

The distribution, relative abundance and diversity of echinoderms in the eastern English Channel, Bristol Channel, and Irish Sea

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The distribution and relative abundance of macroepibenthic echinoderms in the eastern English Channel and Irish Sea is described from beam trawl catches. Echinoderms accounted for approximately 29% (by biomass) of fauna captured. A total of 24 species were recorded, including 12 species of starfish. The most frequently encountered species were *Asterias rubens* and *Psammechinus miliaris*, which were recorded at 85.5% and 56.0% of stations respectively. *Asterias rubens* and *Ophiothrix fragilis* accounted for 63.7% and 25.5% (by biomass) respectively of the echinoderms sampled. Mean echinoderm catches ranged from 0.8-kg h⁻¹ in the north-eastern English Channel to 329-kg h⁻¹ in the south-eastern Irish Sea. The echinoderm fauna was more diverse in the St George's Channel and western Irish Sea (6.7–7.0 species haul⁻¹) than in the north-eastern English Channel (1.9 species haul⁻¹).

INTRODUCTION

Echinoderms are a dominant group in many soft and hard bottom marine assemblages (Falk-Peteren, 1982; McClintock, 1994). The phylum contains a variety of trophic groups, including detritivores, filter-feeders, grazers, scavengers and active predators, and as such play an important role in the structure of benthic communities (Himmelman & Dutil, 1991; McClintock, 1994). Echinoderms may compete for food resources with demersal fish, predate on commercially important bivalves and be a major food source for fish (e.g. Anger et al., 1977; Dare, 1982; Packer et al., 1994). Additionally, they may be useful indicators of pollution (Portocali et al., 1997) and physical disturbance (Kaiser, 1996), and some (e.g. *Echinus esculentus*) are commercially exploited (Conand & Sloan, 1989).

The biogeographical ranges of echinoderms occurring in British waters have been documented (Mortenson, 1927; Falk-Peteren, 1982). Nevertheless, quantitative and descriptive records of echinoderm distribution are only available for the North Sea (Stephen, 1934; Ursin, 1960; Dyer et al., 1982), and certain areas of the English Channel (Allen, 1899; Holme, 1961, 1966) and Irish Sea (Massy, 1913; Mackie et al., 1995). One of the problems in determining the relative abundance of echinoderms in UK inshore waters is that previous benthic surveys have generally used benthic grabs to provide quantitative data (e.g. Ursin, 1960; Mackie et al., 1995). Such gears may be inappropriate for sampling larger epibenthic echinoderms, which are more accurately surveyed by dredge, trawl or diving census (Larsson, 1968; Skjveland, 1973; Kaiser et al., 1994). The current study used the benthic by-catch of beam trawl surveys to describe the relative abundance, distribution and diversity of echinoderms over extensive regions of the eastern English Channel, Bristol Channel and Irish Sea.

MATERIALS AND METHODS

The macroepibenthic by-catch was recorded during two groundfish surveys undertaken by RV 'Corystes'. Sampling stations (Figure 1) in the eastern English Channel and southern North Sea (August 1998, 99 hauls) and the Bristol Channel, St George's Channel and Irish Sea (September 1998, 101 hauls) were at depths ranging from 6–110 m. No sampling was undertaken in the western English Channel. The gear used was a 4 m beam trawl with chain matrix and 40 mm stretched mesh cod-end, as described by Kaiser & Spencer (1995). Tows were of 30 min duration, resulting in an approximate sampling area of 15,000 m². Smaller catches (<10–15 kg) were sorted in their entirety, whereas larger catches were weighed, a subsample of known weight sorted and individual species abundances and weights raised to the total catch. All data were subsequently converted to weight and numbers caught per hour.

Although the catch efficiency of the gear for echinoderms is not known, it is considered that the catch rates for the larger epibenthic species will allow the extent of their distribution and their relative abundance to be estimated. Data for smaller and less frequently caught echinoderms are included for the sake of completeness.

The echinoderm diversity, for those taxa caught, was calculated for all sampling stations using the PRIMER analytical package (Clarke & Warwick, 1994). Values determined were the number of species recorded at each station, the Shannon–Wiener diversity index (H'), Margalef's index of species richness (d) and Pielou's evenness index (J'). PRIMER was also used for the cluster analysis of species-site data to determine which echinoderm species shared similar patterns of occurrence and numerical abundance in beam trawl catches. The similarity of echinoderm catches (by numbers) at stations was compared to five environmental parameters (water depth,

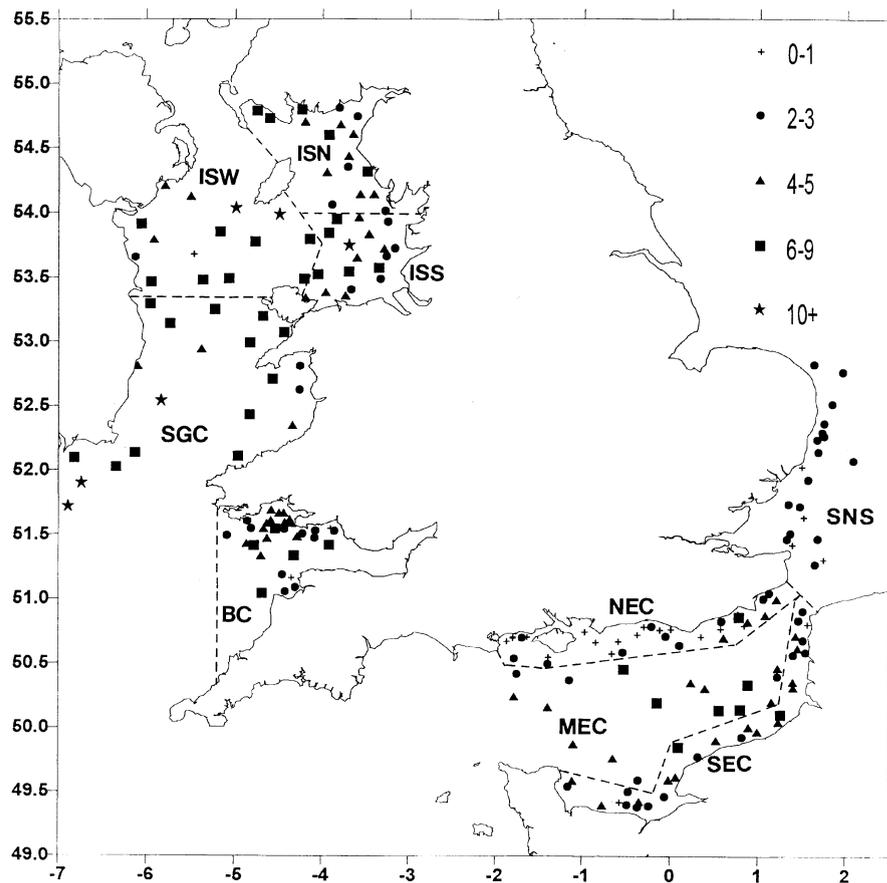


Figure 1. The number of echinoderm species recorded at sampling stations in the southern North Sea (SNS), north-eastern English Channel (NEC), south-eastern English Channel (SEC), mid-eastern English Channel (MEC), Bristol Channel (BC), St George's Channel (SGC), and southern (ISS), northern (ISN) and western (ISW) Irish Sea.

Table 1. Relative proportions of taxa in all beam trawl catches. Values given are the mean percentage of faunal biomass for 200 stations.

Taxa	Mean \pm SD (range)
Fish	32.6 \pm 22.9 (0.3–87.9)
Echinodermata	28.7 \pm 26.4 (0.0–98.8)
Bryozoa ¹	10.4 \pm 20.4 (0.0–95.4)
Crustacea	9.4 \pm 10.6 (0.2–59.5)
Cnidaria ²	7.0 \pm 13.0 (0.0–87.7)
Mollusca	6.8 \pm 10.6 (0.0–81.8)
Porifera	1.9 \pm 7.2 (0.0–63.0)
Worms ³	1.6 \pm 5.2 (0.0–40.2)

¹, mostly *Alcyonidium diaphanum* and *Flustra foliacea*; ², mostly *Alcyonium digitatum* and *Metridium senile*; ³, polychaeta, Hirudinea, Nemertea and Echiura.

latitude and the weights of rocks, sponges and broken shells in the catch) using the BIOENV procedure with Spearman's rank correlation (r_s).

RESULTS

Echinoderms were the dominant invertebrate component of beam trawl catches and, on average, accounted for approximately 29% of the biomass in each sample (Table 1). Twenty-four species of echinoderms were

recorded (Table 2), and these were dominated by the Asterozoa (12 species), with the remaining species belonging to the Ophiurozoa (5 species), Echinozoa (4), Holothurozoa (2) and Crinozoa (1). A maximum of 13 species was observed in any one sample (Figure 1) and, overall, a mean of 4.1 species haul⁻¹ was recorded.

Four species, *Astropecten irregularis*, *Asterias rubens*, *Psammechinus miliaris* and *Ophiura ophiura*, occurred in more than half the hauls taken in either the eastern English Channel or Irish Sea (Table 3). *Ophiothrix fragilis* and *A. rubens* dominated the echinoderm catches by biomass and numerical abundance.

The relative abundance of the 11 most frequently caught species by depth is illustrated in Figure 2. Most of these species had a broad bathymetric distribution, although the relative abundance of some species varied with depth. The largest catches of *A. rubens* occurred in inshore waters (<20 m), whereas *O. fragilis* was abundant in depths of 30–50 m. *Astropecten irregularis*, *Echinocardium cordatum* and *Ophiura ophiura* were observed to be more abundant at depths <25 m, whereas *Anseropoda placenta*, *Crossaster papposus*, *Henricia oculata* and *Echinus esculentus* were less abundant at the shallowest stations. Many of the less frequently caught species were observed in deeper waters, and the number of species of echinoderm recorded per haul significantly increased with depth (Figure 3). The spatial patterns in the relative abundance of individual

Table 2. Taxonomic list of echinoderms recorded in beam trawl catches from the study areas.

Class	Family	Species		
Crinoidea	Antedonidae	<i>Antedon bifida</i> (Pennant)		
Asteroidea	Astropectinidae	<i>Astropecten irregularis</i> (Pennant)		
	Luidiidae	<i>Luidia ciliaris</i> (Philippi) <i>Luidia sarsi</i> Dübén & Koren		
	Poraniidae	<i>Porania pulvillus</i> (Müller)		
	Asterinidae	<i>Anseropoda placenta</i> (Pennant)		
	Solasteridae	<i>Crossaster papposus</i> (L.)		
		<i>Solaster endeca</i> (L.)		
	Echinasteridae	<i>Henricia oculata</i> (Pennant)		
	Stichasteridae	<i>Stichastrella rosea</i> (Müller)		
	Asteroidea	Asteriidae	<i>Asterias rubens</i> L. <i>Leptasterias mülleri</i> (Sars) <i>Marthasterias glacialis</i> (L.)	
		Ophiuroidea	Ophiolopidae	<i>Ophiura albida</i> Forbes <i>Ophiura ophiura</i> (L.)
			Ophiocomidae	<i>Ophiocomina nigra</i> (Alildgaard)
Ophiotrichidae		<i>Ophiothrix fragilis</i> (Abildgaard)		
Echinoidea	Amphiuridae	<i>Amphiura</i> spp.		
		Echinidae	<i>Echinus esculentus</i> L. <i>Psammechinus milaris</i> (Gmelin)	
	Spatangidae	<i>Echinocardium cordatum</i> (Pennant) <i>Spatangus purpureus</i> Müller		
Holothuroidea	Cucumariidae	<i>Pawsonia saxicola</i> (Brady & Robertson) <i>Thyone</i> spp.		

species, as inferred from catch data, are illustrated in the Appendix.

Large catches were recorded for several echinoderm species. Maximum catches (numbers h^{-1}) were approximately 2.4 million for *Ophiothrix fragilis*; 114,000 for *Ophiura ophiura*; 46,000 for *Asterias rubens*, and 24,000 for *P. milaris* (Table 4). The heaviest catches (>1 tonne h^{-1}) were recorded in the Solway Firth and Liverpool Bay, where *A. rubens* dominated, and from *Ophiothrix fragilis* beds in the deeper waters of the eastern English Channel.

Regional differences in echinoderm diversity were observed (Table 5). Stations to the south of the Isle of Man had the greatest number of species (Figure 1) and trawl catches in St George's Channel and the western Irish Sea had the richest and most diverse echinoderm fauna. In contrast, the southern North Sea and north-eastern English Channel had a lower diversity, with approximately 2 species haul $^{-1}$ recorded. Echinoderm catches off the coast of south-eastern England were also comparatively small, with a mean catch rate of 0.8 kg h^{-1} , whereas catches in the deeper waters of the mid-English Channel and eastern parts of the Irish Sea were in excess of 200 kg h^{-1} . Catches in the northeastern English Channel had significantly fewer echinoderm species (t -test, $P < 0.001$) and a lower echinoderm biomass ($P < 0.05$) than catches in either the mid-English Channel or in the south-eastern English Channel.

Cluster analyses of the echinoderm fauna identified those species with similar patterns of spatial distribution and abundance (Figure 4). Within the eastern English Channel, *Ophiura albida*, *O. ophiura*, *A. rubens* and *P. milaris* occurred primarily in the coastal waters of both England

Table 3. Percentage occurrence (%O) of echinoderms in survey hauls and the species composition by biomass (%W) and numbers (%N) in the eastern English Channel/southern North Sea and Bristol Channel/Irish Sea.

Species	Eastern English Channel			Bristol Channel/Irish Sea		
	%O	%W	%N	%O	%W	%N
<i>Antedon bifida</i>	1.0	+	+	8.9	+	0.3
<i>Astropecten irregularis</i>	—	—	—	65.3	1.5	2.7
<i>Luidia ciliaris</i>	—	—	—	7.9	0.5	0.1
<i>Luidia sarsi</i>	—	—	—	3.0	+	0.1
<i>Anseropoda placenta</i>	13.1	+	+	7.9	0.1	0.1
<i>Crossaster papposus</i>	21.2	1.0	0.1	36.6	1.4	0.7
<i>Solaster endeca</i>	—	—	—	2.0	+	+
<i>Henricia oculata</i>	18.2	0.1	+	28.8	0.1	0.1
<i>Stichastrella rosea</i>	—	—	—	3.0	+	+
<i>Asterias rubens</i>	75.6	37.4	4.4	95.0	86.4	39.6
<i>Leptasterias mülleri</i>	—	—	—	1.0	+	+
<i>Marthasterias glacialis</i>	—	—	—	10.9	0.4	0.1
<i>Ophiura albida</i>	29.3	+	0.3	22.8	+	0.3
<i>Ophiura ophiura</i>	22.25	0.1	0.1	70.3	2.7	42.1
<i>Ophiocomina nigra</i>	3.0	+	+	1.0	+	+
<i>Ophiothrix fragilis</i>	23.2	53.7	93.0	27.7	1.0	11.1
<i>Amphiura</i> spp.	2.0	+	+	3.0	+	+
<i>Echinus esculentus</i>	—	—	—	28.7	3.3	0.6
<i>Psammechinus milaris</i>	60.6	3.4	1.7	51.5	1.0	1.4
<i>Echinocardium cordatum</i>	10.1	3.5	0.4	26.7	0.5	0.5
<i>Spatangus purpureus</i>	4.0	0.6	+	12.9	0.9	0.2
Cucumariidae	8.1	+	+	16.8	+	+

+, indicates a value $< 0.1\%$.

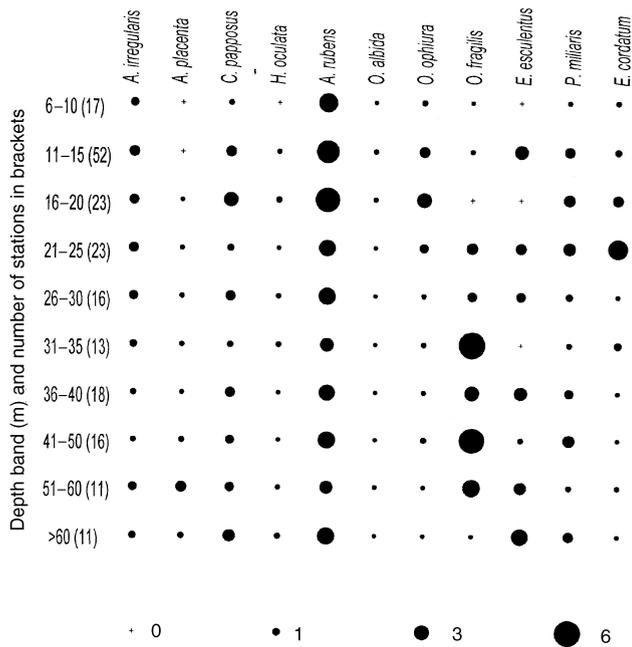


Figure 2. Relative abundance by depth band for the 11 most frequently caught echinoderms. Scale based on the ln (1+ mean biomass per hour, when present). The total number of stations in each depth band is indicated.

and France. A second group of species, *C. papposus*, *Ophiothrix fragilis*, *H. oculata* and *Anseropoda placenta*, occurred in the deeper waters of the eastern English Channel and were generally absent from the southern North Sea. The burrowing urchins *Spatangus purpureus* and *Echinocardium*

cordatum were extremely abundant in localized areas, resulting in their distinctness from other groups (Figure 4A, Appendix).

Similar echinoderm assemblages also occurred in the Irish Sea (Figure 4B). *Spatangus purpureus*, *Astropecten irregularis*, *Asterias rubens*, *O. ophiura* and *E. cordatum* were abundant in the inshore waters of Carmarthen Bay, Liverpool Bay and Solway Firth. The predatory starfishes *Luidia* spp. and *Marthasterias glacialis* were most abundant in the south-western approaches. The remaining species were most abundant in the deeper waters of the western Irish Sea and St George's Channel. These species were either less abundant in other areas (*Anseropoda placenta*, *Porania pulvillus* and *Stichastrella rosea*), or had a wider

Table 4. Maximum values of catch per unit effort (numbers h^{-1}) of the dominant echinoderm species.

Species	Maximum catch (no. h^{-1})
<i>Ophiothrix fragilis</i>	2,404,320
<i>Ophiura ophiura</i>	114,112
<i>Asterias rubens</i>	46,740
<i>Psammechinus milaris</i>	24,360
<i>Echinocardium cordatum</i>	17,808
<i>Ophiura albida</i>	8,690
<i>Astropecten irregularis</i>	2,092
<i>Crossaster papposus</i>	1,174
<i>Echinus esculentus</i>	1,144
<i>Antedon bifida</i>	1,052
<i>Spatangus purpureus</i>	852
<i>Luidia sarsi</i>	546
<i>Marthasterias glacialis</i>	470
<i>Anseropoda placenta</i>	350
<i>Luidia ciliaris</i>	244
<i>Henrica oculata</i>	234

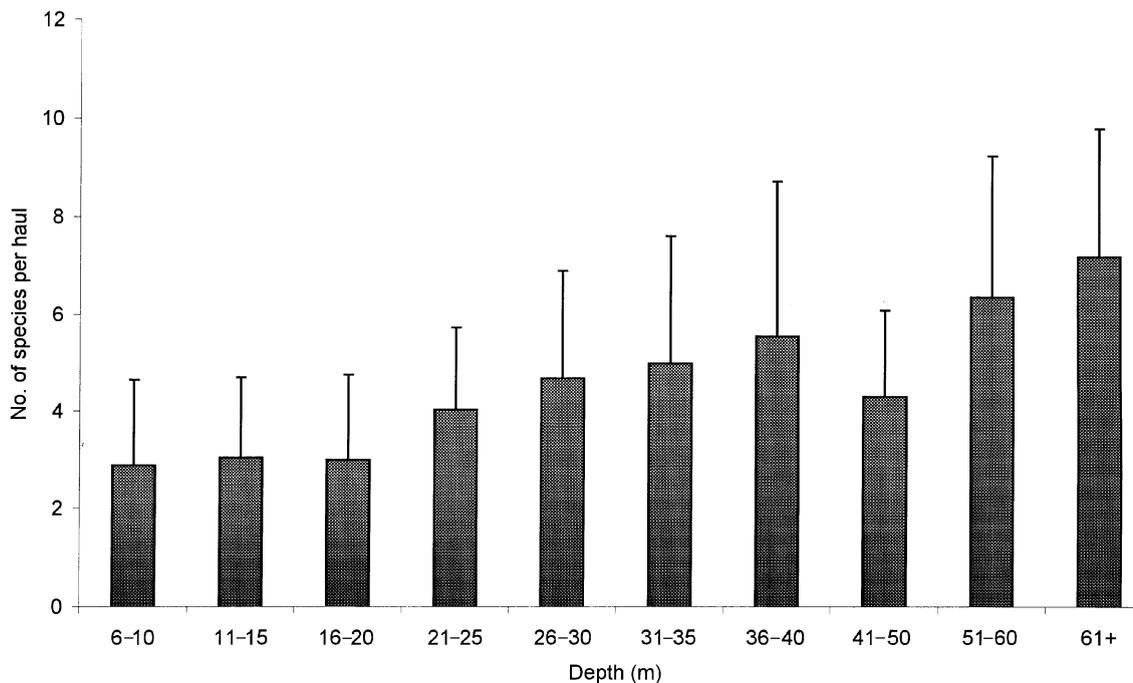


Figure 3. Mean number (\pm SD) of echinoderm species recorded per haul by depth band. The number of stations within each depth band is as indicated in Figure 2.

Table 5. Mean (\pm SD) biomass and number of species of echinoderm per haul, and mean richness, diversity and evenness in the southern North Sea, eastern English Channel, Bristol Channel and Irish Sea. The number of hauls per region (N) is indicated and regions are illustrated in Figure 1.

Region	N	Biomass	No. species	Richness d	Diversity H'	Evenness J'
Southern North Sea	20	39.7 \pm 103.8	2.1 \pm 0.7	0.16	0.32	0.36
North-eastern English Channel	32	0.8 \pm 2.0	1.9 \pm 1.7	0.29	0.34	0.33
South-eastern English Channel	30	186.8 \pm 486.4	3.6 \pm 1.4	0.32	0.52	0.41
Mid-English Channel	17	249.9 \pm 496.3	4.8 \pm 1.6	0.45	0.54	0.39
Bristol Channel	31	19.0 \pm 21.8	4.0 \pm 1.6	0.46	0.62	0.42
St George's Channel	20	68.5 \pm 73.7	7.0 \pm 2.2	0.85	0.97	0.50
Western Irish Sea	15	55.6 \pm 83.5	6.7 \pm 3.1	0.83	1.13	0.61
Northern Irish Sea	17	211.3 \pm 630.7	4.5 \pm 1.5	0.51	0.85	0.58
Southern Irish Sea	18	328.9 \pm 788.4	5.3 \pm 2.3	0.56	0.73	0.44
Total	200	114.9 \pm 391.6	4.1 \pm 2.4	0.46	0.62	0.43

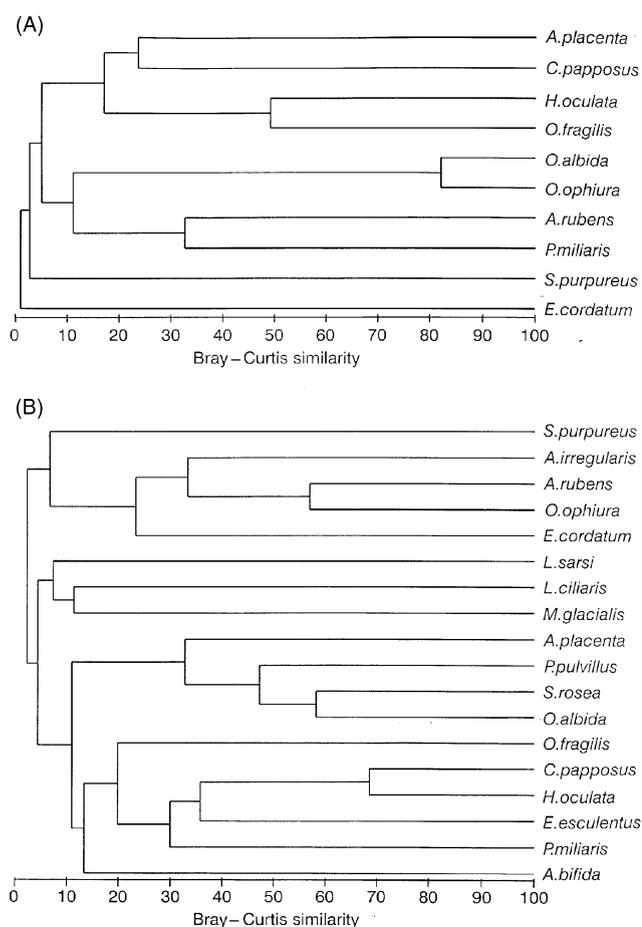


Figure 4. Echinoderm assemblages in the (A) eastern English Channel/southern North Sea and (B) Bristol Channel/Irish Sea.

spatial distribution (*Ophiothrix fragilis*, *C. papposus*, *H. oculata*, *Echinus esculentus*, *P. miliaris* and *Antedon bifida*) (Figure 4B, Appendix).

The BIOENV procedure indicated that the single most important environmental variables affecting echinoderm

catches were depth ($r_s=0.157$) in the eastern English Channel and the weight of rocks in the catch ($r_s=0.299$) in the Irish Sea. The best correlation in the latter survey was a combination of three factors, depth, and the weights of rocks and sponges ($r_s=0.371$). These data indicated that depth and the nature of the substrate were important abiotic factors affecting the spatial distribution and relative abundance of macroepibenthic echinoderms.

DISCUSSION

The broad-scale patterns in the relative abundance of epibenthic echinoderms around the British Isles are, despite their ecological importance, little known. The present study is based on data from 200 stations and provides the most widespread quantitative study of macroepibenthic echinoderms for the areas involved.

During the survey, 24 species were observed, and these were primarily starfish (Asteroidea). Although beam trawls are widely used for sampling large epifauna, the catch efficiencies for echinoderms are not known. Nauen (1978) estimated that a triangular dredge captured 10–32% of starfish, depending on the substrate. Dredges, however, are comparatively small and may be completely filled with material, thus hampering quantification of catches. In this respect, a 4 m beam trawl has some advantages. Catch rates of *Ophiura* spp. and *Asterias rubens* have been reported to increase with increased numbers of tickler chains (Creutzberg et al., 1987) and the presence of a chain matrix on our gear will improve the catch efficiency (Kaiser et al., 1994). Nevertheless, small individuals can pass through the mesh and, even though beam trawls can penetrate several centimetres into finer sediments, burrowing species may also avoid capture.

No one gear will sample all species within a taxon as diverse as the Echinodermata with the same efficiency and it is acknowledged that the trawl used in the present study is not the most efficient gear for the quantitative sampling of infaunal echinoids, ophiuroids and holothurians. However these groups have, for the St George's Channel at least, recently been quantified by grab sampling (Mackie et al., 1995) and our data complement this survey by providing quantitative data for those

species which are sampled more effectively by beam trawl (e.g. starfish and epifaunal echinoids).

Despite our lack of comparable data for the western English Channel, this region has been studied by other workers (e.g. Allen, 1899; Holme, 1961, 1966). *Psammechinus miliaris*, *Spatangus purpureus*, *A. rubens*, *Henricia oculata*, *Anseropoda placenta* and *Crossaster papposus* (common in the eastern English Channel), and *Echinus esculentus*, *Luidia* sp., *Astropecten irregularis* and *Marthasterias glacialis* (uncommon/absent in the eastern English Channel), have all been observed in beam trawl catches in this area (M. Vince, unpublished data).

The number of echinoderm species recorded in hauls increased significantly with depth, supporting the observations of earlier authors (e.g. Drouin et al., 1985). Diversity measures, however, may also be affected by gear type and sampling protocol (Heip et al., 1992). The increase in the number of echinoderm species in the catches from deeper waters (60–100 m) was partly responsible for the increased echinoderm diversity in the western Irish Sea, St George's Channel and off south-east Ireland. Unfortunately no comparable survey data are available for the outer Celtic Sea, although the Bay of Biscay is considered to have a diverse starfish fauna (Sibuet, 1977).

Several species of echinoderms are known to aggregate under certain conditions (e.g. Könnecker & Keegan, 1973; Warner, 1979), and the aggregating of adult echinoderms has been linked to the local abundance of food, reproductive requirements, defensive behaviour and increased efficiency of filter-feeding (Warner, 1979; Vadas et al., 1986). The maximum catches of the dominant species (Table 4) may be indicative of the aggregating nature of echinoderms. High catch rates of *Asterias rubens* were recorded in the Solway Firth and Liverpool Bay and were approximately 3 tonnes h⁻¹ (equivalent to 46,740 kg h⁻¹). Large aggregations have previously been reported in Morecambe Bay (Sloan & Aldridge, 1981) and such large aggregations have been related to high prey densities (Larsson, 1968; Sloan & Aldridge, 1981). The bivalve *Spisula subtruncata*, an important prey species, was also observed in the large catches of *A. rubens* in Liverpool Bay. Large catches of *Ophiothrix fragilis* were observed in the deeper waters of the English Channel, with maximum catches estimated at 2.7 tonnes h⁻¹ (2.4 million h⁻¹). The locations of other *O. fragilis* beds have been given by Warner (1971), Holme (1984) and Aronson (1989), and such beds occur in areas with suitable tidal currents (~20–25 cm s⁻¹) and low sedimentation (Aronson, 1989; Davoult & Gounin, 1995).

There are few published works on echinoderm assemblages. Franz et al. (1981) described six guilds of starfish in the north-western Atlantic according to their spatial distributions (latitude and depth). Due to the restricted latitudinal range of our study area (~5°), echinoderm assemblages were found to be more strongly correlated with depth and substrate, which have been reported as important factors affecting demersal assemblage structure (Kaiser et al., 1999). Within the eastern English Channel, *Ophiura* spp. and *A. rubens* occurred in a soft-bottom assemblage and Skjveland (1973) has previously reported that these species occurred together. A similar soft-bottom assemblage comprised of spatangoids, *Astropecten irregularis*, *Asterias rubens* and *O. ophiura* was also observed in

the Bristol Channel/Irish Sea survey. These species were all observed to be more abundant in shallower waters. The echinoderm assemblage in deeper waters was comprised of *C. papposus*, *Ophiothrix fragilis*, *H. oculata* and, in the Irish Sea, *E. esculentus*.

The low catch rate of echinoderms in the northeastern English Channel is noteworthy, although reasons for this are unknown. Holme (1961, 1966) has previously noted a lower number of echinoderm species in the eastern areas of the English Channel, in comparison with western areas, and suggested that temperature was an important factor. Although the faunistic boundary suggested by Holme (1961, 1966) may explain the low abundance/absence of western species (e.g. *M. glacialis*, *Luidia* spp.), it does not necessarily account for the absence of those species which occur in the western English Channel and North Sea (e.g. *Astropecten irregularis*, *E. esculentus*). Additionally, the present data also indicated that both the number of echinoderm species caught per haul and their biomass (as indicated by kg h⁻¹) were significantly greater off the French coast than along the south coast of England. So, in addition to an east–west faunal boundary, there are north–south differences in the echinoderm fauna of the eastern English Channel. Hoch & Garreau (1998) observed that the surface diatom concentration was greater on the French side of the eastern English Channel during the summer, and this was related to the nutrient-rich inputs of the Seine. It is possible, therefore, that the observed differences in echinoderm catches within the eastern English Channel are in some way affected by local hydrodynamics or spatial differences in the productivity and nutrient levels in this region.

In conclusion, depth and substrate were important factors influencing the structure of macroepibenthic echinoderm assemblages, and the number of species caught by beam trawl increased with depth. Large aggregations of many echinoderm species were observed, which may have been due to optimal feeding conditions. The broad-scale patterns of echinoderm catches indicated two major echinoderm assemblages, an inshore *Asterias*–*Ophiura* guild and a *Crossaster*–*Henricia*–*Ophiothrix* guild in deeper waters, which in our study areas often had coarser substrates. The influence of substrate on echinoderm distribution may be linked to predator–prey interactions, resource partitioning or locomotion. Deeper waters may also provide a more constant hydrodynamic environment, whereas temperature and salinity fluctuations will be greater in shallower waters. Commercial fishing activity may also be an important factor, with some species (e.g. *A. rubens*) possibly benefiting from scavenging on damaged/discarded organisms, and more fragile species (e.g. echinoids) subject to high fishing mortality (Kaiser & Spencer, 1995).

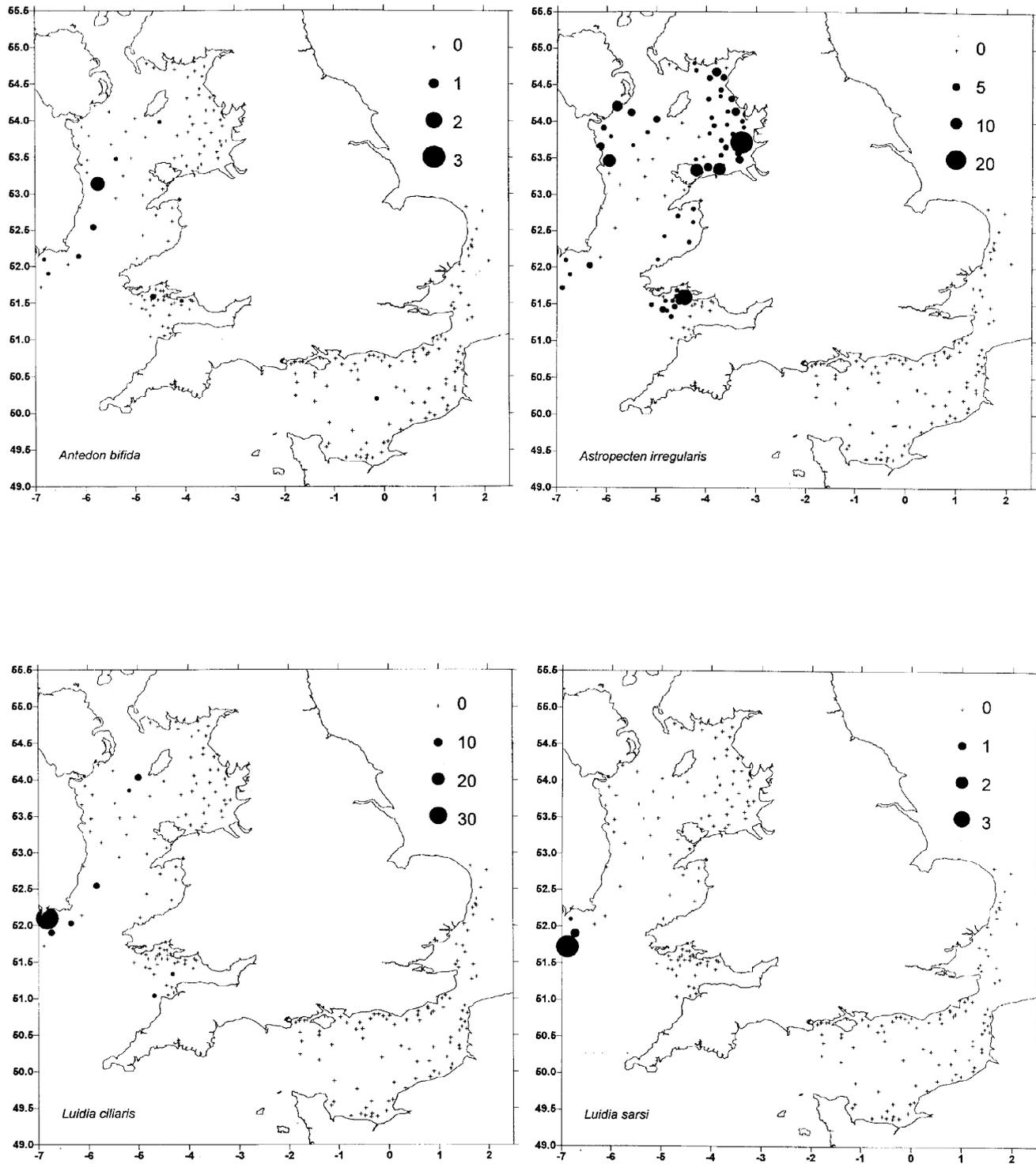
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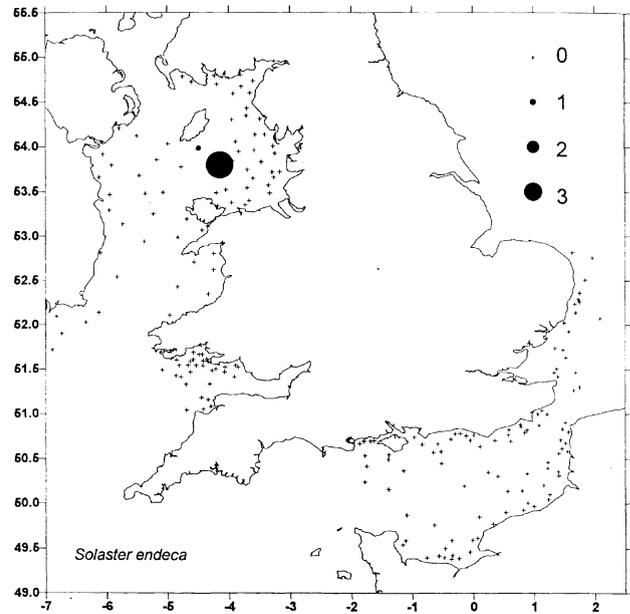
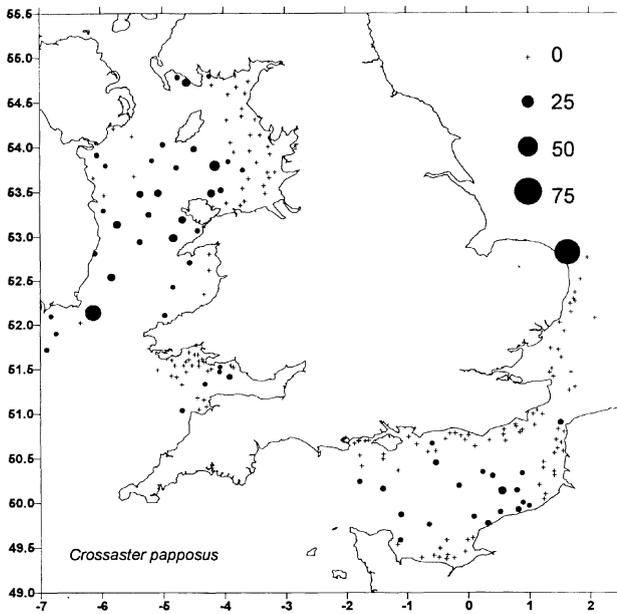
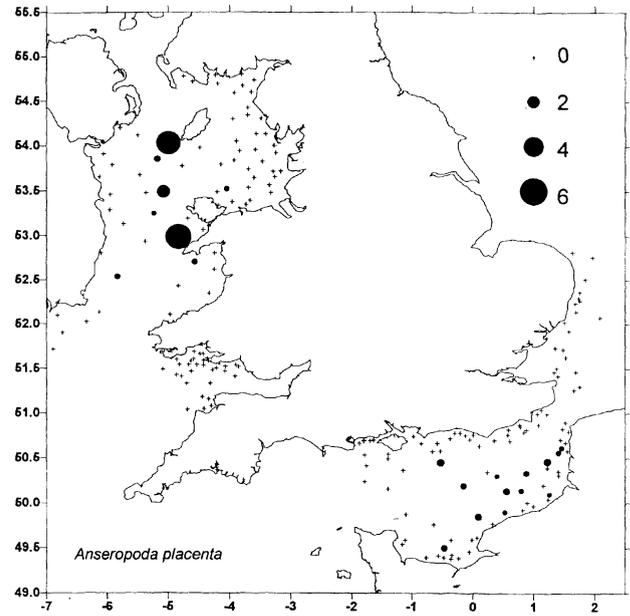
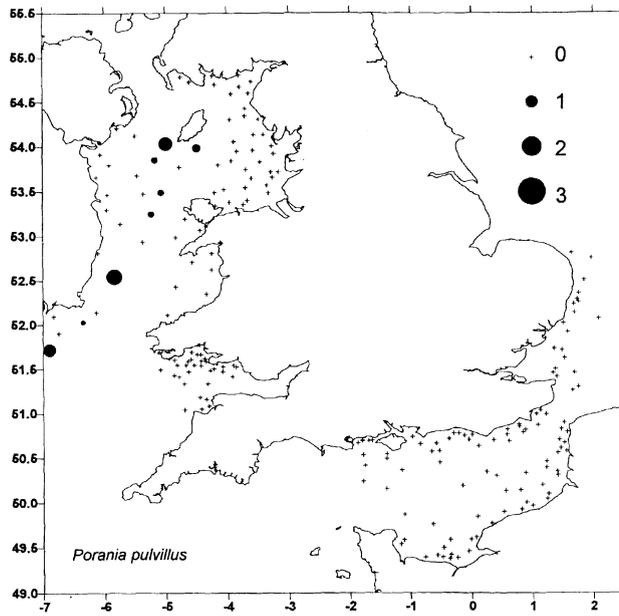
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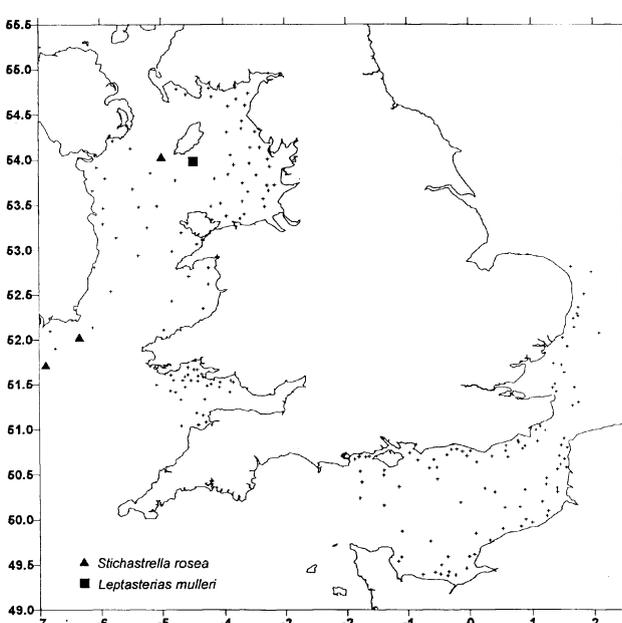
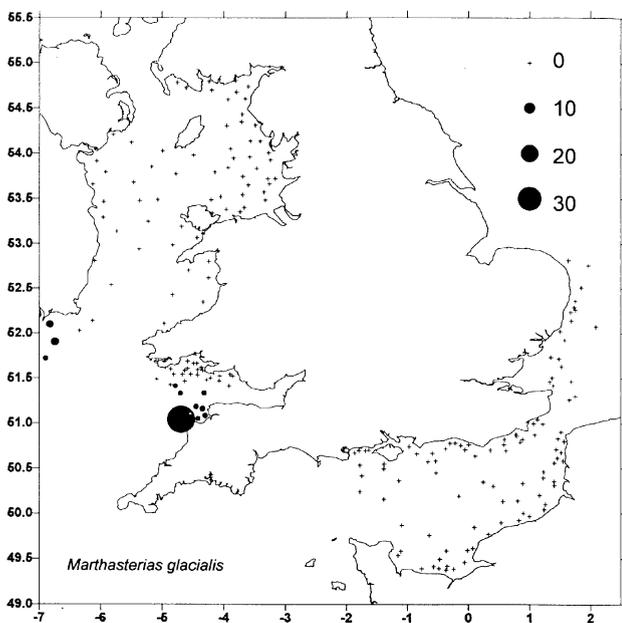
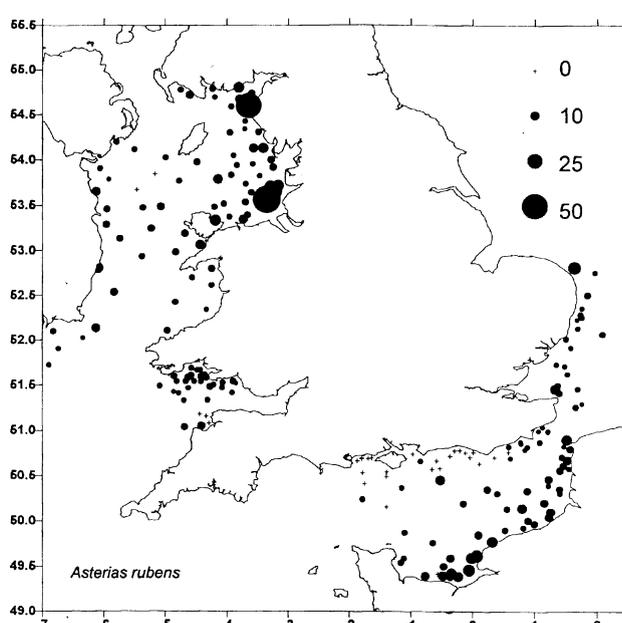
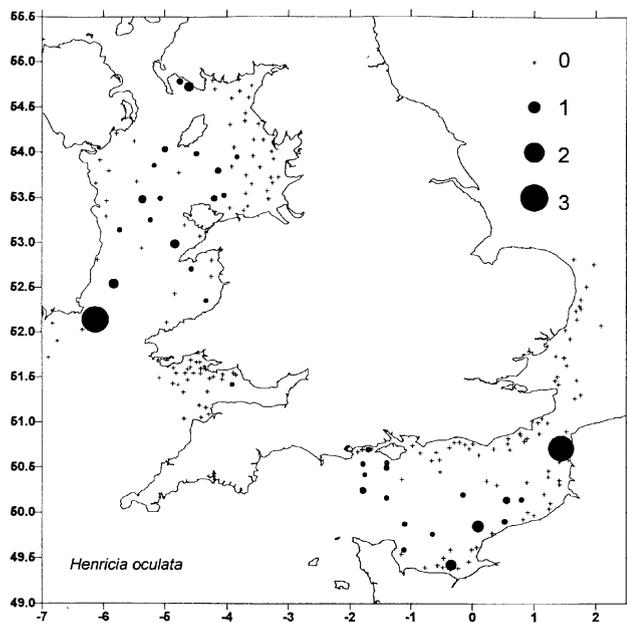
Appendix 1. *Distribution and relative abundance (kg h⁻¹) of echinoderms caught by beam trawl in the eastern English Channel, Bristol Channel and Irish Sea. Catch data for Asterias rubens, Ophiura ophiura, Ophiothrix fragilis, Echinocardium cordatum and Spatangus purpureus have been root transformed. Data for other species are on a linear scale.*



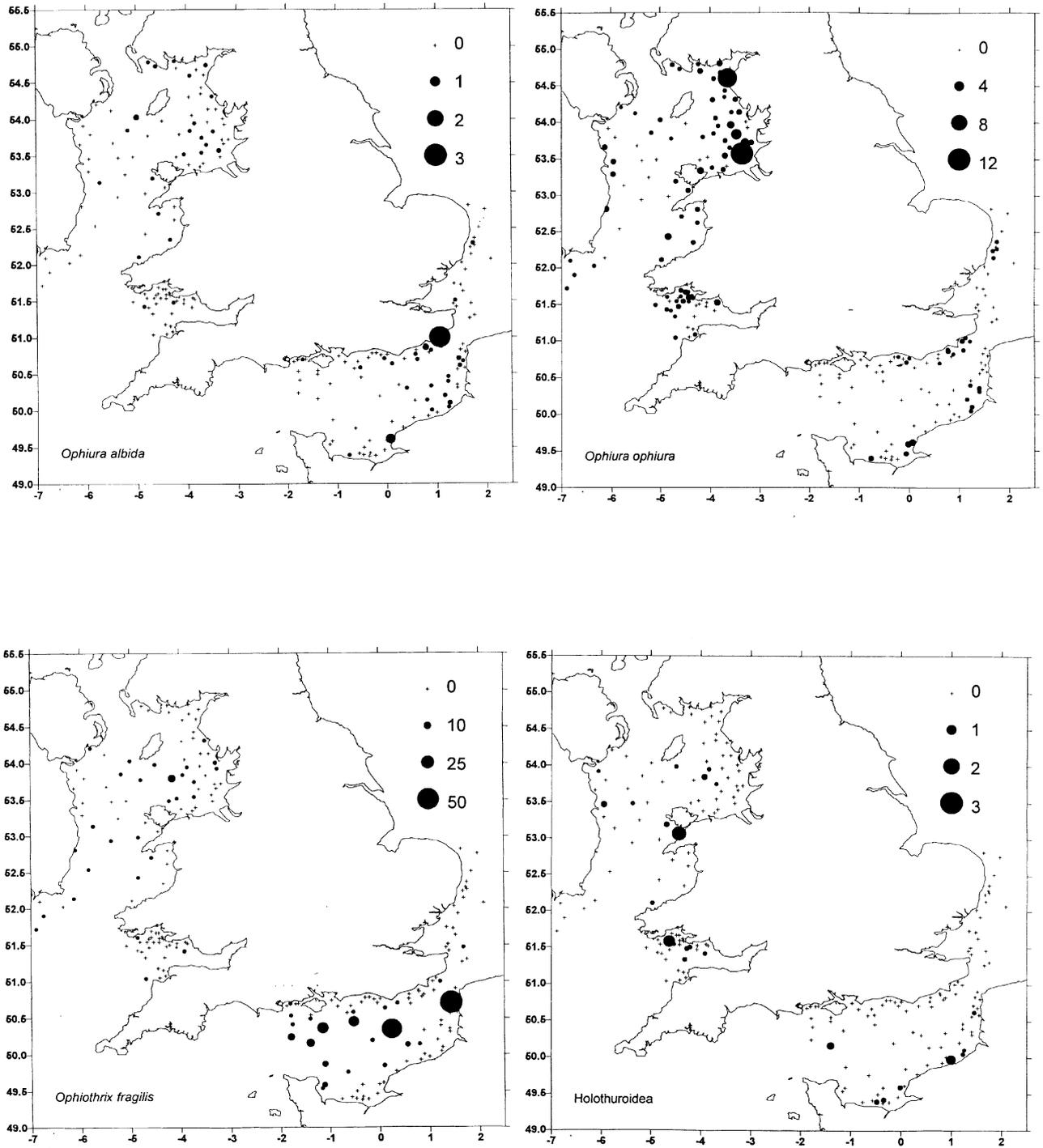
Appendix 1. (Continued).



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Appendix 1. (Continued).

