Abstract: Global fisheries are in decline, calling for urgent evidence-based action. One such action is the identification and protection of fishery-associated habitats such as seagrass meadows and kelp forests, both of which have suffered long-term loss and degradation in the North Atlantic region. Direct comparisons of the value of seagrass and kelp in supporting demersal fish assemblages are largely absent from the literature. Here, we address this knowledge gap. Demersal fish were sampled using a baited camera to test for differences between habitats in (1) the species composition of the fish assemblages, (2) the total abundance and species richness of fishes, and (3) the abundances of major commercial species. Seagrass and kelp-associated fish assemblages formed two significantly distinct groupings, which were driven by increased whiting (Merlangius merlangus) and dogfish (Scyliorhinus canicula) presence in seagrass and higher abundances of pollock (Pollachius pollachius) and goby (Gobiusculus flavescens) in kelp. The abundance, diversity, and species richness did not change significantly between the two habitats. We conclude that seagrass and kelp do support unique demersal fish assemblages, providing evidence that they have different ecological value through their differing support of commercial fish species. Thus, this study improves the foundation for evidence-based policy changes.

Keywords: fish assemblages; eelgrass; laminaria; Zostera; fisheries; biodiversity conservation; species diversity; marine ecosystem; nursery habitat; UK

1. Introduction

The United Nations Food and Agriculture Organisations (FAO) estimated in 2015 that more than one third of global fish stocks were being fished at biologically unsustainable levels to support our ever-increasing human population [1–3]. Key to maintaining fishery stocks is understanding the habitats which are essential for supporting them [4–7].

Nearshore ecosystems, such as the brown algae kelp (Laminaria spp.) and the marine angiosperm seagrass (Zostera marina), can be important fish nursery grounds, crucial for maintaining fish stocks [8–11]. The physical structure of both ecosystems provides shelter from predators, and the large surface areas permit a higher settlement of epiphytes and invertebrates—key food sources for many juvenile fish [7,12,13]. Ribbon-like leaves of seagrass and large blades of kelp rise into the water column, serving to slow water flow through their respective habitats. This relatively benign environment decreases fish energy expenditure, allowing more energy for growth and success [14].

Both habitats are in decline principally due to water quality degradation, anthropogenic development, and climate change [11,15–19]. The availability of habitats like these has been found in some studies to have a stronger effect on the recovery of exploited fish populations than a reduction in fishing effort, making conservation crucial [20].
An important component to protecting these habitats is the knowledge of their associated fish assemblages and their implications on habitat function [21,22]. Top-down control, such as that caused by overfishing, can have similar or more pronounced degradation effects on seagrass and macroalgae than elevated levels of eutrophication [23]. In seagrass meadows, the removal of grazing species causes a trophic cascade of epiphytic dominance, smothering the seagrass and reducing photosynthetic abilities [24,25]. For kelp, the removal of predatory fish results in an increase in herbivorous species abundance, which can demolish the forests [11,26]. For both ecosystems, a downward spiral occurs, wherein less fish results in a weaker habitat, which, in turn, results in lower fish recruitment success.

When assigning ecosystem service values—for example, when creating marine spatial plans—it is necessary to make value judgements about the relative ecosystem functions of different habitats. This is particularly the case when the roles that different habitats play in supporting fish stocks are considered [27,28]. Judgements should be evidence-based, requiring studies and data that make accurate comparisons across habitats in their ecosystem service value [29]. Such comparative studies remain largely absent from the literature with respect to understanding the relative value of kelp forests and seagrass meadows for supporting fish fauna. Of those studies that do exist, they are largely limited both temporally and spatially [30]. In addition, with continued global interest in commercial kelp harvesting, it is particularly important that we develop a more quantitative understanding of kelp-associated fish communities to inform environmental impact assessments of this harvesting activity [27]. Currently, data on kelp-associated fish assemblages are extremely limited, possibly due to the challenges of catching or observing fish in dense kelp forests.

The present study aims to provide a comparison of demersal fish species assemblages associated with seagrass and kelp ecosystems around the UK and identify the spatial and seasonal variation within. Thus, this increases the capacity for evidence-based fishery and biodiversity management strategies.

2. Materials and Methods

Assessments of the fish assemblages in kelp and seagrass ecosystems were completed between April and September 2017 using mono-baited remote underwater video stations (BRUVS) [31]. BRUVS are a cost effective, non-destructive method for assessing species composition, and have little influence on the species present [32–35]. This study did not include a comparison with a denuded ecosystem, following the already established theory of seagrass and kelp supporting higher levels of biodiversity [8–11,27].

2.1. Study Sites

Five sites along the west coast of the United Kingdom were used: two in Pembrokeshire, two on the Llyn Peninsular, and one on the Isle of Skye (Figure 1, Table 1). All the sites had known seagrass meadows (Zostera marina) and kelp forests (Lamnaria spp.) present within 300 m of each other in sheltered waters. Bardsey Island was the exception, with only kelp present.
1. Locations of the baited remote underwater video (BRUV) deployments in seagrass and kelp. Study sites are Loch Eishort, Porthdinllaen, Bardsey Island, Milford Haven, and Skomer Island.

Table 1. Overview of the seagrass and kelp fish assemblage study site characteristics on the west coast of the UK.

| Metrics          | Milford Haven | Skomer    | Porthdinllaen | Bardsey Island | Loch Eishort |
|------------------|---------------|-----------|---------------|----------------|--------------|
| Coordinates      | 51.703711, -5.079408 | 51.738621, -5.279614 | 52.941880, -4.561587 | 52.752350, -4.794178 | 57.164910, -5.941416 |
| Zostera marina   | ✓             | ✓         | ✓             | ×              | ✓            |
| Laminaria spp.   | ✓             | ✓         | ✓             | ✓              | ✓            |
| Industry         | ✓             | ×         | ×             | ×              | ×            |
| Statutory Protection | ×            |            | ✓             | ✓              | ✓            |
| Depth Range (m)  | 3.0–6.2       | 2.6–6.3   | 3.0–7.5       | 2.0–13.5       | 2.5–6.1      |

The “✓” represents presence, the “×” represents absence.

2.2. Fish Assemblage Sampling

The BRUV deployments were by boat during daylight hours, between 09:00 and 16:00, and as close to the spring high tide as possible to minimise the tidal influence on the bait plume size and fish behaviour [36,37]. All the cameras were baited with approximately 100 g of fresh Atlantic mackerel (Scomber scombrus), prawn (Penaeidae sp.), or squid (Loliginidae sp.) [38,39]. The presence of bait, regardless of the bait type, gives the most consistent assemblage representation [40–42].
The project was approved by the Swansea University ethics board with the approval number SU-Ethics-Student-230920/237.

The video cameras (GoPro Hero 4, San Mateo, CA, USA) were set to record at a resolution of 1080p, 30 frames per second, and took 70 min recordings. The first and last five minutes were excluded from analysis to minimise the deployment and retrieval disturbance [30,43,44]. Analysis was made in real time using the specialised SeaGIS software EventMeasure (Version 3.51, www.seagis.com.au). The relative abundance, termed MaxN, was taken as the maximum number of individuals of a taxa per frame, minimising bias from repeated observations and thus giving the most conservative species relative abundance.

2.3. Statistical Analysis

All the summary data are presented as means ± sample standard deviations. The sampling design consisted of three factors: ecosystem (seagrass and kelp), site (Milford Haven, Skomer, Llyn Peninsular and Loch Eishort), and season (spring, early summer, and late summer). Statistical analysis was conducted using PRIMER v7 [45]. The Shannon-Wiener diversity index (H') was calculated to characterise the species diversity.

Univariate analysis of the ecosystem, site, and season permutational analysis of variance (PERMANOVA+) using a Euclidean resemblance matrix was employed to analyse the differences in relative abundance and species diversity between conditions [46]. All the PERMANOVA tests were nested three ways and based on 9999 unrestricted permutations under a reduced model.

Community composition was analysed on square-root transformed data using a Bray-Curtis similarity resemblance measure and visualised using non-metric multidimensional scaling ordination (nMDS) [47]. A two-way analysis of similarity percentages (SIMPER) was performed on Bray-Curtis similarity data with a 50% cut off for low contributions, allowing ecosystem driver species to be identified. Two-tailed t-tests were also performed to identify differences in certain species abundance between the habitats.

3. Results

Out of 116 samples, 49 were suitable for fish assemblage analysis (Appendix A Table A1). In order to provide a consistent sampling regime, samples were excluded when the bait box was not in clear view (e.g., high turbidity), the BRUV system fell over, or the equipment failed. A total of 50 animal taxa were seen across all samples, of which 36 were fish species. Thirty-three animal taxa were observed across the kelp samples, of which 22 were fish, and 33 animal taxa were recorded in seagrass, of which 29 were fish. Only fish species were considered for analysis.

3.1. Abundance

The fish abundance (with habitat and site nested inside season) did not differ significantly depending on the season, site, or habitat (F_{2,40} = 0.27, p = 0.84; F_{3,40} = 3.63, p = 0.23; and F_{3,40} = 0.12, p = 0.91, respectively) (Figures 2 and 3). Across all samples, the mean relative abundance (MaxN) was 19.53 ± 37.52. Kelp had a mean relative abundance of 18.45 ± 32.91 fish per sample; the two-spotted goby (Gobiusculus flavescens) was the most abundant (Table 2). The mean relative abundance found in seagrass was 20.41 ± 41.49, and the most abundant species identified in seagrass was the dogfish (Scyliorhinus canicula). The calculated mean values do not consider the seasonal or spatial variability within the data.
Figure 2. Metric of (a) the relative fish abundance (MaxN), (b) species richness, and (c) Shannon Weiner diversity index ($H'$) from seagrass and kelp sites using mono BRUVs in the UK during 2017. Mean data are shown with standard deviation bars. “All Seasons” shows an average across all data.
Figure 3. Metric of (a) the relative fish abundance (MaxN), (b) species richness, and (c) Shannon Weiner diversity index (H’) from four seagrass and kelp sites using mono BRUVs in the UK during 2017. Seagrass was not assessed at Milford Haven. Mean data are shown with standard deviation error bars.
Table 2. The contribution (%) of the most prevalent four species to kelp and seagrass habitats, from BRUVS deployments across the UK west coast between April and September 2017, in a two-way analysis of similarities (SIMPER) across season and site.

| Ecosystem | Species               | Similarity Contribution (%) |
|-----------|-----------------------|-----------------------------|
| Kelp      | Gobiusculus flavescens| 35.13                       |
|           | Pollachius pollachius | 22.07                       |
|           | Labrus bergylta       | 20.81                       |
| Seagrass  | Scyliorhinus canicula | 30.44                       |
|           | Merlangius merlangus  | 24.7                        |
|           | Callionymus lyra      | 12.31                       |
|           | Pomatoschistus microps| 8.88                        |

3.2. Species Richness

Across all samples, the mean total species count was 4.27 ± 2.34. The mean total species count was higher in kelp (4.41 ± 2.36) than in seagrass (4.14 ± 2.36). The total species count did not differ significantly between the season, site, or habitat (PERMANOVA, F2,40 = 1.06, p = 0.44; F3,40 = 7.06, p = 0.13; and F3,40 = 0.23, p = 0.87, respectively) (Figures 2 and 3).

3.3. Species Assemblage

There was a significant difference recorded (PERMANOVA, F3,40 = 4.71, p < 0.001) between the community composition of fish in kelp forests and seagrass meadows at a 30% similarity level, with the abundance of G. flavescens as the biggest driver of the dissimilarity in compositions (Figure 4, Table 3). Assemblage was not significantly different with respect to the season or site (PERMANOVA, F2,40 = 1.12, p = 0.41; F3,40 = 0.67, p = 0.91, respectively).

Figure 4. Non-metric multidimensional scaling configuration with superimposed Bray-Curtis similarity clusters (30% similarity) for fish assemblage in seagrass and kelp ecosystems across the west coast of the UK. One anomalous seagrass sample was removed from the MDS plot for clearer aesthetics. One conger eel and no other fish were identified in this sample.
Table 3. Inter-habitat dissimilarity, showing the top four fish species present and their percentage of contribution (%) to differences in seagrass and kelp communities from BRUVS deployments across the UK west coast between April and September 2017, following SIMPER analysis on square-root-transformed data.

| Species                  | Dissimilarity Contribution (%) |
|--------------------------|--------------------------------|
| Gobiusculus flavescens   | 12.73                          |
| Pollachius pollachius    | 9.53                           |
| Merlangius merlangus     | 8.92                           |
| Scyliorhinus canicula    | 8.92                           |

3.4. Commercial Assemblage

The key commercial species seen included Atlantic cod (Gadus morhua), Atlantic pollock (Pollachius pollachius), Whiting (Merlangius merlangus), flatfish (Limanda limanda, Platichthys flesus and Pleuronectes platessa), European Sprat (Sprattus sprattus), and Atlantic Mackerel (Scomber scombrus). The three flatfish species were all in low abundance, and so were considered as one grouping under the term “flatfish”.

All the cod recordings occurred from June onwards and at two sites, Llyn and Skomer. The cod abundance was not significantly different between habitats (two-tailed t-test, \( p = 0.83, t = 2.01 \)); however, the presence distribution varied, as individuals were observed across six seagrass samples, whereas only one shoal was observed in kelp (Table 4). Pollock were present across all the seasons and sites, and were significantly more abundant in the kelp forests (two-tailed t-test, \( p < 0.05, t = 2.01 \)). Flatfish were only present in the seagrass samples, where they were observed across all the seasons and sites. Whiting were only present in late summer Llyn seagrass samples. Sprat and Atlantic mackerel were observed, but both in only one sample.

Table 4. The mean abundance (±SD) of commercially important species (cod (Gadus morhua), pollock (Pollachius pollachius), flatfish (Including Limanda limanda, Platichthys flesus, and Pleuronectes platessa), and whiting (Merlangius merlangus)) in seagrass and kelp ecosystems from BRUV samples across the UK from April to September 2017.

| Species                  | Ecosystem | Abundance       |
|--------------------------|-----------|-----------------|
| Gadus morhua             | Kelp      | 0.18 ± 0.85     |
|                          | Seagrass  | 0.22 ± 0.42     |
| Pollachius pollichis     | Kelp      | 2.18 ± 3.40     |
|                          | Seagrass  | 0.63 ± 1.50     |
| Flatfish                 | Kelp      | 0.00 ± 0.00     |
|                          | Seagrass  | 0.22 ± 0.71     |
| Merlangius merlangus     | Kelp      | 0.00 ± 0.00     |
|                          | Seagrass  | 2.2 ± 4.05      |

4. Discussion

The research presented here provides a unique analysis of the fish fauna in seagrass meadows and kelp forests using comparable methods. It highlights that seagrass meadows and kelp forests support significantly differently associated fish assemblages, but do not largely differ in their fish abundance or diversity when examined using baited video. Such direct comparisons are vital for the development of evidence-based legislation to protect habitats that provide more and stronger recruits to diminishing fish stocks [27].

This study provides clear comparable evidence that both seagrass meadows and kelp forests support fish species of commercial significance; this is of importance, given the dearth of data on fish species-associated with kelp forests, particularly in the NE Atlantic region. The present study also builds on existing data, showing the value of three-dimensional seagrass and algal habitats in
supporting more abundant and diverse fish than unvegetated and unstructured habitats [8–11,27]. The present study used mono-baited video, and therefore it is not possible to distinguish age classes reliably, restricting our ability to understand the relative nursery functioning of these systems; however, previous beach seine data indicates that those species found in seagrass in the present study were mostly of a juvenile size range [8].

Species thrive when inhabiting a favoured ecological niche, and the resulting large population can lead to them dominating abundance samples and influencing the community composition [48]. Species of a higher trophic level create increased interspecific competition for resources, whereas an abundance of smaller non-predatory species may provide an ample food source, altering the community structure. The most abundant species observed, dogfish (*Scyliorhinus canicular*) and the two-spotted goby (*Gobiusculus flavescens*), were key drivers in the assemblage differences for these reasons, respectively.

The two-spotted goby was amongst the most abundant species for both ecosystems, reflecting the previous literature and rationalised through their established preference for complex three-dimensional seascapes [5,49,50]. The abundance of the two-spotted goby indicates the availability of small fish in both ecosystems as prey items for predatory commercially valuable species, such as the Atlantic cod and the Atlantic pollock [51].

Several North Atlantic-based studies have identified an abundance of cod in seagrass [8,12,52,53]. Two comparative studies of seagrass meadows and kelp forests also reported higher abundance of Pacific cod [9] and Atlantic cod [30] in seagrass. No significant difference in cod abundance was found between habitats; however, a distinct difference in distribution was observed, with one shoaling group seen in kelp and only individuals seen in seagrass samples. The fine seagrass leaves create a more complex three-dimensional structure, which increases the cod carrying capacity and survival rates. In more exposed environments, such as kelp, cod tends to increase shoaling behaviour, negatively impacting growth and survival through increased intraspecific competition. Pinnegar et al. [54] highlights that Atlantic cod stocks are altering key behaviours such as spawning times and distributions in response to climate change and overfishing, emphasising the importance of expanding our knowledge of their ecological niches in order to maintain sustainable stocks.

Pollock is an adaptable species occupying rocky and sandy coastal habitats alike, forming shoals or developing individual territories [55,56]. The presence of pollock in both kelp and seagrass habitats across all sites and seasons reflects this and supports previous findings [8,30]. Existing studies suggest lower-energy environments, such as seagrass, to be more important for pollock fry, whereas the rockier kelp would identify an abundance of transitional stage pollock, before moving to deeper exposed waters in maturity [57,58].

This study supports the well-reported presence of flatfish in soft-bottomed UK seagrass meadows and their lack of association with rockier kelp forests [8,30,59,60].

Whiting display a preference for sandy or gravel habitats over rocky substrates or emergent structures associated with kelp forests, explaining their observed presence in seagrass but not kelp [61]. The demand for whiting has grown as other key commercial species populations such as cod have declined, increasing their economic value and the need for their consideration within fishery management strategies. Whiting show ontogenetic migrations towards deeper waters, again emphasising the need for studies including age association [62,63].

The relative abundance, species richness, and diversity index also responded in unison to spatial variation, regardless of the ecosystem. The proximity of ecosystems within a site (~300 m) makes it probable that motile fauna moves between the ecosystems, reducing the differences in observed assemblages. The concept of habitat connectivity is proven to enhance populations, as each ecosystem supports one another through bio-physical and biological features [5,64–66].
5. Conclusions

We find that seagrass meadows and kelp forests contain differing fish assemblages, yet the fish abundance and richness did not vary across habitats. Over the time scales assessed, the fish did not change in assemblage, richness, or abundance with respect to location or season. This study provides the first evidence that UK kelp forests and seagrass meadows have different ecological values through their differing support of commercial fish species, increasing the potential for evidence-based policy changes [7,67].

Author Contributions: All authors contributed to the experimental design, execution, and reporting. All authors have read and agreed to the published version of the manuscript.

Funding: This research received no external funding.

Acknowledgments: We thank all at Project Seagrass, SEACAMS2, the Skomer MNR team, and Alun Valed Jake Davies for their field assistance.

Conflicts of Interest: The authors declare no conflict of interest.

Appendix A

Table A1. Successful deployments in seagrass (SG) and kelp (K) ecosystems at the five study sites between April and October 2017. Brackets indicate failed deployments. Total of 116, of which 49 were successful.

| Location     | Ecosystem | April | May | June | July | August | September |
|--------------|-----------|-------|-----|------|------|--------|-----------|
| Loch Eishort | SG        | 5 (3) |     |      |      |        |           |
|              | K         | 4 (3) |     |      |      |        |           |
| Milford Haven | SG      |       | 2 (2) |      |      |        |           |
|              | K         |       | (3) | 2 (2) |      |        |           |
| Skomer       | SG        | 2 (2) | 3   |      |      |        |           |
|              | K         | (3)   | 2 (1)|      |      |        |           |
| Porth Dinllaen | SG | 2 (6) | 4 (1)|      | 13 (3)|        |           |
|              | K         | (4)   | (1) | 4 (4) |      |        |           |
| Bardsey      | K         |       |     |      |      | 10 (13)|           |

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