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The diversity of demersal assemblages of the western English Channel and the Celtic Sea

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ABSTRACT: Adapting the current management of marine resources to align with an ecosystem-based approach is becoming increasingly common. Understanding the communities within an area — their species and distribution — is crucial to managing marine activities whilst maintaining ecological function. We performed a broad-scale community analysis of the demersal assemblages of the western English Channel and Celtic Sea. The diversity of the study area was investigated through *K*-means cluster analysis, indicator species analysis, diversity indices and discussion in relation to relevant environmental variables. The demersal species studied formed 7 distinct demersal assemblages, broadly aligned with environmental variables such as natural disturbance and substrate. Several assemblages were defined by notable characterising species, including Norway lobster *Nephrops norvegicus* in the Celtic Sea, queen scallop *Aequipecten opercularis* in the central western English Channel and boarfish *Capros aper* off the coast of the Cornish peninsula and the Isles of Scilly. The area of the central English Channel dominated by queen scallop had lower diversity relative to neighbouring demersal assemblages. This study provides the most spatially comprehensive delineation of demersal assemblage structure for this region, and is an example of the spatial analyses needed to inform future biodiversity monitoring and marine spatial planning, which are both key aspects of an ecosystem-based approach for the management of human activities in marine waters.

KEY WORDS: Biodiversity · Demersal fish assemblages · Monitoring · Spatial distribution

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1. INTRODUCTION

The Marine Strategy Framework Directive (European Union 2008) requires that biological diversity and sea-floor integrity are monitored to ensure that 'good environmental status' (GES) may be maintained. One of the criteria for GES in relation to biological diversity is to determine the 'composition and relative proportions of ecosystem components' (European Union 2010). Achieving such criteria requires a thorough understanding of the distribution and composition of demersal assemblages. Furthermore, this understanding is an important requirement of the ecosystem-based management (EBM) approach to fisheries, as it can aid the development and design of marine spatial planning, monitoring marine biodiversity, climate adaptation planning and the identification of sites where vulnerable species and habitats occur (Rees et al. 2008, Meyer et al. 2020, Howell et al. 2021). The implementation of such a process has resulted in increased monitoring of environmental and ecological components (Kupschus et al. 2016).

The Channel and the Celtic Sea, collectively termed the 'Southwest Approaches', differ in their currents, tides, sediments and temperatures. These differences create a biologically diverse region with respect to their bottom-dwelling organisms. The Channel is a relatively shallow and narrow strait (30 km

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wide at its most eastern point; an average depth of 100 m) and is tide-dominated with coarse sediments. In comparison, the Celtic Sea is a low-energy environment with muddier substrates in the south and the Celtic Deep, and gravel and sandy substrates in the north (Salomon & Breton 1993, Coggan & Diesing 2011). Whilst both the Channel and the Celtic Sea are influenced by Atlantic water, the Channel also receives input from coastal rivers, creating a transition zone that supports both cold-temperate and warm-temperate organisms (Dauvin 2012). The Southwest Approaches mark the lower latitudinal limit of some fish species as well as the high-latitudinal limit of some southerly (Lusitanian) species (Martinez et al. 2013, Heessen et al. 2015). The range of sedimentary habitats found across the Southwest Approaches, from muddy grounds to rocky habitats, further contributes to this high faunal diversity (Larsonneur et al. 1982, Ellis et al. 2013). Therefore, the region can be considered a hotspot of diversity of benthic assemblages and a potentially important area in which to track climate-driven shifts in species composition in relation to the broader NE Atlantic region (Peck & Pinnegar 2018).

The development of biological classifications to inform EBM is becoming increasingly common. Recent studies have focused on regional-scale comprehensive classification schemes that have been developed to inform a range of management applications (Cooper et al. 2019, O'Brien et al. 2022). Previous studies have described the benthic fauna (infauna and small epifauna) of the western Channel (e.g. Holme 1961, 1966, Glémarec 1973, Bolam et al. 2008), whilst other studies have considered the demersal fish assemblages of the area (Ellis et al. 2000, van der Kooij et al. 2011, Martinez et al. 2013). These latter studies have, to varying extents, been constrained by their temporal and/or spatial coverage. Previously, van der Kooji et al. (2011) analysed 4 yr of survey data from the Channel (that study did not include data from the Celtic Sea). They found little spatial and temporal (interannual) variation in the survey data and reported that species compositions within the strata were stable between years.

The purpose of this study was to conduct a detailed, broadscale analysis of the structure and distribution of the demersal assemblages of the Southwest Approaches, including greater temporal coverage, a larger spatial extent and higher resolution of sampling sites than has previously been completed for this area. Data collected during annual beam-trawl surveys were used to (1) describe and delineate the demersal fish and shellfish assemblages and (2) examine the diversity of those assemblages. The information reported here can be used to support an ecosystem-based approach to management by informing marine spatial planning that considers fisheries management programmes as well as conservation planning for species and habitats, such as marine protected areas (MPAs). This study also improves our overall knowledge of the demersal assemblages of the Southwestern Approaches.

2. MATERIALS AND METHODS

2.1. Study area and sampling

The study area comprised the western Channel (ICES Division 7.e; sampled since 2006) and the Bristol Channel and Celtic Sea (Divisions 7.f–h; sampled since 2013; Fig. S1 in the Supplement at www.int-res.com/articles/suppl/m714p015_supp.pdf). Data on demersal fauna (fish and shellfish) were collected from annual beam trawl surveys conducted by the RV 'Cefas Endeavour' in the spring (February–April) of each year. Our survey, the Southwest Ecosystem Survey, was a random-stratified design comprising 24 strata, which assumed that each stratum is a homogenous demersal assemblage. The data analysed were collected from 73–137 stations sampled per year over 16 yr (2006–2022) (Fig. S2). Spatio-temporal information on fishing activities provided by local fishers was considered during the initial design of the survey, and environmental variables such as depth, substrate and currents were considered by mapping areas defined by fishers over existing oceanographic, bathymetric and geological survey plots to delineate the boundaries of the survey strata (ICES 2019). Demersal fish and shellfish were sampled with two 4 m beam trawls that were deployed simultaneously and towed for distances ranging from 1.7–5.6 km. Fish and shellfish catches were sampled at each station. The lengths, abundance and biomass were recorded for all taxa. Taxa were either fully sampled or sub-samples of known weight were measured and then raised accordingly.

2.2. Data treatment

In total, data were available for 1633 sampling stations. From the 180 species that were recorded, a total of 115 taxa (species and groups of species) were used in the present analysis. These comprised teleosts (89 taxa), elasmobranchs (14), commercial crustaceans (6), cephalopods (2) and bivalve molluscs (2) (Table S1). The current analyses excluded some fish taxa, such as pelagic species and those taxa for which identification has been noted to be difficult (Table S2). Catch data were standardised to the numbers of individuals caught per km^2 swept area (Table S1).

2.3. Spatial distribution of assemblages

Data analysis consisted of establishing the demersal assemblages in the study area, their diversity and their representative species. All analyses were conducted in R v.4.2.1 (R Core Team 2021) with RStudio v.1.4.1717 and were applied to standardised catch data.

To identify the main assemblages through a cluster analysis, the data were transformed into a Hellinger matrix, based on Hellinger distance (Nikulin 2001). This is a function of the square root of the frequencies of abundance, thereby reducing the impacts of relatively abundant species. *K*-means clustering was performed in R. To aid in choosing the number of assemblages, an 'elbow plot' of percentage variation explained (100 × between assemblage SS / total SS, where SS is sum of squares) was plotted against cluster number. The elbow plot shows the amount that the percentage variation explained increased as the number of assemblages increased. This information needs to be balanced against the ecological appropriateness of any potential number of assemblages.

Maps and figures were produced using the 'ggplot2' package v.3.3.6 (Wickham 2016). Nonmetric multidimensional scaling (NMDS) was performed using the 'vegan' package v.2.6-2 (Oksanen et al. 2022). NMDS standardises scaling in the result so that the configurations are easier to interpret, and adds species scores to the site ordination.

2.4. Species composition of assemblages

Each assemblage was characterized by the 10 most common taxa as a percentage of total abundance (see Table 2) and the most frequent taxa as a percentage of sampling stations at which they were present (see Table 3). Indicator species were identified by analysing the association between species patterns and combinations of groups of sites using the 'indicspecies' package v.1.7.9 (De Caceres & Legendre 2009; see Tables 2 & 3). Through the indicator species analysis we obtained a list of indicator species per assemblage with a value of significance for each species. From this list we selected indicator species which were associated with only one assemblage and had a p-value of <0.01. Species diversity, richness and evenness were calculated for each assemblage using the Shannon index, Margalef's index of species richness and Pielou's evenness index (see Table 1).

3. RESULTS

3.1. Spatial distribution of assemblages

A total of 7 demersal assemblages were identified based on the elbow plot from the *K*-means analysis (Fig. 1), the geographical map of these assemblages (Fig. 2) and from ecological observations of the characteristic species in each assemblage. The elbow plot in Fig. 1 provides a summary of the statistical fit of varying numbers of potential assemblages. This plot is not enough on its own to determine the 'correct' number of assemblages and was used in tandem with spatial (Fig. 2) and ecological information (Fig. 3). As shown in Fig. 1, the percentage variation, as indicated by between-assemblage SS, began to decrease at around 7 assemblages. When these 7 assemblage locations were plotted, they were broadly distributed across a gradient from east to west and from the shallow inshore embayments of the English coast to the deeper waters of the Channel and Celtic Sea. In addition, the 7 assemblages were broadly aligned with the environmental variables, such as natural disturbances and substrates, that were considered in

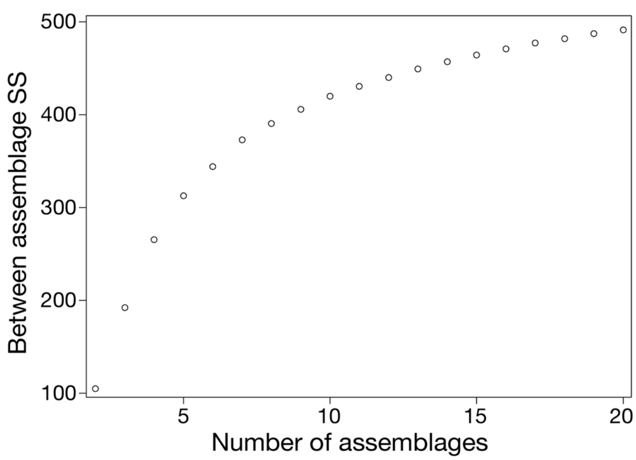

Fig. 1. Elbow plot showing the percentage of variation explained as a function of the number of assemblages. The rate of change in variation explained reduces from 4 assemblages onwards

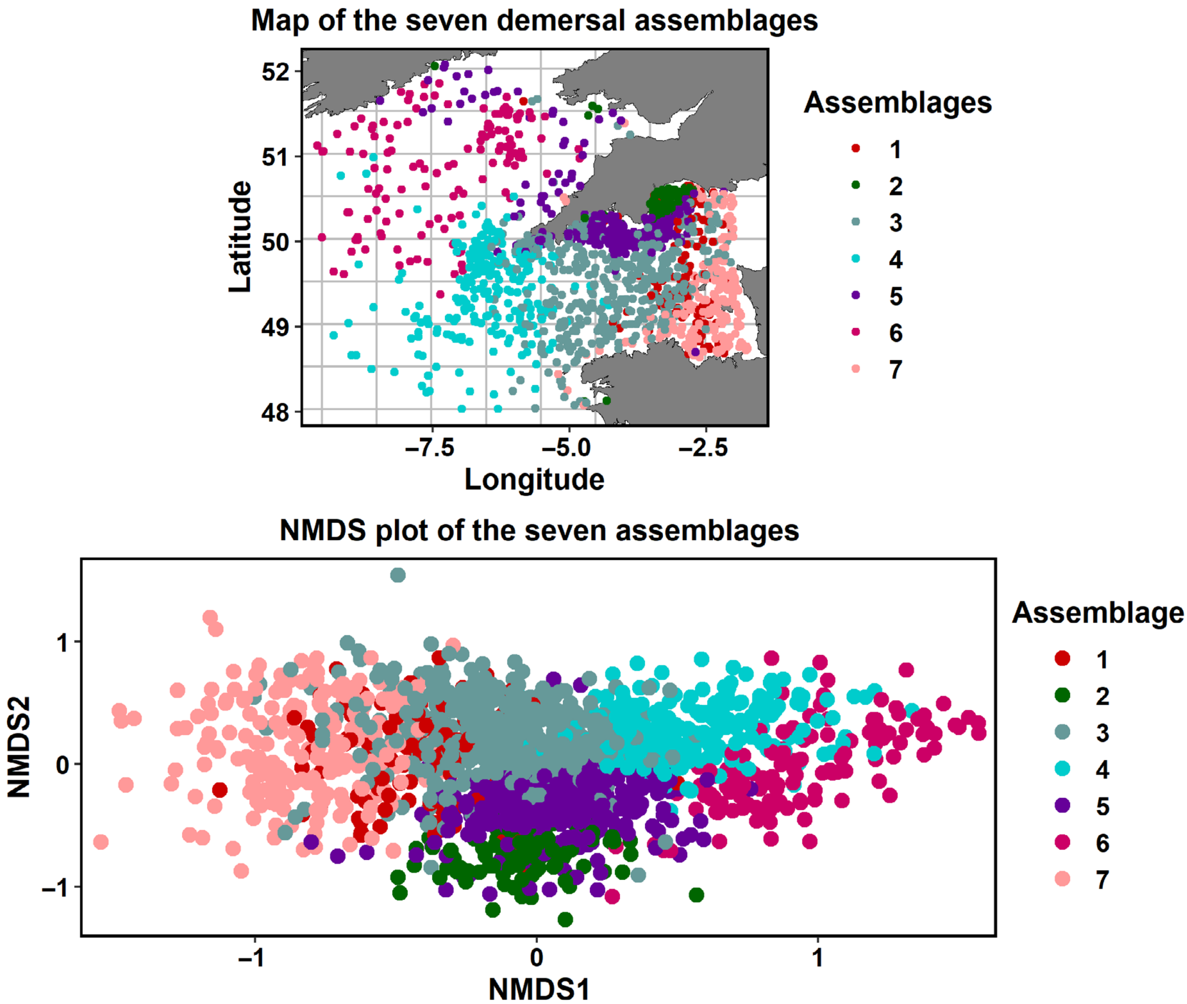

Fig. 2. The 7 demersal assemblages recommended by the *K*-means analysis of the survey stations and the outlines of ICES Divisions and non-metric multidimensional scaling (NMDS) plot of the 7 assemblages, plotted using 'vegan' package v.2.6-2

the survey design. Several assemblages were defined by notable characterising species, including Norway lobster *Nephrops norvegicus* in the Celtic Sea, queen scallop *Aequipecten opercularis* in the central western English Channel and boarfish *Capros aper* off the coast of the Cornish peninsula and the Isles of Scilly (Fig. 3). We explore the assemblages in more detail below.

Assemblages 1 and 7 (119 and 218 stations, respectively; Table 1, Fig. 1, Fig. S3) occupied a band of water dominated by a strong current that stretches across the Channel from the French coast to the English coast (Figs. 2 & 3). Table 1 shows the number of stations whilst Figs. 2 & 3 show the assemblage position. Assemblage 3 (the most sampled assemblage with 454 stations) contained most of the samples from the Channel (Figs. 2 & 3). Assemblages 5 and 2 (335 and 111 stations respectively) were located along the shallow embayments of the southwest English coast, with Assemblage 5 extending around the Cornish peninsula and into the inshore waters of the Bristol Channel and continuing into the shallower waters in the northern Celtic Sea. The more offshore waters of the Celtic Sea indicated a latitudinal split between the northern Celtic Sea (Assemblage 6; 129 stations) and the southern Celtic Sea (Assemblage 4; 267 stations), with the eastern margin of the latter merging with Assemblage 3 at the entrance to the western Channel (Fig. 2).

3.2. Species composition of assemblages

Poor cod *Trisopterus minutus* and lesser-spotted dogfish *Scyliorhinus canicula* were 2 of the 10 most

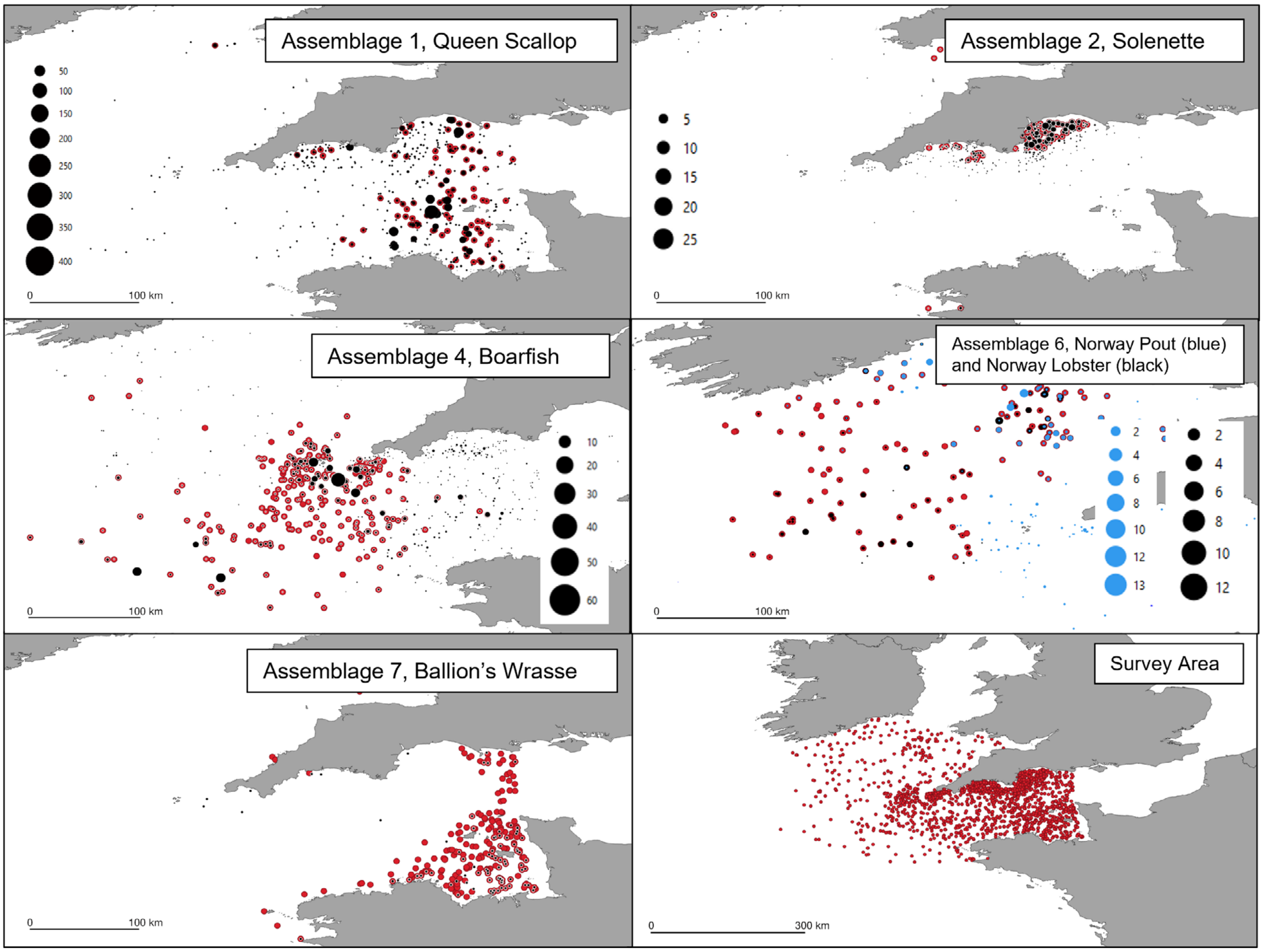

Fig. 3. Abundant indicator species (black or blue) (see Table 2) for Assemblages 1, 2, 4, 6 and 7 (stations in red; species dots are superimposed on station dots). Where species abundance is indicated by size, a scale is shown

Table 1. Diversity indicators (Shannon-Wiener index, Margalef index and Pielou's evenness index) for the 7 assemblages as well as the total number of taxa present per assemblage and the number of stations per assemblage (all years combined, based on the 115 taxa considered)

Assemblage	No. of stations	Total no. of taxa recorded	Shannon index	Margalef index	Pielou's evenness index
1	119	90	1.11	10.65	0.09
2	111	80	2.40	10.87	0.19
3	454	100	2.20	11.82	0.15
4	267	89	2.69	11.69	0.19
5	335	94	2.90	11.30	0.20
6	129	81	2.99	11.66	0.21
7	218	95	2.75	13.10	0.19

abundant species in all 7 assemblages (Table 2), and common dragonet *Callionymus lyra* was one of the 10 most abundant species in 5 of the 7 assemblages, excluding Assemblages 6 and 7 in the English Channel. Furthermore, lesser-spotted dogfish was one of the 10 most frequently occurring species (% of stations) in all assemblages (Table 3). Poor cod and common dragonet were both one of the most frequently occurring species in 6 and 5 of the 7 assemblages, respectively.

Table 2. Abundance of individuals (no. km^{-2}) for each assemblage for all 115 taxa. Species codes are listed in Tables S1 & S2 in the Supplement (www.int-res.com/articles/suppl/m714p015_supp.pdf) and the number of taxa per assemblage is reported in Table 1. The 10 species with the highest abundance per assemblage are indicated in green. Indicator species (see Section 2.4 for calculation) are shown in ***bold italics***

Assemblage	ARG	BBY	BIB	BKS	BLG	BLL	BLR	BLW	BNW	BOF	BRT	BTF	CDT	COD	COE	CRE	CUR	CUW	CWG	DAB
1	0.00	4.55	55.95	39.85	0.67	0.91	0.73	0.32	0.38	0.91	0.00	0.06	54.47	0.21	2.53	5.19	1.18	0.98	0.07	1.06
2	0.00	3.34	5.87	0.30	0.57	0.46	0.30	0.00	0.07	0.37	0.00	0.07	101.56	0.10	0.14	2.85	0.00	0.03	0.00	51.24
3	2.77	3.39	204.55	15.19	0.28	3.56	1.94	0.35	2.56	43.12	0.09	0.17	227.32	3.22	8.04	26.95	8.83	9.22	0.00	6.35
4	7.75	0.47	10.06	0.00	0.00	0.94	0.36	0.10	0.83	***442.50***	0.00	0.00	81.96	2.10	3.08	5.71	***29.71***	1.23	0.00	0.30
5	1.93	5.60	67.37	3.93	0.61	2.59	2.30	0.10	1.02	19.72	0.00	0.03	390.02	1.86	1.31	9.55	4.14	1.04	0.00	164.30
6	6.42	0.07	0.50	0.00	0.00	0.35	0.80	0.00	0.00	6.25	0.00	0.00	18.42	***2.68***	0.54	1.40	2.00	0.00	0.00	4.59
7	0.00	6.15	79.94	53.26	1.65	1.95	3.75	***12.07***	***11.48***	0.44	***0.14***	***0.64***	17.13	0.17	2.75	23.37	0.00	12.15	0.03	0.94

Assemblage	DGN	ECR	EKT	FLE	FRR	FSG	FVR	GDY	GFB	GOB	GPF	GSV	GUG	GUL	GUR	GUS	HAD	HKE	ISF	JOD
1	0.40	0.00	1.43	0.03	0.00	0.95	0.25	3.62	0.00	0.00	1.78	4.26	2.40	0.00	45.04	14.90	0.34	0.13	0.94	1.82
2	0.37	0.00	0.67	***2.23***	0.36	0.41	0.62	0.03	0.00	0.03	2.14	0.03	35.96	0.00	1.11	0.74	0.17	0.37	0.20	1.59
3	0.51	0.10	3.13	0.33	0.60	0.85	1.63	21.20	0.16	0.69	2.33	5.02	9.53	0.54	185.73	19.60	22.84	6.64	80.51	6.94
4	0.10	0.13	0.20	0.00	0.03	0.00	0.03	1.88	1.68	0.00	0.16	0.00	22.51	0.00	60.52	0.13	44.09	20.31	93.74	5.19
5	0.45	0.00	0.17	4.99	0.23	3.66	0.39	2.02	0.13	0.00	3.79	0.24	144.97	0.23	39.73	3.35	45.52	8.60	27.43	14.62
6	0.77	0.07	0.00	0.03	0.42	0.24	0.00	0.07	***3.40***	0.00	0.00	0.00	32.20	0.00	1.12	0.13	105.15	24.90	4.30	1.72
7	1.64	0.00	1.90	0.31	0.21	0.62	1.72	13.86	0.00	***3.33***	1.48	4.77	0.17	0.00	29.04	50.15	0.10	0.07	0.34	1.31

Assemblage	JYG	LBE	LBI	LDM	LEM	LFB	LIN	LIO	LSD	MEG	MER	MON	MUR	NEP	NKT	NNR	NOP	NVB	PAC	PLA
1	0.03	0.94	0.00	0.00	2.59	0.00	0.10	0.04	64.33	0.84	1.12	9.73	4.78	0.00	4.30	0.91	0.88	0.22	0.00	0.00
2	2.32	0.07	0.00	0.00	6.84	0.00	0.03	0.00	30.40	0.03	0.00	4.82	10.51	0.94	1.26	0.03	0.93	0.00	0.10	0.00
3	2.88	2.01	0.00	0.00	41.97	0.13	1.41	0.03	154.54	10.21	4.67	65.12	23.55	0.00	25.60	1.24	14.00	0.45	0.00	0.07
4	0.54	1.12	0.07	0.00	34.19	0.03	0.53	0.03	70.22	160.17	0.26	29.08	3.44	0.33	5.50	0.23	6.92	0.04	0.00	2.63
5	1.52	0.47	0.00	0.00	56.29	0.21	0.33	0.00	166.97	5.42	0.00	45.37	31.85	0.53	14.99	0.07	39.93	0.00	0.00	1.92
6	0.00	0.10	***0.49***	***0.17***	10.63	0.00	0.66	0.00	81.63	93.25	0.03	17.14	0.23	***119.71***	1.41	0.03	***122.95***	0.03	0.00	***46.35***
7	3.48	4.40	0.00	0.00	2.16	0.30	0.10	0.03	93.91	0.04	0.37	6.91	9.26	0.00	2.69	2.06	0.03	0.54	0.00	0.00

Assemblage	PLE	POD	POG	POM	PTR	QSC	RBM	RDT	RKG	RPF	SBC	SBG	SCE	SCR	SDF	SDG	SDR	SDT	SGR	SHR
1	16.79	349.15	2.05	3.14	0.03	***3318.28***	0.00	0.40	0.27	0.00	***0.20***	0.00	48.51	59.83	7.98	0.00	1.88	0.83	0.10	0.00
2	178.35	58.12	***21.59***	***13.76***	1.16	21.04	0.00	0.00	0.07	***0.83***	0.00	0.00	10.90	15.60	150.54	0.00	1.39	4.97	0.00	0.00
3	33.82	2367.85	8.29	3.92	0.10	63.87	0.00	0.37	0.03	0.13	0.00	0.00	108.13	32.49	16.44	0.00	3.03	7.74	0.07	0.03
4	8.24	433.14	0.17	4.38	0.03	1.39	0.00	0.14	0.00	0.00	0.00	0.00	16.22	1.53	8.44	0.00	7.91	4.75	0.00	0.98
5	313.86	945.77	16.04	18.77	1.46	32.22	0.00	1.02	1.13	0.40	0.00	0.00	23.88	19.36	177.09	0.00	11.57	38.08	0.00	0.00
6	11.38	53.76	0.00	0.87	0.54	0.27	***0.14***	0.20	0.03	0.00	0.00	0.00	2.70	4.41	7.80	0.00	6.12	6.90	0.00	0.17
7	7.81	235.86	8.57	0.84	0.07	44.11	0.00	0.13	0.24	0.00	0.13	0.07	82.93	362.23	0.59	0.27	0.95	0.12	0.07	0.00

Assemblage	SKG	SKT	SLO	SMW	SOL	SOS	SOT	SRW	SSN	SYP	TBR	TBS	TBY	THR	TKT	TUB	TUR	UNR	WAF	WEG
1	0.37	0.00	0.33	0.00	14.87	1.22	20.46	0.00	0.03	0.00	0.34	12.14	0.14	6.82	5.93	5.10	0.41	1.82	0.10	0.00
2	0.00	0.00	0.00	0.00	20.00	1.15	***532.98***	0.00	0.00	0.00	0.00	53.56	0.07	8.11	0.16	6.33	0.50	0.10	0.03	0.00
3	0.20	0.00	1.06	0.24	38.84	6.62	3.86	0.00	0.24	0.00	5.95	82.65	0.10	0.84	19.48	17.30	0.94	1.42	3.63	0.23
4	2.37	1.34	1.42	0.00	27.44	1.45	0.11	0.05	0.00	0.40	5.33	45.12	0.03	0.03	0.69	1.99	0.40	0.06	18.93	0.07
5	0.20	0.00	0.65	0.07	83.44	6.23	51.67	0.00	0.03	0.00	0.37	388.43	0.17	4.41	1.98	30.87	0.85	0.47	1.64	0.16
6	***2.37***	0.93	0.03	0.00	8.39	0.13	1.60	0.07	0.00	0.20	1.00	15.39	0.00	0.86	0.27	0.61	0.41	0.00	19.36	0.03
7	0.00	0.00	0.82	***0.40***	19.52	4.72	1.87	0.03	***2.38***	0.00	1.27	1.85	***4.04***	2.25	16.00	3.11	0.37	5.99	0.00	0.06

Assemblage	WEL	WHB	WHG	WIT	WPF	WRA	YBY	SDS2	TSC2	SAN2	SQC2	OMX2	CTC2	MSS2	SHE2
1	0.58	0.71	3.83	0.00	0.04	0.00	0.13	5.77	0.54	0.93	2.53	0.03	19.89	0.03	0.29
2	0.75	0.06	44.42	0.24	0.00	0.00	0.00	3.33	0.13	0.14	3.41	0.13	3.19	0.00	0.03
3	8.96	10.83	41.49	0.40	0.00	0.00	0.62	11.30	0.33	3.09	7.77	0.80	127.77	0.69	0.00
4	2.25	48.00	5.41	1.78	0.00	0.00	0.13	3.03	0.00	0.48	2.56	3.66	46.61	0.00	0.00
5	18.35	3.95	132.65	4.15	0.00	0.03	0.03	8.88	0.36	1.77	12.91	1.04	63.28	0.00	0.77
6	0.07	27.77	33.10	***31.23***	0.00	0.00	0.00	0.84	0.00	0.07	0.83	0.67	0.27	0.00	0.00
7	1.09	0.00	3.72	0.00	0.07	***0.64***	0.15	9.75	0.56	2.17	1.58	0.00	13.50	***0.60***	1.60

Assemblage 1, one of 3 assemblages in the Channel, had 2 indicator species: queen scallop and Couch's seabream *Pagrus pagrus* (Tables 2 & 3). Queen scallop occurred at all stations and was particularly abundant in Assemblage 1; only 5 % of the total abundance of this species was located elsewhere. Although Couch's seabream was not particularly abundant in the Channel (0.2 ind. km^{-2}), it was most frequently encountered here (3.4 % of stations) and only occurred in one other assemblage (at 1.4 % of stations in Assemblage 7). Assemblage 1 had a pattern of abundance similar to adjacent Assemblages 3 and 7. For example, bib *Trisopterus luscus*, red gurnard *Chelidonichthys cuculus* and king scallop *Pecten maximus* were 3 of

Table 3. Percentage of stations at which each species was present, for each assemblage, for all 115 taxa. Species codes are listed in Tables S1 & S2, and the number of taxa per assemblage can be seen in Table 1. The 10 species with the highest frequency per assemblage are indicated in green. The indicator species, determined using 'indicspecies' package v.1.7.9 (De Caceres & Legendre, 2009) are shown in ***bold italics***

Assemblage	Species code																			
	ARG	BBY	BIB	BKS	BLG	BLL	BLR	BLW	BNW	BOF	BRT	BTF	CDT	COD	COE	CRE	CTC2	CUR	CUW	CWG
1	0	37	87.4	53.8	5.9	15.1	10.9	5	5	10.1	0	0.8	89.1	3.4	36.1	55.5	62.2	3.4	10.1	0.8
2	0	34.2	33.3	7.2	5.4	10.8	2.7	0	1.8	5.4	0	1.8	95.5	2.7	2.7	46.8	22.5	0	0.9	0
3	6.8	8.4	89.2	22.9	1.5	17.8	8.1	1.3	5.1	41.2	0.2	0.9	89.9	10.1	30	60.6	63.2	22	20.5	0
4	35.6	4.5	29.2	0	0	8.6	3.7	0.7	3	***93.3***	0	0	80.1	16.1	22.8	31.5	53.2	***77.5***	6.4	0
5	3.9	18.8	62.1	9.3	0.6	17.9	8.1	0.3	4.8	28.4	0	0.3	97.9	10.1	8.1	43.6	56.4	10.7	3.6	0
6	38.8	1.6	6.2	0	0	6.2	6.2	0	0	45.7	0	0	62	***32.6***	10.1	18.6	6.2	24.8	0	0
7	0	20.6	77.5	68.8	5.5	12.4	14.2	***31.7***	***28.9***	1.4	1.8	***6.4***	54.1	1.8	21.6	73.4	27.1	0	26.6	0.5

Assemblage	DAB	DGN	ECR	EKT	FLE	FRR	FSG	FVR	GDY	GFB	GOB	GPF	GSV	GUG	GUL	GUR	GUS	HAD	HKE	ISF
1	16	9.2	0	19.3	0.8	0	5.9	4.2	30.3	0	0	13.4	37	16.8	0	85.7	47.1	1.7	3.4	11.8
2	85.6	4.5	0	5.4	***24.3***	7.2	3.6	10.8	0.9	0	0.9	23.4	0.9	82.9	0	14.4	9	2.7	7.2	2.7
3	11.7	2.6	0.7	11.9	1.5	2.4	2.4	6.8	35.7	0.9	1.5	6.4	11.9	24.2	1.8	88.1	22.7	20.5	18.3	59.7
4	3	0.7	1.5	1.9	0	0.4	0	0.4	11.2	8.6	0	0.4	0	55.4	0	79.4	1.5	74.2	65.5	96.6
5	63.6	2.7	0	0.9	8.4	1.2	2.4	1.8	6.9	0.9	0	18.5	1.5	85.7	1.2	62.1	11.3	30.4	23.6	38.5
6	23.3	9.3	1.6	0	0.8	8.5	0.8	0	1.6	***24.8***	0	0	0	58.1	0	17.1	3.1	80.6	89.9	23.3
7	7.3	12.8	0	15.1	1.8	1.4	2.3	12.8	35.3	0	***4.6***	11	24.8	1.8	0	55.5	70.2	0.9	0.9	1.8

Assemblage	JOD	JYG	LBE	LBI	LDM	LEM	LFB	LIN	LIO	LSD	MEG	MER	MON	MSS2	MUR	NEP	NKT	NNR	NOP	NVB
1	18.5	0.8	17.6	0	0	30.3	0	2.5	0.8	91.6	0.8	13.4	64.7	0.8	42	0	37	14.3	2.5	4.2
2	23.4	2.7	1.8	0	0	61.3	0	0.9	0	80.2	0.9	0	53.2	0	45	0.9	15.3	0.9	6.3	0
3	22.2	5.1	9.7	0	0	55.3	0.9	7	0.2	86.6	18.1	14.8	82.2	0.7	49.6	0	45.2	4.8	5.5	1.3
4	26.6	3.4	8.6	0.4	0	70	0.4	4.9	0.4	84.3	96.6	2.2	78.7	0	22.5	2.6	21.7	1.9	10.1	0.4
5	34	2.7	3.6	0	0	75.2	0.9	2.1	0	86.9	14.6	0	74.3	0	55.5	0.9	35.2	0.6	17.3	0
6	24	0	2.3	***2.3***	***3.1***	47.3	0	12.4	0	87.6	94.6	0.8	79.1	0	4.7	***76***	16.3	0.8	***52.7***	0.8
7	12.8	9.2	28.9	0	0	15.6	2.3	0.9	0.5	88.1	0.5	1.4	36.7	***5***	35.3	0	19.3	14.2	0.5	5.5

Assemblage	OMX2	PAC	PLA	PLE	POD	POG	POM	PTR	QSC	RBM	RDT	RKG	RPF	SAN2	SBC	SBG	SCE	SCR	SDF	SDG
1	0.8	0	0	54.6	95.8	16.8	10.9	0.8	***100***	0	4.2	1.7	0	10.9	***3.4***	0	77.3	89.1	20.2	0
2	1.8	0.9	0	97.3	75.7	***52.3***	***63.1***	7.2	30.6	0	0	0.9	***13.5***	3.6	0	0	45	81.1	100	0
3	4.4	0	0.4	45.2	100	9.5	14.3	0.7	21.6	0	1.8	0.2	0.7	12.6	0	0	73.8	50.4	23.3	0
4	27.3	0	*11.2*	34.5	96.6	1.9	25.1	0.4	6.7	0	0.7	0	0	3.7	0	0	49.4	10.5	28.8	0
5	7.8	0	3	98.2	96.7	24.2	33.7	6.6	24.5	0	4.5	0.6	3	8.7	0	0	49.9	54.9	86.3	0
6	11.6	0	***88.4***	49.6	75.2	0	14.7	3.9	3.9	***2.3***	2.3	0.8	0	1.6	0	0	20.9	18.6	34.9	0
7	0	0	0	28	89.9	29.4	6	0.9	28.9	0	0.9	1.8	0	10.1	1.4	0.5	59.6	100	4.1	0.5

Assemblage	SDR	SDS2	SDT	SGR	SHE2	SHR	SKG	SKT	SLO	SMW	SOL	SOS	SOT	SQC2	SRW	SSN	SYP	TBR	TBS	TBY
1	13.4	42.9	9.2	2.5	2.5	0	0.8	0	6.7	0	74.8	13.4	14.3	29.4	0	0.8	0	8.4	34.5	2.5
2	14.4	19.8	28.8	0	0.9	0	0	0	0	0	87.4	4.5	***100***	42.3	0	0	0	0	80.2	0.9
3	9.9	24.4	13	0.2	0	0.2	0.4	0	3.7	1.3	65.4	15.4	6.2	25.6	0	0.9	0	20	56.4	0.7
4	32.6	15.7	27.3	0	0	8.2	10.1	9	7.1	0	57.3	3.7	1.1	16.5	0.4	0	2.6	23.6	71.2	0.4
5	26.6	17.9	50.1	0	0.3	0	1.2	0	3.9	0.3	87.8	21.5	44.5	40	0	0.3	0	3.3	96.4	0.9
6	30.2	9.3	48.1	0	0	3.1	***30.2***	12.4	0.8	0	51.2	0.8	7	11.6	1.6	0	4.7	11.6	65.9	0
7	6.9	36.2	1.4	0.5	8.7	0	0	0	3.7	***3.7***	56.4	12.8	6	13.8	0.5	***10.6***	0	9.6	9.2	***25.2***

Assemblage	THR	TKT	TSC2	TUB	TUR	UNR	WAF	WEG	WEL	WHB	WHG	WIT	WPF	WRA	YBY
1	22.7	35.3	10.9	25.2	7.6	23.5	2.5	0	7.6	3.4	38.7	0	0.8	0	2.5
2	48.6	3.6	1.8	57.7	12.6	2.7	0.9	0	7.2	1.8	83.8	1.8	0	0	0
3	2.9	36.8	1.5	32.4	4.8	5.1	13.2	1.5	18.9	17.6	41.4	2.4	0	0	3.1
4	0.4	5.6	0	16.5	4.1	0.4	64.4	0.7	11.2	52.1	19.5	12.7	0	0	1.5
5	13.7	9.3	1.8	48.7	6.9	3.9	9.9	0.9	30.7	9.9	75.5	9.6	0	0.3	0.3
6	8.5	2.3	0	12.4	8.5	0	67.4	0.8	1.6	45.7	55.8	***89.1***	0	0	0
7	12.4	47.7	6	12.8	4.1	29.4	0	0.5	7.8	0	17	0	0.5	***2.8***	1.8

the 10 most abundant and frequently encountered species in Assemblages 1, 3 and 7.

Assemblage 2, one of the 2 inshore assemblages, included 5 indicator species (Tables 2 & 3), the most abundant of which was solenette *Buglossidium luteum* (Fig. 3). Assemblages 2 and 5 (both inshore areas) shared 8 of their 10 most abundant species: common dragonet, poor cod and lesser-spotted dogfish, as well as dab *Limanda limanda*, grey gurnard *Eutrigla gurnardus*, European plaice *Pleuronectes platessa*, scaldfish *Arnoglossus laterna* and thickback sole *Microchirus variegatus*.

Assemblage 3, in the eastern Channel, contained no indicator species based on the indicator species analysis. Its most abundant species — excluding poor cod, lesser-spotted dogfish and common dragonet — were bib, red gurnard, imperial scaldfish *Arnoglossus imperialis*, anglerfish *Lophius piscatorius*, king scallop, thickback sole and cuttlefish *Sepia* spp. (Table 2). Five of these taxa (bib, cuttlefish, red gurnard, anglerfish and king scallop) were also the more frequently caught species in Assemblage 3, along with edible crab *Cancer pagurus* and sole *Solea solea.* Imperial scaldfish and thickback sole were not identified among the most frequent species occurring in Assemblage 3.

Assemblage 4, in the southern Celtic Sea and up to the Isles of Scilly, comprised 2 indicator species, namely boarfish and cuckoo ray *Leucoraja naevus*, which occurred at 93 and 77% of the stations, respectively (Table 3). Boarfish was the most abundant species (442.5 ind. km^{-2}; Fig. 3) and was found at much lower abundances in adjacent areas (Assemblages 3 and 6 contained 43.1 and 6.3 ind. km^{-2}). Many of the most abundant species in Assemblage 4 were shared with either Assemblage 3 (red gurnard, imperial scaldfish, thickback sole and cuttlefish) or Assemblage 6 (megrim *Lepidorhombus whiffiagonis*).

Assemblage 5, an inshore assemblage, had no indicator species and was similar in species composition to the adjacent Assemblage 2. The main differences between Assemblages 5 and 2 were that Assemblage 5 had a higher abundance of sole and whiting *Merlangius merlangus*, a lower abundance of solenette and a greater frequency of occurrence of lemon sole *Microstomus kitt*, thickback sole and anglerfish.

Assemblage 6, in the Celtic Sea, contained several indicator species, the most abundant of which were Norway lobster and Norway pout *Trisopterus esmarkii* (Fig. 3). These indicator species were not necessarily the most abundant or frequently occurring species (Tables 2 & 3) but were more characteristic of this assemblage when compared to other assemblages. For example, Atlantic cod *Gadus morhua* was only the 30^{th} most frequently encountered species in Assemblage 6 (32.6% of stations) but occurred much less frequently in other areas (1.8–16.1%).

Assemblage 7, in the channel adjacent to Assemblage 1, contained 9 indicator species (Tables 2 & 3), the most abundant of which was Baillon's wrasse *Symphodus bailloni* (Fig. 3). The 9 indicator species were of relatively low abundance and/or frequency, but were either not found at all or present at a much lower abundance in the other assemblages.

3.3. Diversity of assemblages

For Assemblages 1 to 7, Margalef's index for species richness ranged from 10.65 to 13.10. Assemblage 1 and the adjacent Assemblage 7 had the lowest and highest species richness, respectively (see Margalef's index, Table 1). The Shannon index of diversity was similar in Assemblages 2 to 7 (2.2–3.0) but lower in Assemblage 1 (1.11). Pielou's evenness index score was also similar for Assemblages 2 to 7 (0.15–0.21) and lowest for Assemblage 1 (0.09).

4. DISCUSSION

To track changes in marine biodiversity and to inform conservation and restoration policies, it is important to have robust monitoring of marine habitats, including both historic biodiversity baselines and present conditions (Plumeridge & Roberts 2017). The present study provides the most highly spatially resolved analysis of survey data and has identified 7 ecologically distinct demersal assemblages within the Southwest Approaches — waters encompassing the western Channel and Celtic Sea, and an extensive part of the NW European continental shelf. These assemblages comprise different compositions of species, some similarities in presence–absence of species and, in 5 cases, unique indicator species. The indices of species richness, diversity and evenness were similar in all but one assemblage, which was dominated by queen scallop. Thus, in order to maintain GES as mandated in the UK (Defra 2019) and other European marine waters, our analysis helps to identify the indicators and species that environmental managers should monitor when attempting to detect ecological change.

To successfully enact policies with an EBM approach in the marine environment, there is a need to understand the distribution of both target and nontarget fisheries species during assessments of marine ecosystems (Moriarty et al. 2020). The present study indicates that within the Southwest Approaches, there are 7 distinct demersal assemblages: 2 inshore assemblages (one of which spans the coastline, around the coast of the Bristol Channel and across to the northern Celtic Sea), 3 western Channel assemblages, one assemblage in the southern Celtic Sea and up to the Isles of Scilly, and one which spans most of the northern Celtic Sea. Each assemblage is ecologically distinct with significantly different species compositions. Despite these differences, adjacent assemblages exhibit some similarities in species presence — often with differences in frequencies or abundance of species compared to neighbouring assemblages. Indices for species richness, diversity and evenness were all lowest in Assemblage 1, which was dominated by a high abundance of queen scallop and with much lower values, comparatively, of all other species present in the assemblage. The species richness, diversity and evenness indices were similar across the other 6 assemblages.

Natural environmental variables are known to influence the distribution and composition of demersal assemblages, with broadscale assemblage structure across shelf seas being influenced by depth, substrate, sea temperature, salinity and natural disturbance (Fariña et al. 1997, Ellis et al. 2000, Gomes et al. 2001, Souissi et al. 2001, Ehrich et al. 2009). These are also known to be important environmental factors influencing the demersal assemblages of the western English Channel and Celtic Sea (van der Kooij et al. 2011, Ellis et al. 2013, Fincham et al. 2020a). The effect of depth (inshore to offshore) was often associated with changes in the distribution of the assemblages we identified. Fincham et al. (2020b), using the same species abundance data as the present analysis, reported statistically significant relationships between the abundance and habitat distribution of >50% of the species in the demersal assemblages of the Channel.

Several of the assemblages (Assemblages 1, 4 and 6) were dominated by individual species that appeared to be strongly associated with a preferred habitat characteristic and which were unlikely to be found in great abundance elsewhere. For example, the dominant species of Assemblage 1 (queen scallop) was constrained to relatively deeper Channel waters on mixed sediments of sand and gravel; in Assemblage 6, the majority of the catches of 4 species (Norway lobster, Norway pout, long-rough dab *Hippoglossoides platessoides* and witch *Glyptocephalus cynoglossus*) were all associated with the deeper waters and muddy substrates characteristic of the Celtic Sea; and Assemblage 4 contained most of the abundance and occurrence of boarfish.

The influence of natural disturbance (with kinetic energy used to relate to the background levels of 'natural disturbance') and bottom-trawling by fisheries can have clear impacts on benthic assemblages, and these 2 factors have explained 5–11% of the overall inertia (how the assemblages clustered together in the analysis) of the demersal species considered (Fincham et al. 2020a). Patterns in natural disturbance revealed through a kinetic energy map of the area (JNCC 2018) were aligned with the distribution patterns of the 7 demersal assemblages identified in our study region. For example, a band of higher natural disturbance occurred along the eastern side of the western Channel and was associated with Assemblages 1 and 7, moderate natural disturbance was associated with the embayments of the southwest coast where Assemblages 2 and 5 were located and low levels were associated with the Celtic Sea and western Channel, where Assemblages 6 and 3 were found, respectively. Finally, Assemblage 4 was distributed in a region where currents and tides create unique patterns of natural disturbance. Fishing pressure has also impacted benthic diversity and community composition, causing population declines in some elasmobranch species with slow population growth rates (Rogers & Ellis 2000, Genner et al. 2010). Fishing pressure is often positively associated with species abundance since fishers target areas with higher abundances of their target species (Fincham et al. 2020a). High-value commercial stocks on 'soft' benthic habitats (such as mud or sand) are suitable for bottom-towed gears and are often targeted, as evidenced by the high fishing pressure on Norway lobster (around Assemblage 6) on the muddy Celtic Sea habitats (Fincham et al. 2020a).

Our detailed analysis of benthic species composition has identified species assemblages in the Southwest Approaches that differ somewhat from previous analyses. For example, our analysis identified 3 assemblages in the Celtic Sea compared to 4 assemblages reported by Martinez et al. (2013). However, Martinez et al. (2013) defined the central and deep Celtic Sea as 2 separate assemblages that were pooled as one assemblage (Assemblage 6) in this study. Differences in the spatial distribution of assemblages reported here and in the study by Martinez et al. (2013) are likely due to methodological differences. Benthic sampling by Martinez et al. (2013) was conducted by otter trawl, using a fixed station survey design, while our survey data were collected by beam trawl using a random survey design. Beam trawling will sample smaller demersal fish more effectively and, in our view, a stratified random survey design provides more comprehensive spatial coverage and more accurate delineation of assemblages across the survey area.

Our study provides an example of a spatially comprehensive delineation of the demersal assemblages needed to inform future biodiversity monitoring and marine spatial planning, both of which are key aspects of an ecosystem-based approach to the management of human activities (e.g. Greenstreet et al. 2012). The most recent marine strategy assessment deemed demersal fish communities of the UK to be not in GES (Defra 2019), and the increased information on assemblage distribution provided here can inform the future definition or redesign of spatial management units, MPAs, benthic surveys and more general marine development planning outlined in the UK's Marine and Coastal Access Act 2009 (Marine Management Organisation 2009). For example, a recent large-scale example of new benthic biodiversity protection in UK waters includes the prohibition of bottom-towed gears in a specified area of the Dogger Bank Special Area of Conservation in the central North Sea (Marine Management Organisation 2020), which aims to protect the largest offshore sandbank in UK waters. The byelaw was introduced after consultation on multiple management options, and the mitigating impacts of the presence of alternative fishing grounds were considered during the impact analysis of the management options. An understanding of the fish and shellfish assemblages within management areas supports such challenging decisions.

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