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Vertical Distribution Patterns of Cephalopods in the Northern Gulf of Mexico

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Cephalopods are important in midwater ecosystems of the Gulf of Mexico (GOM) as both predator and prey. Vertical distribution and migration patterns (both diel and ontogenic) are not known for the majority of deep-water cephalopods. These varying patterns are of interest as they have the potential to contribute to the movement of large amounts of nutrients and contaminants through the water column during diel migrations. This can be of particular importance if the migration traverses a discrete layer with particular properties, as happened with the deep-water oil plume located between 1000 and 1400 m during the Deepwater Horizon (DWH) oil spill. Two recent studies focusing on the deep-water column of the GOM [2011 Offshore Nekton Sampling and Analysis Program (ONSAP) and 2015–2018 Deep Pelagic Nekton Dynamics of the Gulf of Mexico (DEEPEND)] program, produced a combined dataset of over 12,500 midwater cephalopod records for the northern GOM region. We summarize vertical distribution patterns of cephalopods from the cruises that utilized a 10 m^2 Multiple Opening/Closing Net and Environmental Sensing System (MOC10). About 95% of the cephalopods analyzed here either move through or live within 1000–1400 m zone. Species accounts include those with synchronous (e.g., *Pterygioteuthis* sp.) and asynchronous (e.g., *Stigmatoteuthis arcturi*) vertical migration. Non-migration patterns of some midwater cephalopods (e.g., *Vampyroteuthis infernalis*) are also highlighted. Ontogenic shifts are noted for some species examined.

Keywords: squid, octopod, vertical migration, DEEPEND, Deepwater Horizon, deep-sea, development

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INTRODUCTION

The Deepwater Horizon (DWH) oil spill generated one of the largest oil spill responses to date, including millions of dollars allocated to scientific research to examine the impacts of this devastating event (i.e., Gulf of Mexico Research Initiative, NAS Gulf Research Program). It was not only a blowout that affected the seafloor immediately surrounding the wellhead, the surface, and coastline, but also a midwater event. One of the questions post-spill was "Where has all the oil gone"? Passow and Hetland (2016) determined that a deep plume of trapped oil formed between 1000 and 1400 m depth (Socolofsky et al., 2011) due to the petrocarbons that became neutrally buoyant in seawater at that depth. This contaminated layer dispersed from the site via subsurface currents that impinged on the continental slope of the region, leaving extensive oiled sediment (Romero et al., 2015).

Two comprehensive, long-term programs established post-spill have examined the faunal groups found within the water column (0–1500 m) in the northern Gulf of Mexico (GOM). The Offshore Nekton Sampling and Analysis Program (ONSAP) and the Deep Pelagic Nekton Dynamics of the Gulf of Mexico (DEEPEND) consortium have compiled an immense dataset for midwater fauna over a period of 8 years (2011–2018) examining biodiversity and contaminant questions about multiple deep-water pelagic faunal groups (Judkins et al., 2016; Burdett et al., 2017; Richards et al., 2018; Romero et al., 2018).

Historically, the oceanic midwater environment has received little attention (Webb et al., 2010), as it is very difficult to study. However, it is the largest biome on Earth (Robison, 2004; Sutton, 2013). Past deep-sea cephalopod inventories include work conducted using various methods such as closing-net systems as well as large, open trawl nets (Nesis, 1972, 1993; Lu and Clarke, 1975a,b; Young, 1978; Vecchione and Pohle, 2002; Judkins et al., 2016). Recently, remotely operated vehicles have been used to collect precise observations on vertical distribution and other properties (Vecchione et al., 2001; Widder et al., 2005; Robison et al., 2017).

Another, less direct technique that has been utilized to assess cephalopod biodiversity and distributional patterns is the examination of stomach contents from predators. Cephalopods are major prey items for many vertebrates, including seabirds, large tunas and billfishes, and marine mammals (Summers, 1983; Williams, 1995; Lansdell and Young, 2003; Xavier et al., 2018). These studies have examined gut contents and through knowledge of the predators and their migrations and feeding grounds, inferred cephalopod distributions, both spatially as well as vertically.

While faunal inventories and indirect methods to assess deep-sea cephalopod diversity and distribution are important, few vertical distribution patterns have been compiled. Efforts in the 1970s reported vertical distribution of cephalopods in various regions (Clarke and Lu, 1975; Lu and Clarke, 1975a,b; Roper and Young, 1975; Young, 1978). Since that time, vertical distribution patterns have been documented for various zooplankton groups such as fish larvae and cephalopod paralarvae (Hopkins, 1982; Ropke et al., 1993; Salman et al., 2003) but larger specimens have not been included. There are approximately 700 species of cephalopods worldwide (Young et al., 2019) with great morphological and genetic variation among the families, especially those of oceanic habitats. Vertical distribution patterns vary among cephalopod taxa and developmental stages.

The deep oil plume of the DWH oil spill was detected in May, 2010 (Dierks et al., 2010) and persisted for months after that (Camilli et al., 2010; Joye et al., 2011; Reddy et al., 2014) as a horizontal plume that moved toward the southwest with deep-water currents (Melvin et al., 2016). There was also an anomaly of low dissolved oxygen observed at depths of 1100–1200 m below the surface (Kessler et al., 2011). This deep-water oil plume exposed any meso- and/or bathypelagic organisms living in or moving through this plume to potential toxicity.

In light of the need to know which cephalopods may have been exposed to the deep oil plume, as well as a need for comprehensive accounts on deep-sea species, this study reports on 39 cephalopod species from the northern GOM, examining the following questions: (1) How many species move through or are found within the deep oil plume located between 1000 and 1400 m? (2) What are the vertical distribution patterns of deep-sea cephalopods in water column of the northern GOM and how does this relate to past accounts of these species? (3) Are there developmental shifts in vertical distribution of these cephalopods?

MATERIALS AND METHODS

Two midwater sampling programs provided all material for this analysis. ONSAP (2011) and the DEEPEND (2015–2018) programs sampled in the northern GOM (**Figure 1**). A 10 m^2 Multiple Opening and Closing Net and Environmental Sensing System (MOC10) (Wiebe et al., 1976) with 3 mm mesh was used by both programs (as described in DEEPEND, 2015). The following depths were targeted on each MOC10 tow during both cruise programs: 1200–1500, 1000–1200, 600–1000, 200–600, and 0–200 m at all 169 stations where cephalopods were collected and tows quantified. Sampling depths were chosen based on the following premise: 1200–1500 m was a depth range below where a subsurface hydrocarbon plume was detected during the initial spill; 1000–1200 m fished through the hydrocarbon plume (Reddy et al., 2012); 600–1000 m fished where the vertically migrating species are known to reside during the day; 200–400 m fished where vertical migrators are known to move through during daily migrations; and 0–200 m fished the epipelagic zone where vertical migrators gather at night (Burdett et al., 2017). Sampling was conducted twice at each station per cruise (∼solar noon and ∼midnight).

Three thousand seven hundred and thirty cephalopods were documented using the MOC10 from both programs. Flow metering on the trawls allowed inference of the amount of water filtered through each net and these were used to standardize abundance per volume of water per tow. The 2150 specimens included in the analyses here were those individuals collected in quantifiable trawl tows. Specimens were measured and identified to species level when possible at sea and either sampled for molecular projects (i.e., Sosnowski, 2017; Timm et al., 2020), frozen, or preserved (10% formalin). Identifications were verified or corrected post-cruise. Non-parametric Kruskal–Wallis analyses were conducted to compare the standardized abundances of the six most abundant species (**Table 1**) among depth bins, day vs. night.

The vertical distribution plots (VDP) include 2150 individuals while the ontogenic shift plots (OSP) include 1820 individuals. The numbers vary between the two analyses due to the lack of measurable size (dorsal mantle length) for the ontogenic shift analyses because of collecting damage to some specimens. Plots of vertical migration and ontogenic shifts were created using the R program (**Figures 3–10** and **Supplementary Materials A, B**)

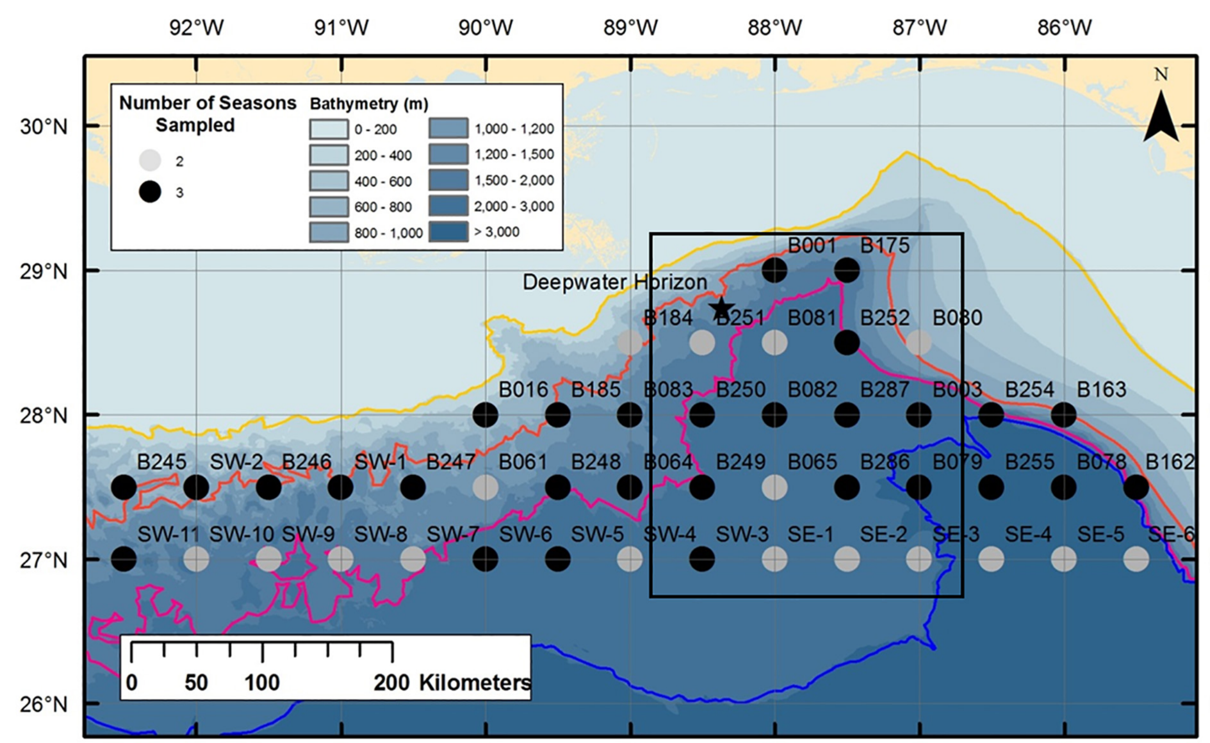

FIGURE 1 | Station sites for ONSAP and DEEPEND MOC10 cruises. Modified from Florida Fish and Wildlife Research Institute SEAMAP cruise stations. Circles, ONSAP stations; black box, DEEPEND stations; star, DWH oil spill site.

(R Core Team, 2013). VDP's were created for cephalopod species where possible and species were grouped according to their VDP patterns (**Figures 3–7** and **Supplementary Material A**). These groups are based on patterns identified for deep-water fishes of the GOM by T. Sutton (unpublished).

We felt it important to include rare species as **Supplementary Material** because reports from multiple projects will eventually allow enough published information to accumulate for ecological patterns to be discerned (Vecchione and Pohle, 2002). We arbitrarily chose 20 individuals as an adequate number of individuals to include in VDP and OSP descriptions.

RESULTS

Cephalopods are found throughout the water column with the mesopelagic zone containing more individuals than the epipelagic or the upper bathypelagic zones (**Figure 2**). Of the 39 species examined for this analysis, 37 species (95%) are found to either live within or move through the 1000–1400 m depth zone (**Table 1**). Occupancy of this zone varied among species (i.e., 2 of 70 *Abralia redfieldi* individuals vs. 21 of 39 *Bathyteuthis* sp. individuals, **Table 1**).

The DEEPEND team is in the process of analyzing vertical distribution patterns for multiple faunal groups including fishes, crustaceans, gelatinous organisms, and cephalopod, pteropod, and heteropod mollusks[1]. T. Sutton et al. (unpublished) examined distributional data for oceanic fishes and the results revealed seven major diel vertical patterns for the 151 fish taxa examined. Based on plots of diel vertical distribution, we grouped cephalopods into six of the seven possible vertical-distributional patterns following T. Sutton et al. (unpublished). Although these patterns were visually obvious in the pooled samples presented in the figures, the Kruskal–Wallis analyses of the underlying data failed to reject the null hypothesis of no statistically significant differences in diel patterns in vertical distribution even for the six most abundant species (**Table 2**). This is likely because of high within-group variance (i.e., variance in abundance among samples within day and night depth bins) not obvious in the pooled figures.

Based on visual assessment of pooled samples, six species were holoepipelagic non-migrators with centers of abundance the upper 200 m day and night (**Figure 3** and **Supplementary Material A**). The seven nyctoepipelagic synchronous vertically migrating species inhabit the meso- and/or the bathypelagic zones during the day and migrate to the epipelagic zone nightly (**Figure 4**). The 14 species of mesopelagic asynchronous vertical migrators are found primarily in the mesopelagic during the day and move into or between the epi- or the upper mesopelagic at night (**Figures 5**, **7** and **Supplementary**

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[1] http://www.deependconsortium.org/images/documents/publications_1-12-18.pdf

TABLE 1 | Midwater cephalopods ordered by abundance; total individuals examined; mantle length range; evidence of vertical migration; evidence of ontogenic shift; percent of species that was found between 1000 and 1400 m.

Species	Total # individuals	Mantle length range (mm ML)	Vertical migration Y/N/weak	Ontogenic shift Y/N/weak	% total located between 1000 and 1400 m
Cranchia scabra	353	4–115	N	N	11
Vampyroteuthis infernalis	157	4–135	N	N	44
Japetella diaphana	153	5–92	N	Y	37
Leachia atlantica	110	7–80	N	N	38
Pyroteuthis margaritifera	106	8–33	Y	Y	17
Stigmatoteuthis arcturi	102	2–69	Y	N	13
Mastigoteuthis agassizii	82	13–110	N	Weak	48
Bolitaena pygmaea	77	6–64	N	Y	43
Abralia redfieldi	70	5–13	Y	N	1
Onychoteuthis banksii	61	4–326	W	Y	13
Grimalditeuthis bonplandi	53	6–84	N	Weak	49
Histioteuthis corona	50	6–46	Y	N	28
Pterygioteuthis gemmata	45	6–28	Y	N	<1
Chiroteuthis sp.	42	6–121	Y/W	N	19
Pterygioteuthis giardi	40	6–37	Y	N	<1
Octopoteuthis sp.	40	5–100	Y	W	<1
Ornithoteuthis antillarum	39	5–40	Y	W	18
Bathyteuthis sp.	39	6–72	N	N	54
Selenoteuthis scintillans	37	8–29	Y	Y	<1
Abraliopsis atlantica	35	6–27	Y	N	<1
Argonauta argo	35	3–7	N	N	1
Brachioteuthis sp.	35	6–47	N	N	11
Helicocranchia pfefferi	32	10–59	N	Y	20
Helicocranchia sp. *A*	31	6–44	N	Y	35
Haliphron atlanticus	29	4–32	N	Y	10
Heteroteuthis dagamensis	27	3–15	Y	N	11
Discoteuthis discus	22	6–50	Y	N	<1
Sandalops melancholicus	20	7–46	N	Y	15
Joubiniteuthis portieri	19	5–159	N	N	21
Cycloteuthis sirventi	18	9–28	N	N	22
Sthenoteuthis pteropus	18	5–25	N	W	11
Macrotritopus defilippi	17	4–12	N	N	18
Walvisteuthis jeremiahi	17	5–24	N	Y	N/A
Bathothauma lyromma	16	5–82	N	W	31
Taningia danae	12	7–34	W	W	N/A
Galiteuthis armata	11	12–53	N	Y	82
Chtenopteryx sicula	10	7–15	Y	W	10
Hyaloteuthis pelagica	9	4–8	N/A	N	22
Ancistrocheirus lesueurii	7	4–18	N/A	N/A	29

Material A). *Chtenopteryx sicula* is placed as a mesopelagic non-migrator (**Supplementary Material A**). There is one species, *Joubiniteuthis portieri*, that falls into the deep meso-/bathypelagic asynchronous migrator category (**Supplementary Material A**). The seven deep-meso/bathypelagic non-migrating species are found between 600 and >1000 m depth during the day and night (**Figure 6** and **Supplementary Material A**). Two squid species (*Leachia atlantica*, *Sandalops melancholicus*) do not fit into a described pattern and are labeled as "unclassified" here (**Figure 7**). The nine species with less than 20 individuals are found in the **Supplementary Material**.

Ontogenic shift plots' were created (**Figures 8–10** and **Supplementary Material B**) and patterns reveal that seven cephalopod species descend deeper as they develop (**Figure 8**). Sixteen species show no evidence of ontogenic shift (**Figures 9A,B**). There are three species for which it appears that the adults live closer to the surface whereas smaller individuals inhabit a deeper zone (**Figure 10**). Those OSP's with less than 20 individuals examined can be found in **Supplementary Material B** (13 species).

Table 1 summarizes the number of individuals included for each VDP, OSP, mantle length (ML) range, whether a species

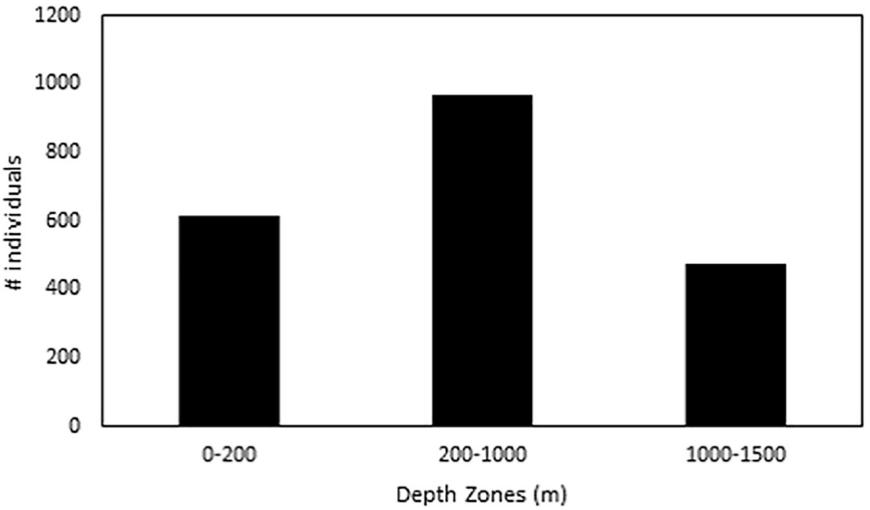

FIGURE 2 | Total cephalopod distribution divided into ocean zones from 0 to 1500 m depth.

is considered a vertical migrator and the percentage of the species that was found between 1000 and 1400 m. Caution is important when using this analysis because the sample sets in some cases are small. Kruskal–Wallis analyses did not reveal any statistically significant results with regard to distributional differences between day and night even for the six most abundant species (**Table 2**).

Family Accounts

Vampyroteuthidae

Among 157 *Vampyroteuthis infernalis* individuals, the majority were below 600 m both day and night (4–135 mm ML). Two individuals (ML = 5 mm, 7 mm) were found between 200 and 600 m. We do not believe that this depth layer is characteristic of juveniles as over 30 individuals of similar MLs found between 600 and 1500 m. Vampires are non-migrators and do not appear to exhibit an ontogenic shift during their life history (**Figures 6**, **9**).

Alloposidae

Twenty-nine *Haliphron atlanticus* were collected from the surface layer down to 1200 m. Mantle lengths ranged from 4 to 32 mm with no evidence of diel vertical migration. Larger *H. atlanticus* were found in the upper layers (**Figures 5**, **10**).

Argonautidae

Thirty-five individuals (3–7 mm ML) were examined for the VDP (**Figures 3**, **9**). Nine were collected during day tows and 26 collected at night. *Argonauta argo* were found in the surface layer both day and night but also down to 1500 m deep. They are classified as holoepipelagic non-migrators here but it should be noted with more sampling, a vertical migration pattern may become apparent. There is no evidence of ontogenic shift.

Octopodidae

Only 5 of 17 *Macrotritopus defilippi* paralarvae (4–12 mm ML) were collected in day tows at the surface (0–200 m) while during the night tows, 12 specimens were collected from 0 to 1500 m. They appear to be holoepipelagic non-migrators (**Figure 3**). Additional material needs to be collected to make firm conclusions on vertical migration and any possible ontogenic shift (**Supplementary Material B**).

Amphitretidae

Seventy-seven *Bolitaena pygmaea* (6–64 mm ML) are distributed from 0 to 1500 m with no diel migration pattern observed. They do shift to deeper water as they develop with all individuals larger than 20 mm ML caught below 600 m (**Figures 6**, **8**). One hundred fifty-three *Japetella diaphana* (5–92 mm ML) follow a similar pattern, with no obvious diel migration pattern, and those larger than 26 mm ML living below 600 m, with one exception where a 44 mm ML specimen was collected between 0 and 200 m (**Figures 6**, **8**). For both species, the peak abundance both day and night was in the 600–1000 m depth zone.

Brachioteuthidae

Thirty-five *Brachioteuthis* sp. (6–47 mm ML) were available for examination of vertical migration and possible ontogenic shifts. Brachioteuthids were found throughout the water column (0–1500 m) during day and night. There is no

TABLE 2 | Results of Kruskal–Wallis test comparing day/night standardized abundances per species per depth bin.

Species	Kruskal–Wallis H	df	Significance
Cranchia scabra	5.782	4	0.216
Japetella diaphana	8.400	4	0.078
Leachia atlantica	4.473	4	0.346
Pyroteuthis margaritifera	5.782	4	0.216
Stigmatoteuthis arcturi	6.545	4	0.162
Vampyroteuthis infernalis	7.354	4	0.118

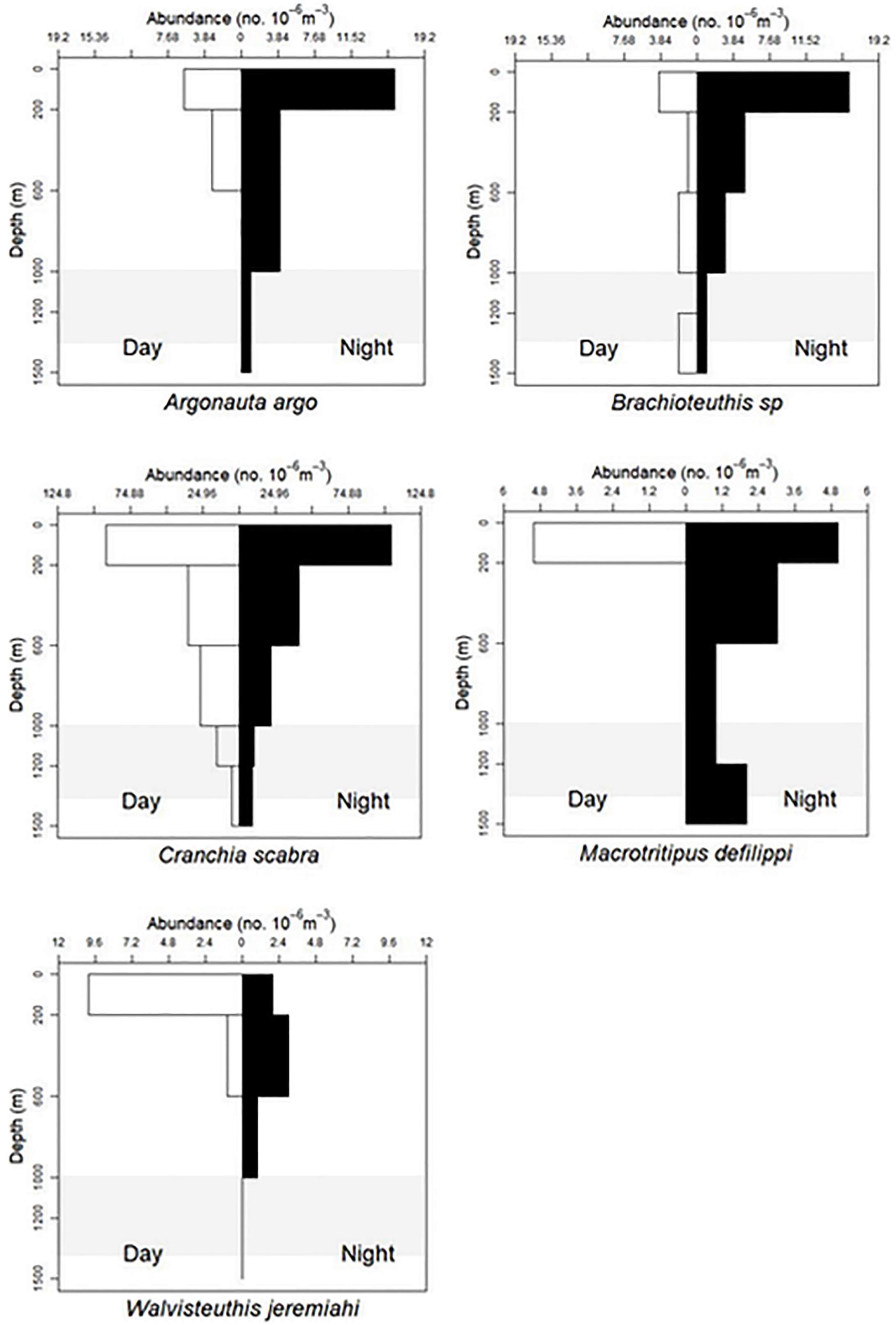

FIGURE 3 | Vertical distribution patterns of five cephalopods. Holoepipelagic non-migration pattern described by T. Sutton et al. (unpublished). *A. argo*, *n* = 35; *Brachioteuthis* sp., *n* = 35; *C. scabra*, *n* = 353; *M. defilippi*, *n* = 17; *W. jeremiahi*, *n* = 17; shaded region indicates the deep oil plume zone.

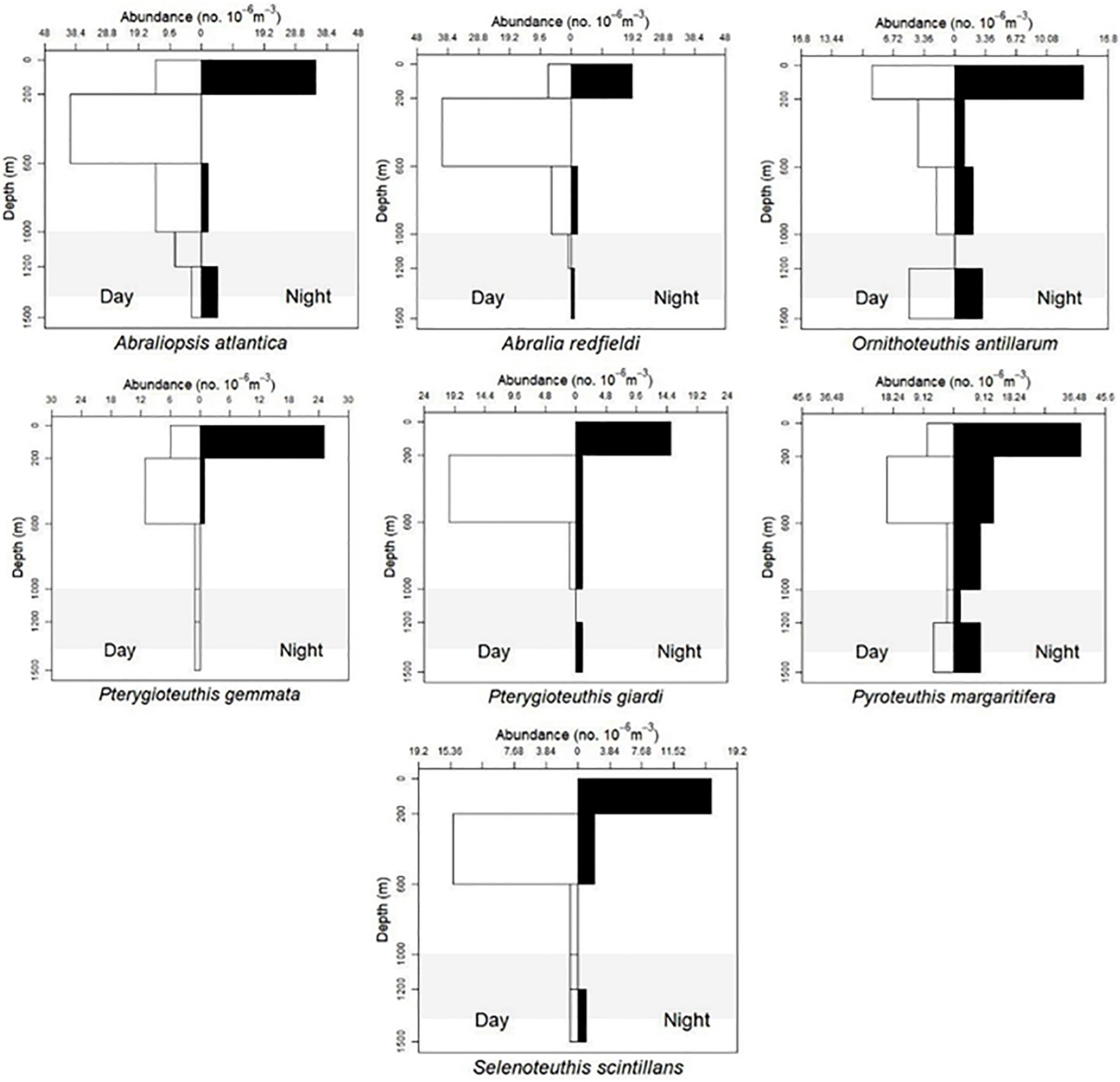

FIGURE 4 | Vertical distribution patterns of seven cephalopods. Nyctoepipelagic synchronous diel migration described by T. Sutton et al. (unpublished). *A. atlantica*, *n* = 32; *A. redfieldi*, *n* = 70; *O. antillarum*, *n* = 39; *P. gemmata*, *n* = 45; *P. giardi*, *n* = 40; *P. margaritifera*, *n* = 106; *S. scintillans*, *n* = 37; shaded region indicates the deep oil plume zone.

evidence in this analysis of vertical migration or ontogenic shift (**Figures 3**, **9**).

Chiroteuthidae

Forty-two *Chiroteuthis* sp. (6–121 mm ML) showed that individuals were caught from 0 to 1500 m during the day and from 0 to 1200 m during the night (**Figure 5**). There is some evidence of diel vertical migration but plots would need to be broken out by species for further clarification. We found no evidence of ontogenic shift for this genus (**Supplementary Material B**). Fifty-three *Grimalditeuthis bonplandi* (6–84 mm ML) were analyzed. They were found from the surface to 1500 m during day and night with the majority of individuals found between 600 and 1500 m. We found no evidence of vertical migration but an ontogenic shift for this species is evident, with larger individuals found in the lower meso- and upper bathypelagic zones (**Figures 6**, **8**).

Joubiniteuthidae

Nineteen *J. portieri* (5–159 mm ML) documented the species living throughout the water column; six were found

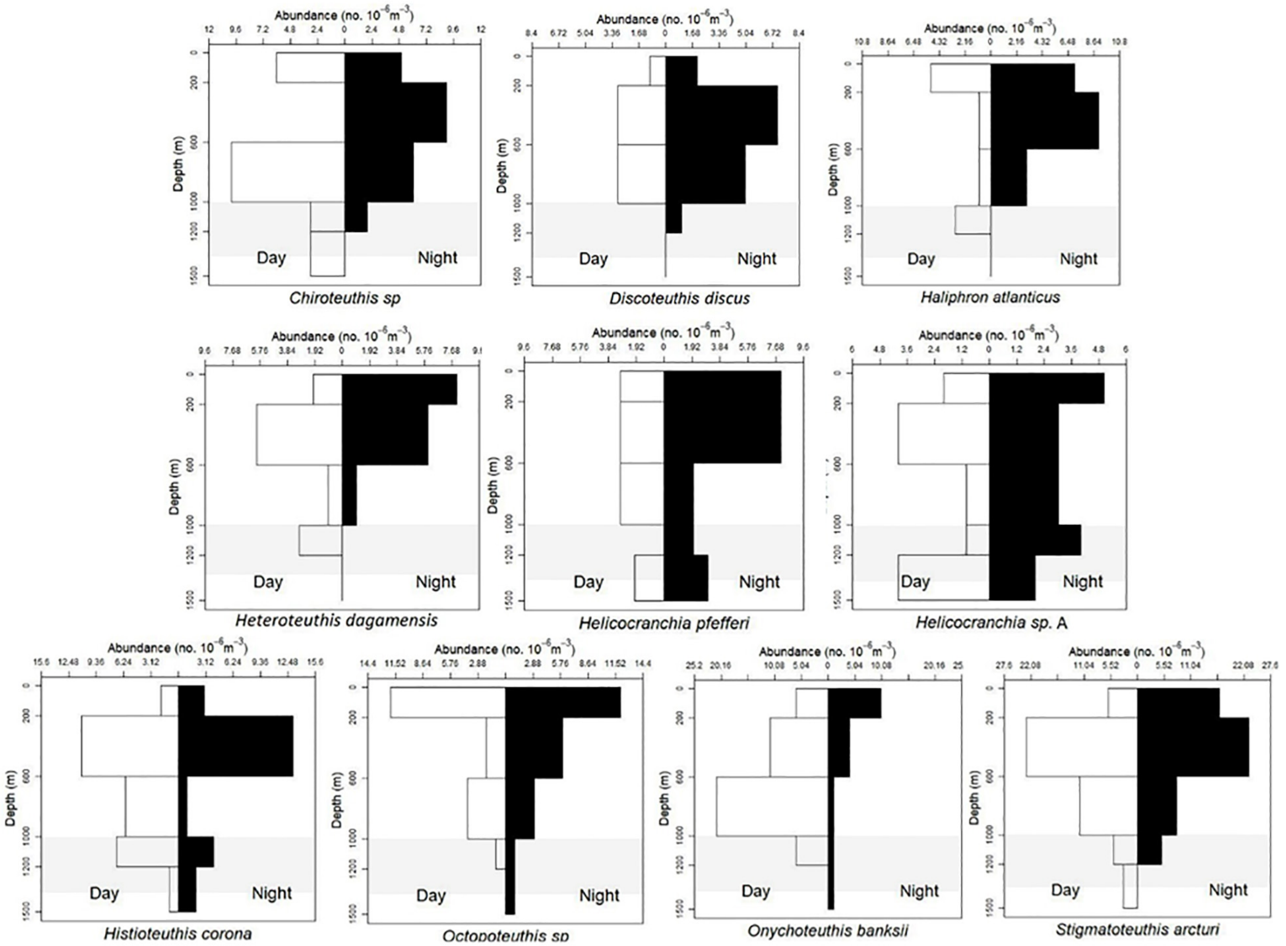

FIGURE 5 | Vertical distribution patterns of 10 cephalopods. Mesopelagic asynchronous migrators as described by T. Sutton et al. (unpublished). *Chiroteuthis* sp., *n* = 42; *Discoteuthis* sp., *n* = 22; *H. atlanticus*, *n* = 29; *H. dagamensis*, *n* = 27; *Helicocranchia* sp. A, *n* = 31; *H. pfefferi*, *n* = 32; *H. corona*, *n* = 50; *O. banksii*, *n* = 61; *S. arcturi*, *n* = 102; *S. melancholicus*, *n* = 20; *Cycloteuthis sirventi*, *n* = 18; *Sthenoteuthis pteropus*, *n* = 18; *Octopoteuthis* sp., *n* = 40; shaded region indicates the deep oil plume zone.

in day tows inhabiting the upper and lower mesopelagic zone while thirteen individuals were collected at night from the surface to 1500 m. There is some evidence of vertical migration but no ontogenic shift for this species (**Supplementary Materials A, B**).

Mastigoteuthidae

The majority of *Mastigoteuthis agassizii* (13–110 mm ML) were found below 600 m. They are deep meso-/bathypelagic non-migrators. There appears to be a weak ontogenic shift to deeper water as this species becomes larger (**Figures 6**, **8**).

Cranchiidae

Three hundred fifty-three *Cranchia scabra* (4–115 mm ML) were used for the VDP and the ontogenic shift analysis. They are found distributed between 0 and 1500 m. There is no evidence of vertical migration or ontogenic shift for this species (**Figures 3**, **9**).

Leachia atlantica (7–80 mm ML) demonstrate a non-migration vertical pattern (*n* = 110) as they are found at all depths (**Figure 7**). They are currently placed as "unclassified" here. There is no evidence of ontogenic shift (**Figures 9A,B**).

Thirty-two *Helicocranchia pfefferi* (10–59 mm ML) were included in the VDP, which showed individuals distributed throughout the water column both day and night with some weak diel vertical migration occurring at the deeper depths (**Figure 5**). There does not appear to be an ontogenic shift for this species (**Figures 9A,B**). The VDP and ontogenic shift patterns for a currently undescribed *Helicocranchia* species, *Helicocranchia* sp. A (6–44 mm ML) show the same diel vertical distribution pattern but the species does appear to move deeper in the water column as it develops (**Figures 5**, **8**).

The diel vertical distribution of sixteen *Bathothauma lyromma* (5–82 mm ML) was skewed, as there were 12 collected during day tows but only four individuals captured at night. This species was found throughout the water column during the day and deeper depths (below

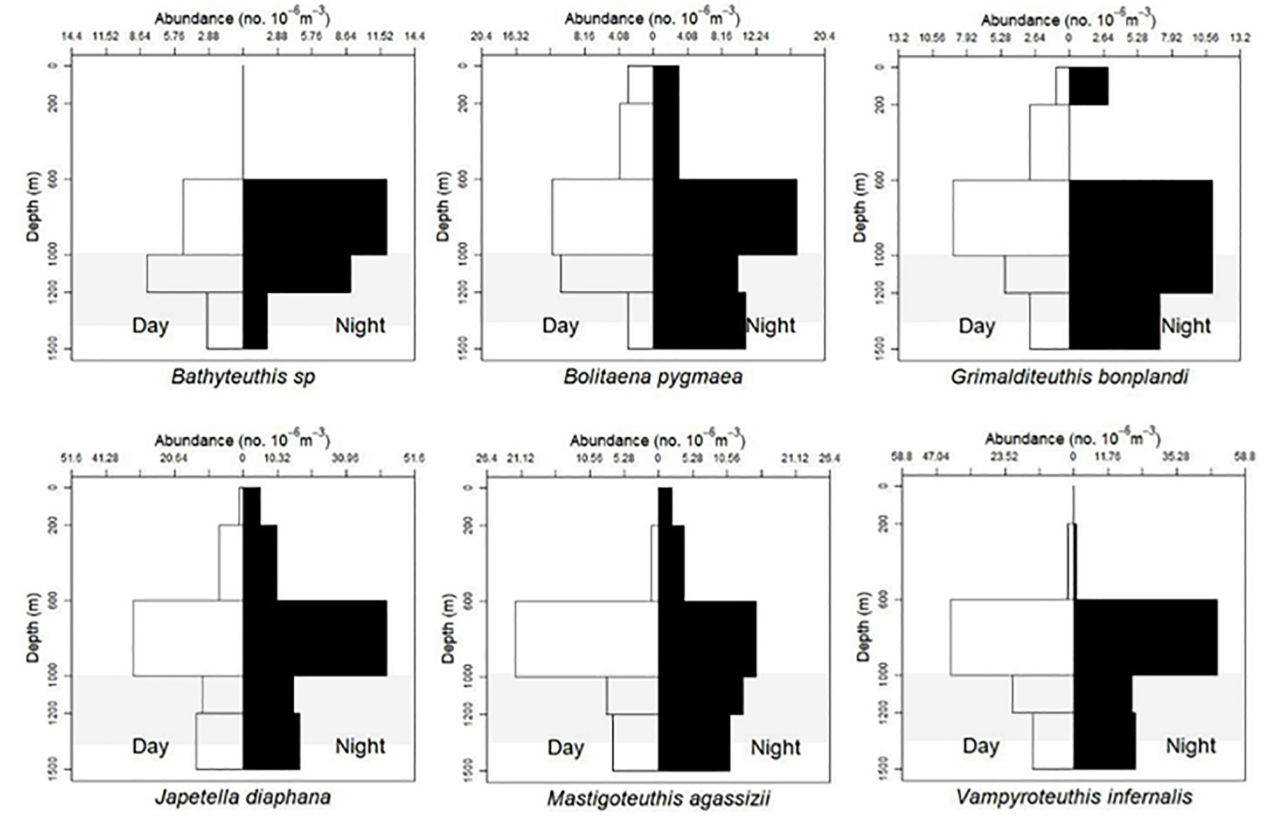

FIGURE 6 | Vertical distribution of six cephalopods. Deep-meso/bathypelagic non-migration as described by T. Sutton et al. (unpublished). *Bathyteuthis* sp., *n* = 39; *B. pygmaea*, *n* = 77; *G. bonplandi*, *n* = 53; *J. diaphana*, *n* = 153; *M. agassizii*, *n* = 82; *V. infernalis*, *n* = 157; shaded region indicates the deep oil plume zone.

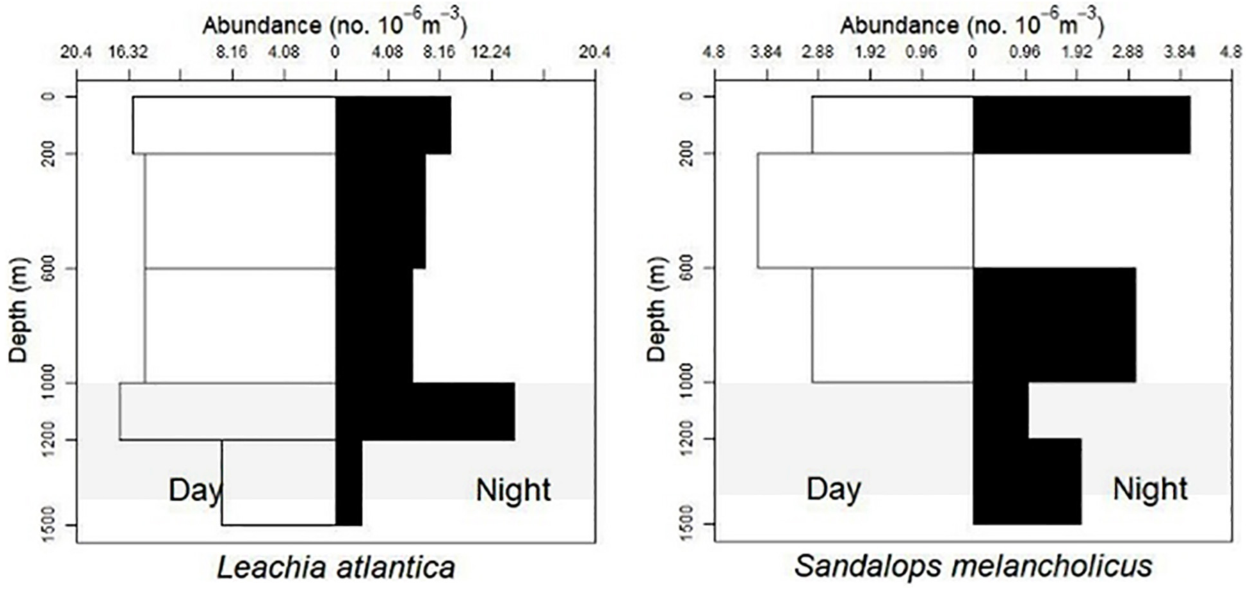

FIGURE 7 | Vertical distribution patterns unclassified. *L. atlantica*, *n* = 110; *S. melancholicus*, *n* = 20; shaded region indicates the deep oil plume zone.

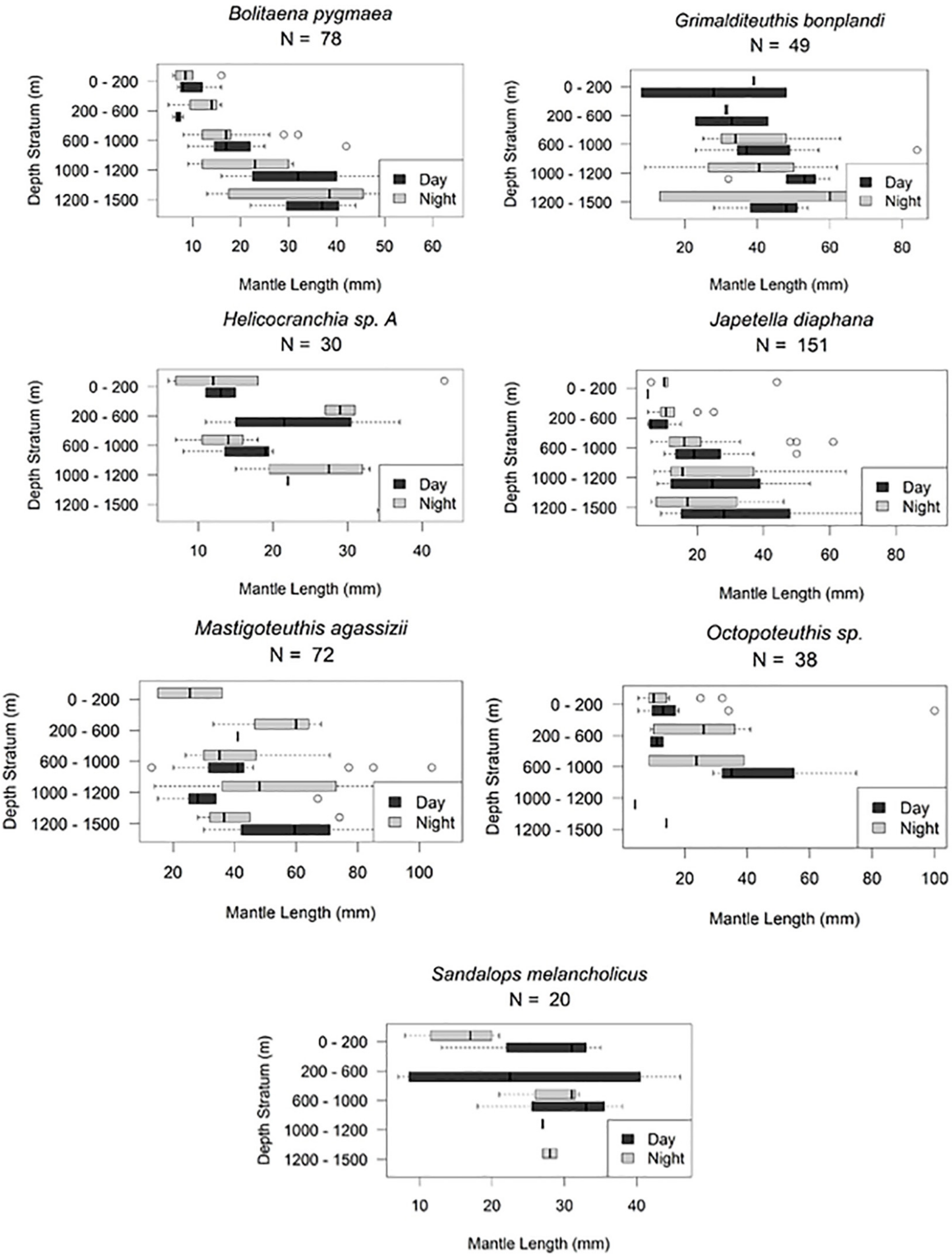

FIGURE 8 | Cephalopod ontogenic shift patterns demonstrating a shift deeper as these species develop. Horizontal line, median; box limits, 1st and 3rd quartiles; circles, outliers.

600 m) at night. A weak ontogenic shift was noted for this species but more material is required to confirm this pattern (**Supplementary Materials A, B**).

The distribution of 20 *S. melancholicus* (7–46 mm ML) encompasses the water column from 0 and 1500 m with no evidence of diel vertical pattern within this small sample set. There appears to be an ontogenic shift with larger animals found at deeper depths (**Figures 7**, **8**).

Eleven *Galiteuthis armata* (12–53 mm ML) were considered for this analysis. All individuals were found between 600 and 1500 m with no evidence of vertical migration. There appears to be an ontogenic shift by this species

(>12 mm ML) but additional material is needed to confirm this (**Supplementary Materials A, B**).

Cycloteuthidae

Cycloteuthis sirventi (*n* = 18) are distributed throughout the water column from 0 to 1500 m depth with more collected during night tows than day tows (9–28 mm ML) (**Supplementary Materials A, B**). *Discoteuthis discus* (*n* = 22) was also documented from the surface to 1200 m and is a mesopelagic asynchronous migrator (6–50 mm ML). No ontogenic shift was apparent for either taxon (**Figure 5** and **Supplementary Material B**).

Ancistrocheiridae

Preliminary findings indicate that *Ancistrocheirus lesueurii* (4–18 mm ML) is found throughout the water column from 0 to 1500 m. Additional records are needed to confirm any pattern of vertical distribution or ontogenic shift as there are only seven specimens available for analysis (**Supplementary Materials A, B**).

Enoploteuthidae

Thirty-five *Abraliopsis atlantica* (6–27 mm ML) and 70 *A. redfieldi* (5–13 mm ML) were plotted and both species are found from 0 to 1500 m. Both are nyctoepipelagic synchronous vertical migrators, living primarily at mesopelagic depths during the day and moving up to the epipelagic zone nightly (**Figure 4**). However, there is no evidence of ontogenic shift for either species (**Figures 9A,B**).

Lycoteuthidae

Selenoteuthis scintillans (8–29 mm ML) are nyctoepipelagic synchronous vertical migrators, moving from mainly the upper mesopelagic zone to the epipelagic zone nightly (*n* = 37). Larger individuals are found in the upper mesopelagic zone (**Figures 4**, **9**).

Pyroteuthidae

One hundred and six *Pyroteuthis margaritifera* (8–33 mm ML) were distributed throughout the water column (0–1500 m) both day and night but overall they are nyctoepipelagic synchronous migrators, with the majority of the population found in the upper mesopelagic zone during daytime and moving to the epipelagic zone nightly (**Figure 4**). Smaller individuals were living at depth whereas larger individuals were shallower (**Figure 10**).

Pterygioteuthis gemmata (6–28 mm ML) were also found mainly in the upper mesopelagic zone in daytime, migrating nightly to the epipelagic zone (**Figure 4**). *Pterygioteuthis giardi* (6–37 mm ML) is also a nyctoepipelagic synchronous migrator (**Figure 4**). Neither of these species appear to undergo an ontogenic shift during development (**Figures 9A,B**) within the limits of our methods.

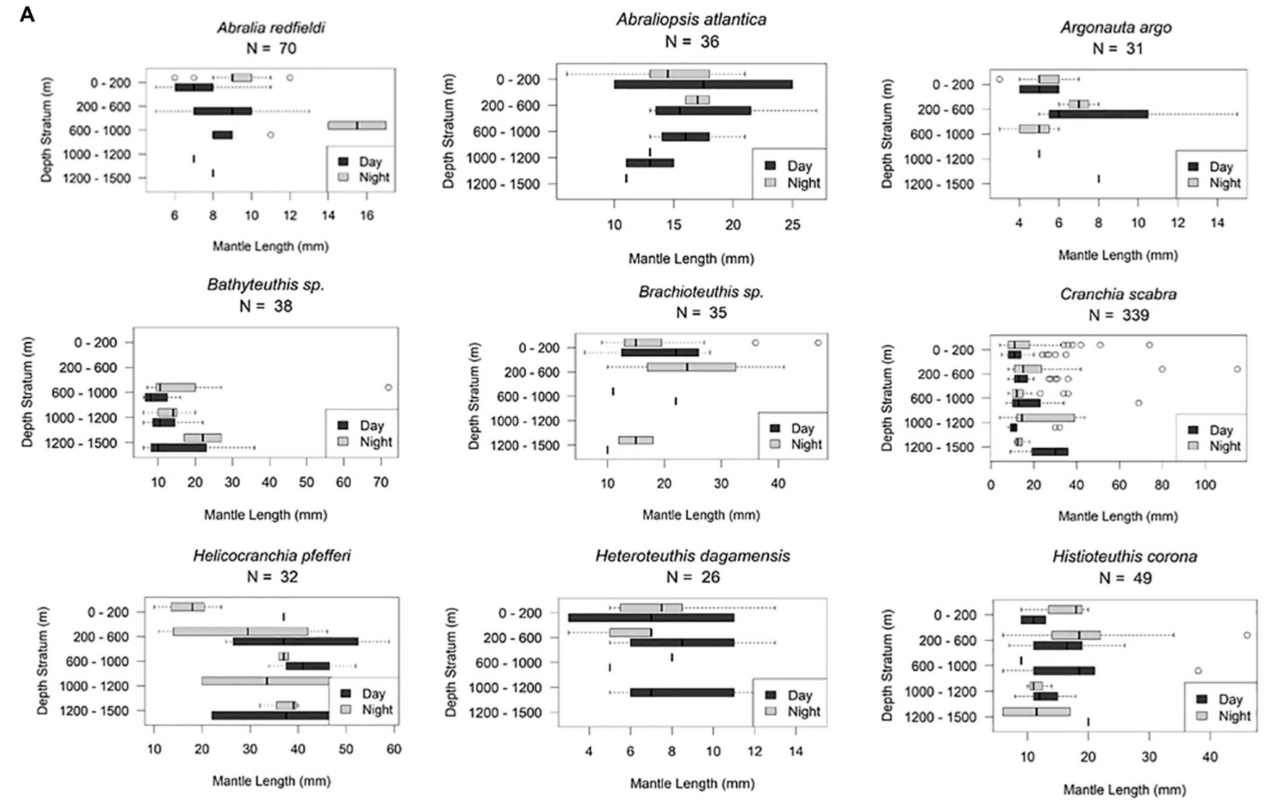

FIGURE 9 | Continued

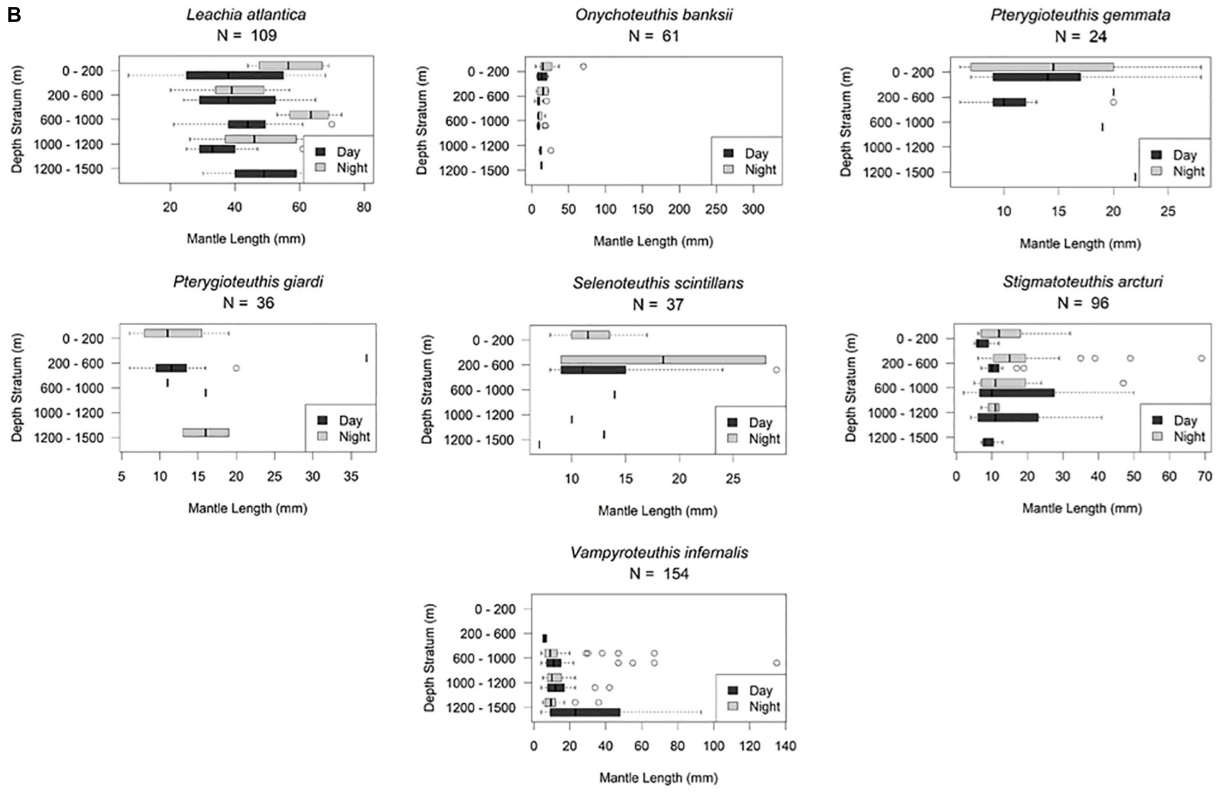

FIGURE 9 | (A,B) Cephalopods showing no evidence of ontogenic shift. Horizontal line, median; box limits, 1st and 3rd quartiles; circles, outliers.

Histioteuthidae

Histioteuthis corona (6–46 mm ML) and *Stigmatoteuthis arcturi* (2–69 mm ML) are found throughout the water column with high concentrations found in the upper mesopelagic zone. They are mesopelagic asynchronous migrators, living primarily from the lower to upper mesopelagic zone at night. We found no evidence of ontogenic shift for either species (**Figures 5**, **9**).

Octopoteuthidae

The two *Octopoteuthis* species (*O. sicula*, *O. megaptera*) found in the northern GOM were combined into one VDP due to the difficulty of identifying specimens confidently to species because many were badly damaged (5–100 mm ML). Forty *Octopoteuthis* sp. display a mesopelagic asynchronous migration pattern (**Figures 5**, **8**).

Twelve *Taningia danae* (7–34 mm ML) were included in a VDP (**Supplementary Materials A, B**) as there is little distribution information in past literature about this species. They were caught from 0 to 1000 m deep with the majority living above 600 m, and indicated a weak vertical migration pattern. Additional material is needed to confirm this assessment (**Supplementary Materials A, B**).

Ommastrephidae

Ornithoteuthis antillarum (5–40 mm ML) follows the nyctoepipelagic synchronous diel migration pattern with some vertical migration from the meso- to the epipelagic zone. Smaller individuals were found throughout the water column (<15 mm ML) while larger individuals (>23 mm ML) were above 600 m (**Figures 4**, **10**). This could be evidence of a weak ontogenic shift for this species moving upwards as they get larger. Eighteen *Sthenoteuthis pteropus* (5–25 mm ML) display a uniform distribution from 0–1500 m (**Supplementary Material A**) with a weak ontogenic shift (**Supplementary Material B**). We include a VDP for *Hyaloteuthis pelagica* (4–8 mm ML) in spite of its rarity because of scarce historical records. Nine specimens show a vertical distribution from 0 to 1200 m. No ontogenic pattern is documented at this time (**Supplementary Materials A, B**).

Onychoteuthidae

Sixty-one *Onychoteuthis banksii* (4–326 mm ML) showed that the species is found from the surface to 1500 m, with more collected during daytime hours than at night. We found evidence of a mesopelagic asynchronous migration for this species (**Figure 5**). There is no strong evidence of ontogenic shift as this species grows (**Figures 9A,B**). *Walvisteuthis jeremiahi* (5–24 mm ML) were documented from 0 to 1000 m as holoepipelagic non-migrators with a similar ontogenic shift pattern (**Supplementary Materials A, B**).

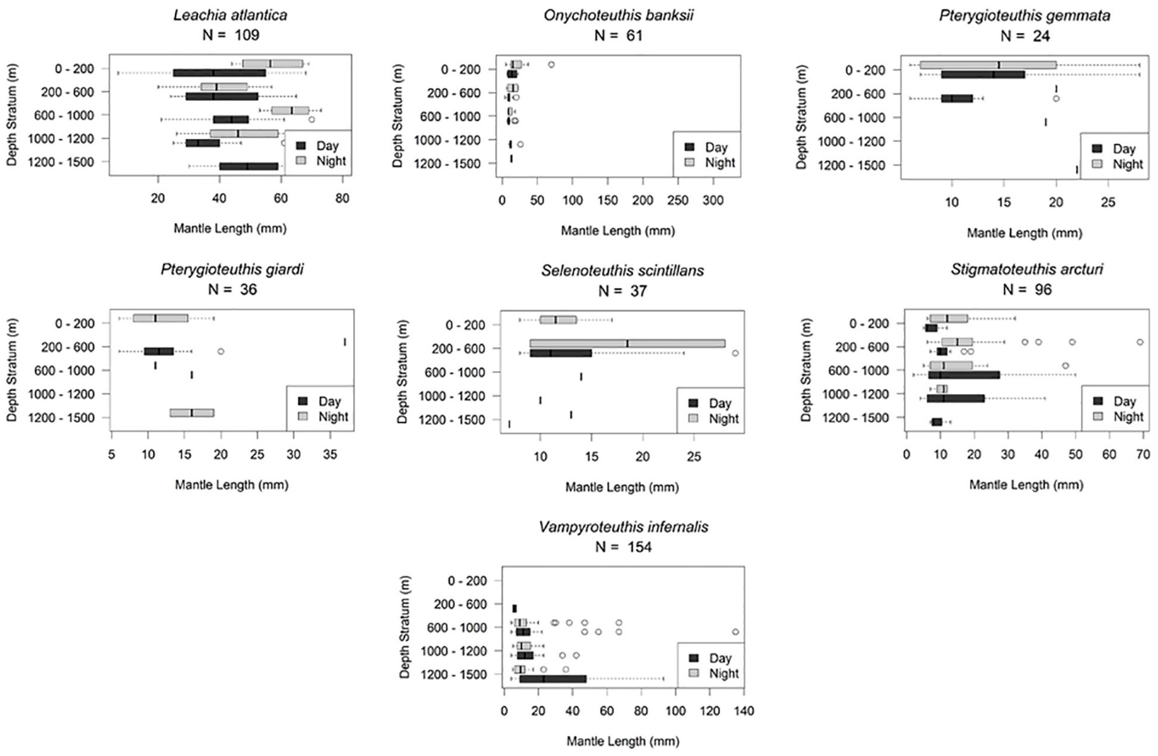

FIGURE 10 | Cephalopods displaying an ontogenic shift from deeper zones to shallow zones as they develop. Horizontal line, median; box limits, 1st and 3rd quartiles; circles, outliers.

Sepiolidae

Heteroteuthis dagamensis (3–15 mm ML) are found from 0 to 1200 m in the northern GOM with evidence of the species being mesopelagic asynchronous vertical migrators. Six larger individuals (>9 mm ML) were found above 600 m while only one was found in the 1000–1200 m depth zone. There is no evidence of ontogenic shift (**Figures 5**, **9**).

Bathyteuthidae

Thirty-nine *Bathyteuthis* sp. (6–72 mm ML) were used to create a VDP that shows they live solely in the lower meso- and upper bathypelagic zones at all sizes. They are considered deep meso-/bathypelagic non-vertical migrators with no evidence of ontogenic shift (**Figures 6**, **9**).

Chtenopterygidae

Although only 10 specimens of *C. sicula* (7–15 mm ML) were collected, a VDP is included due to the scarcity of available literature. They occupy depths from the surface to 1200 m with many inhabiting the upper mesopelagic zone. From the plot, they appear to move down the water column at night but this is likely a product of a low sample size (**Supplementary Material A**). They also exhibit a weak ontogenic shift, as they get larger, they move deeper into the water column (**Supplementary Material B**). More material is needed for a robust assessment.

DISCUSSION

The DWH spill was an ecological disaster from the surface to the seafloor. The midwater plume lasted for months (Camilli et al., 2010; Melvin et al., 2016) and numerous taxa interacted with it as they either lived within it or moved vertically through it on their nightly migrations (Burdett et al., 2017; Romero et al., 2018). Multiple faunal groups are found within the upper bathypelagic zone including fishes, cephalopods, crustaceans, and gelatinous organisms (Pond et al., 2000; Robison et al., 2010; Sutton et al., 2010; Letessier et al., 2011; Cook et al., 2013; Judkins et al., 2016; Hosia et al., 2017). All of these taxa play a role in the carbon flux from the surface to benthic habitats. This biological carbon pump becomes vulnerable as oil drilling moves farther off the coast into deeper waters. When another spill occurs, knowing the migrating and non-migrating populations that may interact with any contamination will provide a baseline of sorts for species that may be impacted in the upper bathypelagic zone.

We found that 95% of oceanic cephalopod species of the northern GOM spend time in the upper bathypelagic zone for some portion of their lives (1000–1500 m), either migrating through or living within it (**Figure 2** and **Table 3**). Past records support these 37 cephalopod species having been collected from similar depths in various regions around the world (Lu and Clarke, 1975a; Roper and Young, 1975; Young, 1978; Lu and Roper, 1979; Vecchione and Pohle, 2002; Shea et al., 2017). Although the Kruskal–Wallis results reveal no significance for

TABLE 3 | Current study species and our placement of cephalopods within the vertical migration pattern categories according to T. Sutton et al. (unpublished) and Roper and Young (1975).

Species	Sutton et al. classification	Roper and Young classification
Cranchia scabra	Holoepipelagic non-migrator	Non-migrator
Argonauta argo	Holoepipelagic non-migrator	Does not fit well by definition
Brachioteuthis sp.	Holoepipelagic non-migrator	First order diel vertical migrator
Macrotritopus defilippi	Holoepipelagic non-migrator	Non-migrator
Walvisteuthis jeremiahi	Holoepipelagic non-migrator	Non-migrator
Bathothauma lyromma	Holoepipelagic non-migrator	Non-migrator
Abraliopsis atlantica	Nyctoepipelagic synchronous diel migrator	First order diel vertical migrator
Abralia redfieldi	Nyctoepipelagic synchronous diel migrator	First order diel vertical migrator
Pyroteuthis margaritifera	Nyctoepipelagic synchronous diel migrator	First order diel vertical migrator
Pterygioteuthis gemmata	Nyctoepipelagic synchronous diel migrator	First order diel vertical migrator
Pterygioteuthis giardi	Nyctoepipelagic synchronous diel migrator	First order diel vertical migrator
Selenoteuthis scintillans	Nyctoepipelagic synchronous diel migrator	First order diel vertical migrator
Ornithoteuthis antillarum	Nyctoepipelagic synchronous diel migrator	Non-migrator
Haliphron atlanticus	Mesopelagic asynchronous migrator	Second order diel vertical migrator
Chiroteuthis sp.	Mesopelagic asynchronous migrator	Second order diel vertical migrator
Helicocranchia pfefferi	Mesopelagic asynchronous migrator	Second order diel vertical migrator
Helicocranchia sp. *A*	Mesopelagic asynchronous migrator	Second order diel vertical migrator
Sandalops melancholicus	Mesopelagic asynchronous migrator	Non-migrator
Histioteuthis corona	Mesopelagic asynchronous migrator	Second order diel vertical migrator
Stigmatoteuthis arcturi	Mesopelagic asynchronous migrator	Second order diel vertical migrator
Cycloteuthis sirventi	Mesopelagic asynchronous migrator	Diel vertical spreader
Discoteuthis discus	Mesopelagic asynchronous migrator	Non-migrator
Sthenoteuthis pteropus	Mesopelagic asynchronous migrator	Non-migrator
Octopoteuthis sp.	Mesopelagic asynchronous migrator	Non-migrator
Heteroteuthis dagamensis	Mesopelagic asynchronous migrator	Second order diel vertical migrator
Onychoteuthis banksii	Mesopelagic asynchronous migrator	Second order diel vertical migrator
Joubiniteuthis portieri	Deep meso-/bathypelagic asynchronous migrator	Diel vertical spreader
Vampyroteuthis infernalis	Deep meso-/bathy non-migrator	Non-migrator
Grimalditeuthis bonplandi	Deep meso-/bathy non-migrator	Non-migrator
Mastigoteuthis agassizii	Deep meso-/bathy non-migrator	Non-migrator
Bolitaena pygmaea	Deep meso-/bathy non-migrator	Non-migrator
Japetella diaphana	Deep meso-/bathy non-migrator	Non-migrator
Bathyteuthis sp.	Deep meso-/bathy non-migrator	Non-migrator
Leachia atlantica	Does not fit well by definition	Non-migrator

any of the six species examined, this is most likely due to small sample sizes and large within-group variation. Erickson et al. (2017) showed that sampling variability is very high in young pelagic cephalopods. Large sample sizes are needed for a robust statistical analysis.

Cephalopods are important links among various components of marine ecosystems. The contribution of nektonic squids to the coupling of energy flows among marine ecosystems during their ontogenic migrations is poorly understood (Arkhipkin, 2013). It is often neglected in ecosystem models despite their capacity to move significant amounts of resources between ecosystems (Arkhipkin, 2013). The vertically migrating squids contribute to this resource flux throughout the water column.

The bathypelagic zone is part of the largest unexplored realm on Earth (Webb et al., 2010). There have been multiple programs to close the gap of deep-sea exploration such as MAR-ECO and CMarZ, both supported by the Census of Marine Life as well as the DEEPEND consortium supported by the Gulf of Mexico Research Initiative (GoMRI). These programs have scratched the surface of the bathypelagic zone which continues to require focused, collaborative sampling efforts. The dataset created here is currently the largest of its kind for midwater cephalopods.

Vertical Migration Patterns

Past studies of cephalopod vertical migration have been conducted using a modified Isaac-Kid midwater trawl (IKMT) or rectangular midwater trawls (RMT 8) (Lu and Clarke, 1975b; Lu and Roper, 1979; Salman et al., 2003; Shea and Vecchione, 2010). One caution using these types of nets, fished either open or with a closing cod-end, is the possibility of organisms being captured during descent or ascent to the desired discreet depth. The RMT8 and MOC10 are opening/closing net systems, which can descend closed to the desired depth and then open, so we have higher confidence in inferred vertical distribution patterns using this type of gear. Roper and Young (1975)

TABLE 4 | Cephalopod species found living between (10% or more of abundance) or moving through 1000–1400 m.

Living between 1000 and 1400 m	Moving through 1000–1400 m
Ancistrocheirus lesueurii	*Abralia redfieldi*
Bathothauma lyromma	*Abraliopsis atlantica*
Bathyteuthis sp.	*Histioteuthis corona*
Bolitaena pygmaea	*Onychoteuthis banksii*
Brachioteuthis sp.	*Ornithoteuthis antillarum*
Chtenopteryx sicula	*Pterygioteuthis gemmata*
Chiroteuthis sp.	*Pterygioteuthis giardi*
Cranchia scabra	*Selenoteuthis scintillans*
Cycloteuthis sirventi	*Stigmatoteuthis arcturi*
Galiteuthis armata	
Grimalditeuthis bonplandi	
Haliphron atlanticus	
Helicocranchia pfefferi	
Helicocranchia sp. A	
Heteroteuthis dagamensis	
Hyaloteuthis pelagica	
Japetella diaphana	
Joubiniteuthis portieri	
Leachia atlantica	
Macrotritipus defillipi	
Mastigoteuthis agassizii	
Pyroteuthis margaritifera	
Sandalops melancholicus	
Sthenoteuthis pteropus	
Vampyroteuthis infernalis	

examined three programs that documented cephalopod vertical migration patterns using IKMTs. They created categories for the cephalopods based on the vertical migration patterns noting that these are not mutually exclusive; some species may exhibit a combination of patterns and that all patterns are not sharply defined (Roper and Young, 1975).

Many of the plots in the current study reinforce the patterns defined by Roper and Young (1975). Some plots (i.e., *P. margaritifera*, *Octopoteuthis* sp., *O. banksii*, *H. pfefferi*, *A. argo*) extend the known depth range for the species. This is likely due to our deeper trawling efforts. The current study found that while some cephalopod species fit within the Roper and Young (1975) categories, others did not because there was not a clear pattern or few individuals included in their original analysis (**Table 4**). We used the categories created by T. Sutton et al. (unpublished) to compare with those of Roper and Young (1975) as they align better with our observations regarding cephalopods. The categories are more specific by depth zones than those reported by Roper and Young (1975) used due to the capability of the MOC10 to collect discreet depth zone samples in this study (**Table 4**). Examples of this can be found when looking at certain species (i.e., *S. melancholicus*, *D. discus*, *S. pteropus*) as Roper and Young (1975) classified them as non-migrators but the patterns exhibited with the current plots demonstrate a nightly upward movement into the upper mesopelagic or epipelagic which places these species into the asynchronous migrator category.

It should be noted that some groups need additional material to strengthen the patterns inferred here (i.e., *Chiroteuthis*, *Brachioteuthis*, and *Octopoteuthis*) because they are grouped by genus and not compared at the species level. As more material becomes available, clearer conclusions can be made.

Ontogenic Shifts

Past studies have focused on ontogenic shifts of various cephalopod groups, notably the ommastrephids (Shigeno et al., 2001; Shea, 2005). Ontogenic examination of deep-water cephalopods is less available; some work has been presented by Villanueva (1992), Quetglas et al. (2010), and Shea and Vecchione (2010). Developmental strategies such as anti-predator behavior changes through ontogeny have been examined as well (York and Bartol, 2016).

Shea and Vecchione (2010) examined paralarvae of three mesopelagic cephalopod species from the North Atlantic Ocean and compared allometric changes with ontogenic changes in their diel vertical migration patterns. They found that the brachioteuthids were caught primarily during the day while we recorded the opposite pattern (**Figure 3**). We examined 35 brachioteuthids ranging in size from 6 to 47 mm ML and found them in the upper 600 m during the day and from 0 to 1500 m at night. This aligns with a holoepipelagic vertical distribution pattern where the majority of the species spends time in the upper 200 m but can be found deeper as well. There does not appear to be an ontogenic shift within the specimens we examined. These findings do not align closely with what Shea and Vecchione (2010) report but this could be due to differences in sampling depths, specimen sizes, or species considered (**Figures 3**, **9**).

Shea and Vecchione (2010) also documented that *C. sicula* paralarvae were found between 0 and 300 m when <6.5 mm ML as well as allometric changes that occur once they are below the euphotic zone. We find that *C. sicula* (7–15 mm ML) are found from 0 to 600 m during the day and from 0 to 1200 m at night. This could align with Shea and Vecchiones' (2010) thought that there is an ecological change that corresponds with allometric change for this group. However, note that our study has only 10 specimens to examine for this comparison (**Supplementary Materials A, B**).

The ontogenic migration of *Histioteuthis reversa* to deeper waters has been observed in the Mediterranean Sea (Quetglas et al., 2010). They concluded that adult females ascend the water column to spawn because spent females have been collected at the surface, as reported elsewhere (Voss et al., 1998). The two histioteuthid species studied here (*H. corona* and *S. arcturi*) were found throughout the water column when smaller than 20 mm ML and the larger animals (>20 mm ML) were found at shallower depths both day and night indicating that the pattern inferred for *H. reversa* may be consistent for the family.

CONCLUSION

Cephalopods are widely distributed throughout the water column down to 1500 m with the mesopelagic zone containing the largest number of individuals. This study reveals that 95% of the species examined spent all or part of their lives in the upper bathypelagic zone which is where the deep oil plume was located during the DWH oil spill. This study provides new details, as there were no baseline data for midwater cephalopods of the GOM prior to the spill. The VDP and ontogenic shifts analyzed with a reliable collection method contribute additional evidence and include large sample sizes for many species, providing reference data for midwater cephalopods in the GOM.

DATA AVAILABILITY STATEMENT

The datasets generated for this study are available on request to the corresponding author.

ETHICS STATEMENT

Ethical review and approval was not required for the animal study because this is not required for cephalopods in the United States at this time.

AUTHOR CONTRIBUTIONS

HJ and MV were responsible for cephalopod collection and identification as well as writing and reviewing the manuscript.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fmars.2020.00047/full#supplementary-material

MATERIAL A | Cephalopod vertical distribution plots for species with fewer than 20 individuals for analysis.

MATERIAL B | Ontogenic shift plots of cephalopods with fewer than 20 individuals for analysis.

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