

Spatial variability in the structure of fish assemblages associated with *Laminaria hyperborea* forests in the NE Atlantic

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ABSTRACT

Understanding fish-habitat associations is critical for ecosystem-based approaches to management and conservation. Kelp species, which are estimated to inhabit around 25% of the world's coastline and underpin highly productive and biodiverse ecosystems, are widely recognised as important nursery and foraging habitats for coastal fish species. However, quantitative assessments of fish assemblages within kelp forests are lacking for many regions. Here, we used Baited Remote Underwater Video (BRUV) and Underwater Visual Census (UVC) to quantify fish assemblages in *Laminaria hyperborea* forests at eight shallow subtidal rocky reefs that spanned 9° of latitude in the United Kingdom (UK). Fish assemblages were a ubiquitous and conspicuous component of kelp forest communities at all sites. BRUV surveys recorded marked regional-scale variability, with latitudinal shifts in assemblage structure and particularly distinct assemblages recorded in southwest England. These patterns were largely due to greater abundances of *Pollachius* spp. (i.e. saithe and pollock) in northern regions and higher numbers of *Gobiusculus flavescens* (two-spotted goby) and labrid species (i.e. rock cook, goldsinny and ballan wrasses) in southern regions. Unlike BRUVs, UVC surveys did not detect significant regional-scale variation in assemblage structure but did detect significant site-level differences, highlighting differences between the two techniques. BRUV surveys also recorded clear latitudinal trends in richness, with more taxa recorded at lower latitudes. Fish assemblages in the NE Atlantic have been, and will continue to be, impacted by ocean warming and fishing activities. Greater spatiotemporal coverage of kelp forest surveys and ongoing robust monitoring is needed to better understand and manage future ecological changes.

1. Introduction

Kelp species are estimated to inhabit around a quarter of the world's coastlines (Jayathilake and Costello, 2020), where they form highly productive and diverse habitats (Steneck et al., 2002; Teagle et al., 2017) and underpin a range of ecosystem services (Bennett et al., 2016; Blamey and Bolton, 2018; Smale et al., 2013). As with other coastal vegetated habitats, such as seagrass meadows and mangrove forests (Bertelli and Unsworth, 2014; Nagelkerken et al., 2002), a key ecosystem service widely attributed to kelp forests is the provision of nursery and foraging habitat for finfish (Bertocci et al., 2015; Bodkin, 1988). This is achieved through the direct provision of complex biogenic habitat that offers refugia from predators and also supports high diversity of plant and animal food sources (Bertocci et al., 2015). Many of

the fish found in kelp forests are commercially important species and, as such, understanding habitat-fish associations is an important aspect of ecosystems based fisheries management (Bertocci et al., 2015; Lefcheck et al., 2019). However, despite their obvious economic and ecological value, quantitative assessments of fish assemblages associated with kelp forests are lacking for many regions (Bertocci et al., 2015; Lefcheck et al., 2019). For example, while spatiotemporal variability patterns of kelp forest fish assemblages have been well characterized in Australasia (Anderson and Millar, 2004; Tuya et al., 2011), California (Bodkin, 1986; Holbrook et al., 1994) and South America (Hüne et al., 2021; Pérez-Matus et al., 2007) they have received less attention in the northeast (NE) Atlantic (but see Furness and Unsworth, 2020; Pita et al., 2018). This is surprising given their importance within coastal food webs and the intensifying pressures on both fish species and kelp forests

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in this region (Eigaard et al., 2016; Smale et al., 2013).

In the NE Atlantic, *Laminaria hyperborea* (Gunnerus) Foslie 1884 dominates rocky subtidal reefs along wave exposed coastlines (Assis et al., 2016; Smale et al., 2013; Smale and Moore, 2017). To date, research conducted on the structure and functioning of fish assemblages associated with *L. hyperborea* forests has been limited, despite the extensive distribution of these habitats along the coastline of northwest Europe (Assis et al., 2016; Pessarrodona et al., 2018). The few studies that have described this aspect of biodiversity have been conducted in Norway or on the Iberian Peninsula (Franco et al., 2020; Norderhaug et al., 2005; Pita et al., 2018), with basic quantitative information lacking for most other regions. Given *L. hyperborea* is threatened by a range of stressors (Smale et al., 2013), this lack of baseline information impedes our ability to monitor and predict environmental change and implement informed management strategies.

Here we used two sampling methods, Baited Remote Underwater Video Surveys (BRUVs) and Underwater Visual Census (UVC), to characterise fish assemblages associated with subtidal *L. hyperborea* forests in the United Kingdom (UK). We conducted surveys at eight sites within four established study regions that spanned 9° of latitude and a 2.5 °C gradient in ocean temperature (Smale et al., 2016; Smale and Moore, 2017; Smale et al., 2020b). Recent work across this gradient has identified clear regional-scale variability in the structure of *L. hyperborea* forests (Smale et al., 2016; Smale and Moore, 2017). In addition, some components of kelp forest biodiversity (e.g. understory algal and invertebrate assemblages) exhibit regional variability and structural shifts with latitude (Bué et al., 2020; Smale et al., 2020a), whereas other components (e.g. kelp holdfast and stipe-associated assemblages) show limited regional structuring and high variability at smaller spatial scales (King et al., 2021; Teagle et al., 2018). Given that fish assemblages are influenced by both large scale drivers (e.g. temperature, exploitation) and small scale processes (e.g. predation, food availability, habitat structure), patterns of variability in assemblage structure are likely to be complex and context-dependent. With this in mind, the overall aims of

the study were to (i) quantify fish assemblages within *L. hyperborea* forests, (ii) examine variability in ecological patterns across multiple spatial scales, from meters to hundreds of kilometres, and (iii) compare the utility of the two survey methods (BRUV and UVC).

2. Methods

2.1. Study area

We examined the structure of fish assemblages at eight subtidal rocky reef habitats situated within four regions, which spanned 9° of latitude in the UK. Adjacent regions were situated between ~180 and 500 km apart (Fig. 1). The four regions (N Scotland, W Scotland, S Wales and S England) are broadly comparable with regards to wave fetch, turbidity and nutrients, but differ in their climatology (see Table S1 for summary and see Smale et al., 2016; Smale et al., 2020b for a full description of the sites and selection criteria). The two northernmost regions are, on average, 2.5 °C colder than the two southernmost regions (Pessarrodona et al., 2018). Within each region we selected two subtidal sites (randomly from a larger pool of potential sites) that were similar in terms of depth, geomorphology and topography (Fig. 1, Table S1). Sites within regions were situated between ~2 and ~13 km apart, and all sites were known to support extensive kelp forest habitat dominated by *Laminaria hyperborea* (Pessarrodona et al., 2018; Smale and Moore, 2017).

2.2. Baited remote underwater video (BRUV)

Given the three-dimensional environment provided by kelp, a combination of benthic and pelagic BRUV systems were used to capture kelp-associated fish assemblages. The pelagic BRUV was modelled on Santana-Garcon et al. (2014) and featured a stainless-steel frame, which was suspended above the kelp canopy while remaining anchored to the benthic BRUV. Pelagic BRUV systems comprised two SJCAM 4000

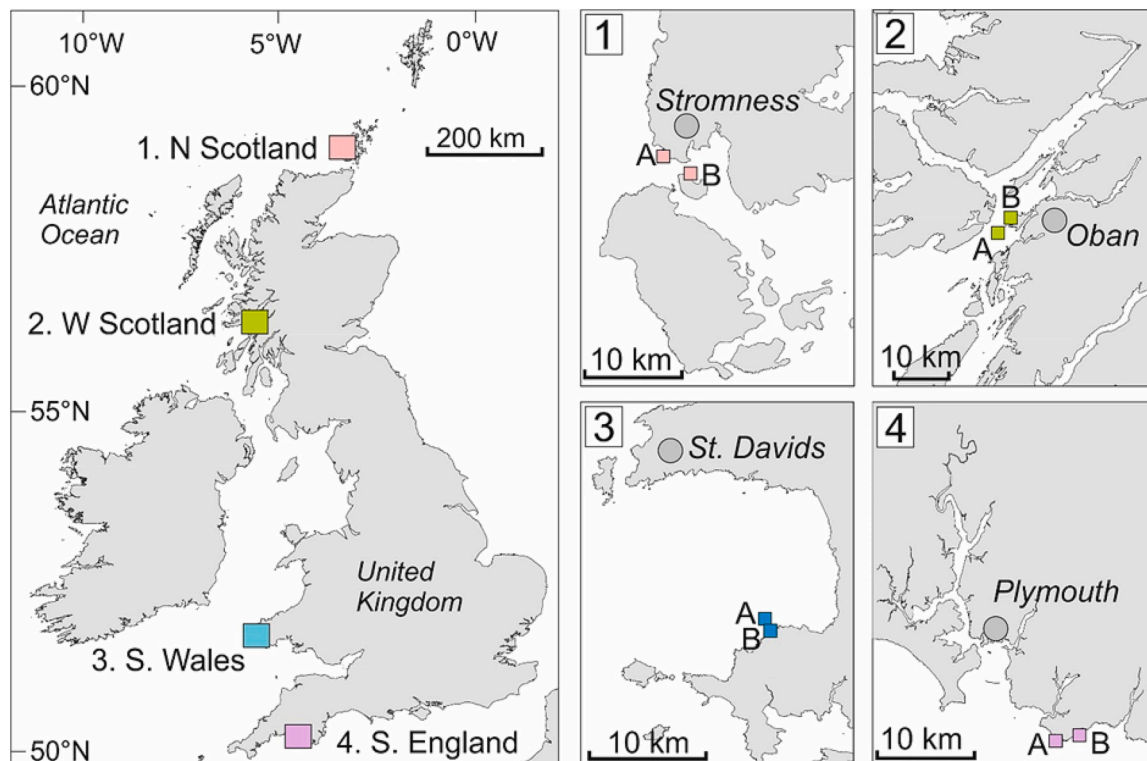


Fig. 1. Main map shows positions of four study regions (1: north Scotland, 2: west Scotland, 3: south Wales, 4: south England). Insets maps indicate the location of the two study sites (A and B) within each region.

(SJCAM Limited, China) action cameras mounted on a base bar inwardly converged at an 8° to gain an optimized field of view (Fig. 2). A bait holder was positioned in front of the cameras at a distance of 0.5 m. As mono camera systems, benthic BRUV systems comprised one SJCAM 4000 action camera facing the bait holder. All systems were baited with a crushed mackerel (*Scomber scombrus*). Five replicate BRUV systems (i.e. combined benthic and pelagic) were deployed by boat at each site during each survey, at distances of >50 m apart and within mature *L. hyperborea*. Ideally, replicate BRUV units would be deployed further apart (i.e. >200 m) to avoid overlap of bait plumes and ensure independence (Langlois et al., 2010). However, due to the extent and patchiness of reef habitat at some sites this was not feasible so the spacing of deployments was reduced and made comparable to UVC coverage. Video systems recorded for a duration of 60 min, which was deemed acceptable as the majority of species usually occur within the first 40 to 60 min of deployment (Unsworth et al., 2014), and allowed for adequate ‘settling’ time following the disturbance of the initial deployment.

BRUV surveys were conducted in late summer (August–September) in both 2016 and 2017. However, due to adverse weather conditions, BRUVs were not deployed in southwest Wales in 2017. Fish assemblage structure and abundance were examined using footage from the left camera only (Right camera was kept in case of camera failure) of the pelagic BRUV and the central camera for benthic BRUV. Fish species were identified to the lowest taxonomic level possible and the conservative measure of relative abundance MaxN was recorded for each species. MaxN is obtained by counting the maximum number of each species visible in a single frame (Cappo et al., 2003; Langlois et al., 2010). Individual fish within ~3 m distance from the camera were identified and enumerated; horizontal visibility through the water was at least 5 m during the surveys (as estimated by divers). This approach has been shown to be robust, enabling an accurate and efficient assessment of fish assemblage structure (e.g. Letessier et al., 2013).

2.3. Underwater visual census (UVC)

UVC surveys were conducted in late summer (August–September 2017 and 2020). At each of the two sites used for BRUV deployments a single SCUBA diver swam along a randomly positioned 25 m by 2 m belt transect. Due to the density of kelp stipes the diver swam above the kelp canopy on the outward leg to capture pelagic species and would swim within the kelp forest on the return leg to capture benthic species. Five replicate transects were undertaken at each site. All fish species were identified and enumerated.

2.4. Data analysis

In total, 70 BRUV deployments (collecting a total of 140 h of footage) and 40 UVC transects (sampling a total area of ~2000 m²) were completed in the study. For BRUV surveys, videos that did not record any fish due to either technical issues or lens obstruction by kelp plants were first removed, resulting in 61 replicates for analysis and an unbalanced design (*n* per site/survey ranged from 3 to 5). Pelagic and benthic BRUV data from the same unit were pooled to investigate fish assemblages across the kelp strata. Both univariate and multivariate analyses were conducted using Primer v7 software (Clarke and Gorley, 2015) with the PERMANOVA add on (Anderson et al., 2008). Initially a full model with the factors Year (fixed), Region (fixed) and Site (random, nested in region) was used to explore variability in fish assemblage structure. In all cases the ‘Year’ factor (and associated interactions) were non-significant at *p* > 0.3 (Table S2) and the year factor was removed to allow for a more robust examination of spatial variability patterns using the Region and Site factors only. Permutations (999 under a reduced model) were based on a Bray-Curtis similarity matrix constructed from square-root transformed abundance data. Square-root transformation was chosen to down weight the importance of numerically dominant fish species. Where the Region factor was significant (*p* < 0.05), pairwise tests were conducted between Regions to determine where differences were present. To determine which taxa contributed the most to the

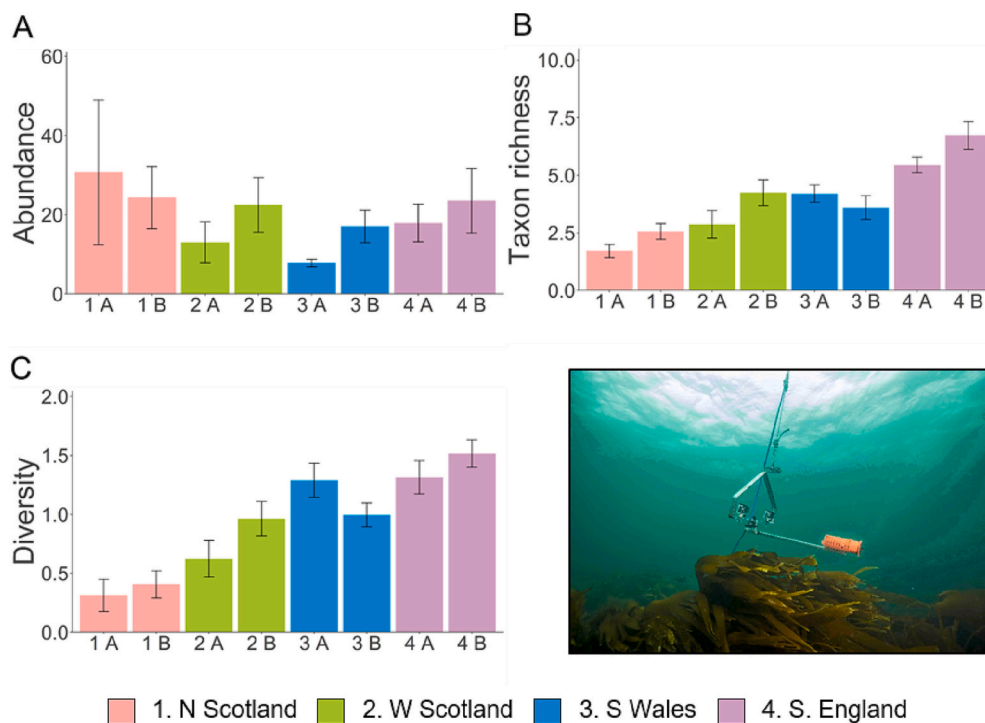


Fig. 2. Total abundance, taxon richness and diversity of fish assemblages at each site within each region, as captured by BRUV surveys. Four study regions were north Scotland (1), west Scotland (2), south Wales (3) and south England (4), with two sites (A and B) surveyed in each region. Bars show mean values ± SE. Image in lower right panel shows a typical deployment of the pelagic BRUV system.

observed dissimilarities a similarity percentage procedure (SIMPER) was carried out. The same statistical approach was undertaken for the UVC data.

Patterns in fish assemblage structure were visualised using principal coordinate analysis (PCO) and constrained canonical analysis of principal coordinates (CAP) plots (Anderson and Willis, 2003). Vectors were overlaid onto CAP plots to illustrate the strength of Pearson's correlations between fish species abundances and CAP axes (using correlations ≥ 0.5 to identify the most influential species). Given some species were only detected with one technique, both BRUV and UVC surveys were also combined to provide a comprehensive assessment of kelp-associated fish assemblages. Here, presence/absence data were used with the same PERMANOVA model based on a Jaccard resemblance matrix. Variability in univariate assemblage metrics (total abundance, taxon richness and Shannon Weiner diversity) for both BRUV and UVC separately (and taxon richness for combined techniques) were analysed using the same permutation-based model described above with Euclidean distance used for the similarity matrices. Prior to analysis, differences in within-group dispersion were examined with the PERMDISP routine. For all assemblage-level univariate response variables, data are presented as mean values \pm SE.

3. Results

Across all surveys, a total of 4636 individuals representing 24 taxa were recorded. A total of 1249 individuals (21 species) were recorded with BRUV surveys, whilst UVC surveys recorded 3387 individuals (16 species). *Pollachius* spp. (saithe and pollack) were found at every site and were generally the most dominant taxa, contributing to $\sim 38\%$ of total abundances, while the two-spotted goby, *Gobiusculus flavescens*, was also often locally abundant.

3.1. BRUV surveys

Total fish abundance ranged from 7.8 ± 2.2 (S Wales A) to 30.7 ± 18.2 (N Scotland A) but did not differ significantly between regions

(Fig. 2A; Table 1). Taxon richness ranged from 1.7 ± 0.29 (N Scotland A) to 6.73 ± 0.6 (S England B) and differed significantly between regions (Fig. 2B; Table 1). Pairwise comparisons revealed all regions were significantly different to one another apart from S Wales and W Scotland. Shannon Weiner diversity ranged from 0.31 ± 0.14 (N Scotland A) to 1.52 ± 0.12 (S England B) with a clear stepwise increase in diversity with decreasing latitude (Fig. 2C; Table 1). Pairwise comparisons revealed all regions were different from one another apart from S Wales and S England.

PERMDISP showed no significant differences in within-factor multivariate dispersion ($F_{(3, 57)} = 0.52, p = 0.5$). Fish assemblage composition captured by BRUV surveys varied significantly among regions and exhibited significant Site(Region) variability (Table 1). Pairwise comparisons showed all regions to be different from one another, while PCO plots suggested strong partitioning between the two northern (N and W Scotland) and two southern (S Wales and S England) regions, with S England particularly distinct from all other regions (Fig. 3A). SIMPER analysis revealed this was driven predominantly through greater abundance of *Pollachius* spp. in northern regions and greater abundances of *Gobiusculus flavescens* in southern regions (Fig. 3B). The distinctness of S England was driven through greater abundances of *Centrolabrus exoletus* and *Ctenolabrus rupestris* (Table S3, Fig. 3B).

3.2. UVC surveys

Total fish abundance ranged from 48 ± 29 (S England A) to 228 ± 50 (W Scotland B) (Fig. 4A). There was no significant differences between regions but significant Site(Region) variability was detected (Table 1). Greatest within-region variability was observed in W Scotland where abundance range from 19.4 ± 4.7 (W Scotland A) to 228 ± 50 (W Scotland B). Taxon richness ranged from 1.6 ± 0.25 (N Scotland B) to 5.4 ± 0.4 (S Wales A) and differed significantly by region, with a clear stepwise increase with decreasing latitude (Fig. 4B; Table 1). Pairwise comparisons revealed all regions were different to one another apart from S Wales and S England. Shannon's diversity ranged from 0.109 ± 0.002 (W Scotland B) to 1.33 ± 0.12 (S Wales A) and differed

Table 1

Results of univariate and multivariate PERMANOVAs to test for differences in fish assemblages between regions (fixed) and sites (random, nested within region), based on each survey technique separately and in combination. Significant differences are highlighted in bold. Where significant differences between regions were detected, the results of pairwise post hoc tests are shown (1: north Scotland, 2: west Scotland, 3: south Wales, 4: south England).

Source	BRUV				UVC				Combined BRUV-UVC			
	df	MS	Pseudo-F	p	df	MS	Pseudo-F	p	df	MS	Pseudo-F	p
	<i>Multivariate assemblage</i>				<i>Multivariate assemblage</i>				<i>Multivariate assemblage</i>			
Region	3	15,116	5.2327	0.001	3	5755.7	1.0941	0.432 (MC)	3	9939.7	3.8449	0.012
Site (Region)	4	2920.1	2.5361	0.001	4	5260.7	4.7869	0.001	4	2586.9	1.9987	0.002
Residual	53	1151.4			32	1113.9			36	1294.3		
Total	60				39				43			
Pairwise tests	1 \neq 2 \neq 3 \neq 4								1 \neq 2 \neq 3 \neq 4			
	<i>Total abundance</i>				<i>Total abundance</i>				<i>Taxon richness</i>			
Region	3	42.671	2.9315	0.186	3	6803.3	0.21946	0.901 (MC)	3	58.654	10.753	0.008
Site (Region)	4	14.617	1.3081	0.277	4	31,001	5.6808	0.003	4	5.4587	2.251	0.089
Residual	53	11.174			32	5457			36	2.425		
Total	60				39				43			
Pairwise tests									1 < 2 = 3 < 4			
	<i>Taxon richness</i>				<i>Taxon richness</i>							
Region	3	47.903	10.153	0.025	3	25.425	145.29	0.001 (MC)				
Site (Region)	4	4.7689	2.5171	0.051	4	0.175	0.125	0.964				
Residual	53	1.8946			32	1.4						
Total	60				39							
Pairwise tests	1 < 2 = 3 < 4				1 < 2 < 3 = 4							
	<i>Diversity</i>				<i>Diversity</i>							
Region	3	3.8777	12.3	0.015	3	1.9019	11.443	0.020 (MC)				
Site (Region)	4	0.31857	2.412	0.062	4	0.1662	1.6323	0.201				
Residual	53	0.13208			32	0.094469						
Total	60				39							
Pairwise tests	1 < 2 < 3 = 4				1 = 2 = 4 < 3							

Note: MC (= Monte Carlo) indicates where P values were estimated with the Monte Carlo routine.

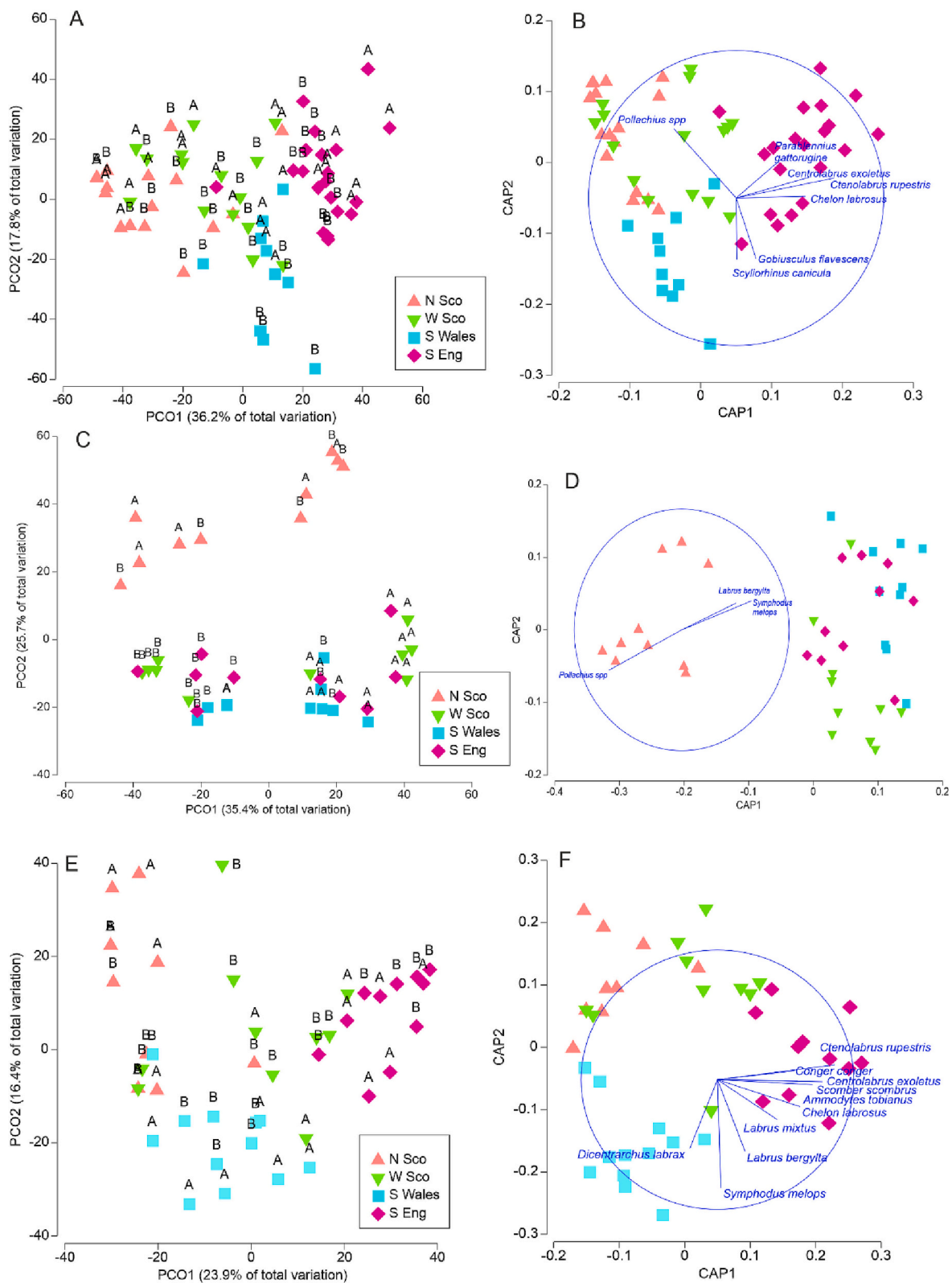


Fig. 3. Principle Coordinate Ordination (PCO) and Canonical Analysis of Principal Coordinates (CAP) plots of fish assemblage sampled at each site within each region as collected by (A, B) BRUVs, (C,D) UVCs and (E,F) both techniques combined. Data were square-root transformed and similarities were based on a Bray-Curtis similarity matrix (or Jaccard similarity for the combined dataset). Vectors overlaid on CAP plots indicate the direction of Pearson correlations between individual fish species and CAP axes (minimum correlation coefficient of 0.5). The four study regions were north Scotland (1), west Scotland (2), south Wales (3) and south England (4), with two sites (A and B) surveyed in each region.

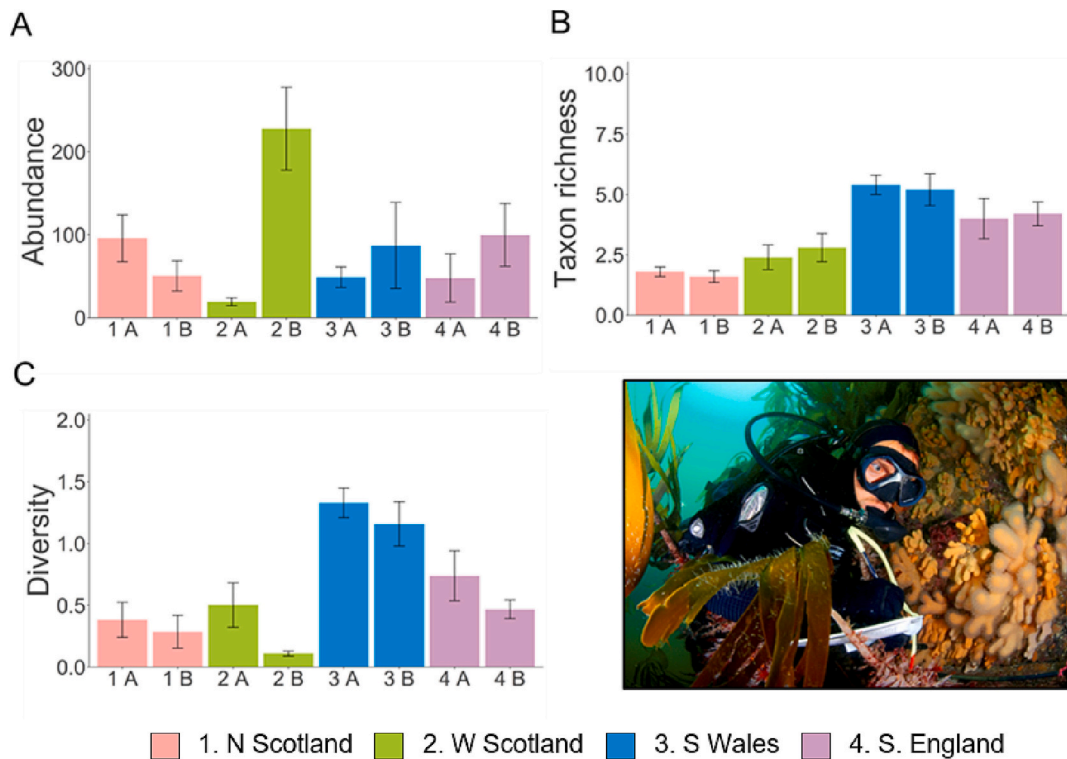


Fig. 4. Total abundance, taxon richness and diversity from UVCs for each site within each region. Four study regions were north Scotland (1), west Scotland (2), south Wales (3) and south England (4), with two sites (A and B) surveyed in each region. Bars show means \pm SE. Lower right panel shows example of diver-conducted UVC.

significantly by region (Fig. 4C; Table 1). Pairwise comparisons revealed S Wales to be significantly greater than all other regions, which were similar to each other.

PERMDISP showed within-factor multivariate dispersion varied significantly between regions ($F_{(3,36)} = 7.62, p = 0.003$). The structure of fish assemblage composition captured by UVC did not vary significantly among regions but significant Site(Region) variability was detected (Table 1). Whilst not significant, PCO plots indicated some partitioning between regions, particularly with N Scotland being distinct from other regions (Fig. 3B).

3.3. Combined surveys

Total taxon richness ranged from 2.8 ± 0.5 (N Scotland A) to 9.8 ± 0.9 (S England B). Taxon richness differed significantly between regions and showed a clear stepwise increase with decreasing latitude (Fig. 5; Table 1). Pairwise comparisons showed all regions to differ from one another apart from S Wales and W Scotland.

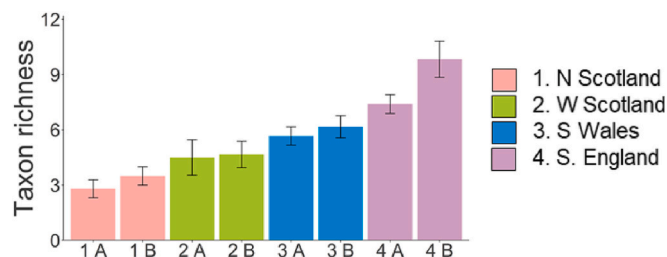


Fig. 5. Taxon richness of fish assemblages captured by both techniques (i.e. BRUV and UVC data combined) at each site within each region. Four study regions were north Scotland (1), west Scotland (2), south Wales (3) and south England (4), with two sites (A and B) surveyed in each region. Bars show means \pm SE.

PERMDISP showed within-factor multivariate dispersion varied significantly between regions ($F_{(3,40)} = 3.36, p = 0.004$). PERMANOVA detected significant regional differences in community structure, as well as significant Site(Region) variability (Fig. 3C; Table 1). Pairwise comparisons showed that all regions were significantly different from one another. This was evident in the PCO plot, which showed clear clustering by region (Fig. 3E). SIMPER analysis revealed that the observed dissimilarity between northern and southern regions was driven by a greater presence of labrid species (*Centrolabrus exoletus*, *Labrus bergylta* and *Symphodus melops*) in southern regions (Fig. 3F, Table S4). Additionally, the mackerel *Scomber scombrus*, the thick lip grey mullet, *Chelon labrosus*, the European conger *Conger conger* and lesser sand eel *Ammodytes tobianus* appeared more often in southwest England than other regions (Fig. 3F, Table S4). Overall, BRUV captured more taxa than UVC (21 versus 16, respectively), although over half of all taxa (13) were detected in both survey techniques (Fig. 6).

4. Discussion

Fish assemblages were a conspicuous and ubiquitous component of kelp forest communities across the study area, highlighting the importance of these habitats for coastal fish species as has been shown elsewhere (e.g. Holbrook et al., 1994; H une et al., 2021; Pita et al., 2018). We recorded significant variability in fish assemblage structure at regional spatial scales (particularly with the BRUV and combined datasets), with clear sequential shifts with latitude and clear separation between northernmost and southernmost regions. Regional structuring of kelp-associated fish assemblages has been previously reported from Australasia (Anderson and Millar, 2004; Tuya et al., 2011) and North America (Konar et al., 2015; Lamy et al., 2018), and has been attributed to biogeographic patterns, temperature gradients, habitat structure, fishing pressure and oceanographic processes.

Assemblage-level patterns in regional structuring can be largely explained by different thermal affinities of particular taxa. In general,

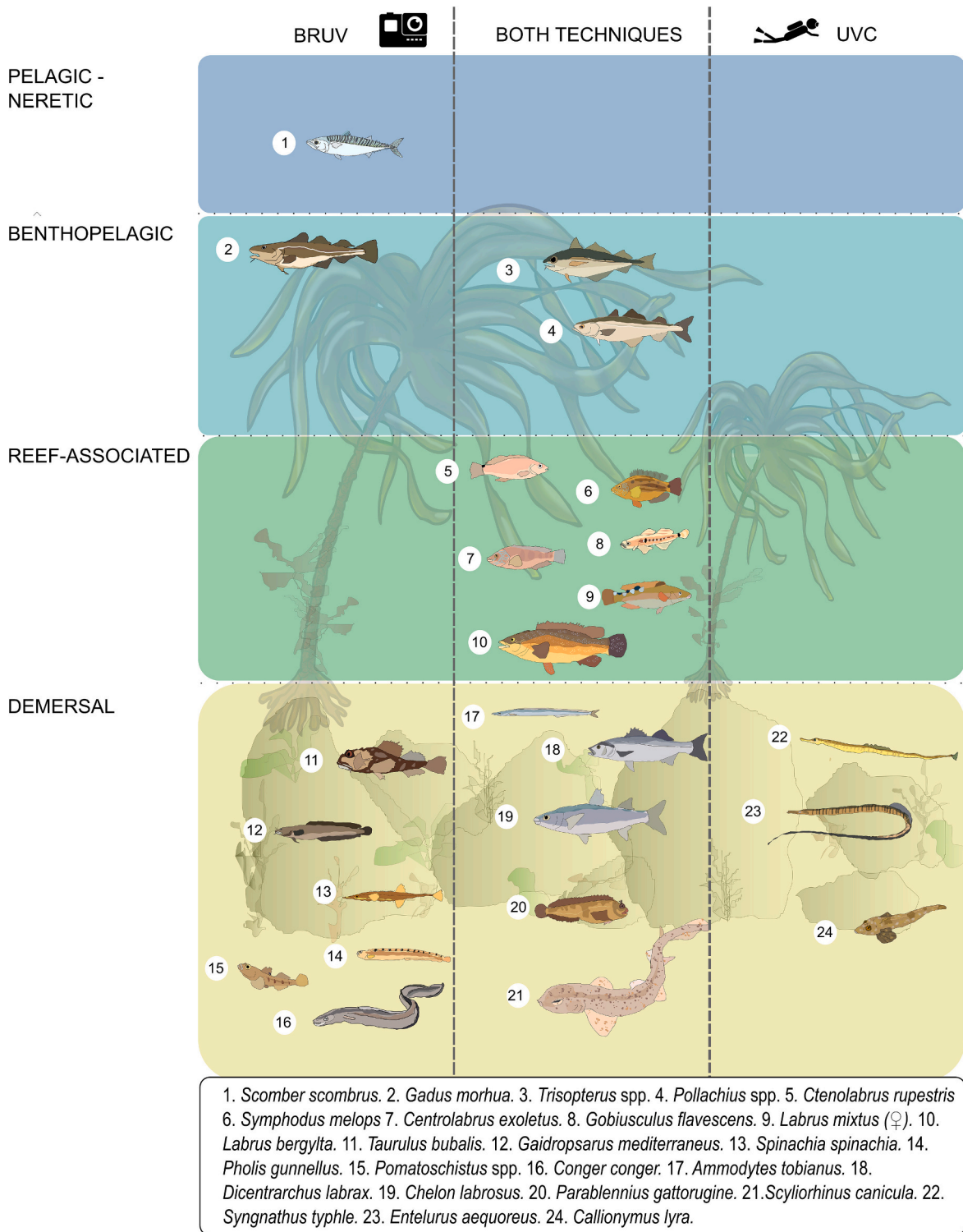


Fig. 6. Schematic showing fish species recorded in kelp forests in the UK with each survey method and their typical vertical position with the habitat.

regional variability patterns were driven by higher abundances of *Pollachius* spp. in northern regions and *Gobiusculus flavescens* in southern regions, while various labrid species were also more abundant at lower latitudes. Both *Pollachius* species recorded here (*P. virens*, ‘saithe’ and *P. pollachius*, ‘pollock’) have distinctly northern boreal distributions (Howes, 1991) and the cooler waters around Scotland suit their cooler thermal affinities. Moreover, current and historical fishing intensity in coastal waters is likely greater at our southernmost regions (Eigaard et al., 2016), which may have influenced population structure. The two-

spotted goby, *Gobiusculus flavescens*, has a more southerly distribution, albeit still cool-temperate (Svensson et al., 2000), whilst reduced predation pressure related to fewer larger carnivorous fishes in southern regions may also explain higher abundances at lower latitudes. The distributions of several labrid species (e.g. *Ctenolabrus rupestris*, goldsinny wrasse, *Labrus bergylta*, ballan wrasse and *Symphodus melops*, corkwing wrasse) extend much further south into warm-temperate areas and, as such, ocean temperatures in our southern regions suits their warmer thermal affinities (Almada et al., 2017; Knutsen et al., 2013).

Additionally, greater abundance and richness of understory macroalgae and associated invertebrates (Bué et al., 2020; Smale et al., 2020a) may support greater population sizes in southern regions, through elevated habitat and food availability.

The most striking finding of the study was the general increase in richness and, to a lesser extent, Shannon's diversity with decreasing latitude. Here, we recorded a greater number of taxa in our southernmost regions compared to the northernmost, particularly in the BRUV surveys and combined dataset. In particular, sites in S England were markedly more diverse and hosted distinct assemblages. Given southwest England sits at the intersection of three ecoregions (i.e. North Sea, South European Atlantic Shelf and Celtic Seas) and is known to represent a biogeographic transition zone (Hiscock et al., 2004; Spalding et al., 2007), higher fish diversity is likely due to the co-existence of warm and cool adapted species. At a broader scale across the eastern Atlantic Ocean, inshore fish diversity has been shown to generally increase from high to low latitudes, largely aligned with increases in functional and phylogenetic diversity (Bosch et al., 2021). Across the spatial gradient examined here, previous work has shown that the richness of understory algal and invertebrate assemblages also increases from north to south (Bué et al., 2020; Smale et al., 2020a), suggesting that the latitudinal diversity gradient may hold for multiple kelp forest components (but see also King et al., 2021; Teagle et al., 2018). As such, the current study combined with previous survey work suggests that kelp forests in southwest England are particularly rich and therefore of high biodiversity and conservation value. It should be noted that our estimates of fish diversity within these habitats are conservative and do not represent 'true' diversity, as surveys did not capture temporal variability and some species (e.g. cryptic, nocturnal, highly mobile) would have likely remained undetected by either survey technique.

Several assemblage-level metrics showed significant variability at the site-level. Fish assemblages, as with other components of kelp forest ecosystems, often exhibit high variability across small to medium spatial scales (Anderson and Millar, 2004; Pita et al., 2018; Smale et al., 2010; Smith et al., 1996; Tuya et al., 2011). Here, variability between sites may have been related to differences in wave exposure, habitat structure, food availability or human activities, as has been suggested elsewhere. Other kelp-associated assemblages, particularly those within holdfasts and on stipes, have been shown to vary markedly between sites across this study area (King et al., 2021; Teagle et al., 2018). Site-level variation is likely to be a ubiquitous feature of these ecosystems, particularly for fish assemblages given the high mobility of coastal species.

With regards to the methods employed, UVC recorded a higher number of individuals compared to the BRUVs (Fig. 6), as has been reported previously (Colton and Swearer, 2010). Taxon richness was, however, higher with the BRUV technique, which is likely a result of the bait attracting a wider range of species (Willis and Babcock, 2000). Furthermore, BRUVs successfully captured some cryptic and timid species that were not observed by divers (e.g. *Taurulus bubalis*, *Pholis gunnellus*, *Pomatoschistus* spp., *Gaidropsarus mediterraneus*, *Conger conger*, *Spinachia spinachia*). Clearly, UVC may modify the behaviour of fish, with some species tending to avoid divers and others approaching them (Dickens et al., 2011; Watson and Harvey, 2007). For example, the labrid *C. rupestris* avoids divers (Sayer et al., 1993) which may explain their comparatively low abundances using UVC. A total of 7 species were exclusively captured by BRUVs, one from the pelagic BRUVs and 6 from the benthic BRUVs while only three species were exclusively captured using UVC (Fig. 6). However, UVC has the advantage of sampling a larger, more defined area whereas BRUV samples a small, less standardised area and is subject to increased variability relating to the bait plume, which in turn is influenced by hydrodynamic processes such as tidal currents and wave action. Given the 3D structure of kelp forests, the combined benthic–pelagic BRUV system used in this study, deployed in conjunction with transect methods, would be the most effective approach to monitoring fish assemblages, as has been suggested

elsewhere (Schramm et al., 2020). Further work should employ stereo-video systems (e.g. Unsworth et al., 2014) to quantify the size structure of fish populations and discern whether kelp forests are serving as important nursery habitats for juveniles (as with commercial shellfish species, see Smale et al., 2022) and/or foraging or spawning grounds for mature individuals.

5. Conclusions

Our study, like others (Furness and Unsworth, 2020; Norderhaug et al., 2005) has demonstrated that *Laminaria* forests are important habitat and feeding ground for fish and, collectively, these observations highlight the need to manage and conserve these ecosystems. Moreover, several species we recorded (e.g. *Pollachius* spp. *Scomber scombrus*, *Dicentrarchus labrax*) are important targets for inshore fisheries, while several labrid species we observed are targeted for the live wrasse fishery for salmon farms. Other species have elevated ecological importance as either prey (e.g. *Ammodytes tobianus*) or as higher predators (e.g. *Conger conger*), playing pivotal roles in coastal foodwebs. As such, these fish assemblages have high socioeconomic and ecological value and should be managed accordingly. Previous surveys have shown that these kelp forests also support populations of socioeconomically important crustaceans (Smale et al., 2022), again highlighting their role in provisioning ecosystem services. The main threats to these assemblages relate to historical and current fishing activities (Gall et al., 2020; Thurstan et al., 2010), as well as ocean warming driving shifts in the distribution and ecological performance of species, leading to changes in communities, foodwebs and entire ecosystems (Heath et al., 2012; Perry et al., 2005). Given that we observed marked shifts in assemblage structure and richness along a gradient of latitude and temperature (Pessarrodona et al., 2018; Smale and Moore, 2017), we can expect continued ocean warming to lead to changes in the distributions of coastal fish species and subsequent alterations to kelp forest communities. Moreover, indirect effects of climate-driven shifts in habitat structure and productivity will likely influence these ecosystems further (Pessarrodona et al., 2019; Teagle and Smale, 2018). Although our study provides only a 'snapshot' of kelp-associated fish assemblages in the UK, it does provide a useful baseline for further monitoring and has demonstrated the efficacy of non-destructive, fisheries-independent survey techniques in these habitats. Clearly, greater spatiotemporal coverage and sustained monitoring will be needed to detect future changes and to inform approaches to management and conservation.

Author contributions

MJ-B, DS and PM conceived the study. MJ-B led collection and processing of samples and data. DS, NK, AR and contributed to field and laboratory work. DS and PM funded the work. MJ-B led development of the manuscript with significant intellectual input from all authors.

Declaration of Competing Interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests:

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Data availability

Data will be made available on request.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.jembe.2023.151899>.

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