoring of physical or biological characteristics in an environment from a distance. Above water, this is generally done by measuring reflected and emitted

Species	Average abundance (m <sup>-2</sup> )	Trophic function
Sponge, encrusting Suberites spp.	0.26	Filter feeder
Hydroid, Obelia geniculata	0.27	Filter feeder (on kelp)
Anemone, Urticina felina	1.54	Predator
Cnidarian, Caryophyllia smithii	0.59	Filter feeder
Annelid, Eupolymnia nebulosa	0.02	Filter feeder
Crustacean, Palaemon serratus	0.016	Predator
Mollusc, Gibbula umbilicalis	0.86	Grazer
Mollusc, Gibbula cineraria	0.06	Grazer
Echinoderm, Asterias rubens (<3 cm diameter)	1.22	Predator
Echinoderm, Marthasterias glacialis	0.41	Predator
Echinoderm, Holothuria forskali	0.39	Suspension feeder
Echinoderm, Echinus esculentus	0.2	Grazer
Ascidian, Aplidium punctum	0.78	Filter feeder
Ascidian, Distomus variolosus	4.99	Filter feeder
Ascidian, Diplosoma spongiforme	0.08	Filter feeder
Vertebrate, Pomatoschistus spp.	0.015	Predator
Vertebrate, Gobiusculus flavescens	0.39	Predator

Table 4.1. A list of indicator species that are consistently associated with healthy *Laminaria hyperborea* forests throughout the year, including their average abundance per m<sup>2</sup> of kelp forest and trophic function

Notes: A lack of these species within an *L. hyperborea* forest may indicate that the ecosystem is unhealthy or that the habitat is small (i.e. a "kelp park"; see Parr, 2020) or comprises mixed kelps.

Reproduced from Schoenrock *et al.* (2020a); licensed under CC BY 4.0 (https://creativecommons.org/licenses/by/4.0/). Note that some genus names have changed since publication.

Data presented in Schoenrock et al. (2021b) were used to synthesise this table.

radiation (light) from a distance (e.g. by satellite, plane or drone; Rossiter *et al.*, 2020); under water, this can be done by measuring reflected sound or light [e.g. by using light detection and ranging (LiDAR), sound navigation and ranging (sonar) or autonomous underwater vehicles (AUVs); see Table 1 in Bennion *et al.*, 2019]. All methods have pros and cons in their application for different habitats, but ground truthing is always necessary to validate the chosen monitoring tool. With kelp forests, the appearance of this subtidal species at the surface of the water is highly variable and this will dictate which tools can be used for remote sensing.

#### 4.2.1 Satellite imagery

Satellite optical imagery has been highly successful for the remote sensing of vegetation of all types on land and, to a limited extent, aquatic vegetation in specific contexts. Floating macroalgal canopies that are apparent at the ocean surface can be mapped using satellite imagery relatively easily (Schroeder *et al.*, 2019; Mora-Soto *et al.*, 2020), but monitoring subtidal canopies such as those around Ireland is more complicated. The lack of infrared (IR) band reflectance from submerged kelp makes the use of all conventional vegetative indices redundant and limits any analysis to the use of the remaining available optical passband imagery. The increasing opacity of the water column with depth due to suspended and dissolved organic matter, combined with the poorer reflectance of the seafloor and the potential confusion of differing seafloor "types" (e.g. sand, mud, rock, or a mixture of all three, combined with varying vegetation coverage), contributes to limiting our ability to fully define these environments using satellite-based remote sensing, particularly those deeply submerged macrophyte colonies. This is particularly relevant to the nearshore marine environment surrounding Ireland, which has not been fully characterised from an Earth observation (EO) perspective. Finally, regular cloud coverage can reduce the number of useable images from optical sensors and it may be necessary to consider satellite types with increased "passes"/ coverage.

Name: Date:

Golden

Wakame

#### EPA - KelpRes Kelp Forest Recorder Form

Contact Information:

Site information (including GPS coordinates):\_\_\_\_

Exposure:	Weather conditions:
Visibility (m):	Depth (m) :

#### Dominant kelp species

Estimated Density Depth (m):

(per m<sup>2</sup>)

Common specie	es	
Cuvie	Laminaria hyperborea	
Oar weed	Laminaria digitata	
Sugar kelp	Saccharina latissima	
Furbellows	Saccorhiza polyschides	
Dabberlocks	Alaria esculenta	
Rare species		

Laminaria ochroleuca

Undaria pinnatifida

### Kelp forest inhabitants

Common species		_	
Common urchin	Echinus esculentus		
Spiny Sea Star	Marthasterias glacial	lis	
Cotton spinner	Holothuria forskali		
Common star	Asterias rubens		
Sea orange	Suberites fiscus		
Kelp fur	Obelia geniculata	% cover ->	
Blue rayed limpet	Patella pellucida	# kelp-1->	

#### Seasonal Species

Edible crab	Cancer pagurus	
Common lobster	Homarus gammarus	
Spiny spider crab	Maja brachydactyla	
Two-spot goby	Gobiusculus flavescens	
Pollock	Pollachius pollachius	
juvenille fish		

#### Any other information:

![](_page_32_Picture_15.jpeg)

To record kelp forests online go to: nuigalway.ie/zoology/research/kelpres/

Figure 4.1. Kelp forest dive slate intended for use by citizen science or recreational dive club groups. The QR code links recorders to an identical online form. All data collected can be directly inputted to the NBDC database. Despite these limitations, it is possible to detect subtidal Laminaria spp. populations remotely, although species delineation remains problematic, as the broad spectral bands used in most orbiting EO missions cannot provide the fine spectral profile necessary to do so: vegetation class separation requires hyperspectral imagery which typically operates in much narrower passbands (5- to 10-nm resolution) than the multispectral approaches currently used in orbit. To date, the only index demonstrated to have verifiable remote-sensing capability of submerged Laminaria spp. is the ratio of red to green wavelengths (Casal et al., 2011). Casal et al. (2011) made use of three broadband optical passbands (XS1 band: 500-590 nm, "G"; XS2 band: 610-680 nm, "R"; and XS3 band: 780-890 nm, "IR") from the EO SPOT-4 (Satellite pour la Observation de la Terre-4) and, in conjunction with ground-truthed data, applied several supervised and unsupervised algorithms to classify submerged kelp forests with ~70% accuracy to 10 m depth at a resolution of 20 m pixel<sup>-1</sup> off the Galician coast. Ideally, an EO platform with a higher spatial resolution, regular cadence duty cycle that supports hyperspectral imaging and bandpass resolution of approximately tens of nanometres would be available for the longterm monitoring of Ireland's kelp ecosystems, but unfortunately no platform like this exists. We assess three currently available EO-based monitoring platforms for use as part of a kelp monitoring programme.

The Sentinel class of EO satellites, operated by the European Space Agency (ESA) on behalf of the European Commission's Copernicus programme, carry multispectral optical instrumentation which has good spatial resolution (swath width of 290 km and a spatial resolution from 10 to 60 m) and frequent temporal sampling (every 2-3 days at 45°N). At the highest spatial resolution (10 m), band "B" (centred at 490 nm), band "G" (centred at 560 nm), band "R" (centred at 665 nm) and band "IR" (centred at 833 nm) are available for use in mapping algal and seagrass habitats in the Atlantic (Jia et al., 2019; Zoffoli et al., 2020), although this is much more difficult at temperate latitudes for the reasons listed previously. Therefore, Sentinel-2 images can provide only presence/absence data to map vegetation to ~10 m depth and this can drop to only 4 m depth in areas or times of lower water clarity (Wilson et al., 2020).

The Landsat programme, operated jointly by the US Geological Survey and the National Aeronautics and Space Administration (NASA), has been operational since the early 1970s and provides freely available multiband imagery at a spatial resolution of 30 m (up to nine optical/IR bands in the most recent missions) with a typical sampling cadence of ~10–15 days. Drawbacks in using this technology are that there is no detection in close coastal cells (within 30 m of the coast) and accuracy is low in certain tidal states, as determined from work on surface canopy kelp forests (Nijland et al., 2019). Using older satellite images would allow potential hindcasting of changes in kelp forest distribution across Ireland from archived images, as achieved by Nijland et al. (2019). Whether or not this historical to present-day Landsat technology would work with submerged forests is uncertain.

Over the past decade, there has been a revolution in the miniaturisation of satellites deployed to orbit, with the U-class (also known as CubeSats) widely launched for a variety of applications, including EO. The market leader is Planet Labs Inc. based in San Francisco, CA, USA, which operates a fleet of over 200 such remote-sensing CubeSats, most of which are 4 kg in mass and 10 cm × 10 cm × 30 cm in size (the "Doves"). The "Doves" imagery is ~3-m resolution in the "B", "G", "R" and "NIR" (near IR) bands, and the plethora of satellites allows observation of the same location multiple times each month, limiting the impact of cloudy, temperate conditions and optimising data collection during low tides (in Ireland there are semidiurnal mixed tides). Limited data are freely available for the academic community (up to 50 2000-km<sup>2</sup> images per day) and discussions have taken place between Planet Labs Inc. and the ESA to permit approved access to ESA scientists as a Third Party Mission. To date, relevant applications have involved the study of seagrasses (Coffer et al., 2020) and coral reefs (Li et al., 2019).

In Figure 4.2, we demonstrate the imaging quality and resolution for these three remote-sensing platforms at a long-term monitoring site in east An Cheathrú Rua (ACR, Keeraunbeg). Figure 4.2a–d shows four contemporary images from Google Earth, Landsat, Sentinel-2 and a Planet Labs Dove CubeSat, highlighting the limitations of the low-spatialresolution imagery. Figure 4.2e shows the results of an unsupervised classification of submerged kelp

![](_page_34_Picture_1.jpeg)

Figure 4.2. The east An Cheathrú Rua (ACR) Keeraunbeg site assessed by remote sensing. True colour imagery from (a) Google Maps (obtained by aerial photography), resolution ~0.1 m [Data: Scripps Institution of Oceanography (SIO), National Oceanic and Atmospheric Administration (NOAA); US Navy; National Geospatial-Intelligence Agency (NGA); General Bathymetric Chart of the Oceans (GEBCO); Image © 2021 National Centre for Space Studies (CNES)/Airbus]; (b) Landsat 8, resolution ~ 30 m; (c) Sentinel-2, resolution ~10 m; and (d) Planet Labs Dove, resolution ~3 m. The result of an unsupervised classification of R/G pixels from the Planet Lab observations (e), prepared using the Integrated Mapping for the Sustainable Development of Ireland's Marine Resource (INFOMAR) bathymetry map of Cuan na Gaillimhe to clip the analysis region to 10-m depth (lowest astronomical tide). The red pixels correspond to the group identified with known kelp beds visible close to the shore in (c) and show the extent of the forest into Cuan Chasla. All data were processed locally using the R statistical programming environment (R Core Team, 2018).

beds using the "R"/"G" band data from the Planet Labs imagery and INFOMAR bathymetry maps of Cuan na Gaillimhe, truncated to a depth of 10 m. This map provides a good assessment of kelp distribution in An Cheathrú Rua, confirmed by scuba diver assessment.

To summarise, the accuracy of kelp habitat classification with satellite imagery tends to be higher in relatively small areas with contiguous habitat coverage, mapped with a high spatial resolution and a degree of tuning to local conditions (as in Figure 4.2e). Some platforms, such Google Earth Engine, can simplify classification by cleaning images (e.g. clouds or ocean glint) and by removing the need to download and store the images locally. Good tools for macroalgal ecosystems are those created within Google Earth Engine to simplify automation of the image analysis (see Nijland *et al.*, 2019) and "hybrid" image processing approaches that use machine learning to boost habitat classification via simple band ratios such as the normalised difference vegetation index (NDVI) and the red–green index, although these are viable only in intertidal and shallow subtidal zones (Wilson *et al.*, 2020). These tools are already used in citizen science projects such as Floating Forests (https://www.zooniverse.org/projects/zooniverse/ floating-forests), although an important consideration would be the phenology of the target species so that the imagery used coincides with optimal coverage periods to assist with mapping success (thus, for *L. hyperborea*, this would be summer).

#### 4.2.2 Sonar mapping

Perhaps a better subtidal mapping approach is single beam or multibeam sonar, which can provide <5 cm resolution with surface-based sensors (Bennion *et al.*, 2019). This method can determine seafloor characteristics (e.g. hard vs soft substrata, flat vs rough), which highlights both substrata suitable for kelp and 3D objects in the water column, for instance the kelp itself (Bajjouk et al., 2015). Sonar data should be ground-truthed with data collected either with a drop-down camera or by a scuba diver (Scally et al., 2020; van Son et al., 2020), but a major benefit is that sonar does not have depth penetration limitations like the optical methods described previously. Although single-beam sonar has less coverage than multibeam methods, single-beam data have less backscatter and have been used to estimate kelp biomass in Norway and Ireland (Blight et al., 2011; Kruss et al., 2017; Rossiter, 2020), and commercial single-beam sonar units with an integrated camera are now available (e.g. BioSonics Inc. Seattle, WA, USA). Multibeam sonar units are also commercially available, but these are not as effective as single-beam methods in identifying kelp forests (Kruss et al., 2017). Sonar mapping must be carried out from the water surface and requires extensive field work, which reduces the scope for completely mapping a coastline. Similarly, LiDAR and AUVs are often operated from a craft; however, these have greater disadvantages for application in Ireland because LiDAR operates poorly in turbid water and AUVs have small ranges and collect fewer data than sonar (reviewed in Bennion et al., 2019).

#### 4.2.3 Future of drone work in this area

Drones are now being used to assess the extent of intertidal algal communities in Ireland, especially with commercial species such as A. nodosum (Rossiter et al., 2020). Subtidal communities are hard to survey with optical sensors as discussed, but drone work also often includes stitching imagery together to cover a site area, which can be complicated by water surfaces. Furthermore, kelp "spectral signatures" are very similar, with a reflectance peak in the range of 500-600 nm from chlorophyll (Chl) c pigments, as well as the typical Chl a and IR bands for seaweeds (Figure 4.3). Kellaris et al. (2019) managed to create predictive models for A. armata coverage in the Azores (but to a depth of only 3-4 m) with low-cost drone equipment and support-vector machine, random forest and artificial neural network methodologies. This study suggested that the Azores is a particularly challenging habitat because of deep waters; however, turbid waters such as those of Ireland would be likely to complicate the application of this methodology even more. Ground-truthing, as in all other survey methods, is necessary with drones, but, if developed, drone work could be a low-cost alternative to in situ surveys (scuba or sonar) and produce higher resolution imagery than satellite data.

![](_page_35_Figure_4.jpeg)

Figure 4.3. In-air reflectance spectra above kelp forests (~2m depth) in An Cheathrú Rua taken with a spectral radiometer (TriOS RAMSES, Germany) in full sunlight.

#### 4.3 Data Pipeline for Continued Kelp Ecosystem Monitoring

We have already outlined that knowledge on the distribution and abundance of kelp ecosystems is lacking in Ireland (section 1.3). To monitor Irish kelp ecosystems and trends in kelp distribution and abundance, we need to facilitate both professional and non-professional research efforts across Ireland. Ideally, the associated biodiversity and hence health of kelp forests should be monitored and recorded at a subset of monitoring sites that are representative of kelp ecosystems in Ireland. This should also include monitoring changes in invasive species or range extensions of warm-water kelp species. Remote sensing of total kelp coverage, as well as related metrics such as biomass, should be attempted following and expanding on the methods described in section 4.2.1. Platforms to achieve this include

Seasearch Ireland and Explore Your Shore (in situ monitoring: https://exploreyourshore.ie/marinebiodiversity-surveys/seasearch-ireland/, https:// exploreyourshore.ie/shore-surveys/) (Figure 4.1) in Ireland (as part of the NBDC) and, at an international level, the Kelp Ecosystem Ecology Network (KEEN; https://www.kelpecosystems.org/) and Floating Forests (Zooniverse; https://www.zooniverse.org/ projects/zooniverse/floating-forests). Currently, the optimal data pipeline is still recording observations through the NBDC; however, this could and should be expanded for kelp ecosystems in Ireland. Avenues for this could be classroom activities, recreational outreach materials such as an infographic developed for KelpRes (Figure 4.4; a similar infographic was used as a popular stamp in California, USA) and activities such as BioBlitzes (National Geographic, https://www. nationalgeographic.org/projects/bioblitz/#).

![](_page_36_Figure_4.jpeg)

Figure 4.4. Kelp forest infographic designed for KelpRes outreach. Illustration by Luczo Illustrative Designs.

### 5 Implications for Resilience of Kelp Ecosystems in Ireland

#### 5.1 Evolutionary versus Ecological Resilience

Two resilience metrics were defined with implications for how kelp ecosystems might recover and resume normal function after large disturbance events:

- genetic diversity in *L. hyperborea* populations across Ireland, which will facilitate adaptation to long-term stressors in these populations;
- the existence of a microscopic "bank" of *L. hyperborea* forms (gametophytes or juvenile sporophytes), which will facilitate community recovery after short-term stressors via recruitment of new kelp.

The results show that *L. hyperborea* has genetically diverse populations in several regions of Ireland, namely the south, north-west and east coasts (two sites in Dublin and Wicklow). The species exhibits isolation by distance across populations (i.e. gene flow is limited by dispersal mechanisms), potentially restricting population recovery if the habitat were to be completely denuded. Furthermore, microscopic kelp "banks" are heterogeneously distributed within kelp forests and are therefore spatially variable. Finally, *L. hyperborea* seems to outcompete congeners for space in the subtidal zone, even at juvenile stages.

#### 5.2 Knowledge Gaps and Future Directions

#### 5.2.1 Modern pressures on kelp ecosystems

Studies outside Ireland have shown that mechanical harvesting has large impacts on biodiversity and food webs for up to 5 years post harvest (Lorentsen *et al.*, 2010; Greenhill *et al.*, 2021). Whether or not mechanical harvesting should be licensed to go ahead in Ireland is under judicial review (Mac Monagail and Morrison, 2020; O'Loughlin, 2021). The data provided in this report show that there are regionally unique genetic stocks of *L. hyperborea* that could be reduced or destroyed by wild harvesting. Genetic diversity is an important basis for resilience in the face of multiple stressors.

Approval for harvesting has been withdrawn for *L. hyperborea* and *S. latissima* by regional seaweed exploitation plans in some countries, such as Spain and Scotland, owing to concerns about sustainability (Araújo *et al.*, 2021). Concerns have been raised about declines in kelp abundance globally, including in Spain, the North Sea and Celtic Sea (Krumhansl *et al.*, 2016). Global climate shifts forcing changes in species distribution ranges are major threats to kelp ecosystems worldwide (Wernberg *et al.*, 2019), and this should stimulate research and monitoring of these ecosystems, as well as carbon mitigation strategies centred on primary producers, to curb national greenhouse gas emissions.

## 5.2.2 Understanding and utilising kelp ecosystem services

The ESs provided by kelp forests include coastal protection, food web and ecosystem structuring, and recreational activities (i.e. nature's contributions to people). Despite understanding these ESs from a global perspective, we still have little understanding of kelp forest food webs in Ireland, for example how kelps contribute carbon to food chains, which fisheries rely on for subsistence or habitat, and what functional redundancy exists in kelp forest communities to buffer them from the effects of climate change or "fishing down food webs". Furthermore, we have no accurate measure of how much kelp exists in Ireland, or of its distribution across depths, along coasts and over seasons. Gathering these data would require a much more intensive monitoring and field programme than is possible during a single 2-year project like KelpRes. Ongoing data collection would be feasible only with the proposed citizen science outreach tools (Chapter 4).

An important research gap relates to the extent to which kelp contributes to "blue carbon", i.e. carbon that is sequestered and buried in ocean sediments and may help to mitigate climate change. Perhaps 11% of carbon from total net primary production in macroalgae is stored, of which about 90% involves sequestration to the deep sea with the remainder being buried in coastal sediments (Krause-Jensen and Duarte, 2016). This is potentially significant for Ireland and globally, considering the large area and coverage of macroalgae.

Signatory countries to the Paris Agreement can count sources, sinks and storage of greenhouse gases as part of their nationally determined contributions (NDCs) towards meeting their greenhouse gas reduction targets. Conservation and restoration of nature, including carbon-storing habitats as "naturebased solutions", can be included as part of each country's actions and mitigation plans within the NDC framework. Currently, the information needed to calculate this for kelp forests is not available in Ireland because the national coverage and biomass of kelp are not known and neither is its precise carbon storage potential, something which is likely to be context dependent (Cott et al., 2021). The scale of carbon sequestered from kelp (L. hyperborea and S. latissima) on Norway's coastline was estimated recently to be 1.7 Mt CO<sub>2</sub> y<sup>-1</sup> (Gundersen et al., 2021) based on the proportions of both particulate and dissolved carbon sequestered to the deep sea and coastal sediments proposed in the meta-analysis of Krause-Jensen and Duarte (2016). Besides kelp, other types of seaweed and seagrass may also make a substantial contribution to blue carbon in Ireland - in Scotland, the carbon storage potential of algae including kelp was found to be 1.8 MtC y<sup>-1</sup> (Burrows et al., 2014b).

## 5.2.3 Informing policy for industry and conservation

A range of resilience metrics were assessed for subtidal kelp forests in Ireland to better understand how to monitor, manage and simply understand these systems and potential responses to climate shifts in nearshore ecosystems.

- We detected strong genetic structure leading to isolated populations. Our data collection constitutes one of the finest-scale population-level sampling efforts in a marine alga over a national coastline. The published results should inform the management of marine habitats in applied and conservation contexts.
- The bank of microscopic kelp forms in nearshore ecosystems is best detected using genetic techniques. We have described the occurrence of microscopic kelp forms in sites around Ireland, a necessary first step towards understanding the evolutionary ecology of these important taxa. This provides knowledge about potential kelp recruitment dynamics and therefore the resilience of these ecosystems to climate change and other disturbance events.
- 3. Past records of kelp ecosystems are insufficient to monitor either distribution and abundance or the status, trends and ecosystem health of kelp ecosystems. We need to shift towards whole ecosystem records, describing the abundance of not only kelp species but also associated taxa that may be indicators of the health of the ecosystem. This can be done with the help of citizen scientists using a recorder form (such as the digital dive slate developed in this project) or directly inputting data to the NBDC. Although an improved description of kelp ecosystem distribution is possible using remote-sensing technologies, for instance using satellite data and sonar, the density and abundance of target kelp species is still measurable only by direct observation (scuba).

### **6** Recommendations

It has been suggested that, in the past, the southern coastline of Ireland had been a glacial refugium for *L. hyperborea*, and this project shows that the southern region remains a highly genetically diverse region of Ireland, although there is also high genetic diversity elsewhere along Ireland's coastline. The evidence from this research suggests that gene flow is relatively low between *L. hyperborea* populations across the regions of Ireland. Low levels of gene flow may reduce resilience of this species by decreasing the chances of recovery following storms or harvesting activities.

Therefore, a cautious approach should be taken to the protection, conservation and management of this wild resource, either under existing legislation, such as the Habitats Directive, or through other legal instruments, including international conventions such as the Convention for the Protection of the Marine Environment of the North-East Atlantic (OSPAR Convention). The potential expansion of Ireland's marine protected area network as part of the public consultation exercise led by the Department of Housing, Local Government and Heritage is a positive step in this regard. Climate change and blue carbon initiatives under the new European Green Deal may also be relevant to the goal of protecting kelp ecosystems.

Banks of microscopic kelp forms were detectable within kelp communities; the existence of these communities may help populations recover after disturbance events. These life cycle stages (from multiple kelp species) vary across sites and seasons and were notably more abundant at shallower depths, although spatially they were highly variable. Some non-native species (*U. pinnatifida*) were present in the microscopic community but were absent as sporophytes. **Substantial knowledge gaps remain around microscopic dynamics in the kelp life cycle, again suggesting that caution is needed in their future exploitation.** 

Hand in hand with protecting kelp resources is the need to conduct monitoring. Our report shows that subtidal records around Ireland's coastline are incidental (there has been only one dedicated monitoring programme in recent years) and mostly one-off records from individual locations. Monitoring the status and trends in distribution and abundance of kelp should therefore be prioritised. We suggest that this would be best achieved with a mix of citizen science and state-sponsored monitoring programmes (to ensure optimal regional coverage). For the latter, the use of remotesensing tools using sonar that is ground-truthed with data collected from drop-down cameras and by scuba divers should be achievable and would allow periodic monitoring. This method can determine seafloor characteristics (e.g. hard vs soft or flat vs rough substrata), highlighting both substrata suitable for kelp and 3D objects in the water column including kelp itself (Bajjouk et al., 2015).

Schemes to continue monitoring kelp ecosystems drawing on citizen scientists, especially with digital dive slates for scuba divers, are important avenues to pursue and fund. To have a better idea of the health of kelp forests, support and growth of Irish citizen science projects including Seasearch Ireland and 'Explore Your Shore!' will enhance our understanding of these habitats contributing to national and international data sets and research networks such as KEEN (https://www.kelpecosystems.org/). Citizen scientists should be encouraged to help improve machine learning algorithms for mapping kelp (as seen in the Floating Forests project) or other assessments of kelp ecosystems along shorelines to build data that can contribute towards protecting the health of these ecosystems, fisheries assessments and national blue carbon inventories.

Given the multiple stressors facing kelp ecosystems globally and their importance in providing ESs, we do not recommend wild harvesting of kelp in Ireland. Without any routine resource assessment currently taking place in Ireland, it is impossible to ensure the sustainability of wild kelp harvesting to ensure populations recover and maintain ESs. Some international efforts are experimenting with reseeding and out-planting kelp individuals (following the degradation and collapse of these ecosystems in some cases), but there is no tried-and-tested method to repair these systems after they collapse. Therefore, the approach to their protection and management in Ireland should be cautious.

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## Abbreviations

AUV	Autonomous underwater vehicle
DBL	Diffusion boundary layer
EO	Earth observation
ES	Ecosystem service
ESA	European Space Agency
HSM	Habitat suitability model
IR	Infrared
KEEN	Kelp Ecosystem Ecology Network
Lidar	Light detection and ranging
MHW	Marine heatwave
NBDC	National Biodiversity Data Centre
SBR	Station Biologique de Roscoff
Sonar	Sound navigation and ranging

#### AN GHNÍOMHAIREACHT UM CHAOMHNÚ COMHSHAOIL

Tá an Ghníomhaireacht um Chaomhnú Comhshaoil (GCC) freagrach as an gcomhshaol a chaomhnú agus a fheabhsú mar shócmhainn luachmhar do mhuintir na hÉireann. Táimid tiomanta do dhaoine agus don chomhshaol a chosaint ó éifeachtaí díobhálacha na radaíochta agus an truaillithe.

## Is féidir obair na Gníomhaireachta a roinnt ina trí phríomhréimse:

**Rialú:** Déanaimid córais éifeachtacha rialaithe agus comhlíonta comhshaoil a chur i bhfeidhm chun torthaí maithe comhshaoil a sholáthar agus chun díriú orthu siúd nach gcloíonn leis na córais sin.

**Eolas:** Soláthraímid sonraí, faisnéis agus measúnú comhshaoil atá ar ardchaighdeán, spriocdhírithe agus tráthúil chun bonn eolais a chur faoin gcinnteoireacht ar gach leibhéal.

**Tacaíocht:** Bímid ag saothrú i gcomhar le grúpaí eile chun tacú le comhshaol atá glan, táirgiúil agus cosanta go maith, agus le hiompar a chuirfidh le comhshaol inbhuanaithe.

#### Ár bhFreagrachtaí

#### Ceadúnú

Déanaimid na gníomhaíochtaí seo a leanas a rialú ionas nach ndéanann siad dochar do shláinte an phobail ná don chomhshaol:

- saoráidí dramhaíola (m.sh. láithreáin líonta talún, loisceoirí, stáisiúin aistrithe dramhaíola);
- gníomhaíochtaí tionsclaíocha ar scála mór (m.sh. déantúsaíocht cógaisíochta, déantúsaíocht stroighne, stáisiúin chumhachta);
- an diantalmhaíocht (m.sh. muca, éanlaith);
- úsáid shrianta agus scaoileadh rialaithe Orgánach Géinmhodhnaithe (OGM);
- foinsí radaíochta ianúcháin (m.sh. trealamh x-gha agus radaiteiripe, foinsí tionsclaíocha);
- áiseanna móra stórála peitril;
- scardadh dramhuisce;
- gníomhaíochtaí dumpála ar farraige.

#### Forfheidhmiú Náisiúnta i leith Cúrsaí Comhshaoil

- Clár náisiúnta iniúchtaí agus cigireachtaí a dhéanamh gach bliain ar shaoráidí a bhfuil ceadúnas ón nGníomhaireacht acu.
- Maoirseacht a dhéanamh ar fhreagrachtaí cosanta comhshaoil na n-údarás áitiúil.
- Caighdeán an uisce óil, arna sholáthar ag soláthraithe uisce phoiblí, a mhaoirsiú.
- Obair le húdaráis áitiúla agus le gníomhaireachtaí eile chun dul i ngleic le coireanna comhshaoil trí chomhordú a dhéanamh ar líonra forfheidhmiúcháin náisiúnta, trí dhíriú ar chiontóirí, agus trí mhaoirsiú a dhéanamh ar leasúchán.
- Cur i bhfeidhm rialachán ar nós na Rialachán um Dhramhthrealamh Leictreach agus Leictreonach (DTLL), um Shrian ar Shubstaintí Guaiseacha agus na Rialachán um rialú ar shubstaintí a ídíonn an ciseal ózóin.
- An dlí a chur orthu siúd a bhriseann dlí an chomhshaoil agus a dhéanann dochar don chomhshaol.

#### **Bainistíocht Uisce**

- Monatóireacht agus tuairisciú a dhéanamh ar cháilíocht aibhneacha, lochanna, uiscí idirchriosacha agus cósta na hÉireann, agus screamhuiscí; leibhéil uisce agus sruthanna aibhneacha a thomhas.
- Comhordú náisiúnta agus maoirsiú a dhéanamh ar an gCreat-Treoir Uisce.
- Monatóireacht agus tuairisciú a dhéanamh ar Cháilíocht an Uisce Snámha.

#### Monatóireacht, Anailís agus Tuairisciú ar an gComhshaol

- Monatóireacht a dhéanamh ar cháilíocht an aeir agus Treoir an AE maidir le hAer Glan don Eoraip (CAFÉ) a chur chun feidhme.
- Tuairisciú neamhspleách le cabhrú le cinnteoireacht an rialtais náisiúnta agus na n-údarás áitiúil (m.sh. tuairisciú tréimhsiúil ar staid Chomhshaol na hÉireann agus Tuarascálacha ar Tháscairí).

#### Rialú Astaíochtaí na nGás Ceaptha Teasa in Éirinn

- Fardail agus réamh-mheastacháin na hÉireann maidir le gáis cheaptha teasa a ullmhú.
- An Treoir maidir le Trádáil Astaíochtaí a chur chun feidhme i gcomhair breis agus 100 de na táirgeoirí dé-ocsaíde carbóin is mó in Éirinn.

#### **Taighde agus Forbairt Comhshaoil**

• Taighde comhshaoil a chistiú chun brúnna a shainaithint, bonn eolais a chur faoi bheartais, agus réitigh a sholáthar i réimsí na haeráide, an uisce agus na hinbhuanaitheachta.

#### Measúnacht Straitéiseach Timpeallachta

 Measúnacht a dhéanamh ar thionchar pleananna agus clár beartaithe ar an gcomhshaol in Éirinn (*m.sh. mórphleananna forbartha*).

#### **Cosaint Raideolaíoch**

- Monatóireacht a dhéanamh ar leibhéil radaíochta, measúnacht a dhéanamh ar nochtadh mhuintir na hÉireann don radaíocht ianúcháin.
- Cabhrú le pleananna náisiúnta a fhorbairt le haghaidh éigeandálaí ag eascairt as taismí núicléacha.
- Monatóireacht a dhéanamh ar fhorbairtí thar lear a bhaineann le saoráidí núicléacha agus leis an tsábháilteacht raideolaíochta.
- Sainseirbhísí cosanta ar an radaíocht a sholáthar, nó maoirsiú a dhéanamh ar sholáthar na seirbhísí sin.

#### Treoir, Faisnéis Inrochtana agus Oideachas

- Comhairle agus treoir a chur ar fáil d'earnáil na tionsclaíochta agus don phobal maidir le hábhair a bhaineann le caomhnú an chomhshaoil agus leis an gcosaint raideolaíoch.
- Faisnéis thráthúil ar an gcomhshaol ar a bhfuil fáil éasca a chur ar fáil chun rannpháirtíocht an phobail a spreagadh sa chinnteoireacht i ndáil leis an gcomhshaol (*m.sh. Timpeall an Tí, léarscáileanna radóin*).
- Comhairle a chur ar fáil don Rialtas maidir le hábhair a bhaineann leis an tsábháilteacht raideolaíoch agus le cúrsaí práinnfhreagartha.
- Plean Náisiúnta Bainistíochta Dramhaíola Guaisí a fhorbairt chun dramhaíl ghuaiseach a chosc agus a bhainistiú.

#### Múscailt Feasachta agus Athrú Iompraíochta

- Feasacht chomhshaoil níos fearr a ghiniúint agus dul i bhfeidhm ar athrú iompraíochta dearfach trí thacú le gnóthais, le pobail agus le teaghlaigh a bheith níos éifeachtúla ar acmhainní.
- Tástáil le haghaidh radóin a chur chun cinn i dtithe agus in ionaid oibre, agus gníomhartha leasúcháin a spreagadh nuair is gá.

#### Bainistíocht agus struchtúr na Gníomhaireachta um Chaomhnú Comhshaoil

Tá an ghníomhaíocht á bainistiú ag Bord lánaimseartha, ar a bhfuil Ard-Stiúrthóir agus cúigear Stiúrthóirí. Déantar an obair ar fud cúig cinn d'Oifigí:

- An Oifig um Inmharthanacht Comhshaoil
- An Oifig Forfheidhmithe i leith cúrsaí Comhshaoil
- An Oifig um Fianaise is Measúnú
- Oifig um Chosaint Radaíochta agus Monatóireachta Comhshaoil
- An Oifig Cumarsáide agus Seirbhísí Corparáideacha

Tá Coiste Comhairleach ag an nGníomhaireacht le cabhrú léi. Tá dáréag comhaltaí air agus tagann siad le chéile go rialta le plé a dhéanamh ar ábhair imní agus le comhairle a chur ar an mBord.

### EPA Research Report 413

The Diversity and Resilience of Kelp Ecosystems in Ireland

![](_page_50_Picture_2.jpeg)

Authors: Kathryn Schoenrock, Stacy Krueger-Hadfield, Kenan Chan, Rory O'Callaghan,Tony O'Callaghan, Aaron Golden and Anne Marie Power

#### **Identifying pressures**

Kelp forests can be found along rocky shorelines in temperate to Arctic coastlines on six continents. In Ireland, kelp dominates rocky substrata along moderately exposed coastline (approximately 3010 km out of the 7524 km of national shoreline). These ecosystems potentially provide a range of ecosystem services (ESs), including important primary and secondary production in local or adjacent habitats, carbon fixation and sequestration, and protection of coastal habitats via physical attenuation of wave action, food web and ecosystem structuring, and recreational activities, however there is still little known about them in this geographic range. We have little understanding of kelp forest food webs in Ireland, such as how kelp contributes carbon to food chains, which fisheries rely on kelp for subsistence or habitat, and what functional redundancy exists in kelp communities to buffer them from the effects of climate change or "fishing down food webs". Furthermore, we have no accurate measure of how much kelp exists in Ireland, or of its distribution across depths, along coasts and over seasons. Gathering these data would require a more intensive monitoring and field programme.

Despite major knowledge gaps in understanding kelp ecosystems, anthropogenic stressors are predicted to affect Irish populations. These include warming oceans, overgrazing due to "fished down food webs", eutrophication, sedimentation, and wild harvesting. The ability to recover from threats can be termed "resilience", defined as the ability of an ecosystem to recover and maintain normal ecological function after a disturbance event. We have examined the resilience of subtidal kelp Cuvie forests in Ireland using both evolutionary and ecological metrics.

### **Informing policy**

Given the multiple stressors facing kelp ecosystems globally and their importance in providing ESs, we do not recommend wild harvesting of kelp in Ireland. In particular, as no routine resource monitoring currently takes place in Ireland, it would be impossible to ensure that wild kelp harvesting is sustainable and that populations would recover and maintain ESs. There is no tried-and-tested method for repairing or restoring these systems after they collapse. Therefore, the approach to their management in Ireland should be cautious. Hand in hand with protecting kelp resources is the need to conduct monitoring.

This cautious approach should be taken to protect, conserve and manage this wild resource either under existing legislation, such as

the Habitats Directive, or through other legal instruments, including international conventions such as the Convention for the Protection of the Marine Environment of the North-East Atlantic (OSPAR). Filling these knowledge gaps would provide important information for calculating Ireland's "blue carbon" mitigation strategies for meeting climate change Paris Agreement and EU Green deal targets. These ecosystems should be specifically identified in both the Marine Strategy Framework Directive and the Water Framework Directive as monitoring targets for good environmental or ecosystem status.

### **Developing solutions**

The report makes recommendations concerning monitoring and preserving kelp ecosystems nationwide. A range of resilience metrics was assessed for subtidal kelp forests in Ireland to better understand how to monitor, manage and simply understand these systems and their potential responses to climate shifts in nearshore ecosystems. Our data collection constitutes one of the finest-scale population-level sampling efforts in marine algae along a national coastline, and the results should inform both the management and the conservation of marine habitats. The bank of microscopic kelp forms in nearshore ecosystems is best detected with genomic techniques, and we use these to describe the occurrence of microscopic kelp forms in sites around Ireland. This is a necessary first step towards understanding the evolutionary ecology of these important taxa. This provides knowledge about potential kelp recruitment dynamics and therefore the resilience of these ecosystems to climate change and other disturbance events.

Past records of kelp ecosystems are insufficient to monitor the distribution and abundance, and the status, trends and ecosystem health of kelp ecosystems. We need to shift towards whole ecosystem records that describe the abundance of not only kelp species, but also associated taxa that may act as indicators of the health of the ecosystem. Monitoring the status of and trends in the distribution and abundance of kelp should be prioritised. We suggest that this would be best achieved with a mix of citizen science and state-sponsored monitoring programmes (to ensure optimal regional coverage). For the latter, the use of remote-sensing tools using sonar that is ground-truthed with data collected from drop-down cameras and by scuba divers should be achievable and would allow periodic monitoring. Schemes to continue monitoring kelp ecosystems drawing on citizen scientists, especially with digital dive slates for scuba divers, are important avenues to pursue.

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