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Abundance and distribution of large calcareous thecosome pteropods in the northern Gulf of Mexico

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Abstract: The ecological role of large thecosome pteropods in the pelagic ecosystem of the northern Gulf of Mexico (GoM) may be substantial, both in the food web and biogeochemical cycling. We analyzed species abundances, vertical and horizontal distributions of large species with calcareous shells (those collected in 3-mm mesh nets). Pteropod samples were collected following the 2010 Deepwater Horizon oil (DWH) spill by two midwater sampling programs: the Offshore Nekton Sampling and Analysis Program (ONSAP 2011) and the Deep Pelagic Nekton Dynamics of the Gulf of Mexico (DEEPEND 2015) projects. All samples were collected using a 10-m^2 Multiple Opening/Closing Net and Environmental Sensing System (MOC10) midwater trawl, with 3-mm mesh. This gear sampled five discrete depths between 0–1500 m. Over 13,000 pteropod specimens were examined, with 25 species identified. *Clio pyramidata* Linnaeus 1767 was the most abundant species during both collection periods. Five genera (*Diacria, Clio, Styliola, Cuvierina, Cavolinia*) demonstrated diel vertical migration from the meso- to epipelagic zone.

Key words: DEEPEND Consortium, Mollusca, vertical migration, sea butterflies

Thecosome pteropods, commonly called “sea butterflies,” are snails that spend their entire lives in the pelagic realm of the world’s oceans. In addition to importance in various ocean food webs (Lalli and Gilmer 1989, Bednaršek *et al.* 2012), they have become biological indicators for assessing the impacts of ocean acidification (Peijnenburg *et al.* 2020). Taxonomically, pteropods included in this study are in the Order Thecosomata, which has two suborders distinguished primarily by the presence of an external aragonite shell (Euthecosomata) versus an internal shell or a cartilaginous pseudoconch (Pseudothecosomata). Only one family within the Pseudothecosomata, the monogeneric Peraclidae, has an aragonitic shell.

Pteropods are cosmopolitan in distribution (Lalli and Gilmer 1989, Bednaršek *et al.* 2012). Similar to other holozooplankton, pteropods exhibit lower biomass but the highest species richness in tropical and subtropical ocean regions (Angel 1993, Bednaršek *et al.* 2012, Pierrot-Bults and Peijnenburg 2015), whereas greatest population densities are in polar regions (Lalli and Gilmer 1989). The Gulf of Mexico (GoM) is an area of substantial human activity that can impact marine carbonate chemistry; in turn, fluctuations in carbonate chemistry can affect shell deposition by pteropods and impact zooplankton ecology. It is noteworthy that relatively few studies are available for the northern GoM. Previous pteropod research has been conducted in the central-southern GoM (Snider 1975, Lemus-Santana *et al.* 2014), the eastern GoM and Caribbean Sea (Tesch 1946, Austin 1971), western Caribbean (Parra-Flores and Gasca 2009), and the Florida Straits (Wormelle 1962, Michel and Michel 1991).

Where pteropod distribution has been studied in detail, especially in the Atlantic for which the GoMex is a marginal basin, Wormelle (1962) and Van der Spoel (1967) found many pteropod species undergo diel vertical migration. Van der Spoel and Dadon (1999), found that in the South Atlantic 50 pteropod species are epipelagic (0–200 m), 29 occur in both the epipelagic and mesopelagic zones (200–1,000 m), four species are mesopelagic only, five are found in both the meso- and bathypelagic zones (>1,000 m), and the bathypelagic zone contains an additional four pteropod species. This decrease in species richness and abundance with depth is common among other planktonic groups (Bsharah 1957, Van der Spoel and Dadon 1999, Costello and Chaudhary 2017).

The Offshore Nekton Sampling and Analysis Program (ONSAP, 2011)and the Deep Pelagic Nekton Dynamics of the Gulf of Mexico (DEEPEND, 2015–2019) programs were developed to assess the midwater community following the Deepwater Horizon oil spill and to establish a baseline of the mid- to deep-pelagic fauna found in the GoM. These two programs collected the largest dataset of midwater fauna from the surface to 1500 m in the GoM to date (Judkins *et al.* 2017). Using data collected from these GoM programs, we address the following questions: What are the spatial distribution patterns of large shelled pteropods in the northern GoM? Were there differences (seasonal or other) in relative abundance of pteropods between 2011 and 2015? What are the vertical distribution patterns of these pteropod species in the northern GoM?

MATERIALS AND METHODS

In 2011, the ONSAP program conducted a three-month (April–June) cruise aboard the M/V *Meg Skansi* sampling 46 stations in the northern GoM. The DEEPEND program sampled in May and August of 2015 aboard the R/V *Point Sur.* The stations were spread across the northern GoM, 27–29°N and 85–93°W (Fig. 1). Of a total of 46 stations, 15 were common to both programs.

Both programs sampled macrozooplankton and micronekton using a Multiple Opening Closing Net and Environmental Sensing System midwater trawl system with a 10 m^2 mouth area (MOC10) rigged with six 3 mm mesh nets to collect samples at five discrete-depth intervals: 0–200 m, 200–600 m, 600–1000 m, 1000–1200 m, and 1200–1500 m, as well as an initial oblique sample (Judkins *et al.* 2017). The MOC10 was deployed twice at each station, once during the day and once at night, to examine diel vertical migration patterns (Judkins *et al.* 2017). A net tow was considered quantitative if it met the following criteria: opening and closing at target depths as determined by the net closing sensor; reasonable flowmeter readings to calculate volume of water filtered; and no signs of mechanical failure or net damage at the end of the tow (DEEPEND 2015). Upon completion of the tow, contents of each net were rinsed down into its cod end with seawater. The oxygen sensors were not working consistently throughout the cruises, so environmental data was unavailable for this project. Sample processing included the identification, counting, weighing (if possible) and measurements of all collected specimens (DEEPEND 2015). Pteropod samples were preserved in either 50% isopropanol or 95% non-denatured ethanol.

A Zeiss Stemi 2000-C Stereo Microscope was used to identify and examine all specimens after preservation. Only calcareous-shelled thecosome pteropods were quantified for this study as they were generally recovered in adequate condition for confident identification. Gymnosomata and non-peraclid Pseudothecosomata (*i.e.*, those without shells or with pseudoconchs rather than calcareous shells) were excluded

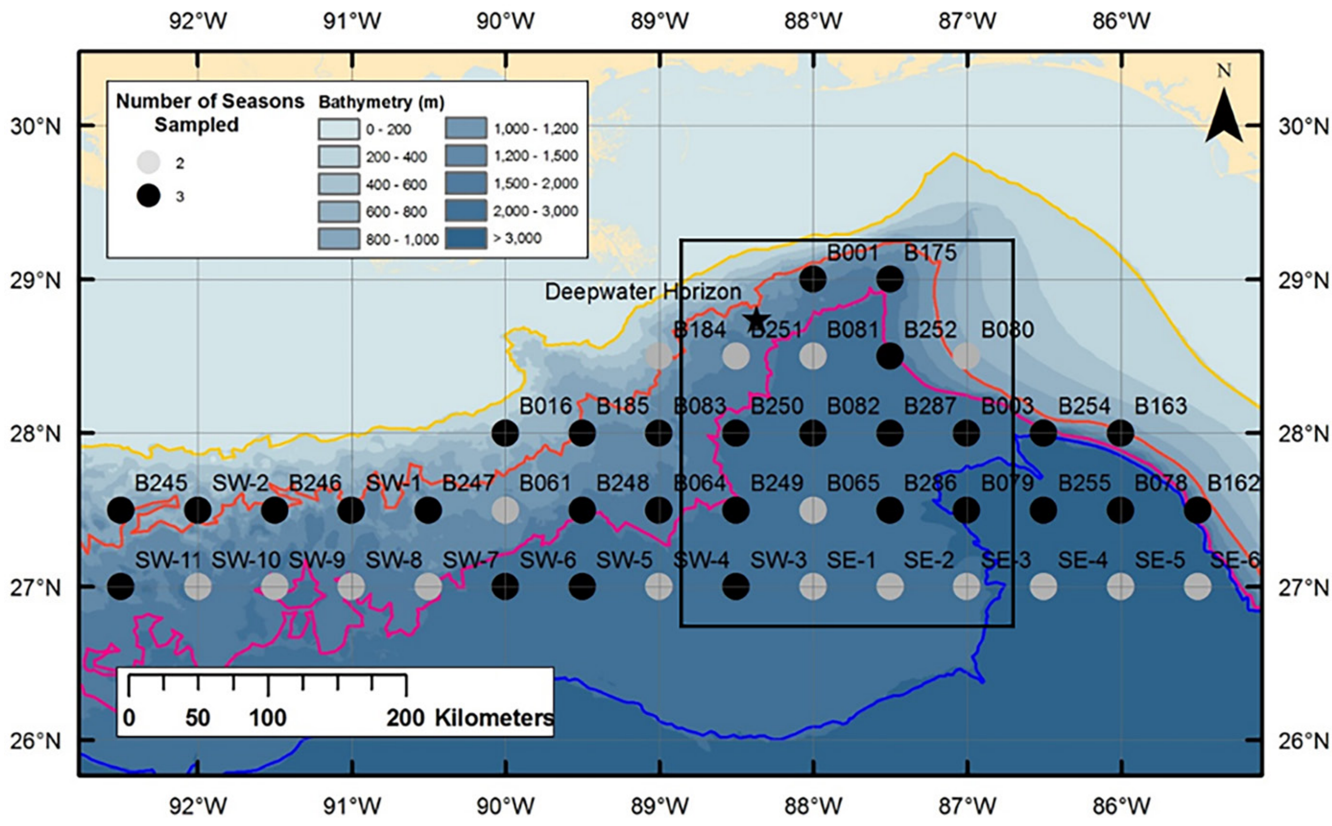

Figure 1. Station sites for ONSAP and DEEPEND cruises. Circles are ONSAP stations; within the black box are DEEPEND stations. The six stations used for quantitative comparisons were: B079, B255, B286, SE-1, SE-3, and SW-3.

because their lack of, or frequent loss of pseudoconch, complicated by damaged gelatinous bodies compromised our ability to identify species confidently.

Spatial distribution of species was plotted by latitude and longitude for all net samples using ArcGIS Desktop 10.5 mapping software (ESRI 2016). Standardized abundance was calculated by dividing the total abundance by the total volume filtered per net. Vertical distribution plots, using abundances standardized to volume filtered, were produced using RStudio version 1.2.1335 software (RStudio 2018). We used an α-value = 0.05 for t-tests.

RESULTS

Abundance

In total, 13,197 pteropods, in nine genera and 25 species, were collected on the cruises (Table 1). Total counts of pteropods collected were greater in 2011 (10,956 individuals) than

Table 1. Pteropod species list and total counts by cruise: ONSAP 2011 and DPND 2015. Specimens identified to the lowest taxonomic level possible. MS7 indicates Meg Skansi cruise #7; DP01 and DP02 stand for DEEPEND cruise 1 and 2.

Species	ONSAP(MS7)	DPND (DP01)	DPND (DP02)	DPND (DP01&02)	Total
Cavolinia gibbosa	109	5	77	82	191
C. inflexa	75	0	0	0	75
C. tridentata	71	5	11	16	87
C. uncinata	284	16	334	350	634
Clio cuspidata	2	1	1	2	4
C. polita	7	0	1	1	8
C. pyramidata	8,315	698	671	1,369	9,684
C. recurva	13	3	14	17	30
Creseis acicula	1	0	0	0	1
Cuvierina columnella	62	0	0	0	62
Diacavolinia constricta	5	0	0	0	5
D. deblainvillei	63	0	1	1	64
D. deshayesi	22	0	0	0	22
D. elegans	6	0	0	0	6
D. flexipes	0	0	1	1	1
D. limbata	3	0	0	0	3
D. longirostris	12	0	19	19	31
D. ovalis	1	0	0	0	1
D. souleyeti	1	0	0	0	1
D. strangulata	1	0	0	0	1
D. vanutrechti	32	0	1	1	33
Diacria major	185	7	20	27	212
D. trispinosa	228	8	135	143	371
Peracle bispinosa	1,050	75	126	201	1,251
Styliola subula	61	0	0	0	61
Cavolinia spp.	136	2	2	4	140
Clio spp.	127	4	3	7	134
Cuvierina spp.	2	0	0	0	2
Diacavolinia spp.	64	0	0	0	64
Limacina spp.	1	0	0	0	1
Totals	**10,956**	**824**	**1,417**	**2,241**	**13,197**

in 2015 (2,241), consistent with the greater sampling effort in 2011. Four hundred and fourteen out of 754 net samples were quantified for abundance relative to volume filtered for this study. Those nets collected 10,684 specimens. Only these specimens from quantitative samples were used for the analysis of vertical distribution patterns.

Clio pyramidata Linnaeus 1767 was the numerically dominant species in both 2011 and 2015 and was collected from every sampling station (Fig. 2A). In 2011, the three most abundant species collected were: *C. pyramidata* (n = 8,315), *Peraclis bispinosa* Pelseneer 1888 (N = 1,050), and *Diacria trispinosa* Blainville, 1821 (n = 228). The three most abundant species collected during 2015 were: *C. pyramidata* (n = 1,369), *Cavolinia uncinata (*d'Orbigny, 1835) (n = 350), and *Diacavolinia longirostris* (Blainville, 1821) (n = 19).

Standardized abundance was calculated primarily to compare nets by depth, but a subset could be used for interannual comparisons. Because the numbers of stations were not equal between the two sampling programs, the six stations in common to both programs were compared, and the differences in available standardized abundance data were not statistically significant (t = 1.78; P = 0.12) (Fig. 3). The most abundant species, *C. pyramidata, P. bispinosa,* and *C. uncinata* were also analyzed individually. Both *C. pyramidata* and *P. bispinosa* showed no significant differences in relative abundance and decreased over time (*C. pyramidata* t = 1.45, P > 0.05; *P. bispinosa* t = 1.87, P > 0.05). *Cavolinia uncinata* showed a significant difference between 2011 and 2015 (t = -3.08, P = 0.006), with an overall increase in individuals in 2015, contrary to the other two species.

Spatial distribution

Clio pyramidata and *Peracle bispinosa* Pelseneer, 1888 were the numerically dominant species found throughout the study area. The former was the only species found at every station. Spatial distribution maps for the four most abundant species, based on combined cruise data (presented in Figs. 2A–D). Generally, abundances were highest around the upper slope and along DeSoto Canyon in the northeastern GoM and were lower west of the Mississippi Canyon and slope. However, spatial distribution patterns and quantities varied greatly among species.

Vertical distribution and diel migrations

Pteropods were present throughout the sampled water column, but the largest number of collected pteropods, standardized to volume filtered, occurred in the depth range of 0–200 m at night, and 200–600 m during the day (Fig. 4). Diel vertical migration patterns were revealed for *D. trispinosa, Styliola subula* Quoy and Gaimard, 1827*, Cavolinia inflexa* (Lesueur, 1813)*, Cuvierina columnella (*Rang, 1827), and *C. pyramidata* (Figs. 5A–E). No diel migration on the scale we sampled was observed for *P. bispinosa*, *Cavolinia tridentata (*Forsskål, 1775), *Clio recurva (*Children, 1823), *C. uncinata*, *Diacria major (*Boas, 1886), *D. longirostris*, *Diacavolinia deblainvillei* van der Spoel, Bleek and Kobayasi, 1993, *Diacavolinia vanutrechti* van der Spoel, Bleek and Kobayasi, 1993, and *Diacavolinia deshayesi* van der Spoel, Bleek and Kobayasi, 1993 (Figs. 6A–I). Migration patterns could not be assessed for 10 additional species due to insufficient standardized data (Shedler 2020).

DISCUSSION

Abundance

Overall, pteropod collections were fewer in 2015 than in 2011, which aligns with declines between 2011 and 2015 in many other taxa, including fishes, cephalopods, crustaceans, and heteropods, another group of pelagic gastropods that have been reported in this region of the northern GoM (Clark *et al.* 2021). The number of stations sampled and trawl volumes filtered were both higher in 2011, which most likely explains the difference in total capture numbers for pteropod species. However, the decline in pteropod abundance was observed when comparing just the small subset of six stations that were sampled for standardized abundances by both programs, albeit not significantly for the three species analyzed. Additional work analyzing the 2016 through 2021 DEEPEND pteropod material would contribute to a larger sample size at various stations, which would lead to further examining trends.

There was a lack of baseline information of the GoM midwater prior to the DWH oil spill. Pteropods were collected at different times of the year for the two programs used sampled (ONSAP: April, 2011) (DEEPEND: May, August, 2015). Seasonal variability may be a factor in the observed abundance decline but additional examination of other years is needed to create a robust dataset for comparison. Additional cruises during multiple seasons could aid in distinguishing whether seasonal patterns exist for these species.

Spatial distribution

Pteropods play key roles in the pelagic ecosystem and the biogeochemistry of the northern GoM. Thecosomatous pteropods prey on planktonic microorganisms (*i.e.*, phytoplankton, micro- and mesoplankton and larvae) that they trap in a mucous food web (Lalli and Gilmer 1989). These interactions lead to the carbon flux of the midwater column (Bednaršek *et al.* 2012, Burridge *et al.* 2017). Primary production occurs year-round in the northern GoM, but is highest in the spring and summer, coinciding with the Mississippi River's peak discharge (Spies *et al.* 2016). Highly productive areas in the northern GoM yield the highest zooplankton abundances in the GoM (Fisher *et al.* 2016). Pteropod

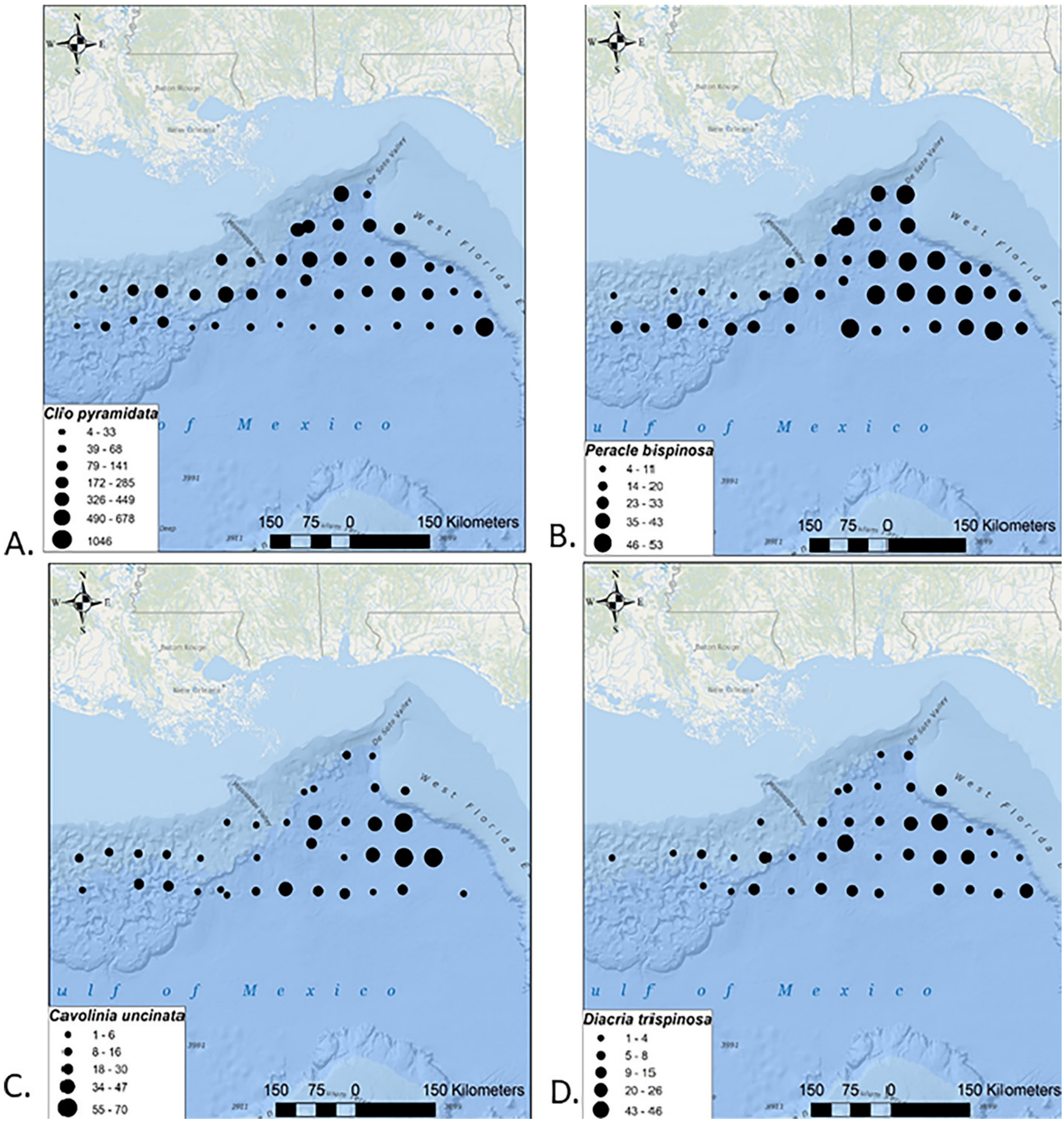

Figure 2. Pteropod spatial distribution for the four most abundant species. A. *Clio pyramidata*, B. *Peracle bispinosa*, C. *Cavolinia uncinata*, D. *Diacria trispinosa.* Each species is plotted to a unique scale.

abundance and spatial distribution reported here follow the same pattern found in previous studies of plankton diversity and abundance, corresponding to unique physical oceanographic features (*e.g.*, Loop Current eddies, basin edges) in the GoM (Wormelle 1962, Xue *et al.* 2013, Fisher *et al.* 2016, Gomez *et al.* 2018).

Considerations to examine in a future study would include measuring pH and other environmental influences

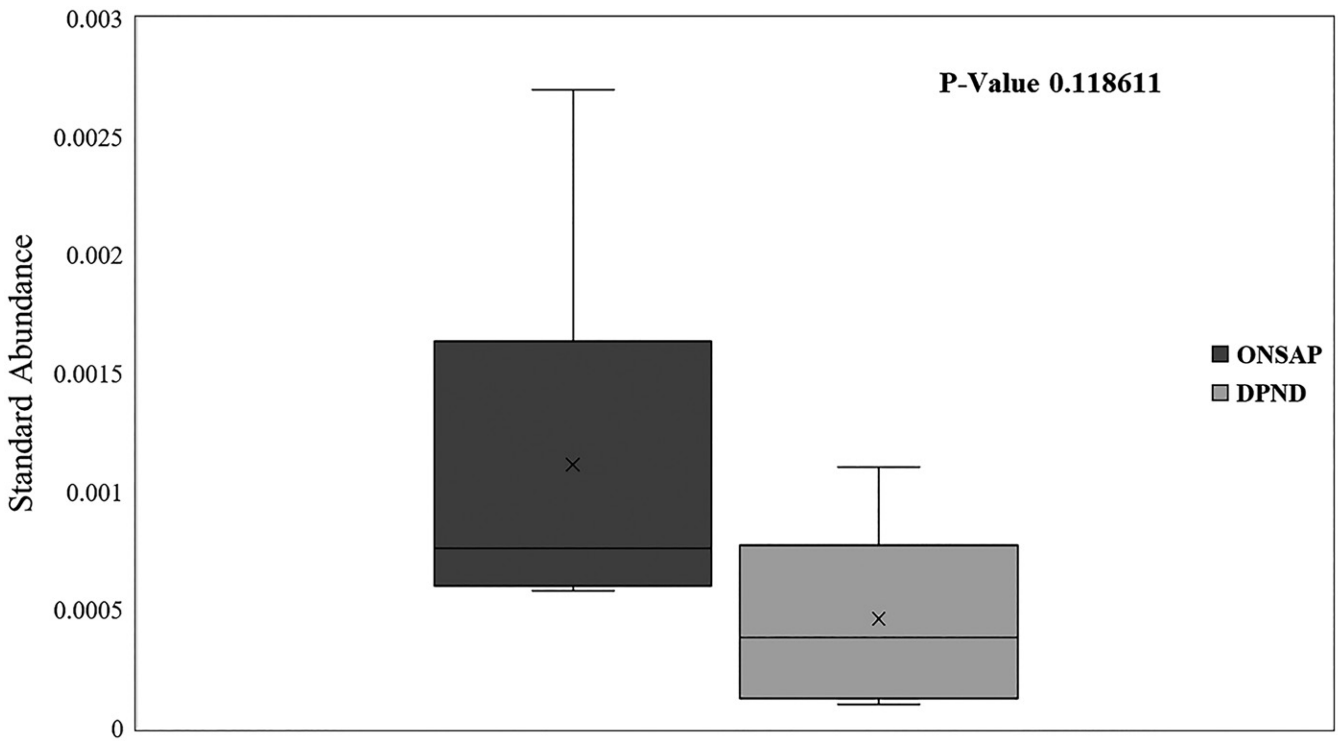

Figure 3. Pteropod abundance standardized by volume of water filtered (No. $10^{-6}m^{-3}$) for six stations, and the t-test used to calculate p-value sampled from ONSAP (2011) and DEEPEND (2015).

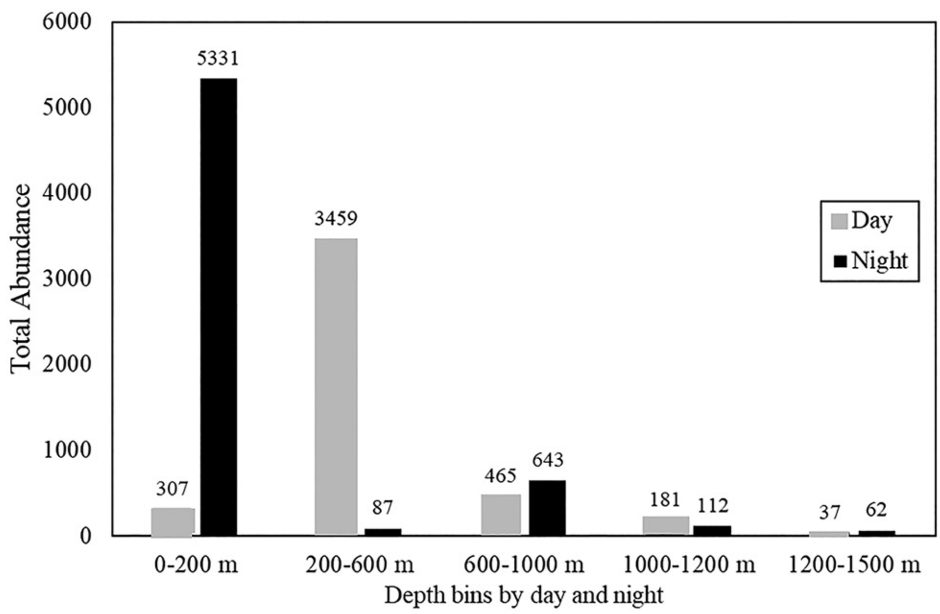

Figure 4. Total number of pteropods collected per depth zone by day/night from 2011 and 2015 combined.

that may impact the distribution of pteropods in the northern GoM. A study by Feely *et al.* (2018) looking at documented changes in acidification levels found that a decrease of aragonite saturation is high in the GoM due to the warmer water temperatures (Feely *et al.* 2018). Another study examined carbonate chemistry of deep sea corals in the GoM,

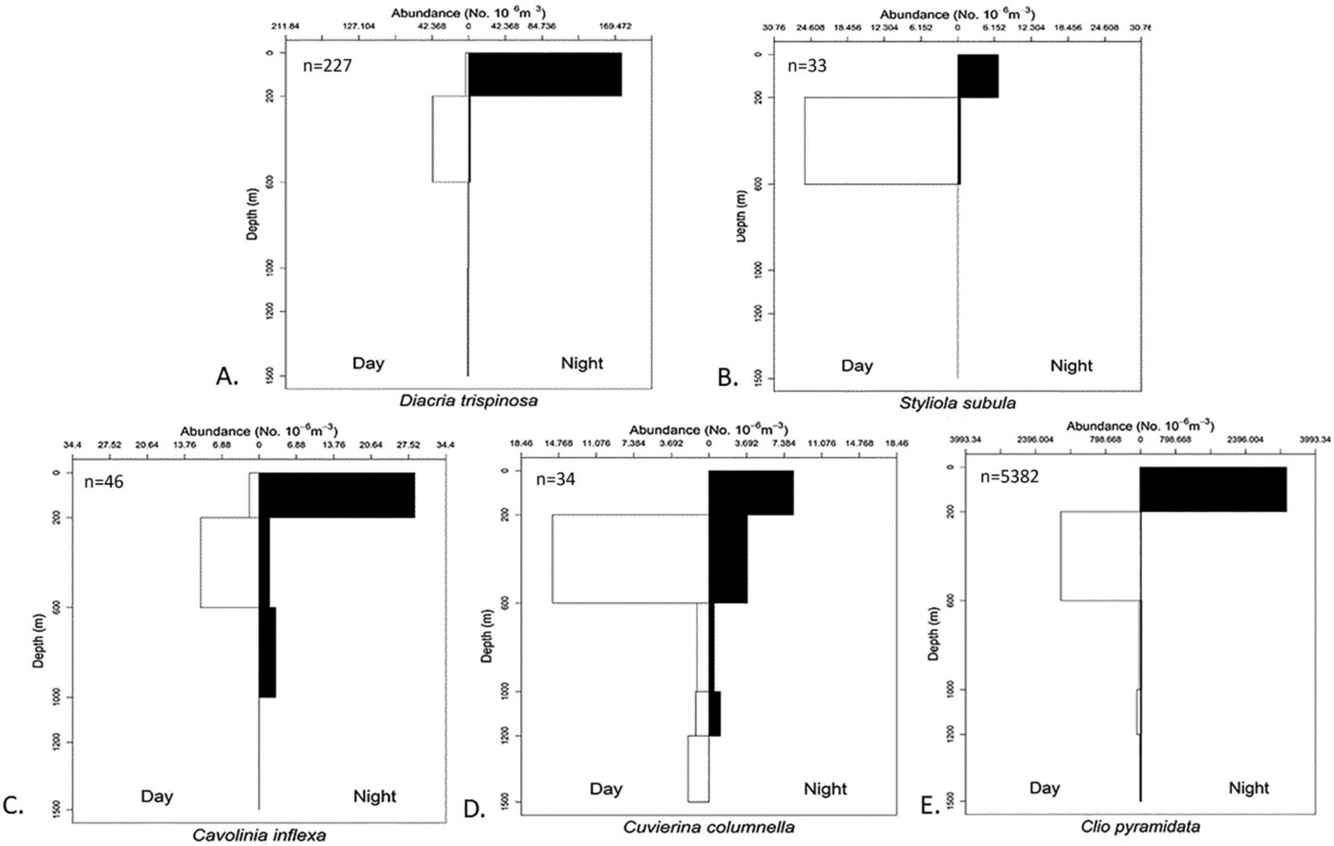

Figure 5. Five large pteropod species exhibiting diel vertical migrations. A. *Diacria trispinosa*, B. *Styliola subula*, C. *Cavolinia inflexa*, D. *Cuvierina columnella*, E. *Clio pyramidata*. Each species is plotted to a unique scale.

finding a quantitative baseline for benthic, cold-water coral systems (Georgian *et al.* 2016). Broadening the current study to include environmental parameters could increase the current knowledge of pteropod resilience in the northern GoM in the face of current climate change.

Vertical distribution and diel migrations

Horizontal and vertical distribution patterns for zooplankton vary by both species and season and are often closely related to hydrographic conditions (*i.e.*, salinity, depth, temperature, freshwater input) (Bsharah 1957, Austin 1971, Vecchione and Grant 1983, Manno *et al.* 2017). Diel differences in depth distribution may differ by location and season due to differences in water clarity and downwelling sunlight, also affecting visibility of plankton to their predators (Almogi-Labin *et al.* 1988, Pierrot-Bults and Peijnenburg 2014). For example, Almogi-Labin *et al.* (1988) observed in the Sargasso Sea during summer months that diel migrators moved to greater depths than in other seasons, without reaching the surface in summer. Vertical distribution and diel migration of pteropods have been extensively studied in the major oceanic basins, but studies in the GoM have been limited to specific regions, such as the Florida Current (Wormelle 1962) and the Florida Straits (Michel and Michel 1991). Snider's (1975) study was extensive and covered most of the GoM outside the 1,828 m isobath and the northwest/central region, but not the northern/northeastern GoM. Snider (1975) noted the problem of variability among samples taken with various nets and mesh sizes. This is a frequent problem with pteropod collection because sizes vary greatly among species and growth stages. As a result, total abundances are underestimated by large-mesh nets such as ours, compromising inferences about overall distributions.

In this study, vertical distribution and diel migrations patterns varied among species. *Cavolinia uncinata* and *C. pyramidata,* were the only species collected at every depth (0 – 1,500 m) during both day and night while others showed no apparent vertical migration. It is interesting to note that *D. vanutrechti* showed an apparent reverse diel migration into deeper depths at night (> 1,200 m) (Fig. 6H). This observation could be investigated further to confirm this behavior, as this was based on small numbers of specimens (n = 30).

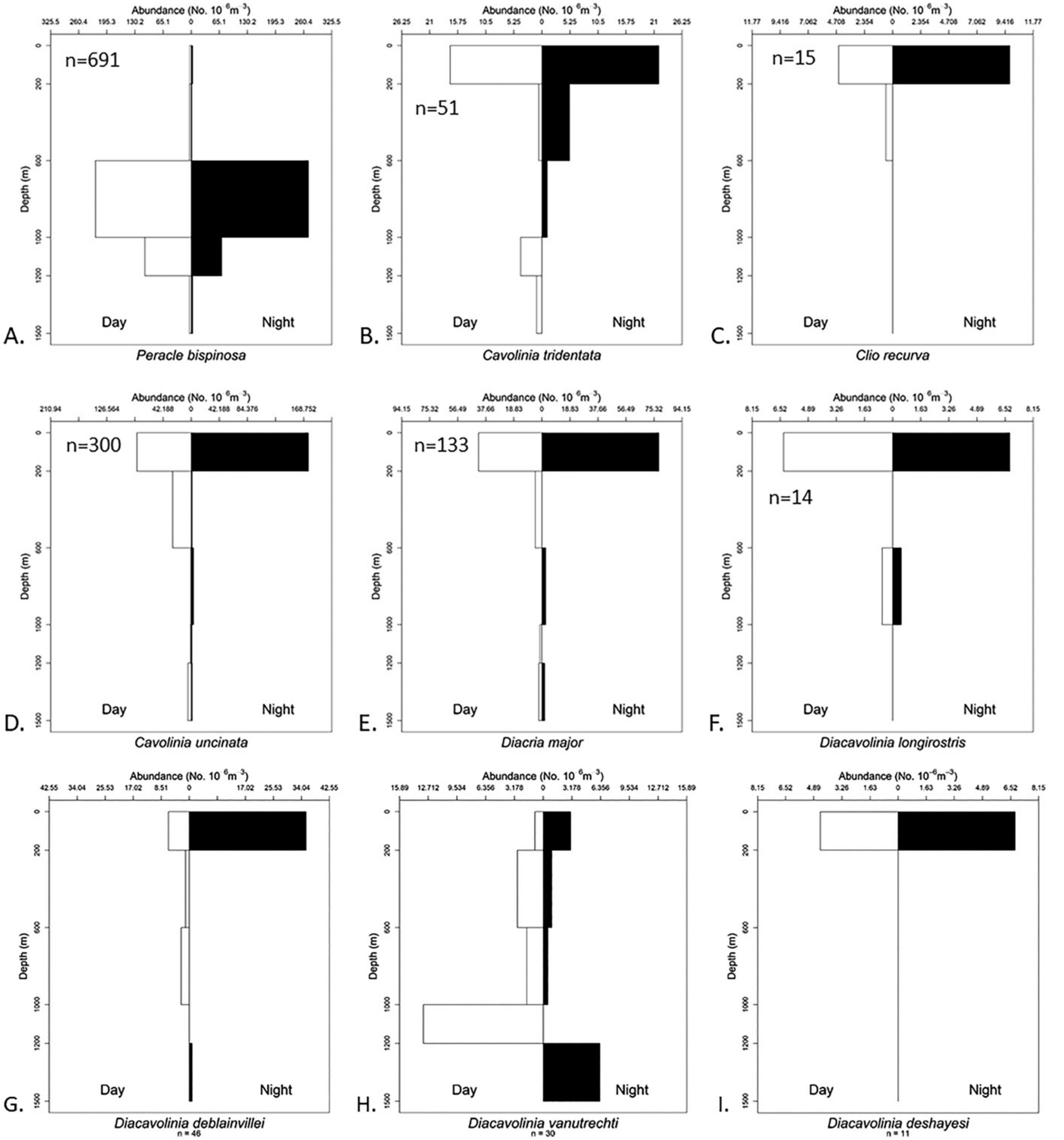

Figure 6. Nine weak or non-vertical migrating species. A. *Peracle bispinosa*, B. *Cavolinia tridentata*, C. *Clio recurva*, D. *Cavolinia uncinata*, E. *Diacria major*, F. *Diacavolinia longirostris*, G. *Diacavolinia deblainvillei*, H. *Diacavolinia vanutrechti*, I. *Diacavolinia deshayesi*. Each species is plotted to a unique scale.

Peracle bispinosa is a mesopelagic species that stayed below 600 m both day and night (Fig. 6A). *Clio recurva, D. major, C. tridentata,* and *Cavolinia gibbosa* d'Orbigny, 1835 were found in the epipelagic zone during both day and night (Fig. 6). Pteropods display a wide range of niche associations, which follows other mollusk patterns in the region (Judkins and Vecchione 2020, Clark *et al.* 2021)

Several studies (Wormelle 1962, Michel and Michel 1991, Snider 1975) concluded from smaller sample sizes that *C. uncinata* is a vertical migrator. Our study had a larger sample size of *C. uncinata* (n = 300) with the size range 3.33–8.3 mm and indicated only a weak vertical migration pattern, as there were individuals found in the epipelagic (0–200 m) during the day (Fig. 6D). There may be a vertical migration pattern of this species that is more refined than the depth bins we analyzed (0-200 m, 200-600 m, 600- 1000 m, 1000-1200 m, 1200- 1500 m). Our results show that the total number of individuals collected at night in the near-surface layer (n = 184) was greater than the total number collected at all depths during the day (n = 116). *Cavolinia uncinata* was also the only species to increase in number of individuals collected from 2011 to 2015, implying that there could be a seasonal variation between spring and summer months.

Other holoplanktonic mollusks have similar patterns in vertical distribution to that of the pteropods studied here in the GoM. Clark *et al.* (2021) found that two of the five large heteropod species examined were diel vertical migrators. Twenty-one cephalopod species from these sampling programs are known to migrate vertically, while only six are classified as non-migrators (Judkins and Vecchione 2020). However, even within these categories, the extent and depths of migration are variable. It appears that midwater mollusks occupy a variety of niches in the northern GoM.

CONCLUSIONS

Nine genera containing 24 shelled pteropod species were collected using MOC10 rigged with 3 mm mesh nets in the northern GoM in 2011, whereas only five genera with 14 species were similarly found in 2015. *Clio pyramidata* and *Peracle bispinosa* were the numerically dominant species found in these samples. Five species showed diel migration patterns while most other species remained primarily in the epipelagic zone. Overall, this study revealed that some pteropod species inhabit a broader depth range than indicated by many previous studies, mainly because of collecting gear and previous lack of deep-water sampling. These data are the first of their kind for the northern GoM and can be used as a baseline for future studies. At scales from local to global, rising anthropogenic CO_2 levels are projected to have major effects on the world's marine ecosystems (Feely *et al.* 1988, Fabry 1990, Orr *et al.* 2005, Bednaršek *et al.* 2016). Because pteropods are important indicators of the anthropogenic effects of changes in carbonate chemistry, knowledge of their current distribution and abundance will contribute to the understanding of these impacts.

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