Assessing novel cultivation methods, baseline fish assemblages and survey methodologies of cultivated and wild kelp in the Southwest of Ireland

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Table of Contents

Declaration

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Acknowledgments

Abstract

Kelp (i.e. large brown macroalgae of the order Laminariales) are important habitat-forming species in coastal ecosystems. Recently, the key role kelp play as part of an expanding blue economy has been recognised in addition to their use as a mitigation tool for climate-driven impacts and other threats posed by anthropogenic activities. Unfortunately, kelp beds and forests globally are under increasing threat due to anthropogenic activities. Paradoxically, kelp has been identified as a mitigation tool for multiple anthropogenically induced environmental impacts. It has arguably never been more urgent to address key knowledge gaps to understand the role kelp play in coastal ecosystem functioning. This study aimed to: (i) address current knowledge gaps surrounding the link between diversity and productivity in relation to biomass production in algal aquaculture (Chapter 2); (ii) describe the fish communities associated with wild kelp beds in SW Ireland (Chapter 3); and (iii) test methods of quantifying fish assemblages associated with kelp farms (Chapter 4). The interaction between juvenile sporophytes of three native Irish kelp species were found to be selective, with a single species dominating in mixed assemblages. The fish communities associated with *Laminaria hyperborea* were mainly composed of species of the families *Gobiidae, Gadidaea* and *Labridae*. Underwater visual census surveys via scuba were identified as an appropriate method for quantifying fish communities at kelp cultivation structures.

Chapter 1: Introduction

Temperate kelp forests face increasing threats from anthropogenic activities (Assis et al., 2016, Franco et al., 2018, Oksanen et al., 2022). At a global scale, ocean warming is driving marine species range shifts poleward (Poloczanska et al., 2013), which may result in changes to community structure and consequently ecosystem functioning in areas of species loss, gain or both (Sorte et al., 2010). At regional and local levels resource extraction, development, introduction of non-native species, high-intensity weather events and pollution threaten the resilience of current kelp habitats to global processes (Smale et al., 2013). As the distribution and abundance of this foundation species changes both regionally and globally, understanding the relationship with its associated communities will be vital for predicting impacts on ecosystem functioning in temperate coasts, which may also affect the wider marine environment indirectly (Viitasalo and Bonsdorff, 2022, Coni et al., 2022).

Kelp species (i.e. large brown macroalgae of the order Laminariales) form a fundamental part of marine coastal systems from the lower intertidal zone to shallow subtidal zone in temperate to polar regions (Araujo et al., 2021). Kelp stands are drivers of primary (White et al., 2021) and secondary (Shelamoff et al., 2020)productivity, facilitating trophic linkages (Schaal et al., 2010) that increase biodiversity (Teagle et al., 2017, Shelamoff et al., 2020). Kelps also have significant cultural and practical importance to society from the ecosystem services provided, for example, coastal defence, nutrient cycling, carbon sequestration (Hasselström et al., 2018). They are also cultivated and harvested for an increasing range of uses from food and feed (Nayar and K, 2014, Monagail et al., 2018), to biofuels (Shushpanova and Kapralova, 2021) and pharmaceuticals (Kang et al., 2016), which has driven an 8% annual increase in commercial macroalgae production over the last decade (Aldridge et al., 2021, Visch et al., 2020b, Walls et al., 2019, FAO, 2018).

Heterogeneity, or complexity, of habitat is a well-known factor in biological productivity, diversity and abundance within biological systems. Physiological diversity within foundation species can exponentially increase overall biodiversity by facilitating habitat niches suitable to a wider range of flora and fauna (Thomsen et al., 2022). Experimental grassland model systems sown in polycultures have resulted in higher biomass yield, utilisation of resources and stability across temporal scales compared to monocultures (Tilman and Wedin, 1996). Species diversity within macroalgal communities has also been shown to influence overall biodiversity-ecosystem functioning in the marine environment (Hall et al., 2018, Vaz-Pinto et al., 2014). Understanding the role macroalgal diversity plays in marine primary productivity can contribute to understanding the ecological mechanisms through which macroalgal diversity influences biodiversity-ecosystem functioning, and how these may be affected by the loss/gain of macroalgal species.

The primary productivity rates of macroalgae have been utilised for commercial exploitation through aquaculture worldwide. In Asia, it is a well-established industry, where China alone produces roughly half of the worlds macroalgal biomass (Visch et al., 2020b). In Europe and North America, a fledgling industry has slowly developed at a small scale to provide biomass for some high-value products, but is unable to grow owing to much higher running costs and lower market demand than in established Asian regions (Grebe et al., 2019). For the industry to grow in Europe, novel cultivation techniques and technologies will be required to increase production while reducing production costs (Hasselström et al., 2020, Bak et al., 2018).

Any negative ecological effects of macroalgal cultivation are relatively unknown in Europe owing to the lack of scaled operation upon which to conduct studies with measurable impacts. Research to date has demonstrated distinct epibiont communities associated with cultivated kelp (Walls et al., 2017a), the contribution of cultivated biomass to marine detrital

pathways (Krause-Jensen and Duarte, 2016), nutrient mitigation capabilities (Visch et al., 2020a), the limited benthic impacts on *Zostera marina* biomass below cultivation sites (Walls et al., 2017b) and a reduction in suspended solids in kelp farming areas owing to reduced turbidity (Jiang et al., 2020). Currently, macroalgal cultivation promises to be a relatively clean activity with relatively low impact compared to finfish aquaculture. Macroalgae have even been proposed for incorporation into Integrated Multitrophic Aquaculture to mitigate excess nutrient outputs from finfish aquaculture (Rugiu et al., 2021).

At the time of writing, there is currently very little published literature on the actual value of macroalgal cultivation sites as semi-natural habitat. Semi-natural habitats can be beneficial to enhancing biodiversity in marine environments (Salomaa et al., 2017). Many species, especially those associated with natural kelp beds, may forage and shelter among cultivated kelp lines consisting of similar species to their native affinity. that matches their preferred natural habitat. Although there has been research on whether the presence of kelp farms influence fish assemblages in the surrounding seabed (Visch et al., 2020b, Leonardo Lara de et al., 2015), no studies to date have tested directly which species utilise the physical structure of cultivated macroalgae as habitat, and thus their effect on fish stocks whether positive or negative remains difficult to estimate.

To accurately assess the use of macroalgal cultivation structures as habitat requires sampling methodologies capable of detecting a broad range of species. It is common and recommended that more than one methodology be utilised when quantifying complete assemblages to maximise the likelihood of recording species that may be more easily detected by one method over another (Jessop et al., 2022). Three methods were deployed to assess habitat usage and test methodological procedures; underwater drone transects, baited traps and underwater

visual census by SCUBA. The results will inform future studies/surveys on appropriate methodologies to deploy.

As anthropogenic activities threaten the distribution, diversity and abundance of kelp beds across temperate regions while interest in its cultivation grows simultaneously, research into the importance of diversity within kelp species on ecosystem functioning, the communities of organisms reliant upon them, a refinement in methodologies and acquiring baseline data will be vital for understanding and managing this resource at regional and global levels.

Chapter 2 - Does greater diversity increase productivity of cultivated kelp?

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Abstract

Macroalgal cultivation and wild harvest continues to grow year on year into the 21st Century. Simultaneously, climate change and anthropogenic activities threaten the distribution and abundance of wild brown seaweeds worldwide. It has, therefore, never been more important to understand how diversity may be related to associated rates of ecosystem functioning/ productivity of macroalgal assemblages. There is also a commercial interest in Europe and North America to improve the economic efficiency of kelp farming in order to compete with established industries in Asia. In this study, it was hypothesised that kelp productivity will increase with greater species richness within macroalgal assemblages. To test this, an experiment was designed based on seven treatments comprised of three monocultures of the common kelp species, *Alaria esculenta*, *Saccharina latissima* and *Laminaria digitata,* three treatments of 2-species mixtures of each species and a 3-species polyculture of all three kelp species. Treatments were established in a hatchery and grown to harvesting size on long lines at a macroalgal cultivation site in Toormore Bay, Co. Cork, Ireland. Total biomass was quantified as proxy for general productivity of each treatment. It was found that interactions between kelp species grown in close proximity appear to be selective rather than complementary. A single species typically dominated within polyculture treatments. The only difference in biomass production occurred between *L. digitata* and the other two monoculture treatments, for which *L. digitata* produced significantly less biomass. These results highlight

our lack of understanding of intraspecific interactions between co-occurring macroalgal species. These findings have implications for both the aquaculture industry and ecological theory. For sites with unpredictable environmental parameters, multi-species seeding of cultivation lines will allow the most suited species to a particular site to proliferate. Influential environmental and ecological parameters at an early developmental stage appear to be the determining factor in wild kelp succession.

Introduction

Comparing productivity of primary producers in a assemblages of varying diversity has been well-studied in a variety of model systems, including grasslands (Dukes, 2001, Hector et al., 2010), terrestrial forests (Haggar and Ewel, 1997), cropland (Picasso et al., 2011) and microalgae (Thomas et al., 2019). Comparatively less research has been undertaken on the productivity of macroalgal communities of varying species diversity (Crowe et al., 2012, Tait and Schiel, 2011). The subsequent knowledge gaps have implications for making predictions on the effects of species loss driven by climate change on coastal ecosystems, best management practices for wild kelp harvest, optimal methods for macroalgal cultivation and the role macroalgal forests play in marine primary productivity in general.

Heterogeneity (or complexity) of communities is a well-known factor in biological productivity, diversity and abundance within biological systems. It is accepted generally that increased diversity of primary producers can result in greater overall rates of primary productivity (Tilman and Wedin, 1996, Loreau and Hector, 2001, Thomas et al., 2019). Diversity within foundation species can also exponentially increase overall biodiversity owing to niche facilitation, provided via secondary and tertiary foundation species to a wide range of species (Thomsen et al., 2022).

Greater diversity has also been linked with increased stability when faced with fluctuating environmental conditions (Godwin et al., 2018), which was thought to be driven by complementarity of species within assemblages (Boyer et al., 2009, Hector et al., 2010). Grassland model systems sown in polycultures have resulted in higher biomass yield, utilisation of resources and stability across temporal scales compared to monocultures (Tilman and Wedin, 1996, Ashworth et al., 2018). This suggests that diversity is an important factor promoting resilience of assemblages to extreme weather events linked to climate change (Isbell et al., 2015). Field studies have further suggested these same diversity-stability/productivity relationships operate in marine foundation species such as kelp (Wernberg et al., 2018).

Temperate kelp forests face increasing threats from anthropogenic activities (Nimbs et al., 2023, Smale et al., 2013). At a global scale, ocean warming is facilitating marine species range shifts (Poloczanska et al., 2013), which is likely to result in changes to community structure and consequently, ecosystem functioning in areas of species loss, gain or both (Sorte et al., 2010). The consequence of ocean warming for kelp species in temperate seas are that their distributions and ranges will shift poleward (Assis et al., 2016, Schoenrock et al., 2020). At regional and local levels resource extraction, development, introduction of non-native species, high-intensity weather events and pollution threaten the stability of current kelp habitats to global processes (Smale et al., 2013). As the identity of key foundation species changes (Duarte et al., 2013), understanding the relationship with its associated communities will be vital for predicting the impacts on ecosystem functioning in temperate coasts, with relevance to the wider marine environment (Himes-Cornell et al., 2018).

Kelps form a fundamental part of marine coastal systems from the lower intertidal zone to shallow subtidal zone in temperate to polar regions (Araujo et al., 2021). Kelp stands are drivers of primary and secondary productivity, facilitating trophic linkages that increase biodiversity (Teagle et al., 2017, Shelamoff et al., 2020). Kelps also have significant cultural and practical

importance to society from the ecosystem services provided such as coastal defence, nutrient cycling, carbon sequestration and utilisation for an increasing range of uses from food and feed, to biofuels and pharmaceuticals, which has driven an 8% annual increase in commercial macroalgae production over the last decade (Aldridge et al., 2021, Visch et al., 2020b, Walls et al., 2019). Kelp aquaculture has been identified as an activity that addresses numerous UN Sustainable Development Goals, such as climate change, water quality, food security and protecting our marine resources (García-Poza et al., 2022).

The kelp cultivation industry in Europe is growing, but remains at a much smaller scale than in the Asian-Pacific region. Europe, combined with the United States, only produced 1.4 % of global gross biomass in 2014 (FAO, 2016). Domestic consumption in Europe of kelp products is typically in the form of specialty cosmetic additives and food products, driving a higher wet weight value than kelp grown in Asia (Grebe et al., 2019). Compared to Asia where macroalgae are a commodity product (Grebe et al., 2019), European kelp production faces higher production costs at smaller scales and overall lower local market demand (Bak et al., 2018). To protect the emergent industry already operating while also encouraging investment and development, unique improvements to current cultivation methods will be necessary to improve European kelp cultivation's cost effectiveness.

This study aimed to test experimentally whether more species rich mixtures of kelp species are more productive than less species rich, or monocultures, of kelp species and for differences among species. Three of the most common kelp species in the NE Atlantic region (*Alaria esculenta*, *Saccharina latissima* and *Laminaria digitata*) were cultivated and grown to harvestable size on long lines in SW Ireland. The hypothesis was that complementarity-driven productivity would result in greater biomass accumulation in the mixture of three species compared to two-species mixtures, which would in turn be greater than the monocultures. Understanding the impact of macroalgal diversity loss (or species identity change) on rates of

primary productivity will be important to predict the indirect effects on trophic linkages and associated ecosystem services. These results will help develop a more precise understanding of the effects of potential primary producer diversity on overall productivity by marine macroalgae.

Methods

Experimental Design

To test the hypotheses that productivity would be greater when algal species richness was greater, an experiment was conducted that manipulated the identity and species richness of three kelp species (*A. esculenta*, *S. latissima* and *L. digitata*) with overlapping distributions and that are suitable for cultivation. Total productivity was estimated by quantifying their total biomass and estimating their growth from gametophyte through to sporophyte phase in each experimental treatment. The experiment included seven treatments comprised of three native kelp species across a gradient of species richness (1, 2 and 3 species present). These were: (i) *A. esculenta* (1 species); (ii) *S. latissima* (1 species); (iii) *L. digitata* (1 species); (iv) *A. esculenta* with *S. latissima* (2 species); (v) A. esculenta with L. digitata (2 species); (vi) S. latissima with *L. digitata* (2 species) and (vii) a mixture of all species *A. esculenta* and *S. latissima* and *L. digitata* (3 species). Each treatment was established as independent experimental units and replicated five times (Figure 1).

The gametophytes for the experimental treatments were cultivated at Bantry Marine Research Station and the sporophyte growth phase was conducted at an existing cultivation site in Toormore Bay, Co. Cork, Ireland (51º 29' 32.711" N, 9 º 37' 44.626" W). The site was situated in approximately 12-20 m depth of water. Open to prevailing south-westerly winds, the site is classified as very exposed (Ballantine, 1961). Sea surface temperatures in the region range

from approximate lows of 9.5 °C in early Spring to 20.5 °C in early Autumn, averaging around 13.5 °C (Marine Institute, 2023)
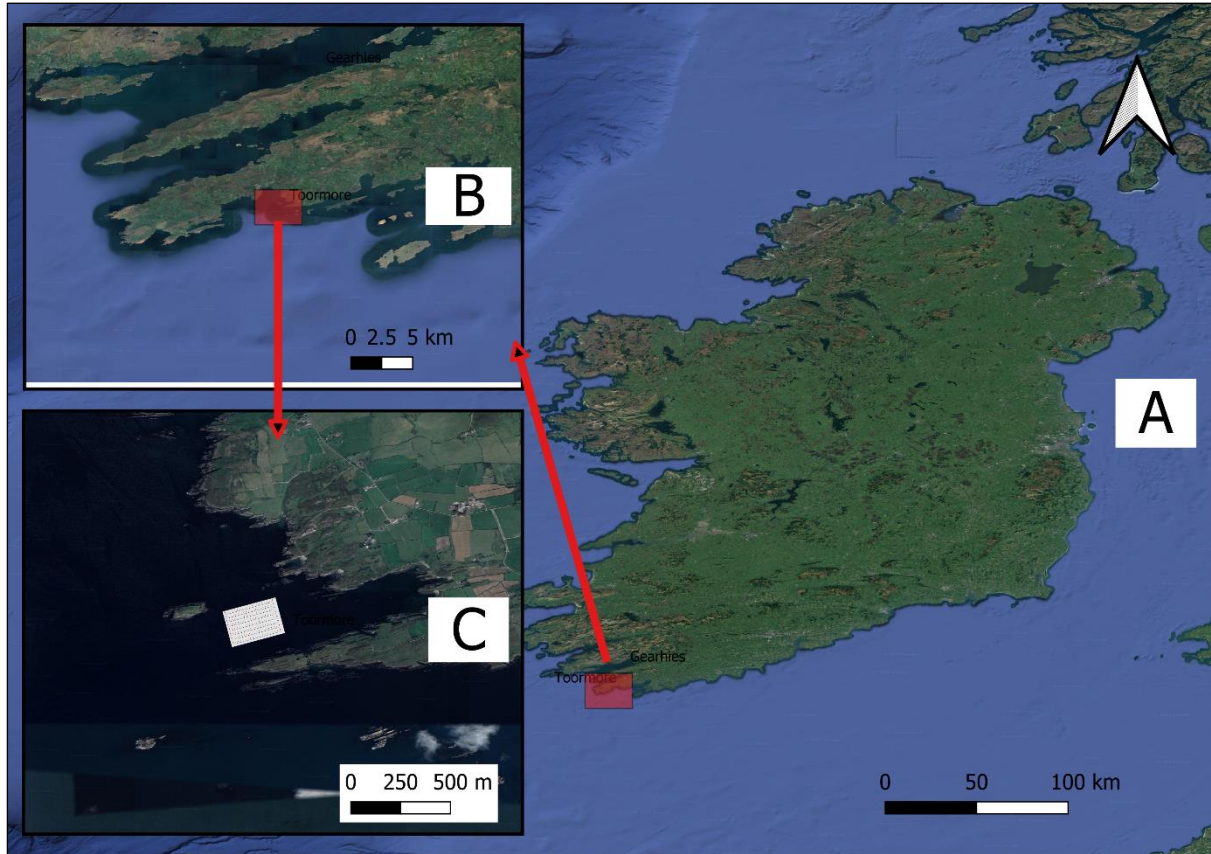

Figure 1: location of the macroalgal cultivation site in Toormore Bay, Co. Cork, Ireland.

The culturing process from sori collection to seeding and sporophyte development at Bantry Marine Research Station followed standard operating procedures (Edwards et al., 2016). Forty sporophytes of each species were collected from close to the hatchery in Bantry, Co. Cork, Ireland. Collections were carried out when the sori were ripe (i.e. April 2021 for *A. esculenta*, June 2021 for *S. latissima* and August 2021 for *L. digitata*). To establish experimental treatments and avoid confounding potential treatment effects with gametophyte density (O'Connor and Crowe, 2005), the density of gametophytes was standardised across all treatments at 14 g·l⁻¹ (estimated following Edwards et al. (2016)). The experimental treatments

were then established by mixing gametophyte cultures at equal ratios of 1:1 for two-species polycultures and 1:1:1 for 3-species polycultures. An electric paint sprayer (Wagner Universal Sprayer W 590 FLEXiO) was used to seed two collectors, facilitating settlement from the plankton to benthic life phase, for each treatment evenly using 600 ml of each treatment's gametophyte culture. These seeded collectors (string) were stored in tanks with UV-filtered seawater at 10 ˚C, light intensity 40 µmol·m^{-2}·sec^{-1}, photoperiod 12:12 for around 6 weeks separated by treatment to avoid cross-contamination and allow development and early growth of each species (Edwards et al., 2016). Seeded string for each of the seven treatments were then deployed at sea in experimental units of 10 m sections of cultivation line ($n = 5$) at predetermined points that were selected randomly across three parallel long-lines (*figure 1.*). The long-lines at the site were 200 m in length, separated by approx. 10 m, where depth varied from 1.5 m – 5 m.

After 66 days of growing at sea (and during the typical harvest period for kelp cultivation) all accumulated algal biomass was quantified. It was noted that one full line and part of another amounting to 13 experimental units in total (2 replicates from each monoculture and two species polyculture and 1 from three-species polyculture) had been lost due to suspected vandalism. Biomass was estimated by full removal of 2 x 0.5 m subsamples on each replicate. Samples taken from each 10 m experimental unit were taken at 1 m and 5 m from the beginning of each section. All algal biomass (stipe and blade material above the holdfast) was removed with a knife by hand. Occasionally some holdfast material was removed with the rest of the biomass in small amounts as is typical in an aquaculture setting, however, the same individual was responsible for sample removal to apply consistency to end sample quality. All biomass samples were collected on the same day and brought immediately to the processing area post-harvest. Samples were shaken five times to remove excess water prior to weighing. Species

within each sample were separated and weighed. Where the biomass of each individual species was not sufficient to trigger a reading on the scales, the value was recorded as 0.01 kg.
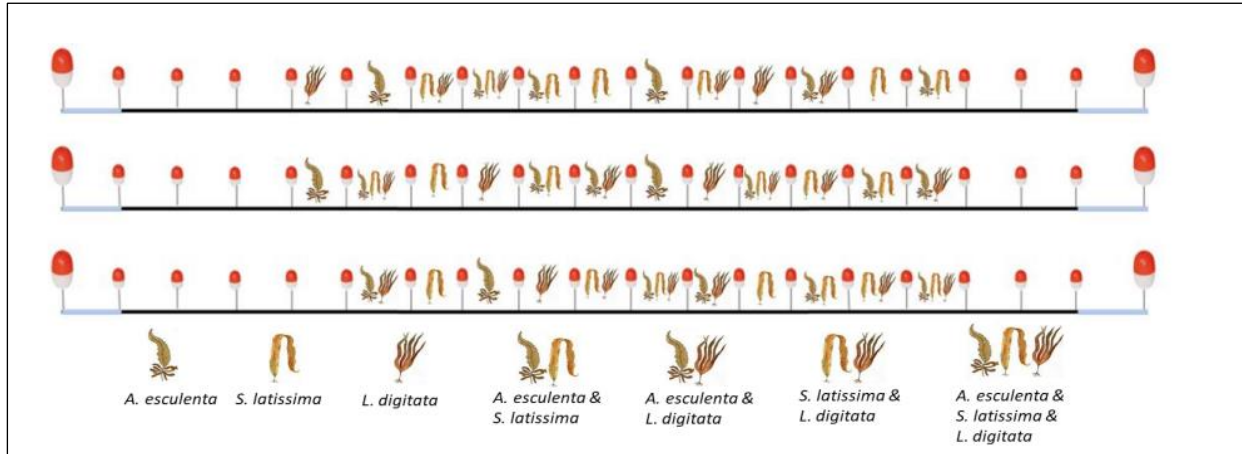

Figure 2. Experimental set-up at Toormore Bay, Co. Cork, from January – April 2022, including all seven experimental treatments; Alaria esculenta *(1 species),* Saccharina latissima *(1 species),* Laminaria digitata *(1 species),* A. esculenta *with* S. latissima *(2 species),* A. esculenta *with* L. digitata *(2 species),* S. latissima *with* L. digitata *(2-species), and a mixture of* A. esculenta*,* S. latissima *and* L. digitata *(3 species).*

Data Analysis

Prior to formal analyses a Shapiro-Wilk test for normality and Levene's test homogeneity of variance were carried out and indicated that total biomass data did not conform with the assumptions required for traditional ANOVA. The data were subsequently analysed using a generalised linear model (GLM). The model was fitted with fixed factor 'Treatment' and the response variable total biomass yield (kg/m^{-1}). There were seven levels of the fixed factor representing each independent experimental treatment: (i) *Alaria esculenta*; (ii) *Saccharina latissima*; (iii) *Laminaria digitata*; (iv) *A. esculenta* with *S. latissima*; (v) *A. esculenta* with *L. digitata*; (vi) *S. latissima* with *L. digitata;* and (vii) a mixture of all species *A. esculenta* and *S. latissima* and *L. digitata*. To determine the model of best fit, the GLM was ran with various

combinations of family functions (gaussian, inverse.gaussian, gamma, quasi) and associated link functions. The model of best fit was determined by lowest AIC value, which was gamma distribution and inverse link function, aligning with the right-skewed distribution of the data as determined visually (Zuur et al., 2009). Significant values from the GLM were analysed further through Holm's post-hoc pairwise comparison (Tressler and Chow, 2013). In addition, the percentage contribution of each species towards each polyculture total biomass was estimated to compare the performance of each species within each treatment. All data analyses were carried out in R (R Core Team, 2022) using the vegan package (Oksanen et al., 2022).

To analyse different species' contributions to the total biomass of each treatment, a PERMANOVA was performed based on a Bray-Curtis dissimilarity matrix (Clarke and Gorley, 2006) created using the ecodist package (Goslee and Urban, 2007) and square-root transformed biomass data for each species in each treatment. Following a significant output, SIMPER analysis was executed using the vegan package in R (Oksanen et al., 2022, R Core Team, 2022) to identify whether the species driving dissimilarity between significantly different groups were driven by the species characterising each specific treatment.

Results

Total algal biomass was found to differ among experimental treatments (*Figure 3.*, pseudo-R^2 = 0.473319). Although subsequent post hoc tests were inconclusive, it appears that *L. digitata* monoculture treatment biomass production was lower compared to the other two monocultures (*Figure 3.*).

Analysis of the composition of the total algal biomass reveals that the initial experimental treatments established at gametophyte stage transformed during the sporophyte growth phase (*Figure 4.*). Multivariate analyses show that there were large differences in composition

between treatments did not reflect their initial even seeding ratios (PERMANOVA, $R^2 =$ 0.828, F = 32.828, p = 0.001 < 0.05). It is clear that *L. digitata* did not perform well in any experimental treatment and that one species has ultimately dominated in each treatment by the end of the experiment.

The species contribution towards the biomass yield within each polyculture treatment was typically dominated by an individual species (*Figure 4.*). *Alaria esculenta* dominated all polyculture mixtures where it was present. *A. esculenta* accounted for 88 % of biomass when grown with *S. latissima*, 98 % when grown with *L. digitata*, and 93.4 % of biomass in the treatment containing all three species.

Similarly to *A. esculenta*, *S. latissima* outperformed *L. digitata* when grown together accounting for 99% of total biomass in this polyculture. However, it was substantially outperformed by *A. esculenta* when co-occurring, only accounting for 12 % and 6 % of biomass when grown together in 2-species and 3-species polycultures respectively.

L. digitata performed poorly within each polyculture mixture where it was present. *L. digitata* yielded only 2 % and <1 % of biomass within the *A. esculenta* and *S. latissima* two-species polycultures respectively. Within the three-species polyculture, *L. digitata* only produced <1 % of biomass on average. Comparing the three species treatment with two-species treatment of *A. esculenta* and *S. latissima*, *L. digitata* contributes the least to the difference between the two treatments than the other two species (SIMPER, *L digitata* = 0.12 % contribution to dissimilarity, p = 0.976 > 0.05). Interestingly, *L. digitata* only produced 92 % of the biomass within its monoculture, with the rest mainly accounted for by *A. esculenta* (~ 8 %).
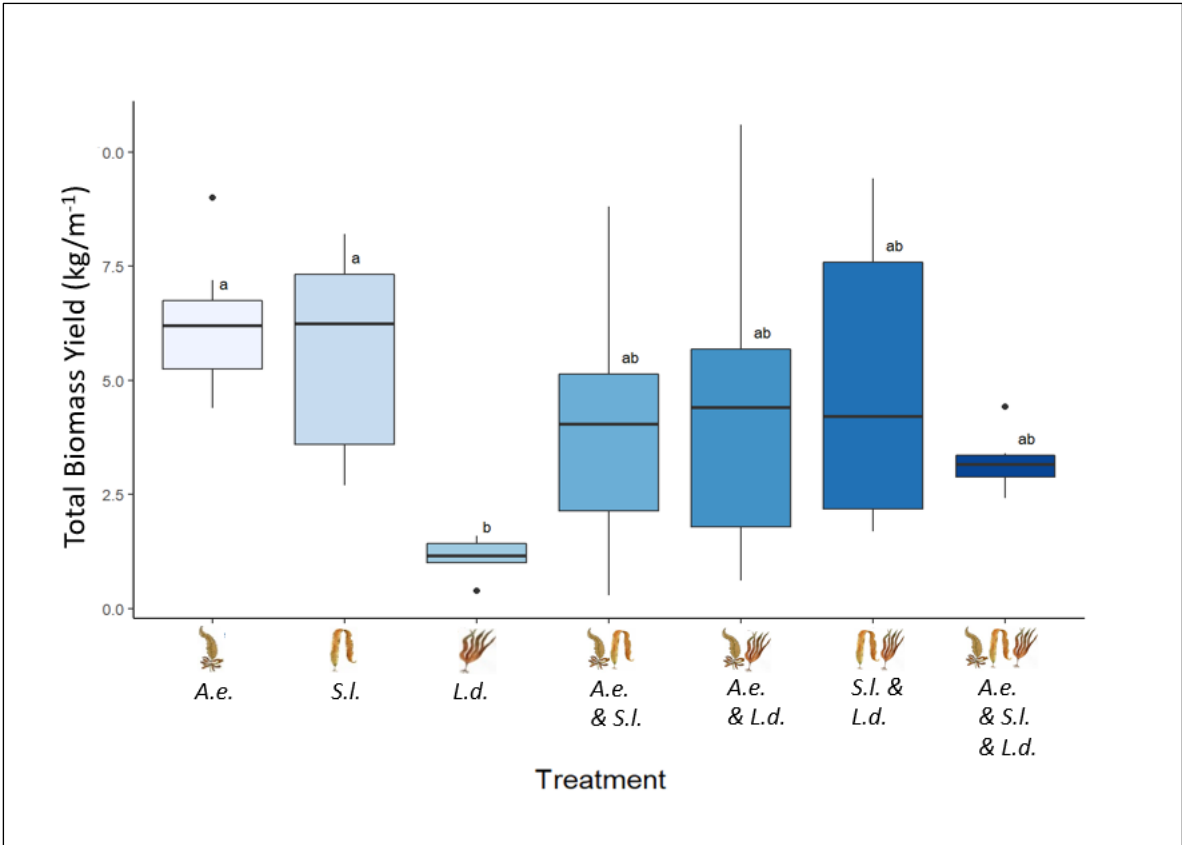
Figure 3. Medians and interquartile ranges of total kelp biomass in experimental treatments with 1, 2 or 3 species of kelp. Lower case letters represent groups of means that are statistically indistinguishable (p < 0.05) based on Holm's post-hoc test.

Figure 4. The percentage contribution of each species towards total accumulated algal biomass in each treatment. X-axis labels represent initial experimental treatments and colours show their final composition at the end of the experiment. A. esculenta *represented in green,* S. latissima *in orange, and* L. digitata *in blue.*

Discussion

This study was designed to test for effects of species richness on algal biomass production, however, the results show that inter-species competition drove variation in individual species responses when in mixtures at their early growth phas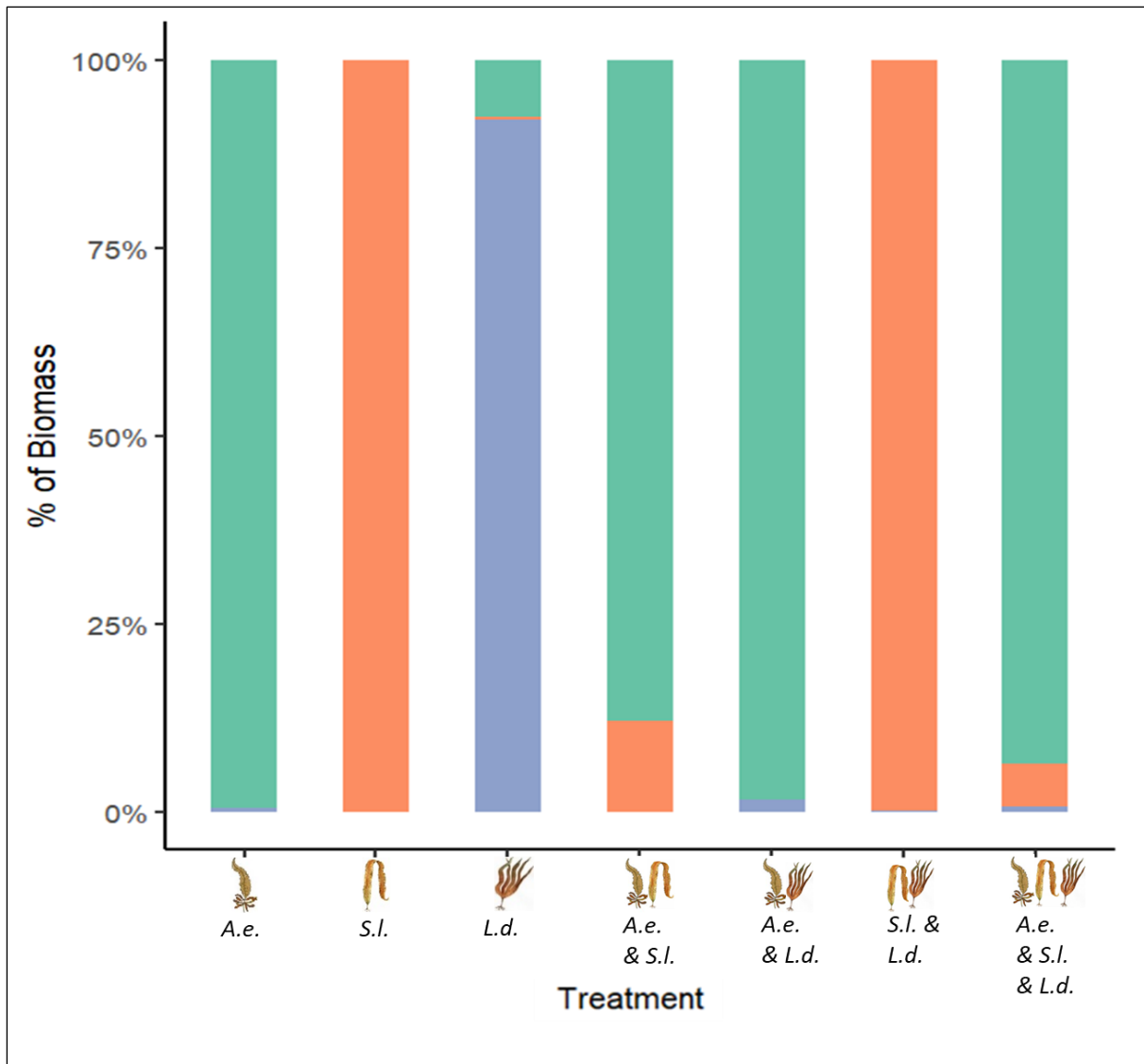e. These findings are not what was expected. It was hypothesised that increased species richness would correspond with an increase in overall kelp biomass production, however the results highlighted how greater species richness can provide stability in primary productivity (i.e. biological insurance; (Yachi and Loreau, 1999, Loreau et al., 2021)) and also identified strong identity effects. Specifically, *L. digitata* did not perform well and treatments that were ultimately dominated by *A. esculenta* or *S. latissima* had greater biomass than *L. digitata* and were similar to each other (suggesting an element of redundancy). It is harder to interpret the 3-species mixture, which shows no sign of complementarity and was similar to the monocultures of *A. esculenta* and *S. latissima*. This experiment shows that when cultivated together *A. esculenta* outcompeted both *S. latissima* and *L. digitata*, however, there was no evidence of enhanced production with greater species richness seemingly because the strength of inter-specific interactions was stronger than any potential complementarity. The findings show that *A. esculenta* is a dominant performer at this site but that in its absence *S. latissima* is just as productive in terms of accumulated biomass.

A. esculenta & S. latissima performed well, and comparatively similar when grown in monocultures. Wild *A. esculenta* is commonly found along the Irish coast in wave exposed areas (Kraan et al., 2000) and is one of the most commonly cultivated species in Irish waters (Walls et al., 2017a). *S. latissima* is also cultivated in Ireland (Aldridge et al., 2021) and is found along the Irish coast in relatively more sheltered sites (Birkett et al., 1998), with an optimal growing temperature of 10-15 ºC (Fortes and Lüning, 1980). This made these species ideal candidates for this study site owing to the likelihood of cultivation success. The stock

culture used were derived from locally obtained sporophylls, following best practice

(Edwards et al., 2016) and ensuring that the strains used were locally adapted.

L. digitata was the lowest performing monoculture and lowest performing species in

polyculture treatments. A native species to Ireland (Schoenrock et al., 2020) *L. digitata* has a

wide thermal tolerance range, with optimal performance at temperatures of 5-15 $^{\circ}$C (Franke et

al., 2021). It is possible that growth rates of *L. digitata* were insufficient at an early

developmental stage to out-compete fouling filamentous algae on the monoculture lines as well

as the other species developing within polycultures. As the longer lived of the study species,

there may be an evolutionary advantage to slower growth, as is the case with late-successional

terrestrial plant species (Bugmann, 2020). This may not be applicable in a cultivation setting,

however, where growing seasons are short compared to wild growing perennial species in

mixed stands. *L. digitata* has been shown to reduced growth in blade size in favour of increased

structural tissue to withstand increased hydrodynamic forces in wave exposed environments

(Millar et al., 2019). The exposed nature of the cultivation site in this study may have

compounded this culture's pre-disposed growth rates.

It is possible that cultivation methods were compromised at the very early life stage in the

hatchery, which may have contributed to the poor *L. digitata* performance. *L. digitata* initially

had the lowest gametophyte density pre fertilisation (14 g l^{-1}) although cultures of the other

two species were diluted to standardise densities. It was noted that the first *L. digitata*

gametophyte culture was contaminated with diatoms and replacement sporophylls were

initially difficult to obtain to create a replacement culture because it was later in the season.

The replacement sporophylls used may have contained poorer quality spores than those

collected initially during the peak reproductive season. Based on these results, *L digitata* spores

should be collected as early in the reproductive season as possible, in large quantities, and

decontamination procedures followed meticulously to reduce the probability of culture

contamination. Redundancy cultures and separating them from cultures of other species would also be advised.

Previous research has shown *A. esculenta* to be dominant over *L. digitata* in early developmental stages when these two species are co-cultivated (Zacher et al., 2019). This was reflected in our biomass yield data for this species combination, where *A. esculenta* was completely dominant over *L. digitata*, and suggests that this dominance can be expected in aquaculture applications. It is likely that this dominance will prevail in wild assemblages where abiotic conditions suit the settlement, development and growth of both species.

Based on the comparable biomass yields of *A. esculenta* and *S. latissima* in monocultures, it would be expected that they would contribute similarly to overall yield when grown co-occurring. This was not the case, as although no difference in yield occurred between their respective monocultures and polycultures, *A. esculenta* clearly out-competed *S. latissima* in polyculture mixtures, regardless of whether *L. digitata* was included. *A. esculenta* is highly tolerant of wave exposure, whereas *S. latissima* generally prefers semi-exposed, but not highly exposed environments (Bak et al., 2018). A transplant experiment by Picard et al. (2022) showed that where naturally *A. esculenta* occurred in an exposed location and not an adjacent sheltered location, and *S. latissima* occurred in both, both species survived in both environments following transplantation. The ability of *S. latissima* to naturally occupy a wider range of ecological niches than *A. esculenta* may be at the expense of a competitive disadvantage. The cultivation site in Toormore Bay was highly exposed, facing directly into the prevailing Southwesterlies off the Atlantic. The site was also subjected to a number of high intensity weather events, and access was limited by sea conditions for much of the growing season. This high level of energetic disturbance may have influenced the success of *A. esculenta.*

S. latissima completely out-competed *L. digitata* when grown together in a two-species polyculture. Similar to when *A. esculenta* was grown with *L. digitata*, this was probably a result of faster growth rates of juvenile *S. latissima* and possibly a sub-standard *L. digitata* culture. Early growth in *S. latissima* would have limited light availability for juvenile *L. digitata* sporophytes, reducing their photosynthetic performance. Lower localised water flow in the *S. latissima* sub-canopy could have also reduced flow rates in the understory. Reduced flow rates reduce nutrient assimilation via diffusion boundary layer (Hurd, 2000), further inhibiting metabolism and consequently growth.

All polyculture treatments effectively developed into monoculture stands as the sporophytes developed. This suggests that competition inhibits the co-habitation of multiple kelp species within immediate proximities. The dominant species in each polyculture probably established itself relatively quickly in the early developmental stages. Asymmetric inter-specific species competition has been shown to occur between microscopic stages of various kelp species, varying depending on environmental conditions (Reed, 1990). Competition at the microscopic stage undoubtedly played a role in the ultimate success of a single species from each of the polyculture treatments under the environmental conditions in the hatchery and field of study.

Although it was not significant, there was a tentative trend towards a reduction in yield within two-species polycultures, compared to the dominant species' respective monocultures. This could be because of a destabilising effect when two kelp species compete immediately post-settlement. With two holdfast morphologies developing in close proximity, energetic input into haptera development may increase to ensure adequate stability. A redirection of energy input into haptera development would lead to a corresponding reduction in energy input towards blade growth, and subsequently, blade biomass accumulation. Species adapted to high energy environments such as *A. esculenta* (Kraan et al., 2000) would be expected to

prioritise holdfast development in early developmental stages. Although there is probably a degree of plasticity in this trait, as with blade and stipe morphology (Coleman et al., 2020, Ronowicz et al., 2022, Fowler-Walker et al., 2006), this may require a larger diversion of energetic input for less exposure tolerant species such as *S. latissima*. Holdfast morphology has also been linked to substratum type (i.e. bedrock or gravel) in certain kelp species (Leal et al., 2021). The long-line material used may have also influenced the early-stage development of each species. If this is the case, the materials of long-lines used for kelp cultivation should be considered for each target species and this warrants further research.

The variability in responses within the 2-species treatments was noticeably wider than the monocultures and 3-species treatments. However, this variation may not have been a natural occurrence. The distances between each long-line were roughly the length of the boat used for the commercial harvest of non-study lines at the site. Samples were taken after commercial harvests and it is possible that patches of the western and eastern-most lines were disturbed by the commercial operations. The site was also subjected to vandalism more than once throughout the season. It may be necessary in future studies to apply an element of discretion to choosing sampling locations, use multiple sites and/or to deploy an excessive number of replicates than would be statistically the most efficient.

The three-species polyculture had the most consistent yield across all treatments. Although *A. esculenta* dominated with some contribution by *S. latissima,* and *L. digitata* practically absent, the low variability between samples contrasted greatly to the two-species treatments. Increased diversity is known to stabilise productivity in ecological systems as a result of niche complementarity, enhancing resource utilisation within a system (Isbell et al., 2015, Loreau, 2010). We cannot clearly identify complementary effects within the three-species polyculture in the current study because of the overwhelming dominance of *A. esculenta.* Our

results do suggest the presence of a 'selection effect' (Loreau and Hector, 2001) as the highest performing monoculture dominated in each polyculture.

This study provides interesting insights within an aquaculture perspective. The planning, development and running of macroalgal cultivation sites outside the Pacific rim are time consuming and costly (Coleman et al., 2022). Our results showed that when multiple species are seeded along the same stretch of long-line, the most dominant, and therefore suitable species will proliferate. In the first year of a cultivation site, using this polyculture seeding method may be the most cost-effective way to prospect the suitability of a variety of species, rather than to divide a site's lines proportionately between the same number of species as monocultures. Successive seasons of these trials can determine the temporal stability of this method compared to monocultures.

Diversity of primary producers, including macroalgae, have been linked to higher abundance and diversity of facilitated biodiversity (Hauser et al., 2006). Biodiversity facilitation has been a highly suggested potential ecosystem service from macroalgal aquaculture (Grebe et al., 2019, Forbes et al., 2022, Gentry et al., 2020, Walls et al., 2019). The relationship between the diversity in macroalgae at kelp farming sites and the biodiversity directly associated with them is likely to be correlated and should be considered by farmers, regulatory bodies and incorporated into future studies.

There may be overlaps between how *A. esculenta* and *S. latissima* compete in aquaculture settings and at locations where high settlement of both species' meiospores occur. The drivers determining the competitive success of either species in this scenario should be investigated further, because it could feed into models predicting species range shifts in response to climate change.

Future studies are recommended to diversify their sampling and monitoring efforts. The lack of regular and predictable access to remote, exposed sites requires a high level of redundancy for maximal likelihood of success. Examples could include excess replicates for each experimental treatment, multiple study sites, loggers deployed on-site as well as spot sampling on site visits for the same environmental parameters (sea surface temperature, light, current, pH etc.). These studies are subjected to a high level of risk to both safety and successful research output. Researchers should expect the unexpected and be prepared to adjust their plans throughout similar studies as unexpected issues arise.

In conclusion, polyculture seeded twine of *A. esculenta, S. latissima* and *L. digitata* do not necessarily develop into mature polycultures. The interaction between these species in close proximity appears to be selective rather than complementary. This competitive interaction may inhibit the potential productivity of the competitively dominant species where multiple species settle in immediate proximity. Further studies are required in order to properly understand interspecific interaction between kelp species across various temporal, spatial and environmental scales.

Chapter 3 - Fish communities associated with Irish kelp (*Laminaria hyperborea*).

Abstract

We currently lack fundamental baseline information describing Irish coastal ecosystems, in particular subtidal habitats, despite threats to their existence. Biogenic habitats, such as kelp forests or beds, pay a key role providing habitat for many species but these have not been identified or characterised in many regions including Ireland. There is a paucity of data describing fish communities associated with Irish kelp beds. Moreover, these habitats are often excluded from independent fisheries data collections for estimating stock densities. As a result, the presence and abundances of fish species predominately residing amongst our kelp beds are largely unknown. Globally, kelp stands are recognised as important habitats to a range of fish species. It is recognised widely that threats to kelp will have direct negative effects on local diversity, which underpins many ecosystem services. Without baseline data we cannot detect changes in ecological status or predict effects of climate-driven species range shifts. This study aims to describe the fish communities associated with kelp forests on the Atlantic coast of SW Ireland. Underwater Visual Census surveys were conducted by SCUBA divers among kelp (*Laminaria hyperborea*) beds at three sites on Co. Cork, Ireland. At all sites, fish communities were mainly composed of species from the families *Gobiidae, Gadidaea* and *Labridae*. Fish species richness, abundance and diversity were similar among all sites. Fish assemblage structure was also similar between sites, suggesting consistency in

communities locally and similarities to other areas across the NE Atlantic region. These findings identify key baseline data in a poorly described habitat and characterise the fish communities associated with *L. hyperborea* kelp forests on the south coast of Ireland. *Pollachius pollachius* likely to be the first species pushed out of this region as ocean warming accelerates. *Ctenolabrus rupestris* is one current species in this region likely to benefit from an increase in ocean temperatures.

Introduction

Habitat forming species, known as biogenic habitats or foundation species, can be defined as spatially dominant habitat-structuring organisms (Angelini et al., 2011). These species enhance biodiversity (Victorero et al., 2018) and ecosystem functioning (Cerrano et al., 2010) through food-web interactions (Diaz and Cabido, 2001), formation of additional ecological niches (Jones et al., 1994) and alleviating physical stressors (Borst et al., 2018). Examples of marine biogenic habitats include mangrove forests (Sahana et al., 2022), salt marsh (Keur et al., 2019), sea grass meadows (Himes-Cornell et al., 2018), coral reefs (Caceres et al., 2020) and kelp forests and beds (Teagle et al., 2017).

Kelp are classified as large brown seaweeds of the order *Laminariales* (Le et al., 2022). Kelps occur in the intertidal and subtidal habitats of temperate and polar regions (Steneck et al., 2002). They are important sources of primary productivity (Krumhansl and Scheibling, 2012) and drivers of secondary productivity (Shelamoff et al., 2020). Kelp beds/forest are important biogenic habitats by scale, comprising a quarter of the worlds coastlines (Hamilton et al., 2022). Kelps are well known examples of ecosystem engineers (Teagle et al., 2017) and are recognised as important habitats for marine biodiversity in general. Kelp are known to increase habitat heterogeneity and complexity in shallow, hard substratum marine environments (Bruno and Bertness, 2001), increasing and diversifying the habitat available

for a wide range of mobile and sessile faunal species (Bologna and Steneck, 1993, Norderhaug et al., 2005, Smale et al., 2013).

The dominant species of kelp in Ireland include *Laminaria digitata*, *Alaria esculenta*, *Saccharina latissima*, and *Laminaria hyperborea*. *L. hyperborea* is a dominant canopy forming species in Irish and Northern European temperate waters (Kelly, 2005), contributing the most towards habitat volume of the subtidal kelp beds. *L. hyperborea* directly facilitates unique macroinvertebrate assemblages (Smale et al., 2015). These assemblages in turn support a large number of ecologically, commercially and socio-culturally important fish, decapod, seabird and marine mammal species. There is evidence to suggest that *L. hyperborea* is replaced by *Laminaria ochroleuca* in warmer more southerly European waters (Pereira et al., 2019), however, these reefs support comparably less biodiversity than *L. hyperborea* (Teagle and Smale, 2018). The predicted northerly range shift of *L. ochroleuca* into the southern limits of *L. hyperborea*'s range (Franco et al., 2018), therefore, poses a threat to the integrity of marine food webs in kelp-dominated cold-temperate coastal regions in Ireland and the UK.

Kelps are widely understood to be positively associated with fish community abundance (Dean et al., 2000, Shelamoff et al., 2020). In turn, healthy carnivorous fish populations can positively affect kelp habitat volume locally by exerting top-down controls on grazing invertebrates (Ling et al., 2015). The importance of this balance between bottom-up and top-down controls has been well documented in regions such as California and Australia, where declines in the charismatic giant kelp, *Macrocystis pyrifera*, forests have been linked to over-harvest of urchin predators, such as California sheephead (*Semicossyphus pulcher*) and southern rock lobster (*Jasus edwardsii),* which has disrupted top-down predator controls on

grazers, resulting in the loss of historically prolific kelp forests from entire regions (Nichols et al., 2015, Grover et al., 2021).

The disruption to ecosystems through overharvest has been exacerbated as the proportion of biologically unsustainable fisheries stocks has increased from 10 % in 1974 to 35 % in 2019 (FAO, 2022). As the appetite for seafood continues to grow globally (Naylor et al., 2021), the pressures to fish stocks and the associated indirect effects on marine ecosystems can be expected to accelerate. Although many stocks throughout the world are monitored and their decline has been recorded, data for many regional, under-developed, and difficult to survey areas are lacking. Acquiring baseline data for these regions will be vital, not just for monitoring the long-term trends in populations and setting quotas, but also for providing targets for restoration efforts in similar degraded environments.

In Irish waters, routine monitoring produces estimates of fish assemblages/stocks in a range of coastal (Connor et al., 2019) and offshore (Marine Institute, 2012) habitats. However, fish surveys on hard bottom marine habitats are often not included in routine monitoring by government bodies, and specific studies into kelp bed fish communities are lacking in Ireland. Trawler surveys, from which the size of many stocks are estimated, only sample soft sediment habitats because of the bottom trawling sampling methodologies employed (Marine Institute, 2012). These methods inevitably lead to some degree of bias, excluding populations/species inhabiting hard-bottom habitats such as kelp beds. This leads to gaps in management scale data. Although local knowledge and studies on similar habitats in nearby regions give a roughly accurate estimate of the fish community structure to be expected (Furness and Unsworth, 2020, Schoenrock et al., 2021, Norderhaug et al., 2005), this has not been quantified by robust studies at regular intervals in the literature focusing on fish specifically at the time of writing in Ireland.

Declining fisheries, species-range shifts, water quality degradation and marine development currently, and will continue to, alter ecosystem functioning in the marine environment (Chapman, 2017). Obtaining baseline data for a range of habitats and incorporating spatial and temporal variation is, therefore, essential to understand the implications of ecosystem changes and to preserving our marine resources where possible. This study aims to describe the current typical abundance and diversity of fish assemblages associated with *L. hyperborea* kelp beds at their southern range on the coast of Ireland, using underwater visual census survey, a non-extractive observational method. It was hypothesised that fish diversity and abundance would be similar among sites, which would enable a characterisation of these communities from which future studies can record potential changes.

Methods

Study Sites

Surveys took place in Roaringwater Bay (51º 48' 87.52" N, 9º 60' 37.21" W), Toormore Bay (51º 49' 31.21" N, 9º 63' 06.77" W) and Galley Cove (51º 46' 10.31" N, 9º 73' 83" W). Sites were selected to be presentative of typical rocky subtidal habitat in the region and taken from longer list of potential sites selected based on their for their hard substrata as observed on Google Earth (Google, 2022), similar depth profiles identified using Navionics WebApp (Garmin, 2022) and similar levels of exposure to prevailing south westerly conditions. Sites were selected in the same general geographic region (within 10 km) to limit any substantial variation in latitude, temperature and other potential oceanographic/geographical influences on fish assemblages.
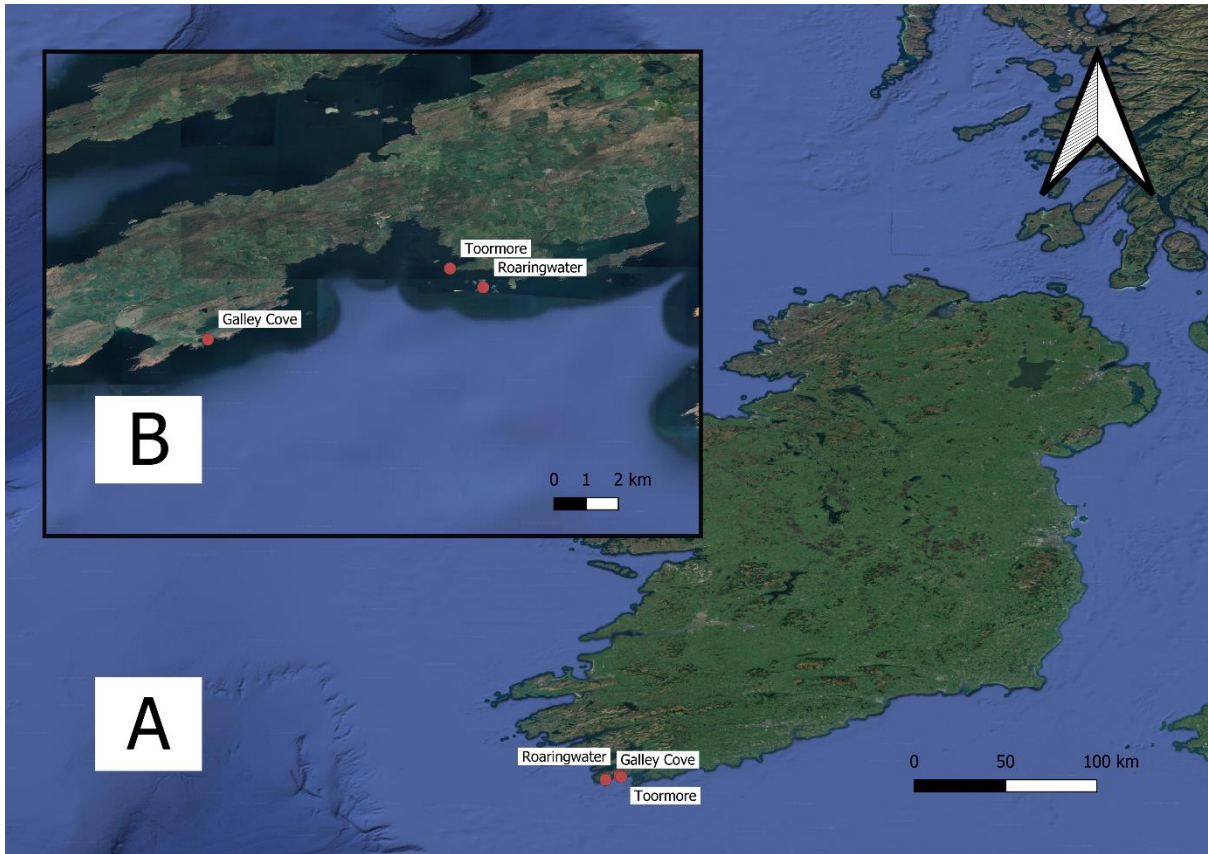
Figure 5. Locations at Galley Cove, Toormore Bay and Roaringwater Bay where dive transects were conducted.

Underwater Visual Census

The following underwater visual census survey methodology was adapted specifically to quantifying mid-water fish assemblages in kelp beds while navigating topographically variable sites with low visibility typical of temperate waters. At each site, divers completed surveys along four transects of 50 m in length at 5 - 6 m depth. At least 10 m distance was given between finishing transects and beginning new ones to prevent fish pushed forward by disturbance from being double counted in following transects. Transect tape/markers, typically used in underwater visual censes (Jessop et al., 2022) were avoided to prevent disturbance of fish prior to surveys.

Visibility was recorded upon descent. One diver held the end of a measuring tape and the other swimming away with the measuring reel until the other diver was no longer visible. Diving in pairs, one diver was tasked with recording fish abundances according to species. The second diver kept track of distance covered. The beginning and end of each transect was determined by one diver using pre-determined fin kick cycles specific to that diver. The fish count diver preceded in a predetermined sampling direction with the fin kick count diver following adjacently but slightly behind to reduce disturbance. After at least 10 m of swimming, the measurement diver tapped the quantifying diver twice to initiate counting. Counts of the number of mid-water and canopy fish for each species within a 2.5 m radius (approximate range for clear identification) of the fish count diver were recorded by that diver. Transects were completed at a slow but steady pace for divers to keep track of their depth, air, and respective counts accurately. Transects were conducted linearly, following the depth contour of the seabed that allowed divers to remain as close to the 5 - 6 m depth range target as possible without making contact with the kelp canopy or bedrock. After 50 m had been determined by the distance count diver, a double tap to the fish count diver's legs indicated the transect was complete. These steps were continued a further three times and repeated in each location. All transects were completed on the same dive at each site, totalling three dives overall. All dives were carried out over a 48 hour period in August 2022.

Data Analysis

Analysis of variance (ANOVA) was carried out on fourth transformed data to meet the assumptions of normality and heterogeneity, with site as random factor (3 levels) to test for differences in fish species richness, total abundance and Shannon Diversity Index. To test for differences in fish assemblage structure among sites all PERMANOVA was performed on fish community data based on a Bray-Curtis dissimilarity matrix (Clarke and Gorley, 2006)

created using the ecodist package (Goslee and Urban, 2007). Simper analysis was performed using the vegan package in R (Oksanen et al., 2022, R Core Team, 2022) using the transformed dataset, grouped by location, to compare and identify the percentage influence for which individual species contributed to the similarity/dissimilarity of assemblage structure between each site..

To attempt to set standardised metric usable for comparisons with other studies using transects of varying dimensions and number to quantify fish assemblages in kelp beds, as well as other habitats, the densities of each species observed per metre cubed of water were also estimated. Count data was averaged between sites, and the count average divided by the total 3D cylindrical transect area ($\pi \cdot 2.5^2 \cdot 50 = 981.75$ m^3) covered per site (4 x m$^3 = 3926.99$ m^3).

Results

A total of 1838 individuals comprised of seven species were observed in total (736 excluding sandeel (*Ammodytes tobianus*)) (Figure 7). Lesser sandeel (*Ammodytes tobianus*) was excluded from analysis as it is a transient species in this habitat (Jiorle et al., 2022) and numbers within shoals could not be quantified accurately by visual counts.

Species richness did not differ between the three sites (ANOVA; $F_{2,9} = 1.8$, $p = 0.22 > 0.05$), which was 3 ($^+/_-$ 0.816) at Roaringwater, 4 ($^+/_-$ 0.816) at Toormore and 3.5 ($^+/_-$ 0.577) at Galleycove (Figure 6). Overall fish abundance did not differ between sites (ANOVA; $F_{2,9} = 1.25$, $p = 0.33 > 0.05$). Mean abundance at Roaringwater, Toormore and Galleycove was 26.5 ($^+/_-$ 14.708), 81 ($^+/_-$ 74.57882) and 76.5 ($^+/_-$ 54.86043) respectively (Figure 6). Shannon diversity also did not differ between any of the sites (ANOVA; $F_{2,9} = 2.53$, $p = 0.14 > 0.05$) (Figure 6). Assemblage structure did not differ between sites (PERMANOVA; $F_{2,9} = 0.9557$

p = 0.46 > 0.05). The only species which differed in contribution to assemblages between locations was *Gobiusculus flavescens* (49%) between Roaringwater and Galleycove (p = 0.011 < 0.05) (Figure 8), where total abundances were 24 and 248 respectively. However this did not affect similarity of assemblages as a whole. Species total abundances at each site ranged from 106 (Roaringwater) to 324 (Toormore).
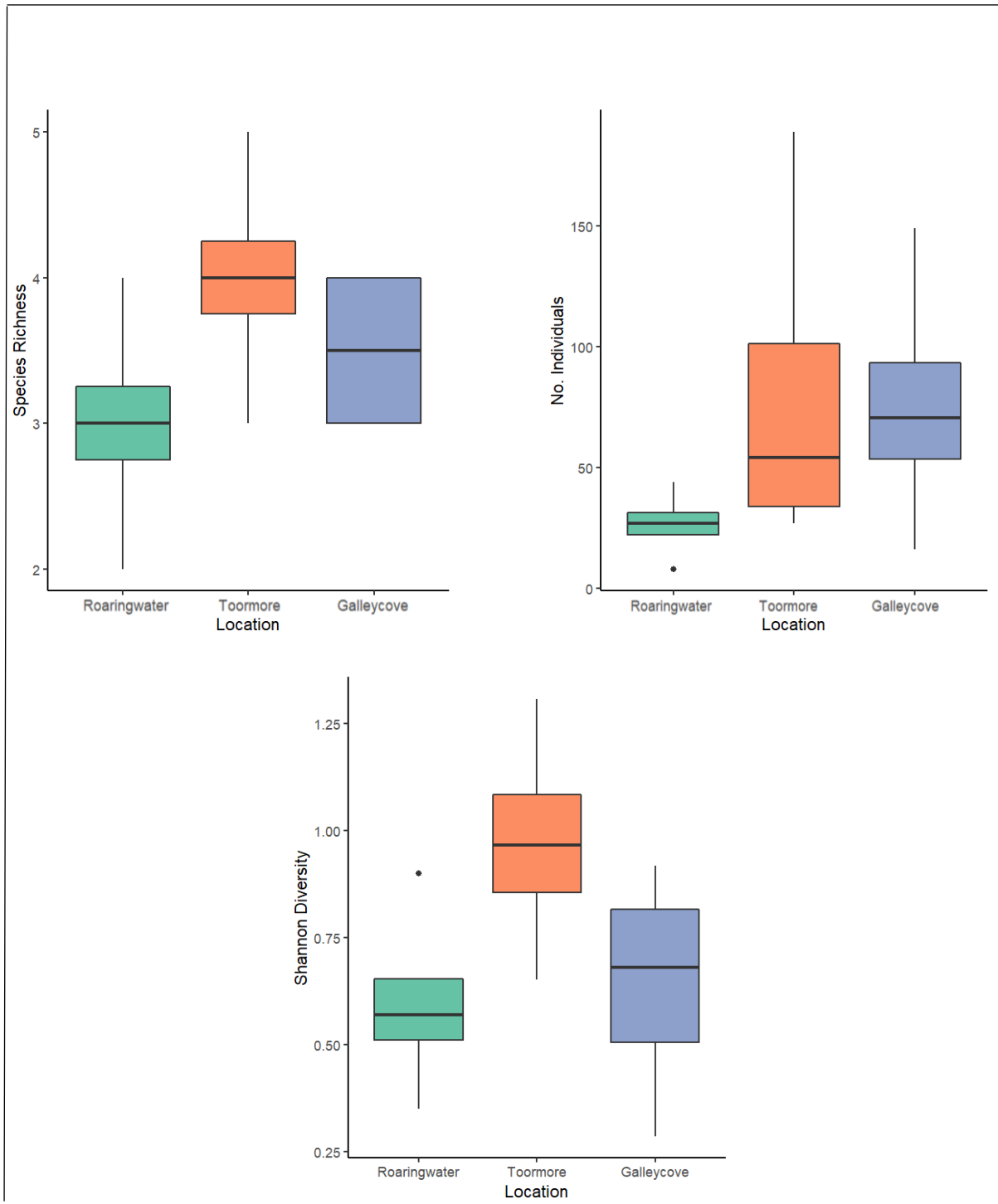
A total of six fish species were recorded during the survey among kelp beds: two spotted goby (*Gobiusculus flavensus*), pollock (*Pollachius pollachius*), ballan wrasse (*Labrus bergylta*), corkwing wrasse (*Symphodus melops*), goldsinny wrasse (*Ctenolabrus rupestris*), and rock cook (*Centrolabrus exoletus*). Four of these species were present at all sites (*G. flavensus, P. pollachius, L. bergylta* and *S. melops).* Toormore was the only site where all six of these species occurred. Lesser sandeel (*Ammodytes tobianus*), was also recorded at each site.
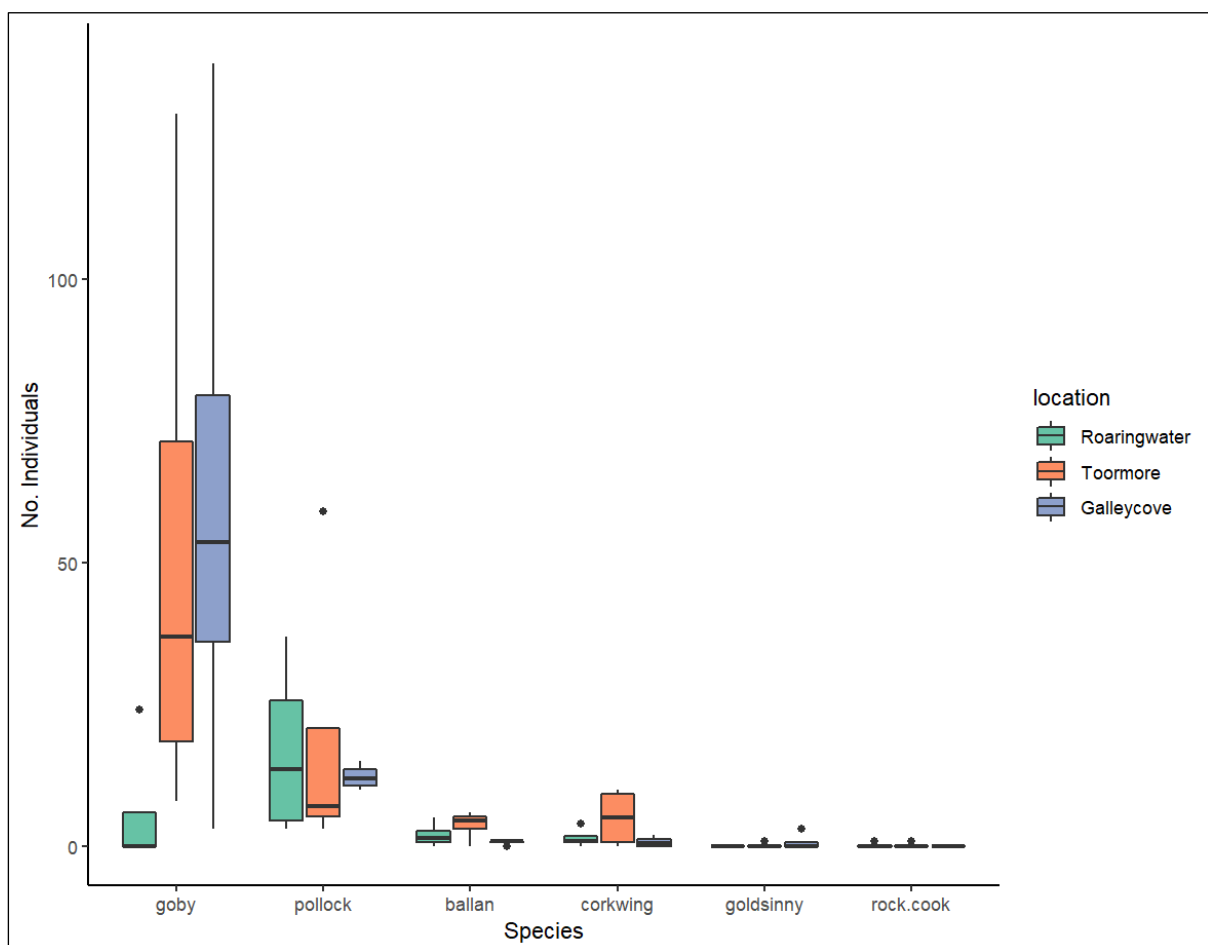
Figure 7. Median and interquartile ranges for counts at each site grouped by species.
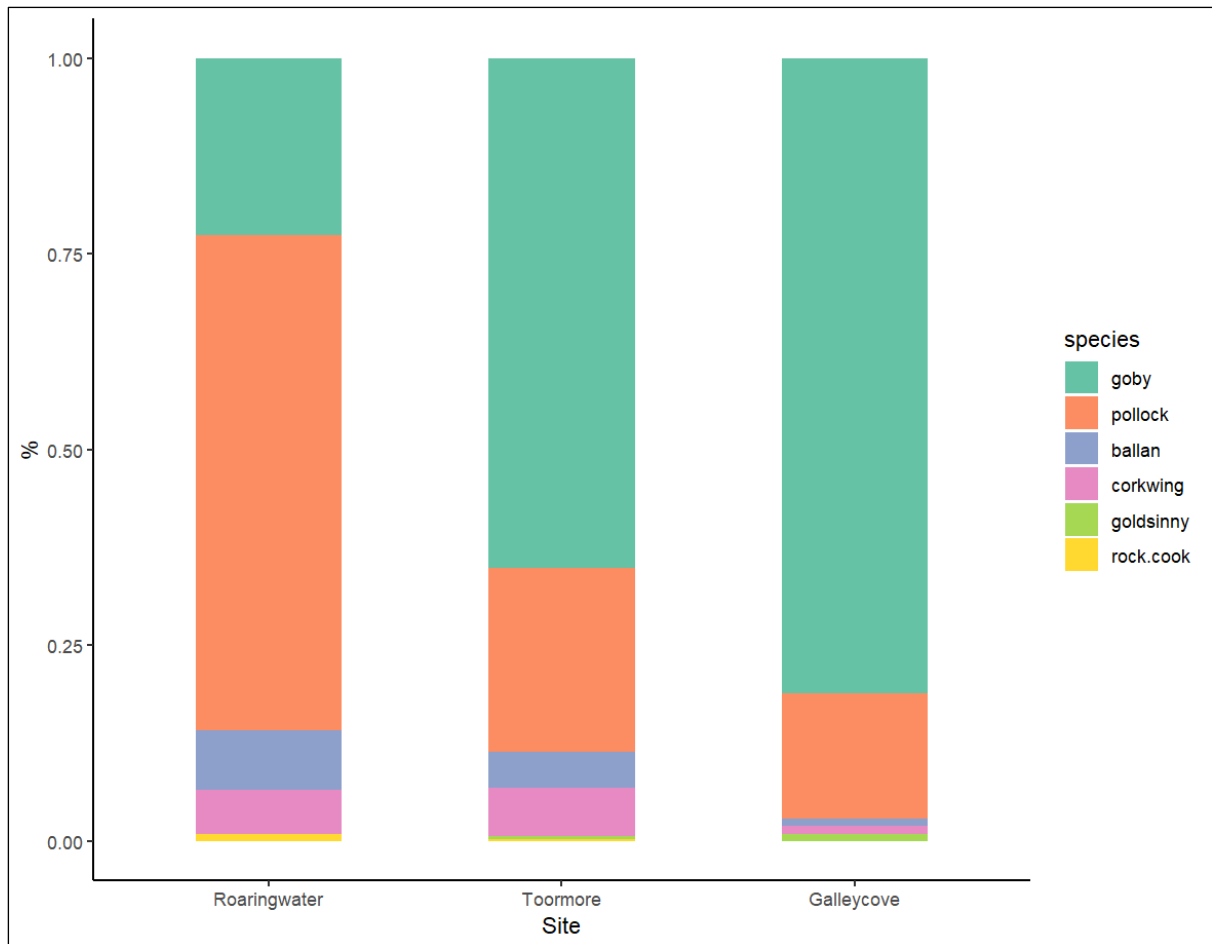
Figure 8. Percentage contribution of each species towards the community structure at each site.

Discussion

Despite widespread acknowledgment of the importance of kelp forests as fish habitat throughout temperate and polar regions, very few studies have characterised fish assemblages in kelp beds around the Irish coast. Existing data describing fish communities associated with NE Atlantic kelp are relatively recent (Jackson-Bué et al., 2023), sparse (Schoenrock et al., 2021), or focus on only one species (Vondolia et al., 2020). The current study area is at the southern geographic range of *L. hyperborea* (Assis et al., 2016). This study aimed to be the first to characterise and quantify fish assemblages at *L. hyperborea* beds on the southern

coast of Ireland and set baseline data in a region at the forefront of range shifts due to warming ocean temperatures.

Our results detected no differences in assemblage composition, overall abundance, species richness or diversity between sites. This indicated a consistent community structure across spatial scales in this region. The community structure identified including species richness, diversity and abundance can therefore be characterised by the findings of these surveys. The particular species observed were consistent with what little research has been conducted on Irish kelp beds generally (Jiorle et al., 2022, Schoenrock et al., 2021).

Many of the fish species identified in this study are of high commercial importance regionally. The salmon aquaculture industry is still reliant on wild-caught labrid species for biological control of sea lice parasites (Bolton-Warberg, 2018). Recreational angling contributes around €555 million to the Irish economy each year (Curtis et al., 2017), with much of this stimulus occurring in rural and coastal areas with often limited economic stimulus otherwise. Pollock (*P. pollachius*) and wrasses (*labridae*) are very popular marine sportfish for anglers fishing on boats and the shoreline, therefore, these kelp beds may play a key role in sustaining recreational fisheries in rural coastal communities through charters, accommodation, hospitality and equipment.

Of the current fish species identified with Irish kelp beds, *C. rupestris* and *S. melops* are likely to retain, and potentially increase their distribution in this region as ocean temperatures rise (Bull et al., 2013). *C. rupestris'* and *S. melops'* preferred physiological temperature tolerances are the highest of those species identified in this study, rising to 15 ºC and 17.2 ºC respectively (Froese and Pauly, 2023). Although this does not take into account genetic adaptability within local populations of these species to regional environmental parameters, it indicates the capability of these species to persist in Irish kelp beds following climate-driven

ocean warming. In contrast, *P. pollachius* is likely to be one of the first endemic species in this region to be negatively affected by sea temperature increase (Heath et al., 2012), having the most northerly southern distribution of the species observed (Dunn, 1992).

This climate-driven shift in fish assemblages could be exasperated by concurrent shifts in macroalgal composition. The south coast of Ireland is situated at the southern extent of *L. hyperborea,* beyond which it is replaced by the warmer temperate species *Laminaria ochroleuca* (Pereira et al., 2019). *L. ochroleuca* has recently been recorded in Irish waters (Schoenrock et al., 2019) and could potentially replace *L. hyperborea* functionally as a habitat forming macroalgae. These two species share similar physiological features. However, *L. ochroleuca* as a habitat forming species has been shown in its northernmost range to facilitate far less diverse and abundant epibiont assemblages than *L. hyperborea* (Teagle and Smale, 2018, Smale et al., 2015). In addition, a reduction in the overall biomass and diversity of invertebrates associated with newly establishing kelp species such as *L. ochroleuca* is almost certain to have negative impacts on fish communities dependant on this production (Teagle and Smale, 2018).

Shifting food web dynamics in response to range shifts of foundation species will certainly be disruptive to predator community structures in their current form in either abundance, diversity or richness. Loss of species owing to warming sea temperature could, however, be compensated in the long-term by new species colonising new areas within their northerly temperature range (Rutterford et al., 2023). For example, the increased occurrence of warmer-temperate fish species, such as *Sparus aurata,* in UK and Irish waters (Coscia et al., 2012), provides a new target for commercial and recreational fishers at a time where formerly regional iconic species, such as cod (*Gadus morhua*), were in decline (Beaugrand and Kirby, 2010). The absence of any species in this study that could be associated as a climate coloniser

in southern Ireland at roughly the warmest time of year suggests that new fish species are yet to colonise southern Ireland's extensive *L. hyperborea* beds in any quantifiable or meaningful numbers. Predicting climate-driven range shifts of fish species is complicated by interactions with various life cycle stages, ability of a particular species to expand range by migration and whether a new region meets all the other environmental/ecological/geological parameters required to persist (Heath et al., 2012).

In conclusion, *L. hyperborea* beds in the southern Atlantic coast of Ireland support an open-water and canopy dwelling fish community comprised of *Gobiusculus flavensus*, *Pollachius pollachius*, *Labrus bergylta*, *Symphodus melops*, *Ctenolabrus rupestris*, and *Centrolabrus exoletus*. This reflects community structure seen in *L. hyperborea* forests elsewhere in Europe. These data provide a baseline describing fish communities in kelp beds upon which to compare any future changes, owing to warming seas and its associated warmer tolerant species, that will arrive in increasing numbers, and the simultaneous withdrawal of warm-intolerant species. This baseline will also contribute to estimates of our inshore fisheries resources. *C. rupestris* and *S. melops* were identified as species which warming seas may favour, and *P. pollachius* a species which is predicted to retreat northward as sea temperatures increase (Bull et al., 2013, Rutterford et al., 2023). The colonisation by warm water-affinity species will be driven by species with pelagic life stages, and will be affected by retreats of existing cold-tolerant or advance of warm-tolerant foundation species and their associated assemblages.

Chapter 4: A comparison of methods for quantifying fish species abundance associated with cultivated kelp lines

Article Type: Note

Target Journal: 'Aquaculture Environment Interactions'

Word Count: 2,608

Abstract

Cultivated kelp has potential to provide novel habitat to a range of fish species depending on the region and their proximity to the shore. Although some studies have investigated the effects of kelp farms on benthic and adjacent fish assemblages, there were a very few studies that aim to quantify the diversity of fish associated with kelp cultivated on long lines at sea. This study tested the efficiency of three fish survey techniques (underwater drone, baited traps and underwater visual census (SCUBA)) to estimate fish abundance at a macroalgal cultivation site at Toormore Bay, West Cork, Ireland. Despite previous studies that reported successful outcomes, none of the methods were successful in quantifying fish on macroalgal cultivation lines, with underwater visual census the only technique that detected any fish (single *Cyclopterus lumpus* individual). Underwater drone transects were challenging to undertake as adverse sea condition and water clarity inhibited its effectiveness. Baited traps also proved fruitless, and trials show that bait had been taken in large mesh traps without a successful capture of the consumer while smaller bottle traps also failed to capture any individuals after both 24 hr and five day periods. Survey methodologies for quantifying fish at kelp farms and other marine aquaculture structures should be carefully considered prior for

practicality, time efficiency and suitability of each for specific conditions likely to be encountered. Underwater visual census surveys via SCUBA undertaken by divers with good fish identification skills should be utilised when surveying for general assemblages to maximise the likelihood of successfully detecting macrofauna.

Introduction

Kelp species form important biogenic habitat, facilitating multitudes of species directly and indirectly (Teagle et al., 2017). Biogenic habitats provide crucial nursery, feeding and refuge habitat for a wide range of reef dwelling and juvenile species. As living organisms, they increase the complexity of the existing substrata around them (Velasco-Charpentier et al., 2021). Kelp also create a network of refugia at various scales that facilitates a range of species from sessile invertebrates within their holdfast, large fish using the blades as cover (Walls et al., 2019, Jackson-Bué et al., 2023).

Increased coastal development and multiple anthropogenic activities resulting in the loss of habitat heterogeneity is one of the primary causes of biodiversity loss in coastal areas (Stone et al., 2019). Much research has been carried out into monitoring artificially altered sea beds and shorelines in order to assess their habitat value compared to natural features, and what changes could be made to enhance their support of marine biodiversity (Vozzo et al., 2021, Levy et al., 2022). These efforts have included altering the texture and features of sea walls (Natanzi et al., 2021), artificial reefs to improve seabed heterogeneity (Nauta et al., 2023) and re-establishment of habitat forming organisms, such as oysters (Searles et al., 2022), coral (McLeod et al., 2022) and kelp (Eger et al., 2022). The increase in coastal and offshore developments will require further research and survey techniques to monitor the impact these activities will have on biodiversity in general.

Aquaculture is an economic activity that has grown substantially globally and increased its impacts on coastal environments as a result (Ahmed and Lorica, 2002). Negative impacts on the environment have been the main focus of research to date, in particular in relation to pollution (Ayeon et al., 2020) and the spread of invasive species (Rech et al., 2018). The cultivation of extractive species, such as bivalves and macroalgae, have however been associated with substantially lower impacts (Camelo-Guarín et al., 2021, Visch et al., 2020b). Integrated multitrophic aquaculture combining the culture of these species with finfish aquaculture has been touted as a potential way to reduce the impact of finfish aquaculture, by removing excess solid and dissolved nutrient outputs arising from excess feed and metabolic outputs of finfish (Paolacci et al., 2022, Khanjani et al., 2022).

Cultivated kelp long-lines may recreate the habitat structure of wild kelp beds by creating three-dimensional structures within the water column that otherwise would not have been there (Walls et al., 2019), facilitating epibionts, grazers and their associated predators. These longlines, however, also differ significantly from wild kelp beds because they are situated usually floating above soft sediment, suspended off the sea floor near the surface. Holdfast and kelp blades provide structure and food source for a range of invertebrates of similar abundance to wild kelp stands (Teagle et al., 2017), which should theoretically encourage utilisation of this habitat by species in higher trophic levels, such as fish. Anecdotal evidence and personal observations point to utilisation of kelp cultivation lines by a variety of species associated with wild kelp, such as lumpsuckers (*Cyclopterus* lumpus), 2-spot goby (*Gobiusculus flavensus*) and pollock (*Pollachius pollachius*).

Cultivated kelp are ultimately harvested, therefore, they only provide temporary habitat for up to 6 months per year. Species that use this habitat for the same purpose for feeding and protection would be displaced annually and could be forced into adjacent habitats. The

transient availability of this habitat could, therefore, act as a recruitment reservoir for adjacent habitats if timed appropriately but this has yet to be tested in the field and the potential abundances of fish utilising kelp farms remains unquantified.

There are various methodologies utilised for quantifying fish presence and abundance because of the wide variety of environments, contexts, species and their specific requirements. Each methodology has its own particular benefits, but each also have potential sampling biases. It is common and recommended that more than one methodology be utilised when quantifying complete assemblages to maximise the likelihood of recording species that may be more easily detected by one method over another (Jessop et al., 2022). For example, certain species may be more prone to disturbance from SCUBA divers than others, while other species may be more active at night than during the day etc. Also, the use of bait can lure fish from a substantial distance away, but may be not be attractive to herbivorous species.

In this study, we tested three fish sampling methodologies at a kelp cultivation site in Co. Cork, Ireland to estimate the abundance and diversity of fish utilising the long-line structures as habitat, and to compare the effectiveness of each sampling method. The methods we tested were based on: underwater drone; baited traps; underwater visual census (SCUBA).

Methodology

Study Site

To identify fish species at kelp long lines and describe abundance patterns, three sampling methods were trialled at macroalgal cultivation site in Toormore Bay, Co. Cork, SW Ireland (51° 29' 32.711" N, 9 ° 37' 44.626" W) during the spring and summer of 2022. The

methodologies implemented were underwater drone transects, baited trap sampling, and underwater visual census via SCUBA.

The cultivation site was situated in water of an approximate depth of 12 – 20m. The seabed type was mainly soft sediment, with adjacent rocky shorelines dominated by *L. hyperborea* kelp beds. The location was highly exposed, directly facing prevailing south-westerly weather conditions from the Atlantic. This was the first year of cultivation at this site. Eight long-lines (220 m) were in operation cultivating several kelps species but mainly *Alaria esculenta*.

Underwater Drone Transects

The underwater drone transects were conducted using Chasing M-2 drone (Chasing-Innovation Technology Ltd.) with a Samsung Galaxy tablet in a waterproof casing as a viewing screen. Four surveys transect (50 m long) were carried out in February and May along the cultivation lines at line level. The drone was operated at a 45° angle to the line so that open water immediately adjacent to the lines, as well as the cultivated kelp itself, were viewed in the pane. All species were recorded as they were seen from live-feed on the operating vessel, and footage reviewed afterwards for verification.

Baited traps

Two trap designs were tested: 1. Large collapsible mesh traps (50 cm length and 25 width, 0.5 cm mesh size,10 cm flapped entry); 2. Small traps constructed with recycled plastic bottles (2 L, 2 mm holes for water circulation and 1.5 cm entry hole). All traps were baited with a combination of mussel, hake and salmon to appeal to a wide of a dietary preference of fish at the sampling locations. Two trap deployments were carried out, in April and May, at randomly appointed locations along kelp cultivation lines, secured by cable ties. Two large

and eight small traps were deployed for a soak time of five days in April and 24 hours in May. Traps were deployed across two separate cultivation lines within the kelp farm.

<center>*Underwater Visual Census Survey*</center>

The following underwater visual census survey methodology was adapted specifically to quantifying fish assemblages on kelp cultivation lines. Four transects (50 m length) were completed along cultivation lines. At least 5 m distance was given between finishing transects and beginning new ones to prevent fish pushed forward by disturbance from being double counted. Transect tape/markers, typically used in underwater visual censes (Jessop et al., 2022) were deemed unnecessary because the cultivation line and its supporting buoys (every 13 m) was used as a marked transect.

Transects were conducted by pairs of divers. One diver was tasked with recording fish abundances according to species. The second diver kept track of distance covered, following the count diver slightly behind to limit disturbance along transects during counts. The beginning and end of each transect was determined by the trailing diver using pre-determined fin kick cycles specific to that diver. The fish count diver preceded in a predetermined sampling direction. The measurement diver tapped the quantifying diver twice to initiate transect counts. Counts of the number of mid-water and canopy fish (Schoenrock et al., 2021) for each species were recorded by the leading diver. Transects were completed at a slow but steady pace for divers to keep track of their depth, air, and respective counts accurately. After 50 m had been determined by the distance count diver, a double tap to the fish count diver's legs indicated the transect was complete. These steps were continued a further three times and repeated in each location. All transects were completed on the same dive, totalling four transects overall. The underwater visual census survey was carried out in early August 2022.

Results

In total, only 1 individual lumpfish (*Cyclopterus lumpus*) was recorded by visual census survey. Both baited trap deployments failed to record any individuals. Both underwater drone transects also recorded no fish.

Traps deployed in April for five days were completely stripped of bait upon recovery. Bait remained relatively intact after a 24 hour deployment in May.

Discussion

Only one individual of one species of fish recorded is an extremely poor result for the volume of time and resources required to deploy these methodologies at a remote site with weather windows for access. *C. lumpus* is a species well-known to utilise cultivated kelp as habitat (Hasselström et al., 2018). Juvenile *C. lumpus* are frequent hitch-hikers on cultivated kelp as it is being harvested, and is one of the few species recorded utilising cultivated kelp as habitat directly (Theuerkauf et al., 2021). It was therefore not a surprising species presence to record, but the abundance was far lower than expected.

The underwater visual census survey was not undertaken until early August. Upon arrival at the site, the remaining line of unharvested *A. esculenta* had been degraded/grazed substantially. This greatly reduced the habitat volume available along the lines for any fish utilising them as physical habitat and likely reduced the abundance of fish, including the expectedly common *C. lumpus*. At the time, only one cultivation line remained intact at the site due to vandalism which further reduced the amount of baseline habitat volume. The size of artificial marine structures can be correlated to the abundance of fish present (Rountree, 1989), and so the reduced cultivation structure size during underwater visual census surveys cannot be compared to the surveys undertaken when all lines remained at the site.

Traps deployed in April had been deployed with an intended soak time of 24 hours. Unfortunately, inclement weather postponed recover of the traps and extended the soak time to 120 hours. The lack of bait within each of the traps suggested that the baited traps had succeeded in attracting scavenging fauna of some description during their soaking period. Although the entrance of the larger traps were one-way, the larger mesh size may have allowed smaller species of fish or crustaceans to enter and exit the trap freely to feed on the bait. The smaller traps although having smaller water-flow holes and entrance, did not have a one-way trap entrance and so organisms after a time would have been able to make their exit. The bottle traps are typically used for periods of a few hours due to their permanently open entrance and are not likely ideal for retaining organisms for multiple days at a time.

The second trap deployment in May was successfully retrieved after a 24 hour soak, however again, no specimens were captured. The bait also remained intact in all traps. This suggested that the soak time was of insufficient length to attract and retain and mobile organisms.

The trap designs utilised had been trialled in Dun Laoghaire and Coliemore Harbours in South Dublin prior to deployment to ensure they were fit for purpose. During soaks between 1 and 3 hours, both traps were able to attract and retain a variety of decapod and fish species, including common prawn (*Palaemon serratus*), green crab (*Carcinus maenas*), velvet crab (*Necora puber*), brown crab (*Cancer pagurus*), lobster (*Homarus gammarus*), three-bearded rockling (*Gaidropsarus vulgaris*) and conger eel (*Conger conger*). Due to the vast array of species caught in trials, it is unlikely that 0 counts from the kelp cultivation site were due solely to trap design. Due to the fact the site had only been present with kelp for a couple of months, it is possible that the kelp was not present for long enough for any quantifiable communities of fish to reside there.

The underwater drone survey was a method that had the potential to provide spatially quantifiable fish abundance data in a non-abstractive manner without the logistics, coordination and time required for SCUBA diving. The first set of transects in February conducted to determine whether any fish were utilising the cultivation structure prior to kelp growth. This initial set of transects was unfortunately hampered by poor weather and less than 1 m visibility. This made it not only difficult to follow the cultivation line, but also extremely difficult to confirm if any fish were present, and particularly uncomfortable for those watching the screen in rolling seas. A repeat of these transects in May was conducted successfully along a mature cultivation line at the site. No fish were observed. The clarity of the footage beyond around 2 metres was not particularly good which also limited the chances of successful counts.

Although studies have investigated the role of cultivated kelp as habitat, those quantifying fish abundance have generally investigated seafloor fauna or cultivated macroalgae in different climates with permanently resident fish assemblages that don't change with the seasons (Visch et al., 2020b). The methodologies tested here were novel in this particular context and region. The trap methodology was deployed in an extremely broad, non-targeted way to attempt the quantify a currently unknown type of or existing assemblage.

We can confirm the presence of lumpfish on cultivated kelp long-lines. What we can also confirm is that they reside on the cultivated lines far beyond the normal harvest season at the end of spring. If cultivated macroalgae does provide habitat for mobile fauna, the displacement of these animals following the harvest and removal of cultivation lines each season should be further investigated to assess their effect, if any, on mobile fauna community structures adjacent to kelp farms.

Chapter 5 - Discussion

Kelp in general has gained increased interest from a variety of perspectives worldwide. The increased attention has been focused around the cultivation potential in regions of new and existing industries, the carbon sequestration potential, the consequences of losing kelp across wide spatial scales and the ecosystem services provided by kelps in order to place a value on their conservation. In fact, kelp has been tied directly as a tool to address a variety of the UN's sustainability goals (García-Poza et al., 2022). My research aimed to address knowledge gaps relating to the cultivation, ecology, ecosystem services and monitoring of kelp in an Irish context, with relevance to the wider northeast Atlantic. The knowledge gaps targeted relate to currently crucial avenues being faced by the kelp cultivation industry, the lack of ecological baseline data related to kelp ecosystems in the face of species range-shifts and coastal development, and the developing methodologies for gathering data in a relatively novel research environment. Framed within an Irish context, these knowledge gaps were targeted due to their wider relevance globally.

The development of the kelp mariculture industry in Europe is currently hindered by its economic viability at current scales (Bak et al., 2020). Compared to established Asian industries, the operating costs at current scales remain extremely high. Although the value of kelp per kg is much higher in Europe than in Asia (Grebe et al., 2019), the overall demand remains relatively low in comparison. One obvious solution to increase the competitiveness and boost growth in North Atlantic kelp mariculture is the development and refinement of new and existing cultivation techniques to improve yield quality and quantity with minimalised inputs.

Polyculture have been utilised in a variety of terrestrial agriculture systems to optimise and diversify yields. The benefits of polycultures in terrestrial agricultural systems can include

increased primary productivity, stability of yields across temporal scales, resistance to disease and more efficient uptake of nutrients (Mitchell et al., 2002). Macroalgae in the marine environment are inherently different to terrestrial plant being immersed within their substrate from which they derive their nutrients. Therefore, the drivers of competition and complementarity derive mainly from access to favourable light levels, nutrient availability, grazing pressure, as well water motion/wave action (Kregting et al., 2016, Smale et al., 2020). How species diversity may influence primary productivity in marine macroalgal dominated systems requires further research to break barriers to understanding biodiversity ecosystem functioning in the marine environment and further develop ecological concepts and more efficient aquaculture systems.

As the kelp cultivation industry strives for growth in Europe, the impacts will have to be carefully monitored and considered. Various potential environmental impacts have been suggested and tested by various researchers over the past decade (Campbell et al., 2019, Loureiro et al., 2015, Badis et al., 2019, Zhang et al., 2009, Walls et al., 2017b, Visch et al., 2020b). The general consensus of these studies has been that any negative environmental impact is either theoretically hypothetical or unquantifiable at the scales at which these impacts are tested. Most macroalgal cultivation sites in Europe likely lack the scale to have a quantifiable impact on a number of environmental and ecological parameters (Campbell et al., 2019). In China for instance, where farms can be hundreds of hectares in size (Jiang et al., 2020), any negative environmental impacts remain limited in their severity compared to finfish aquaculture (Visch et al., 2020a, Zhou, 2012). The potential future effects of macroalgal cultivation expansion in Europe may not be predictable. Standardised monitoring of various ecological and environmental parameters will be needed to be integrated into the development of the macroalgal cultivation industry in order to detect and ameliorate any negative, and quantify any positive impacts.

The loss of current and gain of new species will be an inevitable consequence of species range shifts as a result of climate change. In particular, the shifts in habitat-forming primary producer ranges are likely to result significant bottom-up community structure changes. The stability and productivity of ecosystems undergoing these changes in community compositions cannot be predicted with any certainty. The northward migration of many species into new regions is likely to be sporadic in timing and distribution, and reliant on many interacting factors such as prevailing currents, habitat requirements, life-cycles and their interaction with species in new regions (Rutterford et al., 2023). However, understanding what ecosystem services and level of ecosystem functioning is provided by present community structures will be important in identifying any future biodiversity and ecosystem service level losses or gains as communities change.

Baseline assessments in all areas of our marine environment will be vital both for estimating changes we may expect and what changes actually occur due to climate change. In Ireland, efforts have been made by citizen science and collaborative groups (e.g. Seasearch and The National Biodiversity Data Centre) to collect this baseline data in coastal areas. These initiatives provide data that covers broad temporal and spatial scales that would not otherwise have been collected. As with any citizen science collated data they are biased due to the favour of areas with ease of access and higher populations/footfall, and the ability of data collectors to identify a range of species as accurately and taxonomically broad as possible which likely varies widely (Bowler et al., 2022). Inherently, these surveys are likely to be biased towards more charismatic or noticeable species. It may be necessary for state bodies responsible for the management of these habitats to conduct surveys following standardised sampling methodologies in a wider range of habitats at specified intervals in order to verify data collected citizen scientists is accurate.

Surveys conducted at levels to inform fisheries management decision making in the marine environment are primarily fisheries dependant (Connor et al., 2019). These surveys are generally biased towards habitats, species and locations favoured by commercial fisheries as estimating these stocks are their primary purpose. These neglect other habitats upon which species of commercial interest may be dependent upon directly during other parts of their life-cycle, or indirectly through the food-web connectivity. Narrow habitat availability at specific life stages can act as a significant bottleneck in the life cycles of many fish species (Petitgas et al., 2013). The habitat complexity provided by kelp beds can significantly reduce post-settlement mortality in species which transition from pelagic larval stages to demersal juvenile stages for various commercially and ecologically important species, including Atlantic cod (*Gadus morhua*) and haddock (*Melanogrammus aeglefinus*) (Juanes, 2007). Although kelp beds are generally accepted to be important habitats in the marine environment, they are currently not offered protection under the EU Birds and Habitats Directive (Marine Protected Area Advisory Group, 2020) and as a result have been neglected from any stringent protection measures.

As the expansion of human activities in the marine environment due to increased resource requirements and changes within marine ecosystems due to climate change occur simultaneously, opportunities and challenges will inevitability be encountered. In the right locations, certain industries such as macroalgal cultivation can be implemented with positive outcomes commercially and environmentally. With shifting species ranges due to climate change, current and future marine anthropogenic activities ecological processes may be lost or changed beyond current recognition, and therefore certainty. Protection of current kelp habitats aid their resilience against environmental and anthropogenic stressors, allowing dependant ecosystems an opportunity to adapt and change while functioning at a similar level of productivity across trophic levels. Continued monitoring will allow us to track these

inevitable changes, and put them into context in the face of an increasingly anthropogenically influenced world.

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Appendix

A. Chapter 2 – Summary of results:

Table 1.

Treatment	n	Total kg	Mean	Median	SD	Highest	Lowest
A.e.	8	50	6.25	6.2	1.442	9	4.4
S.l.	6	33.8	5.633	6.25	2.343	8.2	2.7
L.d.	8	9.24	1.155	1.16	0.377	1.6	0.4
A.e. & S.l.	8	33.04	4.13	4.05	2.968	8.8	0.3
A.e. & L.d.	6	27.08	4.513	4.41	3.643	10.6	0.62
S.l. & L.d.	6	29.78	4.963	4.22	3.354	9.42	1.7
A.e. & S.l. & L.d.	6	19.38	3.23	3.16	0.676	4.42	2.42

Table 2.

	Estimate	Std. Error	t value	Pr(>|t|)
Intercept	0.12248	0.03414	3.587	**0.000920**
treatment 2	0.02766	0.04768	0.580	0.565234
treatment 3	0.69852	0.16403	4.258	**0.000125**
treatment 4	0.07922	0.05329	1.486	0.145209
treatment 5	0.04658	0.05576	0.835	0.408588
treatment 6	0.05095	0.05186	0.982	0.331955
treatment 7	0.13262	0.07289	1.819	0.076519

Table 3.

Treatments	1	2	3	4	5	6
2	1.0000	-	-	-	-	-
3	**0.0021**	**0.0224**	-	-	-	-
4	1.0000	1.0000	0.2709	-	-	-
5	1.0000	1.0000	0.2166	1.0000	-	-
6	1.0000	1.0000	0.0917	1.0000	1.0000	-
7	0.3671	1.0000	1.0000	1.0000	1.0000	1.0000

Table 4.

Treatment		Species
1	=	*A. esculenta*
2	=	*S. latissima*
3	=	*L. digitata*
4	=	*A. esculenta & S. latissima*
5	=	*A. esculenta & L. digitata*
6	=	*S. latissima & L. digitata*
7	=	*A. esculenta & S. latissima & L. digitata*

Table 1. Total, mean, median, variance and range for biomass production for each of the experimental treatments where n refers to number of 0.5 m replicates.

Table 2. Output of GLM (gamma distribution, inverse link function) using biomass data. Significant values displayed in bold.

Table 3. Output of Holm's pairwise comparison. Significant interactions displayed in bold.

Table 4. Legend of treatments displaying representative species.

B. Chapter 3 – Summary of results

Table 1. Fish counts per species/total, species richness (S'), total number of species, Shannon diversity index (H) and Shannon equitability index (E_H) for each site.

Species	Roaringwater	Toormore	Galleycove	Mean	Mean/m3
Gobiusculus flavensus	24	211	248	161.000	0.0410
Pollachius pollachius	67	76	49	64.000	0.0163
Labrus bergylta	8	15	3	8.667	0.0022
Symphodus melops	6	20	3	9.667	0.0025
Ctenolabrus rupestris	0	1	3	1.333	0.0003
Centrolabrus exoletus	1	1	0	0.667	0.0002
No. Individuals	106	324	306	245.333	0.0625
Species Richness (S')	3 $^+/_-$ 0.82	4 $^+/_-$ 0.82	3.5 $^+/_-$ 0.58		
Total Species	5	6	5		
Shannon Diversity (*H*)	0.596 $^+/_-$ 0.22	0.972 $^+/_-$ 0.26	0.641 $^+/_-$ 0.26		
Shannon Equitability (*E_H*)	0.563 $^+/_-$ 0.18	0.709 $^+/_-$ 0.17	0.503 $^+/_-$ 0.17		

Table 2. ANOVA outputs for species richness, total abundance, and Shannon diversity.

	df	Sum Sq	Mean Sq	F value	Pr(>F)
Species richness (S')					
Location	2	2	1	1.8	0.22
Residual	9	5	0.5556		
Total abundance					
Location	2	7321	3660	1.25	0.332
Residual	9	26364	2929		
Shannon diversity (H)					
Location	2	0.3372	0.1686	2.528	0.135
Residual	9	0.6003	0.0667		