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Demersal Assemblages in the Irish Sea, St George's Channel and Bristol Channel

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Macro-epibenthic invertebrate and demersal fish assemblages are described from 101 beam trawl stations in the Irish Sea, St George's Channel and Bristol Channel. Cluster analysis was used to identify those stations where catches were similar, in terms of species composition and biomass, and six assemblages were identified. The average similarity within these assemblages ranged from 44 to 58%. Species that were indicative of the differences between the six assemblages were used to describe their biological characteristics. Plaice and dab dominated on fine substrates in inshore waters (*Pleuronectes–Limanda* assemblage), whereas sea urchins and sun-stars dominated on the coarser substrates further offshore (*Echinus–Crossaster* assemblage). Thickback sole and hermit crabs were typical of the transitional area (*Microchirus–Pagurus* assemblage). Norway lobster and witch dominated on the muddy sediments in the Irish Sea (*Nephrops–Glyptocephalus* assemblage). Dead man's fingers beds (*Alcyonium* assemblage) occurred on coarse substrates in inshore waters throughout the study area, whereas common spider crabs were only dominant in the Bristol Channel (*Maja* assemblage). The common starfish (*Asterias rubens*) was an important component of all assemblages. The distribution of these assemblages was primarily correlated with depth, temperature and substrate type. Their spatial distribution was similar to previously described distribution patterns of sediments and infaunal communities in the area.

Keywords: Epifauna; fish catches; diversity; species composition; distribution; beam trawl; benthic surveys; Atlantic Ocean Northeast

Introduction

The offshore distribution and abundance of macro-epibenthic invertebrates and the spatial variation in the composition of demersal assemblages are largely unknown for many areas around the British Isles, and particularly western areas (Rees *et al.*, 1999). There is, however, a current interest in the identification of vulnerable species and habitats in both coastal and offshore environments, since these may require protection from a wide range of anthropogenic impacts. Nature conservation organizations and international fora (e.g. ICES and OSPAR) are currently leading the description of such areas in U.K. waters.

Massy (1912) and Holt (1910) provided detailed descriptions of the invertebrates and fish, respectively, caught in beam trawls in the north-western Irish Sea. Invertebrate catches were not, however, numerically quantified at all stations, and the biomass of neither fish nor invertebrates was recorded. Subsequent research on the demersal and benthic fauna of the region has generally been more localized. Coastal areas monitored in the Irish Sea include the Isle of Man (Jones, 1951, 1956; Bruce *et al.*, 1963), Cumbria

(Jones, 1952; Swift, 1993), North Wales coast (Rogers, 1994), Liverpool Bay (Eagle, 1973; Rees & Walker, 1991), and *Nephrops norvegicus* fishing grounds in the western Irish Sea (Hensley, 1996). The Bristol Channel was also extensively surveyed (e.g. Warwick, 1984; Mettam *et al.*, 1994) while Cardigan Bay and St George's Channel have been little studied (Laurie & Watkin, 1922; Mackie *et al.*, 1995).

The species composition of benthic and demersal faunas observed during surveys depend on the sampling gear and protocol. Previous studies utilized a variety of gears, including Reineck box corers (Swift, 1993), van Veen grabs (Jones, 1951, 1956), Smith-McIntyre grabs (Eagle, 1973), Day grabs (Hensley, 1996; Rees *et al.*, 1999), dredges (Jones, 1951, 1956), underwater video (Patterson, 1984) and small beam trawls (Eagle, 1973; Rees *et al.*, 1999). Jones (1951) also used additional gears, including both otter and Agassiz trawls.

Due to the differences in the gears used, it is difficult to combine the quantitative results of individual studies, and hence surveys with a broad spatial coverage are required (Rees *et al.*, 1999). Only two recent studies have covered a wide geographical area.

Mackie *et al.* (1995) surveyed the southern Irish Sea, St George's Channel and Celtic Deep with Van Veen grab and dredges to sample infauna and small epifauna. More recently, Rees *et al.* (1999) used a 2 m beam trawl at 18 stations in the Irish Sea and Bristol Channel.

The aim of the current study was to describe the demersal fish and macro-epibenthic invertebrate assemblages in the Bristol Channel, St George's Channel and Irish Sea using samples from a broad-scale fisheries survey. The subsequent analyses of these data were designed to determine the spatial variation, composition, broad-scale distribution and diversity of demersal assemblages, and to evaluate the importance of selected physical factors (e.g. depth and substrate) in affecting these patterns. This represents the first such study over a relatively wide geographical area of the western shelf seas of England and Wales and complements similar studies undertaken for the eastern English Channel (Kaiser *et al.*, 1999) and the North Sea (Jennings *et al.*, 1999).

Methods

Sampling stations and sampling protocol

Demersal fish and invertebrates were collected from 101 stations in the Irish Sea, St George's Channel and Bristol Channel (ICES areas VII a, f and g) during a groundfish survey undertaken by the RV *Corystes* in September 1998 (Figure 1). The choice of these stations and their geographical distribution (22 ICES rectangles, latitude ranging from 51·04–54·80°N) reflected the primary needs of the survey, which was to sample juvenile, commercially important flatfish (sole and plaice) over a stratified depth range (6–110 m).

Fishing was conducted with a 4 m beam trawl with chain matrix and 40 mm stretched mesh cod-end (see Kaiser & Spencer, 1994). The net was towed for 30 min at each station and sampled an area of approximately 15 000 m² per tow.

All fish and commercial shellfish were identified, counted, weighed and measured (see Rogers *et al.*, 1998). The remaining invertebrate catch was weighed and a representative sub-sample of known weight sorted. Invertebrates were identified to the lowest taxonomic level possible, weighed, and non-colonial species counted. All data were subsequently converted to weight and numbers caught per hour. The total weight of rocks in each catch was recorded, and the weight of broken shells in the sub-sample was raised to the total catch. The surface water temperature and salinity were recorded from a continuous data logger.

Data analysis

The PRIMER analytical package (Clarke & Warwick, 1994) was used for the cluster analysis of species-site data, using the Bray-Curtis similarity on root–root transformed biomass data. Stations with similar catch compositions were assumed to reflect sites with similar demersal assemblages. Discriminating species for each assemblage were identified using a similarity of percentages procedure (SIMPER). This determined the contribution of each species to the average dissimilarity between clusters.

The cumulative number of species recorded (mean of 10 randomized orders of catch data) was plotted against the cumulative number of hauls, to determine whether the number of taxa sampled gave an adequate description of the species composition of each assemblage. This analysis also permitted the comparison of species diversity between assemblages, where the sampling effort was different.

Dominance curves (cumulative proportion of biomass plotted against species rank) were plotted to determine whether the assemblages were comprised of several abundant species, or dominated by a few species. As colonial taxa (e.g. hydroids, bryozoans and sponges) could not be counted, no analysis of abundance-biomass curves was undertaken.

Species diversity, richness and evenness were calculated for each assemblage using the Shannon–Wiener diversity index (H'), Margalef's index of species richness (d) and Pielou's evenness index (J'). ANOVA and post-hoc Tukey Honest Significant Difference tests were used to determine whether these indices were significantly different between assemblages.

The association of selected abiotic variables with the similarity of catches of demersal fauna was determined using the BIOENV routine (Clarke & Warwick, 1994). The biological similarities of the catches at stations were compared with the following physical variables: latitude, depth, the weights of rocks and broken shell in the catch, and the surface sea water temperature and salinity (as recorded during the research cruise). Other variables included in the analysis were the mean summer and winter bottom water temperatures, temperature stability (i.e. the difference between these values) and the maximum tidal current speeds during mean spring tides. These data were taken from Lee and Ramster (1981). ANOVA and post-hoc Tukey HSD tests were used to determine any significant differences in the physical characteristics of the assemblages.
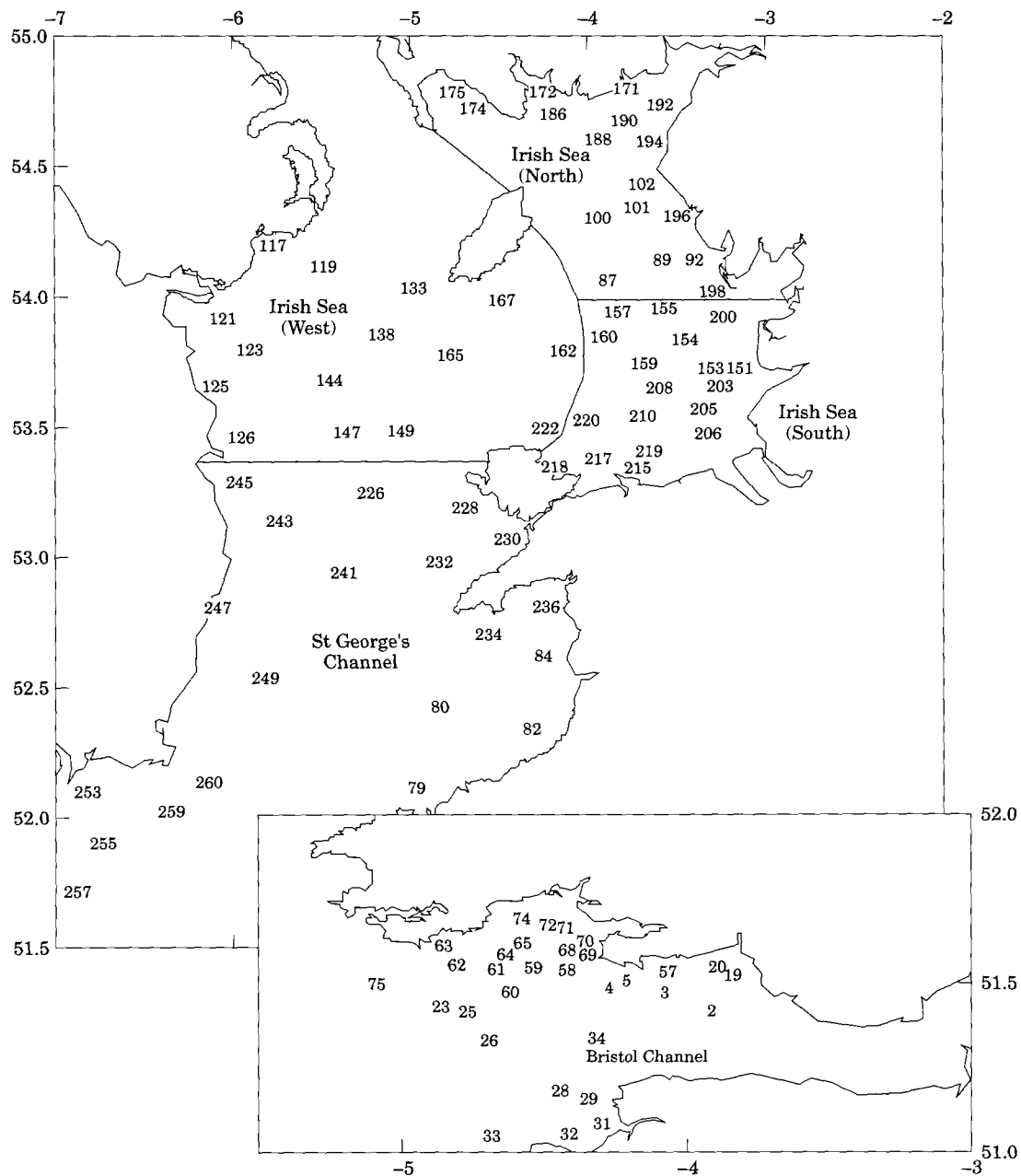
FIGURE 1. Map of study area showing sampling sites in the Irish Sea, St George's Channel and Bristol Channel (inset).

Results

Biological assemblages

Cluster analysis (Figure 2) indicated that 100 of the 101 stations could be attributed to six assemblages, with one outlying station (Station 259 in St George's Channel). The mean similarities of stations within each of these assemblages ranged from 44 to 58%.

The spatial distribution of these assemblages is illustrated in Figure 3, and their biological characteristics are described below and in Tables 1–6. The nomenclature for each assemblage was chosen to indicate the characteristic and typifying species, although these species were not necessarily the most abundant. The common starfish (*Asterias rubens*), for example, was not considered to be a suitable descriptor of
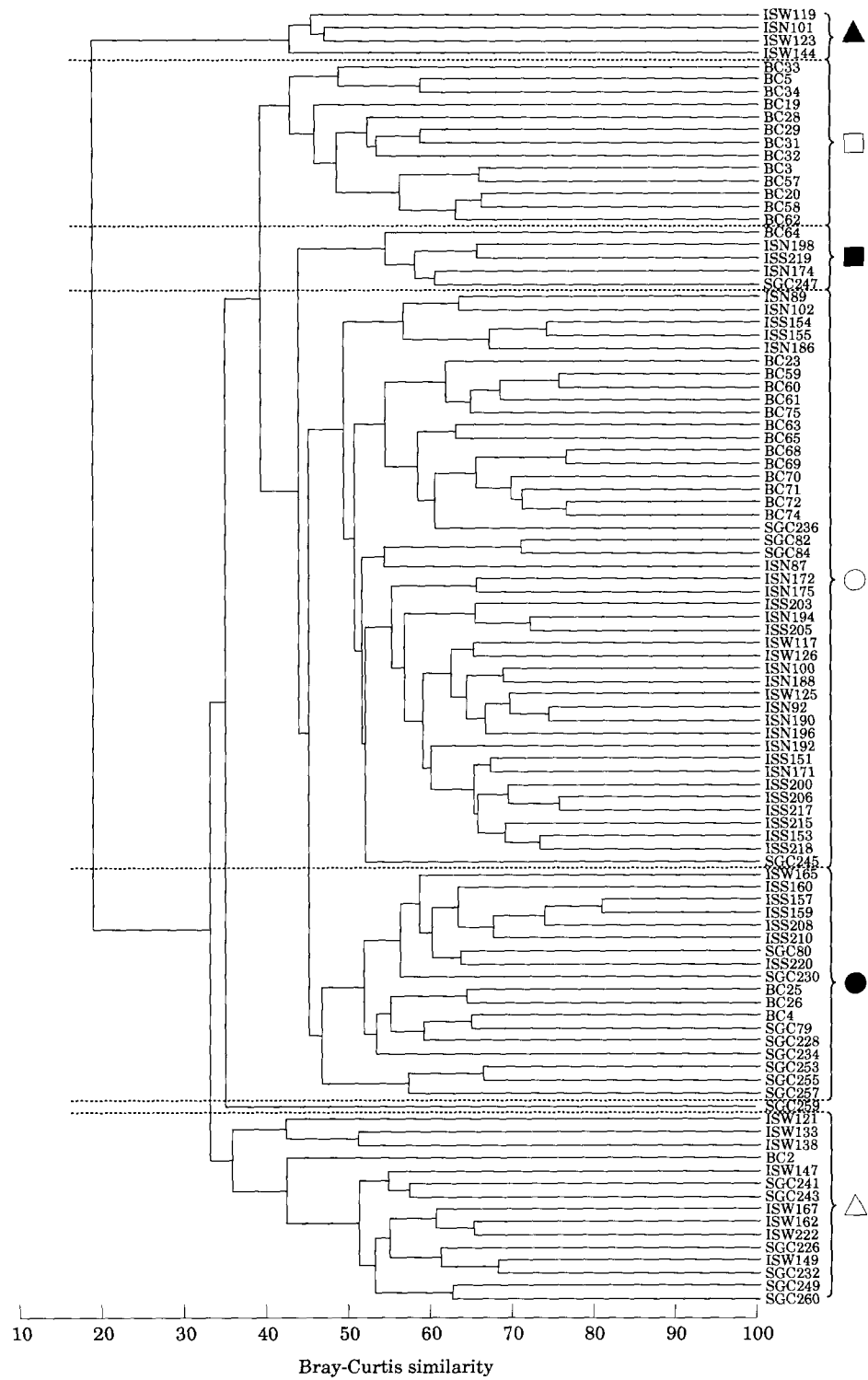
FIGURE 2. Dendrogram showing the Bray-Curtis index of similarity between stations.
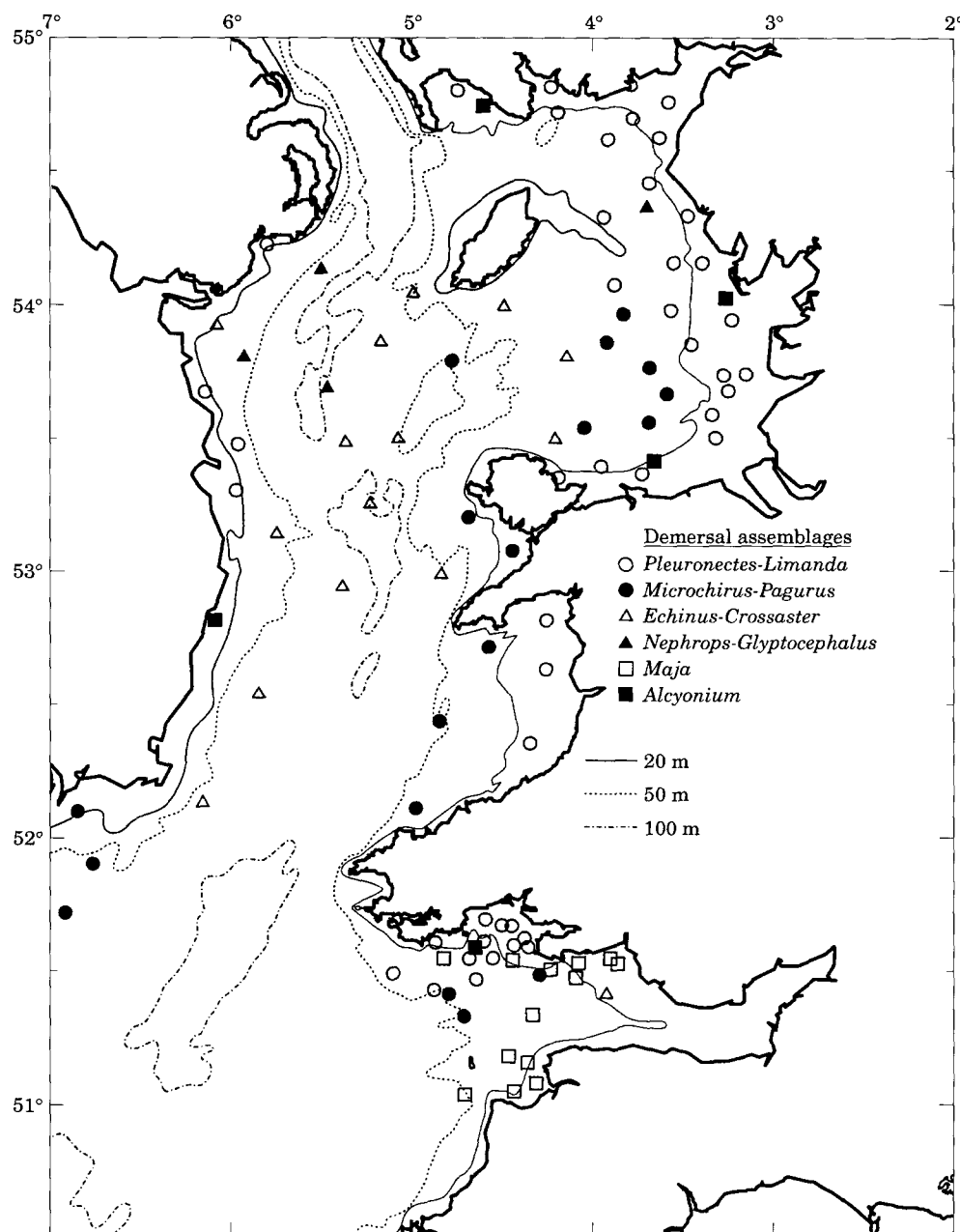
FIGURE 3. Distribution of six demersal assemblage types in the Irish Sea, St George's Channel and Bristol Channel based on the interpretation of Figure 2. 20, 50 and 100 m depth contours also indicated.

assemblages because it was more or less ubiquitous throughout the study area and abundant in all assemblages.

(i) Pleuronectes–Limanda *assemblage.* Flatfish, including dab (*Limanda limanda*) and plaice (*Pleuronectes platessa*) dominated this assemblage, which was recorded at 45 stations in the inshore waters of the eastern and western Irish Sea, and Cardigan and Carmarthen Bays (Figure 3). This assemblage was 54–80% dissimilar to other assemblages. *Asterias rubens*, *L. limanda*, *P. platessa* and sole (*Solea solea*) dominated the assemblage. This assemblage was most similar to the *Microchirus–Pagurus* assemblage (54% dissimilar) described below. Common hermit crab (*Pagurus bernhardus*), sand-star

TABLE 1. Taxonomic list of the major fauna associated with the *Pleuronectes platessa–Limanda limanda* assemblage *(Pleu)*. Fauna were included if they either occurred at ≥80% of stations within the assemblage (%O), or comprised ≥5% of the species composition (by biomass, %W), or if the catch-per-unit-effort (CPUE) was ≥2 kg h⁻¹. *ᵃDenotes the dominant five taxa, as indicated by SIMPER analysis. *Denotes these species caught with notably greater catches (ratio >1·5 in the SIMPER analysis) than at other assemblages *(Microchirus–Pagurus (Micr), Echinus–Crossaster (Echi), Alcyonium (Alcy), Nephrops–Glyptocephalus (Neph)* and *Maja)*

Dominant fauna	% O	% W	Mean CPUE (kg h⁻¹)	Greater abundance cf. other assemblages				
				Micr	Echi	Alcy	Neph	Maja
Hydroids	86·7	0·9	1·4 ± 3·0	—	—	—	—	—
Alcyonium digitatum	55·6	2·1	2·6 ± 6·3	—	—	—	—	—
Metridium senile	53·3	0·7	2·7 ± 11·6	—	—	—	—	—
Aphrodita aculeata	95·6	1·8	2·8 ± 4·6	—	—	—	★	★
Pagurus bernhardus	93·3	2·5	2·0 ± 2·5	—	★	★	—	★
Liocarcinus depurator	73·3	1·3	2·8 ± 5·6	—	—	—	★	—
*Liocarcinus holsatus*ᵃ	100·0	2·4	4·5 ± 7·9	—	—	—	★	—
Buccinum undatum	80·0	3·7	7·0 ± 14·0	—	—	—	★	—
Astropecten irregularis	88·9	2·4	3·3 ± 4·8	—	★	★	★	★
*Asterias rubens*ᵃ	100·0	30·4	202 ± 605	—	—	—	—	—
Ophiura ophiura	95·6	2·1	7·0 ± 26·3	—	—	—	—	—
Ascidiacea	40·0	2·2	2·5 ± 7·9	—	—	—	—	—
Scyliorhinus canicula	73·3	4·6	6·0 ± 8·0	—	—	—	—	—
Merlangius merlangus	84·4	2·8	3·4 ± 5·4	—	—	—	★	—
Eutrigla gurnardus	80·0	0·6	0·5 ± 0·8	—	—	—	★	—
Trigla lucerna	82·2	1·8	1·9 ± 2·8	—	★	—	★	—
Callionymus lyra	95·6	1·7	2·6 ± 3·3	—	—	—	★	★
*Limanda limanda*ᵃ	97·8	8·6	15·2 ± 16·9	—	★	—	★	★
*Pleuronectes platessa*ᵃ	100·0	7·0	9·4 ± 11·1	—	★	—	★	—
Buglossidium luteum	88·9	1·9	2·6 ± 4·1	—	★	—	★	★
*Solea solea*ᵃ	93·3	4·5	5·2 ± 7·9	—	★	—	★	—

(Astropecten irregularis), *L. limanda* and solenette *(Buglossidium luteum)* were important discriminating species in comparison with some of the other assemblages (Table 1).

(ii) Microchirus–Pagurus *assemblage*. This assemblage was comprised of 18 stations, which were generally found further offshore than the *Pleuronectes–Limanda* assemblage, and thickback sole *(Microchirus variegatus)* and the hermit crab *(Pagurus prideaux)* were important discriminating species. This assemblage was 57–81% dissimilar to other assemblages and was dominated by *A. rubens, S. solea* and common dragonet *(Callionymus lyra)* (Table 2).

(iii) Echinus–Crossaster *assemblage*. This group of 15 stations was 54–81% dissimilar to other assemblages. They generally occurred offshore, in the deeper waters of the western Irish Sea, St George's Channel and Bristol Channel. Large echinoderms, particularly common sea urchin *(Echinus esculentus)* and common sunstar *(Crossaster papposus)*, which were important discriminating species, and *A. rubens* dominated this assemblage (Table 3).

(iv) Nephrops–Glyptocephalus *assemblage*. The most distinct assemblage (80–87% dissimilar to others) was comprised of three stations in the western Irish Sea and one off the coast of Cumbria. Important typifying species were witch *(Glyptocephalus cynoglossus)* and Norway lobster *(Nephrops norvegicus)*. Edible crab *(Cancer pagurus)*, red whelk *(Neptunea antiqua)* and *A. irregularis* were also relatively important components of this assemblage (Table 4).

(v) Alcyonium *assemblage*. Dead-mans fingers *(Alcyonium digitatum)* dominated at five stations, and these sites were in Luce Bay and off Barrow-in-Furness, Arklow Head, Llandudno and South Pembrokeshire. The dominant fauna was comprised of *A. digitatum, A. rubens* and *L. limanda*. The high catch rates for *A. digitatum*, plumose anemone *(Metridium senile)*, velvet swimming crab *(Necora puber)*, shore sea urchin *(Psammechinus miliaris)* and *L. limanda* helped to distinguish this from other assemblages (Table 5).

(vi) Maja *assemblage*. A group of 13 stations in the Bristol Channel was 60–83% dissimilar to other

TABLE 2. Taxonomic list of the major fauna of the *Microchirus variegatus–Pagurus prideaux* assemblage. See Table 1 legend for further details of the data presented

Dominant fauna	% O	% W	Mean CPUE (kg h⁻¹)	Greater abundance cf. other assemblages				
				Pleu	Echi	Alcy	Neph	Maja
Hydroids	100·0	1·5	1·3 ± 1·3	—	—	—	★	—
Alcyonium digitatum^a	100·0	9·1	14·4 ± 26·3	—	—	—	★	—
Aphrodita aculeata	94·4	0·8	0·7 ± 0·6	—	—	—	★	—
Pagurus bernhardus	100·0	1·6	1·3 ± 1·2	—	★	★	—	—
Pagurus prideaux	83·3	2·1	1·6 ± 1·7	★	—	★	★	★
Macropodia spp.	94·4	0·1	0·1 ± 0·1	—	—	—	—	—
Inachus spp.	88·9	0·3	0·4 ± 0·6	★	—	—	—	—
Liocarcinus holsatus	88·9	0·4	0·3 ± 0·4	—	—	—	—	—
Buccinum undatum	94·4	2·4	2·0 ± 2·1	—	—	—	★	★
Aequipecten opercularis	72·2	7·0	10·0 ± 19·1	—	—	—	—	—
Luidia ciliaris	11·1	2·5	2·6 ± 9·6	—	—	—	—	—
Asterias rubens^a	100·0	16·2	21·7 ± 29·5	—	—	—	★	—
Ophiura ophiura	88·9	0·3	0·4 ± 0·9	—	—	—	—	—
Psammechinus miliaris	83·3	0·6	0·8 ± 1·1	—	—	—	★	★
Spatangus purpureus	16·7	1·7	5·1 ± 21·5	—	—	—	—	—
Scyliorhinus canicula	77·8	8·4	8·6 ± 11·0	—	—	—	—	—
Raja clavata	55·6	2·7	2·6 ± 3·8	—	—	—	—	—
Callionymus lyra^a	100·0	2·2	2·2 ± 1·6	—	—	—	★	★
Limanda limanda	66·7	3·0	2·9 ± 4·3	—	—	—	—	—
Pleuronectes platessa^a	94·4	2·9	2·6 ± 2·8	—	★	—	★	—
Microchirus variegatus	100·0	1·4	1·1 ± 0·9	★	—	★	★	★
Solea solea^a	100·0	3·0	2·9 ± 2·4	—	★	—	★	—

assemblages. The dominant fauna were *S. solea*, bib (*Trisopterus luscus*) and common spider crab (*Maja squinado*), with the latter being the primary discriminating species (Table 6).

Overall, the average dissimilarity between these assemblages ranged from 54 to 87% (Table 7), with the *Nephrops–Glyptocephalus* assemblage being the most distinct. The biological and physical characteristics of these six assemblages are summarized in Table 8.

Diversity of demersal assemblages

The cumulative number of species recorded in hauls (Figure 4) indicted that the *Alcyonium*, *Echinus–Crossaster* and *Microchirus–Pagurus* assemblages were the most diverse. The least diverse was the *Nephrops–Glyptocephalus* assemblage. Species-dominance curves (Figure 5) indicated that both the *Alcyonium* and *Nephrops–Glyptocephalus* assemblages were dominated by comparatively few taxa, whereas in contrast, the *Microchirus–Pagurus* and, to a lesser extent, the *Echinus–Crossaster* assemblages were composed primarily of several abundant species. Indices of species diversity, richness and evenness broadly supported these visual representations of diversity (Table 8).

Margalef's index of species richness (d) for all non-colonial species was significantly lower in the *Nephrops–Glyptocephalus* assemblage than all other assemblages ($P \le 0.04$) except the *Pleuronectes–Limanda* assemblage. Both the *Microchirus–Pagurus* and *Echinus–Crossaster* assemblages had significantly richer non-colonial fauna than both the *Pleuronectes–Limanda* and *Maja* assemblages ($P \le 0.015$). The *Microchirus–Pagurus* assemblage also had a significantly greater diversity (H') of non-colonial fauna in comparison with the *Pleuronectes–Limanda* assemblage.

Invertebrate species richness at the *Microchirus–Pagurus* and *Echinus–Crossaster* assemblages was significantly greater than at all other assemblages ($P \le 0.015$) and the invertebrate diversity was greater than at the *Pleuronectes–Limanda* and *Maja* assemblages ($P < 0.05$). The analysis of fish catches indicated that the *Nephrops–Glyptocephalus* assemblage had a significantly less diverse (H'=0·74) and less rich (d=0·63) ichthyofauna than other assemblages ($P < 0.025$ and $P < 0.006$ respectively). The *Microchirus–Pagurus* and *Alcyonium* assemblages had the richest and most diverse ichthyofauna (H'=2·13, d=2·61 and H'=1·94, d=2·43, respectively).

TABLE 3. Taxonomic list of the major fauna of the *Echinus esculentus–Crossaster papposus* assemblage. See Table 1 legend for further details of the data presented

Dominant fauna	% O	% W	Mean CPUE (kg h^{-1})	Greater abundance cf. other assemblage				
				Pleu	*Micr*	*Alcy*	*Neph*	*Maja*
Hydroids[a]	100·0	5·6	14·5 ± 35·5	—	—	—	*	—
Alcyonium digitatum	86·7	3·8	6·4 ± 12·0	—	—	—	—	—
Pandalus montagui	86·7	0·6	1·1 ± 1·9	*	*	—	*	—
Pagurus prideaux	80·0	0·5	0·6 ± 1·4	—	—	—	*	—
Hyas coarctatus	86·7	0·1	0·2 ± 0·4	—	—	—	—	—
Inachus spp.	86·7	0·4	0·8 ± 1·1	*	—	—	*	—
Macropodia spp.	100·0	0·2	0·5 ± 1·2	—	—	—	*	—
Liocarcinus holsatus	86·7	0·6	0·6 ± 0·7	—	—	—	—	—
Aequipecten opercularis	80·0	0·2	0·4 ± 0·5	—	—	—	—	—
Alcyonidium diaphanum	46·7	4·4	9·4 ± 35·6	—	—	—	—	—
Flustra foliacea	80·0	3·3	12·2 ± 35·1	—	—	—	—	—
Henricia oculata	86·7	0·1	0·4 ± 0·7	—	—	—	*	—
Crossaster papposus[a]	100·0	5·0	9·0 ± 9·7	*	*	*	*	*
Asterias rubens[a]	93·3	19·4	37·6 ± 38·6	—	—	—	*	—
Ophiothrix fragilis	73·3	2·0	7·9 ± 30·3	—	—	—	—	—
Echinus esculentus[a]	93·3	14·1	24·7 ± 30·3	*	*	*	*	*
Psammechinus miliaris	93·3	1·1	2·9 ± 7·4	*	—	—	*	*
Ascidiacea	93·3	1·0	1·2 ± 1·4	—	—	—	*	*
Scyliorhinus canicula	73·3	3·7	6·2 ± 5·3	—	—	—	—	—
Lophius piscatorius	53·3	2·7	2·4 ± 3·7	—	—	—	—	—
Trisopterus minutus[a]	100·0	2·7	4·2 ± 4·1	*	—	—	*	—
Agonus cataphractus	80·0	0·1	0·2 ± 0·3	—	—	—	—	—
Microstomus kitt	66·7	0·7	2·1 ± 5·4	—	—	—	—	—

TABLE 4. Taxonomic list of the major fauna of the *Nephrops norvegicus–Glyptocephalus cynoglossus* assemblage. See Table 1 legend for further details of the data presented

Dominant fauna	% O	% W	Mean CPUE (kg h^{-1})	Greater abundance cf. other assemblages				
				Pleu	*Micr*	*Echi*	*Alcy*	*Maja*
Nephrops norvegicus[a]	100	12·0	1·3 ± 1·8	*	*	*	*	*
Cancer pagurus[a]	100	12·1	1·5 ± 1·0	*	—	—	—	—
Liocarcinus depurator[a]	100	0·8	0·1 ± 0·05	—	—	—	—	—
Neptunea antiqua	25	10·4	2·0 ± 4·0	—	—	—	—	—
Astropecten irregularis[a]	100	6·3	1·3 ± 2·3	—	*	*	—	*
Asterias rubens	75	7·9	1·6 ± 2·8	—	—	—	—	—
Spatangus purpureus	50	7·7	1·7 ± 3·3	—	—	—	—	—
Scyliorhinus canicula	25	5·9	0·4 ± 0·8	—	—	—	—	—
Glyptocephalus cynoglossus[a]	100	21·1	2·6 ± 2·1	*	*	*	*	*
Solea solea	25	5·4	0·6 ± 1·1	—	—	—	—	—

Environmental characteristics

The BIOENV analysis indicated that the abiotic factors that correlated most closely with the distribution of the demersal assemblages were depth ($r_w = 0·28$), temperature ($r_w = 0·24–0·27$) and the weight of rocks in the catch ($r_w = 0·22$). Tidal currents, latitude, the weight of broken shells in the catch and salinity were of less importance ($r_w = 0·16$, 0·12, 0·04 and 0·01

respectively). The best correlation between the biotic and abiotic data was the combination of three variables: depth, surface water temperature (taken during the survey) and the weight of rocks in the catch ($r_w = 0·455$) (Table 9).

Several physical variables were significantly different between the assemblages (Table 8). The *Echinus–Crossaster* assemblage occurred at sites with a greater mean depth (59·1 m) than the *Alcyonium* (21·0 m),

TABLE 5. Taxonomic list of the major fauna of the *Alcyonium digitatum* assemblage. See Table 1 legend for further details of the data presented

Dominant fauna	% O	% W	Mean CPUE (kg h⁻¹)	Greater abundance cf. other assemblages				
				Pleu	Micr	Echi	Maja	Neph
Porifera	100	1·8	26·7 ± 52·7	★	★	—	—	★
Hydroids	100	2·0	25·8 ± 36·4	★	—	—	—	★
Metridium senile	80	2·4	19·7 ± 19·7	★	★	★	★	★
*Alcyonium digitatum*ᵃ	100	45·0	566 ± 533	★	★	★	★	★
Pandalus montagui	100	<0·1	0·3 ± 0·5	—	—	—	—	★
Maja squinado	20	0·2	2·6 ± 5·8	—	—	—	—	—
Macropodia spp.	100	0·1	0·6 ± 0·5	—	—	—	—	★
Cancer pagurus	100	0·1	0·7 ± 0·5	—	—	—	—	—
Liocarcinus holsatus	100	0·3	3·4 ± 3·2	—	—	—	—	★
Liocarcinus depurator	100	0·2	2·8 ± 1·8	—	—	★	★	★
Necora puber	80	0·2	1·5 ± 0·9	★	★	★	—	★
Modiolus modiolus	60	0·7	7·9 ± 12·3	—	—	—	—	—
Buccinum undatum	80	0·7	5·2 ± 5·7	—	—	—	★	★
Crossaster papposus	40	0·2	2·8 ± 5·1	—	—	—	—	—
*Asterias rubens*ᵃ	100	11·1	81·5 ± 94·4	—	—	—	—	★
Psammechinus miliaris	80	0·4	3·7 ± 3·5	★	★	—	★	★
Echinus esculentus	20	0·2	3·2 ± 7·2	—	—	—	—	—
Alcyonidium dipahanum	80	9·0	109 ± 202	—	—	—	—	—
Flustra foliacea	80	4·4	46·7 ± 80·0	—	—	—	—	—
Ascidiacea	80	12·5	164 ± 257	—	—	—	—	—
*Scyliorhinus canicula*ᵃ	100	1·4	12·5 ± 7·8	—	—	—	★	★
Raja clavata	60	0·3	3·8 ± 7·7	—	—	—	—	—
Merlangius merlangus	80	0·2	1·4 ± 2·1	—	—	—	—	★
Trisopterus minutus	80	0·2	3·8 ± 7·9	—	—	—	—	—
Trisopterus luscus	80	0·2	3·0 ± 5·6	—	—	—	—	—
Myoxocephalus scorpius	60	0·2	2·1 ± 3·2	—	—	—	—	—
Eutrigla gurnardus	100	0·1	0·9 ± 0·3	—	—	—	—	★
Trigla lucerna	80	0·2	2·1 ± 2·3	—	—	★	—	★
Agonus cataphractus	100	0·1	0·7 ± 0·8	—	—	—	—	★
Callionymus lyra	100	0·3	2·8 ± 1·8	—	—	—	—	★
*Limanda limanda*ᵃ	100	2·2	19·8 ± 9·7	—	★	★	★	★
Microstomus kitt	80	<0·1	0·6 ± 0·7	★ —	—	—	—	
*Pleuronectes platessa*ᵃ	100	2·0	15·4 ± 15·3	—	—	★	★	★
Solea solea	100	0·2	2·4 ± 2·2	—	—	★	—	★

Pleuronectes–Limanda (24·5 m) and *Maja* (33·5 m) assemblages (*P*<0·002). The *Nephrops–Glyptocephalus* assemblage occurred in deeper water (62·3 m) than the *Alcyonium* and *Pleuronectes–Limanda* assemblages (*P*<0·008), and the *Microchirus–Pagurus* assemblage was also in deeper water (46·4 m) than the *Pleuronectes–Limanda* assemblage (*P*<0·001). The mean weight of rocks in the catches were significantly higher in the *Echinus–Crossaster* (68·3 kg h⁻¹) and *Maja* (64·8 kg h⁻¹) assemblages in comparison with the *Pleuronectes–Limanda* assemblage (1·9 kg h⁻¹, *P*≤0·03). No significant differences in the weight of broken shells associated with assemblages were observed.

Surface water temperature associated with the *Maja* assemblage of the Bristol Channel (17·6 ± 0·4 °C) was higher than at other assemblages (*P*=0·001–0·05).

The only significant difference in mean surface salinity was between the *Pleuronectes–Limanda* (33·1) and *Echinus–Crossaster* (33·9) assemblages (*P*=0·04). The temperature and salinity regimes of the study area, as determined during the research cruise, are illustrated in Figure 6.

Discussion

Although many intertidal and shallow sub-littoral sites of the British Isles have been studied in great detail, such studies have tended to be localized and comparisons between disparate surveys are complicated by their different sampling times and gears, and sorting protocols. Additionally, many studies attempting to describe the faunal communities of the sea floor have used benthic grabs. This gear is designed to

TABLE 6. Taxonomic list of the major fauna of the *Maja squinado* assemblage. See Table 1 legend for further details of the data presented

Dominant fauna	% O	% W	Mean CPUE (kg h^{-1})	Greater abundance cf. other assemblages				
				Pleu	*Micr*	*Echi*	*Alcy*	*Neph*
Hydroids	92·3	3·9	1·5 ± 1·5	—	—	—	—	★
Alcyonium digitatum	53·8	3·2	3·4 ± 7·7	—	—	—	—	—
Metridium senile	84·6	1·6	0·7 ± 0·9	—	—	—	—	★
Maja squinado[a]	92·3	13·7	10·8 ± 22·0	★	★	★	★	★
Liocarcinus holsatus[a]	100·0	2·7	1·2 ± 1·2	—	—	—	—	★
Alcyonidium diaphanum	61·5	5·7	10·9 ± 35·6	—	—	—	—	—
Asterias rubens[a]	76·9	14·8	12·3 ± 17·0	—	—	—	—	★
Marthasterias glacialis	46·2	1·9	3·1 ± 9·9	—	—	—	—	—
Scyliorhinus canicula	61·5	6·7	6·3 ± 16·5	—	—	—	—	—
Raja clavata	53·8	6·5	3·7 ± 6·0	—	—	—	—	—
Raja microocellata	46·2	4·5	2·1 ± 3·5	—	—	—	—	—
Merlangius merlangus	92·3	2·0	0·9 ± 1·3	—	—	—	—	★
Trisopterus luscus[a]	100·0	2·5	1·3 ± 1·2	—	★	★	—	★
Trisopterus minutus	100·0	1·5	1·0 ± 1·6	★	—	—	—	★
Solea solea[a]	92·3	4·7	2·4 ± 1·3	—	—	★	—	★

TABLE 7. Percentage dissimilarity between the six demersal assemblages

	Pleu	Micr	*Echi*	*Neph*	*Alcy*
Micr	54·6	—	—	—	—
Echi	69·5	57·7	—	—	—
Neph	79·9	81·3	82·3	—	—
Alcy	55·3	56·2	61·2	87·2	—
Maja	61·0	60·3	68·0	83·1	62·0

quantitatively sample infauna, is unsuitable for sampling the larger and more mobile species within communities and is less efficient for the sampling of coarser substrates. Despite early benthic ecologists stating that additional studies regarding the epifauna were required (e.g. Petersen, 1915), there have been few broad-scale studies determining the distribution, composition and diversity of epibenthic assemblages in the north-eastern Atlantic (e.g. Jennings *et al.*, 1999; Rees *et al.*, 1999). Beam trawls are designed primarily for the capture of flatfish and, although not suitable for the quantitative sampling of smaller organisms and infaunal species, they are considered suitable for sampling the larger macro-epibenthic invertebrates and demersal fish. Additionally, as beam trawls can sample greater areas than, for example, benthic grabs, the effects of small-scale heterogeneity is reduced and the results can be assumed to be more representative of general patterns. Using these gears, it has been possible to undertake surveys with a broad

spatial coverage in offshore areas to examine demersal assemblages (Jennings *et al.*, 1999; Kaiser *et al.*, 1999). Such data may have particular relevance to the management of these areas, especially in reference to current environmental initiatives, including the European Union Habitats Directive and Annex V of OSPAR.

Broad-scale surveys of the demersal fauna in the eastern English Channel (Kaiser *et al.*, 1999) and the present study used the same gear and sampling protocol. Additionally, surveys of macro-benthic invertebrates have been undertaken with 2 m beam trawls in the North Sea (Jennings *et al.*, 1999) and British coastal waters (Rees *et al.*, 1999). Although providing detailed taxonomic accounts of the invertebrate fauna, these studies would have under-represented the larger and more mobile members of the demersal communities, including demersal fish.

The distribution of both sediment types and benthic communities in the Irish Sea have previously been described (Dickson & Boelans, 1988; Mackie, 1990; Mackie *et al.*, 1995), and our data indicate that the spatial variation in substrate and infauna are accompanied by changes in the demersal epifauna (see Figure 7). The inshore waters of the Irish Sea are composed primarily of sand and are populated by a ' shallow *Venus* ' community, with scattered patches of finer sediments and associated *Abra* communities (Mackie, 1990). These areas were inhabited predominantly by flatfish (*Pleuronectes–Limanda* assemblage) and *Asterias rubens* was particularly abundant. Both flatfish and *A. rubens* are known to predate a variety of

TABLE 8. Summary table of the six broad categories of demersal assemblage recorded in the Bristol Channel, St George's Channel and Irish Sea. Data provided include the number of stations attributed to each assemblage, the average similarity of the catches within these groups and the spatial distribution of the assemblages. Physical characteristics include depth (mean ± SD and range), temperature (°C) and salinity (mean ± SD) and the weights of rocks and broken shells (kg h^{-1}) in the catch. Biological information includes the catch per unit effort (kg h^{-1}; mean ± SD and range), total number of taxa recorded, the diversity (H'), species richness (d) and evenness (J') of all motile fauna, invertebrates and fish, and the dominant species

| Assemblage	Pleuronectes–Limanda	Microchirus–Pagurus	Echinus–Crossaster	Nephrops–Glyptocephalus	Alcyonium	Maja
No. stations	45	18	15	4	5	13
% similarity	53·4	53·3	47·3	44·4	58·0	48·1
Locations	Inshore waters of the Irish Sea, and Cardigan and Carmarthen Bays	Intermediate sites in the eastern Irish Sea, Cardigan and Carmarthen Bays and south-east Ireland	Offshore waters of the Irish Sea, St George's Channel and Bristol Channel	Western Irish Sea and off Cumbria	Luce Bay, Morecambe Bay, Llandudno, Arklow Head and Pembrokeshire	Bristol Channel
Depth (m)	24·5 ± 11·4 (12–56)	46·4 ± 14·4 (17–74)	59·1 ± 22·4 (28–100)	62·3 ± 34·5 (32–110)	21·0 ± 9·8 (15–38)	33·5 ± 11·3 (19–52)
Temperature	16·1 ± 0·8	16·3 ± 0·7	15·5 ± 0·9	14·8 ± 0·7	16·3 ± 0·7	17·6 ± 0·4
Salinity	33·1 ± 0·9	33·8 ± 0·6	33·9 ± 0·5	33·5 ± 0·9	33·2 ± 0·9	33·7 ± 1·0
Wt. rocks	1·9 ± 4·2	14·7 ± 33·9	68·3 ± 104·5	7·4 ± 13·6	21·9 ± 32·7	64·8 ± 79·5
Wt. broken shells	4·6 ± 14·9	2·1 ± 3·7	4·9 ± 3·1	0·5 ± 0·4	11·6 ± 23·3	0·2 ± 0·3
CPUE	303 ± 671 (21·4–3527)	111 ± 79·4 (45·9–319)	177 ± 138 (25·1–502)	14·7 ± 7·6 (6·6–22·8)	1156 ± 409 (577–1615)	74·6 ± 70·3 (15·7–264)
Total no. of species	133	>133	>140	>30	>91	92
Motile fauna						
Diversity	2·0 ± 0·6	2·4 ± 0·4	2·3 ± 0·3	1·8 ± 0·4	2·0 ± 0·6	1·9 ± 0·6
Richness	3·5 ± 0·8	5·1 ± 0·9	4·7 ± 0·7	2·1 ± 0·3	3·8 ± 0·3	3·7 ± 0·7
Evenness	0·6 ± 0·2	0·7 ± 0·1	0·6 ± 0·1	0·7 ± 0·2	0·6 ± 0·2	0·6 ± 0·2
Invertebrates						
Diversity	1·4 ± 0·5	2·0 ± 0·4	2·1 ± 0·4	1·6 ± 0·3	1·6 ± 0·6	1·4 ± 0·5
Richness	1·8 ± 0·6	3·0 ± 0·7	3·1 ± 0·7	1·6 ± 0·5	1·8 ± 0·3	2·2 ± 0·6
Evenness	0·5 ± 0·2	0·6 ± 0·1	0·6 ± 0·1	0·7 ± 0·1	0·6 ± 0·2	0·5 ± 0·1
Fish						
Diversity	1·8 ± 0·4	2·1 ± 0·3	1·6 ± 0·5	0·7 ± 0·6	1·9 ± 0·4	1·8 ± 0·3
Richness	2·1 ± 0·5	2·6 ± 0·6	2·2 ± 0·6	0·6 ± 0·6	2·4 ± 0·5	2·0 ± 0·4
Evenness	0·7 ± 0·1	0·8 ± 0·1	0·6 ± 0·1	0·7 ± 0·5	0·7 ± 0·1	0·7 ± 0·1
Dominant fauna	A. rubens L. limanda P. platessa S. canicula S. solea	A. rubens A. digitatum S. canicula A. opercularis L. limanda	A. rubens E. esculentus Hydroids C. papposus A. diaphanum	G. cynoglossus C. pagurus N. norvegicus N. antiqua A. rubens	A. digitatum Ascidiacea A. rubens A. diaphanum F. foliacea	A. rubens M. squinado S. canicula R. clavata A. diaphanum
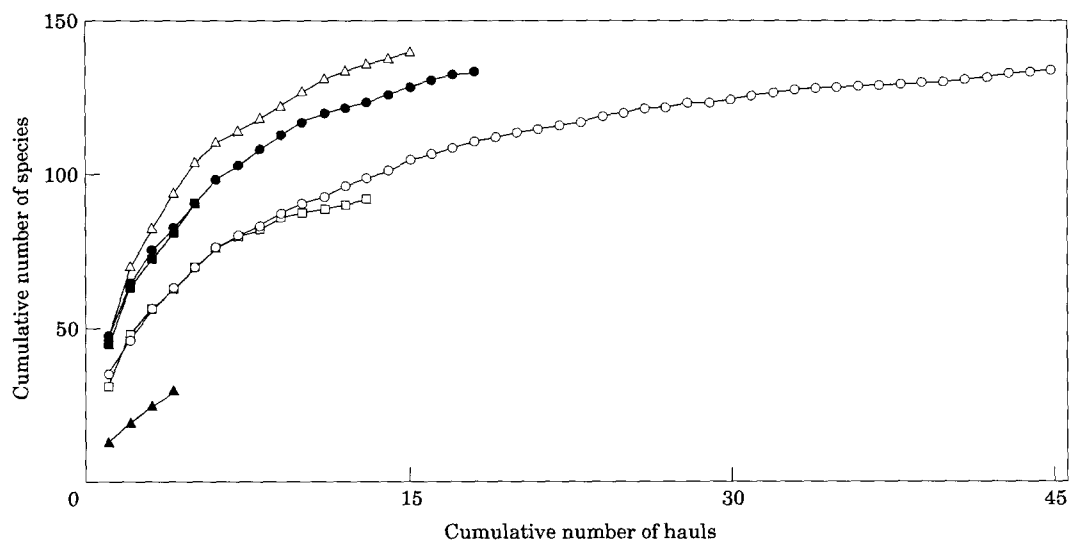
FIGURE 4. Relationship between the mean number of species recorded and the sampling effort (number of hauls) for 10 randomised orders of stations. The standard deviation has been omitted for the purposes of clarity. Open circles, *Pleuronectes–Limanda*; closed circles, *Microchirus–Pagurus*; open triangles, *Echinus–Crossaster*; closed triangles, *Nephrops–Glyptocephalus*; open squares, *Maja*; closed squares, *Alcyonium*.
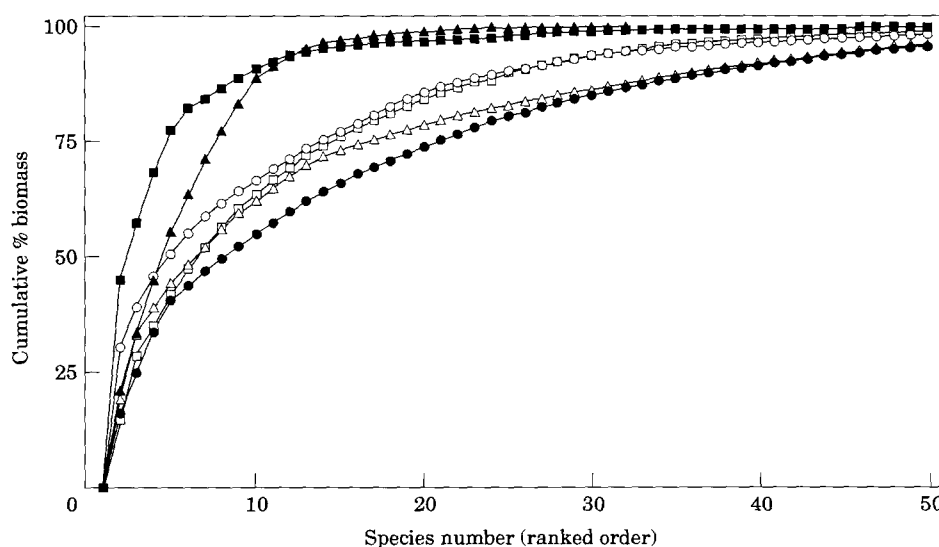

FIGURE 5. Species-dominance curves for the six assemblages, as indicated by the cumulative percentage of biomass. Open circles, *Pleuronectes–Limanda*; closed circles, *Microchirus–Pagarus*; open triangles, *Echinus–Crossaster*; closed triangles, *Nephrops–Glyptocephalus*; open squares, *Maja*; closed squares, *Alcyonium*.

bivalves, e.g. *Abra alba*, *Nucula*, *Tellina* and *Spisula* (Jones, 1952; Allen, 1983) and such bivalves are typical of the 'shallow Venus' community (Mackie, 1990). Rees *et al.* (1999), who also recorded a near-shore muddy-sand community in the coastal waters of the eastern Irish, also recorded a distinct *Crangon crangon* and *Pandalus montagui* assemblage in the estuarine waters of Morecambe Bay.

The muddy basins off the coast of Cumbria and in the north-western Irish Sea have been referred to as a boreal offshore mud association (Jones, 1950) and as a *Brissopsis lyrifer* community (Mackie, 1990), although this burrowing urchin was not recorded in our beam trawl catches. *Cancer pagurus* and *Nephrops norvegicus* were the dominant macro-invertebrates in these areas, with another burrowing crustacean,

TABLE 9. BIOENV analysis giving the correlation (r_w) between environmental and biological variables. *Maximum correlation denoted

Environmental parameter	r_w
Single variable	
Depth	0·28
Mean bottom temperature (summer)	0·27
Mean bottom temperature (winter)	0·26
Temperature stability	0·25
Surface water temperature (cruise)	0·24
Weight of rocks	0·22
Maximal tidal current speed of mean spring tides	0·16
Latitude	0·12
Weight of broken shell	0·04
Surface salinity (cruise)	0·01
Two variables	
Depth/surface water temperature	0·44
Depth/weight of rocks	0·37
Depth/latitude	0·36
Three variables	
Depth/surface water temperature/weight of rocks	0·46*
Depth/surface water temperature/surface salinity	0·41
Depth/surface water temperature/latitude	0·40

Goneplax rhomboides, also comparatively abundant. Indeed, these areas support commercially valuable *Nephrops* fisheries (Briggs, 1985). The fish community in these areas was dominated by *Glyptocephalus cynoglossus* and *Solea solea*, both of which are known to favour mud and muddy-sand substrates (Rogers, 1994). This habitat had the least diverse fauna and was dominated by comparatively few species. Rees *et al.* (1999) also recorded a *N. norvegicus* ground in the Celtic Sea.

Outside these muddy basins, the offshore sediments of the Irish Sea are generally coarser than the inshore sandy substrates and are primarily composed of more heterogeneous gravel and sand substrates (Dickson & Boelans, 1988; Figure 7), which are associated with a 'deep *Venus*' community (Mackie, 1990). The *Microchirus-Pagurus* and *Echinus-Crossaster* assemblages identified in our study equate with the *Psammechinus miliaris-Adamsia carcinopados* (the anthozoan which is commensal with *P. prideaux*) and bryozoan/hydroid assemblages of the coarser grounds in deeper waters reported by Rees *et al.* (1999). The macro-invertebrate assemblages of these offshore sites were still dominated by *A. rubens*, although other large echinoderms, including *Crossaster papposus* and *Echinus esculentus* were also dominant. These latter species are known to be more abundant in offshore
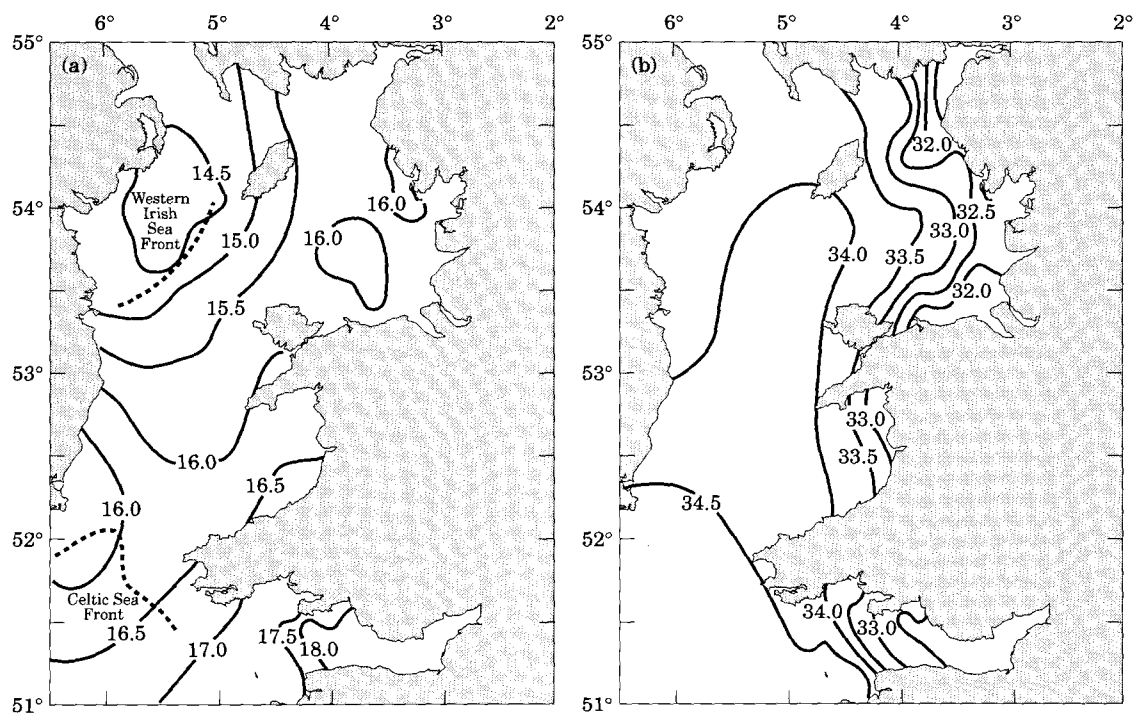

FIGURE 6. Geographical variation in (a) surface water temperature and (b) surface salinity, as recorded during sampling. The locations of the Western Irish Sea and Celtic Sea Fronts, as given by Mackie *et al.* (1995), are indicated (– – –).
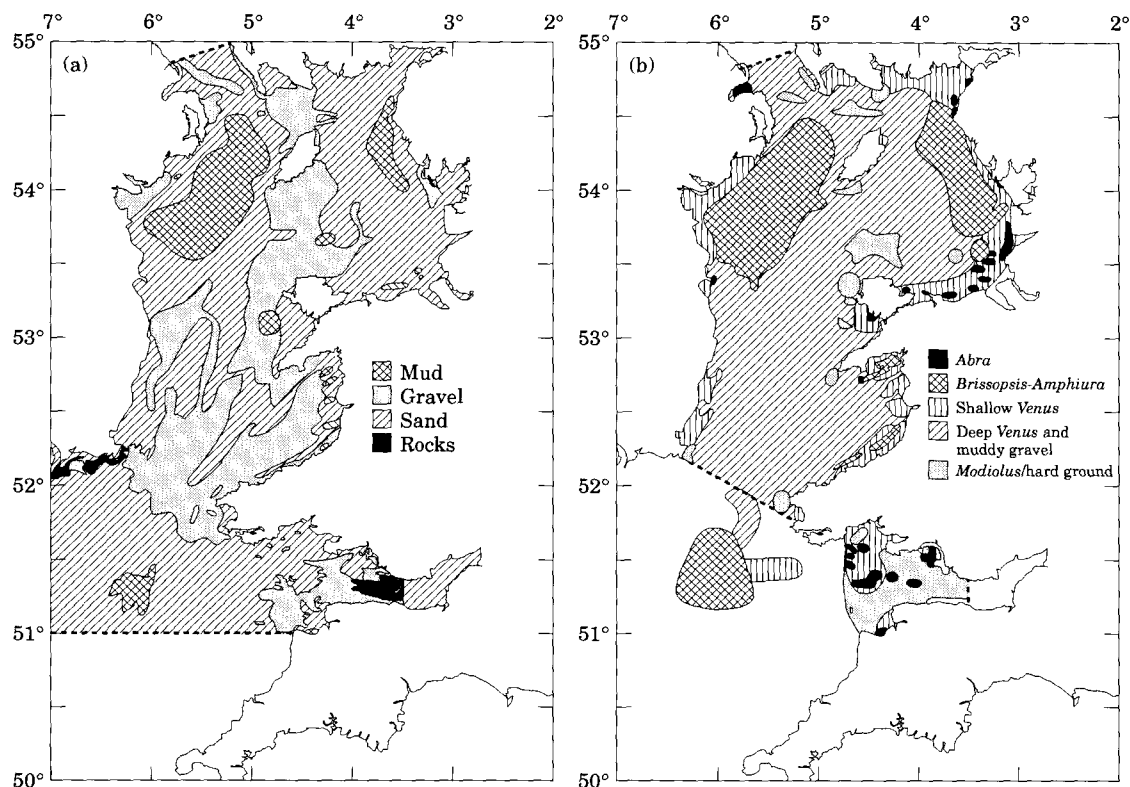
FIGURE 7. Geographical variation in (a) surface sediments and (b) benthic communities (Adapted from Warwick & Davies, 1977; Dickson & Boelens, 1988; Mackie, 1990; Mackie *et al.*, 1995 and British Geological Survey sediment charts).

waters (Ellis & Rogers, 2000). The diversity of these offshore sites, with their coarse and heterogeneous substrates, was generally greater than inshore waters, as has been reported by earlier authors (e.g. Gray, 1974). The current work also provides data on the epifauna of the western Irish Sea, including sites in deeper waters, where Rees *et al.* (1999) did not sample. Certain sites in this area were dominated by *Neptunea antiqua*, a species rarely caught in the eastern areas of the Irish Sea, as noted by Rees *et al.* (1999).

Further south, the demersal fauna of St George's Channel and Cardigan Bay has been less well studied. Laurie and Watkin (1922) deployed a variety of gears, including grabs, dredges and beam trawls, to sample an area of Cardigan Bay known as the ' Gutter ', which was regarded as an important area for flatfish fisheries. The brittlestar *Amphiura filiformis* and the gastropod *Turritella communis* dominated the catches in their grab samples. Mackie *et al.* (1995) sampled a broader area of St George's Channel, Celtic Deep and Cardigan and Caernarfon Bays with grab and dredge, and reported on three broad categories of assemblage. One assemblage was recorded in the soft sediments in the Celtic Deep, where we have no comparable data, a

second was widely distributed in the inshore sands and muddy sands of Cardigan Bay, outer Bristol Channel and off Anglesey, and a third was in the coarser, offshore sediments. The differentiation of an inshore sandy-sediment assemblage and an offshore assemblage with a biota more typical of coarser substrates was supported by our data.

The Bristol Channel has been relatively well surveyed over the last few decades, although many of these studies have focused on intertidal and shallow sub-tidal areas (e.g. Crothers, 1966; Withers, 1977; Shackley, 1981). Swansea Bay has been subject to numerous studies regarding the sediments and benthic communities (e.g. Harkantra, 1982; Shackley & Collins, 1984). Further offshore, detailed studies of the marine fauna have been made over an area extending from Bridgwater Bay to Caldey Island (Warwick & Davies, 1977; Warwick *et al.*, 1978; Warwick & Uncles, 1980; Warwick, 1984; George & Warwick, 1985). These studies used a Day grab for the quantitative sampling of infauna, and a Naturalist's dredge to survey the invertebrate epifauna. The communities described included a *Venus–Spisula* community in the dynamic sandy areas of the central Bristol Channel,

and a *Venus–Tellina* community in the more hard-packed sands in parts of Swansea, Carmarthen and Bideford Bays. *Abra* communities also occurred in the muddy areas of these bays. The coarser substrates that occur in the southern half of the Bristol Channel were referred to as a hard-bottom *Modiolus* community, where 'reefs' formed by the polychaete *Sabellaria spinulosa* also occurred (Warwick & Davies, 1977). The habitats of the eastern areas of the Bristol Channel are heavily influenced by tidal stress, resulting in less diverse communities on both hard and soft substrates (Warwick & Uncles, 1980; Mettam *et al.*, 1994).

The present study indicated that four of our demersal assemblages occurred in the Bristol Channel. Unfortunately, those areas of the Bristol Channel with reduced benthic communities were not sampled. Stations in Carmarthen Bay were representative primarily of the *Pleuronectes–Limanda* assemblage, and scavenging invertebrates (e.g. *Liocarcinus* spp., *Asterias rubens*, *Pagurus bernhardus* and *Buccinum undatum*) were abundant at these sites. The areas off South Gower, outer Swansea Bay and Bideford Bays were distinct from other sites in the survey, due primarily to the abundance of the common spider crab *Maja squinado*. This species is known to migrate seasonally, moving inshore in the spring and summer and offshore during the winter (Hines *et al.*, 1995). *Maja squinado* is reported to be more abundant in the Bristol Channel during summer (Crothers, 1966) and, although it has been recorded off South Gower from March to October (Ellis, pers. obs.), its distribution during the winter is unknown. As characteristic species for denoting communities should preferably be those species which dominate, by numerical abundance and/or biomass throughout the year, and without major seasonal variations (Petersen, 1915), additional studies during winter months would be desirable, in order to verify the biological distinction of these sites. It is possible that, if *M. squinado* moves offshore during the winter, then those shallower sites in the *Maja* assemblage could be more biologically similar to other inshore sites. Other taxa in this assemblage were, however, also indicative of a hard-bottom community, and included *Marthasterias glacialis* and sessile fauna (e.g. hydroids, *M. senile*, *A. digitatum* and *A. diaphanum*). The importance of small-bodied gadoids (*Merlangius merlangus*, *Trisopterus minutus* and *T. luscus*) in the Bristol Channel, as also noted by Rogers *et al.* (1998), is also indicative of a more structurally complex habitat. Stations in the middle of the Bristol Channel were more typical of offshore assemblages.

The descriptions of benthic communities have, traditionally, been categorized according to the typifying and characteristic species (e.g. Petersen, 1915; Shelford *et al.*, 1935). Other authors have given the primary emphasis for community divisions as either the hydrographic conditions (e.g. Molander, 1928) and/or sediments (Einarsson, 1941). Stephen (1933) divided the North Sea into four faunal divisions (littoral, inshore, offshore and *Thyasira–Foraminifera* zones), with sediments acting as a second tier of divisions. A variety of biotic and abiotic factors are known to affect the distribution of marine organisms and assemblages (e.g. Shelford *et al.*, 1935; Spärck, 1935; Warwick & Uncles, 1980; Harkantra, 1982), and certain physical factors are, at least in part, related to other physical factors. In view of this Jones (1950) developed a tiered classification, with a primary division according to the biogeographical region, and subsequent sub-divisions according to the temperature and salinity regime, and then substrate. More recently, Glémarec (1973) proposed a classification based on three étages (infra-littoral, coastal and open sea), which broadly represented the temperature and thermal stability of the areas, and secondary divisions according to substrate. Although we have used the characteristic biota to differentiate between the assemblages identified, the importance of depth and substrate in affecting the distribution and structure of these assemblages has been confirmed and is summarized in Table 8. Similar work in the eastern English Channel also determined that these were important factors correlating with the distribution of demersal assemblages (Kaiser *et al.*, 1999). Temperature was also an important factor in determining the biotic assemblages along the western coasts of England and Wales. The *Maja* assemblage in the Bristol Channel was in significantly warmer water than the other assemblages and several species recorded in the present study, for example small-eyed ray (*Raja microocellata*) tend to have their northern limits in the Bristol Channel. The presence of fronts, particularly the Celtic Sea and western Irish Sea Fronts (Figure 6), may also affect the distribution of certain species. Analysis of potential temporal variation in the demersal assemblages was beyond the scope of the present study, although it is known that fluctuations in the abundance of benthic species can occur over a variety of temporal scales, and these are often related to recruitment success. Nevertheless, major temporal changes in the macro-epibenthic fauna are likely to be slower than, for example, the plankton, due to the longer generation time (Holme, 1953).

Groundfish surveys can, however, provide useful information on the broad range of demersal

assemblages over wide geographical areas, although there are some areas (e.g. shallow waters, extremely rocky grounds and grounds fished with static gears) that could not be sampled. Six contrasting demersal assemblages were observed in the present study and, through the analysis of biological and physical data, these assemblages can be described on the basis of some of their biotic and abiotic characteristics. We have used the typifying and characteristic biota in the nomenclature of these assemblages, in favour of a system based on physical characteristics, as our data were collected from beam trawl catches and, therefore, sampling tows may have passed over several distinct habitats or biotopes. Nevertheless, there was a general tendency for the spatial distribution of demersal assemblages to mirror the distributions of both infaunal communities and sediment types, giving credence to Petersen's (1915) suggestion that ' for each community on the level bottom there exists one or more corresponding epifauna'. Further work regarding the associations of demersal fish and macro-epibenthic invertebrates with particular sediment, temperature and depth regimes may allow a more accurate spatial delineation of demersal assemblages to be made. This will enable coastal managers to gauge the relative importance of selected sites with reference to the abundance of commercial fish and shellfish, species of conservation interest and the diversity of the demersal fauna.

Acknowledgements

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