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Vertical structure, biomass and topographic association of deep-pelagic fishes in relation to a mid-ocean ridge system ☆

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Abstract

The assemblage structure and vertical distribution of deep-pelagic fishes relative to a mid-ocean ridge system are described from an acoustic and discrete-depth trawling survey conducted as part of the international Census of Marine Life field project MAR-ECO ⟨http://www.mar-eco.no⟩. The 36-station, zig-zag survey along the northern Mid-Atlantic Ridge (MAR; Iceland to the Azores) covered the full depth range (0 to >3000 m), from the surface to near the bottom, using a combination of gear types to gain a more comprehensive understanding of the pelagic fauna. Abundance per volume of deep-pelagic fishes was highest in the epipelagic zone and within the benthic boundary layer (BBL; 0–200 m above the seafloor). Minimum fish abundance occurred at depths below 2300 m but above the BBL. Biomass per volume of deep-pelagic fishes over the MAR reached a maximum within the BBL, revealing a previously unknown topographic association of a bathypelagic fish assemblage with a mid-ocean ridge system. With the exception of the BBL, biomass per volume reached a water column maximum in the bathypelagic zone between 1500 and 2300 m. This stands in stark contrast to the general "open-ocean" paradigm that biomass decreases exponentially from the surface downwards. As much of the summit of the MAR extends into this depth layer, a likely explanation for this mid-water maximum is ridge association. Multivariate statistical analyses suggest that the dominant component of deep-pelagic fish biomass over the northern MAR was a wide-ranging bathypelagic assemblage that was remarkably consistent along the length of the ridge from Iceland to the Azores. Integrating these results with those of previous studies in oceanic ecosystems, there appears to be adequate evidence to conclude that special hydrodynamic and biotic features of mid-ocean ridge systems cause changes in the ecological structure of deep-pelagic fish assemblages relative to those at the same depths over abyssal plains. Lacking terrigenous input of allochthonous organic carbon, increased demersal fish diversity and biomass over the MAR relative to the abyssal plains may be maintained by increased bathypelagic food resources. The aggregation of bathypelagic fishes with MAR topographic features was primarily a large adult phenomenon. Considering the immense areal extent of mid-ocean ridge systems globally, this strategy may have significant trophic transfer and reproductive benefits for deep-pelagic fish populations.
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Keywords: Vertical distribution; Mesopelagic zone; Bathypelagic zone; Mid-ocean ridges; Topography; Benthic boundary layer

1. Introduction

The "deep-pelagic" realm of the open ocean, from ~200 m depth to just above the bottom, is by far Earth's largest habitat, containing 95% of the ocean's volume

(Horn, 1972) and thus about ∼94% of the planet's water. Encompassing the meso- (200–1000 m), bathy- (1000–4000 m) and abyssopelagic (>4000 m) zones, the deep pelagial is essentially boundless in three dimensions for most of its extent, being structured physically only by the fluid properties of the water itself (e.g., temperature, salinity, pressure, light absorption, current shear). However, near continental landmasses, seamounts and along mid-ocean ridges, the deep-pelagic realm intersects abrupt topographic features of the seafloor. Of these features, mid-ocean ridges are by far the largest.

Large elevations of bottom topography, such as the Mid-Atlantic Ridge (MAR), influence local and regional circulation patterns (Roden, 1987), which in turn are likely to affect the distribution of deep-pelagic organisms. The MAR has an important influence on the deep-water circulation of the North Atlantic, partly separating deep waters of the eastern and western basins (Rossby, 1999; Bower et al., 2002). Closer to the surface, the ridge system might serve as an important source of ocean mixing through generating internal tides, tidally rectified flows and trapped waves (Holloway and Merrifield, 1999).

In terms of surface area, the mid-ocean ridge system is immense compared to continental shelf and slope habitats, where considerably more research effort on ecological structure has been focused. Lacking the terrigenous nutrient input received by continental slope communities, the deep-water fauna associated with mid-ocean ridges ultimately depends on the generally very limited local surface production. The annual primary production in the southern portion of the North Atlantic is around 45 g $C\,m^{-2}$ (Berger, 1989), though elevated surface chlorophyll concentrations have been observed in the region of the subpolar front (∼50°N; Søiland et al., 2008). Despite generally limited surface production, there is evidence of enhanced near-ridge demersal fish biomass above the MAR (Fock et al., 2002a; Bergstad et al., 2008) and that the mid-ocean ridges are ecologically important for higher trophic levels relative to the surrounding abyssal plains and the open ocean (e.g., blue ling, *Molva dypterygia*, spawning aggregations on the northern MAR; Magnusson and Magnusson, 1995). Three major processes by which organic matter can be transferred to the near-ridge zone include: (1) sinking of aggregates (including marine snow) and the carcasses of larger animals; (2) lateral advection of organic matter from off-ridge sources; and (3) the vertical migration of living animals (i.e., "trophic ladder"; Angel, 1997). The latter process has been found to be important at seamounts near the MAR. Fock et al. (2002b) studied the diets of four dominant demersal fish species at the Great Meteor Seamount and found that their interaction with vertically migrating mesopelagic fauna played a significant role in the maintenance of these fish stocks.

Along the MAR, the complicated topography and its effect on the circulation system and production at seamounts probably act to affect the distribution of the mesopelagic, bathypelagic and benthopelagic fauna. Up-welling processes may be strong enough to establish a considerable upward flux of near-bottom material into the deep pelagial. As most previous studies have been based just off the continental slopes, or in oceanic basins, the understanding of the significance and influence of mid-ocean ridges on biodiversity, distribution and community ecology of the pelagic fauna (and vice versa) is still rudimentary. In this paper we explore the structure and vertical distribution of the deep-pelagic fish assemblages over the northern MAR, from Iceland to the Azores, with the goal of better understanding the nature and magnitude of the interactions between a deep-pelagic nekton assemblage, a mid-ocean ridge system and its associated fauna.

2. Methods

Materials and biophysical data for this investigation were obtained during Leg 1 of the 2004 R/V *G.O. Sars* MAR-ECO expedition (see Wenneck et al., 2008, for more methodological detail) as part of MAR-ECO 〈www.mar-eco.no〉, an international Census of Marine Life (CoML) field project focusing on the ecosystems associated with the northern MAR, from Iceland to the Azores. The principal objectives of MAR-ECO are to describe and understand the patterns of distribution, abundance and trophic relationships of organisms inhabiting the mid-oceanic North Atlantic, as well as to identify and model ecological processes that cause variability in these patterns.

Leg 1 of the expedition, conducted during summer (5 June–3 July), utilized a two-pronged approach to mapping the pelagic fauna: (1) continuous sampling via acoustic methods along the entire cruise track and (2) point sampling at predefined "SuperStations" (SS) to characterize hydrography and biotic composition, abundance and biomass (Fig. 1). A series of sampling methods was employed at each SS, including CTD deployments, plankton net tows and pelagic nekton tows. Some opportunistic sampling was conducted along the track after detection of acoustic features of special interest. The *a priori* station design was chosen to best utilize the available ship time for the pelagic survey, with survey lines set up to allow several transverse crossings of the ridge, particularly at key features such as the Charlie-Gibbs Fracture Zone (CGFZ; Fig. 1). This cruise track did not allow day/night net sampling at each station and as a result fine-scale diel distributional patterns could not be determined within the spatial and temporal resolution of this survey. As most of the net sampling was done below 800 m (over 60% of all samples), the depth below which most diel vertical migrators reside (Angel and Baker, 1982), and daylight prevailed throughout most of the diel cycle due to latitude and season, larger-scale distributional patterns were the primary foci of trawl sampling.

2.1. Acoustic data

A scientific echosounder operating at five frequencies (18, 36, 70, 120, 200 kHz; SIMRAD EK60) was used to
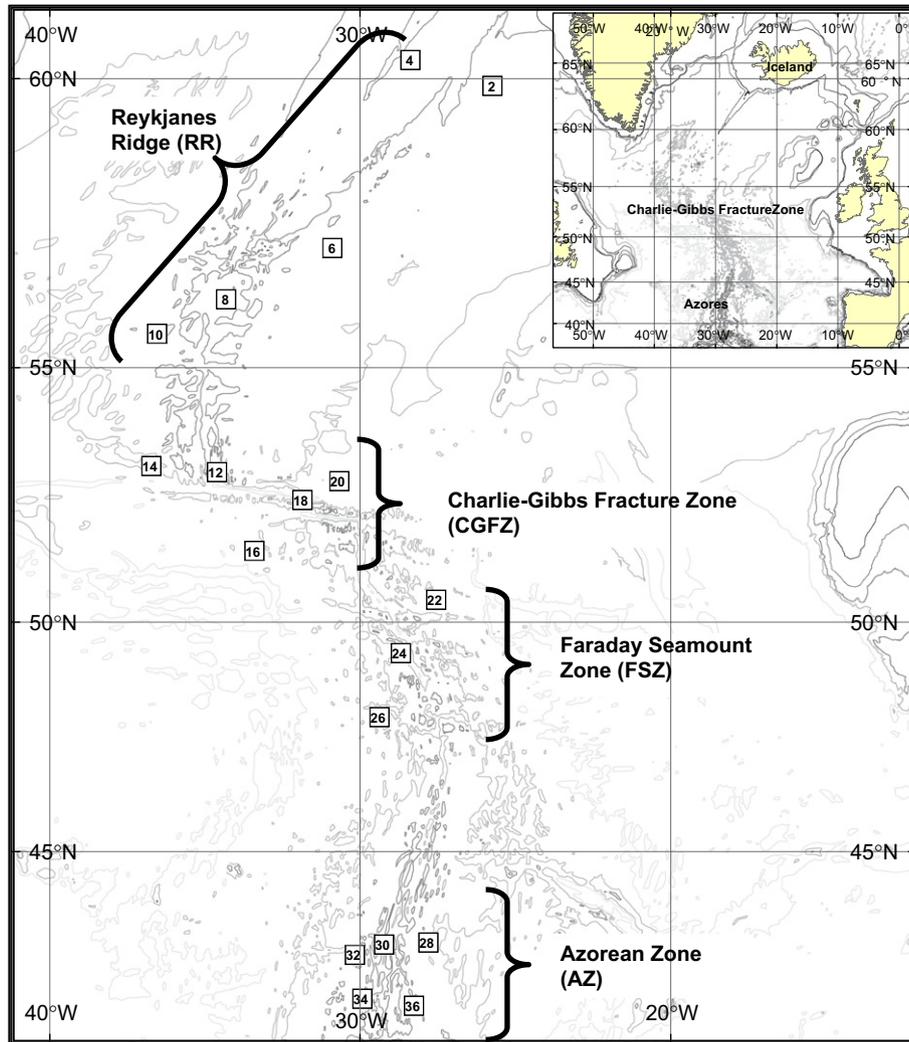
Fig. 1. Trawl sampling stations for Leg 1 of the 2004 R/V *G.O. Sars* MAR-ECO expedition.

map the horizontal and vertical distribution of biological backscatter in the upper 2000–3000 m. The combination of mounting the transducers on a drop keel and the use of an acoustically quiet vessel allowed good quality observations to full ocean depth in most cases. Bathymetry and bottom hardness were monitored during the cruise using a multibeam echosounder (SIMRAD EM300) recording to an Olex data management and navigation system. These data were used to determine proximity of the deepest pelagic trawls to the seafloor.

2.2. Trawl sampling

Three different double-warp midwater trawls, two of commercial fishing-size (a very large 'Egersund' trawl and a large 'Åkra' trawl) and one of oceanographic research-size ('Macroplankton' or 'Krill' trawl), were used to sample from the surface to depths of 3000 + m, bottom depth permitting. The largest net, the Egersund trawl (vertical opening of 90–180 m, door spread of 150 m and cod-end mesh size of 22 mm, stretched), was used to sample acoustic

targets opportunistically, but these data were not quantifiable in terms of the other two gears and thus were not used in this paper other than capture data presented in Appendix A. The latter two trawls (Åkra and Krill) were used at each station to increase the spectrum of deep-pelagic fishes sampled, including larger forms that generally avoid smaller (i.e., standard oceanographic) nets (Kashkin and Parin, 1983; Pearcy, 1983). A detailed description of the trawl gears, with schematics, can be found in Wenneck et al. (2008). These gears and the samples collected with each are discussed in turn.

The Åkra trawl is a medium- to large-sized pelagic trawl used in fishery research to simulate catches made with commercial gear. It has graded-mesh netting with a vertical opening of 20–35 m, a door spread of 110 m and a cod-end mesh size of 22 mm, stretched. For this cruise the trawl body was equipped with a remotely operated multi-sampler with three separate cod ends to sample three depth strata discretely and consecutively during each deployment. This net was used routinely for sampling large and medium-sized deep-pelagic fishes and cephalopods. With respect to

fishes, the Åkra trawl recorded the highest catches as well as the highest species numbers. As is the case with large, graded-mesh trawls, the volume of water filtered was difficult to estimate. For purposes of comparison with the Krill trawl, the Åkra trawl catches were standardized according to catchability (see below) and unit effort (trawl distance).

The Norwegian Krill trawl, with a mouth area of $\sim 36\,\text{m}^2$, is larger than trawls routinely used by oceanographers to sample micronekton. It has a $6 \times 6\text{-m}^2$ mouth opening, $3 \times 3\text{-mm}$ meshes (6 mm, stretched) from the mouth to the cod end, a length of 45 m, and was deployed with standard pelagic trawl doors. For this cruise the gear was equipped with a remotely operated multi-sampler and five 30-m long cod ends to sample five depth strata discretely and consecutively during each deployment. The trawl was equipped with SCANMAR sensors to provide data on actual cod end number, position, UTC time and depth.

In total, 114 discrete-depth samples were used for vertical distribution characterization (Table 1). Samples

Table 1
Trawl samples from the 2004 MAR-ECO expedition used for deep-pelagic fish vertical distribution analysis

SS	Net no.	Sample code	Date	Latitude (°N)	Longitude (°W)	Bottom depth (m)	Max trawl depth (m)	Min trawl depth (m)	Depth zone	Solar cycle	Group no.
2	AK 1-3	1	09-Jun	59.931	25.658	2260	180	0	1	D	X
2	AK 1-2	2	09-Jun	59.900	25.746	2314	750	370	2	D	V
2	AK 1-1	5	09-Jun	59.868	25.826	2264	2070	1500	4	D	IV
2	KT 1-5	8	10-Jun	59.927	25.859	2127	200	10	1	ND	V
2	KT 1-4	3	10-Jun	59.934	25.838	2150	850	200	2	ND	V
2	KT 1-3	4	10-Jun	59.947	25.804	2187	1550	850	3	ND	III
2	KT 1-2	6	10-Jun	59.963	25.766	2219	1900	1550	4	N	III
2	KT 1-1	7	10-Jun	59.970	25.754	2222	2100	1900	bot-3.5	N	III
4	AK 2-3	9	11-Jun	60.314	28.302	1467	200	0	1	D	V
4	AK 2-2	11	11-Jun	60.319	28.356	1397	850	200	2	ND	V
4	AK 2-1	14	10-Jun	60.356	28.421	1419	1260	850	3	ND	III
4	KT 2-5	10	11-Jun	60.239	28.398	1393	175	5	1	D	V
4	KT 2-4	13	11-Jun	60.253	28.398	1393	475	175	2	D	V
4	KT 2-3	12	11-Jun	60.278	28.415	1353	740	475	2	D	V
4	KT 2-2	15	11-Jun	60.300	28.424	1664	1300	745	3	D	III
4	KT 2-1	16	11-Jun	60.307	28.428	1501	1330	1300	bot-3	D	VII
6	KT 3-5	17	12-Jun	57.150	31.250	2315	200	0	1	N	XII
6	KT 3-4	18	12-Jun	57.151	31.223	2321	700	200	2	N	V
6	KT 3-3	19	12-Jun	57.154	31.175	2357	1500	700	3	N	III
6	KT 3-2	20	12-Jun	57.158	31.127	2344	2140	1500	4	N	III
6	KT 3-1	21	12-Jun	57.159	31.116	2309	2170	2140	bot-4	N	IV
8	AK 3-3	22	14-Jun	56.201	34.654	1344	300	0	1	D	V
8	AK 3-2	24	14-Jun	56.243	34.587	1315	800	300	2	ND	V
8	AK 3-1	27	14-Jun	56.285	34.513	1219	1050	800	bot-3	ND	III
8	KT 4-5	23	14-Jun	56.314	34.392	2031	200	0	1	N	V
8	KT 4-4	25	14-Jun	56.314	34.366	1847	760	200	2	N	V
8	KT 4-3	26	14-Jun	56.316	34.324	1680	1280	760	3	N	V
8	KT 4-2	29	14-Jun	56.320	34.275	1552	1330	1280	bot-3	DN	III
8	KT 4-1	28	14-Jun	56.321	34.266	1651	1335	1328	bot-3	DN	III
10	KT 5-5	30	14-Jun	55.536	36.558	2026	202	0	1	D	XII
10	KT 5-4	31	14-Jun	55.552	36.560	2104	751	202	2	D	V
10	KT 5-2	32	14-Jun	55.604	36.569	2144	1920	1500	4	D	III
10	KT 5-1	33	14-Jun	55.609	36.570	2147	1985	1920	bot-4	D	IV
12	AK 4-3	34	16-Jun	52.861	34.668	3239	293	0	1	D	V
12	AK 4-2	36	16-Jun	52.913	34.650	2744	800	300	2	D	V
12	AK 4-1	38	16-Jun	52.959	34.638	2112	1750	815	3	D	III
12	KT 6-5	35	16-Jun	53.047	34.629	1912	200	0	1	D	V
12	KT 6-4	37	16-Jun	53.060	34.616	1808	700	200	2	D	V
12	KT 6-3	39	16-Jun	53.081	34.597	1514	1186	700	3	D	III
12	KT 6-2	40	16-Jun	53.103	34.581	1636	1460	1186	bot-3	D	III
14	AK 5-3	41	16-Jun	53.182	36.783	3102	340	0	1	D	V
14	AK 5-2	43	16-Jun	53.134	36.753	3127	900	340	2	D	V
14	KT 7-5	42	18-Jun	53.083	36.698	3103	200	0	1	D	V
14	KT 7-4	44	18-Jun	53.041	36.702	3055	665	200	2	D	V
14	KT 7-3	45	18-Jun	53.067	36.710	3172	1480	665	3	D	III
14	KT 7-2	46	18-Jun	53.092	36.721	3130	2300	1500	4	D	III
14	KT 7-1	47	18-Jun	53.100	36.724	3153	2530	2300	5	D	III
16	KT 8-5	48	19-Jun	51.448	33.450	3794	238	36	1	D	XII
16	KT 8-4	49	19-Jun	51.420	33.455	3793	678	236	2	D	V
16	KT 8-3	50	19-Jun	51.392	33.465	3764	1488	674	3	D	III
16	KT 8-2	51	19-Jun	51.364	33.474	3710	2248	1496	4	D	III

Table 1 (*continued*)

SS	Net no.	Sample code	Date	Latitude (°N)	Longitude (°W)	Bottom depth (m)	Max trawl depth (m)	Min trawl depth (m)	Depth zone	Solar cycle	Group no.
16	KT 8-1	52	19-Jun	51.346	33.478	3688	3008	2239	5	D	III
18	AK 6-2	56	20-Jun	52.549	31.892	3935	1774	805	4	D	III
18	KT 9-5	53	20-Jun	52.983	30.771	3131	202	2	1	D	V
18	KT 9-4	54	20-Jun	52.995	30.790	3100	676	187	2	D	V
18	KT 9-3	55	20-Jun	53.014	30.821	3106	1502	685	3	D	III
18	KT 9-2	57	20-Jun	53.034	30.847	3095	2256	1518	4	D	III
18	KT 9-1	58	20-Jun	53.055	30.867	3070	2527	2256	5	D	III
20	AK 7-2	61	21-Jun	52.892	30.585	3167	1837	820	3	D	III
20	KT 10-5	59	21-Jun	52.983	30.771	3131	202	2	1	D	V
20	KT 10-4	60	21-Jun	52.995	30.790	3100	676	187	2	D	V
20	KT 10-3	62	21-Jun	53.014	30.821	3106	1502	685	3	D	III
20	KT 10-2	63	21-Jun	53.034	30.847	3095	2256	1518	4	D	III
20	KT 10-1	64	21-Jun	53.055	30.867	3070	2527	2256	5	D	III
22	AK 8-2	67	23-Jun	50.353	27.515	3650	1800	850	3	D	III
22	AK 8-1	69	23-Jun	50.395	27.497	3604	2370	1810	4	D	III
22	KT 11-5	65	23-Jun	50.516	27.486	3177	210	36	1	D	V
22	KT 11-4	66	23-Jun	50.532	27.488	3179	656	227	2	D	V
22	KT 11-3	68	23-Jun	50.559	27.491	3420	1487	647	3	D	III
22	KT 11-2	70	23-Jun	50.582	27.492	3520	2301	1774	4	D	III
22	KT 11-1	71	23-Jun	50.607	27.493	3705	2731	2309	5	D	III
24	AK 9-2	74	24-Jun	49.250	28.683	2606	1800	800	3	D	III
24	AK 9-1	76	24-Jun	49.288	28.662	2672	2230	1800	4	D	III
24	KT 12-5	72	24-Jun	49.590	28.480	3077	211	27	1	N	V
24	KT 12-4	73	24-Jun	49.567	28.483	3366	665	212	2	N	V
24	KT 12-3	75	24-Jun	49.541	28.486	3530	1776	666	3	ND	III
24	KT 12-2	77	24-Jun	49.516	28.485	3494	2338	1528	4	ND	III
24	KT 12-1	78	24-Jun	49.501	28.485	3589	2768	2314	5	ND	III
26	AK 10-2	81	25-Jun	47.967	29.510	3517	1746	800	3	D	VI
26	AK 11-3	79	25-Jun	47.796	29.166	3495	250	0	1	D	X
26	AK 11-2	80	25-Jun	47.810	29.188	3095	603	250	2	D	VI
28	AK 12-2	85	27-Jun	42.814	27.881	2657	1770	829	3	D	I
28	AK 12-1	86	27-Jun	42.809	27.825	3010	2400	1810	4	D	III
28	KT 13-5	83	27-Jun	42.813	27.691	2996	138	7	1	D	IX
28	KT 13-4	84	27-Jun	42.828	27.700	2989	691	151	2	D	VIII
28	KT 13-2	87	27-Jun	42.883	27.733	2822	2308	1475	4	D	III
28	KT 13-1	88	27-Jun	42.901	27.743	2890	2202	2295	5	D	III
30	AK 13-2	91	28-Jun	42.783	29.468	2407	1800	810	3	D	I
30	AK 13-1	93	28-Jun	42.789	29.389	2492	2390	1800	4	D	III
30	KT 14-5	89	28-Jun	42.951	29.257	1949	186	36	1	D	VIII
30	KT 14-4	90	28-Jun	42.953	29.274	2443	598	175	2	D	VIII
30	KT 14-3	92	28-Jun	42.939	29.312	2718	1500	604	3	D	I
30	KT 14-2	94	28-Jun	42.912	29.306	2828	2283	1480	4	D	III
30	KT 14-1	95	28-Jun	42.890	29.303	2839	2383	2265	5	D	XI
32	AK 14-2	97	29-Jun	42.678	30.197	2532	1800	800	3	D	I
32	AK 14-1	99	29-Jun	42.720	30.215	2542	2300	1800	4	D	III
32	KT 15-4	96	29-Jun	42.442	30.145	2364	675	188	2	DN	VIII
32	KT 15-3	98	29-Jun	42.467	30.144	2289	1523	652	3	DN	I
32	KT 15-2	100	29-Jun	42.492	30.145	2411	2005	1495	4	D	III
32	KT 15-1	101	29-Jun	42.515	30.148	2287	1828	2031	bot-4	D	III
34	AK 15-2	104	30-Jun	41.517	29.909	2230	1800	800	3	D	I
34	AK 15-1	106	30-Jun	41.560	29.924	2335	2000	1800	4	D	III
34	KT 16-5	102	30-Jun	41.684	29.999	1927	203	0	1	N	VIII
34	KT 16-4	103	30-Jun	41.698	29.999	2317	684	205	2	N	VIII
34	KT 16-3	105	30-Jun	41.721	29.999	2177	1494	674	3	N	II
34	KT 16-2	108	30-Jun	41.746	30.002	2154	1887	1490	4	N	III
34	KT 16-1	107	30-Jun	41.769	30.007	2524	1981	1887	4	N	III
36	KT 17-5	109	30-Jun	41.486	28.346	2698	180	0	1	N	VIII
36	KT 17-4	110	30-Jun	41.489	28.364	2524	729	218	2	N	VIII
36	KT 17-3	112	30-Jun	41.494	28.392	2602	1493	725	3	N	III
36	KT 17-2	115	30-Jun	41.498	28.425	2441	2036	1489	4	N	III
36	KT 17-1	114	30-Jun	41.499	28.453	2654	1980	2042	4	N	III
36	AK 16-2	111	1-Jul	41.239	28.238	2616	1800	800	3	D	I
36	AK 16-1	113	1-Jul	41.295	28.244	2722	2400	1800	4	D	III

SS = SuperStation (see Fig. 1). Net: AK = Åkra trawl sample; KT = Krill trawl sample. Sample codes are used in later figures for graphical clarity. Depth zones: 1 = 0–200 m; 2 = 200–750 m; 3 = 750–1500 m; 4 = 1500–2300 m; 5 ⩾ 2300 m; bot = near-bottom trawl (depth zone of bottom). Solar cycle: D = day; N = night; DN = dusk; ND = dawn. Group no. = assemblage as defined by multivariate analysis.

generally fell within one of five depth categories: 0–200, 200–750, 750–1500, 1500–2300 and >2300 m; samples that came within 200 m of the bottom were noted specifically; other samples that did not fall within this scheme were excluded from analysis. Samples were classified as daytime (D), dusk (DN), night (N) or dawn (ND) using sunrise and sunset times calculated for each sampling location and time. Sunrise and sunset times were calculated using the CBM model of Forsythe et al. (1995) to estimate day length and the equation of time and longitude to estimate 'noon.' Dusk and dawn samples were defined as those that were taken 1 h before to 1 h after sunset and sunrise, respectively. The solar cycle of samples was examined as an explanatory factor in subsequent multivariate statistical analyses.

For qualitative vertical distribution analysis, relative catch-per-unit-effort data from both trawl types were used to reveal a broader spectrum of deep-pelagic fish vertical distribution patterns. In order to integrate data from the different trawl types the Åkra trawl (graded mesh) results were standardized using the Krill trawl (uniform mesh) as the reference trawl. Catchability (defined as the ratio of Åkra trawl catch numbers to those of the Krill trawl) coefficients were calculated separately *for each fish taxon* (Heino et al., submitted), and the Åkra trawl results were divided by the appropriate catchability coefficient to form an integrated station × species matrix for both trawl types. Most taxa exhibited catchability coefficients much less than that predicted by the differences in mouth area alone, indicating that few deep-pelagic fishes are 'herded' by the large meshes in the mouth of larger trawls. For fully herded species (i.e., highly active swimming fishes), the mouth area of a large trawl with graded meshes may be similar to its effective mouth area (Heino et al., submitted). Catchability coefficients varied greatly across taxa, suggesting that the sampled volume for the Åkra trawl with graded meshes was highly taxon-specific, most likely a function of size, mobility and behavior of the individual fish taxon (Ramm and Xiao, 1995; Sangster and Breen, 1998). For quantitative purposes (abundance and biomass per volume), only the Krill trawl data (with known volume filtered) are reported here, with appropriate caveats regarding the underestimation of larger forms.

2.3. Sample handling

Following trawl retrieval, catches were kept separate on deck by net number, corresponding to the depth stratum sampled, and taken below decks for further processing. Catches were sorted one at a time to prevent potential mixing of specimens from different depth strata. The deepest net catch was routinely sorted first, with the other catches stored in a cold room to prevent sample degradation. The total wet weight of each catch was determined on a motion-compensating scale, recorded, and then the entire catch was rough sorted by major taxonomic group (fish, crustaceans, gelata). Fishes were then sorted by major

taxon and further identified to species by the first two authors (TTS and FMP). Each species was enumerated and weighed on a motion-compensating scale (±0.1 g) before further handling. One of the major benefits of at-sea weighing is that the biomass data do not suffer the rather large variability imposed by 'back-calculating' via volume displacement or length–weight regressions. Samples were then either frozen in lots by species, with an appropriate volume of seawater, or preserved in formalin in cases of rarity or taxonomic uncertainty. In cases where species determination was not feasible in a time appropriate to prevent sample degradation, specimens were frozen or preserved in lots by family, with species identification determined after closer examination by TTS and/or FMP at the Bergen Museum of Zoology, 〈http://collections.uib.no/vertebrate/〉, the permanent repository for all 2004 MAR-ECO expedition pelagic fish specimens. Biotic database updates following taxonomic revisions were handled by Bergen Museum staff.

2.4. Statistical analysis

The overall goal of this study was to characterize the vertical structure of a collection of pelagic fish assemblages subject to different uncontrolled factors, namely latitude/water mass, position relative to the ridge axis, time of day, depth and collection (gear) method. The data matrices analyzed consisted of standardized counts or biomass of species × trawl sample. Some community analyses were carried out on subsets of the total data matrix. Two multivariate techniques were employed to discriminate sample groups, using the PRIMER v.6 software package (Clarke and Gorley, 2006): (1) non-metric multi-dimensional scaling (MDS, Kruskal and Wish, 1978) and (2) hierarchical unweighted pair-group method using arithmetic averages (UPGMA) cluster analysis (Romesburg, 1990). Both methods were based on a triangular matrix of Bray–Curtis similarity coefficients (desirable because joint absences have no effect; Bray and Curtis, 1957; Faith et al., 1987). The independence of joint absence criterion is particularly important relative to this study; species can be absent for many reasons, and in this case it would be inappropriate to infer that two samples are similar because neither contains a particular species. As an example, it would be wrong to suggest that near-surface and lower bathypelagic samples are similar because neither contains species found only in the mesopelagic zone.

For multivariate analyses, and prior to construction of the similarity matrix, the total data matrix was fourth-root transformed to down-weight the importance of the numerically dominant species (namely, *Benthosema glaciale* and *Cyclothone microdon*). Ideally, the optimal degree of data transformation prior to multivariate analysis would be determined using statistical methods (e.g., dispersion-based weighting, Clarke et al., 2006). However, these methods require replication of samples (not possible in this study), so the 'range of values' criterion was employed. The

(non-zero) abundance values upon which analyses were based spanned six orders of magnitude (0.005–970.114 ind. per $10^4 \, m^3$), calling for a strong transformation to discriminate assemblage structure beyond the numerically dominant fish species.

A series of similarity permutation tests (ANOSIM, 999 iterations, $p < 5\%$) were run to test the null hypothesis that there were no differences between groups of samples as a function of five *a priori* defined factors. These factors included: ridge section (Fig. 1); location of sample relative to ridge axis (east, west, or directly over); solar cycle (day/night); collection gear (Åkra vs. Krill trawl); and depth stratum (Table 1). The results of these tests were then used to: (1) indicate the relative 'explanatory power' of each factor and (2) to direct further examination (pairwise comparisons) to determine where the major differences occurred relative to each factor. In cases where the null hypothesis was not rejected, no further pairwise comparisons were attempted.

In order to assess the appropriate similarity level for assemblage discrimination, similarity profile permutation tests (SIMPROF; 1000 iterations, $p < 5\%$) were run to test the null hypothesis that the samples, which were not *a priori* divided into groups (as they were for ANOSIM), did not differ from each other in multivariate structure. The similarity level at which the departure statistic, π, exceeded the 5% probability criterion (i.e., no statistical evidence for substructure at higher similarity levels) was used to define assemblage groups via cluster analysis. This similarity level was then overlain on the MDS plot to assess concordance, and pending that, used to define the groupings (i.e., natural assemblages) for data presentation and pooling for quantitative estimation (abundance and biomass per volume).

3. Results

3.1. Deep-pelagic fish community structure

A total of 205 fish species were collected by midwater sampling during Leg 1 of the 2004 *G.O. Sars* expedition (Appendix A). A detailed treatment covering the overall biogeography and latitudinal variation of the assemblage is underway (Porteiro et al., in prep.), pending the resolution of certain taxonomic issues, but a complete species list is presented for taxon-specific sample size representation. As some of these fishes are among the rarest known, this list also serves to highlight the MAR-ECO/CoML contributions in the Bergen Museum Vertebrate Collection. Of these 205 species, 197 were collected in 114 discrete-depth trawl samples, with these data constituting the basis for the remainder of this paper. The primary faunal contributors to either abundance or biomass will be detailed in a following account by depth stratum.

ANOSIM tests revealed that of the five factors investigated, depth was by far the most important (global $R = 0.452$, $p < 0.1\%$), followed by ridge section (global $R = 0.141$, $p < 0.1\%$). Gear type as a factor was weakly significant (global $R = 0.094$, $p < 2.2\%$). The null hypothesis (no differences between groups) could not be rejected for position relative to ridge axis (global $R = 0.021$, $p < 14.6\%$) or solar cycle ($R = -0.029$, $p < 67.2\%$), negating any further analysis. Relative to ridge section, the strongest differences were found between the Azorean (AZ) samples and those of the two northern regions (Reykjanes Ridge, $R = 0.273$, and CGFZ, $R = 0.287$, both with $p < 0.1\%$). The Faraday Seamount region (FSZ) differed weakly from the region to the north (CGFZ, $R = 0.095$, $p < 3.8\%$) and to the south (AZ, $R = 0.126$, $p < 1.7\%$). There was no statistical evidence suggesting differences between samples from the Reykjanes Ridge region and either the CGFZ ($R = -0.004$, $p < 51.2\%$) or the FSZ ($R = -0.015$, $p < 59.1\%$). As depth proved to be the primary assemblage composition determinant, the remainder of this paper will deal primarily with vertical structure, with some treatment of biogeographic differentiation as appropriate.

3.2. Large-scale vertical distribution patterns

The largest-scale view of the vertical distribution of fish abundance and biomass along the northern MAR is simply one of depth across the entire region sampled (Iceland to the Azores). Pooled quantitative data (all 81 Krill trawl samples) are plotted in Fig. 2 with respect to the five depth intervals sampled, plus a representation of data from samples taken within 200 m of the ridge, defined here as the MAR benthic boundary layer (BBL), irrespective of depth below the surface. Several large-scale features were apparent from these results. Abundance showed an expected decline with depth to approximately 1500 m, but then increased by roughly half relative to the overlying water before decreasing to a minimum below 2300 m. Pelagic fish densities rose dramatically within the BBL, rivaling values from the upper 750 m. The trend in biomass with depth differed from that of abundance, though the increase in the BBL was even more dramatic. In fact, the highest biomass values found during this survey occurred in this layer. Biomass values in the top 2300 m were somewhat surprising in that the expected exponential decline with depth did not occur; indeed the midwater biomass maximum was found between 1500 and 2300 m, resulting from the larger average size of fishes taken within this stratum (since abundances were lower). Not surprisingly, the water column minimum in biomass was observed below 2300 m but above the top of the BBL. In order to extract explanatory details within this large-scale view, we must look in more detail at the nature of the sample groupings.

A two-dimensional (2-D) spatial plot of ordination (MDS) resulted in a stress level (a measure of the dimensionality of an ordination) of 0.17, suggesting that the ordination could give a useful 2-D picture if used in tandem with another multivariate technique such as cluster
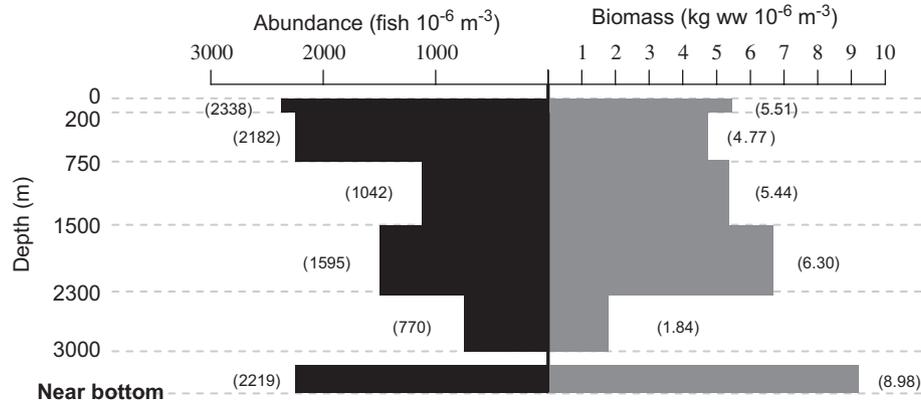
Fig. 2. The pooled vertical distribution of deep-pelagic fish abundance and biomass (ww = wet weight) along the northern Mid-Atlantic Ridge (Reykjanes Ridge to the Azores archipelago). Exact values listed in parentheses. Results based on 81 discrete-depth Krill trawl samples. "Near bottom" data include all samples within 200 m of the bottom, irrespective of depth from the surface (range = 750–2300 m).

analysis. Three-dimensional (3-D) plots resulted in a lower stress value, 0.12, but the gain was offset by the increased difficulty in visualizing the configuration in 3-D. Similarity profile tests (SIMPROF) of cluster analysis results identified 12 major assemblages at a similarity level of 33% ($\pi = 3.87$, $p < 0.1\%$). SIMPROF found no statistical evidence for substructure at higher similarity values (at 40% $\pi = 2.92$, $p < 20.8\%$). The dendrogram output of cluster analysis was too complex to be presented in its entirety, so a condensed version is provided in Fig. 3, with factorial characteristics listed for each cluster. Linking cluster analysis results to the MDS plot (Fig. 4) further corroborates this level of discrimination; subclusters were not organized spatially within major clusters when based on higher similarity values.

The finding that depth was the predominant factor with respect to group composition, more so than geographic region, is evidenced by the characteristics of the largest group, Group III. While 52 of the 53 samples included in Group III were taken at deep meso-/bathypelagic depths, these samples were apportioned almost evenly across the four main geographic regions (Fig. 3).

A spatial synopsis of these statistical analyses is presented in Fig. 5. The dominant feature was the widespread, deep-living assemblage of fishes between 750 and 3000 m (Group III), from the northern Reykjanes Ridge all the way to the Azores. Some zonation was apparent in the northern and southern ends of this large depth stratum, with six smaller assemblages of fishes exhibiting limited distributions. Of these six, the largest was an assemblage of fishes (Group I) found mainly in the Azorean Zone between 750 and 1500 m. Three smaller assemblages were found in close association with the ridge itself, two (Groups IV and VII) in the Reykjanes Ridge region and one (Group XI) in the Azorean Zone, the latter being very deep (>2300 m). An assemblage was observed at night between 750 and 1500 m in the Azorean Zone (Group II), and another assemblage was detected spanning 250–750 m in the Faraday Seamount Zone (Group VI).

As might be expected given the presence of a subpolar front in the CGFZ (Søiland et al., 2008), much more spatial variation was observed in the upper 750 m of the water column. Within this depth stratum the dominant feature was an assemblage of fishes (Group V) that stretched from the Reykjanes Ridge region to the southern end of the Faraday Seamount Zone, but not into the Azorean Zone. An unexpected finding was that for much of its extent this assemblage spanned the epi- (0–200 m) and upper mesopelagic (200–750 m) depth intervals. This finding will be treated in more detail in the following faunal account. Group V fish assemblage was replaced in the upper waters of the Azorean Zone by the more subtropical Group VIII assemblage. The remaining three assemblage groupings were distributed across the epipelagic zones of the four geographic regions, one being shared by the Reykjanes and Faraday Zones (Group X), one being shared by the Reykjanes and CGFZ (Group XII) and one found only in the Azorean Zone (Group IX).

3.3. Faunal account by depth stratum

In this section the major groups mentioned above will be treated in more quantitative and taxonomic detail, organized by depth stratum encompassing each group. In some cases the depth stratum will be an aggregate of multiple depth intervals as dictated by the depths of the samples making up each group. In this passage, the terms "group" and/or "cluster" refer to the sample set, while the term "assemblage" refers to the faunal elements of the sample sets. Any references to numbers, abundance or biomass are to values per unit volume filtered. Fish family names are given in parentheses on first usage.

3.3.1. 0–200 m

Of the 12 major groups of trawl samples, three (Groups IX, X and XII), were contained wholly within the top 200 m. Group IX, represented by one daytime sample from the Azorean Zone, was characterized by overall low
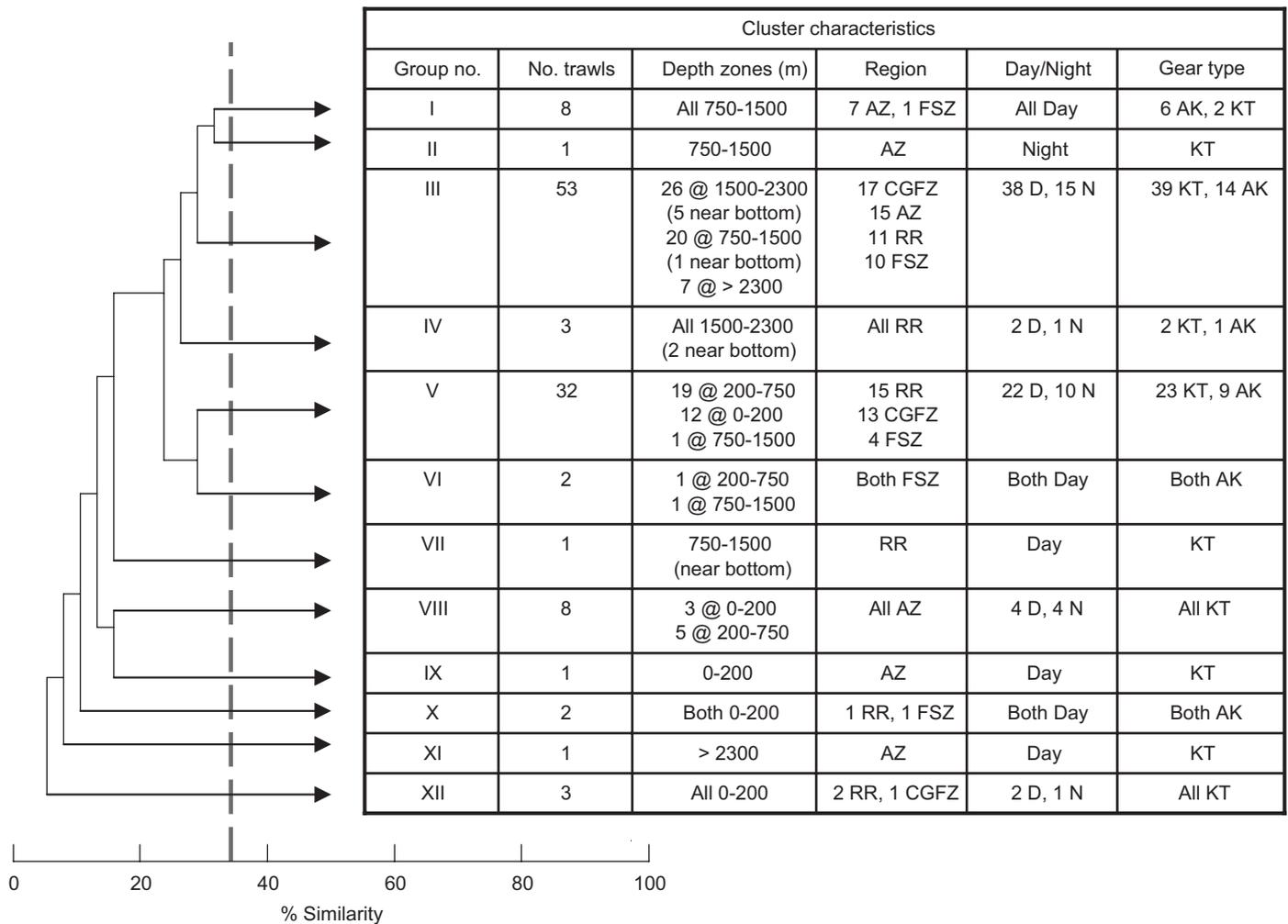
Cluster characteristics					
Group no.	No. trawls	Depth zones (m)	Region	Day/Night	Gear type
I	8	All 750-1500	7 AZ, 1 FSZ	All Day	6 AK, 2 KT
II	1	750-1500	AZ	Night	KT
III	53	26 @ 1500-2300 (5 near bottom) 20 @ 750-1500 (1 near bottom) 7 @ > 2300	17 CGFZ 15 AZ 11 RR 10 FSZ	38 D, 15 N	39 KT, 14 AK
IV	3	All 1500-2300 (2 near bottom)	All RR	2 D, 1 N	2 KT, 1 AK
V	32	19 @ 200-750 12 @ 0-200 1 @ 750-1500	15 RR 13 CGFZ 4 FSZ	22 D, 10 N	23 KT, 9 AK
VI	2	1 @ 200-750 1 @ 750-1500	Both FSZ	Both Day	Both AK
VII	1	750-1500 (near bottom)	RR	Day	KT
VIII	8	3 @ 0-200 5 @ 200-750	All AZ	4 D, 4 N	All KT
IX	1	0-200	AZ	Day	KT
X	2	Both 0-200	1 RR, 1 FSZ	Both Day	Both AK
XI	1	> 2300	AZ	Day	KT
XII	3	All 0-200	2 RR, 1 CGFZ	2 D, 1 N	All KT

Fig. 3. Classification results comparing deep-pelagic fish samples taken during the 2004 MAR-ECO expedition, with cluster separation at 33% similarity. Region codes (see Fig. 1): RR = Reykjanes Ridge; CGFZ = Charlie-Gibbs Fracture Zone; FSZ = Faraday Seamount Zone; AZ = Azorean Zone. Gear type codes (see Table 1): AK = Åkra trawl; KT = Krill trawl.

abundance (237 fish 10^{-6} m^{-3}), and biomass (1.5 kg wet weight [ww] 10^{-6} m^{-3}), with a large contribution (56% numbers, 95% biomass) of the barracudina *Lestidiops sphyrenoides* (Paralepididae). The lightfish *Vinciguerria poweriae* (Phosichthyidae) was a distant second in both categories. Group X, represented by two daytime Åkra trawl samples north of the Azorean Zone, was characterized by the dominance (up to 95% of sample) of the pearlside *Maurolicus muelleri* (Sternoptychidae) and little else. Group XII, represented by three samples from northern stations (2 RR, 1 CGFZ), was again characterized by low overall abundance (333 fish 10^{-6} m^{-3}) and biomass (0.87 kg ww 10^{-6} m^{-3}), with nearly total domination (92% numbers, 56% biomass) by the snake pipefish, *Entelurus aequoreus* (Syngnathidae). Identity of this typically inshore species was confirmed by Byrkjedal.

3.3.2. 0–750 m

This aggregate depth stratum contained samples taken from 0–200 and 200–750 m depth intervals, a counter-intuitive arrangement at first until the entire scope of the water column is considered. As we have seen already, certain fishes appeared to be strong indicators of a near-surface existence (e.g., *E. aequoreus* and *M. muelleri*), separating these samples by their dominance, and, as we will see below, certain fishes were strong indicators of a bathypelagic existence (e.g., Platytroctidae). The lower epipelagic (particularly at night) and mesopelagic zones, on the other hand, were characterized by a diverse assemblage of fishes whose vertical distributions change on a diel and/or seasonal basis. Relative to the epi- and bathypelagial, samples from these strata (0–200 and 200–750 m) tended to cluster together based on common species at different times of day.

Two large groups shared this vertical distribution pattern; one (Group V) containing samples from the Reykjanes Ridge to the lower Faraday Seamount Zone, including the CGFZ, and the other (Group VIII) containing samples from the Azorean Zone. In both clusters the split between upper (0–200 m) and lower (200–750 m) samples favored the lower by roughly a 3:2 margin.
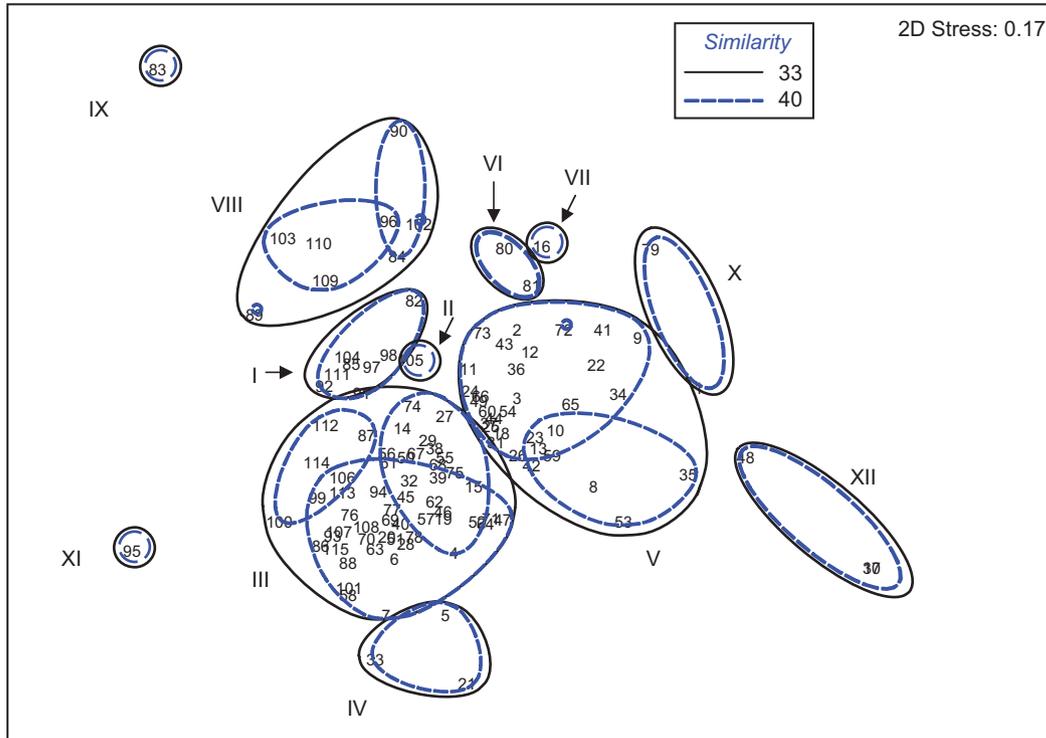
Fig. 4. Ordination (MDS) results comparing deep-pelagic fish trawl samples taken during the 2004 MAR-ECO expedition. Circled groups are based on classification results (see Fig. 3): solid lines equal discrimination at the 33% similarity level; dashed lines equal discrimination at the 40% similarity level. Sample codes are as listed in Table 1 for graphical clarity.
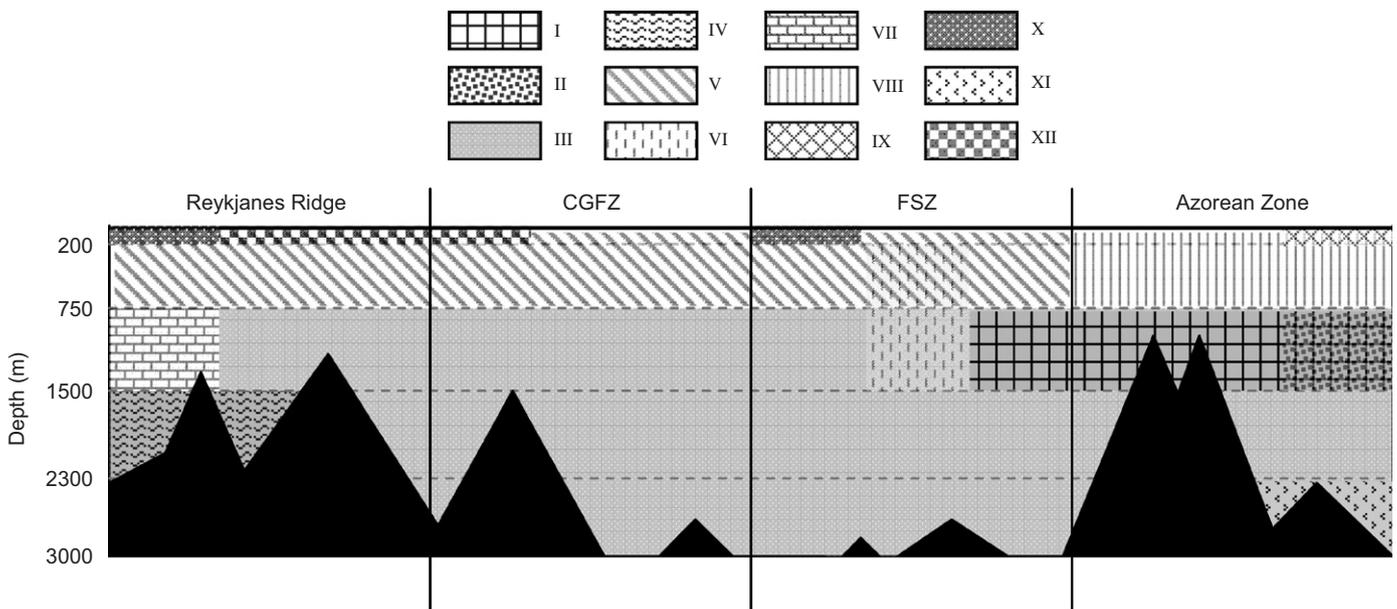

Fig. 5. Diagrammatic representation of the large-scale vertical distribution patterns of deep-pelagic fishes along the northern Mid-Atlantic Ridge, from Iceland (left) to the Azores (right). Patterns are based on multivariate analysis groupings (Groups I–XII; Figs. 3 and 4), scaled in size for location and depth. Bottom topography, smoothed from concurrent bottom profiling, indicated in solid black; peaks represent transverse ridge crossings. Depths below the maximum trawling depth (3000 m) were not plotted to avoid unfounded extrapolation. CGFZ = Charlie-Gibbs Fracture Zone; FSZ = Faraday Seamount Zone.

Group V was the second-largest cluster along the MAR in terms of samples (32) and the first- and second-largest assemblage in terms of abundance (2580 fish $10^{-6}\,m^{-3}$) and biomass (5.15 kg ww $10^{-6}\,m^{-3}$; Table 2), respectively. The

faunal assemblage was characterized by the high relative proportion of the lanternfish *B. glaciale* (Myctophidae), both in numbers and biomass (51% and 28.5% of total, respectively). Two other northern lanternfishes,

Table 2
Dominant faunal constituents of the 0–750 m pelagic fish assemblage from the Reykjanes Ridge to the Faraday Seamount Zone (Group V) over the northern Mid-Atlantic Ridge

A. Abundance: ind. 10^{-6} m^{-3} (% of total)		B. Biomass: g ww 10^{-6} m^{-3} (% of total)	
Benthosema glaciale	1318 (51.1)	Benthosema glaciale	1465 (28.5)
Cyclothone microdon	623 (24.1)	Chauliodus sloani	556 (10.8)
Protomyctophum arcticum	219 (8.5)	Serrivomer beanii	522 (10.1)
Entelurus aequoreus	100 (3.9)	Cyclothone microdon	389 (7.6)
Maurolicus muelleri	56 (2.2)	Bathylagus euryops	297 (5.8)
Myctophum punctatum	39 (1.5)	Lampanyctus macdonaldi	251 (4.9)
Chauliodus sloani	31 (1.2)	Stomias boa ferox	241 (4.7)
Other fishes	194 (7.5)	Myctophum punctatum	203 (3.9)
Total	2580 (100)	Scopelogadus beanii	182 (3.5)
		Borostomias antarcticus	178 (3.5)
		Other fishes	865 (16.8)
		Total	5149 (100)

A. Abundance of species contributing at least 1%; B. Biomass of species contributing at least 3%.

Table 3
Dominant faunal constituents of the 0–750 m pelagic fish assemblage from the Azorean Zone (Group VIII) over the northern Mid-Atlantic Ridge

A. Abundance: ind. 10^{-6} m^{-3} (% of total)		B. Biomass: g ww 10^{-6} m^{-3} (% of total)	
Lobianchia dofleini	252 (18.6)	Sigmops elongatus	343.0 (14.0)
Cyclothone microdon	193 (14.2)	Serrivomer lanceolatoides	253.8 (10.4)
Cyclothone braueri	110 (8.1)	Nemichthys scolopaceus	226.3 (9.3)
Vinciguerria poweriae	83 (6.1)	Lobianchia dofleini	179.2 (7.3)
Benthosema glaciale	76 (5.6)	Xenodermichthys copei	136.9 (5.6)
Notoscopelus bolini	56 (4.2)	Scopelogadus m. mizolepis	98.0 (4.0)
Argyropelecus hemigymnus	41 (3.1)	Benthosema glaciale	92.6 (3.8)
Diaphus rafinesquii	41 (3.1)	Chauliodus sloani	87.2 (3.6)
Hygophum hygomii	37 (2.7)	Cyclothone microdon	79.9 (3.3)
Lampanyctus pusillus	34 (2.5)	Argyropelecus aculeatus	71.0 (2.9)
Myctophum punctatum	32 (2.4)	Bathylagichthys greyae	69.1 (2.8)
Argyropelecus aculeatus	24 (1.8)	Lampanyctus crocodilus	60.9 (2.5)
Bolinichthys indicus	22 (1.6)	Diaphus rafinesquii	59.4 (2.4)
Cubiceps gracilis	22 (1.6)	Hygophum hygomii	51.3 (2.1)
Hygophum benoiti	22 (1.6)	Diretmus argenteus	50.9 (2.1)
Sternoptyx diaphana	22 (1.6)	Cubiceps gracilis	47.4 (1.9)
Gonichthys cocco	20 (1.4)	Tetragonurus cuvieri	42.8 (1.8)
Bathylagichthys greyae	15 (1.1)	Vinciguerria poweriae	39.8 (1.6)
Valenciennellus tripunctulatus	14 (1.1)	Notoscopelus bolini	35.2 (1.4)
Other fishes	235 (17.6)	Sternoptyx diaphana	31.8 (1.3)
Total	1351 (100)	Trachurus picturatus	27.7 (1.1)
		Cyclothone braueri	25.5 (1.0)
		Other fishes	335.8 (13.7)
		Total	2445.5 (100)

A. Abundance of species contributing at least 1%; B. Biomass of species contributing at least 1%.

Protomyctophum arcticum and Myctophum punctatum, ranked 3rd (8.5%) and 6th (1.5%) in abundance. The other species contributing at least 1% of the assemblage numbers were, in order of abundance, the bristlemouth C. microdon (Gonostomatidae; 2nd), E. aequoreus (4th), M. muelleri (5th), the latter two again taken near the surface but not as dominants, and the dragonfish Chauliodus sloani (Stomiidae; 7th). These seven species represented 92.5% of the entire assemblage numbers. In terms of biomass, three predatory dragonfishes were among the top 10: C. sloani (2nd), Stomias boa ferox (7th) and Borostomias antarcticus (10th). Other species contributing at least 3% of the assemblage biomass were: the sawtooth eel Serrivomer beanii (Serrivomeridae; 3rd), C. microdon (4th), the deep-sea smelt Bathylagus euryops (Microstomatidae [sensu Nelson, 2006]; 5th), the lanternfishes Lampanyctus macdonaldi (6th) and M. punctatum (8th), and the big-scale Scopelogadus beanii (Melamphaidae; 9th). These 10 species represented 83.2% of the total assemblage biomass.

The Azorean Zone 0–750 m group (Group VIII) could just as easily be called the "Lanternfish Group," as 29 myctophid species contributed half (50.8%) of the total assemblage numbers and one-quarter of the biomass (26.9%) (Table 3). Unlike Group V, however, the

numerically dominant species was the lanternfish *Lobianchia doefleini*, not *B. glaciale* (ranked 5th), followed closely by *C. microdon*. Diversity was higher overall in this assemblage, with 19 species contributing at least 1% of total abundance. This diversity was also manifest in the distribution of biomass, as no species contributed more than 15% of the total, and 22 species contributed at least 1%. Larger but rarer species contributed more heavily to the biomass totals of this assemblage, as evidenced by the high biomass percentages of fishes such as the bristlemouth *Sigmops elongatus* (*Gonostoma elongatum* of some authors), the eels *Serrivomer lanceolatoides* and *Nemichthys scolopaceus* (Nemichthyidae), the smooth-head *Xenodermichthys copei* (Alepocephalidae) and the southern bigscale *Scopelogadus mizolepis mizolepis*. As is the usual case in lower latitude waters of higher diversity (Hopkins and Gartner, 1992), the abundance and biomass of the 0–750 m assemblage of the Azorean Zone was less than that of the Reykjanes→Faraday Zone (Group V), in this case by half (Tables 2 and 3).

3.3.3. 200–1500 m

This aggregate depth stratum contained two samples taken from contiguous depth intervals (200–750 and 750–1500 m; Group VI in Fig. 3) in the Faraday Seamount Zone during daytime. The faunal assemblage of this cluster was dominated by *B. glaciale*, which alone contributed 72% of total numbers. The bristlemouth *Bonapartia pedaliota* was a distant second (7.5%), followed closely by *C. sloani* (5%). Of the five remaining species contributing at least 1%, four were lanternfishes (*Notoscopelus bolini*, *Lampanyctus crocodilus*, *P. antarcticum*, and *Symbolophorus veranyi*), while one was the great swallower *Chiasmodon niger* (Chiasmodontidae). The most distinctive feature of this assemblage was the absence of *C. microdon*, which appeared in all other samples from these depth intervals. As both samples were taken with the Åkra trawl, only relative abundance values are presented. High numbers of *C. microdon* in other Åkra samples tend to rule out gear selectivity here.

3.3.4. 750–1500 m

Three groups were characterized by distinct assemblage structure within this depth stratum. The largest, Group I, contained eight daytime samples, primarily (seven) from the Azorean Zone. The second, Group II, contained a single sample taken at night, also in the Azorean Zone. The third, Group VII, contained a single sample taken near the bottom at 1500 m over the Reykjanes Ridge. This group will be detailed separately in a treatment of near-bottom assemblages.

Group I assemblage was characterized by the moderate dominance of *C. microdon*, with this single species representing 63% of the assemblage numbers. The loosejaw dragonfish *Malacosteus niger* was a distant second (3.5%), while three big-scale species (*Scopeloberyx robustus*, *S. beanii* and *Poromitra megalops*) each contributed

between 2% and 4%. *Cyclothone pallida*, *B. glaciale* and *N. bolini* were the remaining species contributing at least 2%. Twenty-eight other species, 10 of which were deeper-living lanternfishes, each contributed 0.5–1.5% of numbers. Abundance for this assemblage was approximately half (717 fish $10^{-6}\,\mathrm{m}^{-3}$) that of the 0–750 m Azorean Zone assemblage directly above it (Group VIII; 1351 fish $10^{-6}\,\mathrm{m}^{-3}$). The biomass of Group I, however, (3.70 kg ww $10^{-6}\,\mathrm{m}^{-3}$), was greater than that of Group VIII (2.4 kg ww $10^{-6}\,\mathrm{m}^{-3}$; Table 3). This resulted from the greater contribution of larger species, such as *M. niger* (ranked 1st, 18.4%), the fangtooth *Anoplogaster cornuta*, *C. sloani*, the deep-sea smelt *Melanolagus bericoides*, *S. beanii* and *S. lanceolatoides*, all contributing at least 6%. *C. microdon*, in comparison, contributed only 5.7% despite its high numbers.

Group II assemblage was an "admixture" group, with numerical co-domination by both *C. microdon* (43.5%) and *B. glaciale* (30.6%). This point can be made graphically by noting the position of Group II in the ordination plot (Fig. 4), sandwiched firmly between Group V (dominated by *B. glaciale*) and Group I (dominated by *C. microdon*). *Chiasmodon niger* and the pelican eel *Eurypharynx pelecanoides* (Eurypharyngidae) were the only other species contributing at least 3% of numbers. The abundance of this assemblage was less than Group I at 570 fish $10^{-6}\,\mathrm{m}^{-3}$. As with Group I, the biomass contribution of *C. microdon* was low, ~5% of the total. The main biomass contributions were spread out over a diverse group of fishes: *E. pelecanoides* (22%), the tubeshoulder *Normichthys operosus* (Platytroctidae; 18%), the silver spinyfin *Diretmus argenteus* (Diretmidae; 16%), *B. glaciale* (12%) and *C. sloani* (12%). The biomass of this assemblage, 2.52 kg ww $10^{-6}\,\mathrm{m}^{-3}$, was similar to the 0–750 m Azorean Zone assemblage (Table 3).

3.3.5. 750 to >2300 m

That approximately half of all trawl samples (53 of 114) was found in one large group (Group III) in this aggregate depth stratum suggests that for much of its extent, the waters below 750 m over the northern MAR were populated by one large bathypelagic fish assemblage during the time of this survey. The even distribution of samples with respect to the four geographic regions (see Fig. 1) was striking, with a north→south ratio of 11:17:10:15. Likewise for depth, there were 20 samples between 750 and 1500 m, 26 between 1500 and 2300 m, and seven at depths >2300 m. In Fig. 2, the maximum fish biomass per volume across the entire ridge transect occurred in the 1500–2300 m depth interval. The majority of samples that contributed to this value was contained in this group.

Group III was dominated by *C. microdon*, which comprised 88% by number (Table 4). Of the 64 other species caught in quantitative (Krill trawl) samples from this group, only four contributed more than 1% of total abundance: *B. euryops* (2.3%), *S. beanii* (1.5%), *Sigmops bathyphilum* (1.4%) and *L. macdonaldi* (1.1%). Rare

Table 4
Dominant faunal constituents of the 750–>2300 m pelagic fish assemblage (Group III) over the northern Mid-Atlantic Ridge

A. Abundance: ind. 10^{-6} m^{-3} (% of total)		B. Biomass: g ww 10^{-6} m^{-3} (% of total)	
Cyclothone microdon	1292 (88.0)	*Cyclothone microdon*	1206.2 (20.6)
Bathylagus euryops	34 (2.3)	*Bathylagus euryops*	957.5 (16.4)
Scopelogadus beanii	22 (1.5)	*Serrivomer beanii*	886.5 (15.2)
Sigmops bathyphilum	21 (1.4)	*Scopelogadus beanii*	489.8 (8.4)
Lampanyctus macdonaldi	16 (1.1)	*Sigmops bathyphilum*	428.5 (7.3)
Scopeloberyx robustus	13 (0.9)	*Poromitra crassiceps*	356.5 (6.1)
Poromitra crassiceps	9 (0.6)	*Eurypharynx pelecanoides*	275.0 (4.7)
Serrivomer beanii	9 (0.6)	*Lampanyctus macdonaldi*	145.4 (2.5)
Benthosema glaciale	9 (0.6)	*Borostomias antarcticus*	145.3 (2.5)
Eurypharynx pelecanoides	4 (0.3)	*Maulisia microlepis*	139.8 (2.4)
Cyclothone pallida	4 (0.2)	*Herwigia kreffti*	114.4 (2.0)
Chauliodus sloani	3 (0.2)	*Malacosteus niger*	93.8 (1.6)
Malacosteus niger	2 (0.2)	*Chauliodus sloani*	93.0 (1.6)
Protomyctophum arcticum	2 (0.1)	*Anoplogaster cornuta*	72.5 (1.2)
Scopeloberyx opisthopterus	2 (0.1)	*Scopeloberyx robustus*	48.5 (0.8)
Melamphaes microps	2 (0.1)	*Saccopharynx ampullaceus*	42.7 (0.7)
Poromitra megalops	2 (0.1)	*Bathytroctes microlepis*	42.7 (0.7)
Stomias boa ferox	2 (0.1)	*Melanocetus johnsonii*	38.0 (0.6)
Borostomias antarcticus	1 (0.1)	*Stomias boa ferox*	37.0 (0.6)
Maulisia microlepis	1 (0.1)	*Kali macrurus*	28.0 (0.5)
Other fishes	16 (1.1)	Other fishes	202.2 (3.5)
Total	1466 (100)	Total	5843.3 (100)

A. Abundance of species contributing at least 0.1%; B. Biomass of species contributing at least 0.5%.

species were frequent in this assemblage; almost three quarters (47 spp.) contributed less than 0.1% of abundance. Group III abundance, at 1463 fish 10^{-6} m^{-3}, was similar to the overlying waters in the Azorean Zone (Table 3), but approximately half that of the overlying waters in the northern regions (Reykjanes→Faraday; Table 2). As each vertical net series started at the deepest depth interval and worked upwards (i.e., Group III samples were dragged through the meso- and epipelagic layers), the lack of the more abundant, shallow-living species provides some corroboration that the sampling system successfully kept the samples in discrete-depth fashion.

C. microdon was the largest contributor in terms of biomass (Table 4). *B. euryops* (16.4%) and *Serrivomer beanii* (15.2) were a close second and third, followed by *S. beanii*, *S. bathyphilum* and another species of big-scale, *Poromitra crassiceps*. The overall distribution of biomass among species was much more even than was abundance, with 14 species contributing at least 1%. At a higher taxonomic level, there were five tiers of biomass contributors, listed in descending order: (1) the dominant Gonostomatidae (28%); (2) three families, the Microstomatidae, Melamphaidae and Serrivomeridae, contributing 15–16.5% each; (3) the Stomiidae (6.3%); (4) three families, the Platytroctidae, Alepocephalidae and Myctophidae, contributing ~3% each and (5) all other families (<9%).

Several families were archetypal of the bathypelagic zone over the MAR. For example, eight species of big-scales (Melamphaidae) were taken, six of which appeared among

the top 20 of the most abundant species in this assemblage (Table 4). It is also at these depths that we begin to see species from otherwise demersal families (*sensu* Merrett and Haedrich, 1997) such as the slickheads (Alepocephalidae; 6 spp.), grenadiers (Macrouridae; 2 spp.) and cuskeels (Ophidiidae; 1 sp.). The Platytroctidae were also a conspicuous component of the bathypelagic layer, particularly the species *Maulisia microlepis*, which dominated the biomass of some individual trawl samples. The Krill trawl apparently undersampled the Platytroctidae. As an example, the Åkra trawl caught 35 times more *Normichthys operosus* than the Krill trawl per unit distance trawled. This suggests that the quantitative abundance and biomass presented here for this family should be considered to be minimum estimates and that their ecological importance with respect to the deep-pelagic fish assemblage over the MAR is likely underestimated. In order to investigate this further the relative percentages of platytroctid biomass in the Krill trawl samples (presented above; $n = 37$) were compared with those of the Åkra trawl ($n = 16$). The result was that while the relative percentages of the major families listed above stayed remarkably consistent between the two gears, the platytroctid contribution in the Åkra samples was higher (8.2% vs. 3.4%).

3.3.6. >2300 m

One "ultra-deep" Krill trawl sample from the Azorean Zone exhibited a discrete assemblage structure (Group XI), but the most outstanding feature of this sample was its paucity. Only four fishes were sampled, one *Bathytroctes microlepis* (Alepocephalidae), one *P. megalops*, one

S. bathyphilum and one *Lepidophanes guentheri* (probably a contaminant caught on the way up). All that will be said about this assemblage is that it fits with the abundance and biomass minima for this depth interval when not in proximity to the bottom (Fig. 2).

3.3.7. Near-bottom samples

Interactions between deep-pelagic fauna and near-ridge demersal fauna (Bergstad et al., 2008) are central to understanding mid-ocean ridge ecosystems. Two near-bottom pelagic assemblages were unique, Groups IV and VII, both occurring in the Reykjanes Ridge Zone. The deeper of the two, Group IV, consisted of one Åkra and two Krill trawl samples taken between 1500 and 2300 m depth. This assemblage had relatively low abundance (183 fish $10^{-6}\,\mathrm{m}^{-3}$), but high biomass (4.7 kg ww $10^{-6}\,\mathrm{m}^{-3}$) due to the larger fish species collected, and had an absence of *Cyclothone* species. By biomass the primary constituents included *E. pelecanoides* (42%), *B. euryops* (27%), *S. bathyphilum* (17%) and the big-scale species *Scopeloberyx robustus* (12%). The shallow assemblage, Group VII, was collected in a single sample taken close to the Reykjanes Ridge summit between 750 and 1500 m depth. This assemblage exaggerated the previous trend, with low abundances (429 fish $10^{-6}\,\mathrm{m}^{-3}$) and high biomass (18.6 kg ww $10^{-6}\,\mathrm{m}^{-3}$). This catch was at least triple the pelagic fish biomass per unit volume caught anywhere along the cruise track. The primary contributor to this biomass was the sawtooth eel *Serrivomer beanii*, a bathypelagic fish whose abundance and biomass peaked within the boundary layer relative to the same depths in open water. The remaining dominant species were also high-level predators, including *B. antarcticus*, *C. niger* and *C. sloani*.

Six BBL samples also clustered within Group III, the large pan-MAR bathypelagic fish assemblage. When all samples of Group III were split into BBL and off-bottom treatments, increases in density and biomass were observed within the BBL. Density within the BBL was nearly double that of the water column (2634 vs. 1352 fish $10^{-6}\,\mathrm{m}^{-3}$) and biomass was approximately 50% higher (8.7 vs. 5.6 kg ww $10^{-6}\,\mathrm{m}^{-3}$). The same species in this group (III) as in the previous two groups (IV and VII) also peaked in density and biomass within the BBL, but in a different order: *B. euryops*, *Serrivomer beanii* (these two contributing nearly half of the total biomass of the BBL samples), *E. pelecanoides* and *B. antarcticus*. These species, plus *S. bathyphilum*, *S. beanii*, and *S. robustus*, constitute a group of bathypelagic fishes that aggregate near topographic features of a mid-ocean ridge system.

Supporting evidence of a bathypelagic faunal aggregation over the MAR was observed in the acoustic data recorded continuously during Leg 1 of the *G.O. Sars* cruise (Fig. 6). When the cruise track crossed the Reykjanes Ridge (Fig. 6A) and the Azorean MAR (Fig. 6B) in transverse fashion, discernable biological 'features of interest' were observed 100 m off the bottom near valleys and peaks. While these locations were not trawled, we

suggest that backscatter from these regions may have originated from assemblages of bathypelagic fishes. These backscatter patterns were similar to other signals from the mesopelagic deep scattering layer (DSL) and the trawl-derived densities of fishes in the mesopelagic stratum were similar to those of the near-bottom layer. The DSL is not limited to fish taxa, so the observed near-bottom aggregations could be composed of demersal fishes or invertebrates. Some large demersal fish species were caught in the pelagic gear, the larger of which (Åkra) was twice the mouth size of the demersal trawl, suggesting that if dense concentrations of demersal fishes were aggregating in the water column, it is likely that they would have been sampled by the pelagic gear. The corollary, pelagic fishes being caught in bottom trawls, was the case; Bergstad et al. (2008) excluded as much as 60% of individual bottom trawl samples as pelagic fish 'contaminants' prior to their analyses. While these specimens could have been caught during retrieval and/or deployment of the bottom trawl, the high numbers taken relative to fishing effort compared to numbers from pelagic trawls suggest that these fishes were captured during bottom trawling. Higher densities of invertebrates near the bottom relative to open water are not mutually exclusive of elevated vertebrate densities, as dense aggregations of invertebrate prey may be attracting vertebrate predators. These acoustic data provide corollary evidence supporting the trawl-based discrimination of an assemblage of bathypelagic fishes that aggregates over a mid-ocean ridge system.

3.3.8. Faunal account by depth zone: summary

In order to reduce the complexity of these results with respect to biodiversity and faunal composition, a brief summary is presented here. Few assemblages were found wholly within the epipelagic zone, and of these only four species were abundant (a pipefish in the Reykjanes Ridge region and three shallow mesopelagic fishes near the Azores). Two large, vertically migrating mesopelagic assemblages were found: (1) a northern (60–45°N), low-diversity, high-abundance assemblage dominated by three lanternfishes (*B. glaciale*, *P. arcticum* and *M. punctatum*), a dragonfish (*C. sloani*), a pearlside (*M. muelleri*) and a bristlemouth (*C. microdon*) and (2) a southern (Azorean) assemblage of high diversity (29 lanternfishes alone; 19 "dominant" species) and low abundance (half that of northern assemblage). Two discrete deep-meso/upper-bathypelagic assemblages were found near the Azores, with *C. microdon*, the loosejaw dragonfish (*M. niger*), and three large melamphaid species (*S. beanii*, *S. robustus* and *P. megalops*) the dominant fishes. The bathypelagic zone was characterized by the presence of a single, large (half of all trawl samples) assemblage spanning the entire northern MAR. This assemblage was dominated numerically by *C. microdon*, while the main biomass contributors were *C. microdon*, the deep-sea smelt (*B. euryops*), the sawtooth eel (*S. beanii*), two melamphaids (*S. robustus* and *P. crassiceps*) and a tubeshoulder (*M. microlepis*). The
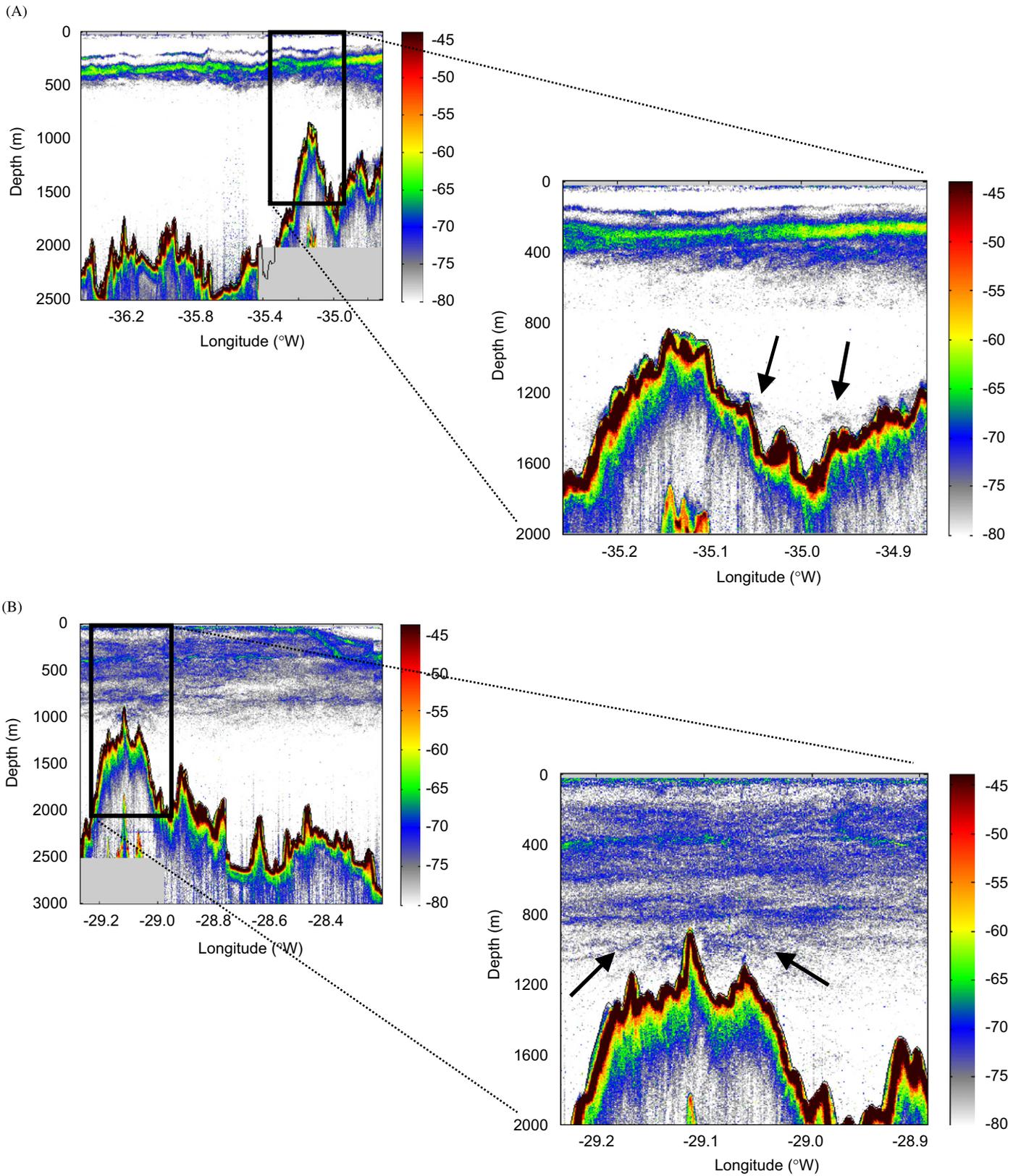
Fig. 6. 18 kHz mean volume backscatter (Sv) data (SIMRAD EK60 echosounder) showing pelagic–benthic biotic interactions along the Mid-Atlantic Ridge. (A) Reykjanes Ridge cross-ridge section (SS 9) and (B) Azorean Zone cross-ridge section (SS 26). Arrows indicate regions of enhanced, near-ridge backscatter.

BBL over the ridge itself (variable depths between 750 and 2300 m) exhibited low diversity (seven main species) but contained the highest numbers and biomass per volume for the entire water column over the MAR. Putative bathypelagic aggregators near the ridge itself include *B. euryops*, *S. beanii*, *Serrivomer beanii*, *E. pelecanoides*, *B. antarcticus*, *S. bathyphilum* and *S. robustus*.

4. Discussion

In this paper, we have described and quantified the assemblage structure and vertical distribution of the deep-pelagic fishes occurring over a mid-ocean ridge system, broken down into discrete assemblages. As a detailed biogeographic account will appear elsewhere, here we focus our discussion on the major depth-related patterns and how these relate to a mid-ocean ridge ecosystem as a whole.

4.1. Faunal structure with depth

The overall vertical distributions for most of the dominant fishes taken during this survey have been reported in the literature, and the records from this survey generally fit the reported patterns. In the 0–200 m stratum the dominant fishes were *M. muelleri*, a species often taken in large numbers in shallow waters (Bergstad, 1990; Quéro et al., 1990a), and the pipefish *E. aequoreus*, whose occasional presence in the oceanic Mid-Atlantic had previously been reported (Dawson, 1986), but whose oceanic vertical distribution is reported for the first time here.

The 0–750 m depth stratum is largely the realm of the vertically migrating Myctophidae, and samples over the MAR were generally dominated numerically either by *B. glaciale*, with a known distribution of 100–850 m in the North Atlantic (Halliday, 1970; Craddock et al., 2002; but occasionally >1000 m south of 40°N; Angel, 1993), or *L. doefleini*, recorded in the upper 600 m (Karnella, 1987). Other important myctophid species above 750 m along the MAR included *Protomyctophum arcticum* (80–850 m; Hulley, 1984) and *Myctophum punctatum* (0–750 m; Craddock et al., 2002). One unusual finding of this study was the occurrence of *C. microdon* in 9 of 20 0–200-m trawl samples, often in large numbers. This species has been reported as shallow as 300 m in the Southern Ocean (Lancraft et al., 1989), but is usually found well below 500 m (Backus et al., 1969; Badcock, 1984; Quéro et al., 1990b). We are not aware of any records of this species above 200 m (J. Craddock, A. Harold, pers. comm.). Either this represents a new vertical range extension for the species, or the multiple cod-end system used in this survey was prone to selective contamination by this species. As for the latter, contamination can be a problem with multiple cod-end samplers (Pearcy, 1983). Fish specimens can become entangled in the fore-net in one depth level and then wash down to the cod-end while fishing at another level. The presence of other surface species (e.g., *E. aequoreus*) suggested that these particular

net tows fished properly within the 0–200 m stratum. The possibility that *C. microdon* was retained by the deeper nets and released in the shallow net also seems unlikely, as the catch numbers for the 0–200 m nets were often quite higher than the net below (200–750 m). Some degree of contamination was seen with other deep-living species (e.g., *M. niger*, *S. bathyphilum*), but these were usually one- or two-fish occurrences. Additionally, all recorded data pertaining to the shallow net samples in which *C. microdon* was caught were examined, and this revealed no data entry or other human errors. Thus, the occurrence of this fish in the upper 200 m does not appear to be artifactual, and represents another indication that the abundance and distribution of deep-pelagic fishes over the MAR differs from the 'typical' open ocean patterns.

Many of the dominant deep-mesopelagic fishes of the North Atlantic exhibited distributions well into the bathypelagic zone (>1500 m) over the MAR. The depth ranges for *L. macdonaldi*, previously known to 1000 m (Hulley, 1984), and *C. sloani*, known from 50 to 1800 m (Gibbs, 1984; Sutton and Hopkins, 1996) are extended downwards, as they were routinely taken between 1500 and 2300 m over the MAR. With the exception of *M. niger*, a non-migrator with maximum abundances between 700 and 900 m (Sutton, 2003), the remaining dominant lower meso- and bathypelagic species occupy a wide range of depths. In the North Atlantic, *C. microdon* has been found primarily between 800 and 2700 m (Badcock, 1984), *S. bathyphilum* between 700 and 3000 m (Badcock, 1984), *E. pelecanoides* between 500 and 7500 m (Nielsen and Bertelsen, 1990), *S. beanii* between 800 and 2500 m (Mauchline and Gordon, 1984; Maul, 1990), and *B. euryops* between 500 and 3000 m (Mauchline and Gordon, 1983; Cohen, 1984). Larger individuals of the latter two species have been reported as catches in demersal trawls in the Rockall Trough (Mauchline and Gordon, 1983, 1984), suggesting a benthopelagic affinity that results of this study confirm for the latter four species.

In the only semi-quantitative study of deep-pelagic fishes over the MAR prior to this one, Fock et al. (2004) examined a series of 250–3200 m samples taken during a 1982 cruise in a frontal gradient area just south of the CGFZ (45–50°N). While the focus of this study was primarily biogeographic and the trawling gear and sampling strategy differed (they used a larger mesh and no opening/closing device), some parallels to this study can be drawn. Using similar statistical methods, Fock et al. (2004) discriminated six clusters of species groups. Even without *Cyclothone*, which was excluded from their analysis, the Gonostomatidae (primarily *S. bathyphilum*) dominated net catches at bathypelagic depths. The authors also found increased relative abundances of the Stomiidae, Melamphaidae, Serrivomeridae and Eurypharyngidae over the ridge, the same near-ridge dominants reported in this study. Direct comparisons with their values are not possible given their catch standardization (no. fish h⁻¹ towing). In a complementary analysis of the vertical

distribution of the gulper eel *Saccopharynx ampullaceus* (Saccopharyngidae), Fock et al. (2004) found that the minimum depth of occurrence of this species rose from 2550 m over the Porcupine Abyssal Plain to 1000 m over the MAR, a finding similar to our observation of reduced minimum depth of occurrence of *C. microdon*. They concluded that special features of the MAR environment likely cause changes in the ecological structure of the fish assemblage. Our study differed from that of Fock et al. (2004) in that they found that surface features (i.e., chlorophyll, temperature, salinity) affected the composition of the lower meso- and bathypelagic fish assemblages, whereas we found assemblages below 750 m to be remarkably consistent from north to south, with some differentiation near particularly shallow ridge regions (Reykjanes Ridge and near the Azores). Perhaps the primary difference was the impact of *C. microdon* in our study, which had the overall effect of uniting the deepest pelagic strata by its abundance, even after severe data transformation. Differences notwithstanding, the parallels between their more localized study with different methods and the one presented here are notable.

4.2. Biomass as a function of depth

Oceanic ecosystems ultimately rely on near-surface primary production for fuel, with the possible exception of highly localized chemosynthetic communities. The primary consequence for the deep-pelagic fauna is a decrease in food supply with depth as a function of an increasing separation from the euphotic zone. Over the MAR this effect is evident in the decline in fish abundance below 200 m, except for the near-bottom (BBL) assemblage. In open ocean ecosystems deep-pelagic zooplankton and micronekton biomass has been shown to decrease exponentially with depth (Angel and Baker, 1982; Angel and Boxshall, 1990), up to within ~100 m of the bottom. In this near-bottom layer an elevated biomass of zooplankton (Wishner, 1980a–c; Angel and Baker, 1982; Wishner and Gowing, 1987; Childress et al., 1989) and nekton (Angel and Baker, 1982; Hargreaves, 1984, 1985; Domanski, 1986) has been reported. Our data show a somewhat different vertical distribution of deep-pelagic fish biomass, with a midwater maximum between 1500 and 2300 m, a sharp decline below 2300 m, and then a dramatic increase in the BBL. In a recent study utilizing manned submersible ("Mir-1") observations in the near-bottom layer over the CGFZ, Vinogradov (2005) reported elevated abundances of macroplankton, particularly larvaceans, within 150 m of the seafloor. It is difficult to compare results of different studies using different gears, but if we accept the sizable body of literature that demonstrates the exponential decline in biomass with depth, and if we accept the accuracy of the data presented here, then it is reasonable to support the supposition that the deep-pelagic ecosystem over the northern MAR differs in structure from that of 'typical' open ocean regimes, at least with respect to fishes, but probably also other taxa. Furthermore, the multivariate statistical

results presented here suggest that this pattern is consistent along much of the ridge rather than being an isolated phenomenon.

4.2.1. Increased bathypelagic biomass over the MAR

Mid-ocean ridges differ markedly from continental slopes in: (1) the lack of terrigenous organic input and (2) the depths at which deep-pelagic nekton impinge upon the topography. The lack of terrigenous sedimentation suggests that water column-derived energy sources primarily drive the ridge ecosystems. One such energy source is the pelagic biota (Vinogradov, 1968; Angel, 1985; Longhurst and Harrison, 1989). Most of what we know about deep-pelagic/deep-demersal trophic interactions is based on studies of the continental slopes, and to a lesser extent the abyssal plains. Such studies have revealed important connections between the demersal fauna and their pelagic prey (Marshall and Merrett, 1977; Merrett, 1986; Roe et al., 1990; Bergstad, 1991; Gordon, 2001). In a study on the slopes of the Rockall Trough, Mauchline and Gordon (1991) found that the depth and biomass distributions of benthopelagic fishes corresponded to the daytime depths of their vertically migrating mesopelagic prey. Haedrich and Merrett (1992) gave further evidence of the dependence of deep-demersal slope fishes on mesopelagic prey; 35% of the demersal species in the Porcupine Seabight fed on pelagic prey, 52% on mixed pelagic/benthic prey, while only 13% were reliant on benthic food. These studies show the importance of deep-pelagic prey to deep-demersal communities. A second major difference between mid-ocean ridge systems and continental slopes is depth—for most of its extent only a small area of the mid-ocean ridges is shallower than 1000 m. Even when the summit of the MAR penetrates the 1000 m isobath, the bulk of the vertically migrating mesopelagic fauna is well above this depth (Fig. 6). Therefore, the primary pelagic prey resource of the near-ridge demersal fauna appears to be the bathypelagic component of the deep-pelagic fauna. The findings presented here of increased bathypelagic fish biomass relative to the 'typical' biomass/depth profiles reported over abyssal ecosystems take on added significance. Bergstad et al. (2008) found that abundance and biomass of demersal fishes over the MAR were highest at stations at or near the summit of the ridge. These depths correspond to the depth stratum of maximal deep-pelagic fish biomass (1500–2300 m) reported here. The dominant components of this biomass maximum, the Melamphaidae, Microstomatidae, Platytroctidae, Stomiidae, and Serrivomeridae, are known prey of the dominant biomass components of the demersal nekton (Pereyra et al., 1969; Haedrich and Henderson, 1974; Pearcy and Ambler, 1974; Sedberry and Musick, 1978; Clarke, 1985; Blaber and Bulman, 1987; Gartner et al., 1997). Thus, lacking the terrigenous input of allochthonous organic carbon, increased demersal fish diversity and biomass over the MAR relative to the abyssal plains may be maintained by increased bathypelagic food resources.

4.3. Bathypelagic aggregation over a mid-ocean ridge system

The higher biomass per fish ratio of the deep-pelagic fishes taken in the BBL over the MAR (Fig. 2) suggests that the BBL assemblages contained larger individuals relative to the water column assemblages. In addition to a higher biomass contribution *per se*, this finding could be ecologically meaningful as well. In a study of specimens of the family Stomiidae deposited in worldwide ichthyological collections, Porteiro (2005) found that a significant proportion were caught by bottom trawls surveying slope habitats, and that these specimens were larger than those caught by pelagic gear (average standard length 159.9 vs. 79.2 mm). The Stomiidae, as well as the Gonostomatidae, Myctophidae, Paralepididae and Melamphaidae have been found to adopt an adult benthopelagic life strategy (Novikov et al., 1981; Vinnichenko, 1997). This topographic aggregation strategy may be important for the individual species in question because it could serve two functions. First, it could increase the trophic efficiency of larger specimens. Even though the mean water mass currents around the MAR are relatively weak, tidal currents are quite strong, in many cases 20–30 cm s^{-1} and in some cases up to 50 cm s^{-1}, and these currents are important for mixing (Søiland et al., 2008). Higher-level predators situated near the ridge could sit and wait for food to be advected in horizontally by tidal currents, or intercept prey swimming downward from above, and thus be 'topographically trapped,' i.e., reduced in space from three dimensions to two by an impenetrable surface (Isaacs and Schwartzlose, 1965). Planktivores would benefit from the higher concentrations of zooplankton in the BBL (Wishner, 1980a–c; Angel and Baker, 1982; Lorz et al., 1983; Vinogradov, 2005), and need not exert as much energy searching for food. However, as discussed above, this trophic benefit might have a mortality cost via predation from the demersal fauna. What might swing the balance ecologically could be the second, longer-term function of topographic association, the concentration of the largest, 'fittest' males with the largest (and most fecund), 'fittest' females for reproduction, thus increasing the relative percentage of offspring from the 'best' of the gene pool. Given the immense areal extent of the global mid-ocean ridge system, any increase in spawning activity at these sites by the bathypelagic fauna may have a non-trivial effect on the ocean-wide genetic structure and evolution of bathypelagic populations.

5. Summary

1. The deep-pelagic fish assemblage was taxonomically diverse, with 205 species from 52 families taken during Leg 1 of the 2004 RV *G.O. Sars* MAR-ECO expedition. Of these, 197 species were collected in discrete-depth trawls and formed the basis for further distributional analysis.
2. From Iceland to the Azores, the primary factor determining the pelagic fish assemblage composition was depth, with geographic region secondary. Little or no effect of gear type, time of capture, and position relative to the ridge axis was detected. Pairwise comparison of pelagic fish samples showed the greatest differences between the Azores and the Reykjanes Ridge/Charlie-Gibbs Fracture Zone regions. Samples from the Faraday Seamount region differed slightly from those taken in the regions just north and south. Reykjanes Ridge and Charlie-Gibbs Fracture Zones samples did not differ statistically ($p < 5\%$).
3. Abundance per volume of deep-pelagic fishes over the MAR was highest in the surface zone (0–200 m) and in the benthic boundary layer (BBL) extending ~200 m off the bottom. Minimal abundance occurred between 2300 and 200 m above the seafloor.
4. Biomass per unit volume of deep-pelagic fishes over the MAR reached a maximum within the BBL, revealing a previously unknown topographic association of a bathypelagic fish assemblage with a mid-ocean ridge system.
5. Biomass per unit volume of waters above the BBL reached a midwater maximum in the bathypelagic zone between 1500 and 2300 m, in contrast to previously studied abyssal regimes whose biomass decreases exponentially from the surface downwards. As much of the summit of the MAR extends into this depth layer, a likely explanation for this midwater maximum is ridge association.
6. Multivariate statistical analyses suggest that the dominant biomass component of the deep-pelagic fishes over the northern MAR was a wide-ranging bathypelagic assemblage (Group III; Figs. 3 and 5) that occurred along the length of the MAR from Iceland to the Azores. Eleven other smaller assemblages were discriminated according to depth, with most of these occurring above or below the bathypelagic assemblage.
7. Integrating these results with those of previous studies in oceanic ecosystems, there appears to be adequate evidence to conclude that special hydrodynamic and biotic features of mid-ocean ridge systems cause changes in the ecological structure of deep-pelagic fish assemblages relative to abyssal ecosystems.
8. Lacking terrigenous input of allochthonous organic carbon, increased demersal fish diversity and biomass over the MAR relative to the abyssal plains may be maintained by increased bathypelagic food resources.
9. The aggregation of bathypelagic fishes with MAR topographic features is primarily a large fish phenomenon (high biomass per fish ratio in the BBL). Considering the immense areal extent of the mid-ocean ridge systems globally, this type of aggregation may have significant trophic transfer and reproductive benefits for the individual populations.

Appendix A

Deep-pelagic fishes collected during Leg 1 of the 2004 *G.O. Sars* MAR-ECO expedition over the northern Mid-Atlantic Ridge (Table A.1).

Table A.1
Orders and families listed in phylogenetic order, following Nelson (2006); species listed by numerical abundance within each family

Order	Family	Species	N	WW	Range
Anguilliformes	Derichthyidae	*Derichthys serpentinus*	16	465.9	RR–AZ
		Nessorhamphus ingolfianus	5	345.2	RR–AZ
	Nemichthyidae	*Nemichthys scolopaceus*	9	449.2	RR–AZ
		Avocettina infans	1	32.8	FSZ
	Serrivomeridae	*Serrivomer beanii*	1062	78,217.7	RR–AZ
		Serrivomer lanceolatoides	8	526.4	AZ
Saccopharyngiformes	Eurypharyngidae	*Eurypharynx pelecanoides*	95	7395.6	RR–AZ
	Saccopharyngidae	*Saccopharynx ampullaceus*	4	756.6	CGFZ–FSZ
Argentiniformes	Opisthoproctidae	*Opisthoproctus soleatus*	3	19.7	FSZ–AZ
		Bathylychnops exilis	2	88.6	CGFZ–AZ
		Opisthoproctus grimaldii	2	1.8	AZ
		Dolichopteryx longipes	1	7.0	RR
	Microstomatidae	*Bathylagus euryops*	4543	190,026.9	RR–AZ
		Bathylagichthys greyae	100	699.7	AZ
		Melanolagus bericoides	15	307.9	CGFZ–AZ
		Nansenia sp.	14	886.1	RR–AZ
		Dolicholagus longirostris	4	40.0	AZ
		Nansenia tenera	3	48.6	FSZ–AZ
		Nansenia atlantica	2	61.3	AZ
		Microstoma microstoma	1	30.6	AZ
	Platytroctidae	*Maulisia microlepis*	931	96,481.4	RR–AZ
		Holtbyrnia anomala	283	11,545.0	RR–AZ
		Normichthys operosus	261	5088.8	RR–AZ
		Holtbyrnia macrops	32	970.0	RR–AZ
		Searsia koefoedi	10	409.5	RR–AZ
		Sagamichthys schnakenbecki	4	51.0	RR–FSZ
		Maulisia argipalla	2	120.9	FSZ–AZ
		Maulisia mauli	2	132.0	RR–AZ
	Bathylaconidae	*Herwigia kreffti*	5	1167.0	AZ
		Bathylaco nigricans	2	374.7	AZ
	Alepocephalidae	*Xenodermichthys copei*	43	1001.2	RR–AZ
		Bajacalifornia megalops	35	2461.3	RR–AZ
		Bathytroctes microlepis	8	1060.0	CGFZ–AZ
		Mirognathus normani	3	54.8	CGFZ
		Bathyprion danae	2	119.0	FSZ–AZ
		Einara macrolepis	2	162.0	AZ
		Photostylus pycnopterus	2	18.0	RR
		Bathytroctes macrolepis	1	33.0	FSZ
		Rouleina attrita	1	73.3	RR

Table A.1 (*continued*)

Order	Family	Species	*N*	WW	Range
Stomiiformes	Gonostomatidae	*Cyclothone microdon*	7430	6556.5	RR–AZ
		Sigmops bathyphilum	564	10,939.0	RR–AZ
		Sigmops elongatus	112	1973.0	RR–AZ
		Cyclothone braueri	82	33.9	RR–AZ
		Bonapartia pedaliota	71	151.0	CGFZ–AZ
		Cyclothone pallida	53	39.1	RR–AZ
		Margrethia obtusirostra	33	84.2	AZ
		Gonostoma denudatum	18	207.3	AZ
		Cyclothone pseudopallida	10	3.1	RR–AZ
	Sternoptychidae	*Maurolicus muelleri*	3379	4469.5	RR–AZ
		Argyropelecus hemigymnus	329	246.2	RR–AZ
		Sternoptyx diaphana	261	473.2	CGFZ–AZ
		Argyropelecus aculeatus	116	393.8	RR–AZ
		Argyropelecus olfersii	25	144.4	RR–FSZ
		Sternoptyx pseudobscura	14	35.7	RR–AZ
		Valenciennellus tripunctulatus	6	0.9	AZ
		Argyropelecus gigas	1	2.3	AZ
	Phosichthyidae	*Vinciguerria poweriae*	281	190.0	FSZ–AZ
		Ichthyococcus ovatus	13	15.1	FSZ–AZ
		Vinciguerria attenuata	5	3.4	AZ
		Pollichthys mauli	2	0.6	FSZ–AZ
	Stomiidae	*Chauliodus sloani*	897	21,700.9	RR–AZ
		Stomias boa ferox	256	5962.5	RR–AZ
		Malacosteus niger	235	9453.0	RR–AZ
		Borostomias antarcticus	139	11,495.9	RR–AZ
		Melanostomias bartonbeani	11	381.2	FSZ–AZ
		Photostomias guernei	8	39.5	AZ
		Pachystomias microdon	5	188.9	FSZ–AZ
		Astronesthes niger	4	30.4	AZ
		Flagellostomias boureei	4	133.9	CGFZ–AZ
		Neonesthes capensis	4	64.6	RR–AZ
		Leptostomias sp.	2	64.1	FSZ–AZ
		Aristostomias tittmanni	1	9.0	AZ
		Astronesthes gemmifer	1	12.2	AZ
		Bathophilus longipinnis	1	3.0	AZ
		Bathophilus vaillanti	1	3.2	AZ
		Melanostomias macrophotus	1	12.0	AZ
		Photonectes margarita	1	40.0	AZ
		Trigonolampa miriceps	1	393.0	RR
Aulopiformes	Notosudidae	*Scopelosaurus lepidus*	6	355.9	RR–FSZ
		Ahliesaurus berryi	2	30.1	AZ
		Scopelosaurus schmidtii	1	2.5	AZ
	Scopelarchidae	*Benthalbella infans*	4	48.0	FSZ–AZ
		Scopelarchus analis	2	8.6	AZ
		Scopelarchus guentheri	1	4.0	AZ
	Evermannellidae	*Evermannella balbo*	11	91.0	RR–FSZ
	Alepisauridae	*Alepisaurus brevirostris*	8	137.2	FSZ–AZ
		Omosudis lowei	1	15.0	AZ
	Paralepididae	*Lestidiops sphyrenoides*	81	201.8	FSZ–AZ
		Arctozenus risso	65	1047.9	RR–FSZ
		Anotopterus pharao	27	5886.1	RR–AZ
		Lestidiops jayakari	14	142.7	FSZ–AZ
		Magnisudis atlantica	8	59.5	FSZ–AZ
		Paralepis brevirostris	5	43.7	AZ
		Paralepis coregonoides	2	19.7	RR–AZ
Myctophiformes	Myctophidae	*Benthosema glaciale*	16640	24,502.6	RR–AZ
		Lampanyctus macdonaldi	4095	101,685.1	RR–AZ
		Notoscopelus kroyeri	3630	28,918.7	RR–AZ
		Myctophum punctatum	2418	11,217.2	RR–AZ

Table A.1 (*continued*)

Order	Family	Species	N	WW	Range
		Protomyctophum arcticum	1289	1245.7	RR–FSZ
		Lobianchia dofleini	406	355.3	FSZ–AZ
		Diaphus rafinesquii	315	710.9	FSZ–AZ
		Hygophum hygomii	309	628.7	AZ
		Diaphus holti	281	472.4	AZ
		Electrona risso	237	788.9	RR–AZ
		Lobianchia gemellarii	216	1707.5	FSZ–AZ
		Hygophum benoiti	214	309.5	AZ
		Symbolophorus veranyi	191	671.9	FSZ–AZ
		Notoscopelus bolini	145	736.2	FSZ–AZ
		Nannobrachium atrum	139	966.9	RR–AZ
		Lampanyctus crocodilus	124	926.2	RR–AZ
		Ceratoscopelus maderensis	102	270.3	FSZ–AZ
		Lampadena speculigera	94	2386.7	RR–AZ
		Bolinichthys indicus	52	66.3	AZ
		Bolinichthys supralateralis	34	171.4	RR–AZ
		Lampanyctus intricarius	34	360.4	RR–AZ
		Lampanyctus pusillus	32	49.6	AZ
		Lampadena anomala	30	844.1	AZ
		Diaphus metopoclampus	28	111.3	AZ
		Diaphus effulgens	18	200.8	FSZ–AZ
		Lampanyctus photonotus	15	67.4	AZ
		Lampadena urophaos atlantica	14	226.1	FSZ–AZ
		Gonichthys cocco	13	12.1	AZ
		Lampanyctus festivus	10	42.4	AZ
		Hygophum reinhardtii	9	6.7	AZ
		Lampadena chavesi	7	28.4	AZ
		Diaphus mollis	5	6.4	AZ
		Lepidophanes guentheri	4	6.0	AZ
		Nannobrachium lineatum	3	25.3	AZ
		Taaningichthys bathyphilus	3	7.3	CGFZ–AZ
		Notolychnus valdiviae	2	0.2	FSZ–AZ
		Benthosema suborbitale	1	1.8	AZ
		Ceratoscopelus warmingii	1	1.0	AZ
		Diaphus bertelseni	1	13.6	AZ
		Diogenichthys atlanticus	1	1.6	AZ
		Lepidophanes gaussi	1	3.5	AZ
		Loweina interrupta	1	7.2	AZ
		Nannobrachium achirus	1	8.4	RR
		Nannobrachium cuprarium	1	0.9	AZ
Gadiformes	Macrouridae	*Coryphaenoides rupestris*	12	92.0	RR–CGFZ
		Bathygadus melanobranchus	3	5.7	AZ
		Odontomacrurus murrayi	1	4.2	AZ
	Moridae	*Halargyreus johnsonii*	1	35.2	CGFZ
	Melanonidae	*Melanonus zugmayeri*	12	56.0	FSZ–AZ
	Merluccidae	*Lyconus brachycolus*	1	61.6	AZ
Ophidiiformes	Ophidiidae	*Brotulotaenia crassa*	2	914.0	AZ
Lophiiformes	Melanocetidae	*Melanocetus johnsonii*	3	333.3	CGFZ–FSZ
	Oneirodidae	*Lophodolos acanthognathus*	10	104.8	RR–AZ
		Leptacanthichthys gracilispinis	4	24.3	FSZ
		Chaenophryne draco	1	225.0	RR
		Danaphryne nigrifilis	1	54.0	RR
		Dolopichthys longicornis	1	4.0	AZ
		Microlophichthys microlophus	1	70.0	CGFZ
		Oneirodes eschrichtii	1	156.0	CGFZ
		Oneirodes macrosteus	1	24.3	AZ
		Phyllorhinichthys micractis	1	33.1	AZ
	Ceratiidae	*Ceratias holboelli*	2	97.5	CGFZ–AZ
		Cryptopsaras couesii	1	99.3	FSZ

Table A.1 (continued)

Order	Family	Species	N	WW	Range
	Gigantactinidae	*Gigantactis vanhoeffeni*	1	166.4	FSZ
	Linophrynidae	*Linophryne macrodon?*	1	1.0	AZ
Stephanoberyciformes	Melamphaidae	*Scopelogadus beanii*	2152	47263.6	RR–AZ
		Melamphaes microps	255	5667.5	RR–AZ
		Scopeloberyx robustus	239	1159.1	RR–AZ
		Poromitra crassiceps	215	9455.6	RR–AZ
		Scopelogadus m. mizolepis	96	336.2	CGFZ–AZ
		Poromitra megalops	82	324.5	RR–AZ
		Poromitra capito	58	670.4	AZ
		Scopeloberyx opisthopterus	11	6.5	CGFZ–AZ
		Melamphaes suborbitalis	7	101.7	RR–AZ
		Melamphaes typhlops	1	1.0	AZ
	Rondeletiidae	*Rondeletia loricata*	5	84.2	CGFZ–AZ
	Cetomimidae	*Gyrinomimus meyersi*	3	259.6	CGFZ
		Cetomimus sp.	2	100.7	RR–CGFZ
		Cetostoma regani	1	15.0	AZ
		Procetichthys kreffti	1	72.9	FSZ
	Megalomycteridae	*Ataxolepis apus*	1	0.4	AZ
Beryciformes	Anoplogastridae	*Anoplogaster cornuta*	26	2767.0	RR–AZ
	Diretmidae	*Diretmus argenteus*	9	190.8	FSZ–AZ
Gasterosteiformes	Syngnathidae	*Entelurus aequoreus*	160	775.2	RR–FSZ
Scorpaeniformes	Scorpaenidae	*Sebastes mentella*	4	8013.5	RR
		Sebastes sp.	4	3264.0	RR
	Liparidae	*Psednos* sp.	1	1.0	CGFZ
Perciformes	Percichthyidae	*Howella brodiei*	18	138.8	FSZ–AZ
	Epigonidae	*Epigonus constanciae*	1	1.1	AZ
		Microichthys coccoi	1	0.3	AZ
	Carangidae	*Trachurus picturatus*	1	16.4	AZ
	Caristiidae	*Caristius maderensis*	1	34.0	FSZ
		Platyberyx opalescens	1	319.2	CGFZ
	Zoarcidae	*Melanostigma atlanticum*	5	18.0	RR–CGFZ
	Anarhichadidae	*Anarhichas minor*	1	1056	CGFZ
	Chiasmodontidae	*Chiasmodon niger*	91	1837.6	RR–AZ
		Pseudoscopelus altipinnis	9	265.5	AZ
		Kali macrodon	5	413.4	CGFZ–AZ
		Dysalotus alcocki	4	129.8	RR–AZ
		Kali indica	4	270.4	CGFZ–FSZ
		Kali macrurus	2	213.8	FSZ–AZ
		Pseudoscopelus obtusifrons	1	68.0	AZ
		Pseudoscopelus scutatus	2	35.0	AZ
		Pseudoscopelus sp. 1[a]	1	68.0	AZ
	Gempylidae	*Diplospinus multistriatus*	1	3.8	AZ
	Trichiuridae	*Benthodesmus elongatus*	1	13.0	FSZ
		Lepidopus caudatus	1	3.8	AZ
	Centrolophidae	*Schedophilus medusophagus*	1	638.5	FSZ
	Nomeidae	*Cubiceps gracilis*	99	1616.0	FSZ–AZ
	Tetragonuridae	*Tetragonurus cuvieri*	9	155.3	AZ
	Caproidae	*Capros aper*	1	2.0	AZ

N = total number of specimens collected, uncorrected for volume sampled/gear type. WW = total wet weight (g), determined at-sea with motion-compensating scale. Range designations follow Fig. 1: RR = Reykjanes Ridge; CGFZ = Charlie–Gibbs Fracture Zone; FSZ = Faraday Seamount Zone; AZ = Azores Zone.
[a]Specimen will serve as paratype for new species description underway (M. Melo, pers. comm.)

References

Angel, M.V., 1985. Vertical migrations in the oceanic realm: possible causes and probable effects. Contributions in Marine Science 27 (Suppl.).

Angel, M.V., 1993. Biodiversity of the pelagic ocean. Conservation Biology 7 (4), 760–772.

Angel, M.V., 1997. Pelagic biodiversity. In: Ormond, R.F.G., Gage, J.D., Angel, M.V. (Eds.), Marine Biodiversity: Patterns and Processes. Cambridge University Press, Cambridge, 449pp.

Angel, M.V., Baker, A., 1982. Vertical distribution of the standing crop of plankton and micronekton at three stations in the Northeast Atlantic. Biological Oceanography 2, 1–30.

Angel, M.V., Boxshall, G.A., 1990. Life in the benthic boundary layer: connections to the mid-water and seafloor. Philosophical Transactions of the Royal Society of London A 331, 15–28.

Backus, R.H., Craddock, J.E., Haedrich, R.L., Shores, D.L., 1969. Mesopelagic fishes and thermal fronts in the western Sargasso Sea. Marine Biology 3, 87–106.

Badcock, J., 1984. Gonostomatidae. In: Whitehead, P.J.P., Bauchot, M.-L., Hureau, J.-C., Nielsen, J., Tortonese, E. (Eds.), Fishes of the North-eastern Atlantic and the Mediterranean, vol. 1. UNESCO, Paris, pp. 284–301.

Berger, W.H., 1989. Global maps of ocean productivity. In: Berger, W.H., Smetacek, V.S., Wefer, G. (Eds.), Productivity of the Ocean: Present and Past. Wiley, New York, pp. 429–455.

Bergstad, O.A., 1990. Ecology of the fishes of the Norwegian Deep: distribution and species assemblages. Netherlands Journal of Sea Research 25, 237–266.

Bergstad, O.A., 1991. Distribution and trophic ecology of some gadoid fish of the Norwegian Deep. 2. Food-web linkages and comparison of diets and distributions. Sarsia 75, 315–325.

Bergstad, O.A., Menezes, G., Høines, Å., 2008. Demersal fish on a mid-ocean ridge: distribution patterns of fishes captured by longlines on the Mid-Atlantic Ridge.

Blaber, S.J.M., Bulman, C.M., 1987. Diets of fishes of the upper continental slope of eastern Tasmania: content, calorific values, dietary overlap and trophic relationships. Marine Biology 95, 345–356.

Bower, A.S., Le Cann, B., Rossby, T., Zenk, W., Gould, J., Speer, K., Richardson, P., Prator, M.D., Zhang, H.-M., 2002. Directly measured mid-depth circulation in the northeastern North Atlantic Ocean. Nature 419, 603–607.

Bray, J.R., Curtis, J.T., 1957. An ordination of the upland forest communities of Southern Wisconsin. Ecological Monographs 27, 325–349.

Childress, J.J., Gluck, D.L., Carney, R.S., Gowing, M.M., 1989. Benthopelagic biomass distribution and oxygen consumption in a deep-sea benthic boundary layer dominated by gelatinous organisms. Limnology and Oceanography 34, 913–930.

Clarke, K.R., Gorley, R.N., 2006. PRIMER v6: User Manual/Tutorial. PRIMER-E, Plymouth.

Clarke, K.R., Chapman, M.G., Somerfield, P.J., Needham, H.R., 2006. Dispersion-based weighting of species counts in assemblage analyses. Marine Ecology Progress Series 320, 11–27.

Clarke, M.R., 1985. The food and feeding of seven fish species from the Campbell Plateau, New Zealand. New Zealand Journal of Marine and Freshwater Research 19, 339–363.

Cohen, D.M., 1984. Bathylagidae. In: Whitehead, P.J.P., Bauchot, M.-L., Hureau, J.-C., Nielsen, J., Tortonese, E. (Eds.), Fishes of the North-Eastern Atlantic and the Mediterranean, vol. 1. UNESCO, Paris, pp. 392–394.

Craddock, J.E., Hartel, K.E., Flescher, D., 2002. Lanternfishes: order myctophiformes. In: Collette, B.B., Klein-MacPhee, G. (Eds.), Fishes of the Gulf of Maine, pp. 198–204.

Dawson, C.E., 1986. Syngnathidae. In: Whitehead, P.J.P., Bauchot, M.-L., Hureau, J.-C., Nielsen, J., Tortonese, E. (Eds.), Fishes of the North-eastern Atlantic and the Mediterranean, vol. 2. UNESCO, Paris, pp. 628–639.

Domanski, P., 1986. The near-bottom shrimp faunas (Decapoda: Natantia) at two abyssal sites in the Northeast Atlantic Ocean. Marine Biology 93, 171–180.

Faith, D.P., Minchin, P.R., Belbin, L., 1987. Compositional dissimilarity as a robust measure of ecological distance. Vegetatio 69, 57–68.

Fock, H.O., Pusch, C., Ehrich, S., 2002a. The 1982-cruise of FRV Walther Herwig II to the Mid-Atlantic Ridge. In: Bergstad, O.A. (Ed.), The Census of Marine Life: Turning Concept into Reality. ICES, Copenhagen.

Fock, H.O., Matthiessen, B., Zidowitz, H., von Westernhagen, H., 2002b. Diel and habitat-dependent resource utilization by deep-sea fishes at the Great meteor seamount: niche overlap and support for the sound scattering layer interception hypothesis. Marine Ecology Progress Series 244, 219–233.

Fock, H.O., Pusch, C., Ehrich, S., 2004. Structure of deep-sea pelagic fish assemblages in relation to the Mid-Atlantic Ridge (45–50°N). Deep Sea Research I 51, 953–978.

Forsythe, W.C., Rykiel Jr., E.J., Stahl, R.S., Wu, H., Schoolfield, R.M., 1995. A model comparison for daylength as a function of latitude and day of year. Ecological Modelling 80, 87–95.

Gartner, J.V., Crabtree, R.E., Sulak, K.J., 1997. Feeding at depth. In: Randall, D.J., Farrell, A.P. (Eds.), Deep-Sea Fishes. Academic Press, San Diego, pp. 115–193.

Gibbs Jr., R.H., 1984. Chauliodontidae. In: Whitehead, P.J.P., Bauchot, M.-L., Hureau, J.-C., Nielsen, J., Tortonese, E. (Eds.), Fishes of the North-eastern Atlantic and the Mediterranean, vol. 1. UNESCO, Paris, pp. 336–337.

Gordon, J.D.M., 2001. Deep-water fisheries at the Atlantic Frontier. Continental Shelf Research 21, 987–1003.

Haedrich, R.L., Henderson, N.R., 1974. Pelagic food of *Coryphaenoides armatus*, a deep benthic rattail. Deep-Sea Research 21, 739–744.

Haedrich, R.L., Merrett, N.R., 1992. Production/biomass ratios, size frequencies, and biomass spectra in deep-sea demersal fishes. In: Rowe, G.T., Pariente, V. (Eds.), Deep-Sea Food Chains and the Global carbon Cycle. Kluwer Academic Publishers, Dordrecht, pp. 157–182.

Halliday, R.G., 1970. Growth and vertical distribution of the Glacier Lanternfish, *Benthosema glaciale*, in the northwestern Atlantic. Journal of the Fisheries Research Board of Canada 27, 105–116.

Hargreaves, P.M., 1984. The distribution of Decapoda (Crustacea) in the open ocean and near-bottom over an adjacent slope in the northern north-east Atlantic Ocean during 1979. Journal of the Marine Biological Association, UK 64, 829–857.

Hargreaves, P.M., 1985. The distribution of Mysidacea in the open ocean and near-bottom over slope regions in the northern North-east Atlantic Ocean during 1979. Journal of Plankton Research 7, 241–261.

Heino, M., Porteiro, F., Sutton, T., Falkenhaug, T., Godø, O. R., Piatkowski, U., submitted. Catchability of pelagic trawls for sampling deep-pelagic nekton in the mid North Atlantic. ICES Journal of Marine Science.

Holloway, P.E., Merrifield, M.A., 1999. Internal tide generation by seamounts, ridges and islands. Journal of Geophysical Research 104, 25937–25951.

Hopkins, T.L., Gartner Jr., J.V., 1992. Resource-partitioning and predation impact of a low-latitude myctophid community. Marine Biology 114, 185–197.

Horn, M.H., 1972. The amount of space available for marine and freshwater fishes. Fishery Bulletin 70, 1295–1297.

Hulley, P.A., 1984. Myctophidae. In: Whitehead, P.J.P., Bauchot, M.-L., Hureau, J.-C., Nielsen, J., Tortonese, E. (Eds.), Fishes of the North-eastern Atlantic and the Mediterranean, vol. 1. UNESCO, Paris, pp. 429–483.

Isaacs, J.D., Schwartzlose, R.A., 1965. Migrant sound scatterers: interactions with the sea florr. Science 150, 1810–1813.

Karnella, C., 1987. Biology of midwater fishes of Bermuda Ocean Acre. Family Myctophidae, lanternfishes. Smithsonian Contributions in Zoology 452, 51–168.

Kashkin, N.I., Parin, N.V., 1983. Quantitative assessment of micro-nektonic fishes by nonclosing gear (a review). Biological Oceanography 2, 263–287.

Kruskal, J.B., Wish, M., 1978. Multidimensional Scaling. Sage Publications, Beverly Hills, CA.

Lancraft, T.M., Torres, J.J., Hopkins, T.L., 1989. Micronekton and macrozooplankton in the open waters near Antarctic Ice Edge Zones (AMERIEZ 1983 and 1986). Polar Biology 9, 225–233.

Longhurst, A.R., Harrison, W.G., 1989. The biological pump: profiles of plankton production and consumption in the open ocean. Progress in Oceanography 22, 47–123.

Lorz, H.V., Pearcy, W.G., Fraidenburg, M., 1983. Notes on the feeding habits of the yellowtail rockfish, *Sebastes flavidus,* off Washington and in Queen Charlotte Sound. California Fish and Game 69, 33–38.

Magnusson, J.V., Magnusson, J., 1995. The distribution, relative abundance, and biology of the deep-sea fishes of the Icelandic slope and Reykjanes Ridge. In: Hooper, A.G. (Ed.), Deep-water Fisheries of the North Atlantic Oceanic Slope. Kluwer Academic Publishers, London, pp. 161–199.

Marshall, N.B., Merrett, N.R., 1977. The existence of a benthopelagic fish fauna in the deep sea. In: Angel, M. (Ed.), A Voyage of Discovery. Pergamon Press, Oxford.

Mauchline, J., Gordon, J.D.M., 1983. Diets of clupeoid, stomiatoid and salmonoid fish of the Rockall Trough, northeastern Atlantic Ocean. Marine Biology 77, 67–78.

Mauchline, J., Gordon, J.D.M., 1984. Occurrence and feeding of berycomorphid and percomorphid teleost fish in the Rockall Trough. Journal du Conseil International pour l'Exploration de la Mer 41, 239–247.

Mauchline, J., Gordon, J.D.M., 1991. Oceanic pelagic prey of benthopelagic fish in the benthic boundary layer of a marginal oceanic region. Marine Ecology Progress Series 74, 109–115.

Maul, G.E., 1990. Melamphaidae. In: Quéro, J.C., Hureau, J.C., Karrer, C., Post, A., Saldanha, L. (Eds.), Check-list of the fishes of the eastern tropical Atlantic (CLOFETA), vol. 2. JNICT, Lisbon; SEI, Paris; and UNESCO, Paris, pp. 612–618.

Merrett, N.R., 1986. Biogeography and the oceanic rim: a poorly known zone of ichthyofauna interaction. In: Pelagic Biogeography UNESCO Technical Paper 49, pp. 201–209.

Merrett, N.R., Haedrich, R.L., 1997. Deep-Sea Demersal Fish and Fisheries. Chapman & Hall, London.

Nelson, J.S., 2006. Fishes of the World, fourth ed. Wiley, Hoboken, NJ, 601pp.

Nielsen, J.G., Bertelsen, E., 1990. Eurypharyngidae. In: Quéro, J.C., Hureau, J.C., Karrer, C., Post, A., Saldanha, L. (Eds.), Check-list of the Fishes of the Eastern Tropical Atlantic (CLOFETA), vol. 1. JNICT, Lisbon; SEI, Paris; and UNESCO, Paris, 206pp.

Novikov, N.P., Kodolov, L.S., Gavrilov, G.M., 1981. Preliminary list of fishes of the Emperor Underwater Ridge. In: Parin, N.V. (Ed.), Fishes of the Open Ocean. Moscow, pp. 32–35.

Pearcy, W.G., 1983. Quantitative assessment of the vertical distributions of micronektonic fishes with opening/closing midwater trawls. Biological Oceanography 2, 289–310.

Pearcy, W.G., Ambler, J.W., 1974. Food habits of deep-sea macrourid fishes off the Oregon Coast. Deep Sea Research 21, 745–759.

Pereyra, W.T., Pearcy, W.G., Carvey, F.E., 1969. *Sebastodes flavidus,* a shelf rockfish feeding on mesopelagic fauna, with consideration of ecological implications. Journal of the Fisheries Research Board of Canada 26, 1969.

Porteiro, F.M.P., 2005. Biogeography and biodiversity of stomiid fishes in the North Atlantic. Ph.D. Dissertation, University of Liverpool.

Quéro, J.-C., Njock, J.C., de la Hoz, M.M., 1990a. Sternoptychidae. In: Quéro, J.-C., Hureau, J.C., Karrer, C., Post, A., Saldanha, L. (Eds.), Check-list of the Fishes of the Eastern Tropical Atlantic (CLOFETA), vol. 1. JNICT, Lisbon; SEI, Paris; and UNESCO, Paris, pp. 278, 279.

Quéro, J.-C., Njock, J.C., de la Hoz, M.M., 1990b. Gonostomatidae. In: Quéro, J.-C., Hureau, J.C., Karrer, C., Post, A., Saldanha, L. (Eds.), Check-list of the Fishes of the Eastern Tropical Atlantic (CLOFETA), vol. 1. JNICT, Lisbon; SEI, Paris; and UNESCO, Paris, pp. 283–292.

Ramm, D.C., Xiao, Y., 1995. Herding in groundfish and effective pathwidth of trawls. Fisheries Research 24, 243–259.

Roden, G.I., 1987. Effect of seamount chains on ocean circulation and thermohaline structure. In: Boehlert, G.W. (Ed.), Geophysical Monograph 43. American Geophysical Union, Washington, DC, pp. 335–354.

Roe, H.S.J., Billet, D.S.M., Lampitt, R.S., 1990. Benthic/midwater interactions on the Madeira Abyssal Plain; evidence for biological transport pathways. Progress in Oceanography 24, 127–140.

Romesburg, H.C., 1990. Cluster Analysis for Researchers. Robert E Kreiger Publishing Company, Malabar, FL.

Rossby, T., 1999. On gyre interaction. Deep-Sea Research II 46, 139–164.

Sangster, G.I., Breen, M., 1998. Gear performance and catch comparison trials between a single trawl and a twin rigged gear. Fisheries Research 36, 15–26.

Sedberry, G.R., Musick, J.A., 1978. Feeding strategies of some demersal fishes of the continental slope and rise off the Mid-Atlantic Coast of the USA. Marine Biology 44, 357–375.

Søiland, H., Budgell, P., Knutsen, Ø., 2008. The physical oceanographic conditions along the Mid Atlantic Ridge north of the Azores in June–July 2004.

Sutton, T.T., 2003. Stomiiformes: dragonfishes and relatives. In: Thoney, D., Loiselle, P. (Eds.), Fishes I. Grzimek's Animal Life Encyclopedia, vol. 4. Gale, New York, pp. 421–430.

Sutton, T.T., Hopkins, T.L., 1996. The species composition, abundance and vertical distribution of the stomiid (Pisces: Stomiiformes) fish assemblage of the Gulf of Mexico. Bulletin of Marine Science 59 (3), 530–542.

Vinnichenko, V.I., 1997. Russian investigations and deep water fishery on the Corner Rising seamount in subarea 6. NAFO Science Countries Studies 30, 41–49.

Vinogradov, G.M., 2005. Vertical distribution of Macroplankton at the Charlie-Gibbs Fracture Zone (North Atlantic), as observed from the manned submersible "Mir-1. Marine Biology 146, 325–331.

Vinogradov, M.E., 1968. Vertikalnoe Raspredelenie Okeanicheskogo Zooplanktona. Nauka, Moscow.

Wenneck, T. de Lange, Falkenhaug, T., Bergstad, O.A., 2008. Strategies, methods, and technologies adopted on the RV *G.O. Sars* MAR-ECO expedition to the Mid-Atlantic Ridge in 2004.

Wishner, K.F., 1980a. The biomass of the deep-sea benthopelagic plankton. Deep-Sea Research 27, 203–216.

Wishner, K.F., 1980b. Near-bottom sound scatterers in the Ecuador Trench. Deep-Sea Research 27, 217–223.

Wishner, K.F., 1980c. Aspects of the community ecology deep-sea benthopelagic plankton, with special attention to gymnopleid copepods. Marine Biology 60, 179–187.

Wishner, K.F., Gowing, M.M., 1987. In situ filtering and ingestion rates of deep-sea benthic boundary-layer zooplankton in the Santa Catalina Basin. Marine Biology 94, 357–366.