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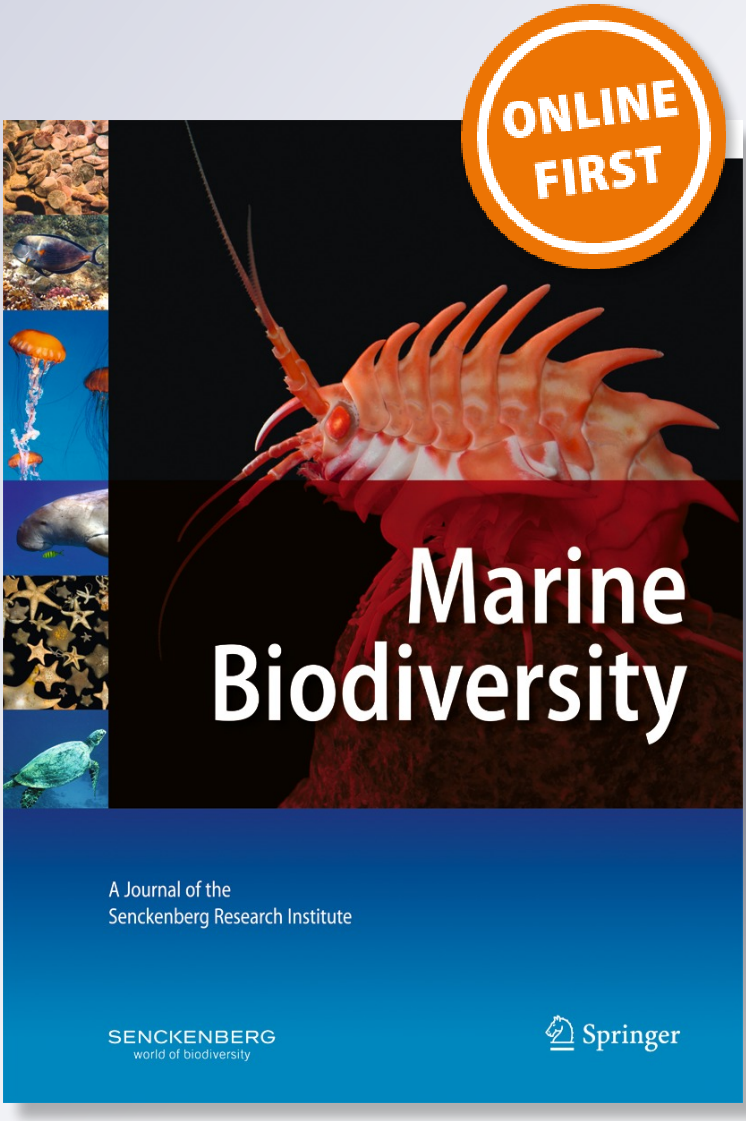

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Diversity of midwater cephalopods in the northern Gulf of Mexico: comparison of two collecting methods

H. Judkins[1] · M. Vecchione[2] · A. Cook[3] · T. Sutton[3]

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Abstract The *Deepwater Horizon* Oil Spill (DWHOS) necessitated a whole-water-column approach for assessment that included the epipelagic (0–200 m), mesopelagic (200–1000 m), and bathypelagic (>1000 m) biomes. The latter two biomes collectively form the largest integrated habitat in the Gulf of Mexico (GOM). As part of the Natural Resource Damage Assessment (NRDA) process, the Offshore Nekton Sampling and Analysis Program (ONSAP) was implemented to evaluate impacts from the spill and to enhance basic knowledge regarding the biodiversity, abundance, and distribution of deep-pelagic GOM fauna. Over 12,000 cephalopods were collected during this effort, using two different trawl methods (large midwater trawl [LMT] and 10-m^2 Multiple Opening and Closing Net Environmental Sensing System [MOC10]). Prior to this work, 93 species of cephalopods were known from the GOM. Eighty cephalopod species were sampled by ONSAP, and additional analyses will certainly increase this number as hard-to-identify taxa are resolved. Of these species, seven were previously unknown in the GOM, including two probable undescribed species. Because additional work is continuing using only the MOC10, cephalopod species composition of the LMT and MOC10 trawls are compared here for possible differences in inferred diversity and relative abundance. More than twice as many specimens were collected with the LMTs than the MOC10, but the numbers of species were similar between the two gear types. Each gear type collected eight species that were not collected by the other type.

Keywords Deep sea · Cephalopods · Gulf of Mexico · MOCNESS · Trawl

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Introduction

Cephalopods of the Gulf of Mexico (GOM), from the inshore areas to the deep sea, include many species of squids, octopods, and their relatives. Neritic regions of the GOM have been well-studied, whereas the cephalopods of the deep ocean remain poorly known. Modern, comprehensive systematic studies began with G. Voss, who reported 42 neritic and oceanic species in 1956 (Voss 1956). Since then, many oceanic species have been added to the list (Voss and Voss 1962; Roper 1964; Voss 1964; Roper et al. 1969; Lipka 1975; Passarella 1990). In this region, the composition of the cephalopod fauna off southern Florida is the best-studied, while the fauna of the rest of the GOM has received much less attention. Overall abundance and distribution of cephalopods in the GOM have been documented (Voss 1956; Passarella 1990; Vecchione 2003; Judkins 2009), but none of these studies has focused specifically on the meso- and bathypelagic zones (0–1500 m) of the GOM.

The *Deepwater Horizon* Oil Spill (DWHOS) was unique in the volume of oil released and in the depth at which the release occurred (~1500 m), necessitating assessment of the whole water column, including the epipelagic (0–200 m), mesopelagic (200–1000 m), and bathypelagic (>1000 m) biomes. The latter two biomes collectively form the deep-pelagic realm

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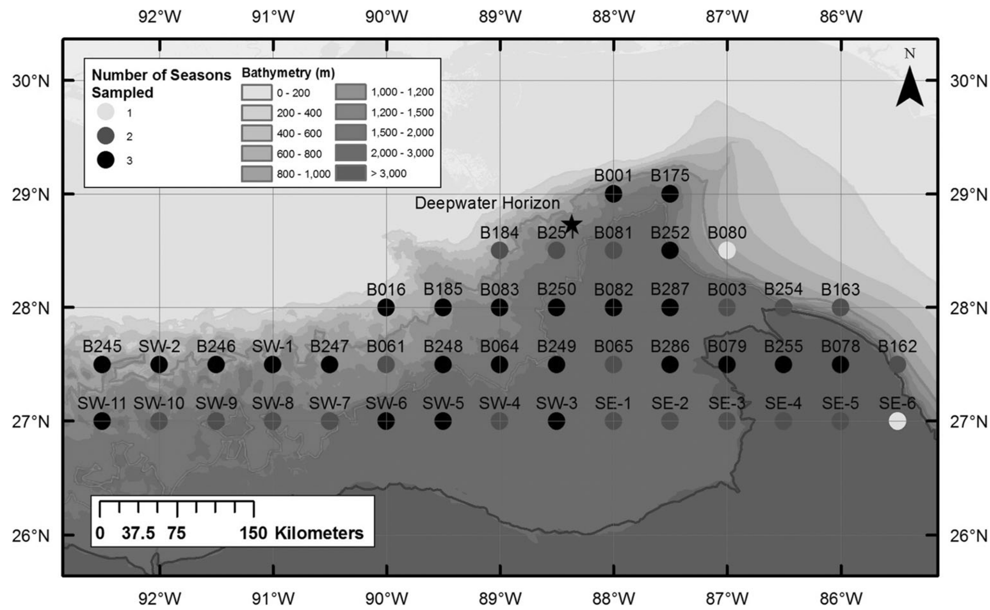


Fig. 1 Offshore Nekton Sampling and Analysis Program (ONSAP) sampling stations, all cruises. These are stations that are used by the long-term Southeast Area Monitoring and Assessment Program (SEAMAP) in the Gulf of Mexico

(Sutton 2013), the largest habitat in the GOM. This habitat received the initial oil/methane discharge from the DWHOS, resulting in persistent deep (800–1300 m) plumes that amounted to one-third of the total mass of discharged hydrocarbons. Because of the lack of comprehensive data regarding biodiversity, quantitative abundance, and distribution of the deep-pelagic fauna (see Webb et al. 2010), a large-scale program, the Offshore Nekton Sampling and Analysis Program (ONSAP), was developed and implemented in 2010–2011 as part of the Natural Resource Damage Assessment (NRDA). The deep-pelagic nekton sample set obtained by ONSAP is the largest of its kind ever collected. We report here the ONSAP cephalopod results, including a taxonomic breakdown by family group. Because a follow-up sampling project continues but uses only one of the two major ONSAP sampling gear types, we focus on comparison of the two net types used throughout ONSAP. The vertical-distribution results are not reported here, as they will be included with the additional discrete-depth samples that are being collected in the follow-up research.

Materials and methods

The station map (Fig. 1) summarizes stations visited throughout ONSAP. Two types of gear were used to collect fishes and invertebrates during ONSAP. One type, referred to collectively here as large midwater trawls (LMT), included several trawls with a variety of specific details, because gear damage and timely availability of replacement nets necessitated changes during the sampling. All of the LMT gear had mouth openings an order of magnitude larger than the MOC10

Table 1 Offshore Nekton Sampling and Analysis Program sampling cruises: ship names, cruise number, dates, net type and size

Cruise name	Cruise number	Dates	Net type	Net size
NOAA Ship *Pisces*	PC8	12/1/10–12/20/10	HSRT	336.64 m^2 EMA[a]
NOAA Ship *Pisces*	PC9	3/22/11–4/11/11	HSRT and IYGPT	336.64 m^2; 171.3 m^2 EMA
NOAA Ship *Pisces*	PC10	6/23/11–7/13/11	Irish herring trawl	165.47 m^2 EMA
NOAA Ship *Pisces*	PC12	9/8/11–9/27/11	Irish herring trawl	165.47 m^2 EMA
M/V *Meg Skansi*	MS6	1/27/11–3/30/11	MOC10	10 m^2
M/V *Meg Skansi*	MS7	4/18/11–6/30/11	MOC10	10 m^2
M/V *Meg Skansi*	MS8	7/18/11–9/30/11	MOC10	10 m^2

[a] Effective mouth area (EMA) is the fishing circle in front of the 80-cm mesh section for each net. *HSRT* high-speed rope trawl, *IYGPT* International Young Gadoid Pelagic Trawl, *MOC10* 10-m^2 Multiple Opening/Closing Net and Environmental Sensing System

described below, a very important characteristic when sampling cephalopods (Hoving et al. 2014). Table 1 details the ships used, sampling dates, net types, and mesh sizes for each cruise. The National Oceanic and Atmospheric Administration (NOAA) research vessel (R/V) *Pisces* trawled with a high-speed rope trawl (HSRT) in December 2010. The cruise in March 2011 used the HSRT and then, after damage to the HSRT, the International Young Gadoid Pelagic Trawl (IYGPT). The June and September cruises of 2011 used an Irish herring trawl. The latter, plus the HSRT and the IGYPT, comprise our LMT category. The LMT nets had very wide mesh in the wings, tapering to small mesh at the cod end. Additionally, a 10-m^2 mouth area Multiple Opening and Closing Net and Environmental Sensing System (MOC10) with 3-mm mesh was used on separate cruises throughout the project. The six nets of the MOC10 were 3-mm mesh size throughout and are therefore more quantitative. The MOC10 also allows inference of discrete depths at which organisms were captured. Our study of cephalopod vertical distribution continues in a follow-up project (www.deependconsortium.org) using only the MOC10. Cruises using each gear type were conducted throughout the year, with multiple stations repeated by both. As with vertical distribution, seasonal and interannual variability will be addressed after the follow-up MOC10 sampling is completed.

LMT sampling took place 24 h day^{-1} with two daytime tows and two nighttime tows per station. For each diel period, one LMT tow fished from 700 m to the surface. A second tow targeted a maximum depth of 1400 m, and was slowly hauled obliquely to 700 m over a period of 1 h; once it reached 700 m, the net was hauled back at a faster winch speed. In total, 169 tows were conducted with the LMTs. During the *Pisces* cruises, field identification of cephalopod species was attempted, and then the animals were placed in containers of 10 % formalin/seawater mix. After the cruises, field identifications were verified or corrected by H. Judkins and M. Vecchione.

To assess the vertical distribution (0–1500 m) of macroplankton and micronekton, the MOC10 was used during January, June, and September of 2011 by sampling in

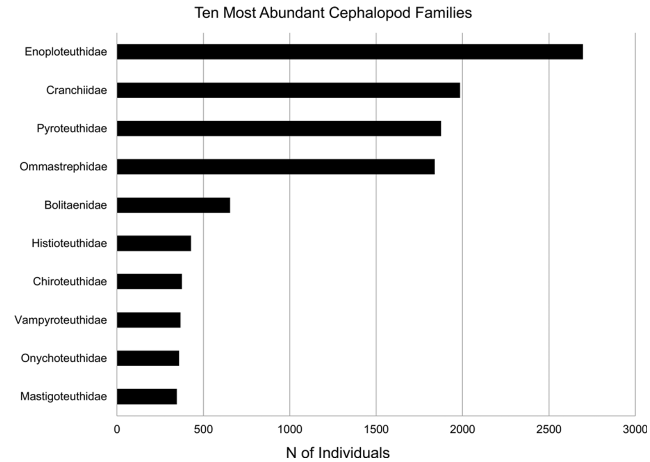


Fig. 2 Number of individuals for the ten most abundant cephalopod families from ONSAP

discrete depth intervals at the offshore stations aboard the M/V *Meg Skansi*. The MOC10 was deployed twice (one day tow, one night tow) at each station. Each tow lasted 4–6 h and was timed to optimize the differences in diel distribution patterns. The first net, designated net 0, was open from the surface to the deepest depth sampled (Table 2). Upon commencing the oblique tow back to the surface, nets were opened and closed to target the depth bins in Table 2. A total of 251 MOC10 tows were conducted during the *Meg Skansi* cruises. The *Meg Skansi* specimens were preserved immediately after net recovery. All samples were transported to T. Sutton's lab and sorted into major taxon groups. Cephalopod identification occurred in H. Judkins' lab, with M. Vecchione verifying identification.

Six common cephalopod species were selected for size-class comparisons by the two net types (Figs. 4, 5, 6, 7, 8, and 9), including *Cranchia scabra*, *Vampyroteuthis infernalis*, *Mastigoteuthis agassizii*, *Haliphron atlanticus*, *Bathyteuthis* sp. (*B. abyssicola*, sp. A, and possible sp. B), and *Abralia*

Table 2 Offshore Nekton Sampling and Acoustics Program MOC10 (see Table 1 for details) depth bins for each of the six nets

Net number	Depth bin (m)
Net 0	0–1500
Net 1	1500–1200
Net 2	1200–1000
Net 3	1000–600
Net 4	600–200
Net 5	200–0

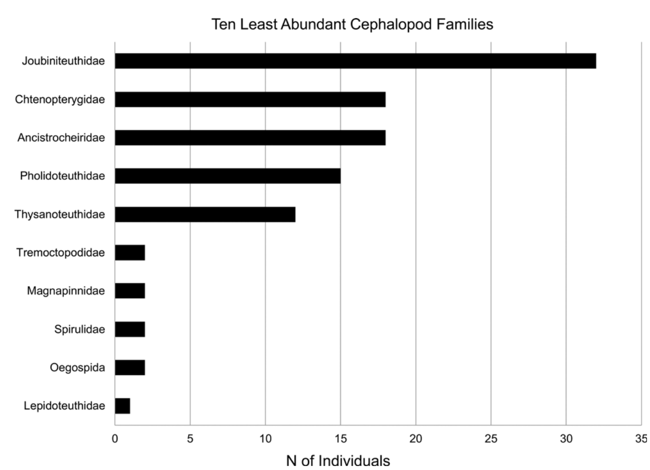


Fig. 3 Number of individuals for the ten least abundant cephalopod families from ONSAP

Table 3 Offshore Nekton Sampling and Analysis Program cephalopod species list with number of specimens measured and minimum, mean, and maximum mantle lengths (mm) for MOC10 and large midwater trawl (LMT) specimens

Classification	Species	Number of MOC 10 specimens	MOC10 size (mm ML)	Number of LMT specimens	LMT size (mm ML)
			Min-Mean-Max		Min-Mean-Max
Class Cephalopoda					
Order Vampyromorpha					
Vampyroteuthidae	*Vampyroteuthis infernalis*	117	4-13-93	180	10-37-103
Order Octopoda					
Family: Argonautidae	*Argonauta argo*	31	3-6-15	15	8-15-26
Family: Alloposidae	*Haliphron atlanticus*	28	3-11-32	18	17-88-235
Family: Tremoctopodidae	*Tremoctopus violaceus*			2	41-43-45
Family: Octopodidae	*Callistoctopus macropus*	1	10-10-10		
	Macrotritopus defilippi	12	4-7-12		
	Octopus vulgaris	1	15-15-15		
	Pteroctopus tetracirrchus			4	12-15-17
	Scaeurgus unicirrhus	1	12-12-12	1	10-10-10
	Tetracheledone spinicirrhus	1	10-10-10		
Family: Amphitretidae	*Bolitaena pygmaea*	53	5-18-64	21	18-29-41
	Japetella diaphana	98	5-20-55	72	
Order: Oegopsida					
Family: Brachioteuthidae	*Brachioteuthis* sp.	34	6-19-47	28	17-52-112
Family: Chiroteuthidae	*Asperoteuthis acanthoderma*			6	117-518-1370
	Chiroteuthis joubini	1	54-54-54	20	19-67-132
	Chiroteuthis mega	8	58-83-121	7	61-109-201
	Chiroteuthis veranyi			1	
	Grimalditeuthis bonplandi	42	9-43-84	71	21-71-111
	Planctoteuthis danae				
	Planctoteuthis lippula	1	28-28-28	1	122-122-122
Family: Joubiniteuthidae	*Joubiniteuthis portieri*	11	8-32-39	16	40-83-163
Family: Magnapinnidae	*Magnapinna pacifica*	2	28-30-31		
Family: Mastigoteuthidae	*Echinoteuthis atlantica*	2	15-24-32	7	44-100-194
	Mastigoteuthis agassizii	73	13-44-110	169	30-69-126
	Mastigopsis hjorti	4	13-19-22	14	47-87-147
	Magnoteuthis magna	8	10-22-49	13	41-82-189
Family: Cranchiidae					
Subfamily: Cranchiinae	*Cranchia scabra*	304	4-16-115	312	10-34-135
	Leachia atlantica	106	7-44-73	103	32-54-76
	Leachia lemur	7	23-30-46	10	30-45-63
	Liocranchia reinhardti	2	29-29-29	9	26-47-121
Subfamily: Taoniinae	*Bathothauma lyromma*	12	5-18-82	29	39-88-154
	Egea inermis	4	9-23-39	4	65-167-213
	Galiteuthis armata	10	18-28-45	107	18-109-465
	Helicocranchia papillata			1	46-46-46
	Helicocranchia pfefferi	21	13-32-59	96	18-40-62
	Helicocranchia sp. A	17	5-18-61		
	Liguriella podophthalma	8	8-12-30	1	25-25-25
	Megalocranchia sp.	15	11-57-300	10	25-89-205
	Sandalops melancholicus	14	7-27-46	10	17-40-83
	Taonius pavo	3	20-24-28	10	48-121-235
	Teuthowenia megalops	1	10-10-10	1	242-242-242

Table 3 (continued)

Classification	Species	Number of MOC 10 specimens	MOC10 size (mm ML)	Number of LMT specimens	LMT size (mm ML)
Family: Cycloteuthidae	*Cycloteuthis sirventi*	7	9-19-32	5	41-76-142
	Discoteuthis discus	12	6-18-50	15	25-54-104
	Discoteuthis sp.	6	5-8-13	2	40-49-58
Family: Ancistrocheiridae	*Ancistrocheirus lesueurii*	5	4-11-23	13	12-29-54
Family: Enoploteuthidae	*Abralia redfieldi*	59	5-9-17	453	5-23-46
	Abralia veranyi	12	6-11-23	224	11-28-43
	Abraliopsis atlantica	28	11-17-27	331	9-23-41
	Abraliopsis morisii	1	10-10-10	5	15-20-24
	Enoploteuthis anapsis	2	13-15-17	161	11-26-75
	Enoploteuthis leptura			31	17-39-70
Family: Lycoteuthidae	*Lampadioteuthis megaleia*	1	4-4-4	2	20-20-20
	Lycoteuthis lorigera	1	13-13-13		
	Lycoteuthis sp.	4	5-8-10		
	Lycoteuthis springeri	1	7-7-7		
	Selenoteuthis scintillans	29	7-13-29	89	14-27-41
Family: Pyroteuthidae	*Pyroteuthis margaritifera*	80	7-16-115	392	11-25-40
	Pterygioteuthis gemmata	12	9-15-22	13	10-16-19
	Pterygioteuthis giardi	18	10-16-37	46	13-19-28
Family: Histioteuthidae	*Histioteuthis bonnellii*				
	Histioteuthis corona	42	6-15-46	77	11-53-183
	Histioteuthis reversa			7	25-49-73
	Stigmatoteuthis arcturi	82	2-14-50	80	11-43-180
Family: Lepidoteuthidae	*Lepidoteuthis grimaldii*			1	83-83-83
Family: Octopoteuthidae	*Octopoteuthis danae*	1	32-32-32	21	20-54-145
	Octopoteuthis megaptera	4	18-32-41		
	Octopoteuthis sp.	28	4-14-39	95	17-50-172
	Taningia danae	9	7-19-30	19	17-72-170
Family: Pholidoteuthidae	*Pholidoteuthis adami*	1	21-21-21	5	16-68-176
	Pholidoteuthis massyae			8	33-65-99
Family: Neoteuthidae	*Neoteuthis thielei*	8	19-34-56	10	30-68-114
	Narrowteuthis nesisi	6	27-40-51	15	30-66-110
Family: Ommastrephidae	*Hyaloteuthis pelagica*	9	4-8-17	1	68-68-68
	Ommastrephes bartramii	13	5-8-16	206	13-50-523
	Ornithoteuthis antillarum	36	3-9-23	1066	12-55-151
	Sthenoteuthis pteropus	17	5-10-25	84	14-68-317
Family: Onychoteuthidae	*Onychoteuthis banksii*	58	4-12-37	180	15-41-93
	Onykia carriboea			9	26-41-63
	Onykia sp.			2	37-45-52
	Walvisteuthis jeremiahi	14	5-10-24	12	22-49-80
Family: Thysanoteuthidae	*Thysanoteuthis rhombus*	5	7-8-11	6	15-70-108
Order: Sepioidea					
Family: Sepiolidae	*Heteroteuthis dagamensis*	3	8-11-13	17	10-17-27
	Heteroteuthis sp.	20	3-7-15	14	10-18-24
Order: Spirulida					
Family: Spirulidae	*Spirula spirula*	1	16-16-16	1	21-21-21
Family: Bathyteuthidae	*Bathyteuthis abyssicola*	6	6-15-27	14	28-46-97
	Bathyteuthis sp. A	27	6-15-72	51	12-40-67
Family: Chtenopterygidae	*Chtenopteryx sicula*	10	7-10-15	8	18-38-64

Table 4 Species found in only MOC10 or large midwater trawl (LMT) samples from the Offshore Nekton Sampling and Analysis Program

MOC10 only species	LMT only species
Callistoctopus macropus	*Asperoteuthis acanthoderma*
Liguriella podophthalma	*Chiroteuthis veranyi*
Macrotritopus defilippi	*Enoploteuthis leptura*
Magnapinna pacifica	*Helicocranchia papillata*
Octopus vulgaris	*Histioteuthis bonnellii*
Planctoteuthis danae	*Histioteuthis reversa*
Planctoteuthis lippula	*Pholidoteuthis massyae*
Tetracheledone spinicirrhus	*Tremoctopus violaceus*

redfieldi. These six were selected due to confidence in species identification and because they were abundant in the samples. The dorsal mantle length (DML) was measured on all specimens that were in adequate condition.

We also compared the two gear types with respect to the expected number of species that were collected in each. Rarefaction is a diversity method used to correct for unbalanced sampling structure. The rarefaction curve is produced by repeatedly re-sampling the pool of N individuals or samples (Gotelli and Colwell 2004). It is dependent on the shape of the species abundance curve rather than the absolute number of specimens per sample. This method is valid when the same groups of organisms are being compared and contrasted—in this case, deep-sea cephalopods in respective trawling methods. Rarefaction curves were created using EstimateS software (Colwell 2013). Cephalopods identified only to family level ($n = 1429$ cephalopods) were not included in rarefaction analyses.

Results

In total, 12,076 cephalopods were examined for ONSAP from all cruises. The *Pisces* cruises collected 8749 and the *Meg Skansi* cruises 3327 cephalopods. Included in the combined total are 85 species in 30 families. The ten most abundant families collected during the current study are presented in Fig. 2. Figure 3 presents the ten least abundant cephalopod families. At least seven species were previously unknown in the region. Cephalopods that are new records for the GOM include *Heteroteuthis dagamensis*, *Magnapinna pacifica*, *Lampadioteuthis megaleia*, *Neoteuthis thielei*, *Narrowteuthis nesisi*, *Bathyteuthis* sp. A and a possible sp. B, *Helicocranchia* sp. A; and possible additional undescribed species of Taoniinae which will require additional study. *Walvisteuthis jeremiahi* is an onychoteuthid that has been recently described from the GOM and was found in this study (Vecchione et al. 2015). A complete species list, including minimum, mean, and maximum mantle lengths by species, is included in Table 3.

Gear comparison

The two gear types, LMT and MOC10, collected a wide diversity of cephalopods (Table 3). The LMT captured a total of 77 species in 169 tows, while the MOC10 captured a total of 76 species in 251 tows. The number of individuals per tow for each gear type was 52 individuals tow^{-1} for the LMT and 13 individuals tow^{-1} for the

Fig. 4 *Cranchia scabra* size class comparison by net type; pelagic trawl = large midwater trawls (LMT)

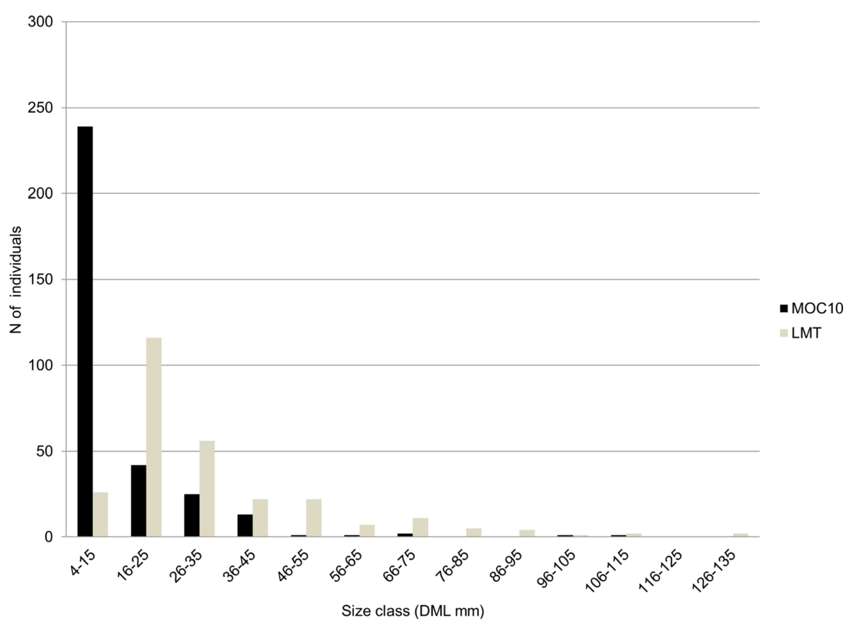
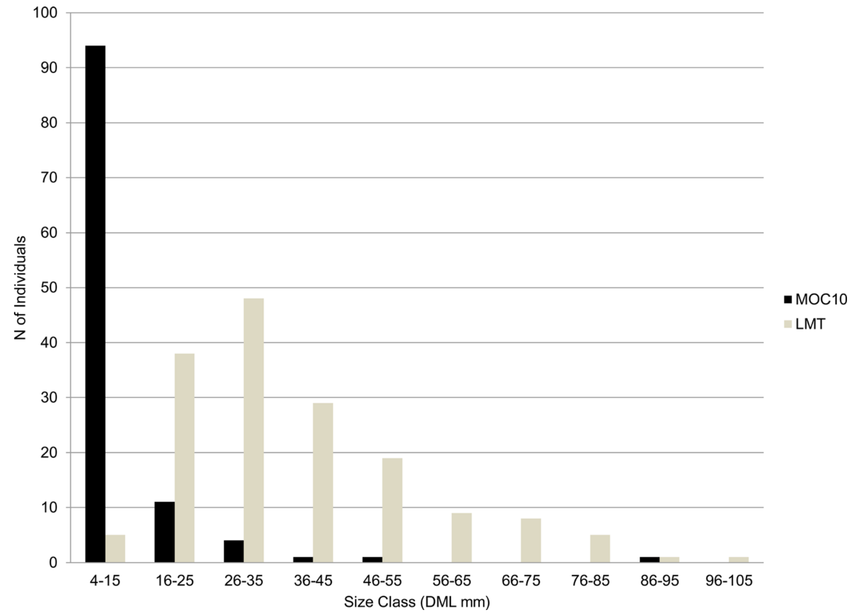


Fig. 5 *Vampyroteuthis infernalis* size class comparison by net type; pelagic trawl = LMT

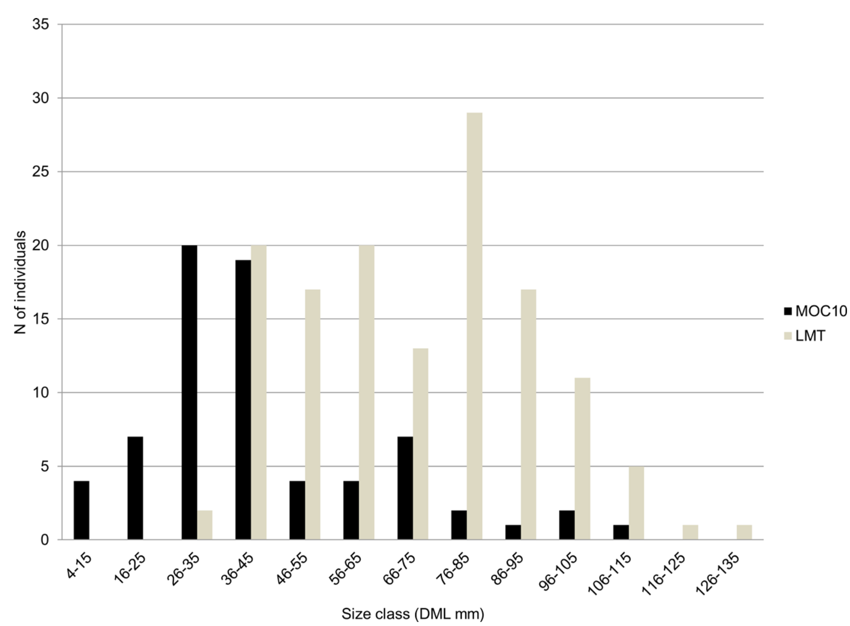


MOC10. Thus, with fewer tows, the LMTs captured more than twice as many individuals as the MOC10. Eight species were found in the LMT that were not in the MOC10, and eight species were found solely in the MOC10 (Table 4). The six cephalopod size-class histograms (Figs. 4, 5, 6, 7, 8, and 9) show that for these species, smaller animals were captured in higher numbers with the MOC10 net, while larger animals were caught using the pelagic LMT across the six species chosen. The rarefaction curves (Fig. 10) depict the LMT nearly reaching asymptote and accumulating species faster at a smaller total N than the MOC10. The MOC10 curve did not reach asymptote. The confidence levels indicate that the two gear types collected a similar overall number of species for sample sizes up to 2863 individuals.

Discussion

Although it is the largest ecosystem on Earth, the deep ocean is also the least explored and understood (Ramirez-Llodra et al. 2010). What little we know indicates that the deep sea supports levels of biodiversity that are among the highest on Earth (Sanders 1968; Snelgrove and Smith 2002; Stuart et al.

Fig. 6 *Mastigoteuthis agassizii* size class comparison by net type; pelagic trawl = LMT



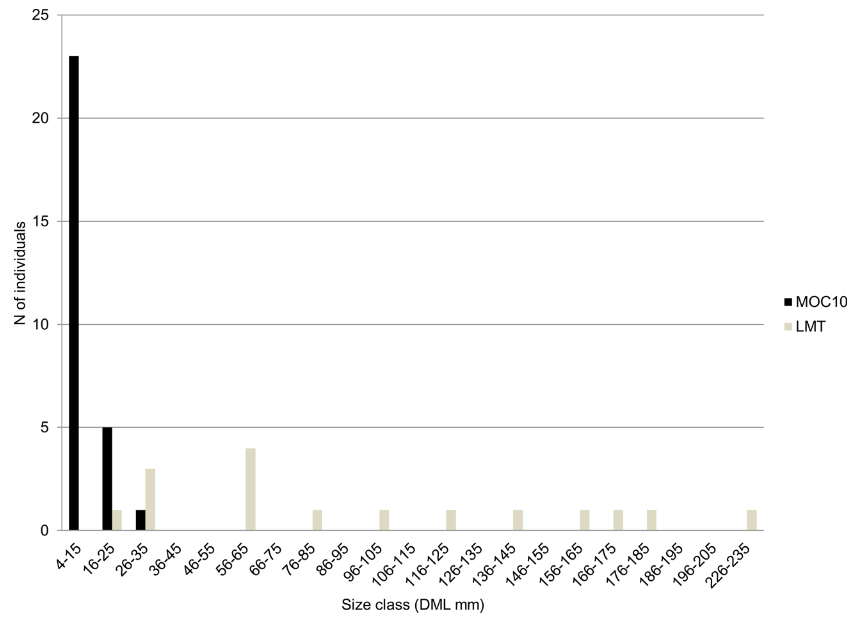


Fig. 7 *Haliphron atlanticus* size class comparison by net type; pelagic trawl = LMT

2003). The ONSAP program is the most comprehensive study to date of nekton in the water column at the regional scale of the northern GOM.

The total number of cephalopods captured (12, 076) is the largest such collection from the GOM. Previous studies have been focused on smaller or coastal areas. One deepwater study in the same region of the GOM, the Sperm Whale Acoustic Prey Study (SWAPS), was conducted in January through March of 2010 using a double-warp midwater trawl similar to our LMT category. It collected 3767 cephalopods in 41 tows (Judkins et al. 2013). The current study was conducted over a 1-year period, with 169 comparable LMT tows providing detailed distribution, abundance, and seasonal collection of specimens. Whereas approximately 60 species were collected during the winter SWAPS study, just before the oil spill, the year-round ONSAP pelagic-trawl sampling collected 77 species. The most numerous families were similar between the two studies.

There are approximately 800 cephalopod species worldwide. Judkins (2009) documented 129 species in the Broad Caribbean, with 32 families and 93 species in the GOM, including the neritic groups. Only three families reported by Judkins (2009) were not collected

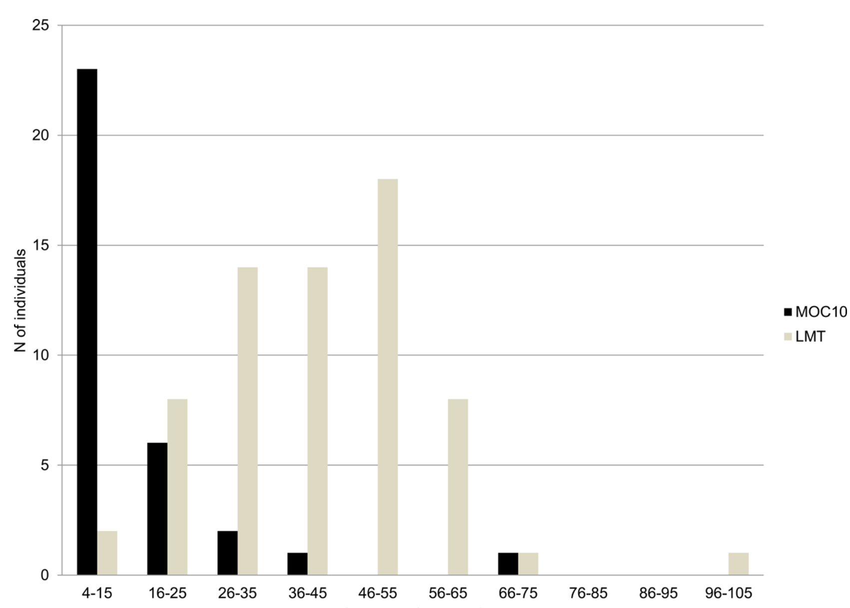


Fig. 8 All *Bathyteuthis* sp. size class comparison by net type; pelagic trawl = LMT

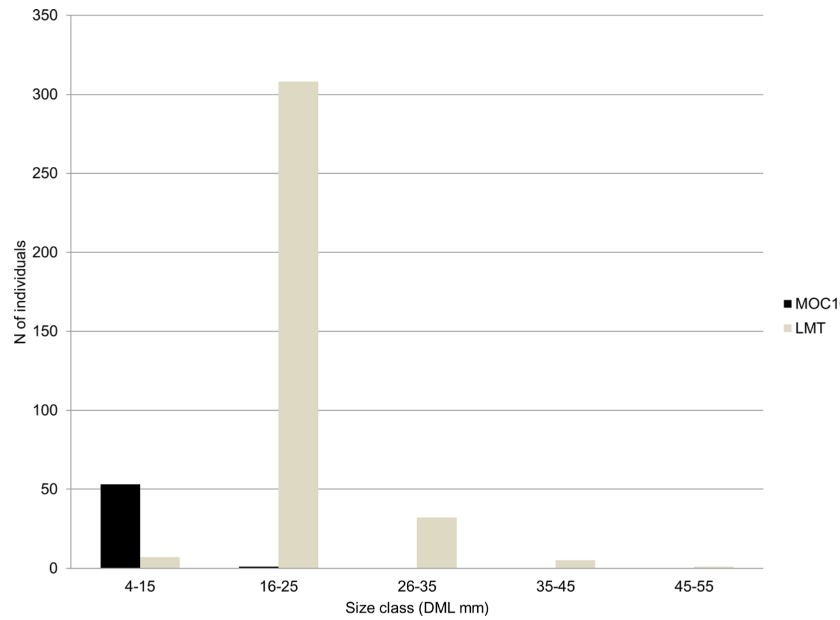


Fig. 9 *Abralia redfieldi* size class comparison by net type; pelagic trawl = LMT

during this study: Ocythoidae, Opisthoteuthidae, and Loliginidae. Loliginids are inshore squids, opisthoteuthids are bathybenthic octopods, and ocythoids are very rare pelagic octopods (Mangold et al. 2014). The two most abundant families caught in the MOC10 were Onychoteuthidae and Cranchiidae, and in the LMT were Cranchiidae and Enoploteuthidae (Fig. 2). The ten least abundant families (Fig. 3) indicate that there are rare species in the GOM that are not often caught, but may be important in the ecosystem because many grow to large sizes and are important prey for large vertebrates.

The rarefaction results (Fig. 10) indicate that both gear types are equally successful at estimating overall species richness of midwater cephalopods. Rarefaction suggests that the LMT collected close to the expected diversity for the region, while the MOC10 had not reached asymptote. Although both were adequate for inferring diversity of cephalopod species, using multiple gear types is an advantage for life history studies due to size-class differences that each net type collects (Table 3). Because each gear type collected species not found in the other, the use of multiple gear types may increase our overall knowledge of the diversity of rarely encountered species.

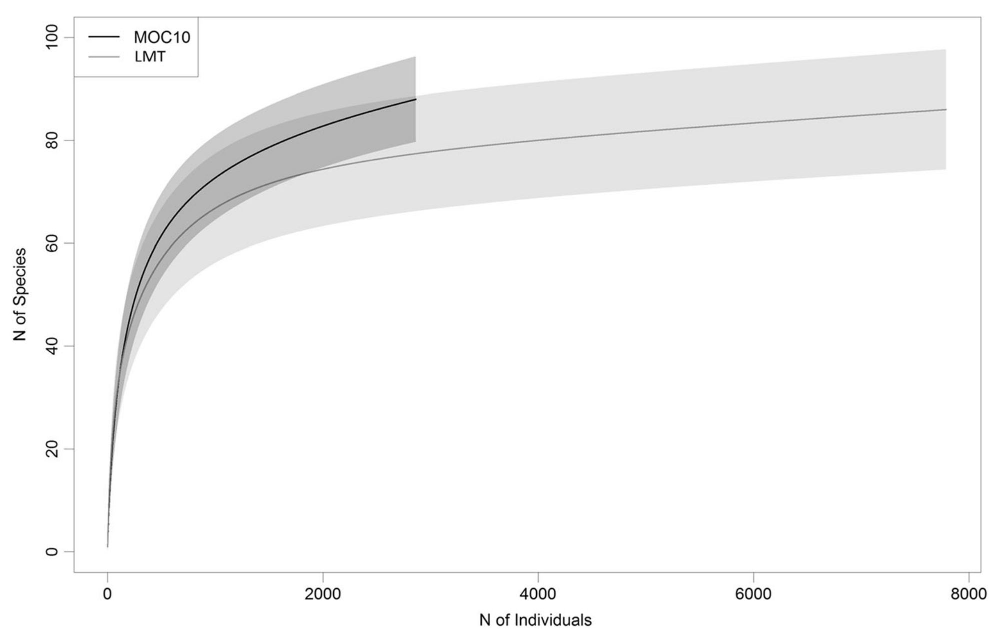


Fig. 10 Rarefaction curve to estimate cephalopod biodiversity comparing two gear types: MOC10 and LMT

Incorporation of multiple net systems has been shown to improve documentation of cephalopod biodiversity within a region (Vecchione et al. 2010). The problems involved in sampling cephalopods with respect to the characteristics of various types of sampling devices have long been recognized (Roper 1977; Clarke 1977). Hoving et al. (2014) provide a review of the advantages and disadvantages of various gear types used for deep-sea cephalopod research. Trawls are effective and widely used for collecting nekton, because they sample large volumes of seawater, which is necessary for collecting specimens of sparsely distributed organisms. A single type of trawl cannot perform well for all types of nekton, which range in size from a few centimeters to several meters. Overall trawl size, which largely determines the ability to capture fast-swimming organisms, and mesh size, which determines the retention of small organisms, are the two primary trade-offs in midwater trawling. Fine-meshed trawls cannot be towed at speeds high enough to capture species that are effective at gear avoidance (Heino et al. 2011). If one chooses a multi-gear approach, care is needed so that the sampling design is sufficiently balanced to allow quantitative merging of the data from different sources (Heino et al. 2011).

Using multiple types of gear to sample an ecosystem is both an opportunity and a challenge. It is important to remember that a single gear type is most effective for only a component of the cephalopod assemblage (Hoving et al. 2014). One of the challenges with the LMT is that during collection, some species become entangled in large meshes in the forenet and never enter the cod end. This applies to cephalopods, large cnidarians, and fish species like eels and dragonfishes. The cause of entanglement could be passive (cnidarians) or an active behavioral response (Sutton et al. 2008). If an animal is stuck in the mesh as the net is being reeled in, it may not be extracted due to haul-in conditions, and the animal may not be recovered for examination. A study targeting the whole life cycle of a species might need to use both small and large trawls. Furthermore, different trawls may catch entirely different species (Heino et al. 2011). Sutton et al. (2008) suggested that such challenges are potentially manageable. Two trawls will sample a broader range of species, as well as a broader size spectrum within a species, than a single trawl. The two gear types used in this study, the LMT and the MOC10, collected many of the same species but at different life stages, as well as eight unique species found in each net type. These 16 species (Table 3) are rarely captured by these types of gear in the GOM, and their occurrence in one gear or the other likely results from random variability of rare encounters rather than gear bias.

Despite the deep-pelagic ocean being the largest biome on Earth, knowledge of it lags behind that of nearly every other biome (Sutton 2013). The ecological roles of cephalopods in these environments are critical, as they are important links between the nutrients at the surface of the ocean and both the top predators and benthic communities. The 12,076 cephalopods documented in this work add an important piece to the knowledge of deep ocean biodiversity. Continued monitoring and use of a multi-net approach is needed to understand the distribution and abundance patterns for many such understudied taxa and their life histories.

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