



Diversity and community structure of pelagic fishes to 5000 m depth in the Sargasso Sea

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ARTICLE INFO

Article history:

Received 18 September 2010

Accepted 18 September 2010

Available online 21 September 2010

Keywords:

Midwater fish
Bathypelagic
Mesopelagic
Diversity
Vertical distribution

ABSTRACT

The diversity, abundance and distribution of pelagic fishes from 0–5000 m in the Sargasso Sea, northwestern Atlantic Ocean, were investigated, with primary focus on fishes between 1000–5000 m. A large-volume, fine-mesh (335- μ m), discrete-depth sampling system was used to sample the latter strata in 1000-m intervals. Species composition and total biomass of fishes collected in these strata were compared with samples taken 0–1000 m using a smaller midwater trawl. Samples were collected in association with the Census of Marine Zooplankton at-sea DNA-sequencing effort, allowing the determination of genetic barcodes of taxa for which species descriptions do not currently exist (e.g., many male ceratioid anglerfishes). A total of 3965 fish specimens were collected, representing minimally 127 species (84 genera), from 42 families. The bristlemouth, *Cyclothone braueri*, dominated the catches both above (47%) and below (41%) 1000 m. The Myctophidae and Stomiidae were the most species-rich taxa, while the deep-sea anglerfish suborder Ceratioidei was the most diverse bathypelagic taxon. Thirty species of fish were sequenced and data submitted to GenBank. New Ocean Biogeographic Information System location records for the Sargasso Sea were logged for 84 fish species. Hydrographic data revealed separation of the region into three physical regimes within the top 1000 m (northern, transition, and southern), while the sub-1000 m stratum was fairly homogeneous. Though species richness, abundance, and diversity were highest in the southern Sargasso, diversity indices of whole water column (0–5000 m) samples were not significantly different between regions. Below 1000 m, the 1000–2000 m stratum held the most diverse assemblage across the entire transect, but high diversity was exhibited below 3000 m at two of four stations. Ordination discriminated 13 pelagic fish assemblages, with these related to depth far more than region. Geometric abundance class analysis revealed profound differences in relative species abundances between the meso- and bathypelagic zones with the former demonstrating a much higher percentage of common species. This finding tracks the hydrographic patterns observed: increased stability in the bathypelagic zone favors increased numbers of rare species relative to the mesopelagic zone, where hydrographic complexity favors higher numbers of common species.

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1. Introduction

One of the initial driving forces of the Census of Marine Life (CoML, www.coml.org) was the desire to assess the abundance and diversity of marine fishes (Anonymous, 1998; Ausubel, 1999, 2001). A primary impediment of this ambitious goal is the lack of information on the fishes of the bathypelagic zone of the world ocean. Occupying 7.5 times the total volume of the terrestrial environment, and over 60% of the world ocean (Herring, 2002), the bathypelagic zone would be expected to contain a large portion, if not the majority, of the planet's fishes (*ergo* vertebrates). At present, for a variety of reasons, we do not have

a realistic quantitative assessment of the fishes in the bathypelagic, much less a comprehensive understanding of the biodiversity and community structure of the deep ocean.

The Sargasso Sea, comprising ~12% of the volume of the North Atlantic, is an anticyclonic gyre that forms the western portion of the North Atlantic subtropical region (Brooks, 1972). The physical oceanography of the Sargasso Sea has been well studied (e.g., Schroeder and Stommel, 1969; Brooks, 1972). Briefly, the prominent hydrographic feature of the Sargasso Sea is the seasonally persistent presence of 18 °C/36.5 ppt salinity seawater between 200–400 m ("18° water" hereafter), formed off Bermuda by winter cooling of surface water (Worthington, 1976). The Sargasso Sea is divided into northern and southern sectors by the Northern Subtropical Convergence located between 26–30°N. Faunal differences between north and south have been reported (Backus et al., 1977) and attributed to the seasonal breakdown of

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the winter thermocline in the north, hence euphotic zone nutrient replenishment, which is lacking in the south (Ryther and Menzel, 1961). A seasonal thermocline (20–27 °C above, 18–19 °C at transition) exists between 25–150 m from April (the time of this study) to November, with maximum development in August. A permanent deep thermocline exists between 500–1100 m, having the general characteristics of North Atlantic central water. In this stratum temperature decreases from ~18 °C to 6 °C and salinity from ~36.2 to 35.0 ppt. Below this stratum, temperatures range from ~5.5 to 4 °C and salinity is fairly uniform at 35.0 ppt. Lastly, a prominent feature of the northern Sargasso Sea is the prevalence of mesoscale cyclonic eddies spun off from the Gulf Stream (Wiebe et al., 1976; Ring Group, 1981), which have the capacity to entrain and transport midwater fauna in and out of specific locations within the Sargasso Sea (Backus and Craddock, 1982). It is also possible that the Sargasso Sea is impacted by eddies originating from the Mediterranean outflow (McDowell and Rossby, 1978). Thus, the Sargasso Sea is a low-to-mid-latitude region characterized by oceanographic complexity, likely contributing to the high biodiversity among its pelagic fish fauna (e.g., Gartner et al., 1989).

The biological characteristics of the upper depth strata (< 1000 m) of this region have been studied fairly extensively with respect to plankton (e.g., Menzel and Ryther, 1961; Steinberg et al., 2001) and mesopelagic fishes (Backus et al., 1969, 1977; Backus and Craddock, 1977; Gibbs and Krueger, 1987; Gartner et al., 1989; Bangma, 2003), but depths below 1000 m, as for most of the world ocean, have rarely been studied. Prior to Angel and Baker's (1982) work in the Northeast Atlantic, we know of no published discrete-depth, quantitative data on pelagic fishes from depths greater than 2000 m. In particular, knowledge is almost wholly lacking for these depth zones of the small "Lilliputian" fishes characteristic of deep subtropical/tropical seas (Murray and Hjort, 1912). Fishes smaller than 50 mm are known to dominate the bathypelagic ichthyofauna numerically (e.g., *Cyclothone*; McClain et al., 2001), but their overall contribution to biodiversity and community structure is very poorly known. A habitat as vast as the bathypelagic realm, often considered the oldest and most stable on Earth, is sure to contain a diverse fauna, even if biomass is low due to size limitation. Our collecting gear also reduced damage to the fragile structures of the bathypelagic ichthyofauna that are critical for taxonomic discrimination. In order to understand the transition between the meso- and bathypelagic fish fauna we sampled the upper 1000 m and will contrast the biodiversity and community structure of these zones.

In this paper we describe the species composition, vertical and horizontal distribution, and abundance of the epi- to bathypelagic fishes of the Sargasso Sea, with emphasis on fishes occurring between 1000–5000 m. Material for this study was collected in association with the Census of Marine Zooplankton (CMarZ, www.cmarz.org), an ocean realm field project of CoML. Sampling for this study was conducted using a large (10-m²) mouth-area MOCNESS midwater trawl (Wiebe et al., 1985) outfitted with fine-(335- μ m) mesh nets for discrete depth pattern characterization. This gear configuration, the first of its kind, provided a unique opportunity to sample and census the "Lilliputian" fishes characteristic of deep subtropical/tropical seas (Murray and Hjort, 1912).

2. Methods

2.1. Sampling and sample processing

This study is based on samples collected during the CMarZ biodiversity survey of the deep tropical/subtropical Western North Atlantic, 10–30 April 2006, on the NOAA ship R/V *Ronald*

H. Brown (Cruise Report, 2006). Sampling was conducted at five stations along a transect from the northern Sargasso Sea to the equatorial waters northeast of Brazil (Fig. 1). Hydrographic data of the sampling area were collected using the CTD sensors of the MOCNESS systems (described below) and presented in Wiebe et al. (2010) and Bucklin et al. (2010). Findings will be summarized as relevant to fish distributions.

The primary trawling gears for deep-pelagic fishes were 1-m² and 10-m² mouth-area MOCNESS (Midwater Opening/Closing Net and Environmental Sensing System) trawls (MOC-01 and MOC-10, respectively, hereafter) outfitted with multiple 335- μ m mesh nets (Wiebe et al., 2010), each fished within discrete, pre-defined depth strata (excepting the initial 0–5000 m deployment net of 3-mm mesh on the MOC-10). This finer mesh size was smaller than that generally used to sample fishes, so avoidance and/or pressure effects (Kashkin and Parin, 1983) may have affected abundance estimates. The magnitude of this potential bias is unknown. The MOC-01 was fished from 0–1000 m, with one descending oblique net haul (0–1000 m) and eight ascending discrete-depth net hauls (Table 1). The MOC-10 deployments consisted of an initial descending oblique net haul (0–5000 m) and four ascending, discrete-depth net hauls from 5000–1000 m, in 1000-m intervals (Table 1). Side deflector and net flaps were installed to prevent contamination of bathypelagic samples during the initial trawl descent through the epi- and mesopelagic zones. Trawl speed was 1.5–2.5 knots and net depths were monitored/controlled on-the-fly. Only those net samples whose depth intervals conformed to the *a priori* design were used in quantitative analyses. The remaining samples (early trips, unintentional obliques, etc.) were used only for the total species list.

Immediately following gear retrieval, cod-end samples were washed down and stored in a cold room to await sequential processing. Whole cod end samples were digitally photographed with large labels and then all fish specimens were removed. All specimens were identified and measured to the nearest 0.1 mm (standard length) at sea, prior to preservation. Tissue samples

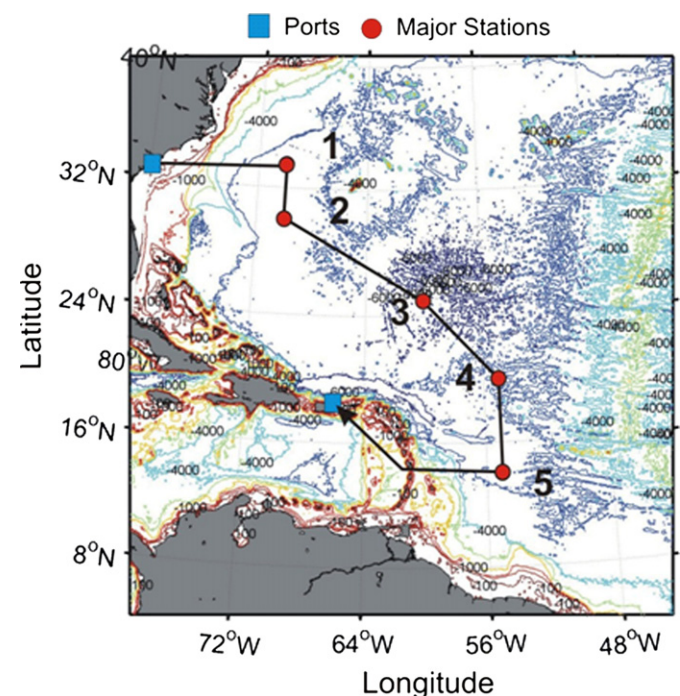


Fig. 1. Cruise track and stations during the Census of Marine Zooplankton/NOAA ship *Ronald H. Brown* cruise 06-03 to the western subtropical and tropical North Atlantic, 10–30 April 2006.

Table 1
Sample data for MOCNESS trawling on the April 2006 CMarZ cruise, Sargasso Sea. Sample nomenclature: gear.station.tow.net number. Code nomenclature: gear [SM – small MOCNESS, LM – large MOCNESS].station number.depth zone.solar cycle. Station 2=replicate trawl on station. Code designations used in multivariate analysis graphical presentation.

Sample	Depth zone	Vol. filtered (m ³)	Station	Code	Solar cycle
moc10.1.1.0	0-5000	66763	1	LM1ob	dn
moc10.1.1.1	4000-5000	147297	1	LM1z	n
moc10.1.1.4	1000-3000	69563	1	LM1w	n
moc10.2.2.0	0-4315	153130	2	LM2ob	d
moc10.2.2.1	4315-3500	34546	2	LM2y	d
moc10.3.3.0	0-5000	61591	3	LM3ob	n
moc10.3.3.1	4000-5000	28665	3	LM3z	n
moc10.3.3.2	3000-4000	35051	3	LM3y	dn
moc10.3.3.4	1000-3000	44849	3	LM3w	d
moc10.3.4.0	0-5000	39641	3.2	LM3.2ob	n
moc10.3.4.1	4000-5000	38177	3.2	LM3.2z	nd
moc10.3.4.2	3000-4000	64341	3.2	LM3.2y	d
moc10.3.4.3	2000-3000	49301	3.2	LM3.2x	d
moc10.3.4.4	1000-2000	53128	3.2	LM3.2u	d
moc10.4.5.0	0-4500	64469	4	LM4ob	n
moc10.4.5.1	4000-4500	33551	4	LM4z	nd
moc10.4.5.2	3000-4000	55233	4	LM4y	d
moc10.4.5.3	2000-3000	52965	4	LM4x	d
moc10.4.5.4	1000-2000	55328	4	LM4u	d
moc10.5.7.0	0-5000	92207	5.2	LM5.2ob	d
moc10.5.7.1	4000-5000	54074	5.2	LM5.2z	d
moc10.5.7.2	3000-4000	55371	5.2	LM5.2y	dn
moc10.5.7.3	1000-3000	114404	5.2	LM5.2w	n
Moc10.5.7.4	0-1000	62573	5.2	LM5.2em	n
moc01.1.2.0	0-993	1653	1	SM1ob.d	d
moc01.1.2.1	797-993	802	1	SM1h.d	d
moc01.1.2.2	600-797	925	1	SM1g.d	d
moc01.1.2.3	400-600	820	1	SM1f.d	d
moc01.1.2.4	200-400	1194	1	SM1e.d	d
moc01.1.2.5	100-200	472	1	SM1d.d	d
moc01.1.2.6	50-100	264	1	SM1c.d	d
moc01.1.2.7	25-50	178	1	SM1b.d	d
moc01.1.2.8	0-25	272	1	SM1a.d	d
moc01.2.3.0	0-998	913	2n	SM2ob.n	n
moc01.2.3.1	790-998	667	2n	SM2h.n	n
moc01.2.3.2	600-790	943	2n	SM2g.n	n
moc01.2.3.3	400-600	1218	2n	SM2f.n	n
moc01.2.3.4	200-400	961	2n	SM2e.n	n
moc01.2.3.5	100-200	667	2n	SM2d.n	n
moc01.2.3.6	50-100	548	2n	SM2c.n	n
moc01.2.3.7	25-50	312	2n	SM2b.n	n
moc01.2.3.8	0-25	289	2n	SM2a.n	n
moc01.2.4.0	0-1000	1234	2d	SM2ob.d	d
moc01.2.4.1	800-1000	783	2d	SM2h.d	d
moc01.2.4.2	600-800	755	2d	SM2g.d	d
moc01.2.4.3	400-600	822	2d	SM2f.d	d
moc01.2.4.4	200-400	896	2d	SM2e.d	d
moc01.2.4.5	100-200	412	2d	SM2d.d	d
moc01.2.4.6	50-100	204	2d	SM2c.d	d
moc01.2.4.7	25-50	151	2d	SM2b.d	d
moc01.2.4.8	0-25	306	2d	SM2a.d	d
moc01.3.7.0	0-1000	2626	3d	SM3ob.d	d
moc01.3.7.1	800-1000	1065	3d	SM3h.d	d
moc01.3.7.2	600-800	1092	3d	SM3g.d	d
moc01.3.7.3	400-600	1059	3d	SM3f.d	d
moc01.3.7.4	200-400	1020	3d	SM3e.d	d
moc01.3.7.5	100-200	807	3d	SM3d.d	d
moc01.3.7.6	50-100	411	3d	SM3c.d	d
moc01.3.7.7	25-50	373	3d	SM3b.d	d
moc01.3.7.8	0-25	407	3d	SM3a.d	d
moc01.3.8.0	0-1000-800	3068	3n	SM3ob.n	n
moc01.3.8.1	600-800	1484	3n	SM3g.n	n
moc01.3.8.2	400-600	1093	3n	SM3f.n	n
moc01.3.8.3	200-400	977	3n	SM3e.n	n
moc01.3.8.4	100-200	1160	3n	SM3d.n	n
moc01.3.8.5	50-100	872	3n	SM3c.n	n
moc01.3.8.6	25-50	634	3n	SM3b.n	n
moc01.3.8.7	0-25	201	3n	SM3a.n	n
moc01.4.9.0	0-1000	2656	4d	SM4ob.d	d
moc01.4.9.1	800-1000	363	4d	SM4h.d	d
moc01.4.9.2	600-800	1005	4d	SM4g.d	d
moc01.4.9.3	400-600	908	4d	SM4f.d	d
moc01.4.9.4	200-400	946	4d	SM4e.d	d

Table 1 (continued)

Sample	Depth zone	Vol. filtered (m ³)	Station	Code	Solar cycle
moc01.4.9.5	100–200	1230	4d	SM4d.d	d
moc01.4.9.6	50–100	1019	4d	SM4c.d	d
moc01.4.9.7	25–50	409	4d	SM4b.d	d
moc01.4.9.8	0–25	259	4d	SM4a.d	d
moc01.4.10.0	0–1000	4220	4n	SM4ob.n	n
moc01.4.10.1	800–1000	1190	4n	SM4h.n	n
moc01.4.10.2	595–800	928	4n	SM4g.n	n
moc01.4.10.3	400–595	852	4n	SM4f.n	n
moc01.4.10.4	200–400	989	4n	SM4e.n	n
moc01.4.10.5	100–200	893	4n	SM4d.n	n
moc01.4.10.6	50–100	480	4n	SM4c.n	n
moc01.4.10.7	25–50	270	4n	SM4b.n	n
moc01.4.10.8	0–25	327	4n	SM4a.n	n
moc01.5.11.0	0–1000	1801	5d	SM5ob.d	d
moc01.5.11.1	799–1000	922	5d	SM5h.d	d
moc01.5.11.2	600–799	839	5d	SM5g.d	d
moc01.5.11.3	400–600	945	5d	SM5f.d	d
moc01.5.11.4	198–400	1044	5d	SM5e.d	d
moc01.5.11.5	100–198	475	5d	SM5d.d	d
moc01.5.11.6	50–100	666	5d	SM5c.d	d
moc01.5.11.7	25–50	1125	5d	SM5b.d	d
moc01.5.11.8	0–25	216	5d	SM5a.d	d
moc01.5.12.0	0–1000	2093	5n	SM5ob.n	n
moc01.5.12.1	800–1000	1017	5n	SM5h.n	n
moc01.5.12.2	600–800	704	5n	SM5g.n	n
moc01.5.12.3	400–600	1189	5n	SM5f.n	n
moc01.5.12.4	200–400	1386	5n	SM5e.n	n
moc01.5.12.5	100–200	650	5n	SM5d.n	n
moc01.5.12.6	50–100	341	5n	SM5c.n	n
moc01.5.12.7	25–50	364	5n	SM5b.n	n
moc01.5.12.8	0–25	361	5n	SM5a.n	n
moc01.5.13.0	0–547	2233	5d_s	SM5ds1	d
moc01.5.13.1	547–527	367	5d_s	SM5ds2	d
moc01.5.13.2	527–516	262	5d_s	SM5ds3	d
moc01.5.13.3	515–496	379	5d_s	SM5ds4	d
moc01.5.13.4	496–488	389	5d_s	SM5ds5	d
moc01.5.13.5	488–477	222	5d_s	SM5ds6	d
moc01.5.13.6	477–473	289	5d_s	SM5ds7	d
moc01.5.13.7	473–464	294	5d_s	SM5ds8	d
moc01.5.13.8	464–461	252	5d_s	SM5ds9	d

were taken of selected species for DNA-barcoding analyses (see Bucklin et al. and Wiebe et al., 2010). Specimens were preserved in 10% (v/v) formalin:seawater for later accurate identification in lab. Biomass (g wet weight) was estimated for all specimens using taxon-specific length/weight regressions derived from previous sampling of the deep North Atlantic (Sutton et al., 2008; Sutton, unpublished). Abundance and biomass data were then pooled for each net sample, tow, and station to gain a quantitative view of fish assemblage structure in terms of biodiversity, relative composition, vertical distribution, and water mass association.

2.2. Statistical analysis

Data matrices consisted of abundance and biomass (per 10⁵ m³ water filtered) of fish species × trawl sample. Data matrices were fourth-root transformed prior to analysis to down-weight the importance of numerically dominant taxa such as *Cyclothone*. The degree of transformation severity was determined using the 'range of values' criterion (Sutton et al., 2008). The range of non-zero abundances in this study upon which analyses were based spanned six orders of magnitude (0.7–10169.5 ind. 10⁻⁵ m⁻³), justifying the strong transformation.

Diversity of samples was expressed as a series of indices. In addition to species richness (*S*, the number of species present in a

sample) Shannon diversity indices (Shannon and Weaver, 1949) were calculated according to the equation:

$$H' = -\sum_i (p_i \ln p_i) \quad (1)$$

where p_i is the proportion of the total count arising from the i th species. In order to express equitability, or the distribution of individuals among the species, Pielou's evenness indices (Pielou, 1975) were calculated according to the equation:

$$J' = H'/H'_{\max} = H'/\log S \quad (2)$$

where H'_{\max} is the maximum possible value of Shannon diversity (that value achieved if all species were equally abundant).

Ordination by non-metric multidimensional scaling (MDS, Kruskal and Wish, 1978) was employed to discriminate assemblages using the PRIMER v.6 software package (Clarke and Gorley, 2006). Ordination is generally preferable to classification (clustering) *per se* in studies such as these because of the relative proximity of sample sites and the likelihood of a steady gradation in community structure across sampling sites in response to gradations in environmental factors (Clarke and Warwick, 2001). Therefore, assemblage structure is presented in a series of MDS plots. Hierarchical unweighted pair-group method using arithmetic averages cluster analysis (UPGMA CA) was used to help in the initial assemblage discrimination (Romesburg, 1990). The appropriate similarity level for assemblage discrimination was

determined using a concordance technique (Sutton et al., 2008). 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, 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 sub-structure 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. Both UPGMA CA and MDS were based on a triangular matrix of Bray-Curtis similarity coefficients (Bray and Curtis, 1957; Faith et al., 1987).

3. Results

3.1. Hydrographic setting

A hydrographic transition was apparent along the cruise track, occurring between Stations 2 and 3 (Fig. 1) and coinciding with the Northern Subtropical Convergence between $\sim 26\text{--}30^\circ\text{N}$ (Backus et al., 1977). At the two northern stations, the “18° water” was present from near the surface to ~ 400 m (Fig. 2 in Wiebe et al., 2010). Below this layer the main thermocline extended to approximately 1000 m, within which temperature decreased uniformly to $\sim 5^\circ\text{C}$. Between 1000–5000 m, temperatures decreased slowly to $\sim 3^\circ\text{C}$. Station 3 was characterized by warmer (24°C), lower salinity (< 36.5 ppt) surface water in the top 100 m, and a replacement of the stable “18° water” stratum seen in Stations 1 and 2 with a steadily decreasing temperature profile to 1000 m. Below 1000 m, the temperature/salinity (T/S) profile of Station 3 was similar to Stations 1 and 2. Shifts between low near-surface salinities and salinity maxima between 100–140 m (Subtropical Underwater) became more exaggerated at the two southern-most stations. A water-column salinity minimum occurred between 800–1000 m at these stations (Antarctic Intermediate Water), with a secondary salinity maximum around 1400 m that decreased slightly to 5000 m. Surface temperature increased from Station 4 (25°C) to Station 5 (27°C). At Station 4, temperature decreased $\sim 8^\circ\text{C}$ between 100–300 m, and then decreased uniformly to 5°C at 800 m. At Station 5, this trend was exaggerated, with a decrease of $\sim 17^\circ\text{C}$ between 100–250 m. Also at Station 5, a thermohaline staircase (Kunze et al., 1987) was observed between 250–550 m. At Stations 4 and 5, temperature profiles below 1000 m were similar to those of the northern stations.

3.2. Ichthyofaunal diversity

A total of 3965 fish specimens was collected, representing minimally 127 species (84 genera) from 42 families. Ninety-eight species were taken in discrete-depth tows and 29 in 0–5000 m oblique tows. A complete species list, with raw abundances (not normalized for volume filtered) by station is presented in Appendix A. Of the epi- to bathypelagic fishes collected in this survey, only 27 species (\sim one-third of the total) are currently listed for the study area in the Ocean Biogeographical Information System (OBIS; www.iobis.org). Eighty-four species location records for the Sargasso Sea will be added to OBIS as a result of this study. The remaining 16 taxa were not identified to species (e.g. larvae, damaged forms, and works in progress).

The Myctophidae was the most species-rich family sampled, with minimally 31 species represented. Additional species may have been present in the unidentified fish larvae, which were the focus of a separate CMarZ project. The Stomiidae was the second-most speciose family with 18 species, at least one of which (*Leptostomias*

sp. A) appears to be new to science (Sutton and Baldwin, in preparation). A second stomiid (*Astronesthes*) and two additional taxa (*Pseudoscopelus* and *Macroparalepis*) are being investigated for novelty (Appendix A). The remaining families contributing more than five species were the Gonostomatidae (11 species), Sternoptychidae (6 species) and Melamphaidae (5 species), though the last family is certainly underestimated. The taxonomy of the Melamphaidae is currently undergoing large-scale revision (Bartow and Sutton, 2008), so the species number for the genus *Melamphaes* was assigned a value of one and designated as “*Melamphaes* TBD” (Appendix A), pending proper diagnosis of numerous undescribed forms from the region. In deference to higher taxonomic levels, which some consider to be a more desirable measure of diversity (Pielou, 1975), the deep-sea anglerfish Suborder Ceratioidei (Lophiiformes) was the most ‘heirarchically’ diverse higher taxon; 14 individuals, nine of which were ‘Lilliputian’ males, represented five families and at least six genera. DNA sequencing of a 700 base-pair “DNA barcode” region of mitochondrial cytochrome oxidase subunit I (mtCOI) was done for 30 species of fish (Bucklin et al., 2010). These sequences were submitted to the BArCODE section of the NCBI GenBank database (see www.ncbi.nlm.nih.gov) and can be located by the GenBank Accession Numbers (GU071722–GU071752).

Before discussing diversity indices among samples, we must first address sampling bias. Two types of trawls were used for discrete-depth sampling, one smaller (MOC-01; 0–1000 m) and one larger (MOC-10; 0–5000 m oblique and > 1000 m discrete-depth). In order to assess the effects of gear type on the spectrum of fishes sampled, we calculated Shannon diversity indices for all trawl samples that contained fish, pooled values for each gear type, and ran a single factor ANOVA. This exercise revealed a significant added variance component among gear types ($p \leq 0.001$, $F_{0.05[1,91]} = 3.95$, $F = 50.63$). A *t*-test revealed that the mean diversity index of the larger trawl ($H' = 2.33$) was significantly ($p < 0.001$) higher than that of the smaller ($H' = 1.06$). Therefore, we will limit comparisons between stations to values from the same trawl type fished at the same depths, forgoing comparisons of diversity indices above and below 1000 m generated from the different trawls. One MOC10 deployment at Station 5 included a 0–1000 m discrete-depth sample (Table 1), allowing meso-/bathypelagic comparison at this site.

3.3. Diversity as a function of depth and water mass

Temperature/salinity (T/S) data suggested three primary upper-water-column (< 1000 m) hydrographic regimes in the study area: northern (Stations 1 and 2), transition (Station 3), and southern (Stations 4 and 5). Pooling the northern and southern stations, respectively, and replication of the transition station allowed for first order comparisons of diversity trends relative to hydrographic regime and depth. 0–5000 m oblique trawls were made at each station with the MOC10. Indices of diversity and equitability of these samples are presented in Table 2. Species richness, total abundance, and diversity (H') were all highest at the southern-most station; however, single-factor ANOVA revealed no significant added variance component among sample sites relative to whole-water-column oblique samples. Evenness (J') indices were nearly identical for all oblique samples, owing to the relative similarity in abundances across all species and the relatively moderate numerical contribution of the genus *Cyclothone* in the MOC10 0–5000 m oblique samples. In order to assess diversity differences among regions as a function of depth, diversity indices are presented in 1000-m depth increments (Table 3). Diversity in the top 1000 m was quite consistent among stations, the lower value from Station 1 notwithstanding. Below 1000 m, it appeared that

Table 2

Indices of diversity and equitability among 0–5000 m oblique trawl samples from the Sargasso Sea. Sample codes as in Table 1. S =species richness, N =total number of ind. 10^{-5} m^{-3} filtered, J' =Pielou's evenness index, H' =Shannon diversity index.

Station	Sample	S	N	J'	H'
1	LM1ob	12	14.92	0.99	2.47
2	LM2ob	18	19.88	0.98	2.84
3	LM3ob	12	18.92	0.98	2.44
3	LM3.2ob	11	15.38	1.00	2.39
4	LM4ob	15	18.85	1.00	2.69
5	LM5.2ob	22	28.77	0.98	3.04

Table 3

Indices of diversity per depth zone per station. 0–1000 m indices based on MOC01 samples, 1000–5000 m indices based on MOC10 samples. S =species richness, H' =Shannon diversity index.

Depth zone	Station 1		Station 2		Station 3		Station 4		Station 5	
	S	H'	S	H'	S	H'	S	H'	S	H'
0–1000	4	1.29	10	2.28	9	2.12	8	2.03	9	2.03
1000–2000	13	2.48	nd	nd	16	2.74	20	2.95	8	2.03
2000–3000	13	2.48	nd	nd	3	1.08	0	0	8	2.03
3000–4000	nd	nd	23	3.05	2	0.69	1	0	5	1.60
4000–5000	nd	nd	nd	nd	0	0	1	0	19	2.89

the 1000–2000 m stratum held the most diverse assemblage across the entire transect, but high diversity was exhibited below 3000 m at two of the four stations for which we had discrete-depth data. The 3000–4000 m stratum at Station 2 contained the highest-diversity assemblage in the study, though as stated above the MOC01 likely underestimated diversity in the top 1000 m.

In order to gain an understanding of the pattern of relative species abundances versus a single summary diversity statistic (as presented above), average ranked species abundance curves and geometric species abundance class curves are plotted by major depth stratum ($<$ or $>$ 1000 m; Fig. 2). Plotting the distribution of abundance across species allows extraction of the overview features of community structure irrespective of the specific taxa present. The average ranked species abundance curves (Fig. 2A) are based on the ranking of species in decreasing order in terms of abundance, and are presented on a log scale to better visualize the more common species. The geometric species abundance class curves (Fig. 2B) are based on size classes defined by how many individuals (in this case, no. ind. 10^{-5} m^{-3} , non-transformed data) represent each species (e.g., class 1=1 ind., class 2=2–3 ind., class 3=4–7 ind., etc., with geometrically expanding bin sizes). The latter plot is sometimes used to indicate environmental perturbation (Gray and Pearson, 1982); in “non-disturbed” communities there are many rare species and the curve would be expected to be smooth and highly skewed to the left. While the average ranked species abundance curves were similar for both strata (Fig. 2A), owing to the numerical domination of the genus *Cyclothone* in both zones (see Section 3.1 below), the geometric abundance class plot differed profoundly between zones (Fig. 2B), with a much higher percentage of common species in the mesopelagic zone.

3.4. Faunal account

3.4.1. Relative abundance and biomass

The bristlemouth *Cyclothone braueri* was the most abundant species in both the meso- and bathypelagic zones (47% and 41% of totals, respectively, Table 4). Its congeners, *C. pallida* and

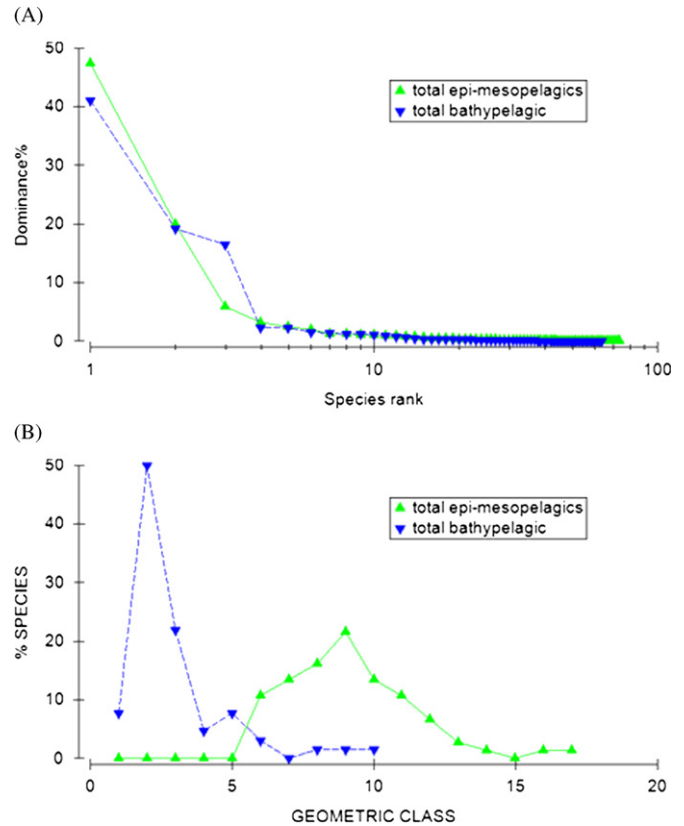


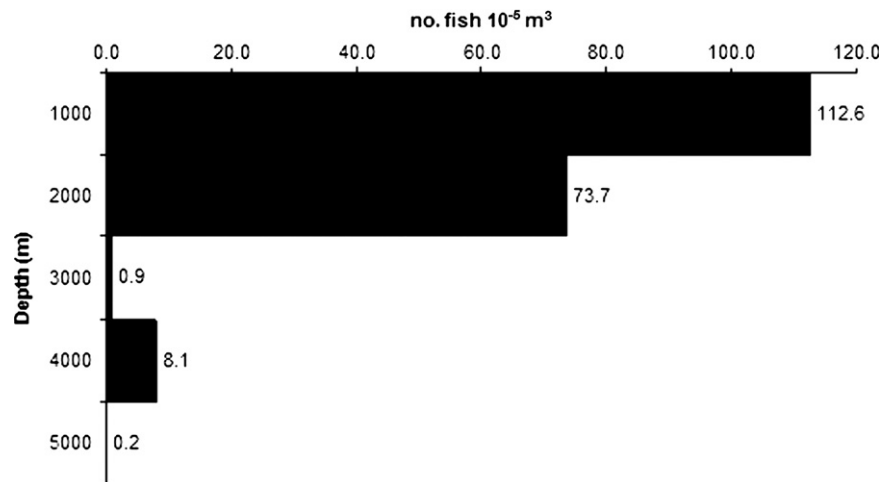
Fig. 2. Plots of the patterns of relative fish species abundance above (green solid line) and below (blue dashed line) 1000 m in the Sargasso Sea, western North Atlantic: (A) average ranked species abundance curve; (B) plot of O_2 geometric abundance classes (Gray and Pearson, 1982). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

C. microdon alternated second and third place rankings in the two depth zones. No other species contributed more than 6% of total abundance. *Cyclothone pseudopallida* ranked fourth and fifth in the meso- and bathypelagic, respectively. In the mesopelagic, the lanternfishes *Lepidophanes guentheri*, *Lobianchia dofleini*, and *Ceratoscopelus warmingii*, ranked 5th–7th, respectively, just ahead of three aggregate taxa of fish larvae and two species of the hatchetfish genus *Argyropelecus*. In the bathypelagic zone, the hatchetfish *Sternoptyx diaphana* ranked fourth, followed by another *Cyclothone* species, *C. acclinidens*, the *Melamphaes* species complex, and the two *Arygropalecus* species bracketing *Ceratoscopelus warmingii*. No other species contributed more than 1% of total abundance in either zone.

As is usually the case in low-latitude bathypelagic ecosystems far removed from topographic features (i.e. seamounts, mid-ocean ridges), fish biomass was low. The genus *Cyclothone* dominated the biomass of the total assemblage, similar – but to a lesser degree – to its dominant contribution to abundance patterns. The biomass contribution by large, single fishes from other genera was substantial in some cases. For example, one extremely large dragonfish specimen (*Rhadinesthes decimus*) accounted for 76.9% of all fish biomass between 1000–2000 m, while *Cyclothone* spp. accounted for 23%. This is the first western Atlantic record for *Rhadinesthes decimus*. The vertical distribution of fish biomass (presented in Fig. 3) was highest in the top 1000 m, but as mentioned previously, this figure may be underestimated if larger, rarer fishes disproportionately avoid the smaller trawl used. *Cyclothone* spp. contributed 65% of biomass in this layer, with *C. pallida* ranking ahead of *C. braueri* due to larger average

Table 4Abundances of the common (> 1% of total ind.) epi-, meso-, and bathypelagic fishes of the Sargasso Sea. Abundance values are no. ind. 10^{-5} m^{-3} .

0–1000 m			1000–5000 m		
	Abundance	%		Abundance	%
<i>Cyclothone braueri</i>	93208.0	47.5	<i>Cyclothone braueri</i>	602.0	41.0
<i>Cyclothone pallida</i>	39154.8	19.9	<i>Cyclothone microdon</i>	282.5	19.3
<i>Cyclothone microdon</i>	11592.7	5.9	<i>Cyclothone pallida</i>	240.9	16.4
<i>Cyclothone pseudopallida</i>	6190.3	3.2	<i>Sternoptyx diaphana</i>	34.1	2.3
<i>Lepidophanes guentheri</i>	4940.1	2.5	<i>Cyclothone pseudopallida</i>	33.5	2.3
<i>Lobianchia dofleini</i>	4023.6	2.0	<i>Cyclothone acclindens</i>	24.0	1.6
<i>Ceratoscopelus warmingii</i>	2539.9	1.3	<i>Melamphaes</i> TBD	21.5	1.5
Bothid larvae	2390.3	1.2	<i>Argyropelecus aculeatus</i>	19.2	1.3
Perciform larvae	2270.0	1.2	<i>Ceratoscopelus warmingii</i>	18.7	1.3
Eel leptocephalus larvae	2113.8	1.1	<i>Argyropelecus hemigymnus</i>	16.3	1.1
<i>Argyropelecus hemigymnus</i>	2029.4	1.0			
<i>Argyropelecus aculeatus</i>	2008.4	1.0			

**Fig. 3.** Vertical distribution of fish biomass (g wet weight) in the Sargasso Sea. Depths listed are the maximum depth within each bin.

size. The biomass between 1000–2000 m was fairly high, due primarily to the large *Rhadinesthes*. Biomass decreased sharply by nearly two orders of magnitude between 2000–3000 m. An increase in biomass between 3000–4000 m was observed, due primarily to the contribution of *Cyclothone microdon* (~two-thirds of biomass in this layer). Biomass below 4000 m decreased sharply to a water column minimum. MOC-10 trawls were kept well above the benthic boundary layer for safety purposes, so it is unknown whether there was near-bottom enhancement of pelagic biomass (e.g., Porteiro and Sutton, 2007).

3.4.2. Vertical and horizontal distribution

Twenty-one fish species/taxa were taken solely in the upper 1000 m of the water column (Table 5), with one-third of these being myctophids and one-third being larvae/juveniles. The remainder consisted of mesopelagic stomiiform fishes and the epi-/mesopelagic codlet, *Bregmaceros atlanticum*. Twenty-four species/taxa were taken solely below 1000 m. Ceratioid anglerfishes, particularly males, were the best-represented taxon, with minimally seven taxa (species keys do not exist for many males of several families). Six additional species included stereotypical bathypelagic taxa: platytroutids, *Eurypharynx*, *Saccopharynx*. Four of the 24 species taken solely below 1000 m are known to occur in the mesopelagic zone as well. Based on literature accounts, an additional four species sampled in the bathypelagic could be classed as epi-/mesopelagic contaminants (e.g., *Exocoetus obtusirostris*). Forty species were taken in discrete-depth samples both above and below 1000 m. These species can be divided into

three categories, based on capture depths: (1) spanners — species with broad vertical distributions in the meso- and bathypelagic zones; (2) vacillators — meso- and upper-bathypelagic species that occur primarily around the 1000 m isobath for all (non-migrators) or part (migrators) of the diel cycle; and (3) contaminants — epi- and mesopelagic species inadvertently collected in bathypelagic cod-ends during descent/retrieval. Again using literature records as a guide, 13 species occurring in bathypelagic samples appeared to be contaminants captured during net descent through the top 1000 m. These included small myctophid species (*Notolychnus*, *Diaphus*, *Benthoosema*) and small-bodied stomiiforms (*Vinciguerria*, *Valenciennellus*, *Margrethia*, *Argyropelecus*). Seventeen species can be classified as spanners, with broad vertical ranges and comparable abundances above and below 1000 m. These include all five *Cyclothone* species, several stomiids and melamphids, an assortment of taxa such as *Serrivomer*, *Gigantura* and *Melanonus*, and transforming larval bothids and eels that may have been in the process of settling to the benthos. The remaining vacillator species include those that live in the lower mesopelagic and upper bathypelagic and do not vertically migrate (*Sternoptyx*, *Scopeloberyx robustus*), as well as species undertaking broad vertical migrations that take them into the bathypelagic zone during daylight (*Ceratoscopelus*, *Hygophum*, *Lampanyctus*, *Melamphaes*).

3.4.3. Multivariate community analysis

In order to discriminate fish assemblages as a function of space, time, and gear, ordination by non-metric MDS was applied to the species \times station matrix after transformation.

Table 5

Faunal breakdown of fish species as a function depth collected in the Sargasso Sea during discrete-depth sampling. Fishes listed in rank order of abundance within depth category. Thirteen of 98 species not listed in this table were captured only in deployment (0–5000 m) nets.

Solely taken in < 1000-m tows	Taken in > and < 1000-m tows	Solely taken in > 1000-m tows
<i>Lobianchia dofleini</i>	<i>Cyclothone braueri</i>	<i>Dolicholagus longirostris</i>
Perciform larva	<i>Cyclothone pallida</i>	<i>Maulisia juvenile</i>
<i>Hygophum hygomii</i>	<i>Cyclothone microdon</i>	<i>Notoscopelus resplendens</i>
<i>Bregmaceros atlanticus</i>	<i>Cyclothone pseudopallida</i>	<i>Eurypharynx pelecanoides</i>
spotted larvae – TBD	<i>Lepidophanes guentheri</i>	<i>Lampanyctus nobilis</i>
<i>Bolinichthys photothorax</i>	<i>Ceratoscopelus warmingii</i>	gigantactinid male
<i>Diaphus dumerilii</i>	Bothid larva	<i>Eustomias fissibarbis</i>
<i>Hyporhamphus juvenile</i>	Eel leptocephalus larva	<i>Photonectes braueri</i>
<i>Coryphaena hippurus</i>	<i>Argyropelecus hemigymnus</i>	<i>Platytrectes apus</i>
<i>Ichthyococcus ovatus</i>	<i>Argyropelecus aculeatus</i>	<i>Rhynchactis male</i>
red-tailed fish larva	<i>Cyclothone acclinidens</i>	Ceratiid male
<i>Lobianchia gemellarii</i>	<i>Notolychnus valdiviae</i>	<i>Macroparalepis brevis</i>
<i>Lampanyctus alatus</i>	<i>Lampanyctus pusillus</i>	<i>Saccopharynx leptocephalus</i>
Echeneid juvenile	<i>Diaphus roei</i>	oneirodid male
Gempylid juvenile	<i>Sternoptyx diaphana</i>	<i>Diaphus cf. fragilis</i>
<i>Bonapartia pedalota</i>	<i>Lampanyctus photonotus</i>	<i>Exocoetus obtusirostris</i>
<i>Diplophos taenia</i>	<i>Idiacanthus fasciola</i>	Himantolophid male
<i>Gonostoma atlanticum</i>	<i>Benthoosema suborbitale</i>	<i>Poromitra capito</i>
<i>Diaphus taaningi</i>	<i>Melamphaes TBD</i>	<i>Rhadimnesthes decimus</i>
<i>Eustomias obscurus</i>	<i>Thunnus juvenile</i>	<i>Argyropelecus gigas</i>
Lophiiform larva	<i>Howella brodiei</i>	<i>Lophodolos acanthognathus</i>
	<i>Nannobranchium cuprarium</i>	<i>Omosudis lowii</i>
	<i>Diaphus rafinesquii</i>	<i>Scopeloberyx robustus</i>
	<i>Paralepis brevirostris</i>	<i>Sigmops elongatum</i>
	<i>Chauliodus danae</i>	
	<i>Diaphus brachycephalus</i>	
	<i>Vinciguerria poweriae</i>	
	<i>Hygophum taaningi</i>	
	<i>Margrethia obtusirostre</i>	
	<i>Scopelogadus m. mizolepis</i>	
	<i>Chauliodus sloani</i>	
	<i>Nesiarchus nasutus</i>	
	<i>Scopeloberyx opisthopterus</i>	
	<i>Poromitra crassiceps</i>	
	<i>Hygophum reinhardtii</i>	
	<i>Cryptopsaras couesii</i>	
	<i>Valencienellus tripunctulatus</i>	
	<i>Melanonus zugmayeri</i>	
	<i>Gigantura indica</i>	
	<i>Serrivomer beanii</i>	

Initial results revealed that two samples, SM1d.d (MOC-01, Station 1, 100–200 m, day) and SM4e.d (MOC-01, Station 4, 200–400 m, day), were highly dissimilar to each other and to all of the remaining samples. Sample SM1d.d contained a single specimen of *Hygophum taaningi*, which was the only time the species was encountered during the survey; sample SM4e.d contained a unique combination of myctophid larvae and deep-living hatch-*et*fish (*Sternoptyx*) juveniles. Since inclusion of these statistical outliers resulted in a tight grouping of all other samples and prevented discrimination of the remaining samples, these two samples were removed and multivariate analyses were re-run. Similarity profile tests (SIMPROF) of cluster analysis results determined a similarity level of 22% ($\pi=2.2$, $p < 2.41\%$) as an appropriate value for assemblage discrimination. SIMPROF found no statistical evidence for sub-structure at higher similarity values (e.g., at 26%, $\pi=1.35$, $p < 16.4\%$). At 22% similarity, 13 pelagic fish assemblages were discriminated. When MDS points (stations) represented in two dimensions were grouped according to this value, overlap was apparent (Fig. 4). However, the moderate 2-dimensional stress value (0.13) suggested that MDS provided a useful 2-D representation of assemblage structure. Stress values were not radically improved (decreased) via a 3-dimensional ordination (stress=0.1).

Characteristics of each assemblage are presented in Table 6. Despite the wide vertical distribution ranges of many species

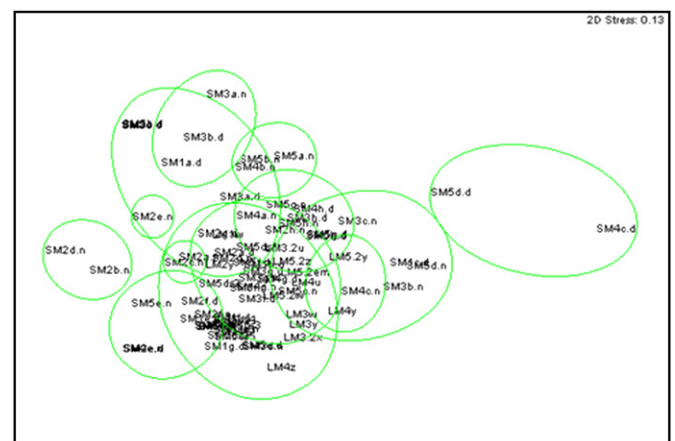


Fig. 4. Multi-dimensional scaling ordination plots of Sargasso Sea deep-pelagic samples collected during the CMarZ/Ronald H. Brown cruise. Circled groups are based on the classification results discriminated at the 22% similarity level. Sample codes are as in Table 1.

(Table 5), vertical zonation of faunal communities was readily discernable. Larval fishes dominated the ichthyofauna from 0–50 m, with three assemblages (III, IV, VI, Table 6) sharing this pattern. These assemblages were dispersed among the five

Table 6
 Characteristics of pelagic fish assemblages of the Sargasso Sea as discriminated by multivariate analyses. *N* – number of samples in group; SM – small (1-m²) MOCNESS; LM – large (10-m²) MOCNESS. No order is intended with assemblage numbering.

Assemblage	<i>N</i>	Gear	Assemblage characteristics
I	2	all SM	Station 2; 25–200 m; night; larval stomiiforms dominant
II	1	SM	Station 2; 200–400 m; night, few fish, no myctophids
III	5	all SM	4 of 5 Stations; 25–50 m; 4 of 5 night; misc. larval fish dominant
IV	8	all SM	4 of 5 Stations; 50–200 m; 3 d/5 n; misc larval fish, small myctophids, <i>Bregmaceros</i>
V	1	SM	Station 2; 50–100 m; night; diverse assemblage of myctophids, stomiiforms, perciform larvae
VI	6	all SM	Station 3(4), 2(1) and 5(1); 0–200 m, most top 50 m; all day; very sparse, low diversity, misc. fish larvae
VII	2	all LM	Stations 4, 5; 3000–4000 m; day; very sparse; one <i>Cyclothone</i> specimen in each sample
VIII	8	all SM	Station 5(4), 4(2), 3(1), 2(1); 4 d/4 n; 600–1000 m; dominated by <i>Cyclothone pallida</i>
IX	4	all SM	Stations 1,2,4,5; 2 d/2 n; 200–400 m; all samples contained <i>Argyropelecus</i>
X	8	all LM	All 5 Stations; 5 d/3 n; 1000–5000 m; dominated by multiple <i>Cyclothone</i> spp., high diversity
XI	5	2 SM, 3 LM	Station 3(3), 4(1), 5(1); 3 d/2 n; 100–400 and 2000–4500 m; very sparse catches with <i>Cyclothone braueri</i> plus few other taxa.
XII	8	all SM	Station 3(3), 4(2), 5(2), 1(1); 5 d/3 n; 400–1000 m; <i>Cyclothone pallida</i> and <i>braueri</i> co-dominant
XIII	19	all SM	All 5 Stations; 11 d/6 n; 400–800 m; <i>Cyclothone braueri</i> over 90% of samples

stations and throughout the diel cycle. They differed from each other mainly in relative abundance of certain taxa and diversity; day samples were much more depauperate than night. It should be noted that all of these assemblages contained only MOC-01 samples, which may select for less-mobile larval fishes over more active swimmers. Two assemblages (I, II) spanning the top 200 m were represented by a small number of samples each and larval fishes were conspicuous components. One assemblage, represented by a single sample (V) taken between 50–100 m at night at Station 2, contained a diverse assemblage of myctophids and stomiiform fishes, ostensibly at the apex of their diel vertical migration. Two assemblages were found between 200–400 m both day and night; one (IX) was characterized by the presence of the sternoptychid *Argyropelecus*, while the other included a subset of assemblage XI, characterized by sparse catches with low numbers of *Cyclothone braueri*. Two large assemblages were centered between 400–1000 m and were widespread among all stations both day and night. The largest assemblage (XII), represented by 19 samples, was characterized by the domination of *C. braueri*, which contributed over 90% of individuals from the samples. Assemblage XII, with eight samples, was characterized by the co-dominance of *C. braueri* and *C. pallida*. All samples comprising these assemblages were taken with the MOC01. Assemblage VIII, also represented by all MOC01 samples, was centered between 600–1000 m and was characterized by the domination of *C. pallida*. The majority of the MOC10 samples (eight in total) comprised the next-deepest assemblage (X), found between 1000–5000 m. This assemblage, spanning all five stations both day and night, was characterized by multiple *Cyclothone* species as well as generally higher diversity, especially among the rarer forms (e.g., male ceratioid anglerfishes). The final assemblage (VII), with two MOC10 samples, was differentiated mainly in its lack of fish – each sample contained a single *Cyclothone* specimen.

4. Discussion

The overall picture from physical oceanographic data collected during this survey was that the upper 1000 m of the Sargasso Sea is divided into three hydrographic regimes, while the bathypelagic was relatively uniform across the transect. This finding mirrors those of previous studies (Brooks, 1972; Worthington, 1976). The environmental gradation observed was not manifest in the faunal composition data, however, as multivariate analysis found depth to be a much stronger influencing factor; in the seven discriminated assemblages containing at least five samples, three or more stations were represented, irrespective of depth. In comparison, only one assemblage (XI) contained samples from

disjunct depth strata. The effect of depth on diversity was revealed by geometric abundance class analysis – the character of relative species abundance distributions between the meso- and bathypelagic zones were fundamentally dissimilar (Fig. 2). The epi- and mesopelagic zones exhibited a much higher percentage of common species, while the bathypelagic exhibited a much higher percentage of rarer species. This finding tracks the depth-dependent hydrographic patterns observed. Namely, increased stability in the bathypelagic zone favors increased numbers of rare species relative to the mesopelagic zone, where hydrographic and physical complexity (i.e., disturbances) favor higher numbers of common species relative to rare species.

DNA barcodes (i.e., short DNA sequences for species recognition and discrimination) determined for 30 described species of deep-sea fishes from the Sargasso Sea (Bucklin et al., 2010) represent a significant contribution to understanding patterns of diversity. A global effort is underway to determine DNA barcodes for all fishes: FISHBOL (Ward et al., 2009), yet few specimens of deep-sea fishes have been barcoded due to the challenges of appropriate sampling and preservation to allow molecular analysis. Notable among the species sequenced were male ceratioid anglerfishes; at present no key exists for males of many families (Pietsch, 2005) and DNA barcodes are particularly useful for this group to allow matching identified males with morphologically identified females. DNA barcoding of this group represents a major step towards understanding fish diversity in Earth's largest habitat.

Given the large distances between stations in this study, and the likely physical and ecological boundaries that were missed between stations, a detailed zoogeographical analysis is not warranted. However, as this study represents the deepest concerted sampling effort in the region, comparisons with available data can be made to infer large-scale biodiversity characteristics of the Sargasso Sea deep-pelagic environment. The most extensive mesopelagic sampling in the study area was that of the Woods Hole Oceanographic Institution, whose researchers conducted multiple cruises over multiple years to describe and explain the patterns of geographic distribution of micronekton in the North Atlantic (Backus et al., 1965, 1971, 1977). Although these surveys used different gear and sampled opportunistically (i.e., depth strata sampled according to acoustic backscatter intensity rather than depths chosen *a priori*), some faunal comparisons can be made. Backus et al. (1969) sampled depths primarily < 600 m and collected 105 species from 66 genera, 30 families, and eight orders, from 25 midwater trawl hauls in the western Sargasso between the Antilles and the Gulf Stream. Their data suggested a division of the study region into North and South Sargasso Sea Provinces, with the Subtropical Convergence Zone (STCZ) separating the two. This pattern was not

manifest in our data. Results of this study are more in agreement with those of Hulley and Krefft (1985), who found that the two provinces are distinguished primarily by differences in species abundance rather than ichthyofaunal structure. Their results were based on multivariate techniques similar to those used in this study. Fasham and Foxton (1979), in an examination of the distribution of pelagic shrimps, did not find the STCZ to be a biogeographic boundary in the eastern North Atlantic. The STCZ, in the western North Atlantic at least, appears to be a seasonal feature, forming in fall and winter and dissipating in summer months (Halliwell et al., 1991; Miller and McCleave, 2007). It should be noted that this study and Hulley and Krefft (1985) were based on fewer samples than Backus et al. (1977), so the latter's finding of biogeographic separation may have been influenced more by cold season sampling. A possible difference between their findings and ours may have been that the breakdown of the STCZ was occurring during our cruise, allowing remixing of fish assemblages. Our conclusion would be that the division of the Sargasso Sea into discrete biogeographic provinces based on mesopelagic species warrants further seasonally-integrated examination.

Integration of current knowledge on species' vertical distributions with catch data from this cruise suggests some degree of contamination effects from shallower depth strata, particularly from mesopelagic myctophid species (*Diaphus*, *Lepidophanes*), but this amount was not major compared to the taxa that are considered truly bathypelagic. These taxa include the ceratioid anglerfishes (eight species from five families), the bathypelagic eels (*Eurypharynx*, *Saccopharynx*, and *Serrivomer*), the great swallows (*Chiasmodon* and *Pseudoscopelus*), and the whalefishes (*Cetostoma* and *Rondeletia*). Perhaps the best indicator of the discreteness of the bathypelagic sampling in these waters was what was not captured in deep trawl hauls. The upper mesopelagic zone of the Sargasso Sea is generally dominated by myctophids (*Diaphus*, *Notolychnus*, *Myctophum*), lightfishes (*Vinciguerra* and *Pollichthys*) and shallow-living hatchetfishes (*Maurolicus*, *Valenciennellus*) (Gibbs and Krueger, 1987). These represented a minor component of abundance and biomass, but did add to the species richness total. A sampling foray into the mesopelagic zone during the last MOC 10 deployment (MOC10.5.7.4 in Table 1) showed fairly conclusively that the low catches observed in the deep tows was a true measure of the low biomass at depth rather than a flaw in the fishing ability of the new MOCNESS configuration.

Within the bathypelagic zone there appears to be three classes of ichthyofauna, not including the 'contaminant' species previously mentioned: spanners, vacillators, and holobathypelagic occupants. Spanners are those species that occur throughout the water column, with little regard for the 1000-m isobath. These include the numerical dominants such as *Cyclothone* spp. (Marshall, 1971; Kobayashi, 1974). As a general rule, these species do not migrate on a diel basis (Sutton, 2003), as this is a defining characteristic of the holomesopelagic fish fauna

(e.g., myctophids; Hopkins and Gartner, 1992). Their broad vertical ranges are largely due to ontogenetic migration, with smaller fish occurring shallower and larger occurring deeper (Brooks and Saenger, 1991; McClain et al., 2001). Vacillators include species whose distribution either hovers between 800–1500 m, also not migrating on a diel basis, such as *Serrivomer* and *Bathylagus*, or species that vertically migrate with an amplitude that takes them below 1000 m during the day, such as *Ceratoscopelus* and *Notoscopelus*. Revisiting the aforementioned studies of Backus et al. (1965, 1971, 1977), after adjustment for currently accepted taxonomy and validity (104 current species, 66 genera, 26 families, 11 orders), 46 (44%) of their species were also collected in this study. After removal of nine species captured in this survey in non-discrete trawl hauls, 10 of the 46 shared species were caught only above 1000 m in this study, 24 were caught both above and below 1000 m, and three were caught only below 1000 m. This suggests that spanning meso- and bathypelagic depths is a common phenomenon, and adds considerably to the ichthyofaunal diversity of the world ocean below 1000 m.

The holobathypelagic ichthyofauna includes true bathypelagic forms (i.e., those species rarely taken above 1000 m). These include fishes such as adult ceratioid anglerfishes (juveniles are captured shallow), eurypharyngid and saccopharyngid eels, and the Chiasmodontidae. It is of this holobathypelagic group that our global species inventory is particularly incomplete. Recent species descriptions of these taxa rival the South American ostariophysans in frequency among all fishes (e.g., Prokofiev and Kukuev, 2005, 2006; Pietsch and Baldwin, 2006; Melo et al., 2007; Pietsch, 2007; Melo, 2008), and far eclipse the ostariophysans in terms of frequency relative to the species number of their taxon. This reconfirms the notion of Robison (2004) that the bathypelagic is among the least known habitats on Earth in terms of biodiversity and community structure.

Acknowledgments

We would like to thank the NOAA Office of Ocean Exploration for their support, as well as the crew of the NOAA ship *Ronald H. Brown* for their excellent shiptime services. We thank L. Waterhouse, K. Parsons, V. Carmo and C.J. Sweetman for critically reading this manuscript. Support for this cruise was provided by the NOAA Ocean Exploration Program Grant #NA06OAR4600091, the Sloan Foundation, and the Census of Marine Life (CMarZ) project.

Appendix A

Pelagic fishes collected from 0–5000 m in the Western Subtropical and Tropical North Atlantic (R/V *Ronald H. Brown* cruise 06-03, April, 2006) is shown in Table A1.

Table A1

Pelagic fishes collected from 0–5000 m in the Western Subtropical and Tropical North Atlantic (R/V *Ronald H. Brown* cruise 06-03, April, 2006).

Taxon	Station 1	Station 2	Station 3	Station 4	Station 5	Cruise totals
ANGUILLIFORMES						
NEMICHTHYIDAE						
<i>Avocettina infans</i>	0	2	0	0	0	2
Nemichthyid leptocephalus	0	1	0	0	0	1
CONGRIDAE						
<i>Ariosoma leptocephalus</i>	0	0	0	1	0	1
SERRIVOMERIDAE						
<i>Serrivomer beanii</i>	0	1	1	0	2	4

Table A1 (continued)

Taxon	Station 1	Station 2	Station 3	Station 4	Station 5	Cruise totals
SACCOPHARYNGIFORMES						
EURYPHARYNGIDAE						
<i>Eurypharynx pelecanooides</i>	0	0	0	0	2	2
SACCOPHARYNGIDAE						
<i>Saccopharynx leptocephalus</i>	0	0	1	0	0	1
Eel leptocephalus larva	1	2	5	3	14	25
ARGENTINIFORMES						
MICROSTOMATIDAE						
<i>Dolicholagus longirostris</i>	1	1	0	0	2	4
PLATYTROCTIDAE						
<i>Platytrectes apus</i>	0	1	0	0	0	1
<i>Maulisia juvenis</i>	0	1	0	0	3	4
STOMIIFORMES						
GONOSTOMATIDAE						
<i>Bonapartia pedaliota</i>	0	3	1	1	1	6
<i>Cyclothone acclinidens</i>	0	0	0	7	165	172
<i>Cyclothone alba</i>	0	0	1	2	0	3
<i>Cyclothone braueri</i>	138	412	214	142	367	1273
<i>Cyclothone microdon</i>	131	99	45	41	64	380
<i>Cyclothone pallida</i>	217	83	181	66	383	930
<i>Cyclothone pseudopallida</i>	18	52	1	0	23	94
<i>Cyclothone</i> (damaged)	1	0	1	1	0	3
<i>Cyclothone</i> larvae	0	10	0	0	0	10
<i>Diplophos taenia</i>	0	0	0	0	1	1
<i>Gonostoma atlanticum</i>	0	0	0	0	2	2
<i>Margrethia obtusirostra</i>	0	0	0	1	1	2
<i>Sigmops elongatum</i>	1	0	0	0	3	4
PHOSICHTHYIDAE						
<i>Ichthyococcus ovatus</i>	0	0	0	0	1	1
<i>Vinciguerria nimbaria</i>	0	0	0	0	1	1
<i>Vinciguerria poweriae</i>	1	2	0	1	2	6
STERNOPTYCHIDAE						
<i>Argyropelecus aculeatus</i>	2	15	0	2	6	25
<i>Argyropelecus gigas</i>	0	0	0	0	5	5
<i>Argyropelecus hemigymnus</i>	2	12	10	11	13	48
<i>Argyropelecus</i> larva	0	0	2	1	4	7
<i>Sternoptyx diaphana</i>	3	16	2	6	9	36
<i>Sternoptyx</i> juvenile	1	1	1	1	1	5
<i>Valencienellus tripunctulatus</i>	0	2	6	0	5	13
<i>Sternoptychid</i> larvae	0	1	2	0	0	3
STOMIIDAE						
<i>Aristostomias xenostoma</i>	0	0	0	0	1	1
<i>Astronesthes cf indicus</i>	0	0	0	0	1	1
<i>Astronesthes micropogon</i>	0	0	0	0	1	1
<i>Astronesthes similis</i>	0	0	0	0	1	1
<i>Astronesthes</i> juvenile	0	0	0	0	2	2
<i>Chauliodus danae</i>	0	2	4	2	0	8
<i>Chauliodus sloani</i>	1	3	0	1	0	5
<i>Eustomias</i> (<i>Biradiostomias</i>) sp.	0	0	0	1	0	1
<i>Eustomias fissibarbis</i>	0	1	0	0	0	1
<i>Eustomias macrurus</i>	0	0	0	0	1	1
<i>Eustomias obscurus</i>	1	1	0	0	0	2
<i>Eustomias</i> postlarva	0	0	0	1	0	1
<i>Idiacanthus fasciola</i>	0	2	0	1	8	11
<i>Leptostomias</i> sp. A	0	0	0	0	1	1
<i>Malacosteus niger</i>	0	0	0	0	2	2
<i>Photonectes cf. achirus</i>	0	0	0	0	1	1
<i>Photonectes braueri</i>	0	1	0	0	0	1
<i>Photonectes dinema</i>	0	1	0	0	0	1
<i>Photostomias goodyeari</i>	0	1	0	0	0	1
<i>Rhadinesthes decimus</i>	0	0	0	1	0	1
<i>Stomias affinis</i>	0	0	0	0	1	1
<i>Stomiid</i> larvae	2	5	2	0	2	11
<i>Stomiiform</i> larvae	0	20	0	0	0	20
AULOIFORMES						
GIGANTURIDAE						
<i>Gigantura indica</i>	0	0	0	0	2	2
PARALEPIDIDAE						
<i>Macroparalepis cf. brevis</i>	0	0	1	0	0	1

Table A1 (continued)

Taxon	Station 1	Station 2	Station 3	Station 4	Station 5	Cruise totals
<i>Paralepis brevisrostris</i>	0	0	1	0	1	2
Paralepidid juvenile	1	1	0	0	0	2
OMOSUDIDAE						
<i>Omosudis lowii</i>	1	0	0	0	0	1
SCOPELARCHIDAE						
<i>Benthalbella infans</i>	0	0	1	0	0	1
Scopelarchid juvenile	0	0	0	0	1	1
EVERMANNELLIDAE						
<i>Coccorella atlantica</i>	0	1	0	0	0	1
MYCTOPHIFORMES						
MYCTOPHIDAE						
<i>Benthoosema suborbitale</i>	0	2	0	0	8	10
<i>Bolinichthys indicus</i>	1	0	0	0	0	1
<i>Bolinichthys photothorax</i>	0	2	1	1	7	11
<i>Bolinichthys</i> juvenile	0	0	0	0	3	3
<i>Ceratoscopelus warmingii</i>	1	1	10	9	31	52
<i>Diaphus brachycephalus</i>	0	0	1	1	6	8
<i>Diaphus dumerilii</i>	0	0	0	1	2	3
<i>Diaphus effulgens</i>	0	0	0	0	1	1
<i>Diaphus cf fragilis</i>	0	0	0	1	0	1
<i>Diaphus lucidus</i>	0	0	0	0	9	9
<i>Diaphus rafinesquii</i>	0	1	0	0	1	2
<i>Diaphus roei</i>	0	0	0	0	9	9
<i>Diaphus subtilis</i>	0	0	0	0	4	4
<i>Diaphus taaningi</i>	1	0	0	0	0	1
<i>Diaphus</i> juv.	0	0	1	0	3	4
<i>Gonichthys cocco</i>	0	0	0	1	0	1
<i>Hygophum benoiti</i>	0	1	0	0	0	1
<i>Hygophum hygomii</i>	10	7	0	0	0	17
<i>Hygophum macrochir</i>	0	0	0	1	5	6
<i>Hygophum reinhardtii</i>	0	0	2	0	1	3
<i>Hygophum taaningi</i>	1	0	1	0	10	12
<i>Lampadena luminosa</i>	0	0	0	0	1	1
<i>Lampanyctus alatus</i>	0	0	0	0	2	2
<i>Lampanyctus nobilis</i>	0	0	0	0	8	8
<i>Lampanyctus photonotus</i>	0	0	12	3	4	19
<i>Lampanyctus pusillus</i>	0	8	0	1	2	11
<i>Lampanyctus</i> juvenile	0	0	0	0	2	2
<i>Lepidophanes guentheri</i>	0	2	1	2	75	80
<i>Lobianchia dofleini</i>	0	25	0	0	0	25
<i>Lobianchia gemellarii</i>	0	2	0	1	2	5
<i>Nannobranchium atrum</i>	0	0	2	0	0	2
<i>Nannobranchium cuprarium</i>	2	4	3	1	0	10
<i>Notolychnus valdiviae</i>	2	0	1	2	9	14
<i>Notoscopelus resplendens</i>	1	1	0	0	0	2
Myctophid larvae	18	26	7	6	55	112
BELONIFORMES						
EXOCOETIDAE						
<i>Exocoetus obtusirostris</i>	0	0	0	1	0	1
HEMIRHAMPHIDAE						
<i>Hyporhamphus</i> juvenile	0	0	0	0	3	3
LAMPRIDIFORMES						
REGALECIDAE						
<i>Regalecus glesne</i>	0	1	0	0	0	1
STYLEPHORIDAE						
<i>Stylephorus chordatus</i>	0	0	0	0	1	1
GADIFORMES						
MELANONIDAE						
<i>Melanonus zugmayeri</i>	1	1	0	0	1	3
BREGMACEROTIDAE						
<i>Bregmaceros atlanticus</i>	0	0	1	2	8	11
LOPHIIFORMES						
HIMANTOLOPHIDAE						
Himantolophid male	0	0	0	1	0	1
ONEIRODIDAE						
<i>Lophodolos acanthognathus</i>	1	0	0	0	0	1
Oneirodid male	0	0	0	0	3	3
CERATIIDAE						
<i>Ceratias holboelli</i>	0	0	0	0	1	1

Table A1 (continued)

Taxon	Station 1	Station 2	Station 3	Station 4	Station 5	Cruise totals
<i>Cryptosaras couesii</i>	0	2	0	0	0	2
Ceratiid male	0	0	1	0	0	1
GIGANTACTINIDAE						
<i>Rhynchactis</i> male	0	0	1	0	0	1
Gigantactinid male	0	0	0	0	2	2
LINOPHRYNIDAE						
<i>Linophryne</i> sp. male	1	1	0	0	0	2
Ceratioid larva	0	0	0	1	0	1
Lophiiform larva	0	1	0	0	0	1
STEPHANOBERYCFORMES						
MELAMPHAIIDAE						
<i>Melamphaes</i> TBD*	5	5	5	3	3	21
<i>Poromitra capito</i>	0	0	0	1	0	1
<i>Poromitra crassiceps</i>	0	1	1	0	0	2
<i>Scopeloberyx opisthopterus</i>	6	0	0	0	2	8
<i>Scopeloberyx robustus</i>	1	0	0	0	0	1
<i>Scopelogadus mizolepis mizolepis</i>	0	0	2	1	0	3
Melamphaid juvenile	0	0	2	0	0	2
RONDELETIIDAE						
<i>Rondeletia bicolor</i>	0	0	0	0	1	1
CETOMIMIDAE						
<i>Cetostoma regani</i>	0	0	1	0	0	1
BERYCFORMES						
DIRETMIDAE						
<i>Diretmus argenteus</i>	0	0	0	1	0	1
SCORPAENIFORMES						
Scorpaenid larva	0	0	0	0	1	1
PERCIFORMES						
HOWELLIDAE						
<i>Howella brodiei</i>	0	0	1	0	3	4
EPIGONIDAE						
Epigonid larvae	0	0	0	1	0	1
BRAMIDAE						
<i>Brama caribbea</i>	0	0	0	0	1	1
CHIASMODONTIDAE						
<i>Chiasmodon niger</i>	1	0	0	0	0	1
<i>Pseudoscopelus</i> "sp. A" cf <i>obtusifrons</i>	0	1	0	0	0	1
CORYPHAENIDAE						
<i>Coryphaena hippurus</i>	0	0	1	0	0	1
ECHENEIDAE						
Echeneid juvenile	0	0	0	1	0	1
GEMPYLIDAE						
<i>Nesiarchus nasutus</i>	1	1	0	1	1	4
Gempylid juvenile	0	0	2	1	0	3
SCOMBRIDAE						
<i>Thunnus</i> juvenile	0	0	0	1	0	1
Scombroid larva	0	1	1	1	2	5
Perciform larva	1	2	0	0	0	3
PLEURONECTIFORMES						
Bothid larva	2	0	10	0	11	23
TETRAODONTIFORMES						
Tetraodontiform juvenile	1	0	0	0	0	1
LARVAL FISHES – TBD**	35	4	40	66	77	223
Minimum no. species	36	49	39	45	72	127
No. fish	617	859	594	408	1487	3965
Biomass (g)	32.96	87.89	12.15	174.68	187.40	495.08

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