Evaluating the status and prospects of blue carbon in Ireland and the North-East Atlantic

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DECLARATION

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ABSTRACT

Since its conception in 2011, the concept of “blue carbon” has been valuable to focus the field of ecosystem services on carbon sequestration by marine macrophytic communities, which has been historically overlooked. In this thesis, three studies investigate the status and prospects of blue carbon in Ireland and the North-East Atlantic through: A) a direct evaluation of a naturally-occurring *Zostera noltei* seagrass meadow in Dublin Bay and its potential value for carbon sequestration (Chapter 1); B) A systematic review of the methods used to determine the fate of macroalgal carbon (Chapter 2); And C), a study quantifying the amount of carbon released to the local environment from an experimental *Saccharina latissima* kelp farm in Strangford Lough, Northern Ireland (Chapter 3). The combination of these three approaches gives both case-specific insight into the status of blue carbon in Ireland and a general overview on the potential for blue carbon sequestration in the North-East Atlantic region.

KEYWORDS

Blue carbon, carbon sequestration, seagrass, ecosystem services, marine macrophytes, *Zostera noltei*, *Saccharina latissima*, kelp, macroalgal carbon.

INTRODUCTION

Blue carbon is a term which describes the carbon stored in both living and non-living aquatic sediments and biomass (Mcleod *et al.*, 2011). Coastal macrophytic systems, such as seagrass meadows, saltmarshes, and mangroves, capture up to 70% of marine organic carbon (Smith, 1981; Duarte, Middelburg and Caraco, 2005), which makes them intense carbon sinks despite only covering a relatively small amount (~7%) of the total ocean (Borges, Delille and Frankignoulle, 2005). Although blue carbon systems have a lesser spatial extent than terrestrial systems globally, their net contribution to carbon sequestration is similar or greater in absolute terms (IUCN, 2009). The considerable carbon sequestration of vegetated coastal systems is the result of high photosynthesis and biomass production, converting inorganic carbon to excess organic carbon, which is stored in underlying sediments over geologically relevant timescales or exported beyond the ecosystem boundary (Duarte and Cebrián, 1996; Barrón *et al.*, 2003; Gattuso *et al.*, 2006; Fourqurean *et al.*, 2012). Conserving, restoring, and creating these natural carbon sinks is a strategy to mitigate global warming, which will compliment a general approach of emissions reduction (Macreadie *et al.*, 2017). Arguably, every potential climate mitigation strategy should be considered given the dramatically elevated levels of atmospheric CO_2 from 280 ppm to over 400 ppm since the industrial revolution and the consequent global warming and ocean acidification (Koch *et al.*, 2013; Hill *et al.*, 2015; Lovelock and Duarte, 2019).

Blue carbon strategies for climate change mitigation have gained popularity since 2009 when the publication of two reports demonstrated the magnitude of carbon sequestration potential by coastal macrophytes worldwide (IUCN, 2009; Nellemann *et al.*, 2009). Despite their ecological importance and relevance for climate regulation, these macrophytic communities are under threat of degradation from nutrient loading, coastal development, sediment contamination, chemical pollution, land use change, and invasive species, amongst other stressors (Waycott *et* *al.*, 2009; Pendleton *et al.*, 2012; Beaumont *et al.*, 2014; Davidson *et al.*, 2018). There is an additional direct threat of large-scale mechanical macroalgal harvesting across much of Europe (Mac Monagail and Morrison, 2020). Degradation of these systems may result in their conversion from carbon sinks to carbon sources (Cullen-Unsworth and Unsworth, 2013). It is imperative, therefore, to appropriately manage these important ecosystems, and to quantify the carbon stored in them for accurate global carbon models. In the Irish context specifically, the overall condition of the marine environment is not well understood due to a chronic lack of baseline data (Marine Protected Area Advisory Group, 2020).

Recently published research in the blue carbon field tends to reference one of several key synthesis papers which assert the magnitude and importance of carbon sequestration in blue carbon systems (eg. Cebrian, 1999; Hill *et al.*, 2015; Trevathan-Tackett *et al.*, 2015; Duarte, 2017; Macreadie *et al.*, 2017; Krause-Jensen *et al.*, 2018). These papers compile data on carbon flows through a large range of different marine communities and provide valuable baseline figures for carbon balances. These results are broad however, and contain many derived, extrapolated, or estimated figures from a small sample size, which limits their usefulness in identifying, measuring, and managing specific blue carbon systems for carbon dioxide mitigation (e.g. Krause-Jensen and Duarte, 2016). Direct measurement of carbon flows from and within site-specific coastal macrophytic communities is needed to design national and local management and conservation strategies which optimize carbon sequestration (Macreadie *et al.*, 2017). This is especially true as a lack of data on the global extent of vegetated coastal habitats, and variability of carbon flux estimates, results in international blue carbon estimates with a range greater than an order of magnitude (Duarte, 2017).

Regarding the carbon sequestration processes of net autotrophic vegetated coastal communities, the two organic carbon pathways which are most studied are local burial and export (Ver, Mackenzie and Lerman, 1999). Carbon may be buried in the sediment underlying the blue carbon system or exported from the system as particulate matter or dissolved organic carbon (up to 40% of net primary productivity, Duarte and Cebrián, 1996). Owing to macroalgal canopies often overlying rocky substrata, local burial in macroalgal systems is extremely limited, and the fate of exported macroalgal productivity is a longstanding unknown in blue carbon accounting (Krause-Jensen *et al.*, 2018; Ortega *et al.*, 2019). Excluding macroalgae from blue carbon assessments incurs error, as macroalgae are the most productive marine macrophytes on a global scale (Duarte, Middelburg and Caraco, 2005). With this in mind, this thesis on the topic "*Evaluating the status and prospects of blue carbon in Ireland and the North-East Atlantic*", aims to examine the status of blue carbon in Ireland in the context of global coastal carbon sequestration research. This will be achieved by direct primary investigation of two types of blue carbon systems in Ireland, one naturally occurring (Chapter 1) and one artificial (Chapter 3), and by conducting a systematic review to identify opportunities for primary research in response to the prominent question of the fate of macroalgal production (Chapter 2). This thesis consists of three chapters presented as manuscripts prepared for publication and an additional brief discussion.

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CHAPTER ONE

Article type: Full paper

Title: The importance of seagrass, *Zostera noltei,* in Dublin Bay**:** Potential for blue carbon sequestration

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ABSTRACT

A *Zostera noltei* (Hornemann, 1832) seagrass meadow in Dublin Bay, Ireland was surveyed during October 2019 and July 2020 to characterise the associated community and to assess potential value for carbon sequestration. This area is of particular interest because it is within a UNESCO biosphere reserve and has been exposed to heat pollution and eutrophication since the early 1900's. This study quantified several biological and environmental variables associated with the local seagrass community in Dublin Bay, including *Z. noltei* dimensions and population density, composition of the associated community, adjacent sediment nutrient content, and water quality. During the sampling periods the seagrass was shaded by the epiphytic macroalgae *Ectocarpus siliculosus* and *Percursaria percursa* with an average biomass greater than or similar to the aboveground *Z. noltei* biomass. In addition, there was a negative relationship between macroalgal cover density and aboveground seagrass biomass (R^2 = 0.86), between macroalgal cover density and belowground seagrass biomass (R^2 = 0.63), and between macroalgal cover density and seagrass shoot density (R^2 = 0.66). The aboveground *Z. noltei* biomass was dramatically lower in October than in July but the belowground biomass did not differ between the two sampling periods. The mean % sediment organic matter at the site was 1.5%, slightly lower than estimates recorded during this season from other seagrass sites which were situated closer to the equator.

Key words: seagrass, blue carbon, Dublin Bay, *Ectocarpus*, sequestration, eutrophication, community

INTRODUCTION

Industrialisation in the 20th century has resulted in a dramatic increase in atmospheric carbon dioxide (IPCC, 2019). This has endangered marine life, because disturbed global thermal regimes have desynchronized important phenological events (Thackeray *et al.*, 2010) and carbonic acidification is reducing the mortality and fecundity of marine calcifers (Andersson and Mackenzie, 2012). In addition to this, the existential threat of climate change to humankind is necessarily an inspiration for action to mitigate atmospheric carbon dioxide concentrations. For these reasons, there has been an increased interest in seagrass meadows, along with mangroves and tidal marshes, often described as 'blue carbon' ecosystems, that is those which perform carbon sequestration in coastal marine environments (Herr, Pidgeon and Laffoley, 2011; Fourqurean *et al.*, 2012; Beaumont *et al.*, 2014; Macreadie *et al.*, 2014).

Not only do seagrasses photosynthesise and direct carbon to the underlying sediment through leaf litter and root exudates (Moriarty, Iverson and Pollard, 1986; Jiang *et al.*, 2018), the structural complexity of their canopies also effectively traps and precipitates allochthonous carbon from marine, terrestrial, and fluvial sources (Kennedy *et al.*, 2010). Sediments beneath seagrass communities also rapidly accrete (Gacia, Duarte and Middelburg, 2002; Bos *et al.*, 2007), circumventing any limitations to carbon sequestration imposed by carbon saturation in a steady state soil (Stewart *et al.*, 2007). It is estimated that seagrasses sequester CO_2 in their sediments up to two orders of magnitude faster than temperate forest ecosystems as a result of these traits (Mcleod *et al.*, 2011). Aside from carbon sequestration, these seagrass meadows are important coastal habitats, which provide ecosystem services, such as shoreline stabilization (Bos *et al.*, 2007), nutrient cycling, and provision of habitat for fish, bird, and invertebrate species (Heck, Hays and Orth, 2003; Nordlund *et al.*, 2018).

Unfortunately seagrasses have been declining globally throughout the 20th century (Waycott *et al.*, 2009), with 30% of European seagrass being lost from 1869 to 2016 as a result of disease, poor water quality, and pressures from coastal development. The potential of any seagrass meadow as a blue carbon system will be threatened if it is degraded. Carbon which was previously immobilized within the sediment may be remineralized and released to the atmosphere (Pendleton *et al.*, 2012; Cullen-Unsworth and Unsworth, 2013; Salinas *et al.*, 2020). The density of seagrass at some European sites has been stable or increasing since the 2000's, however, with much of the trend reversal attributable to local increases in *Zostera* spp. (Santos *et al.*, 2019). Given the recent recovery of *Zostera* spp. habitats, there is an opportunity to amplify this improvement by empirically assessing populations and the factors which affect their health. This would be more accurate than assuming seagrass systems are functionally similar globally, which is understandably the default approach for large-scale assessments (Postlethwaite *et al.*, 2018).

Particularly regarding carbon sequestration, site-specific rates of organic carbon storage are more appropriate for national management strategies in comparison to values from the general blue carbon literature (Emmer *et al.*, 2015). Depending on the seagrass species and their associated communities, depth, turbidity, climate, and level of anthropogenic stressors, the organic carbon content in the sediment beneath a seagrass meadow may vary considerably (Kindeberg *et al.*, 2019; Mazarrasa *et al.*, 2021). There has been a great amount of research on rates of organic carbon burial beneath seagrass systems in the last two decades. The residence time or longevity of organic carbon directed to seagrass sediments is less frequently evaluated however (Belshe *et al.*, 2017). This research gap may lead to overestimation of carbon sequestration potential, as losses from bacterial remineralisation are not accounted for.

Considering the aforementioned rationale supporting local environmental assessments, and the current legislative and policy development for marine protection in Ireland, this study aimed to provide a snapshot of the ecological status of a *Zostera noltei* community in Dublin Bay. The Dublin Bay UNESCO Biosphere is the world's only UNESCO Biosphere located entirely within a capital city and provides valuable habitat for several protected species including *Z. noltei* (Hornemann, 1832) [also commonly known as *Z. noltii*]. This is a small perennial intertidal seagrass species, which is common in shallow bays and estuaries across Western Europe (Vermaat, Hootsmans and Nienhuis, 1987). There is an estimated 60 km^2 of seagrass in Ireland, with approximately 17 km^2 being *Z. noltei*, and the vast majority of the rest being the larger subtidal relative *Z. marina* (45 km^2; Beca-Carretero, Varela and Stengel, 2020). Nationally, this represents potential carbon stocks of 0.6 Mt carbon (Cott, Beca-Carretero and Stengel, 2021). Although it is a perennial, aboveground *Z. noltei* biomass dies back at the end of autumn, and the plant persists by redirecting carbon stores to belowground rhizomes over winter.

This study aimed to characterise a *Z. noltei*-associated community and threats to its health in central Dublin Bay. We described the fauna and epiphytes associated with *Z. noltei* to identify baseline biodiversity at this site for future monitoring efforts. We tested for a relationship between epiphytic macroalgal abundance and *Z. noltei* density/ biomass to assess whether macroalgae limits *Z. noltei* growth and thereby the potential role of this species for carbon sequestration in the Bay. We quantified carbon content in the upper sediment beneath this seagrass site and compared the results to other seagrass sites to provide a global frame of reference. If the carbon content is lower in the sediment beneath this site compared to others it arguably has less potential as a carbon sequestration environment. Despite the protected status of Dublin Bay, it is the busiest port in Ireland and there have been considerable disturbances to the natural systems of the area associated with the capital city's increased industrialisation and urbanisation throughout the 20th century (Brooks *et al.*, 2016; Harris *et al.*, 2019; Grey *et al.*, 2021).

From as early as 1908, but particularly in the last two decades, this part of Dublin Bay has been known to suffer from heat pollution and over-loading with organic particulate nitrogen from wastewater and riverine sources, causing occasional macroalgal blooms and the deposition of extensive green and brown macroalgal mats (Jeffrey *et al.*, 1995; Wilson, Brennan and Murray, 2002; Higgins and Wilson, 2005; Jennings and Jeffrey, 2005). More recently, the Ringsend Wastewater Treatment Plant, upgraded in 2005, has been informally identified as a possible cause of macroalgal blooms (Jones, 2019). When macroalgal mats deposit over seagrass canopies they may cause shading of the blades, prevent photosynthesis, pollination, and seed dispersal and also may generate hypoxic, anoxic, and subsequently sulphuric conditions in the underlying sediment (den Hartog, 1994; Sundbäck *et al.*, 1996). Prolonged eutrophication may lead to the redundancy and under-development of seagrass root systems, reducing the allocation of resources to biomass belowground (McLeod *et al.*, 2011). Nutrient loading as a result of anthropogenic run-off has been found to trigger shifts from seagrass- to macroalgae-dominated systems and subsequent seagrass deterioration (Liu *et al.*, 2017). Considering this, we were motivated to determine whether opportunistic macroalgae were present and whether their presence/ abundance was correlated with the abundance and density of the *Z. noltei* population.

MATERIALS AND METHODS

This study was carried out at the intertidal *Z. noltei* meadow on the southern side of Dublin Bay, Ireland (53° 19' 03.8" N, 6° 12' 14.4" W), at a site where the tidal amplitude is shallow, not exceeding 2 m (Fig. 1). The proximity of this site to developed residential and industrial areas meant it was easily accessed and is representative of an Irish *Zostera* site, which is exposed to anthropogenic stressors. The seagrass meadow has decreased in absolute extent from at least 0.017 km^2 to 0.015 km^2 since the 1990s (Madden, Jennings and Jeffrey, 1993) and further monitoring of cover density over time will be required to determine whether the site is declining further. The site is emergent for several hours at low tide each day and, owing to its close proximity (< 20 m) to residential areas, is subjected to traffic from bird watchers and dog walkers (Wilkes *et al.*, 2017). There is a small freshwater stream which enters the bay approximately 200 m south of the Z. *noltei* meadow and flows northward across the seagrass. The Booterstown Nature Reserve, which is managed by An Taisce the National Trust for Ireland, borders the site to the south (An Chomhairle Oidhreachta, 2013).

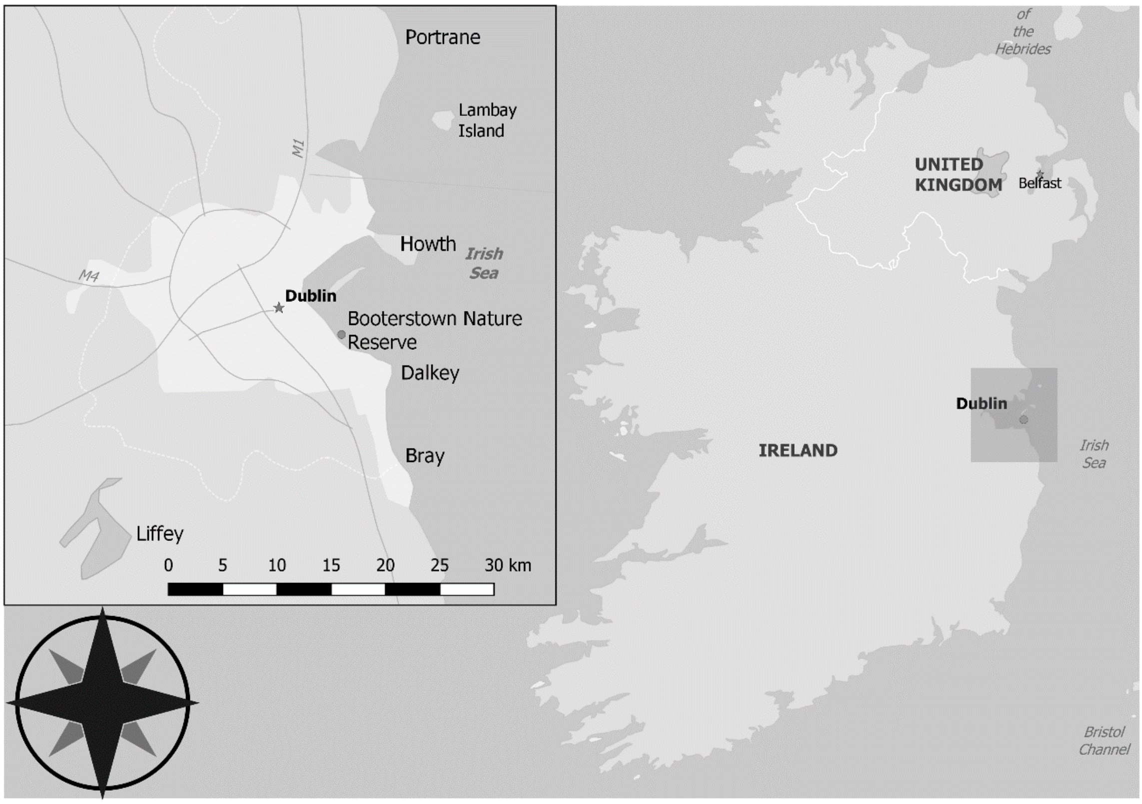

Figure 1— Study site location (○) at the Booterstown Nature Reserve near Dublin, Ireland and surrounding towns.

This survey was adapted from the MarineGEO-designed sampling protocols (MarineGEO, 2019). All the following biomass measurements were conducted by placing samples in a drying oven at 60°C until they registered a constant mass (usually 1-2 days). Except where stated, all following samples were collected in October 2019 and July 2020. Water temperature, salinity, dissolved oxygen (DO), and pH were measured in triplicate *in situ* at each sampling date with a thermometer and HQ40D portable Multi Meter (Hach, Düsseldorf).

To estimate absolute seagrass shoot density, six quadrats (25 cm x 25 cm) were placed randomly along three transects (3 x 50 m; n = 18), one in each of three zones (i.e. inner, middle and outer meadow to represent the whole site), and the number of blades within each quadrat were counted. To estimate cover density of this seagrass population, twelve quadrats (50 cm x 50 cm) were placed randomly along all three transects (3 x 50 m), yielding a total of 36 quadrats (n = 36). The percentage cover density of each sessile species and any bare sediment within the quadrat was estimated and recorded following the Braun-Blanquet cover density scale (Table 1; Fourqurean *et al.*, 2001).

Table 1 - Discrete percentage cover classifications according to the Braun-Blanquet scale (Fourqurean *et al.*, 2001)**.**

Bin	**Interpretation**	**Cover**
0	Absent	0%
0.1	A single shoot	< 5%
0.5	A few shoots	> 5%
1	Some cover	5-25%
2	Moderate cover	25-50%
3	Majority cover	50-75%
4	Total or near total cover	75-100%

To estimate the dimensions of the *Z. noltei* blades, six shoot samples were randomly taken along each of three transects (3 x 50 m; n = 18). The blade length (mm), blade width (mm), and sheath length (mm) were recorded. The blade mass (mg) and fouling biomass (mg) of epiphytic algae and sessile invertebrates were estimated by removing fouling biomass from each blade and drying until a constant mass was obtained. In order to estimate the biomass of macroalgae per area, six quadrats (50 cm x 50 cm) were randomly placed along each transect (3 x 50 m; n = 18). For each sample, all loose macroalgae within the quadrat were collected and the dry biomass (mg) was quantified.

To test whether the biomass of aboveground and belowground *Z. noltei* biomass was correlated with the biomass of overlying filamentous macroalgae, three core samples (diameter = 15 cm, depth = 20 cm) were taken randomly along each transect (n = 9) using a PVC corer. Seagrass and macroalgal biomass were sorted according to species. The seagrass biomass was sorted into above- and belowground biomass. The dry biomass of each algal species and above- and belowground biomass (mg) was quantified.

To estimate the organic matter content of the sediment beneath the *Z. noltei* meadow, three syringe samples (diameter = 2 cm, depth = 5 cm) were randomly taken along each transect (n = 9). Visible fauna, shells, and organic debris were removed from the sample and dry biomass (mg) was quantified. The samples were then combusted at 520 °C for six hours and weighed again. The loss-on-ignition (LOI) was calculated as the difference in mass before and after combustion divided by initial mass of sample and multiplied by 100. LOI was converted to % sediment organic matter (SOM) according to the following equation:

$$Y = 0.851 * X - 0.560$$

where Y represents % SOM and X represents % LOI (Davies, 1974). This organic matter content was compared to sediment samples taken from seagrass sites at 13 taken from the MarineGEO project, all of which used this standardised protocol. Linear regression analysis was used to identify relationships between macroalgal cover density, aboveground and belowground *Z. noltei* biomass, shoot density, and sediment organic matter. Independent two-sample t-tests were used to test the strength of these relationships.

To quantify the total nitrogen and carbon in the sediment in the seagrass meadow, three syringe samples (diameter = 2 cm, depth = 5 cm) were randomly taken along each of the three transects ($n = 9$). Each sample was dried to a constant weight, sieved, and ground to a fine powder. Total nitrogen and total carbon in the sediment samples were determined using an elemental analyser (Elementar VARIO EL-III Cube). Two 30 mg subsamples of each sample were weighed into tin foils using a micro-balance. The tin foils were carefully sealed and combusted in the elemental analyser in pure oxygen at 950°C and the gases produced in combustion were analysed by thermal conductivity to identify % by weight of nitrogen and carbon in the sample. Elemental analysis was repeated in October, November, and December of 2019, and in January 2020 to investigate whether there was monthly variability in the nitrogen and carbon concentrations within the upper sediment.

To identify mobile macrofauna associated with the *Z. noltei* community, samples were taken twice using a 50 m seine net (width = 3.5 m, height = 1.5 m, mesh size = 30 mm), one between the inner and middle transects and one between the middle and outer transects. The tide was approximately 1 m high at the time of sampling. The identity, number, and total length of all visible individuals (> 5 cm) was recorded, with the carapace length recorded in the case of crabs captured. To identify epifauna and epiphytes associated with the Z. *noltei* population, six epifaunal samples were randomly taken using mesh bags (300-micron mesh) along each transect ($n = 18$). The mesh bag was lowered over the canopy and once above the surface of the sediment the drawstring was tightly closed, releasing all exposed shoots, epifauna, and epiphytic macroalgae into the bag. Epibionts captured were identified and their individual biomass was quantified. Epifauna were identified and passed through nested sieves in order to determine their size. Faunal surveys were only conducted in July 2020 when abundance is highest in Dublin Bay (King and Green, 2004; Koutsogiannopoulou and Wilson, 2007).

RESULTS AND DISCUSSION

At the sampling date of October 2019, the water temperature was 13 °C and the water salinity was 21.1 ppt, which is more estuarine than marine and typical of most *Z. noltei* sites (Plus *et al.*, 2001). At the sampling date of July 2020, the water temperature was 18 °C and the water salinity was 28.0 ppt. The average dissolved oxygen (DO) level above the *Z. noltei* meadow was 2.2 ± 0.1 mg/L compared to 0.5 ± 0 mg/L above adjacent macroalgal mats and 1.7 ± 0 mg/L above adjacent bare sediment. The average pH level at the site was 7.7 ± 0.1.

The mean seagrass shoot density in October was 146 ± 96 per 0.0625 m^{-2} quadrat (2342 m^{-2}), with a minimum of 10 shoots in a quadrat along the outer transect and a maximum of 312 shoots in a quadrat along the inner transect. The mean shoot density in July was higher and more variable, 291 ± 287 per 0.0625 m^{-2} quadrat (4650 m^{-2}), with a minimum of 15 in a middle quadrat and a maximum of 1223 in an inner quadrat. Two species of macroalgae, *Ectocarpus siliculosus* and *Percursaria percursa,* were identified as growing attached to or deposited over the *Z. noltei* population in both October 2019 and July 2020, with the cover density of macroalgae being greater in October (Fig. 2). Both species of filamentous algae appeared to be in a state of decay based on their coloration and structural integrity.

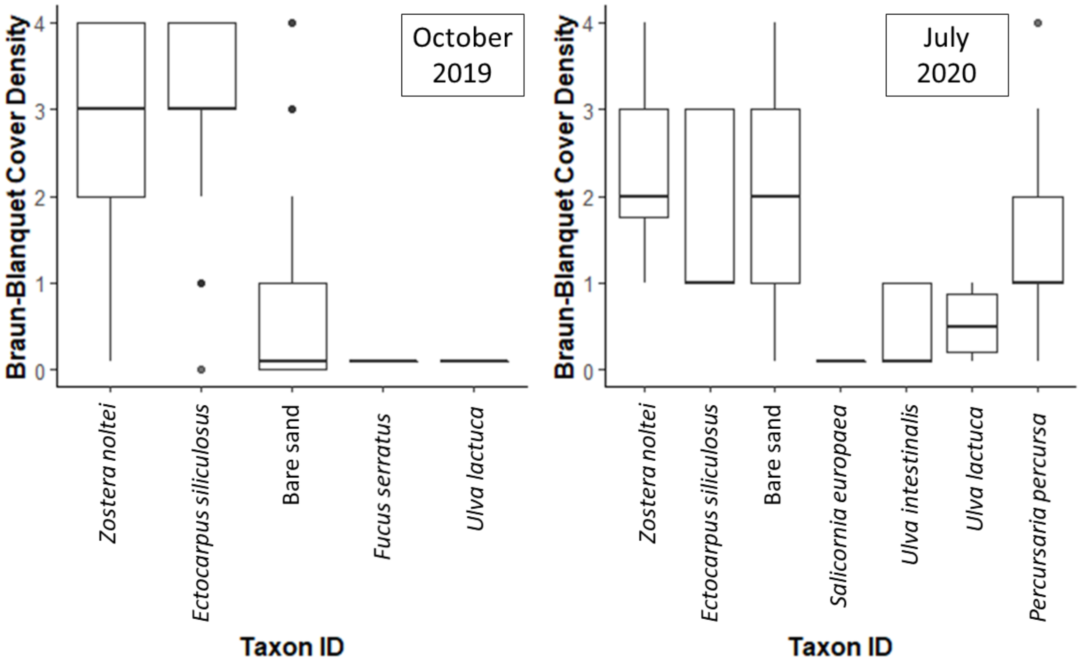

Figure 2 — Median cover density (± IQ range) of macrophyte or bare sand per quadrat (50 cm x 50 cm) in October 2019 and July 2020 according to the Braun-Blanquet scale (*n* = 12).

The only sessile macroinvertebrates present were lugworms (*Arenicola marina*) which are classified as infauna and not cover. The higher DO levels above the seagrass in comparison to those above the neighbouring mat of deposited macroalgae may indicate that the seagrass is either releasing DO while photosynthesising or that DO is being depleted as algae decompose, although evidence for this would require controlled testing (García-Robledo *et al.*, 2008; García-Robledo and Corzo, 2011). Low oxygen availability in water has been shown to negatively affect the physiology, morphology, and general photosynthetic efficiency of the closely related *Z. marina* (Holmer and Bondgaard, 2001).

The mean *Z. noltei* shoot biomass was 0.01 ± 0 g DW in both October and July. The average length was 114 ± 9 mm in October and 98 ± 12 mm in July. In October, the average epibiont biomass per blade was comparable to the shoot itself (0.01 ± 0 g DW) but in July it was significantly lower at 0.004 ± 0 g DW. The estimates of shoot density and shoot size at this site are low within the range of other recently studied *Z. noltei* sites in the Mediterranean (Plus *et al.*, 2001; Pergent-Martini *et al.*, 2005). Shoot biomass and dimension varied seasonally in a manner similar to the closely related *Z. marina* on the west coast of Ireland suggesting that intra-annual variation of shoot size is regular in this case (Beca-Carretero *et al.*, 2019).

Table 2 – Results summary table. All biomass results are in dry weight (g). All values are mean ± S.E.

Description	October 2019	July 2020
Z. noltei shoot density	146 ± 96 0.0625 m^{-2}	291 ± 287 0.0625 m^{-2}
Z. noltei shoot biomass	0.01 ± 0 g	0.01 ± 0 g
Epibiont biomass per blade	0.01 ± 0 g	0.004 ± 0 g
Z. noltei shoot length	114 ± 9 mm	98 ± 12 mm
Biomass of macroalgae per area (quadrat)	84.6 ± 68.8 g m^{-2}	30.4 ± 0 g m^{-2}
Biomass of macroalgae per area (core)	0.2 ± 0.3 g ≈ 12 g m^{-2}	1.1 ± 1.6 g ≈ 61 g m^{-2}
Belowground *Z. noltei* biomass	0.9 ± 0.4 g ≈ 51 g m^{-2}	1.2 ± 1.8 g ≈ 68 g m^{-2}
Aboveground *Z. noltei* biomass	0.2 ± 0.1 g ≈ 12 g m^{-2}	0.7 ± 0.5 g ≈ 38 g m^{-2}
% Sediment organic matter	1.4 ± 0.3 %	1.5 ± 0.1 %

The average biomass of macroalgae on the seagrass meadow was more than 3 times higher in October than July, 84.6 ± 68.8 g m^{-2} and 30.4 ± 0 g m^{-2} respectively. The sampled belowground biomass of the *Z. noltei* population always remained greater than the aboveground component and the biomass measurements were generally highly variable as seen in the high standard deviations following. In July 2020, the average belowground biomass per core was 1.2 ± 1.8 g (≈ 68 g DW m^{-2}), which was almost twice the average aboveground biomass of 0.7 ± 0.5 g (≈ 38 g DW m^{-2}). The biomass of macroalgae present was on average 1.1 ± 1.6 g (≈ 61 g DW m^{-2}). In October 2019, the average aboveground *Z. noltei* biomass was 0.2 ± 0.1 g (≈ 12 g DW m^{-2}), a third of the July biomass. The average macroalgal biomass was similarly reduced to 0.2 ±

0.3 g (≈ 12 ± 19 g DW m^{-2}). The belowground *Z. noltei* biomass was much less affected by the non-growth period, with an average biomass of 0.9 ± 0.4 g (≈ 51 g DW m^{-2}), four times higher than the aboveground biomass. The aboveground *Z. noltei* biomass is particularly lower in October as the shoots die back, which also coincides with the arrival of the visiting light-bellied Brent geese (*Branta bernicla hrota*) that graze on the *Z. noltei* seagrass. These brent geese feed on this meadow each October as a staple food source until it is depleted (Ganter, 2000). The higher allocation of biomass to belowground, particularly during this grazing period, is advantageous for carbon storage (Mazarrasa *et al.*, 2018).

We identified a strong negative relationship between macroalgal cover density and aboveground seagrass biomass (R^2 = 0.86; Fig. 3A); and also a negative relationship between macroalgal cover density and belowground seagrass biomass (R^2 = 0.63; Fig.3B); a relationship between macroalgal cover density and shoot density (R^2 = 0.66; Fig.3C); no relationship between macroalgae DW per m^2 and the cover density of seagrass (R^2 = 0.31; Fig.3D); no relationship between sediment organic matter and belowground seagrass biomass (R^2 = 0.23; Fig.3E); and no relationship between macroalgae DW per m^2 and shoot density (R^2 = 0.34; Fig.3F).

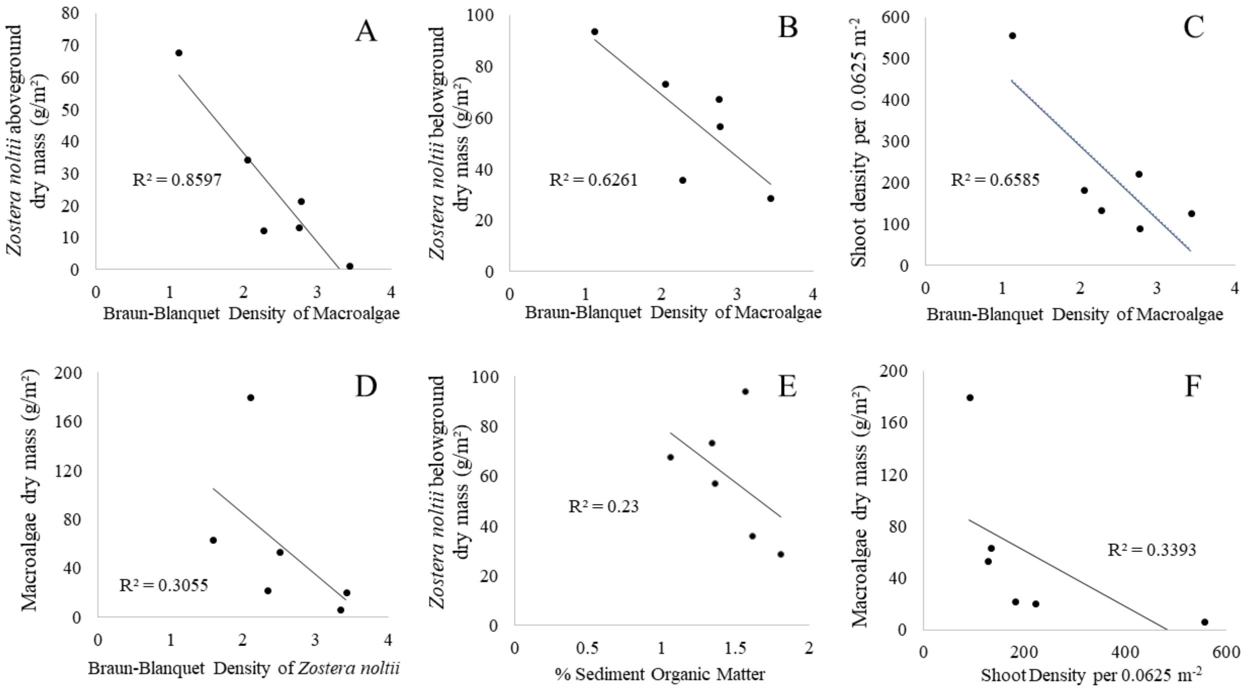

Figure 3 – Relationships between seagrass community characteristics. Black lines represent the linear regression line (n = 6). **A)** A strong negative relationship between macroalgal cover density and aboveground seagrass biomass (p-value = 0.065). **B)** A negative relationship between macroalgal cover density and belowground seagrass biomass (p-value = 0.002). **C)** A negative relationship between macroalgal cover density and shoot density (p-value = 0.028). **D)** No relationship between macroalgae DW per m² and the cover density of seagrass (p-value = 0.089). **E)** No relationship between sediment organic matter and belowground seagrass biomass (p-value = 0.002). **F)** No relationship between macroalgae DW per m² and shoot density (p-value = 0.073).

The negative relationships discovered between macroalgae (cover density/ DW per m^2) and seagrass (cover density/ shoot density) are of concern because as the *Z. noltei* canopy is reduced, the sediment organic carbon beneath is vulnerable to increased shear velocity from tides and currents (Lovelock *et al.*, 2017). This causes erosion of sediments and oxic conditions such that the carbon in the upper profile risks being remineralized (Marbà *et al.*, 2015). This process may be exacerbated by bioturbation by the lugworm population present. Macroalgae may contribute to the remineralization of recalcitrant seagrass detritus via cometabolism (Liu *et al.*, 2020). In previous monitoring projects at this site, blooms of ectocarpoid brown algae were observed, but as significant amounts were not found in subsequent visits, the opportunistic algae was not considered a threat (Wilkes *et al.*, 2017). Interactions between macroalgae and seagrass are not necessarily negative, for example Ouisse, Migné and Davoult (2010) found that macroalgae in seagrass ecosystems compensate community productivity when *Zostera* sp. die back in winter. For this reason, the direct interactions between the overlying macroalgae and seagrass should be investigated in greater detail.

There was no significant difference in SOM in the top 5cm of the meadow between October 2019 and July 2020. In October 2019 % SOM was 1.4 ± 0.3 % and in July 2020 it was 1.5 ± 0.1 %. Although these % SOM values were within the range of MarineGEO international values, they were lower than sites nearer to the equator such as south Korea, Mexico and Belize (Fig. 4; Fourqurean *et al.*, 2012). Additionally, a recent study of unvegetated mudflats and saltmarsh habitats in North Dublin Bay found significantly higher organic matter content in the sediments beneath these communities, 4.3 % and 22.5 % respectively. Most highly cited papers on the carbon sequestration potential of seagrass communities focus on the Mediterranean seagrass, *Posidonia oceanica.* There is large variability in SOM beneath seagrass meadows, depending on environmental conditions and species, and thus the data from *Posidonia* populations should not be generalised other regions with different species. In a study of 17 Australian seagrass communities of varying species composition, sediment organic carbon stocks were found to vary up to 18-fold (Lavery *et al.*, 2013). Different species of seagrasses do not necessarily have similar or even comparable potential to sequester carbon and this must be accounted for in blue carbon estimates and management strategies, as opposed to extrapolating global estimates on data collected from tropical and sub-tropical climates alone (Miyajima *et al.*, 2015; Mazarrasa *et al.*, 2018).

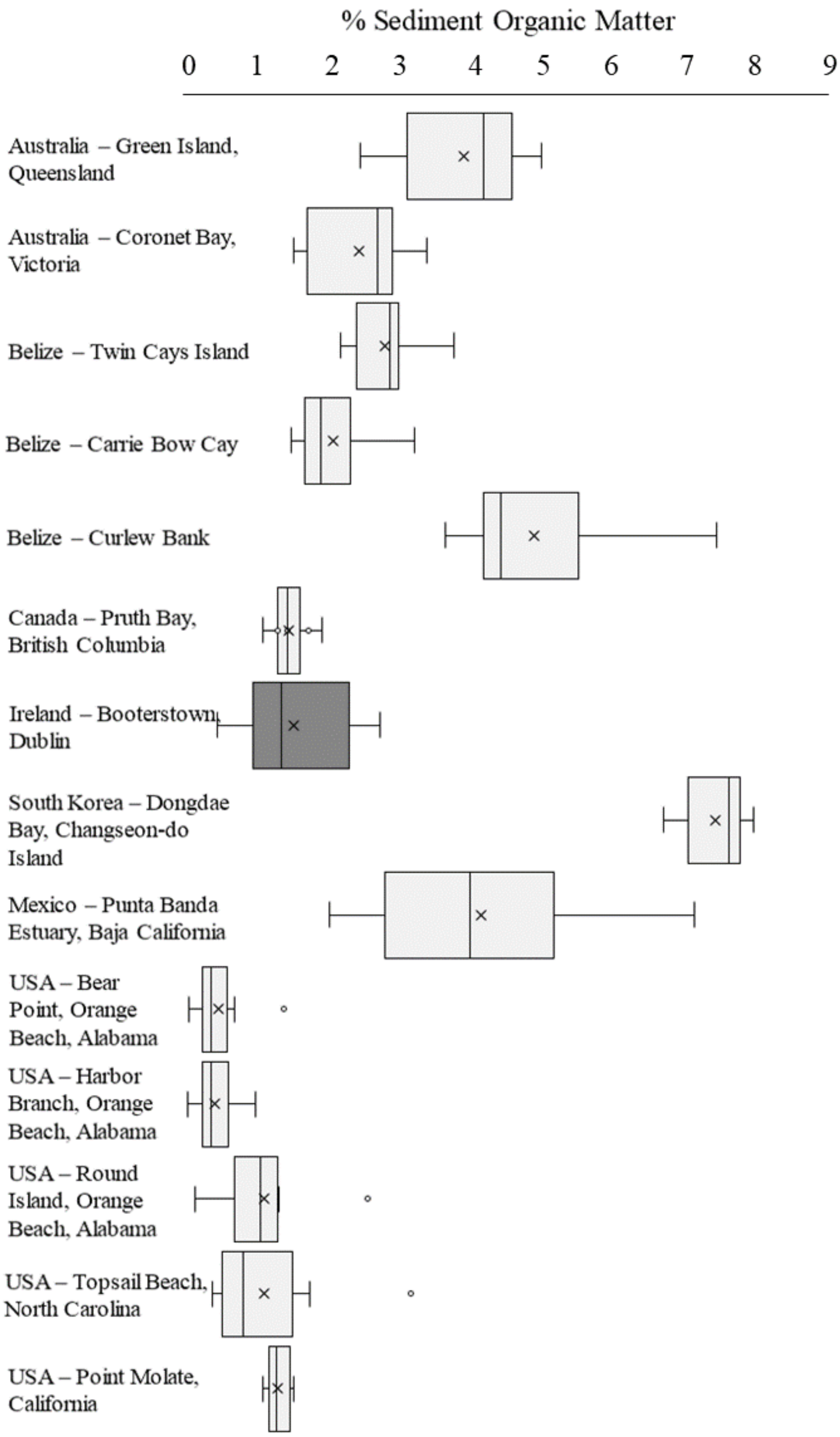

Figure 4 - The % sediment organic matter in the top 5 cm of material beneath the seagrass meadow in Ireland compared to various other regions (*n* = 9). Some of these had different dominant seagrass species (data from MarineGEO, 2019).

Mean nitrogen content of sediment sampled in four months (October, November, December 2019, January 2020) was 0.06% (Fig. 5) and the mean carbon content was 1.3% (Fig. 6). This supports the values obtained by the loss on ignition method. There were no significant observable trends with regards to the sediment elemental analysis (Fig. 5, Fig. 6). If there had been high % C and % N in October at the end of the growth period, which declined over the subsequent months, this would be indicative of organic matter in the soil which was degraded over time and had a low residence time. If the % C had increased over time we might hypothesize that carbon was being leached from the roots during the non-growth period (Moriarty, Iverson and Pollard, 1986). Future research at this site should make use of deeper sediment cores, at least 50 cm deep, in order to comprehensively assess the stock of carbon beneath the site.

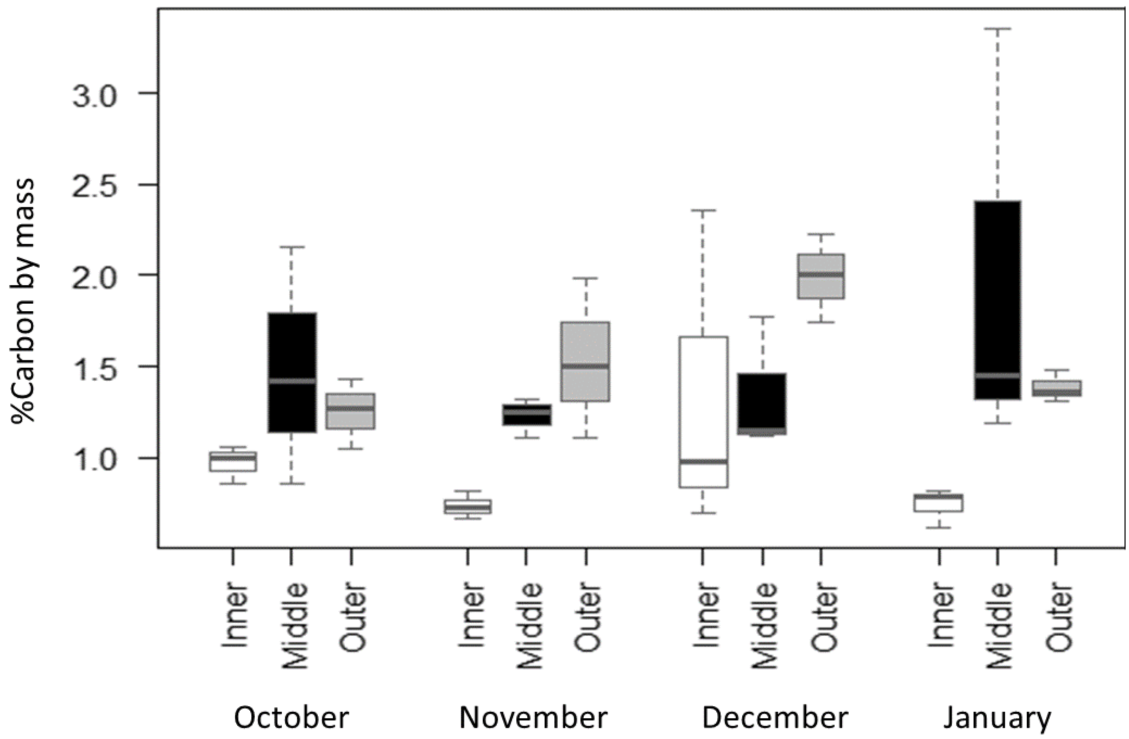

Figure 5 - Median (± IQ range) total carbon by percentage dry mass for each month by transect.

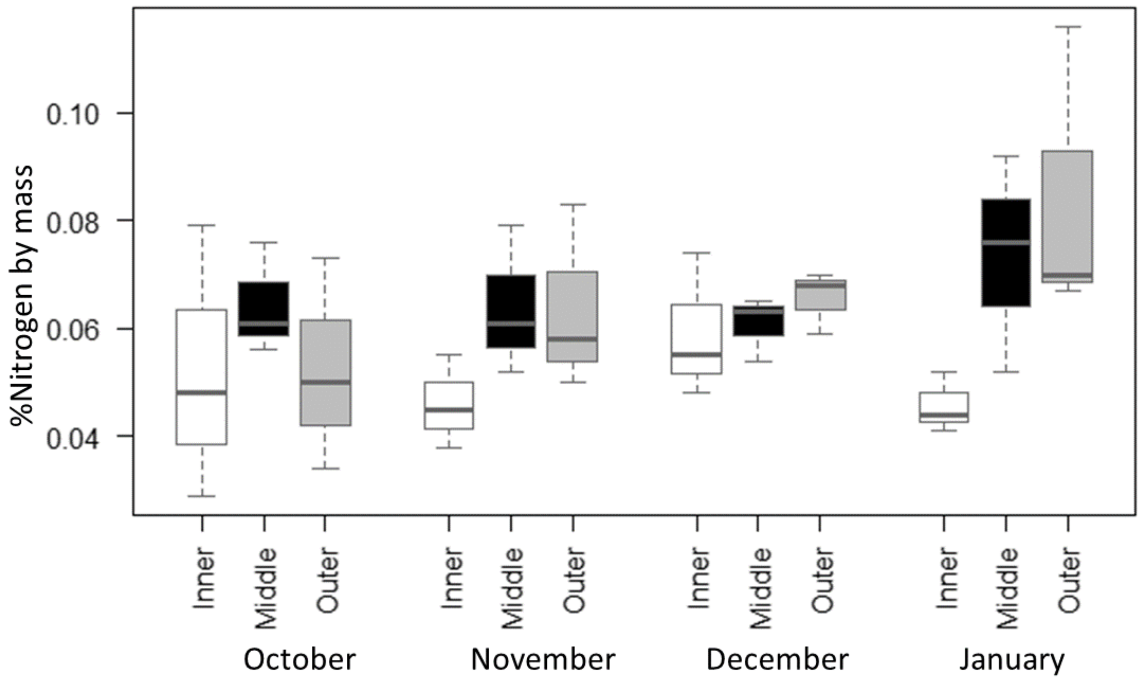

Figure 6- Median (± IQ range) total nitrogen by percentage dry mass for each month by transect.

Fifty-six individual mobile macrofauna were recorded during the two fish seines conducted. 24 were juvenile brill *Scophthalmus rhombus* (58 ± 5.6 mm), 30 were common prawn *Palaemon serratus* (32 ± 1.2 mm), one was a sand goby *Gobius minutus* (70 mm), and one was a common shore crab *Carcinus maenas* (52 mm). The most common epifauna identified was the mudsnail *Hydrobia ulvae* (3662 in total, 203 ± 112 per sample) the majority of which were ~1 mm. Also identified were two *Carcinus maenas* (4 mm, 5.6 mm), one Galeommatacea sp. (4 mm), one blue mussel *Mytilus edulis* (2.8 mm), two common cockle *Cerastoderma edule* (2 mm, 8mm), three scallop *Chlamys varia* (2 mm), and one banded wedge shell *Donax vittatus* (2 mm). The epiphytes identified were *Percursaria percursa* (18 samples, 0.2g dry biomass per sample), *Ectocarpus siliculosus* (11 samples, 0.2g dry biomass per sample), *Ulva intestinalis* (8 samples, 0.2g dry biomass per sample), *Ulva lactuca* (3 samples, 0.01g dry biomass per sample), and *Bryopsis hypnoides* (2 samples, 0.2g dry biomass per sample). The epifauna and fish identified in this survey are components of a typical estuarine food web, with primary consumers including *Hydrobia ulvae* and Brent geese. Other juvenile animals identified use seagrass canopy for nurseries and shelter as opposed to a food source (Heck, Hays and Orth, 2003). Unlike other seagrass communities in which large grazers may be a factor controlling growth of seagrass leaves, grazing at this site is limited throughout the summer without frequent or intense defoliation. Lugworms present may be promising for carbon burial due to their bioturbation activity (Thomson *et al.*, 2020).

CONCLUSION

The ecological status of this *Z. noltei* meadow is comparable with other global seagrass ecosystems, but its value as a blue carbon sink may be threatened by overlying opportunistic macroalgae. The organic matter content of the sediment beneath this site is lower than tropical seagrass communities, indicating that not all seagrass meadows are similar in their potential for carbon sequestration, and they must be evaluated directly.

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CHAPTER TWO

Article type: Review

Title: Whole system analysis is required to determine the fate of macroalgal carbon: a systematic review

Running page head: Determining the fate of macroalgal carbon

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ABSTRACT

The role of marine primary producers in capturing atmospheric CO_2 has received increased attention in the global mission to mitigate climate change. Yet, our understanding of carbon sequestration performed by macroalgae is limited to a relatively small number of studies that have estimated the ultimate fate of macroalgal-derived carbon. This systematic review provides a timely synthesis of the methods used to determine the fate of macroalgal carbon in this rapidly expanding research area and provides suggestions for more effective future research. We found that the most common methods to estimate the fate of macroalgal carbon can be categorised into groups based on those that quantify: (i) export of macroalgal carbon to other environments – known as horizontal transport; (ii) sequestration of macroalgal carbon into deep sea sediments – known as vertical transport; (iii) burial of macroalgal carbon directly beneath a benthic community; (iv) the loss of macroalgal carbon as particulate carbon or dissolved carbon to the water column; (v) the loss of macroalgal carbon to primary consumers; and finally (vi) those studies that combined multiple methods in one location. Based on this review, several recommendations for future research were formulated, most of which require the combination of multiple methods in a whole system analysis approach.

Key words: Macroalgae, biomass, pool, sequestration, blue, kelp, seaweed, carbon

INTRODUCTION

Blue carbon is the carbon stored in aquatic sediments and biomass, whether living or dead (Mcleod *et al.*, 2011). Despite only covering a small area of the total ocean (~7%) (Borges, Delille and Frankignoulle, 2005), coastal macrophytic systems such as seagrass meadows, macroalgae forests, saltmarshes, and mangroves capture as much as 70% of marine organic carbon (Smith, 1981; Duarte, Middelburg and Caraco, 2005). This makes these marine systems intense blue carbon sinks. The rise of blue carbon research and publications is associated with the publication of two reports in 2009 which demonstrated the magnitude of carbon sequestration potential by coastal macrophytic systems worldwide (IUCN, 2009; Nellemann *et al.*, 2009).

Macroalgae in particular are the most extensive and productive of all the blue carbon vegetated coastal habitats, covering 2 - 6.8 million km^2 globally and exporting > 44% of their primary production as biomass, dissolved organic carbon (DOC), and particulate organic carbon (POC) (Duarte *et al.*, 2013; Krause-Jensen and Duarte, 2016; Jayathilake and Costello, 2020). Furthermore, it has been estimated that up to 25% of this macroalgal carbon exported from the area of productivity is sequestered in coastal or deep-sea sediments (Ortega et al. 2019). Owing to their extent, export, and high productivity, macroalgae have long been believed to be important contributors to the global carbon sink (Smith, 1981), and oil deposits derived from macroalgae dated back ~500 million years provide evidence that macroalgae do mediate carbon sequestration on geologically relevant timescales (Sun *et al.*, 2013). Generally, once macroalgal carbon has entered the deep sea it is considered as sequestered, regardless of the fate of the carbon, because whether it is buried, grazed, mineralized or suspended in a nepheloid layer, this carbon will not return to the atmosphere for centuries (Krause-Jensen and Duarte, 2016).

Despite the growing focus on blue carbon and the carbon sink, which coastal marine macrophytes represent, the process of macroalgal carbon burial is not well understood (Pedersen *et al.*, 2020). As most macroalgae grow on rocky substrata, do not have root systems, and do not accumulate carbon-rich sediments directly beneath the community, the contribution of macroalgae to carbon sequestration has probably been underestimated (Hill *et al.*, 2015; Krause-Jensen *et al.*, 2018). Previous reviews have highlighted the importance of carbon sequestration by macroalgae (S1). Yet the ultimate fate of macroalgal carbon remains unknown in most coastal ecosystems which prevents their inclusion in national carbon budgets and accounting (e.g. Cott et al. 2021).

This deficiency of fundamental information must be amended in order to constrain accurate global carbon models and to justify the conservation of macroalgal forests, particularly as macroalgae are under threat from warming, eutrophication, coastal development, sediment contamination, chemical pollution, and invasive species (Wernberg *et al.*, 2011; Smale *et al.*, 2013; Beaumont *et al.*, 2014; Duarte, 2014; Davidson *et al.*, 2018). There is an additional novel threat of large-scale mechanical macroalgal harvesting across Europe (Mac Monagail and Morrison, 2020). If macroalgal systems are significantly impaired by these stressors and are subsequently degraded they may ultimately convert from carbon sinks to carbon sources (Pendleton *et al.*, 2012; Cullen-Unsworth and Unsworth, 2013).

The aim of this study was to systematically review the experimental methods employed to date to quantify the fate of macroalgal carbon in marine ecosystems. Once identified, the caveats and potential improvements to each method are discussed to ensure that the most appropriate data is available to inform ecosystem models. Carbon sequestration is defined here as the effective removal of carbon from the atmosphere without the likelihood of it being immediately released or redirected into detrital food webs (Osman-Elasha *et al.*, 2005). It is hoped that this review will serve as a beneficial overview and give direction to those designing future experiments on the fate of macroalgal carbon.

METHODS

A systematic review was completed using Web of Science (1864-present) according to the 2020 PRISMA statement (Page *et al.*, 2021) and PRISMA-EcoEvo, a recent extension designed for systematic reviews and meta-analyses within ecological and evolutionary biology research fields (O'Dea *et al.*, 2021). All databases available on Web of Science were searched using the field 'topic' which searches title, abstract, author keywords, and Keywords Plus® for search terms. An initial scoping review was conducted in order to develop the first set of search terms. Subsequently an additional root term of "kelp" was added prior to commencing the systematic review. Thirty-two search term combinations were applied as described in Table 1 using the Boolean operator "AND".

Table 1 – Search term combinations used to query the databases stored within Web of Science

Root term	**First additional term**	**Second additional term**
Carbon	Macroalgae/ Macroalgal/ Seaweed/ Kelp	Pool/ Storage/ Fate
Sequester	Macroalgae/ Macroalgal/ Seaweed/ Kelp	
Sink	Macroalgae/ Macroalgal/ Seaweed/ Kelp	
Detritus	Macroalgae/ Macroalgal/ Seaweed/ Kelp	
Export	Macroalgae/ Macroalgal/ Seaweed/ Kelp	

Selection criteria for inclusion in the review were clearly defined *a priori* and were designed to select for novel primary research articles in English, which present empirical data and quantitative outputs (Table 2).

Table 2 – Criteria for inclusion or exclusion from the review

Inclusion/Exclusion criterion	**Rationale for inclusion/exclusion**
Must contain novel research about the fate of carbon from naturally occurring macroalgal communities.	Cultivated macroalgae are negligible in scale in comparison to naturally occurring macroalgal communities. Theoretical models and other reviews were excluded in favour of primary research.
Must not contain research conducted solely in laboratory settings.	Laboratory experiments alone cannot be used to determine whole ecosystem productivity or the fate of that productivity.
Must report quantitative data on macroalgal carbon displacement, ideally constrained by time and area.	Quantitative information on carbon flux between different pools is required for the comparison of macroalgae to other communities and for integration into large scale carbon models.
Must contain information on the fate of productivity and not productivity alone.	Information on productivity alone is not sufficient to determine the fate of this productivity.
Must be in English	There was no capacity to translate publications in languages other than English.

Two hundred and fifty-two publications were identified by the search process for assessment and 48 were selected that met the stated criteria for review (Fig. 1). Plot digitization software was used to include data from figures (https://apps.automeris.io/wpd/).

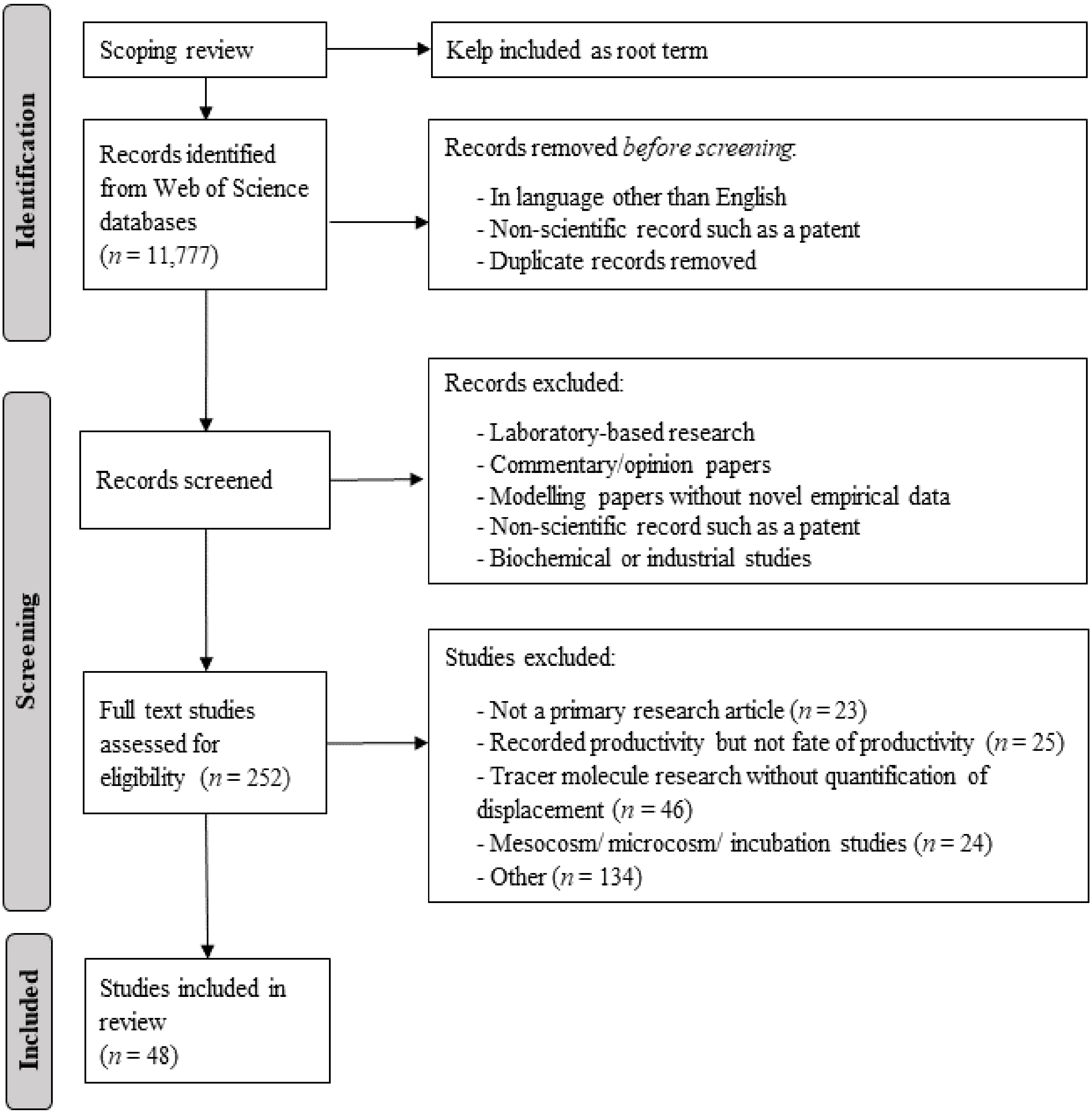

Figure 1 – PRISMA style flowchart of the systematic review methodology used

Publications excluded for review were predominantly other reviews; studies on macroalgal productivity alone; studies using tracer molecules to investigate carbon flow without quantification; and mesocosm or microcosm studies (Table 3, S1).

Table 3 – Most common types of paper identified by the initial search but excluded from review and the rationale for exclusion. See S1 for more detail and citations.

Type of paper	Description and reason for exclusion	Number of studies identified
Other reviews	Commented on or reviewed some aspect of macroalgal carbon but excluded in favour of primary quantitative research.	23
Productivity alone	Described community respiration and productivity within macroalgal dominated ecosystems without describing the fate of the macroalgal carbon.	25
Tracer molecules	Identified movement of macroalgal carbon from its source but without quantification of the fate of the carbon.	46
Microcosm or mesocosm	Measured macroalgal productivity and carbon sequestration in the laboratory without the possibility of scaling these rates up.	24

RESULTS AND DISCUSSION

The 48 reviewed studies experimentally determined either: (i) horizontal transport, that is the export of macroalgal carbon to other environments; (ii) vertical export and sequestration of macroalgal carbon in the deep sea; (iii) burial of macroalgal carbon directly beneath the community; (iv) loss as particulate carbon or dissolved carbon to the water column; (v) loss of carbon to primary consumers; or (vi) a combination of these approaches (Fig. 2, Fig. 3).

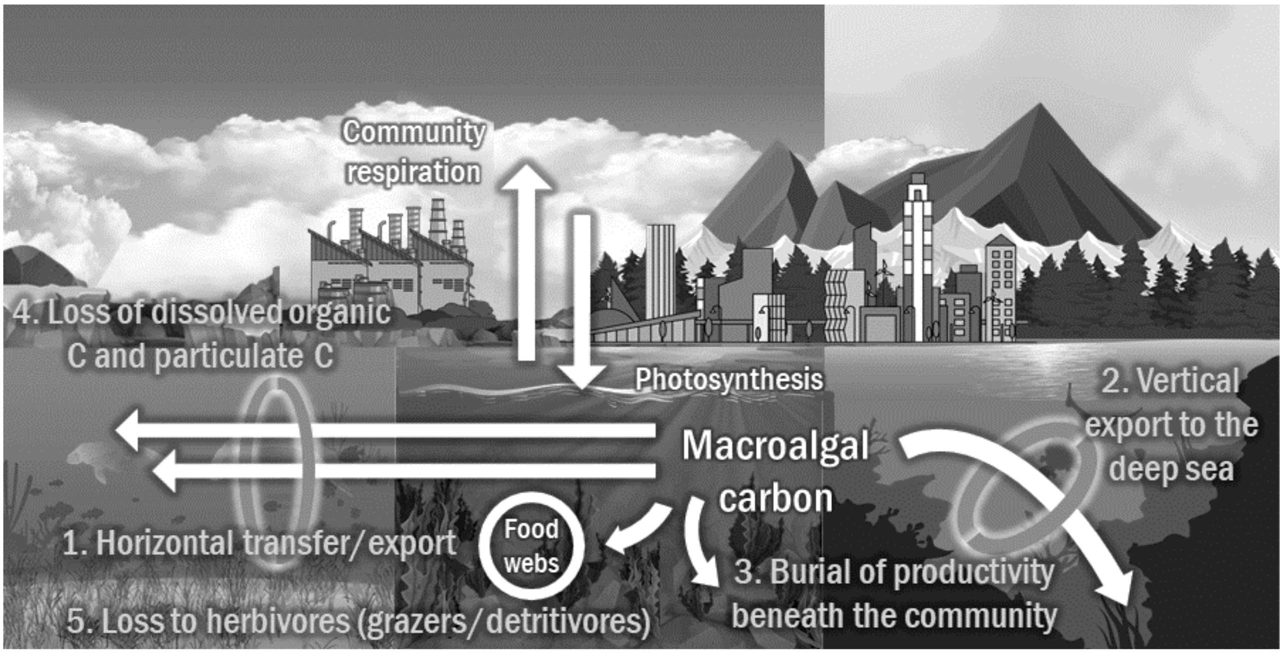

Figure 2 – Carbon flux from and within macroalgae systems

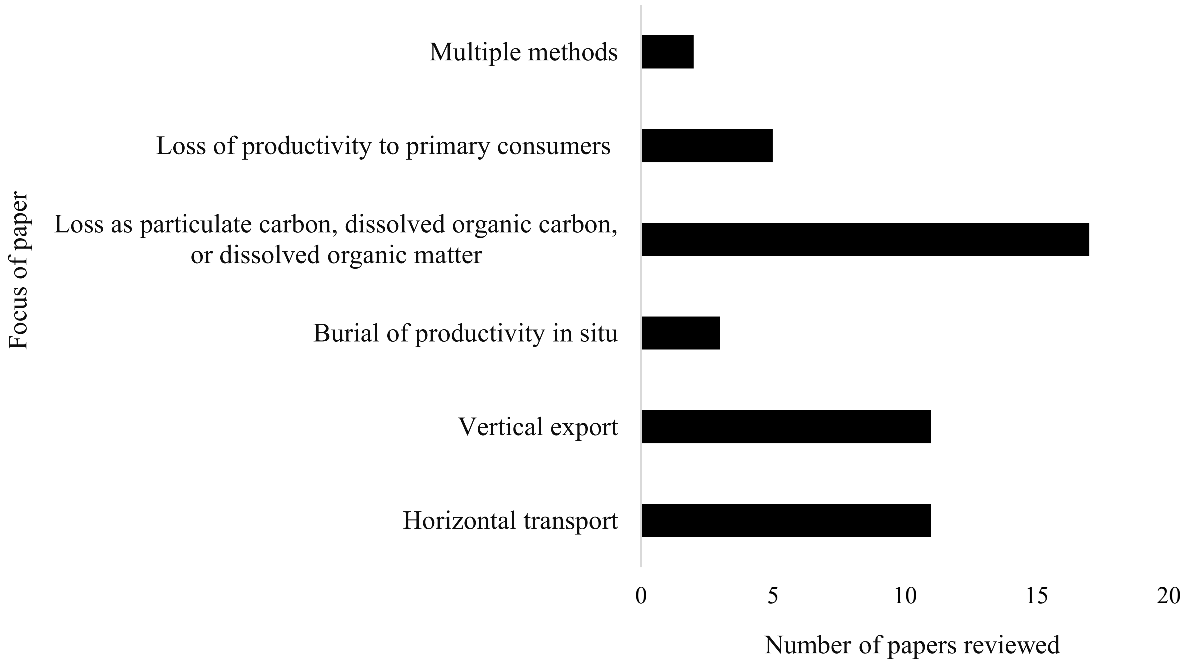

Figure 3 – Studies estimating fate of macroalgal carbon included in this review.

Horizontal transport

Eleven studies estimated horizontal transport from macroalgal communities, which is the export of detached macroalgal biomass beyond the community boundaries to other environments by physical agents, such as currents and waves. With this type of approach, the most that can be done is to identify a macroalgal carbon source, sink, and pathway of export, quantify the displacement of macroalgal carbon from the source, and quantify the deposition of macroalgal biomass in the sink environment. Of the studies reviewed, two described a macroalgal source, sink, and pathway of export but did not quantify displacement (Wernberg *et al.*, 2006; Filbee-Dexter and Scheibling, 2012). Although in these cases displacement is not quantified, the transport pathway has now been recorded and consequently can be studied in more detail. The occurrence of extreme climate events in areas of long-term monitoring are prime opportunities for this type of study. For example, Filbee-Dexter & Scheibling (2012) recorded a post-hurricane pulse of detrital Phaeophyta biomass from macroalgal forests to deeper waters, a reduction of canopy cover from 71% to 39%. This reduction could be updated to estimate biomass or carbon loss if a further survey would relate canopy cover to biomass at the same site.

Three studies quantified the export of macroalgal biomass to an unknown sink (Quartino and Boraso De Zaixso, 2008; Wilmers *et al.*, 2012; Pessarrodona *et al.*, 2018). For example, the seasonal loss of *Laminaria hyperborea* fronds per area was recorded as 187.8 ± 165 g C m^{-2} yr^{-1} lost in cold waters and 101.7 ± 59.6 g C m^{-2} yr^{-1} lost in warm waters (Pessarrodona *et al.*, 2018). These data would be more informative on the fate of macroalgal carbon if a follow-up experiment was conducted to track the dispersal of biomass using tagged or artificial blades.

Owing to the relative ease of shore sampling, the five studies that quantified deposition of macroalgal carbon in a sink environment described marine to terrestrial pathways (Harrold and Lisin, 1989; Kotwicki *et al.*, 2005; Dugan *et al.*, 2011; Lastra *et al.*, 2014; Orr *et al.*, 2014). Considering that < 3% of macroalgal production is estimated to strand ashore (Lastra *et al.*, 2014), there may be an over-representation of macroalgal carbon transport to shores as opposed to subtidal sinks in the literature.

Most studies describing the export of macroalgal biomass to shorelines measure the deposition of fresh weight per area accumulated over time from an unknown donor site, in varying units of mass and time. For example, Orr et al. (2005) estimated daily deposition of up to 140 mg dry wt km^{-1} to shores in British Columbia, while Dugan et al. (2011) calculated the macrophyte deposition on shoreline at Santa Barbara, California to be on average 1.7 kg wet wt m^{-1} day^{-1}. This loading rate was adjusted to account for feeding by the abundant talitrid amphipod populations at the same study beach, yielding a more refined estimated annual macroalgal transport rate of 548 kg wet wt m^{-1} $year^{-1}$. One of these studies (Harrold and Lisin, 1989) demonstrated that it is possible to determine the origin of deposited macroalgal carbon on shores by tagging naturally occurring rafts of *Macrocystis pyrifera* with radiotransmitters along the shoreline of Monterey Peninsula, California. This approach gave a more ecosystem-scale perspective than other shore deposition studies and allowed the authors to estimate that 130,000 t wet wt of *M. pyrifera* is exported from the macroalgal forests at this site to nearby shorelines each year.

Nineteen studies were identified, which did not meet the selection criteria, but investigated the degradation of deposited macroalgal carbon in a sink environment. This common experimental method is conducted *in situ* using naturally occurring macroalgal deposits (Trimmer *et al.*, 2000; Sutula *et al.*, 2014) or more often by "detrital enrichment", that is using artificially loaded or experimentally buried macroalgal biomass in mesh bags (Alkemade and Van Rijswijk, 1993; Mews, Zimmer and Jelinski, 2006; Rossi, 2007; Olabarria *et al.*, 2010; Rossi *et al.*, 2011, 2013; Dufour, Probert and Savage, 2012; Eereveld *et al.*, 2013; Lastra *et al.*, 2014; Gómez *et al.*, 2018; Lastra, López and Rodil, 2018; Rodil *et al.*, 2019; Haram, Sotka and Byers, 2020). These types of experiments are conducted mostly on sandy shore ecosystems, but similar degradation experiments have been conducted in benthic subtidal habitats (de Bettignies *et al.*, 2020;

Pedersen *et al.*, 2021), estuarine sandflats (Gladstone-Gallagher *et al.*, 2016), and in specific seabed hollows where algal blades are known to accumulate (Norkko *et al.*, 2004).

Detached macroalgal biomass, which has been exported and deposited subtidally, cannot necessarily be treated as detritus because it has been found to be actively respiring and growing, without degrading or contributing carbon to the underlying sediments (Frontier *et al.*, 2021). In these experiments, the amount of mass lost from the detritus deposited over time, or the change in concentration or amount of carbon mass in the underlying sediment or pore water (Barreiro *et al.*, 2013) serves as a measure of carbon transferred through abiotic decay or detritivore activity. Rarely are results provided as mass of carbon transferred per unit of time, which prevents comparison to other environments or integration into carbon models. Species-specific and ecosystem-specific degradation rates such as these should be paired with anticipated or measured loading rates to estimate carbon flux from detritus to sediment (Pedersen *et al.*, 2021).

Vertical export

Eleven reviewed studies described vertical export. Despite consumption and transformation, once in the deep sea, macroalgal carbon can be considered to be sequestered from the atmosphere as it is removed from the ocean-atmosphere boundary for geologically relevant amounts of time. Vertical export was originally investigated using cameras attached to remote vehicles which were used to identify and estimate the amount of macroalgal detritus on some deep-sea floors (Alongi, 1990; Harrold, Light and Lisin, 1998; Vetter and Dayton, 1999; Britton-Simmons *et al.*, 2012; Filbee-Dexter and Scheibling, 2014; Filbee-Dexter *et al.*, 2018; Ramirez-Llodra *et al.*, 2021). In most studies, results were presented in rough quantitative terms such as percentage cover (Vetter and Dayton, 1999) or number of pieces of drift macrophytes or drift piles per film segment (Britton-Simmons *et al.*, 2012). Once the presence of macroalgal detritus has been identified, however, this information can be combined with previously determined turnover rates and standing stock data of nearby macroalgal forests to estimate displacement (Ramirez-Llodra *et al.*, 2021), e.g. 45.2 mg C m^{-2} d^{-1} of *M. pyrifera* exported to the Cannel Submarine Canyon benthos (Harrold, Light and Lisin, 1998). More recently, video surveys have been combined with dive observations and tagged samples have been tracked in order to confirm a suspected source of production (Filbee-Dexter *et al.*, 2018).

Alternatively, vertical export to the deep sea has been studied using stationary drift nets at canyon mouths which act as the conduits through which macroalgal detritus reaches deep sea plains (Josselyn *et al.*, 1983). The link between a macroalgal carbon source to deep sea sink has also been established using powerful global observation methods which should be further pursued (Dierssen *et al.*, 2009; Kokubu *et al.*, 2019). For example, the striking loss of 588 km^2 *Colopmenia* sp. detritus on the eastern part of the Great Exuma Bank to the nearby Tongue of the Ocean (>1,800m) was hypothesized using satellite imagery before and after a Langmuir supercell event (Dierssen *et al.*, 2009). It was estimated that this represents a pulsed export of >7 x 10^{10}g of macroalgal carbon exported to the deep sea, approximately the same amount of the carbon sequestered daily by sinking phytoplankton carbon across the entire subtropical North Atlantic.

The most information a vertical export study can provide is the source of the macroalgal tissue exported to the deep sea, the exact area to which it is exported, and the amount of carbon per area of macroalgal forest which is directed to deep sea sediment. For example, benthic sediment cores were collected at depths from 70-262m along the Norwegian coast and distant *L. hyperborea* forests were identified as a source of carbon to the sediments given the similarity of the carbohydrate and phenolic content of the organic matter within the cores to the *L. hyperborea* (Abdullah, Fredriksen and Christie, 2017). The observed rate of organic deposition in the area (approximately 0.46 kg C m^{-1} yr^{-1}) and the high productivity of the donor *L.*

hyperborea (3 kg C m^{-2} yr^{-1}) gave an indication of the amount of *L. hyperborea* carbon which was sequestered in these deep-sea sediments.

Burial of productivity in situ

Given that macroalgae tend to grow on rocky substrata, it is rare that macroalgal productivity is buried directly beneath the canopy. In some cases, however, macroalgae communities overly soft sandy or muddy sediments, allowing the displacement of carbon to the sediment beneath them to be measured (Atwood *et al.*, 2018; Gorain *et al.*, 2018; Sfriso *et al.*, 2020). In a study of organic carbon storage in the Great Barrier Reef, Atwood et al. (2018) measured 2.05 mg organic carbon (OC) ha^{-1} in the upper 0-5 cm layer of sediment (corresponding to the last 40 years) and 2.04 mg OC ha^{-1} in the sediment 5-14 cm deep (corresponding to the last 40-111 years).

Macroalgal blooms often occur in shallow waters such as bays and estuaries, where they overly soft sediment which can be sampled using cores. Gorain et al. (2018) measured the amount of organic carbon from macroalgal blooms directed to underlying "muck", ranging from just 7.6g m^{-2} $month^{-1}$ for *Pithophora oedogonia* blooms to 135.4g m^{-2} $month^{-1}$ for *Rhizoclonium tortuosum*, a small proportion of the biomass yields of these blooms. There are high biomass turnover rates in macroalgal blooms, and they are rapidly degraded through bacterial assimilation, meaning blooms don't act as long-term carbon sequestration, and direct little or no carbon to the sediment below in the form of organic matter (e.g. Corzo, Bergeijk and García-Robledo, 2009; Lanari et al., 2017).

Based on $CaCO_3$ content, microcalcareous epiphytic seaweeds in Italian transitional water systems were estimated to have the capacity to bury between 0.70 and 2.47 tonnes of CO_2 per hectare as oxidized surface sediments, depending on the species (Sfriso *et al.*, 2020). Studies that describe the carbon in the sediment below a macroalgal community, without associated burial rates, or studies that evaluate "carbon stocks" referring to the carbon in standing biomass will be of less value for building marine carbon models or informing management strategies. Valuable data on carbon in sediment with a macroalgal origin (e.g Gilson and Davies, 2020) would be greatly advanced if combined with complementary studies on burial rates or carbon dating.

The IPCC Wetlands Guidance recommends that sediment carbon stocks are standardized to a depth of 1 m below 1 m^2, but of the studies screened for review, sampling depths were much shallower and rarely exceeded 50 cm (IPCC, 2014). To standardize a 10 cm deep sample to 1 m by multiplying by 10 would unrealistically assume a uniform distribution of carbon in the sediment profile.

Loss as particulate carbon, dissolved carbon, or dissolved organic matter

Carbon, either in particulate or in a dissolved form, is released rapidly from marine macroalgae which are actively photosynthesising. Seventeen studies in total were identified which quantified the release of macroalgal carbon as POC, DOC, or dissolved organic matter (DOM). Six of these studies measured DOC and POC loss by observation of biomass change as a result of chronic blade erosion, often alongside measurements of loss through entire plant dislodgement (Dean and Hurd, 2007; Krumhansl and Scheibling, 2011; de Bettignies *et al.*, 2013; Halat *et al.*, 2015; Pessarrodona *et al.*, 2018; Pedersen *et al.*, 2020). Of these, only Dean & Hurd (2007) did not quantify export in terms of area but rather calculated an average *Undaria pinnatifida* sporophyte erosion rate of 0.24 cm d^{-1} to 0.79 cm d^{-1}, which would require accompanying information of sporophyte density to estimate carbon lost from the community. The quantification of these export rates is hugely valuable, and they could be beneficial in answering the question of the fate of macroalgal carbon if combined with tracer studies to track the dispersal of this carbon once released into the environment. For example, Wada & Hama

(2013) used the humic-like fluorophore components of suspended dissolved organic matter released from *Ecklonia cava* to trace its dispersal throughout and beyond Oura bay (Wada and Hama, 2013).

Ten reviewed studies measured the contribution of a macroalgal community to the DOC pool by scaling up mass-specific estimates of DOC release rates from short-term incubations (Fankboner and de Burgh, 1977; Abdullah and Fredriksen, 2004; Wada *et al.*, 2008; Wada and Hama, 2013; Yorke *et al.*, 2013; Barrón, Apostolaki and Duarte, 2014; Ruiz-Halpern, Vaquer-Sunyer and Duarte, 2014; Reed *et al.*, 2015; Egea *et al.*, 2020; Weigel and Pfister, 2020). During an incubation experiment, blades or parts of a macroalgal sample are enclosed in a chamber or plastic bag and the change in concentration of DOC is measured either directly or by proxy. DOC release may then be standardized by net primary productivity (NPP) and scaled up using published rates of community values NPP, which is particularly accessible if the incubation experiment is completed in the context of a longer research programme (e.g. Reed et al. 2005). Incubations such as these offer more control and greater resolution than measuring carbon release via changes in biomass, although the small size of incubation chambers arguably presents an issue for taking representative samples of macroalgal communities. If a single dominant species of macroalgae is incubated to measure DOC loss and export, this data alone is not representative of the true value of macroalgal contribution to the DOC pool, as the release of DOC from other elements of the community and from degrading detrital biomass is not accounted for.

Furthermore, the short duration of incubation experiments in comparison to long term monitoring may incur error as they are understandably conducted in daylight hours and calm weather suitable for fieldwork, although more recent examples have conducted control experiments in the night (e.g. Weigel & Pfister 2020). Tracer molecules, such as radiolabelled sodium bicarbonate, have been used in incubation studies since at least the 1970s, wherein the incubated sample is experimentally enriched with a tracer molecule and its emission monitored (Fankboner and de Burgh, 1977). This method has yielded results of low DOC loss however, equivalent to 0.002 % of blade primary productivity. More recent incubation experiments of *Nereocystis luetkeana* and *M. pyrifera* have shown that of total exuded DOC, less than 20% originated from recently fixed labelled carbon, suggesting that only reporting exuded DOC which is labelled will underestimate DOC release rates (Weigel and Pfister, 2020).

Newly produced DOC is highly labile and is quickly consumed by bacteria, but a large proportion of this consumed DOC is thus transformed to refractory material (Barrón, Apostolaki and Duarte, 2014). The refractory DOC pool in the water column has a turnover period of hundreds to thousands of years (Watanabe *et al.*, 2020) and if exported below the mixing layer of the water column it may be stored for a geologically relevant period of time. One paper which was reviewed monitored the release of DIC and DOC through incubation, and also conducted subsequent degradation experiments to determine the proportion of DOC released which was refractory DOC (RDOC) (Watanabe *et al.*, 2020). RDOC was defined as that DOC which is not remineralized 150 days after release. Net release of DOC from the *S. horneri* community was equivalent to 35% and 6% of net community productivity (NCP) in February and March respectively and it was concluded that the *S. horneri* community exported 5-20% of its productivity as RDOC. Experimental design such as this strengthens the evidence that exuded DOC is relevant to global carbon sequestration.

Loss of productivity to primary consumers

Most quantification of the primary consumption of macroalgae occurs exclusively in a lab setting where consumers can be studied in detail (e.g. Gilson, Smale and O'Connor, 2021; Wernberg and Filbee-Dexter, 2018; Ito *et al.*, 2019), which excluded these studies from review. Five studies were reviewed, however, which directly measured the loss of macroalgal biomass to herbivores in the field (grazers, detritivores, shredders and others) (Itoh *et al.*, 2007; Krumhansl and Scheibling, 2011; Norderhaug and Christie, 2011; Filbee-Dexter *et al.*, 2020; Gutow *et al.*, 2020). These studies quantified the macroalgal carbon directed to primary consumption in the field by combining *in situ* measurements with either lab experiments or previous data sets. For example, Norderhaug and Christie (2011) determined that in the case of Norwegian *L. hyperborea* forests secondary production by *L. hyperborea* consumers was 3% of primary productivity at low wave exposure, and 8% at medium and high wave exposure. They combined their novel data on secondary production rates, based on community composition of mobile macrofauna, with primary production data personally communicated from Pedersen at the same sites.

Studies of primary consumers may be motivated by observations of a particularly voracious grazer. For example, the stipe-burrowing herbivorous amphipods *Sunamphitoe lessoniophila* and *Bircenna sp.,* were estimated to cause a maximum loss of 24–44% of biomass from the *Lessonia berteroana* kelp forests in northern-central Chile (Gutow *et al.*, 2020). Less dramatically, grazing rates of gastropod *Lacuna vincta* on *Saccharina longicruris* and *Laminaria digitata* in Nova Scotia were measured as a maximum of 1% and 1.5% of blade area respectively (Krumhansl and Scheibling, 2011). The type of results from these grazing loss studies could be converted into carbon fluxes if scaling relationships were to be established between blade area or mass and carbon content, and the density of blades per area were known. This analysis is particularly feasible if a grazing survey is part of a larger study on macroalgal production and erosion at one site. The urchins *Strongylocentrotus droebachiensis* and *Echinus esculentus* were studied in Malangen Fjord, Northern Norway and it was calculated that between 1.3 and 10.8kg of fresh biomass are shredded annually per square metre of macroalgal forest (Filbee-Dexter *et al.*, 2020). The rate of macroalgal detritus produced in the area was required for this calculation, which was available in Pedersen *et al.* (2020), which again demonstrates how useful multiple studies in the same site can be for a comprehensive understanding of the carbon flow in a macroalgal community.

Whole system analysis

Two studies, which were reviewed, combined multiple approaches to quantify macroalgal carbon sequestration (Takai *et al.*, 2010; Queirós *et al.*, 2019). Queirós et al. (2019) used eDNA sequencing and Bayesian Stable Isotope Mixing Modeling to identify sources of detrital macroalgal biomass on the seabed 13 km south-southwest of Plymouth, UK, Station L4. The export of POC from identified macroalgal carbon sources was measured according to detritus production rates in the same area, published by Pessarrodona *et al.* (2018). This carbon export pathway was combined with benthic-pelagic process measurements derived using incubated box cores to determine the fate of detrital macroalgal carbon once deposited on the seabed. The incubation of box core samples from the sediment allowed the direct measurement of processes such as POC burial, POC flushing (bioirrigation), POC burial through bioturbation, and the production of DIC, suggesting average annual carbon sequestration of 4.89 ± 5.50 mol $m^{-2}yr^{-1}$, 0.73 ± 0.82 mol $m^{-2}yr^{-1}$ of which was macroalgal carbon sequestration (Queirós *et al.*, 2019). Twenty-three mesocosm or microcosm studies were excluded from this review, all of which described carbon flow from macroalgal detritus to the water column, sediments, or consumers (S1). If these mesocosms were representative of a certain ecosystem and the mass processes of macroalgal import and export from that ecosystem were known, the carbon sequestration of that ecosystem type could be calculated as per Quierós et al. (2019).

Despite using less advanced technology, Takai *et al.* (2010) also used a whole system analysis to establish a transport link between macroalgal carbon source and sink, quantified that link, and indicated the fate of the macroalgal carbon which was deposited. The amount of macroalgal detritus on the seafloor around the Izu Peninsula, Japan was measured by dredging and trawling. The source and transport pathway of the macroalgal detritus was determined based on similarities in species compositions. This was verified using carbon and nitrogen stable isotope ratios. Stable isotope analysis was conducted on the SOM beneath the detrital accumulations, which indicated that macroalgae contribute relatively little to the carbon in the sediment.

The use of multiple methods does not necessarily mean a study on macroalgal carbon will be informative on carbon sequestration. For example, Pfister, Altabet and Weigel (2019) used a remarkable number of different methods to compare the seawater chemistry inside and outside *N. luetkeana* and *M. pyrifera* forests along the Olympic Peninsula of Washington state. Within each forest and 200-400m away, the carbonate content and DOC content of the water was measured, productivity was estimated based on *chl* a concentration, and both eDNA and isotopic investigations were conducted. These comparative observations gave strong evidence that macroalgae contribute to nearshore carbon cycling, but the experimental design did not facilitate quantification of this cycling.

CONCLUSIONS

Once a macroalgal carbon source-sink pair has been identified, measurements of carbon sequestration can be scaled up to all national habitats of the same type. These figures can then be integrated into global carbon models and used by decision makers for effective management and conservation of carbon stocks. Multiple approaches, either combined in the same study (Takai *et al.*, 2010; Queirós *et al.*, 2019), in separate studies on the same site (Harrold and Lisin, 1989; Norderhaug and Christie, 2011; Queirós *et al.*, 2019; Filbee-Dexter *et al.*, 2020), or in one study in the scope of a larger project (Reed *et al.*, 2015; Atwood *et al.*, 2018) offer the most comprehensive insight into the fate of macroalgal carbon.

We conclude that many macroalgal carbon studies could be greatly expanded by complimentary experiments that quantify some related aspect within the same source-transport-sink system. For example, existing species-specific and ecosystem-specific detritus degradation rates could be paired with deposition rates in a sink environment to estimate carbon flux from detritus to sediment. Similarly, sediment deposition rates or sediment dating could be combined with previous studies of sediment carbon content to determine carbon burial rates. Percentage biomass loss due to grazers could be converted into area-standardized carbon fluxes if combined with the density of blades per area. Finally, rates of macroalgal import to an ecosystem can be combined with representative mesocosm studies to estimate carbon sequestration of that ecosystem type.

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<u>CHAPTER THREE</u>

Article type: Full paper

Title: The contribution of cultivated seaweed to the blue carbon sink

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<u>ABSTRACT/ IMPACT STATEMENT</u>

Many governments are currently evaluating carbon sinks to design tools to mitigate the impacts of climate change. These nature-based solutions include cultivation of aquatic plants and macroalgae to sequester carbon dioxide directly from the atmosphere. This requires accurate estimates from the field to be integrated into predictive models. This study estimated potential rates of carbon sequestration of cultivated macroalgae in the NE Atlantic, by quantifying the amount of carbon released to the local environment from an experimental kelp, *Saccharina latissima,* farm in Strangford Lough, Northern Ireland. On average > 40% of net primary productivity (NPP) of the cultivated kelp was lost prior to harvest following blade falloff, while 43% of NPP was lost through exudation of dissolved organic carbon, and 0.2% of NPP was lost through chronic erosion of the blades during the cultivation period (approximately 6-9 months). The sum of these processes of estimated carbon loss resulted in a sizeable average of 84% of NPP being lost from the cultivated macroalgae per longline, equivalent to an average of 20 kg of carbon sequestered per 100 m longline at the Strangford Lough site in 2016. This amount of sequestration is similar to the that by agroforestry schemes which are funded by the Irish Department of Agriculture, Food and the Marine. Thus, this ecosystem service could be

subsidised in order to incentivise farmers and entrepreneurs to develop the macroalgae industry sustainably.

Key words: *Saccharina latissima,* carbon, sequestration, cultivated, macroalgae, kelp, Strangford Lough

INTRODUCTION

Given the urgent need to limit global greenhouse gas (GHG) emissions, many governments are now re-evaluating proprietary carbon sinks with a novel focus on aquatic plants and macroalgae (Muraoka, 2004; Gundersen *et al.*, 2010; Sondak and Chung, 2015; Jiao *et al.*, 2018). In the last two decades, and particularly since the publication of the UN report, 'Blue Carbon: A Rapid Response Assessment' (Nellemann *et al.*, 2009), attempts to quantify CO_2 sequestration by marine macrophytes have increased. This report introduced the concept of 'Blue Carbon' and highlighted its importance by estimating that marine macrophytes perform at least 50% and up to > 70% of carbon sequestration in ocean sediments.

Although naturally occurring macroalgae conduct significant carbon sequestration (Hill *et al.*, 2015; Trevathan-Tackett *et al.*, 2015), cultivated macroalgae have also been proposed as potential carbon sinks (Chung, Sondak and Beardall, 2017; Duarte *et al.*, 2017; Zhang *et al.*, 2017). Macroalgae are primarily cultivated for food, phyllocolloids (gelling agents), cosmetics, nutraceuticals, bioenergy, fertilizer, feed for livestock and cultured finfish, and for novel medical applications (van den Burg *et al.*, 2016; Buschmann *et al.*, 2017). The global production of macroalgae more than tripled between 2000 - 2018, from 10.6 million tonnes to 32.4 million tonnes (Food and Agriculture Organization of the United Nations, 2020) and macroalgae have been identified as a major focus for mariculture development in Europe (Barbier *et al.*, 2019; The Aquaculture Advisory Council, 2021).

Macroalgae, particularly the Phaeophyta (brown algae including kelp), have very high rates of primary productivity (Mann, 1973). Cultivated macroalgae absorb large amounts of inorganic carbon in the water column for photosynthesis, which subsequently reduces the partial pressure of CO_2 in the water and raises alkalinity (Jiang *et al.*, 2013; Lin *et al.*, 2019). This increases the gas transfer velocity of atmospheric CO_2 across the air-sea boundary layer into the ocean (Delille, Borges and Delille, 2009; Zhang *et al.*, 2012; Jiang *et al.*, 2015), although the magnitude of this increase will depend on air-sea equilibration timescales and the residence time of CO_2-depleted seawater in the surface mixed-layer (Jones *et al.*, 2014; Bach *et al.*, 2021). It is for this reason that efforts are being made to test cultivated macroalgae as a measure to offset national carbon emissions through voluntary carbon credits and protocols (Oceans 2050 Foundation, 2019).

Thus far, the majority of studies that have investigated the potential of macroalgae farms as carbon sinks have focussed on the 'removable' carbon, that is the carbon in biomass harvested from the farm (Turan and Neori, 2010; Chung *et al.*, 2011; Tang, Zhang and Fang, 2011; Zhang *et al.*, 2017; Jiao *et al.*, 2018). The macroalgal carbon removed during harvesting, however, will probably return to the atmosphere through respiration and in waste streams. Life cycle assessments of macroalgal cultivation, refinery, and usage of products indicate that for every dry ton of macroalgae cultivated, there is an overall sequestration of 0.13 tons of atmospheric CO_2 over a 100-year period (Seghetta *et al.* 2016). Alternatively, comparative studies have been conducted that contrast the sediment beneath intensive macroalgal cultivation zones to control sites (Ren *et al.*, 2014; Juanjuan *et al.*, 2019; Pan *et al.*, 2019). It is important to note, however, that this approach may underestimate carbon sequestration, as macroalgal detritus is known to travel across community boundaries for kilometres over the space of several days (e.g. Dierssen *et al.*, 2009; Filbee-Dexter and Scheibling, 2012, 2016; Filbee-Dexter *et al.*, 2018; Queirós *et al.*, 2019). For this reason, localised environmental impact assessments on the sediment directly beneath cultivated macroalgae should be considered conservative.

Cultivated macroalgal carbon may be released into the environment as dissolved organic carbon (DOC), through processes of erosion and exudation, or particulate organic carbon (POC) because whole individuals may fall away from the cultivation platforms or lower parts of the tissue may break off before they are harvested. Carbon loss from a *Saccharina japonica* farm in China has been estimated as > 60% of gross biomass production (Zhang et al., 2012). More recently, seafloor investigations under the KELPPRO (2017-2020) project in Norway showed that annually, 8 - 13% of harvested *Saccharina latissima* biomass is released to the environment from the cultivation site, equivalent to 630-880 kg C ha^{-1} yr^{-1} (63-88 g C m^{-2} yr^{-1}). This loss can increase dramatically to > 50% of the harvested biomass if the harvest is conducted later in the cultivation period. Moreover, the subsequent fate of these different forms of lost carbon remains understood poorly. Other than the results from these two studies, there is currently a lack of quantitative data characterising the loss of biomass from cultivated macroalgae, particularly in the Atlantic region. Research on the environmental impacts of macroalgal cultivation has been dominated by several Asian-Pacific countries, which make up the vast majority of global production (Sondak *et al.*, 2017, but see Walls *et al.*, 2017; Visch *et al.*, 2020). More accurate predictions of expected loss of biomass from cultivated macroalgae are needed to efficiently grow the required harvest to meet market demand. The aim of this study was to: 1. Quantify the growth of sugar kelp (*S. latissima)* on a seaweed farm in the NE Atlantic using a typical longline cultivation method; 2. Quantify the proportion of net primary productivity (NPP) lost through processes of erosion, exudation, and dislodgement of entire individuals during kelp cultivation periods; and 3. Estimate the carbon sink that this lost biomass represents. Robust estimates such as these are required to quantify the current contribution of cultivated macroalgae to the carbon sink and to build accurate predictive models as this sector expands rapidly.

Definitions of carbon sequestration vary according to different opinions on the necessary retention time of carbon to be considered as a ‘sink’ (Marland, Fruit and Sedjo, 2001; Herzog, Caldeira and Reilly, 2003; Olson *et al.*, 2014). Here we consider carbon sequestration as the effective removal of atmospheric carbon dioxide with little risk of it being re-released for hundreds of years (Osman-Elasha *et al.*, 2005).

MATERIALS AND METHODS

To quantify the amount of production lost during a typical year of *S. latissima* cultivation, data were analysed which were collected as part of the SeaGas project (BBSRC: SeaGas) at an experimental seaweed farm at Queen’s University Belfast Marine Laboratory, Portaferry. *S. latissima* is a subtidal phaeophyte (kelp) with a large undivided blade and a rubbery texture. It attaches to the benthos or cultivation substratum using a holdfast and stipe. The cultivation site is located within the semi-enclosed, fully saline Strangford Lough, Co. Down, Northern Ireland (54.4° N, 5.58° W; Fig. 1).

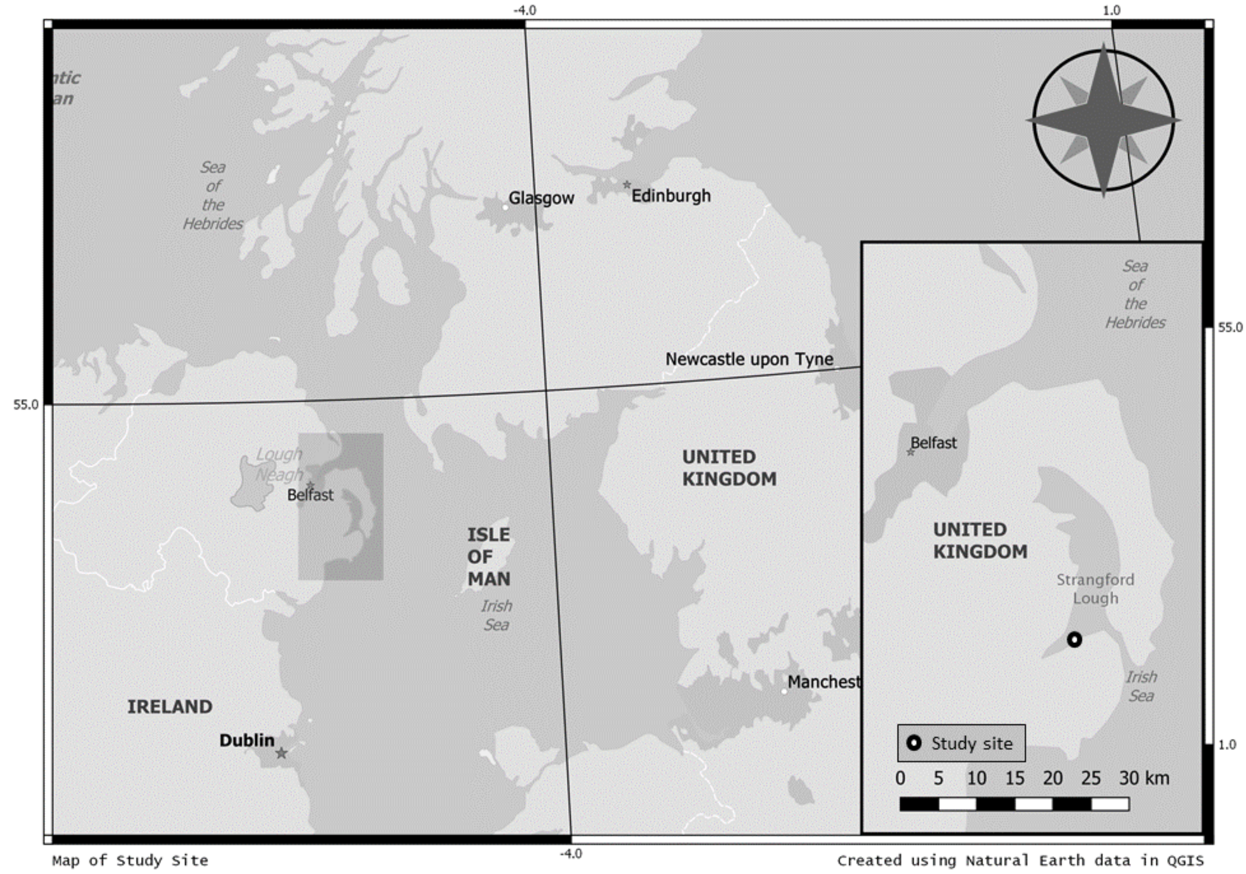

Figure 1 — Location of experimental seaweed farm at Strangford Lough.

The Lough is approximately 130 km^2 in size, 31 km in length, 4-7 km wide, and is connected to the Irish Sea via the Strangford Narrows (Boyd, 1973). The farm site is over waters 2-11m deep off the southern shore and is relatively sheltered with an average current speed of 0.3 ms^{-1} which runs predominantly west to east (Mooney-McAuley *et al.*, 2016). The SeaGas project was designed to optimize the cultivation methods of macroalgae for use as a feedstock for biogas generation through anaerobic digestion. Thus, the aim of the production method was to enhance biomass production during the optimal cultivation period.

Sporophyte growth (hatchery cultivation)

Reproductive material was collected from a local shore or crossed in the laboratory from previously cultured strains. Reproductive sori were stress-induced to release zoospores which were grown to gametophytes. Once fertilization of gametophytes occurred, sporophytes developed for 3-5 months and were then sprayed on culture twine which was wrapped around collectors. These collectors were further cultivated for 4-6 weeks until the sporophytes attached were sufficiently mature to survive deployment at sea and weather conditions were deemed suitable. Alternatively, the culture twine was "direct seeded", that is sprayed or dipped in a solution of unfertilized zoospores.

Longline deployment at sea

100 m longlines were deployed into the adjacent Strangford Lough, which consisted of header ropes buoyed at about 0.5 m – 1 m beneath the surface of the water, attached to anchor blocks at each side. The twine with attached juvenile sporophytes was wound around the header rope during deployment. The first cultivation period spanned from January 2016 to June 2016, for which 12 longlines were deployed. The second cultivation period took place from October 2016 to September 2017, for which 21 longlines were deployed.

Sampling to quantify algal production

The growth and blade morphology of cultivated *S. latissima* was monitored throughout each cultivation period. Five 30 cm sacrificial samples were selected randomly from the deployed 100 m longlines each month during the growing period. In the first cultivation period, 6 longlines were sampled and in the second cultivation period 4 longlines were sampled. All biomass within each 30 cm sample was removed and the number of individuals present were counted. The 12 largest individuals from each 30 cm sample were selected for measurement because these generally formed the majority of the biomass. The remainder of biomass from the 30 cm sample was weighed. Maximum length and width of individual blades, blade wet and dry biomass, and stipe length were all measured. At the end of each cultivation period, all the biomass was removed from the longlines and weighed.

Data analysis

The carbon lost from the macroalgal farm was assumed to represent blade falloff and loss of DOC through erosion and exudation. The net growth rate of individual sporophytes was obtained according to the formula:

$$\text{Net growth rate in weight (g day}^{-1}\text{)} = \frac{M_f - M_i}{T_f - T_i}$$

Where M_f and M_i represent the wet biomass of the sporophyte at the present time of measurement T_f and at the last time of measurement T_i respectively. Loss of carbon as DOC, either through erosion or exudation, was estimated following methods described by Broch and Slagstad (2012), who estimated the productivity, growth, and nutrient contents of *S. latissima*. More recent models exist which describe the energy and growth of *S. latissima* but these do not detail the carbon contents nor the amount of biomass lost through erosion or exudation (eg. Vondolia *et al.*, 2020). For each sampling interval lasting approximately 30 days, the amount of DOC lost through erosion and exudation was estimated. These values were summed to describe the overall cultivation periods.

The frond of *S. latissima* is constantly being eroded at the apex and erosion increases with increased tissue age and water motion (Sjøtun, 1993). The model for erosion applied to the data was in terms of blade area lost which was subsequently converted to wet and dry biomass using scaling relationships from the data, and to carbon lost by assuming that there is 0.18 g of carbon per 1 g of dry structural biomass (Broch and Slagstad, 2012). Erosion was estimated as:

$$v(A) = \left(\frac{10^{-6}\exp(\varepsilon A)}{\left(1 + 10^{-6}(\exp(\varepsilon A) - 1)\right)}\right)$$

Where ε is a frond erosion parameter. A model was built using scaled digitized herbaria samples from the 'Macroalgal Digitization Project' (Macroalgal Digitization Project, 2021) to describe frond area using length and width as inputs. 104 specimens were analysed using ImageJ for this purpose, and care was taken to ensure representative specimens of varying maturity and diverse morphologies were included. Similar to many other macroalgal species, the morphology of *S. latissima* is highly variable depending on the environmental conditions of its growth. Most specimens of *S. latissima* are much longer than they are wide but occasional individuals are almost circular. Specimens also have varying degrees of ruffling along the lateral edges of the blades. Although this is not addressed here, it does increase the surface area of the blade in sheltered localities to provide a larger area for nutrient uptake (Sjøtun, 1993). This diversity of form was the reason a model of generalized dimensions as described by Peteiro and Freire (2013) was not applied.

The model for exudation is in terms of carbon and describes both actively excreted compounds, such as laminarin and mannitol, and leaked carbohydrates (Wada *et al.*, 2007; Sharma *et al.*, 2018; Becker *et al.*, 2020). Exudation was estimated as:

$$E(C) = 1 - \exp\,[\gamma(C_{\min} - C)]$$

Where parameter γ controls the rate at which carbohydrates are exuded and is set to $\gamma = 0.5$, C_{min} is the minimal reserve carbon pool, and C is the total carbon in the kelp at the time (Broch and Slagstad, 2012).

The number of blades lost per sampling interval was determined by comparing the blade density between sampling dates. The biomass and carbon content of the blades lost were calculated based on the average size of blades between the sampling dates and assuming that there is 0.18 g of carbon per 1 g of dry structural biomass (Broch and Slagstad, 2012). The amount of carbon in blades lost for the entire cultivation period was the sum of the blades lost across each sampling interval. Once the amount of carbon lost through break-off of whole blades (macroalgal detritus) or through erosion and exudation (DOC) was determined, the carbon sink which this lost biomass represents was approximated according to the coarse estimates within Krause-Jensen and Duarte (2016). The carbon lost was compared to the carbon harvested at the end of the cultivation periods and the carbon fixed through net primary production was assumed to be equal to the sum of carbon released to the environment and the carbon harvested.

Throughout the two cultivation periods, environmental conditions, such as light intensity, nutrient concentrations (nitrate, nitrite, and phosphate), and water surface temperature were recorded at the experimental site.

RESULTS

Daily growth rates initially increased linearly early in both cultivation periods despite the differing times of year (Fig. 2). Individual daily growth rates ranged between -0.75 g and 7.54 g wet biomass day^{-1}. Growth rates plateaued during the late stages of cultivation period 2 as the individuals reached their maximum size (300 g wet biomass, 313 cm blade length; Fig. 2).

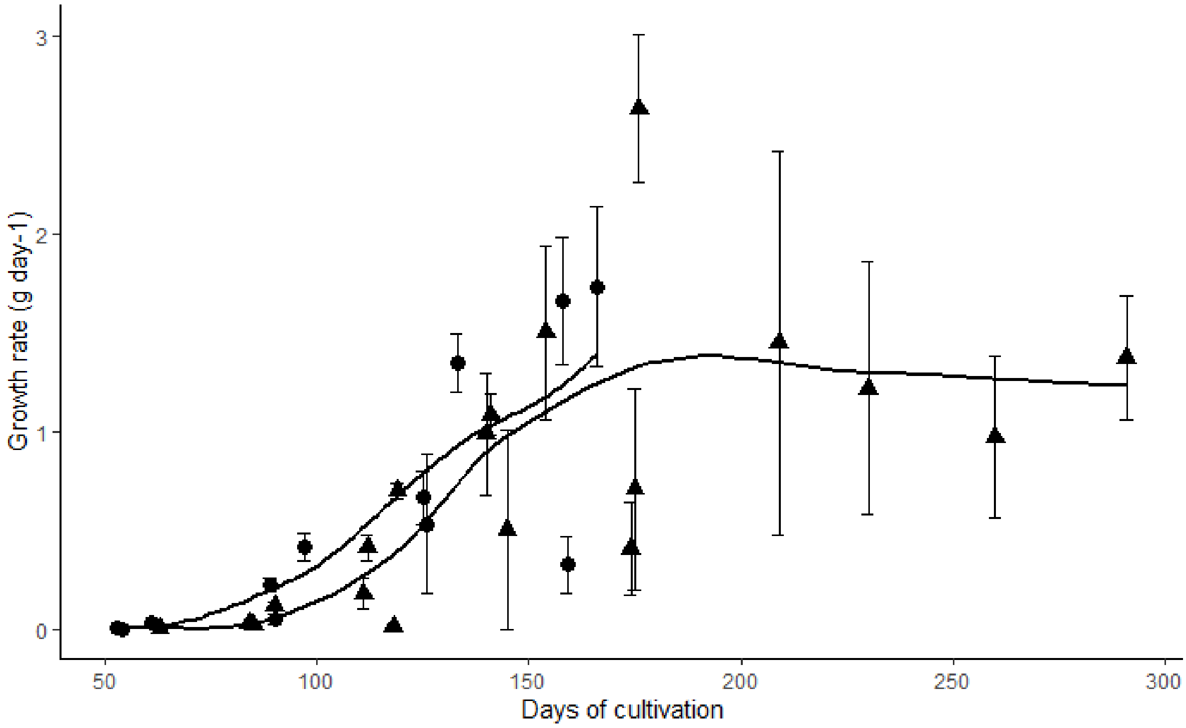

Figure 2 — Mean biomass accrual (± S.E.) (*n* = 5-15) of individual sporophytes of *S. latissima* (g wet biomass day^{-1}). Cultivation period 1, January 2016 - June 2016: ●. Cultivation period 2, October 2016 - September 2017: ▲. Locally weighted smoothing line applied shows the local mean.

There was a logarithmic relationship between maximum blade length (cm) and wet biomass (g) (Fig. 3). The average amount of carbon harvested per 100 m longline was 9.5 kg, although this varied considerably between a minimum of 1kg and a maximum of 19.9 kg.

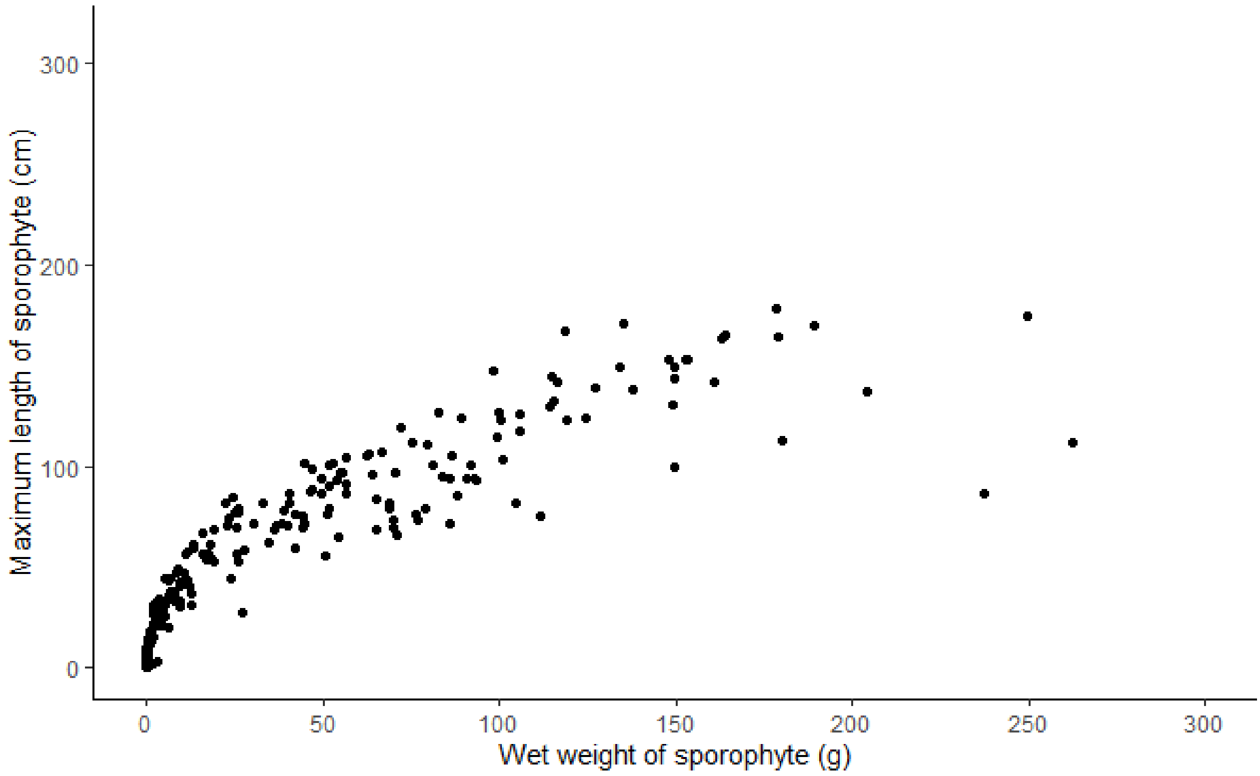

Figure 3 — Relationship between the wet biomass and maximum length of sporophytes of *S. latissima* (n = 231) from all individuals sampled across both cultivation periods.

Area relationship

Multiple linear regression with an interaction effect was the most suitable model to describe the relationship between the area of a *S. latissima* blade and the maximum length and maximum width of that same blade ($R^2 = 0.97$). Blade area was estimated as:

$$A = 0.458ML - 0.863ML.MW + 0.655ML.MW - 1.609$$

Where ML represents maximum length and MW represents maximum width.

Blade fall-off

Density of individuals per 30 cm was highly variable and ranged from 3050 to 0. An initial high density of juveniles dropped over the course of both cultivation periods as a result of competition for space (Fig. 4).

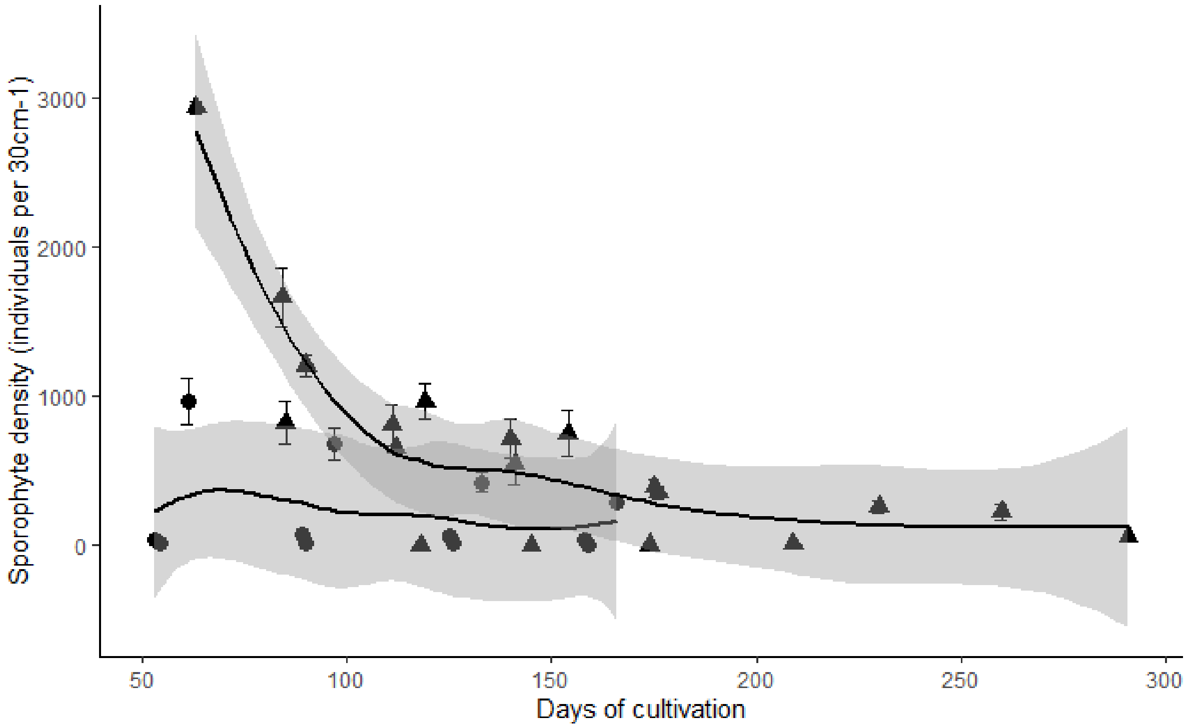

Figure 4 — Mean (± S.E.) number of individuals of *S. latissima* per 30cm of mariculture rope (*n* = 5-15). Cultivation period 1, January 2016 - June 2016: ●. Cultivation period 2, October 2016 - September 2017: ▲. Locally weighted smoothing line shows the local mean ±1.96 S.D.: —

On average, 41% of NPP was lost as blade fall-off per 100 m longline (Fig. 5). There was a positive linear relationship between NPP and the proportion of NPP lost to blade falloff (R^2 = 0.78) (Fig. 6). The most productive longline fixed 360 kg of carbon over 291 days and 62% of this was lost to blade falloff. The minimum amount of NPP lost as fall-off was 24%. There was a logarithmic relationship between the amount of carbon lost through blade fall-off and the amount of carbon harvested (R^2 = 0.75). The least productive longlines lost approximately the same amount of carbon to falloff as the amount of carbon harvested (Fig. 5).

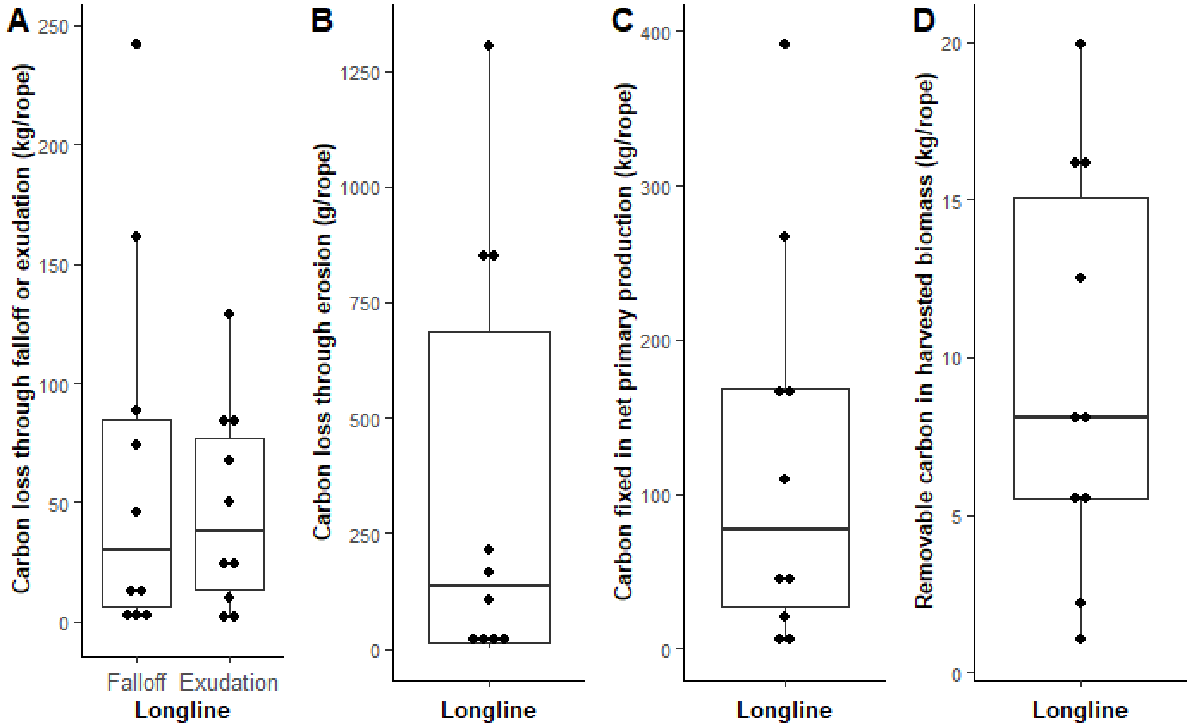

Figure 5 — **A)** Median (± IQ range) mass of carbon lost through blade falloff and exudation, and **B)** erosion per longline sampled across both trials (*n* = 10). **C)** Median (± IQ range) mass of carbon fixed in biomass and **D)** harvested per longline sampled across both trials (*n* = 10).

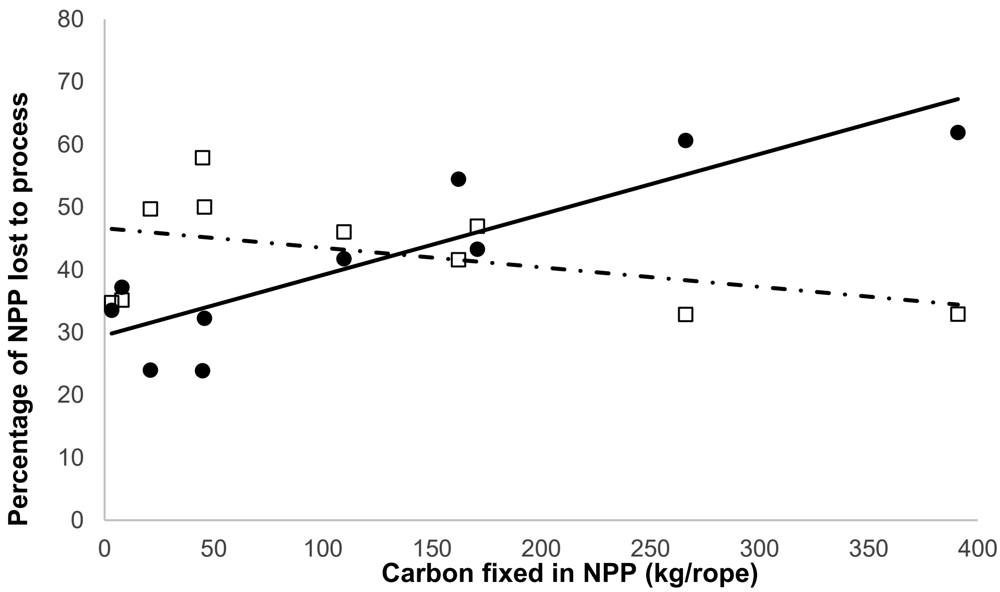

Figure 6 — Mean percentage of net primary productivity (NPP) lost through either blade falloff or exudation per longline sampled across both trials (*n* = 10) versus mean NPP per longline across both trials. Exudation: □. Falloff: ●.

Exudation

The loss of NPP through exudation of DOC per longline was on average 43% and varied from 33- 58% (Fig. 5). There was a positive linear relationship between the amount of carbon lost through exudation and the amount of carbon harvested ($R^2 = 0.80$). There seemed to be a negative relationship between productivity and proportional exudation (Fig. 6), although more replicates across a greater and more even range of productivities would be required to investigate this further. There was a strong positive relationship between the daily growth rate and the daily carbon exudation rate of individual blades (Fig. 7).

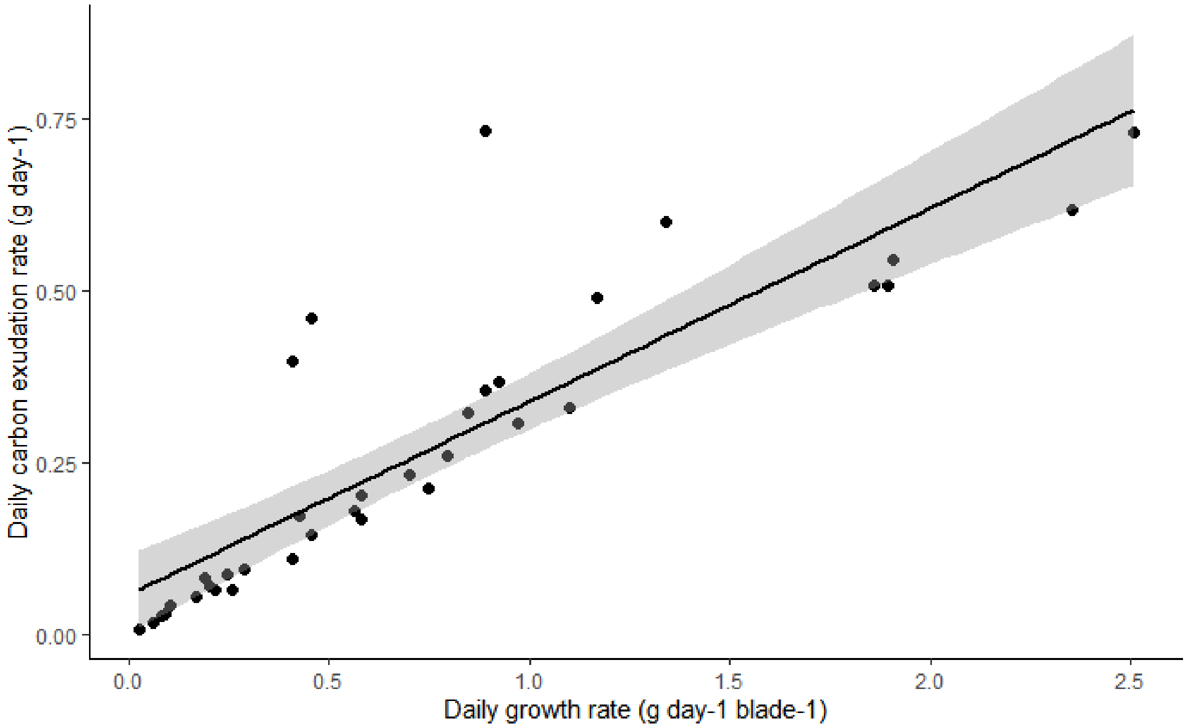

Figure 7 — Mean (± S.E) daily carbon exudation rate ($n = 36$) versus daily growth rate of individual *S. latissima* sporophytes. Locally weighted smoothing line applied shows the local mean.

Erosion

The amount of carbon which was lost as DOC through erosion was lower by orders of magnitude in comparison to the amount lost through exudation and blade falloff. An average of 353.5 g of carbon was lost through erosion per 100 m longline (Fig. 5), equivalent to 0.2% of carbon fixed in NPP per longline.

Water temperature fluctuated from 5.6 °C to 23.5 °C throughout the study period (January 2016 – September 2017), reaching a minimum value in February and maximum values in late May. The greatest light intensities were in March and April and reached over 24000 lumen m^{-2}. There was a clear trend of decreasing nitrate and phosphate concentrations in the water column during both cultivation periods (Fig. 8), which may ultimately result in the availability of these nutrients being limiting factors in growth.

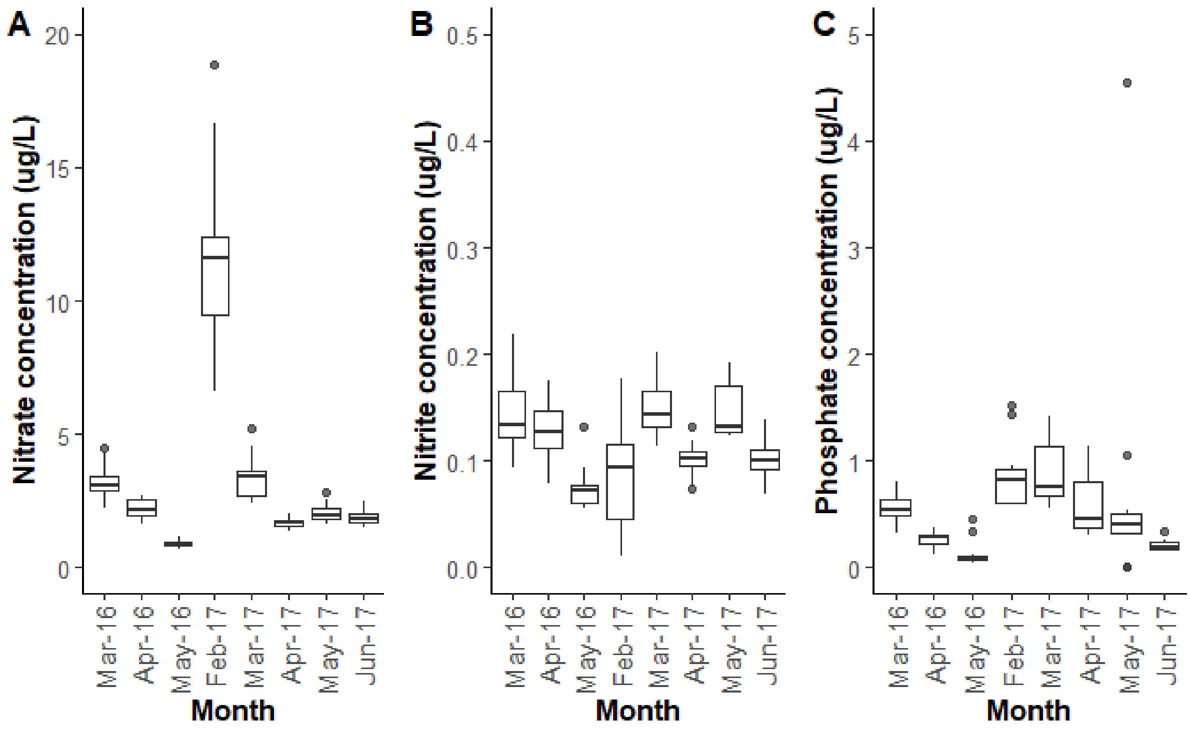

Figure 8 — Median concentrations of nitrate, nitrite, and phosphate in surface waters at the *S. latissima* farm, Strangford Lough. n = 12 water samples at each date.

DISCUSSION

Our results show that longlines of cultivated kelp, which were the most productive during the cultivation period, also lost most macroalgal carbon predominantly through blade falloff. This is in contrast to the findings of a previous study of *S. japonica* in China (Zhang *et al.* 2012), which described blade fall-off as a relatively unimportant process, only contributing to the loss of 4% of gross production at their cultivation site. Our findings show that the less productive longlines appeared to lose carbon predominantly as DOC through exudation, which is in line with estimated rates of DOC exudation from wild macroalgae populations (Broch and Slagstad, 2012; Khailov and Burlakova, 1969; Hatcher, Chapman and Mann, 1977; Wada *et al.*, 2007). The sum of all these processes of estimated carbon loss resulted in a sizeable average of 84% of NPP being lost from the cultivated macroalgae per longline.

The rates of erosion derived from the Broch and Slagstad model (2012) never exceeded 1% of NPP and it is acknowledged that there are some limitations with this current model's erosion estimates. These calculated erosion rates were very low in comparison to previously reported rates of erosion in both cultivated and wild macroalgae (de Bettignies *et al.*, 2013; Pessarrodona *et al.*, 2018; Pedersen *et al.*, 2020). The Broch and Slagstad model may have previously been empirically adjusted against a population in which the majority of individuals were juvenile or showed few signs of erosion for other reasons, such as the absence of wave action, temperature stress, or mechanical stress (Krumhansl and Scheibling, 2011; Krumhansl, Lauzon-Guay and Scheibling, 2014). Alternatively, the proportion of DOC lost from *S. latissima* may have been misattributed between erosion and exudation. Another study of a cultivated kelp, *Undaria pinnatifida*, in Japan estimated that erosion of DOC was 30-40% of biomass production in March and > 80% of production in April (Yoshikawa, Takeuchi and Furuya 2001). In comparison, the greatest rate of erosion calculated for any of the lines sampled in the current study in either the first or second cultivation period was 0.8% of NPP. We recommend that future studies should pair the modelling approach used in the current study with direct measurements of erosion using the hole punch method or similar (Mann, 1972).

A previous review of DOC released from macroalgae estimated that approximately 33% can be considered sequestered because this carbon is exported below the mixed layer in the water column and removed from interaction with the atmosphere for thousands of years (Krause-Jensen and Duarte 2016). In our study system, this equates to an average of 12 kg of DOC burial per 100 m kelp longline over one growth period at this site. When DOC is released from macroalgae, it may be converted to recalcitrant DOC (RDOC) by bacterial activity. This means it is very stable and increases the likelihood of this carbon being stored in deeper waters. One experiment estimated the loss of DOC from the phaeophyte *Sargassum horneri* in Japan, and determined the proportion released DOC which was recalcitrant in the water column (Watanabe *et al.* 2020). The net release of DOC from the *S. horneri* sampled was equivalent to 35% of net community productivity, 56% of which was recalcitrant, that is humic and not remineralized 150 days after release. In this example and others (e.g. Zhang *et al.*, 2017; Li, *et al.*, 2018; Weigel and Pfister, 2020), it is clear that the DOC released from cultivated macroalgae should not be disregarded as a potential sequestration process. With regards to blade fall-off, 4% of the carbon in the blades, which fell from the rope can be considered sequestered in continental shelf sediments, and 10% of this carbon can be considered sequestered in the deep sea (Krause-Jensen and Duarte, 2016). This corresponds to an average of 2 kg of carbon buried in the continental shelf per longline and 5.4 kg buried in the deep sea per longline over one cultivation period at this site. In sum, these sequestration processes equate to an average of 20 kg of carbon sequestered per 100 m longline at the Strangford Lough site in 2016.

Local burial of detritus is rare in naturally occurring macroalgal forests (0.4% of primary productivity) because they attach to hard substratum (bedrock). Local burial may be more common in cultivated macroalgae systems, however, because they are often grown over sedimentary seafloors. At Strangford Lough, burial of detritus in underlying sediment is assumed to be zero because blades and detritus have not been noted to accumulate beneath the installed farm, most likely because of the tidal currents in the area. In future studies, it would be valuable for macroalgal blades or artificial blades to be marked at the cultivated site, released, and tracked in order to determine where they may be deposited.

This study has demonstrated how carbon sequestration, a key ecosystem service, provided by cultivated macroalgae can be monitored and assessed. The amount of carbon lost through both exudation and erosion may be slightly overestimated, as the average blade size at any given time was derived from the 12 largest blades per destructive sample. Additionally, the model for carbon burial and sequestration from different pools should be improved and adapted to local conditions (Krumhansl and Scheibling 2012). Despite these shortcomings, we recommend this approach over previous studies (e.g. Zhang *et al.*, 2017), in which the carbon sink of national cultivated macroalgae is estimated based on published rates of exudation, erosion, and the export of large detritus particles from naturally occurring macroalgal forests. Previous approaches may be inaccurate because the suspension of blades from a cultivation platform is physically distinct from the growth of blades up from holdfasts on the ocean floor. Blade dislodgement or loss in a mariculture system may be more common owing to the smaller area of attachment or the greater physical disturbance in the surface waters. A macroalgal farm is not entirely comparable to a naturally occurring macroalgae forest, which contains a mixture of species at different stages of maturity in a more heterogenous environment (Wood *et al.*, 2017). The direct measurement of the loss of carbon from a macroalgal farm in this study highlights the importance of empirically assessing ecosystem services instead of assuming them.

There is an argument to be made that macroalgae farmers should be compensated for facilitating carbon sequestration, just as European farmers are subsidised for adopting climate-friendly farming practices, for example (Alliance Environnement, The Thünen Institute and European Commission, 2017). It is reasonable and appropriate to compare the amount of estimated carbon sequestered in this case study to a typical agroforestry scheme, such as the Afforestation Scheme provided to landowners by the Irish Department of Agriculture, Food and the Marine from 2014-2020. Under this scheme, financial support of €6,220 is provided to establish a tree plantation on land being used for farming and an annual premium of up to €680/ha is paid. Under this scheme, for example, an established forest of 1 hectare planted with silver birch (*Betula pendula* Roth) would receive a premium of €575/ha as a broadleaf plantation other than oak or beech. Under the terms of the scheme, the biomass may be harvested and combusted, releasing the carbon stored in above ground biomass (Department of Agriculture Food and the Marine, 2015). The amount of carbon sequestered in birch soil can be negligible over time (Uri *et al.*, 2012; Friggens *et al.*, 2020), thus a generous estimation of the rate of carbon flux from young trees through plant litter is 1.2 t^{-1} ha^{-1} (Uri *et al.*, 2012), assuming that this litter is buried and not remineralized. Thus, the landowner receives €575 in a year in exchange for the carbon sequestration of 1.2 tonnes of carbon. If 100 longlines of cultivated *S. latissima* such as those described in our study covering an area of 6 ha (spacing the 100 m longlines out by 6 m) were deployed they would capture nearly two tonnes of carbon each growing periods.

As a note of caution, it should not be assumed that cultivated macroalgal installations are environmentally beneficial in all circumstances. For example, some large-scale cultivation sites that have been utilized continuously for many subsequent years are now depleted in nitrogen (Wang *et al.*, 2018). The extent of large-scale cultivation may slow the supply of nutrients entering the upper layer of the cultivation area by weakening hydrodynamic forces (Li *et al.*, 2017). This then requires fertilization or artificial upwelling interventions in order to continue cultivating macroalgae at the site, which negates the regulating ecosystem service that the installation might have previously provided. If seaweed cultivation is to be intensified and expanded, then the environmental impacts must be carefully monitored. Although seaweed cultivation has many associated ecosystem benefits, any form of large commercial activity risks negatively affecting the natural habitat (Campbell *et al.*, 2019).

CONCLUSIONS

This study shows how the carbon sequestration (a key ecosystem service integral to our natural capital) provided by farmed macroalgae can be assessed and remunerated. Future studies should also quantify erosion directly and install sediment traps below the deployed cultivation lines to estimate detrital inputs directly (Ren *et al.*, 2014). Subsidising this ecosystem service in order to incentivise farmers and entrepreneurs to develop the macroalgae industry sustainably should be considered by government and regulatory agencies (Mac Monagail and Morrison, 2020).

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DISCUSSION

Since its inception in 2011, the term "blue carbon" has been a valuable concept to focus the field of ecosystem services (more recently natural capital) on marine macrophytic communities, which have been somewhat overlooked (Macreadie *et al.*, 2019). The development of this concept is particularly timely in the Irish context, as the Climate Action Bill has been signed into law not more than a month ago and the seminal governmental report "Expanding Ireland's Marine Protected Area Network" is open for public consultation (Marine Protected Area Advisory Group, 2020). As national attention is on climate and our marine systems, there is an opportunity to push for bigger, better connected, and well-funded marine protected areas (MPAs) which protect blue carbon. This is long overdue and will be required to facilitate large scale climate mitigation tools within management strategies, such as Ireland's Marine Planning and Development Management Bill and the National Marine Planning Framework, which is the first of its kind. In order to appropriately designate and protect marine areas, however, there must be reliable scientific records of marine communities. This presents a challenge, as perhaps the most consistent conclusion from this thesis is that there is a critical lack of primary empirical research on coastal blue carbon systems.

This knowledge gap must be amended as quickly as possible because it has led to an over-reliance on coarse estimates from several key papers (e.g. Fourqurean *et al.*, 2012; Krause-Jensen and Duarte, 2016) to demonstrate the carbon sequestration of marine macrophytic communities. For example, the journal One Ecosystem was recently criticized for publicizing a study by claiming it demonstrated the ability of kelp forests to sequester carbon (Bayley *et al.*, 2021). This article, however, simply inferred the potential regional values of macroalgae-mediated carbon sequestration based on population distribution and using the same coarse estimate from 2016 mentioned above (Krause-Jensen and Duarte, 2016), which was derived from just 11 studies. This criticism applies to Chapter 3 of this thesis also – although the loss of carbon from the cultivated longlines was directly studied, the fate of this lost carbon was not observed and thus we had to defer to the limited literature to calculate the potential sequestration this represents. Similarly, a large proportion of the available data on seagrass sediments are derived from tropical climates and are used to extrapolate to global seagrass carbon estimates (Miyajima *et al.*, 2015). This does not yield realistic values of seagrass' blue carbon, however, because as we have seen in Chapter 1 the sediment carbon beneath seagrass meadows differs considerably between climatic regions. Additionally, the lack of data on the fate of macroalgal carbon (Chapter 2) has prevented policy makers from acting to conserve and account for carbon (eg. Beaumont *et al.*, 2014; Cott, Beca-Carretero and Stengel, 2021).

Using the best available alternative data is a better approach than neglecting the field entirely. There is a risk, however, that subsequent studies may misinterpret blue carbon figures derived from disjunct environments as if they are local and present them as such. The error caused by the interpretation of these figures may then lead to the overestimation of national carbon stocks or underestimate the significance of blue carbon systems and exclude them from conservation (e.g. Watson *et al.*, 2020). In the case of over-estimation, large amounts of CO_2 may be emitted with the unfounded certainty that these emissions will be offset by blue carbon sinks, which are highly effective in rapidly sequestering atmospheric CO_2 for long periods of time (Belshe *et al.*, 2017). The urge to over-emphasize associated ecosystem services from these ecosystems must, therefore, be resisted.

The lack of empirical evidence of marine carbon sequestration also results in missed opportunities. Regarding Chapter 3, Irish seaweed growers could have been cultivating seaweed for carbon sequestration and receiving subsidies to expand, particularly as hand harvesting and cultivation of macroalgae are proposed to be the most appropriate methods of expanding the macroalgae industry in Ireland (Bord Iascaigh Mhara, 2020; Mac Monagail and Morrison, 2020). Without solid evidence, however, it is difficult to argue for payment of ecosystem services. The entire framework of nature-based solutions and ecosystem services is designed to put a value on natural systems such that policy makers consider them in decision making processes (Hein *et al.*, 2020). This cannot happen if the ecosystem services are not evaluated directly and are spatially-explicit. In summary, it must be accepted that there can be no conclusive statement made on the blue carbon sequestration potential in areas where there is a lack of baseline information (Macreadie *et al.*, 2019).

The knowledge gap on blue carbon in many regions complicates the inclusion of marine carbon in national greenhouse gas (GHG) inventories and voluntary carbon markets. Inclusion into GHG inventories or carbon credit schemes and protocols requires stringent methodologies and the existing blue carbon science does not seem mature enough to allow for this. Of priority are the Nationally Determined Contributions under the Paris Agreement, which was adopted by all 196 Parties to the United Nations Framework Convention on Climate Change at the Conference of Parties 21. These NDCs are revised every five years and function as national pledges containing detailed actions on how a country will avoid average global warming above 2°C. One of the measures which may be included in an NDC is the conservation and restoration of nature to mitigate climate change. This is an opportunity for the formal recognition of blue carbon ecosystems (Gallo, Victor and Levin, 2017). In fact, a 2016 survey found that, of the 151 countries who have ratified the Paris Agreement, 28 of them have mentioned blue carbon or shallow coastal ecosystems (SCEs) in their NDCs as useful for carbon sequestration, and 59 countries mentioned these systems as useful for climate change adaptation (Martin et. al, 2016).

One of the goals in Ireland's Climate Action plan (now bill) is to reduce the emission of 26.8 Mt of CO_2 equivalent through "Land Use, Land-Use Change and Forestry" actions from 2021 to 2030, most of which are actions towards better management of grasslands, tillage land and non-agricultural wetlands (Department of Communications Climate Action and Environment, 2019). Therefore, Ireland's NDC which must contain specific, legally binding targets, may be the most appropriate place in which to formalize the national conservation of blue carbon ecosystems and subsequently be used as support to drive further detailed evaluation of these systems (Gallo, Victor and Levin, 2017).

Although a significant evidence gap regarding national carbon stocks and fluxes exists, a recent study demonstrated that the upper sediments in the UK Exclusive Economic Zone (EEZ) contain ~530 Mt of organic carbon and 2,500 Mt of inorganic carbon (Smeaton *et al.*, 2021). Similarly, two earlier Scottish studies (Porter *et al.*, 2020; Smeaton, Austin and Turrell, 2020) determined that the upper sediments in the Scottish EEZ alone contain ~200 Mt of organic carbon and ~1,500 Mt of inorganic carbon. The authors of these studies were thus able to identify sites, which function as points of organic carbon accumulation, such as fjords, estuaries, and coastal muds. These sites can then be prioritized for conservation (Parker *et al.*, 2020). A survey similar to this in the Irish context may provide both a roadmap for conservation of blue carbon systems in the emerging MPA network, and also provide a baseline figure for carbon accounting mechanisms.

One of the specific reasons why it is difficult to incorporate marine blue carbon into carbon credit schemes is the question of permanence. In terrestrial systems, carbon credits are bought and sold under the assumption that stored carbon is permanently removed from the atmosphere under a bog or forest for example (Osman-Elasha *et al.*, 2005). This is not possible in marine systems as permanence is not guaranteed. Although the deposition of organic matter in blue carbon systems may be observed, there is not enough primary data to say how long this carbon will remain in the sediment. Realistically some proportion of this deposited carbon will leak back into the atmosphere in the process of ocean circulation, and certainly a considerable amount will be remineralised and re-enter the water column (Krause-Jensen and Duarte, 2016). This ought to be a consideration for terrestrial systems too because a policy on how sequestration permanence affects carbon pricing is yet to be published (Ruseva *et al.*, 2020).

A more appropriate method of carbon accounting may be in "renting" carbon credits as opposed to purchasing them, in accordance with their residence times in some carbon sink (Marland, Fruit and Sedjo, 2001). This is not to suggest that carbon credits are less valuable if they are rented. In fact, recent modelling efforts suggest that, in the North Atlantic, the average time from carbon remineralization on the deep seafloor to exposure to the atmosphere is between 700-900 years and this average increases to over 1400 years in the North Pacific (DeVries and Holzer, 2019). These are considerable timespans for carbon storage considering that carbon storage initiatives on land, such as afforestation or bog restoration, have sequestration times estimated to be decades to a century (Smith, Haszeldine and Smith, 2016). Therefore, the use of carbon renting schemes would not diminish the importance of blue carbon sequestration in comparison to traditional terrestrial carbon sequestration, but rather be a more accurate reflection of global carbon stocks and fluxes. Regardless of the method of carbon accounting, mechanisms such as these should not replace rapid decarbonization of the economy in the face of extreme climate change. It should also be mentioned here that, despite the titular carbon in "blue carbon", these systems ought to be valued for the many other ecosystem services which they provide, such as protection from coastal erosion, nurseries, and foraging habitats, and should also be valued for the biodiversity that they harbour (Barbier *et al.*, 2011; Cullen-Unsworth and Unsworth, 2013; Smale *et al.*, 2013; Lovelock and Duarte, 2019; Schoenrock *et al.*, 2020).

By nature, marine systems are highly interconnected which presents another issue for carbon accounting. There is concern around doubly accounting for marine carbon (Oreska *et al.*, 2018). For example, if a macroalgal forest exports carbon which is counted as sequestered, and if that carbon ends up beneath a seagrass meadow and is counted again the value of blue carbon in that region will be overestimated. Sources and sinks may be very great distances away, particularly in the case of macroalgae, which poses a difficulty in evaluating carbon sequestration as discussed in Chapter 2. We agree with recent suggestions that both carbon sink habitats and carbon source habitats should be protected for the purposes of carbon sequestration (Smale *et al.*, 2018). If clearly identified, the transport corridors between source and sink might also be conserved under blue carbon initiatives. Although long and narrow marine protected areas sound impractical, similar approaches have been taken to conserve marine areas for the migration routes of cetaceans (Notarbartolo di Sciara, 2007). This strong inter-connectivity will have relevance for the development of Ireland's MPA network. The use of blue carbon systems as nurseries and habitats, for example, will only be achievable if these communities are not patchily distributed and species can move between them.

In the same way that marine communities must not be considered as distinct but connected, the different components of a blue carbon community must not be isolated from one another. Blue carbon communities must be managed holistically or using a whole system approach, as opposed to protecting the feature of carbon sequestration alone. Comprehensive management of these systems requires a whole site approach, and the feature based, reductionist approach may have contributed to mismanagement and deterioration of Ireland's marine environment (Solandt *et al.*, 2020). Of course, blue carbon ecosystems may still be chosen and conserved on the basis of the carbon sequestration they provide, but the whole ecosystem must be considered and conserved as opposed to the priority features or species alone (Chapter 2).

Thus far, we have discussed promoting blue carbon systems through protection and conservation alone. Restoration is another approach to maximizing blue carbon systems, however, which is less often discussed. It is less passive and requires more investment but recent examples such as Project Seagrass in the United Kingdom (Project Seagrass, 2021) have demonstrated the possibility of active, large-scale seagrass restoration. Restoration approaches are similarly being researched for macroalgal forests but the lack of a robust macroscopic propagule like seeds in the life cycle presents a difficulty (Vanderklift *et al.*, 2020). The use of "green gravel", small stones coated in young sporophytes of macroalgae and dropped into waters of an appropriate depth are more cost effective than those approaches that require divers to fix material to the seafloor or coastal walls (Fredriksen *et al.*, 2020).

In the context of global anthropogenic emissions, the impact of blue carbon ecosystems may seem negligible. In order to keep global temperature rise below 1.5 °C by 2050, global greenhouse gas emissions must be heavily reduced. If blue carbon systems were conserved and expanded internationally, and the cultivated macroalgal sector was expanded, this would still only account for 1.4% of the emissions reductions required to meet this 2050 target (Hoegh-Guldberg *et al.*, 2019). Although this may seem like a small amount, this reduction in emissions is approximately equivalent to the annual emissions from coal power plants worldwide. Fundamentally, in the context of biodiversity decline on the scale of a mass extinction, and global warming occurring at an unprecedented rate of change, we simply cannot afford to neglect climate-regulating natural ecosystems any longer (Cafaro, 2015).

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SUPPLEMENTARY MATERIAL 1. FULL TEXT PAPERS EXLCUDED FROM REVIEW

1. Other reviews

Previous reviews, meta-analyses, and synthesis papers which may include first order estimates of the fate of macroalgal carbon. These estimates set a valuable baseline, however they are averaged across disparate ecosystems, tend to have very large ranges, are often based on a number of assumptions, use calculations with low sample numbers, and in some cases were interpreted from qualitative information - all of which incur error. Commentary papers located by the initial search make valuable contributions to the discussion of macroalgal carbon but fail to address the fate of macroalgal carbon.

Citation	Article summary
(Cebrian, 1999, 2002; Chung *et al.*, 2011; Krumhansl and Scheibling, 2012; Trevathan-Tackett *et al.*, 2015; Krause-Jensen and Duarte, 2016; Davidson *et al.*, 2018; Krause-Jensen *et al.*, 2018; Ortega *et al.*, 2019)	Compared the absolute magnitude of different routes of carbon flow in macroalgal communities during and after production, quantifying how much carbon is directed to absolute consumption, decomposition, export, or refractory accumulation.
(Duarte and Cebrián, 1996; Krause-Jensen and Duarte, 2016)	Compared the percentage of production exported from macroalgal communities during and after production, quantifying how much carbon is directed to absolute consumption, decomposition, export, or refractory accumulation.
(Hill *et al.*, 2015; Sondak and Chung, 2015; Filbee-Dexter and Wernberg, 2020)	Estimated the potential national carbon stock provided by macroalgae based on areal extent or standing biomass.
(Duarte, 2017)	Highlighted the need for accurate carbon fluxes of vegetated coastal habitats, including macroalgae forests.
(Duarte *et al.*, 2018)	Argued that the capacity for carbon sequestration through macroalgal photosynthesis is threatened by ocean warming and acidification.
(Froehlich *et al.*, 2019; Watson *et al.*, 2020)	Argued that if macroalgal productivity does indeed provide a carbon sink then the national proprietary macroalgal forests should be evaluated as capital and traded as carbon credits.
(Duarte *et al.*, 2013; Krause-Jensen *et al.*, 2018; Macreadie *et al.*, 2019)	Argued that for macroalgal carbon to be accounted as mitigating climate change, both national and internationally agreed guidelines must be amended.
(Smale *et al.*, 2018)	Argued that terrestrial carbon budgeting approaches may not be transferrable to marine environments due to the high connectivity between marine environments.
(Raven, 2018).	Argued that the role of macroalgae in carbon storage will depended on the dominant form of macroalgae (calcareous/ haptophytic/ pleustophytic).

2. Productivity alone

The second notable type of paper which did not meet the selection criteria of this systematic review were those monitoring processes such as community respiration and productivity within macroalgal dominated ecosystems. Productivity measurements were informative on how much photosynthesis occurs but not on the fate of this newly captured organic carbon and thus these papers were excluded.

Citation	Article summary
(Mann, 1972a, 1972b; Smith, 1981; Attwood *et al.*, 1991; Vadas, Sr., Wright and Beal, 2004; King *et al.*, 2020; Smale *et al.*, 2020; Menge *et al.*, 2021)	Measured macroalgal productivity by increase in foliar length or biomass accrual over time. Argued that this high productivity likely represents a significant global carbon sink.
(Hatcher, Chapman and Mann, 1977; Golléty, Migné and Davoult, 2008; Bordeyne, Migné and Davoult, 2015; Kim *et al.*, 2015; Tait *et al.*, 2015; Spector and Edwards, 2020)	Measured intertidal macroalgal community productivity and respiration locally or *in-situ* using benthic chambers. Measured carbon dioxide consumption or oxygen generation as a proxy for carbon dioxide consumption through photosynthesis.
(Attard *et al.*, 2015, 2019; Ikawa and Oechel, 2015; Rovelli *et al.*, 2019)	Measured subtidal macroalgal community productivity and net metabolism *in-situ* using aquatic eddy covariance (AEC). Measured oxygen flux as a proxy for the balance between community production and respiration.
(Tait and Schiel, 2011; South *et al.*, 2016; Figueroa *et al.*, 2021).	Measured macroalgal community net primary productivity using pulse amplitude modulated (PAMs) fluorometry.
(Towle and Pearse, 1973; Bensoussan and Gattuso, 2007; Delille, Borges and Delille, 2009)	Measured macroalgal community metabolism using the change in dissolved inorganic carbon as a proxy for carbon dioxide consumption through photosynthesis.
(Randall *et al.*, 2019)	Measured macroalgal productivity using a combination of the techniques above in order to assess their utility and accuracy.

3. Tracer molecules

Tracer molecules are used to investigate the flow of macroalgal carbon from its origin to another community. While these papers provide useful information, they do not give insight into the amount of carbon immobilized in sediment in terms of spatial units and this prevents the comparison of macroalgae to other communities. Stable isotopes, environmental DNA (eDNA), sterols and *n*-alkanols of varying chain length, and biomarkers such as lignin, lipids, carotenoids, alkanes and amino acids have all been used to trace macroalgal carbon.

Citation	Article summary
(Alldredge, Carlson and Carpenter, 2013; Gabara, 2020)	Identified the export of macroalgal carbon to a previously unrecognized or significant carbon sink/receiver site using stable isotope ratios.
(Ortega *et al.*, 2019; Ortega, Geraldi and Duarte, 2020)	Identified the export of macroalgae to the open ocean or the deep sea using eDNA (environmental DNA) samples.
(Simenstad and Wissmar, 1985; Duggins, Simenstad and Estes, 1989; Simenstad, Duggins and Quay, 1993; Rodríguez, 2003; Vizzini and Mazzola, 2008; Wai *et al.*, 2008; Crawley *et al.*, 2009; Tallis, 2009; Mayr *et al.*, 2011; Miller and Page, 2012; Leclerc *et al.*, 2013; Koenigs, Miller and Page, 2015; Renaud *et al.*, 2015; Zenteno *et al.*, 2018; Elliott Smith, Harrod and Newsome, 2018; Tuntiprapas *et al.*, 2019; Udy *et al.*, 2019; Alurralde *et al.*, 2020; Sandoval *et al.*, 2020; Santos *et al.*, 2020; Kahma *et al.*, 2020).	Identified the flow of a particular macroalgal carbon source into and throughout some food-web using stable isotope ratios. These papers had varying levels of detail and included a varying number of trophic levels.
(Fischer and Wiencke, 1992; Smit *et al.*, 2006; Zaborska *et al.*, 2016; Abdullah, Fredriksen and Christie, 2017; Dauner *et al.*, 2017; Atwood *et al.*, 2018; Garcias-Bonet *et al.*, 2019; Hidayah, Rozaimi and Nadzir, 2019; Kindeberg *et al.*, 2019; Santos *et al.*, 2019; Saavedra-Hortua *et al.*, 2020)	Identified organic carbon attributable to macroalgae in a particular sediment using stable isotope ratios. This includes sediments beneath other "blue carbon" systems, such as mangroves and seagrass beds.
(Kaehler *et al.*, 2006; Bearham *et al.*, 2020)	Identified organic carbon attributable to macroalgae in a particular water body using stable isotope ratios.
(Bode, Alvarez-Ossorio and Varela, 2006; Wai *et al.*, 2008; Kelly, Krumhansl and Scheibling, 2012; Paar *et al.*, 2019; Both *et al.*, 2020; Fey *et al.*, 2020; Venturini *et al.*, 2020)	Used stable isotope ratios in combination with another tracer molecule to resolve uncertainty through cross validation.
(Hyndes, Lavery and Doropoulos, 2012)	Experimentally enriched wild macroalgae with labelled isotopes in order to trace the isotopic signature to another community.

4. Mesocosm, microcosm, and incubation studies

Mesocosms, microcosms, and lab-based incubations are valuable in comparing physiological responses of macroalgal productivity and carbon sequestration under different conditions of light, temperature, pH, and more. Unfortunately, the complexity of a macroalgal canopy cannot be reproduced in a laboratory, in particular the self-shading and light limitation caused by multiple individuals (Sand-Jensen, Binzer and Middelboe, 2007). For this reason, these experiments alone cannot be used to determine whole ecosystem productivity or the fate of that productivity.

Citation	Article summary
(Barrón *et al.*, 2003; Hardison *et al.*, 2010; Ravaglioli *et al.*, 2019; Tsubaki *et al.*, 2020)	Macroalgae in mesocosms were artificially enriched with carbon, which may have been isotopically labelled, in order to trace carbon flow into macroalgal tissue and through to faunal tissue and sediments under varied abiotic conditions.
(Kaladharan, Veena and Vivekanandan, 2009; Zuñiga-Rios *et al.*, 2021)	Measured macroalgal productivity under varied abiotic conditions.
(Naumann *et al.*, 2013)	Combined laboratory measured rates of production with *in situ* macroalgal density data to estimate net primary production of entire communities.
(Barrón *et al.*, 2003; García-Robledo *et al.*, 2008; García-Robledo and Corzo, 2011; J. Chen *et al.*, 2020; S. Chen *et al.*, 2020)	Identified the forms in which macroalgal carbon occurs in the components of an experimental system over time, eg. in the sediment or water.
(Sundbäck *et al.*, 1990; McGlathery, Anderson and Tyler, 2001; Braeckman *et al.*, 2019; Liu *et al.*, 2020).	Investigated carbon flows within and through community assemblages which included macroalgae.
(Koop, Newell and Lucas, 1982; Robinson, Mann and Novitsky, 1982; Ruiz-Halpern *et al.*, 2010; Sosik and Simenstad, 2013; Dethier *et al.*, 2014; Ito *et al.*, 2019; Yorke, Page and Miller, 2019; Diaz-Pulido and Barrón, 2020)	Investigated and quantified the method of loss of carbon from macroalgae, eg. via macrofaunal grazing or passive exudation. This may have been combined with *in situ* data on import and export of macroalgal detritus from a certain community.

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