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Large Thecosome Pteropods of the Northern Gulf of Mexico: Species Abundance, Spatial and Vertical Distribution With a Temporal Comparison of Shell Thickness

by

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A thesis submitted in partial fulfillment
of the requirement for the degree of
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Abstract

Large thecosome pteropods have a significant role in the pelagic ecosystem of the northern Gulf of Mexico (GoM). This research analyzed species abundances, vertical and horizontal distributions, and trends in shell thickness between 2011 and 2015. Pteropod samples were collected following the 2010 Deepwater Horizon oil 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). All samples were collected using a 10-m^2 Multiple Opening/Closing Net and Environmental Sensing System (MOC10) midwater trawl, with 3-mm mesh size. This gear sampled five discrete depths between 0–1500 m. To date over 13,000 pteropod specimens have been examined, and 25 species identified. *Clio pyramidata* was the most abundant species during both collection periods and five genera (*Diacria, Clio, Styliola, Cuvierina, Cavolinia*) demonstrated diel vertical migration from the meso- to epipelagic zone. Shell thickness comparisons between 2011 and 2015 were significantly different for several species, showing an increase in shell thickness in 2015. There was a slight positive correlation between shell length and thickness in several species.

1. Chapter One: Introduction

1.1 Objectives

Following the 2010 Deepwater Horizon oil spill (DWH), vast sampling and collection efforts occurred in the northern Gulf of Mexico (GoM). Sampling for pelagic nekton incidentally collected many large pteropods, capitalizing on these collection efforts, this study aims to address the following questions related to large pteropods: 1. What are the species abundance and distribution patterns in the northern GoM? 2. What are the patterns of vertical distribution for pteropod species from 0–1500 m? 3. Are there any allometric and isometric shell length-to-thickness growth correlations among pteropod species? This is the first comprehensive pteropod study in the northern GoM following the 2010 DWH.

1.2 Taxonomy and Biology

Pteropods are holoplanktonic marine snails of the phylum Mollusca, class Gastropoda, subclass Heterobranchia, and order Pteropoda (Lalli & Gilmer, 1989; Klussmann-Kolb & Dinapoli, 2006; Bouchet et al., 2017). There are three Pteropoda suborders (Bouchet & Rocroi, 2005) commonly referred to as pteropods: those generally having a shell (Thecosomata) and those without a shell (Gymnosomata) (Lalli & Gilmer, 1989; Klussmann-Kolb & Dinapoli, 2006; Bouchet et al., 2017; Rampal, 2017). The two suborders of Thecosomata are separated based upon whether the shell is internal or/only present during larval stage (Pseudothecosomata) or external (Euthecosomata) (Lalli & Gilmer, 1989).

Terrestrial and benthic snails use the typical gastropod sole-like foot for locomotion. In pteropods, the foot has evolved into a pair of modified wings (parapodia) for locomotion. The common name "pteropod" stems from (ptero-) meaning swimming wings and (-poda) meaning foot, "wing-footed" (Lalli &Gilmer, 1989). Their modified pair of swimming wings enable them to adapt to holopelagic life successfully, and they have a wide distribution from tropical to polar latitudes and a wide depth range from the surface to the bathypelagic zone (Chen & Bé, 1964; Van der Spoel, 1967; Lalli & Gilmer, 1989).

In 1804, Cuvier established Pteropoda as a separate order of mollusk, and in 1824 de Blainville distinguished the two suborders, Thecosomata and Gymnosomata (Chen & Bé, 1964). Klussmann-Kolb & Dinapoli (2006) revealed a close relationship between the orders Thecosomata and Gymnosomata, based on molecular work. 'Pteropods' were the unofficial but commonly used name for these suborders (Corse et al., 2013; Burridge et al., 2017; Rampal, 2017; Janssen et al,. 2019). Classification of thecosomes, especially the euthecosomes, has undergone frequent revisions and disputations at the (super)family level (Burridge et al., 2017). The euthecosome classification consists of the extant superfamilies Limacinoidea and Cavolinioidea. According to the widely accepted classification by Janssen (2003), Cavolinioidea has eight extant genera within four families: Cavoliniidae, Clioidae, Creseidae, and Cuvierinidae. In this study we follow Janssen's (2003) classification (Table 1) and focus on pteropods, excluding formae and subspecies, of the Euthecosomata superfamily Cavolinioidea and the family Peraclidae from Pseudothecosomata. The term "pteropod" refers hereafter to the shelled thecosome pteropods.

Each family within Cavolinioidea has unique external anatomical features that distinguish the families (Figure 1). The Cavolinioidea have lost the spiral coil of the shell and internal microstructure; it contains the largest euthecosome (*Clio recurva*) (Lalli & Gilmer 1989). Cavoliniidae shells are bilaterally symmetrical consisting of various shapes and sizes from globular or inflated (*Cavolinia* & *Diacavolinia*), bean/bottle-shaped (*Cuvierina*), long, straight and pointed (*Creseis*), rounded top-cross (*Diacria*), to an inverted triangular/pyramidal (*Clio*). Peraclidae, genus *Peracle*, is the primitive family of the pseudothecosomes and superficially resembles the primitive euthecosome genus *Limacina*, due to its external (internal when body is fully extended) sinistrally (counterclockwise) coiled shell and operculum (Lalli & Gilmer, 1989). Peraclidae are within Pseudothecosomata because their wings are not paired like the Euthecosomata but fused into a single wingplate; they also have two cephalic tentacles, an operculum, and a proboscis (Lalli & Gilmer, 1989).

All thecosome pteropods use a spherical mucous web to capture and entangle planktonic food particles (Gilmer, 1974), can retract their bodies into their shells for protection, and use parapodia for swimming. Thecosomes are protandrous hermaphrodites: maturing and functioning first as males, then as females (Van der Spoel, 1976; Lalli & Gilmer, 1989). Thecosomes typically release free-floating egg masses or gelatinous egg strings, from which veliger larvae hatch (Lalli & Gilmer, 1989), or are ovoviviparous and exhibit brood protection. The pteropod life span is approximately one to two years (Wells, 1976; Lalli & Gilmer, 1989), but is variable by species and location.

Thecosomes are small, ranging in size from less than a millimeter to 30 mm in shell length (Lalli & Gilmer, 1989). The Euthecosomes (and *Peracle bispinosa*) possess a thin external aragonite shell that is fragile, and that allows for weight reduction in the water column.

This thinner and lighter shell might have been advantageous for thecosomes from an evolutionary perspective, allowing them to flourish in new niches within the pelagic realm (Lalli & Gilmer, 1989; Bednaršek et al., 2014); but it could now lead to dissolution of their shells. Their aragonite shells are very sensitive to seawater carbonate chemistry changes that can cause aragonite dissolution (Byrne et al., 1987). As a result of their sensitivity, they are identified as indicators of anthropogenic ocean acidification (OA) (Maas, 2012).

1.3 Pteropod Distribution

Pteropods exhibit a cosmopolitism distribution occurring in every ocean; and tend to live in the epipelagic and upper mesopelagic depths of tropical and subtropical waters from the surface down to ~500 meters (Lalli & Gilmer, 1989). The vertical distribution of tropical and subtropical pteropods is less understood than the geospatial information for these species. Pteropods have the highest species richness and abundance in the epipelagic, while species richness and abundances decline in the meso- and bathypelagic zones (Pierrot-Bults & Peijnenburg, 2014). Van der Spoel and Dadon (1999), found four pteropod species in the bathypelagic zone (1000–4000 m), while 50 species occurred in the epipelagic (0–200 m) in the South Atlantic.

Pteropods are very abundant in surface waters (25–50 m) during the day, and their contribution to sound-scattering, from their shells, is most important at near-surface depths and at high frequency (Lavery et al., 2007). Pteropod shells can contribute up to 30% of pteropod oozes in certain regions of the open ocean, marginal seas and enclosed basins where water depths are shallower than the aragonite compensation depth (Chen & Bé, 1964; Melkert et al., 1992).

Studies using standard plankton nets, with varying net mesh sizes, can underestimate abundance and distribution of pteropods due to their wide range in size and larger species ability to avoid slower moving nets (Vecchione, pers comm, 2018).

There are few studies on pteropods in the GoM to date. Previous pteropod research in the southern regions of the GoM (Snider, 1975; Lemus-Santana et al., 2014), western Caribbean (Parra-Flores & Gasca, 2009), and the Florida Straits and Current (Wormelle, 1962; Michel & Michel, 1991) collected data on vertical and horizontal distribution of pteropods. Currently, the northern GoM is understudied in terms of pteropod horizontal and vertical distribution patterns.

1.4 Shell thickness and length

Pteropod shells come in all different shapes, sizes, lengths and thickness. The aragonite shells are very thin, ranging from 6 µm to 100 µm in thickness. The shell provides ballast and stability in the water column as well as offering protection from parasites and predators (Lalli & Gilmer, 1989; Howes et al., 2017). Aragonite is more soluble than other forms of calcite, making pteropod shells very susceptible to changes in oceanic carbonate chemistry (LeRoy, 1975; Byrne et al., 1987; Feely et al., 1988). Considering pteropod shell sensitivity to changes in carbonate chemistry, they are biological indicators of ocean acidification (OA) and ecosystem health (Betzer et al., 1984; Byrne et al., 1987).

Shell length varies by species and can range from the smallest < 1 mm to 30 mm in the largest species *Clio recurva* (Lalli & Gilmer 1989). Variations in shell length and thickness not only vary by species, but also by growth phases (ontogenic).

1.5 The Northern Gulf of Mexico (GoM)

The entire GoM encompasses an area approximately 1.6 million km^2 (Fisher et al., 2016) and is a semi-enclosed body of water (Judkins, 2009). The continental shelf (0–200 m) and slope together have depth ranges from 180–3,000 m and represents approximately 20% of the GoM (Fisher et al., 2016). The deeper regions, greater than 4,000 m, are part of the abyssal plain and comprises another 20% of the GoM (Gore, 1992). As described by Fisher et al. (2016), the deep pelagic environment is the domain that represents 90% of the GoM's volume. The mesopelagic (200–1,000 m) is about 30% of the volume and the bathypelagic (> 1,000 m) includes the remaining 60% of the volume (Fisher et al., 2016). The northern GoM represents a relatively substantial portion of the GoM approximately 7.5 x 10^4 km^2 and is a unique area with features such as the Loop Current (Judkins, 2009; Lemus-Santana et al., 2014; Fisher et al., 2016; Judkins et al., 2017).

Gomez et al. (2018), discusses that the large spatial differences in plankton productivity and biomass in the GoM can range from being oligotrophic in the Loop Current to highly productive in the northern shelf. The Mississippi-Atchafalaya (MS-A) river system contributes to, and influences, the productivity in the northern shelf GoM area because of its vast river input and discharge (21,524 m^3 s^{-1}) (Aulenbach et al., 2007), and contribution of more than 80% of the total dissolved inorganic nitrogen (DIN) load and exports to the deep ocean (Xue et al., 2013). Nutrients from the river are transported offshore and stimulate phytoplankton blooms that contribute to the organic carbon flux in the deep pelagic waters and sediments (Fisher et al., 2016).

Phytoplankton are primary producers and an important functional group that comprises the base of the marine food-web. Pteropods contribute to the export of organic carbon out of the euphotic zone and into the deep by several different methods, such as: sinking of their negatively buoyant fecal pellets, pseudo-feces from their mucous web collecting non-sinking particles, and by active transport during vertical migration when they respire (Tréguer et al., 2003; Bednarsek et al., 2012). After pteropods die, their aragonite shells sink from the surface down through the water column and into the deep; therefore, they contribute to the transfer of inorganic material from the surface into the deep (Byrne et al., 1987). Deep-sea benthic organisms depend on this flux of organic and inorganic material from the surface waters for food.

1.6 Deep Pelagic Research Programs in the Gulf of Mexico

One of the National Oceanic and Atmospheric Administration (NOAA) programs designed to assess damage to natural resources from human activities is the Natural Resource Damage Assessment (NRDA) program. Following the DWH in 2010, the Offshore Nekton Sampling and Analysis Program (ONSAP), was developed as part of NRDA, to evaluate impacts from the spill and improve basic knowledge of abundance, distribution, and biodiversity of deep-pelagic GoM fauna (Judkins et al., 2017). In 2011, the M/V *Meg Skansi* was used to assess the distribution of macroplankton and micronekton across the northern GoM as part of the ONSAP program. There were three cruises in 2011, each cruise used a 10 m^2 multiple opening and closing net and environmental sensing system (MOC10) to examine vertical distribution. The deep-pelagic nekton sample set collected by ONSAP is the largest of its kind in the GoM (Judkins et al., 2017).

Following ONSAP, the Deep Pelagic Nekton Dynamics of the GoM (DEEPEND) Consortium, sponsored by the Gulf of Mexico Research Initiative (GoMRI), was created to continue investigating possible consequences of the DWH oil spill in the water column from 2015–2018. The focus of DEEPEND is to fill the void in reference data for the water column (0–1500 m) in the GoM, by conducting a four-year quantitative sampling, sensing, modeling, and laboratory-analysis program to assess ecosystem dynamics, identify drivers of variability, and investigate possible consequences of the spill on ecosystem attributes (DEEPEND Consortium, 2017). The data collection from 2015–2018 is established a time-series showing possible ecosystem shifts or detectable responses that occurred since 2011 (DEEPEND Consortium, 2017).

In this study, we used data collected from the two GoM programs to address the following questions: 1) What are the spatial distributions of large pteropods in the northern GoM? 2) What are the vertical distribution patterns of these pteropod species throughout the water column in the northern GoM? 3) How does the pteropod species composition differ in the northern GoM between 2011 and 2015 samples? 4) Is there a correlation within selected pteropod species between shell length and thickness from 2011 to 2015?

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Table 1. Pteropod subdivision of the Thecosomata based upon Janssen (2003) classification.

Phylum Mollusca
Class Gastropoda
Subclass Opisthobranchia
Order Pteropoda – Thecosomata de Blainville, 1824
Suborder Euthecosomata Meisenheimer, 1905
Superfamily Limacinoidea Gray, 1847
Family Limacinidae Gray, 1847
Superfamily Cavolinioidea Fischer, 1883
Family Creseidae Rang, 1828
Family Cuvierinidae van der Spoel, 1967
Family Clioidae van der Spoel, 1967
Family Cavoliniidae Fischer, 1883
Suborder Pseudothecosomata Meisenheimer, 1905
Superfamily Peraclidoidea Tesch, 1913
Family Peraclididae Tesch, 1913
Family Cymbuliidae Cantraine, 1841
Family Desmopteridae Chun, 1889

Figure 1. Four pteropod species from the northern GoM. Photographs by Danté Fenolio. (DEEPEND Consortium, 2017). Starting from top left clockwise: *Clio pyramidata, Cavolinia gibbosa, Clio recurva, Clio recurva* also.

2. Chapter Two: Abundance, distribution and diel migration of large pteropods in the northern Gulf of Mexico

2.1 Introduction

Thecosome pteropods spend their entire lives in the pelagic realm across the world's oceans. "Sea butterflies" or "pteropods" are the common names used for the species possessing a shell in the order Pteropoda. The Thecosomata has two suborders divided by the presence of an external shell (Euthecosomata) or internal shell (Pseudothecosomata). There is one family within Pseudothecosomata that possess an external shell, the Peraclidae family and has only one genus *Peracle*. According to Janssen (2003), one of the two superfamilies in Euthecosomata, Cavolinioidea consists of four families: Cavoliniidae, Cliidae, Creseidae, and Cuvierinidae. Pteropod life span is approximately one to two years (Wells, 1976; Lalli & Gilmer, 1989).

Pteropods have a cosmopolitan distribution and play an important role in the biogeochemistry and ecosystems of the waters they inhabit (Seibel & Dierssen, 2003; Bednarsek et al., 2012). Even though considerable data on pteropod distribution have been compiled, relatively few studies and data available for the Gulf of Mexico (GoM). Previous pteropod research focused on different areas of the wider Caribbean such as the central-southern region of the GoM (Snider, 1975; Lemus-Santana et al., 2014), eastern region and Caribbean Sea (Tesch, 1946; Austin, 1971), western Caribbean (Parra-Flores and Gasca, 2009), and the Florida Straits (Wormelle, 1962; Michel & Michel, 1991).

Horizontal and vertical distribution patterns vary by species and season and are often closely related to hydrographic conditions (Bsharah, 1957; Austin, 1971; Vecchione & Grant, 1983). Similar to other holozooplankton, pteropods exhibit the typical horizontal distribution patterns in several ways, including lower biomass but the highest species richness in tropical and subtropical oceans (Angel, 1993; Pierrot-Bults & Peijnenburg, 2015), and greatest population densities in polar regions (Lalli & Gilmer, 1989).

Although pteropods occur throughout the water column, most species and higher abundances are usually found in the epipelagic and upper mesopelagic zones. Wormelle (1962) and Van der Spoel (1967) found many pteropod species undergo diel vertical migration, feeding near the surface at night and migrating to deeper depths during the day. Van der Spoel and Dadon (1999), found that 50 species are epipelagic (0–200 m) in the South Atlantic, 29 occur in both the epipelagic and mesopelagic (200–1,000 m), four are mesopelagic only, five are in both the meso- and bathypelagic (>1,000 m), and the bathypelagic zone contains an additional four species. This decrease in species richness and abundance with depth is common among other planktonic groups (Bsharah, 1957).

The Offshore Nekton Sampling and Analysis Program (ONSAP), and the Deep Pelagic Nekton Dynamics of the Gulf of Mexico (DEEPEND) programs were developed to asses and establish a baseline of the mid- to deep-pelagic fauna found in the GoM. These two programs collected the largest dataset, to date, of midwater data from the surface to 1500 m in the GoM.

Using data collected from these GoM programs, this study addresses the following questions: 1) What are the spatial distributions of large pteropods in the northern GoM? 2) Are there differences (seasonal or other) in relative abundance between 2011 and 2015? 3) What are the vertical distribution patterns of each of these large pteropod species in the northern GoM?

2.2 Materials and Methods

In 2011, the ONSAP program conducted three cruises aboard the research vessel M/V *Meg Skansi* over nine months sampling 46-stations in the northern GoM and collected specimens (Figure 2). ONSAP cruise (MS7) sampled discrete depths by a Multiple Opening Closing Net and Environmental Sensing System (MOC10) midwater trawl net with a 10-m^2 mouth area and six 3-mm mesh nets, collected samples at five discrete-depth intervals ranging from: 0–200 m, 200–600 m, 600–1000 m, 1000–1200 m, and 1200–1500 m (Judkins et al., 2017). The MOC10 was deployed twice at each station, once during the day and once at night for 4-6 hours to examine the differences in diel migration patterns (Judkins et al., 2017). Due to the 3-mm mesh net size, larger and adult pteropod species were collected.

The sampling stations spanned the northern GoM from 27–29°N and 85–93°W, making it the largest deep macroplankton and micronekton sampling set collected at the time.

The DEEPEND sampling (2015-2018) occurred aboard the R/V *Point Sur.* Midwater sampling also used the MOC10 with 10-m^2 mouth and 3-mm mesh net as well as the same depth scheme, stations, and protocols as the ONSAP (2011) cruise. They sampled each station twice, but for six hours specifically around solar noon (1000 h – 1600 h) and centered at midnight (2200 h – 0400 h) (DEEPEND, 2015). Pteropods from the first two DEEPEND cruises, DP01 and DP02 were included in this study.

Each net was rinsed down with seawater into each cod end for processing. Sample processing, while at sea, included the identification, cataloging, weighing (if possible) and measurements of all collected specimens (DEEPEND, 2015). Once a sample was completely subsampled and persevered in either 50% isopropanol or 95% non-denatured ethanol (EtOH), the remaining sample was fixed in 10% buffered formalin and all samples included a detailed station label (DEEPEND, 2015). A tow was considered quantitative having met the criteria of: proper opening and closing at set depths; proper flowmeter (volume) readings; correct net behavior during deployment; and no signs of mechanical failure or net damage (tears or holes) (DEEPEND, 2015).

A dissecting Zeiss Stemi 2000-C Stereo Microscope was used to identify and examine all specimens. Shell length and thickness were measured (mm) using an LT-4237-000 electronic digital caliper. Specimen wet weight (g) by species in each vial was taken using a Mettler Toledo PL303 310-gram max digital scale. Taxonomic identification, number of individuals, shell length (mm), shell thickness (mm), total wet weight (g) and station data were recorded and correlated to all cruise data of each station. There were several identification tools used including: the Marine Species Identification Portal (Van der Spoel, Newman et al. 1997) and identification guides (Chen & Bé 1964; Van der Spoel, 1967; Van der Spoel, 1972; Van der Spoel, 1976; Lalli & Gilmer, 1989; Van der Spoel et al., 1993; Van der Spoel and Dadon, 1999), used to identify specimens to the lowest taxonomic level possible.

Only shelled Thecosome pteropods were chosen for this study due to identification confidence and material available for examination. Gymnosomata and unshelled Pseudothecosomata were excluded from this study due to no external shell, complications with damaged gelatinous bodies, and difficulty in identification.

All data was recorded and transferred to a Microsoft Excel (2016) spreadsheet for analysis. Spatial distribution was plotted by latitude and longitude data for all net samples by species using ArcGIS Desktop 10.5 mapping software (ESRI, 2016). Vertical distribution plots using standardized abundances were produced using RStudio version 1.2.1335 software (RStudio Team, 2018).

2.3 Results

In total, 13,197 pteropods were collected by ONSAP and DEEPEND cruises (Table 2). Quantified specimens totaling 10,684 were considered ‘quantitative,’ having met the criteria of: proper opening and closing at prescribed depths; 2) proper flowmeter (volume) reading; 3) proper net behavior (mouth angle, net speed) during deployment; and 4) no signs of mechanical failure (tears, holes) (DEEPEND, 2015), were included for the vertical distribution patterns and analysis.

Total counts of pteropods collected were greater in 2011 (10,956 individuals) than in 2015 (2,241). In 2011, 46 stations across the northern GoM were sampled (Figure 2), and in 2015 a total of 15 stations were sampled (Table 3). Specimen collection was highest in 2011 for many species, with *Clio pyramidata* being the dominant species collected in both 2011 and 2015 and collected from every sampling station (Figure 7a). In 2011, the top three species collected were: *C. pyramidata* (N= 8,315), *Peracle bispinosa* (N= 1,050), and *Diacria trispinosa* (N= 228). The top three species collected during 2015 were: *C. pyramidata* (N=1,369), *Cavolinia uncinata* (N=350), and *Diacavolinia longirostris* (N=19).

The standardized abundance was used to compare nets by depth and accounts for the amount of water that flowed through each net. Standardized abundance was calculated by taking the total abundance divided by the total net volume per net, which gives us quantitative net data to use for analysis. Fifteen stations in common between the two sampling programs were evaluated using their standardized abundances to examine if there was a significant difference between 2011 and 2015. There were seven stations from 2011 and eleven stations from 2015 that had standardized abundance data available. There was a significant difference found (p=0.044779) in standardized abundance between 2011 and 2015 (Figure 3). Since the number of stations were not equal, the six shared stations that both programs had standardized abundance data for were analyzed and there was not a significant difference found (p=0.118611) (Figure 4). Pteropods were present throughout the sampled water column, but the majority of pteropods were found in mid- and upper-mesopelagic depths of 600 m and above (Figure 5). The largest number of collected pteropods occurred at night in the 0–200 m and during the day in the 200–600 m depth range (Figure 6).

Spatial distribution maps were created for each species from combined cruise data and the top four species are shown in Figure 7 (a-d). The remaining maps are in Appendix A. Generally, pteropod concentrations were highest around the upper slope and along DeSoto Canyon in the north-eastern GoM and were lower west of the Mississippi Canyon and slope. However, pteropod spatial distribution patterns and quantities varied greatly among species.

Vertical migration patterns for *D. trispinosa, S. subula, C. inflexa, C. columnella, C. pyramidata* are in Figure 8 (a-e). Vertical distribution for the non-migrators, *P. bispinosa*, *C. tridentata*, *C. recurva*, *C. uncinata*, *D. major*, *D. longirostris*, *D. deblainvillei*, *D. vanutrechti*, *D. deshayesi* are in Figure 9 a-i. Several species (N=10) did not have standardized data available to assess vertical distribution, therefore their diel migration patterns are unknown.

2.4 Discussion

2.4.1 Abundance and Spatial Distribution

The data gathered for these assemblages of large pteropod in the northern GoM contributes information on the biodiversity, abundance, and distribution of holopelagic GoM invertebrates. This research presents the species diversity of northern GoM large pteropods and provides a baseline for future research.

In 2015, pteropods catches were lower than in 2011, this is also true when comparing the 15 and 6-stations standardized abundances that were sampled by both programs. Similar trends have been found in many other taxa groups including fishes, cephalopods, crustaceans, and the closely related heteropods in this region of the northern GoM (Sutton et al., in prep). However, the number of stations sampled, and trawl volumes filtered were both higher in 2011 which could possibly contribute to the difference in capture rates.

Samples were collected in April through June during ONSAP (2011) while DEEPEND sampled in May and August of 2015. Three common stations (B175, B252, and B287) were examined for possible trends between years. *Clio pyramidata, P. bispinosa,* and *C. uncinata* were analyzed at these stations in 2011 and 2015. Both *C. pyramidata* and *P. bispinosa* showed no significant differences in the number of captured individuals ($p>0.05$). *Cavolinia uncinata* showed a significant difference $p<0.05$ ($p = 0.005874$) between 2011 and 2015 with an overall increase in individuals in 2015, unlike the other two species which decreased. Seasonal variability and trawl volumes filtered can be factors in this abundance decline. However, it is challenging to fully distinguish the cause(s) of declining abundances for pteropods in the GoM due to the lack of midwater column baseline knowledge in this area before the DWH spill.

The 2010 Deep Water Horizon oil spill was a tragic but unique incident because of the depth at which the spill occurred at (~1,500 m), amount of oil released (~160 million gallons), and length of time (87 days) until containment within the northern Gulf of Mexico (EPA, 2017). In response to this disaster, the ONSAP and DEEPEND programs established a reference dataset to assess the midwater biodiversity. The data from this study can aid in establishing a long-term monitoring program to examine pteropod seasonal variability, abundance differences, and pattern changes over time for this region.

Pteropods play key roles in the ecosystem and biogeochemistry of the northern GoM and contribute to the micronekton community that support higher trophic levels of the food web. The primary food source for pteropods is planktonic in nature (i.e. phytoplankton, mesoplankton and larvae), and they consume the contents of their mucous food web (Lalli & Gilmer, 1989). 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). The highest nitrate concentrations are found near the Mississippi River plume extending onto the continental shelf, and high chlorophyll *a* concentrations occur, to the east of the Mississippi River plume. This highly productive region is coupled with the Mississippi River plume and in-part due to the unique physical characteristics of seasonal water masses being pulled off the shelf by eddies that break off from the Loop Current (LC), and seafloor topography found in the GoM (Austin, 1971; Rowe, 2017). These highly productive areas in the northern GoM yield the highest zooplankton abundances in the GoM. Pteropod abundance and spatial distribution in the GoM follow the same patterns found in previous studies of phyto-, meso- and zooplankton diversity and abundance corresponding to these unique physical oceanographic features (i.e. LC, eddies, basin shape) in the GoM (Wormelle, 1962; Xue et al., 2013; Fisher et al., 2016; Gomez et al., 2018).

Distribution patterns of individual species are closely related to biogeochemical parameters of the GoM. To evade predation during the day most pteropods stay in the mesopelagic zone (<200 m) and will feed at the surface at night (Figure 5). Pteropod assemblages found near the surface, in this study, are associated with the highly productive upper surface waters near the shelf break and upper slope region used for nightly feeding in this region.

2.4.2 Vertical Distributions and Diel Migrations

Hydrographic conditions influence vertical distribution and diel migration patterns and the differences are visible during day and night but differ by place and season (Pierrot-Bults and Peijnenburg, 2014). 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 lower regions, such as the Florida Current (Wormelle, 1962) and the Florida Straits (Michel & Michel, 1991). Snider's (1975) study was extensive and covered a majority of the GoM outside the 1,828 m isobath and northwest/central region, except the northern/northeastern GoM. Snider (1975) noted the problem of variability between samples taken with various nets and mesh sizes. This is a frequent problem with pteropod collection due to their varying sizes and as a result, abundances and distributions may be underestimated.

In this study, vertical distribution and diel migrations patterns varied by species. *Cavolinia uncinata* and *C. pyramidata,* were the only species collected at every depth (0 – 1500 m) during both day and night. Five large pteropod species exhibited diel migration and are known to be vertical migrators (Figure 8 a-e). Ten other species showed weak or no diel migration (Figure 9 a-i). *Clio polita*, *Clio cuspidata*, *Creseis acicula* and seven *Diacavolinia* spp. did not have enough data to assess vertical distribution or migration patterns. It is interesting to note that *D. vanutrechti* showed a reverse diel migration into deeper depths at night (>1,200 m) but were found in all depth zones during day and night (Figure 9 i). This observation could be investigated further to validate this observation. *Peracle bispinosa* is a mesopelagic species that stayed below 600 m both day and night (Figure 9 a). *Clio recurva, D. major, C. tridentata,* and *C. gibbosa* were found in the epipelagic zone during both day and night. All of these showed either weak or no evidence of vertical migration (Figure 9). *Cavolinia uncinata* shows evidence of having a weak vertical migration pattern (Figure 9 d).

Many studies (Wormelle 1962, Michel & Michel 1991, Snider 1975) concluded that *C. uncinata* is a vertical migrator, while using smaller sample sizes. In this study, *C. uncinata* had a larger sample size (N=300) but showed a weak vertical migration pattern, as there were individuals found at the surface (0–200 m) during the day (Figure 9 d). Michel & Michel (1991), did note that "although *C. uncinata* was fairly common in day tows that passed through the upper 300–400 m, there is no clear evidence of population movement to greater depths in these data." Our results show that the total number of individuals collected at night at the surface (N=184) was greater than the total number collected at multiple depths during the day (N=116). *Cavolinia uncinata* was also the only species to increase in number of individuals collected in 2015, implying that there could be a seasonal variation.

2.5 Conclusion

In summary, nine genera containing twenty-five large pteropod species were identified for this study. With twenty-four large pteropod species inhabiting the northern GoM in 2011, but only fourteen species found in 2015. *Clio pyramidata* and *Peracle bispinosa* are the numerically dominant large species found in this area. *Clio pyramidata* was the only species at every station and every depth sampled that showed a diel vertical migration pattern. *Peracle bispinosa* was found at almost every station as well but is not a vertical migrator. This is a deeper mesopelagic species that stays below 600 meters. Overall, the total number of individuals captured was higher in 2011, when the standardized abundance and the common stations between programs was taken into account, the results were not significantly different, but the downward trend was still evident. Additional data is needed from the same stations over time and season to validate this decrease in abundance trend from 2011 to 2015.

This data is the first of its kind for the northern GoM and can be used as a baseline for future studies. Five species showed diel migration patterns while most other species remained primarily in the epipelagic zone. The results from this study can be used to drive future studies that use similar gear, sampling area, and seasons in order to make accurate comparisons.

Overall, this study shows that pteropod assemblages included deeper depth profiles than many previous studies, mainly because of collection gear and previous lack of deep-water sampling. Pteropods play an important part in the food web and biogeochemistry of the Gulf of Mexico and throughout the world's oceans.

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Table 2. Pteropod species catalogue and counts. Specimens identified to lowest taxonomic identification by cruise.

Species	ONSAP (MS7)	DPND (DP01)	DPND (DP02)	DPND (DP01 & 02)	Sub-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	8315	698	671	1369	9684
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	1050	75	126	201	1251
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	10956	824	1417	2241	13197

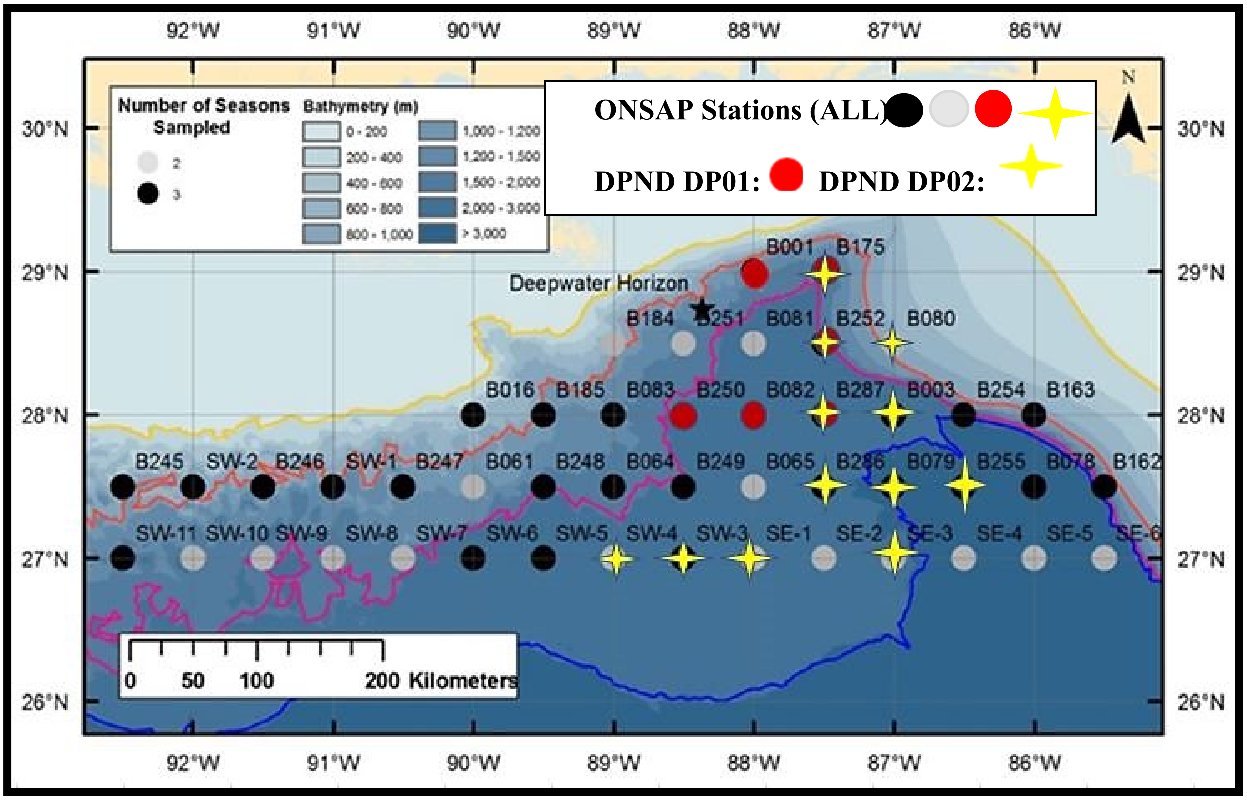


Figure 2. Sampling stations from the northern Gulf of Mexico, showing 2011 ONSAP stations and 2015 DEEPEND DP01 and DP02 sampling stations.

Table 3. Fifteen common stations sampled between in 2011 and 2015.

Stations	MS7 (2011)	DP01 (2015)	DP02 (2015)
B001	Apr-11	May-15	N/A
B003	Apr-11	N/A	Aug-15
B079	Jun-11	N/A	Aug-15
B080	Apr-11	N/A	Aug-15
B082	May-11	May-15	N/A
B175	Apr-11	May-15	Aug-15
B250	May-11	N/A[a]	N/A
B252	Apr-11	May-15	Aug-15
B255	Jun-11	N/A	Aug-15
B286	Jun-11	N/A	Aug-15
B287	Apr-11	May-15	Aug-15
SE-1	Jun-11	N/A	Aug-15
SE-3	Jun-11	N/A	Aug-15
SW-3	Jun-11	N/A	Aug-15
SW-4	N/A[a]	N/A	Aug-15

N/A[a] no data was collected at the station

N/A stations were not sampled

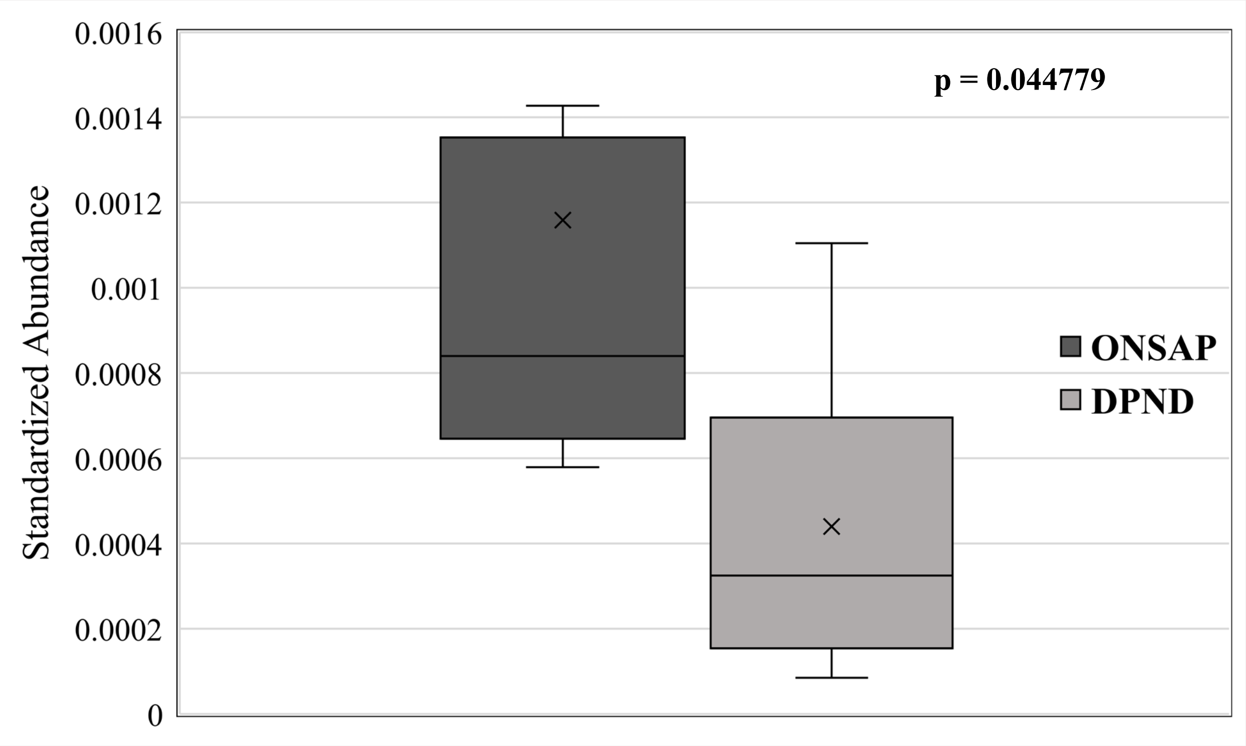


Figure 3. Pteropod standardized abundance of 15-stations sampled from ONSAP (2011) and DEEPEND (2015).

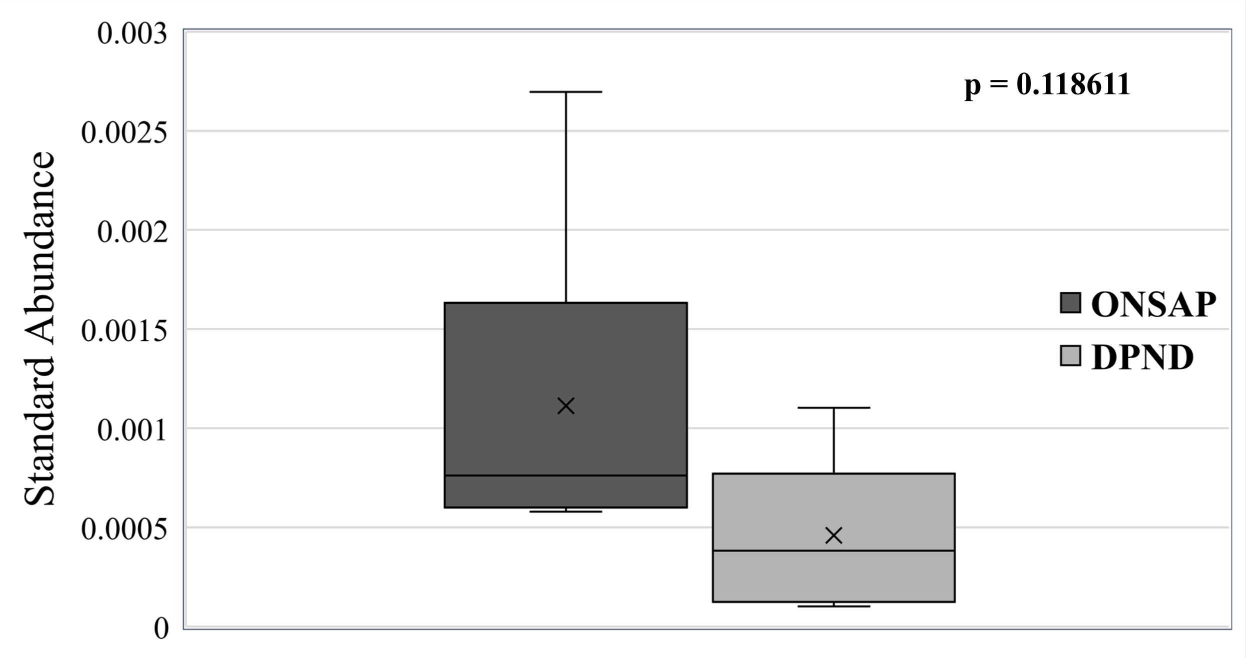


Figure 4. Pteropod standardized abundance of six stations sampled from ONSAP (2011) and DEEPEND (2015).

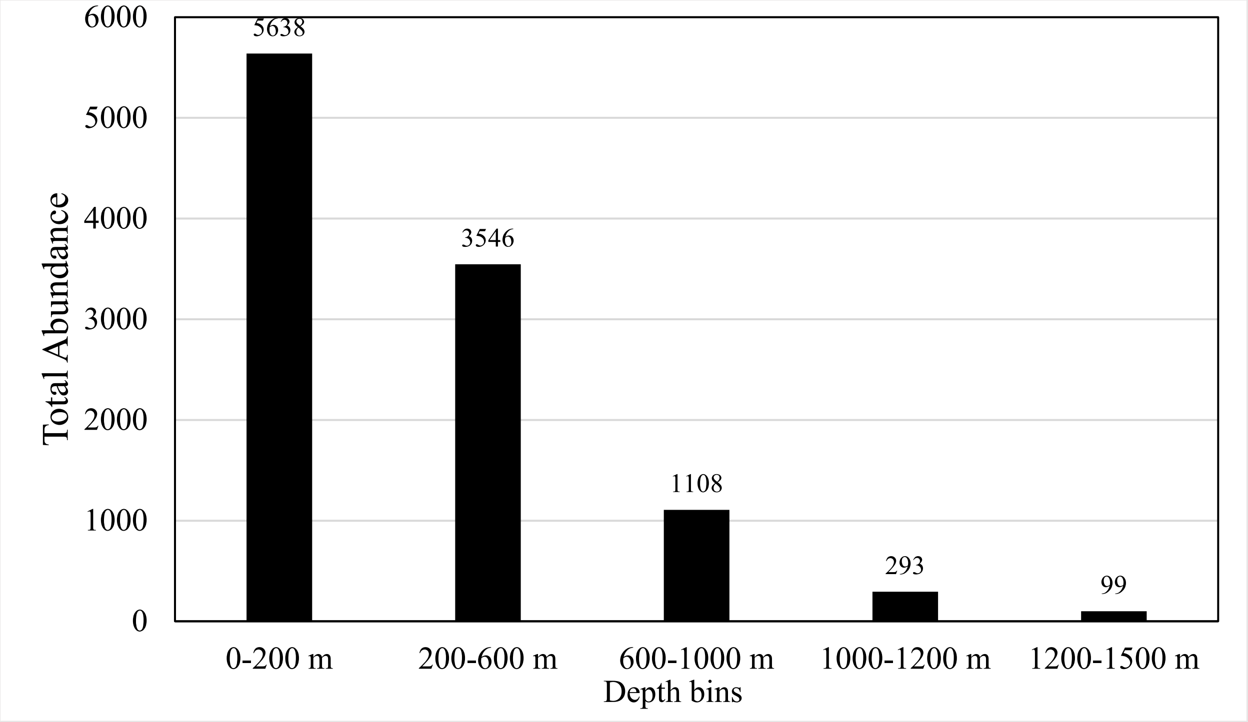


Figure 5. Total number of pteropods collected per depth zone by from 2011 and 2015 combined.

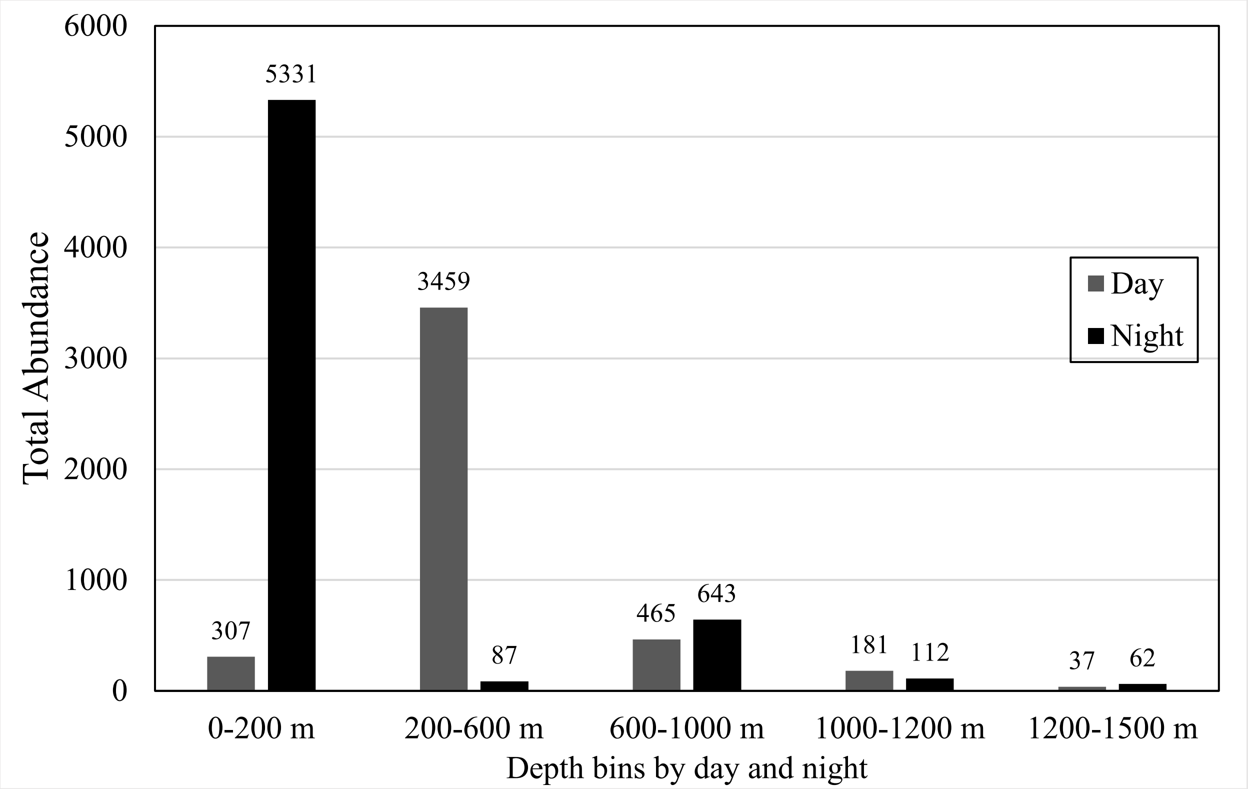
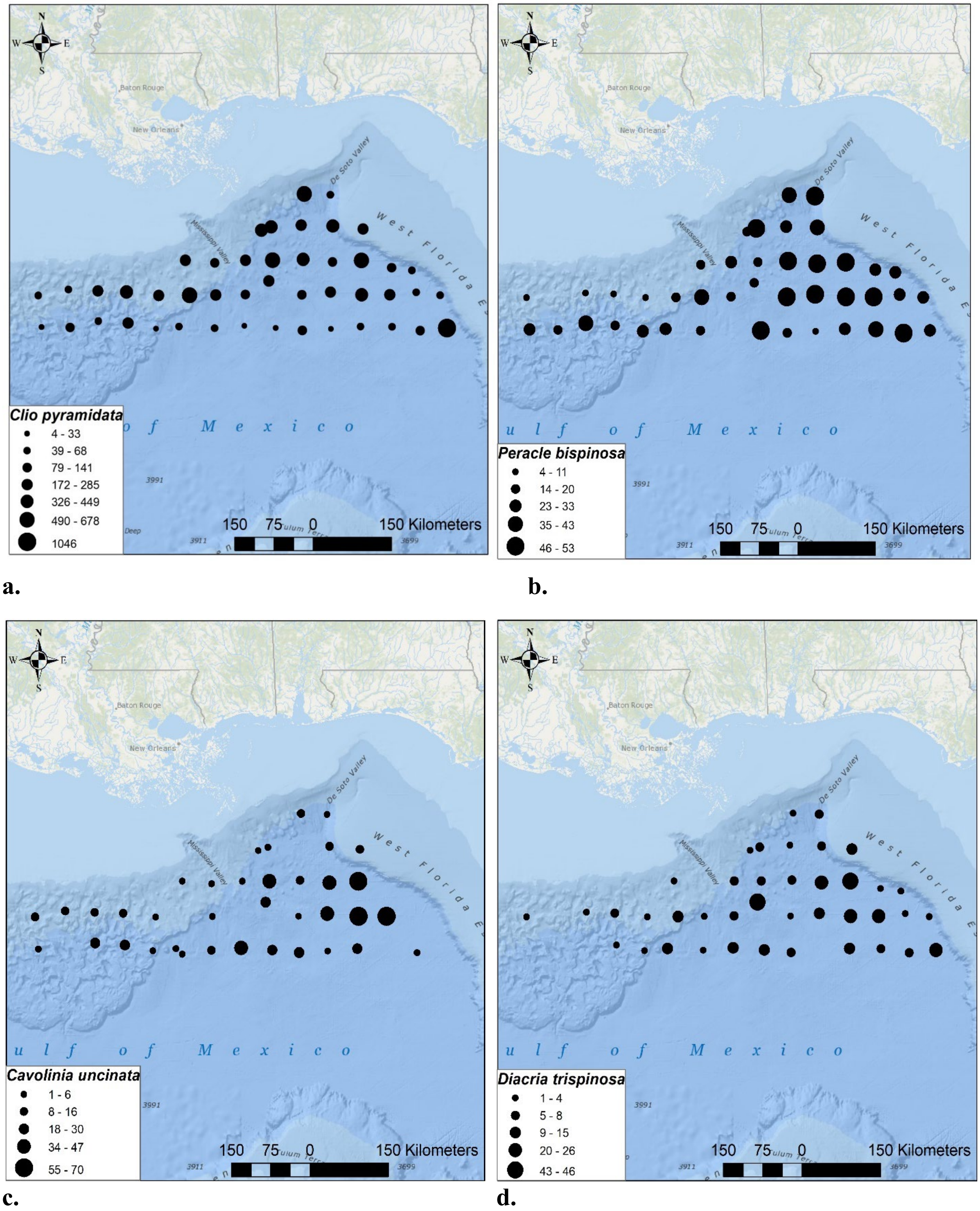


Figure 6. Total number of pteropods collected per depth zone by day/night from 2011 and 2015 combined.



a.

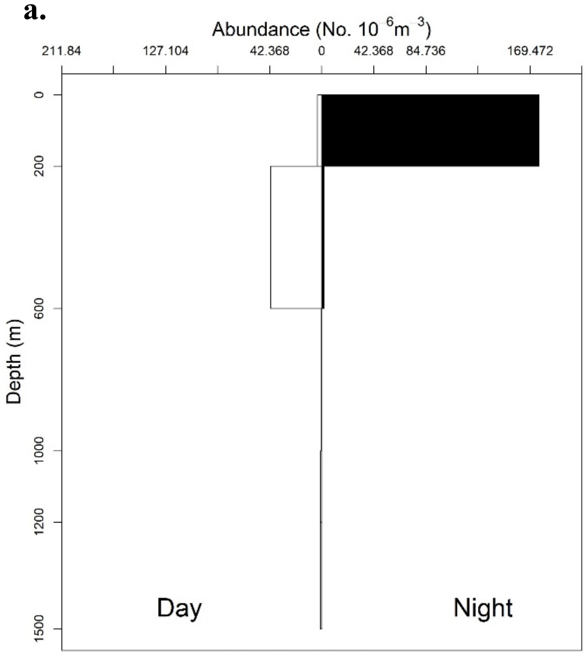
b.

c.

d.

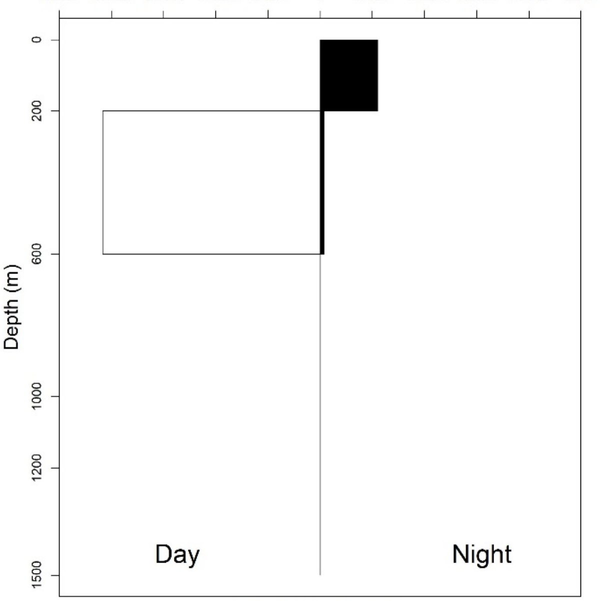
Figure 7 a-d. Pteropod distribution for the top four most abundant species. **a**. *Clio pyramidata* **b**. *Peracle bispinosa* **c**. *Cavolinia uncinata* **d**. *Diacria trispinosa*

a.



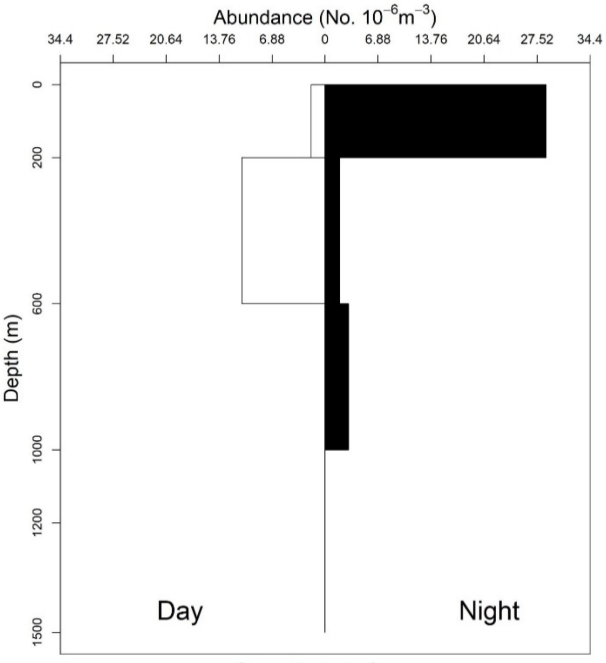
Diacria trispinosa
n = 227

b.



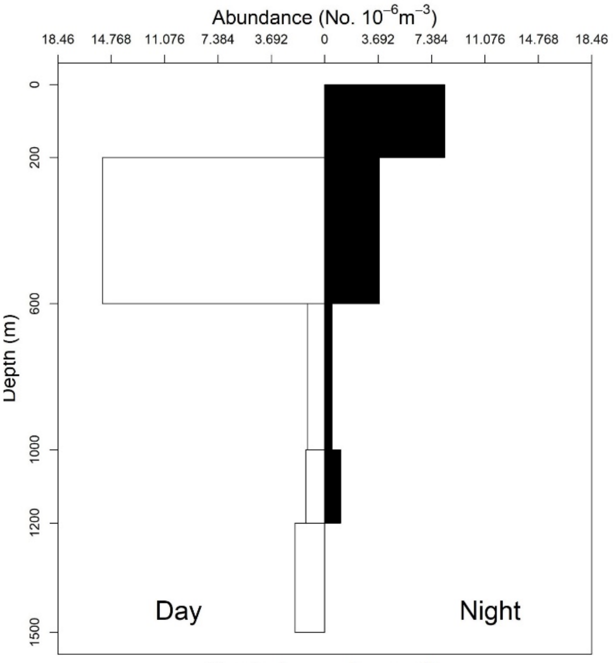
Styliola subula
n = 33

c.



Cavolinia inflexa
n = 46

d.



Cuvierina columnella
n = 34

e.

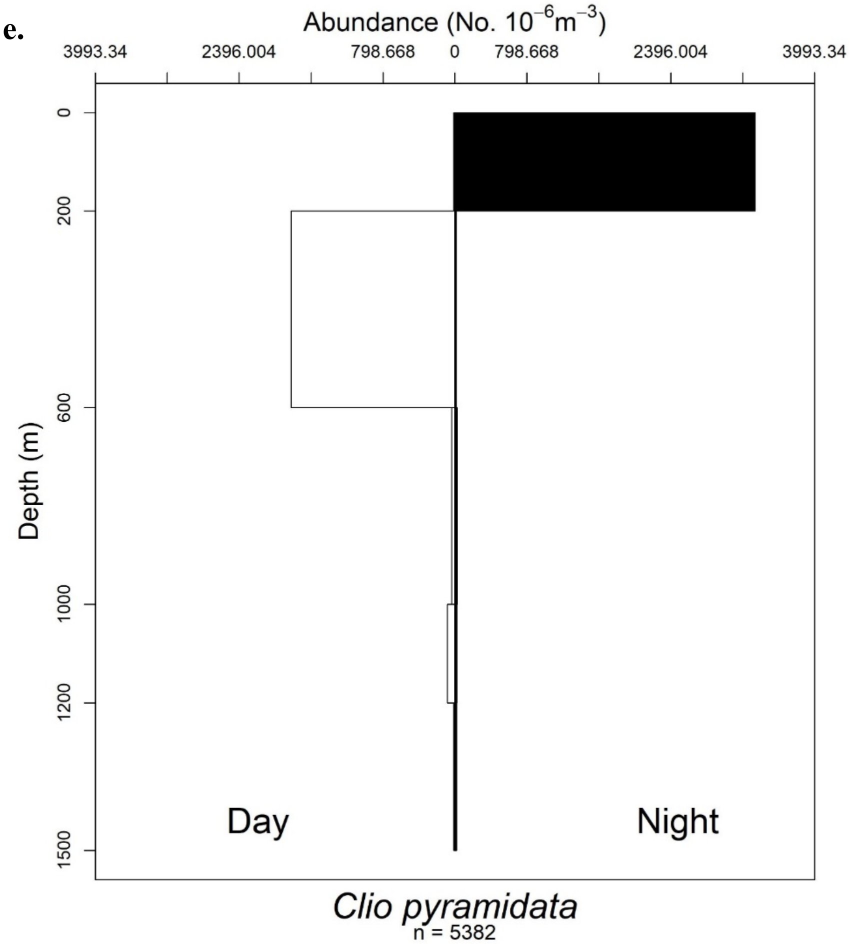
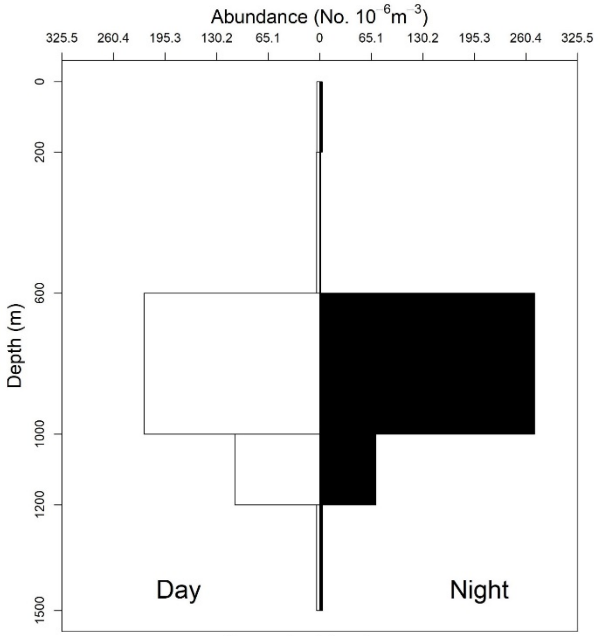


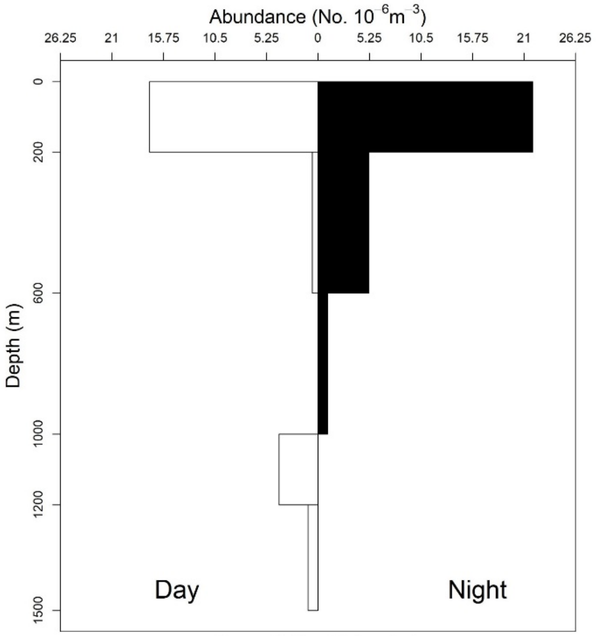
Figure 8 a-e. Five large pteropod species exhibiting diel vertical migrations. **a**. *Diacria trispinosa* **b**. *Styliola subula* **c**. *Cavolinia inflexa* **d**. *Cuvierina columnella* **e**. *Clio pyramidata*

a.



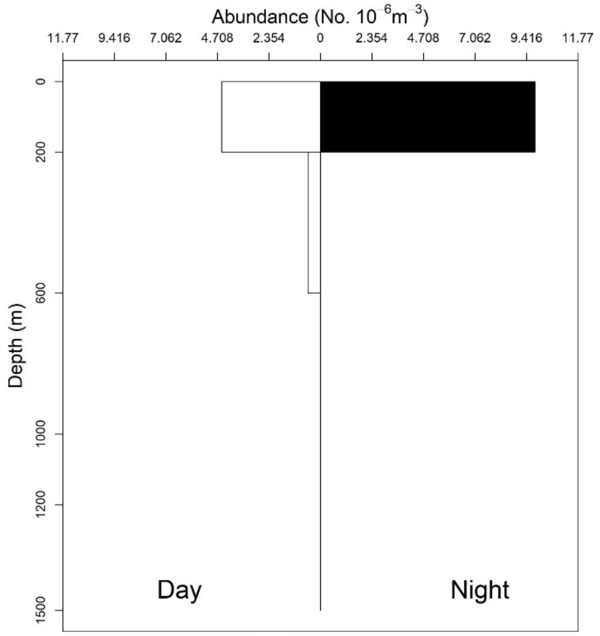
Peracle bispinosa
n = 691

b.



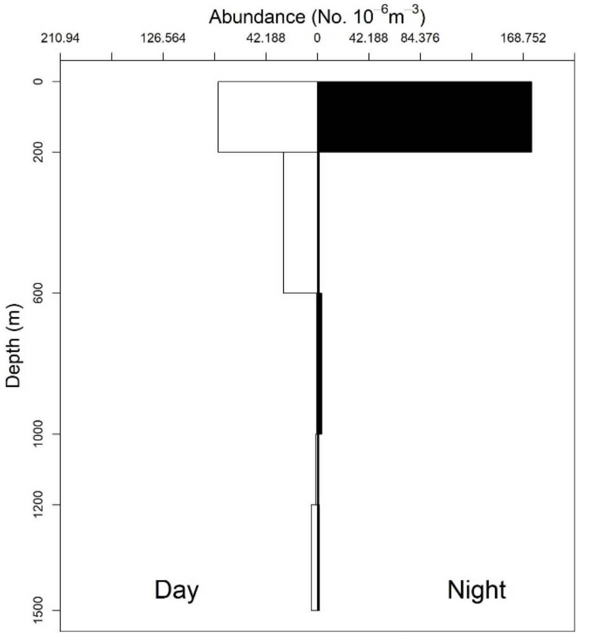
Cavolinia tridentata
n = 51

c.



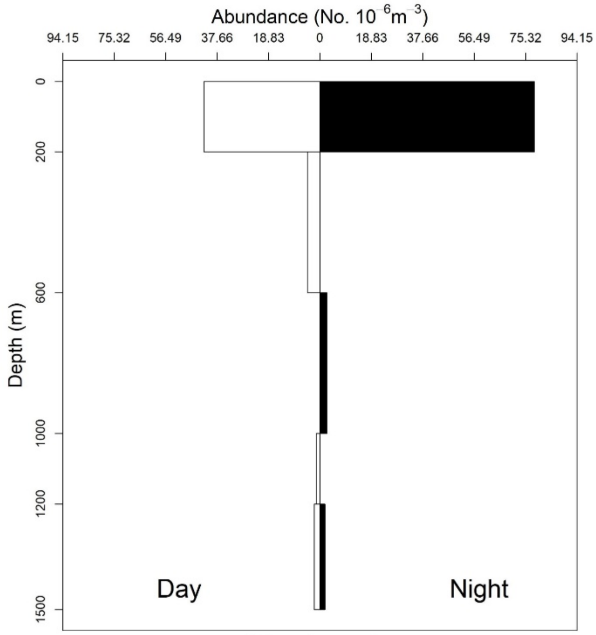
Clio recurva
n = 15

d.



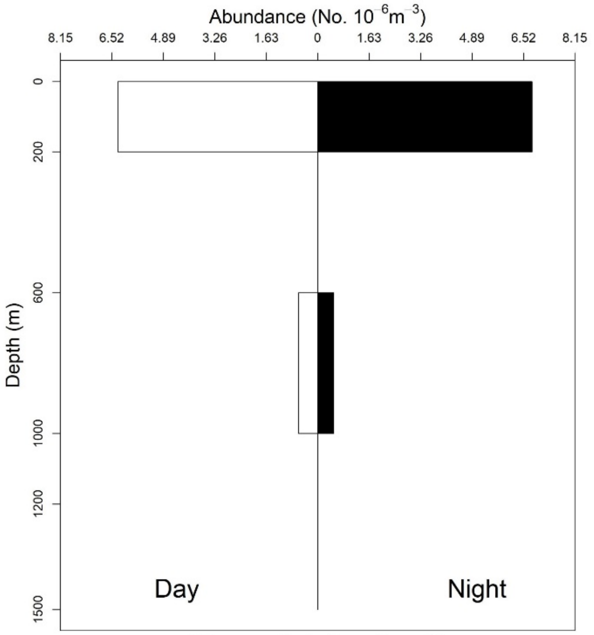
Cavolinia uncinata
n = 300

e.



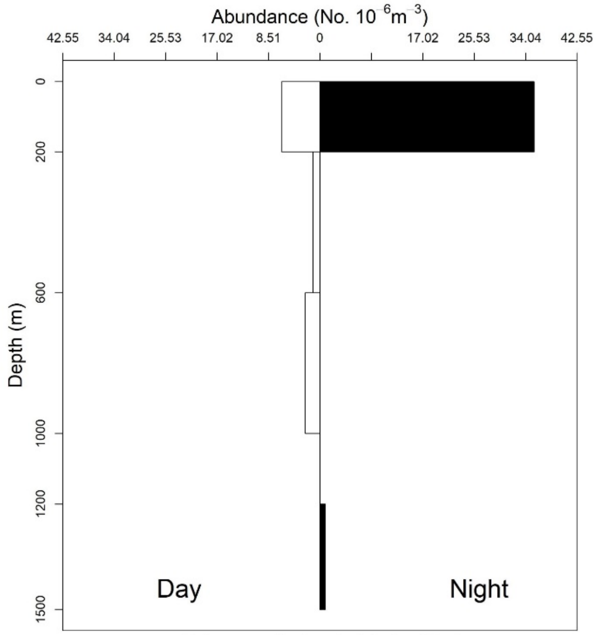
Diacria major
n = 133

f.



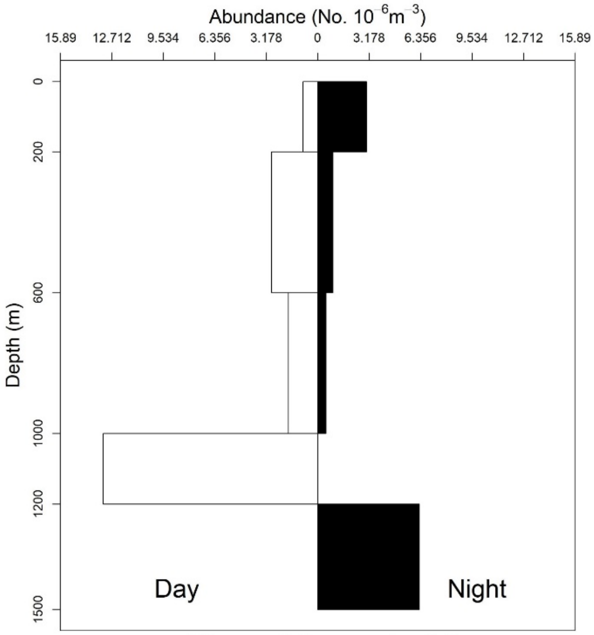
Diacavolinia longirostris
n = 14

g.



Diacavolinia deblainvillei
n = 46

h.



Diacavolinia vanutrechti
n = 30

i.

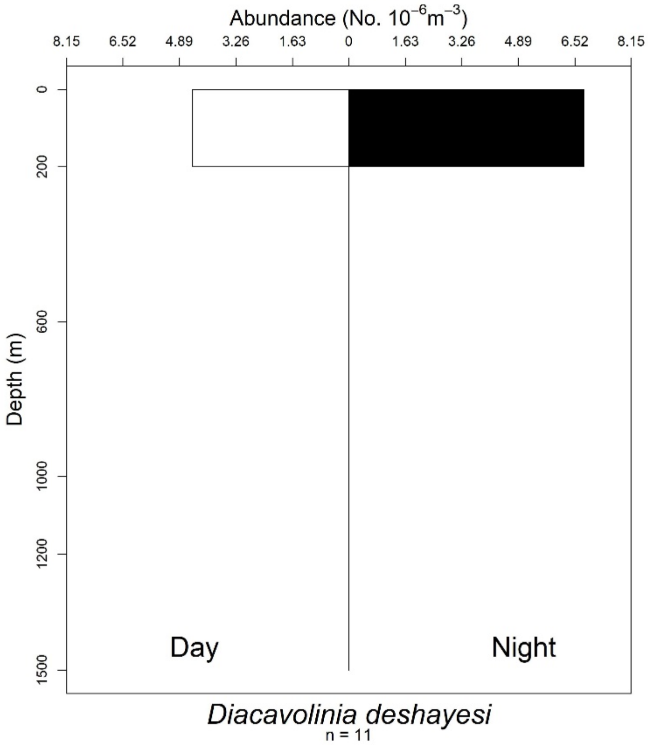


Figure 9 a-i. Nine weak or non-vertical migrating species. **a.** *Peracle bispinosa*, **b.** *Cavolinia tridentata* **c.** *Clio recurva* **d.** *Cavolinia uncinata* **e.** *Diacria major* **f.** *Diacavolinia longirostris* **g.** *Diacavolinia deblainvillei* **h.** *Diacavolinia vanutrechti* **i.** *Diacavolinia deshayesi*

3. Chapter Three: Shell thickness and length assessments of large pteropods in the northern Gulf of Mexico

3.1 Introduction

Pteropods shells come in various lengths, shapes, and shell thickness depending on species. All pteropod shells are aragonite, a form of calcium carbonate which dissolves easier than calcite in seawater (Bé et al., 1972; Berger, 1978; Betzer et al., 1984; Byrne et al., 1987, Lalli & Gilmer, 1989; Fabry, 1990), and provides them protection (Lalli & Gilmer, 1989; Howes et al., 2017). Pteropod shells exist in the fossil record dating back 66-79 million years ago and make up a considerable part of pteropod oozes in certain regions (Diester-Haass and Van der Spoel, 1978, Yvonne, 1998).

Pteropods have extremely fragile and thin aragonite shells. Their thinner and lighter shells may have been advantageous from an evolutionary standpoint and allowed them to adapt to a holopelagic life but increasing ocean acidification is leading to shell dissolution (Lalli & Gilmer, 1989).

Shell growth in members of the family Cavoliniidae occurs in two phases, first with the shell reaching maximum length and final shape, and second, the entire shell thickens inward, and continuous thickening occurs for remainder of animal's life during the second phase (Bé et al. 1972; Lalli & Gilmer, 1989). The shell length only slightly increases during this second phase. Lalli & Gilmer (1989) indicate that shell size is not a reliable indicator of age in cavoliniids and reject the idea of the "minute" and "skinny" forms of pteropods as "there does not seem to be any reason to suppose that shell deposition in pteropods differs from that of other mollusks; the mantle appears to be the primary organ responsible for the production of the shell."

Ontogenic habitat shifts are changes in habitat during various stages of an animal's life cycle. Ontogenic habitat shifts can be utilized as a survival technique to ensure maximal growth rates while minimizing predation risks. Ecological niche theory interconnects facets of an environment or habitat to an individual or population's needs, development, and success at life (Giller, 1984). Pteropod habitat shifts are not yet fully understood, and there is not published studies evaluating the distinctions in pteropod niches and adaptations. This research investigated pteropod niche development by examining changes in total shell length to depth.

The ONSAP and DEEPEND midwater programs collected pteropod specimens using a MOC10 net system and collected data used from 2011 and 2015 for this study. Since members of the family Cavoliniidae reach maximum length first and shell thickness is continuous throughout the pteropod's life, I aim to test the hypothesis that shell length is positively correlated to shell thickness for species present in sample sets from 2011 and 2015. Secondly, does shell thickness differ between 2011 and 2015 for *Clio pyramidata*? Lastly, are there any ontogenic migration patterns for these species?

3.2 Materials and Methods

Pteropod samples were collected during 2011 from the Offshore Nekton Sampling and Analysis Program (ONSAP), and the 2015 Deep Pelagic Nekton Dynamics of the Gulf of Mexico (DEEPEND) programs (Figure 2). Over 13,000 pteropods were identified and measurements were recorded. Standardized shell length to thickness analysis for eight species was calculated in Microsoft Excel (2016) (Figure 11 a-h). Nine species that had thirty or more shell length measurements and quantitative net data were analyzed for possible ontogenic shifts (Figure 12 a-e). Twenty *Clio pyramidata* individuals, ten from 2011 and ten from 2015, were selected for Scanning Electron Microscopy (SEM) shell thickness measurements, to compare to digital caliper measurements for accuracy.

A dissecting Zeiss Stemi 2000-C Stereo Microscope was used to identify and examine all specimens. Shell length and thickness were measured (mm) using an LT-4237-000 electronic digital caliper. Specimen wet weight (g) by species in each vial was taken using a Mettler Toledo PL303 310-gram max digital scale. Taxonomic identification, number of individuals, shell length (mm), shell thickness (mm), total wet weight (g) and station data were recorded and correlated to all cruise data including date, time, depth of sample, station trawl information and latitude/longitude of each station. There were several identification tools, the Marine Species Identification Portal (Van der Spoel et al., 1997), and identification guides (Chen & Bé, 1964; Van der Spoel, 1967, 1972, 1976; Lalli & Gilmer, 1989, Van der Spoel et al., 1993; Van der Spoel and Dadon, 1999), used to identify specimens to the lowest taxonomic level possible.

Once all organisms were identified, data were recorded on bench data sheets and transferred into Microsoft Excel (2016) for analysis. Shell length (mm) was defined as total length from tip or bottom of shell (dependent on shell shape) to tip or top of shell (also dependent on shell shape) (Figure 10 a-i). Shell thickness measurements were taken at or near the aperture.

3.3 Results

Correlation of shell length to shell thickness was calculated for *Cavolinia gibbosa, Cavolinia tridentata, Cavolinia uncinata, Clio pyramidata, Clio recurva, Diacria trispinosa, Diacria major,* and *Peracle bispinosa* species (Figures 11 a-h). A zero to a slight positive correlation between shell length and thickness in *C. gibbosa*, *C. tridentata*, *C. recurva*, and *D. major* was observed in both 2011 and 2015 (Figures 11 a, b, c, e). The other four species showed a negative correlation in one cruise and zero/positive in the other (*C. uncinata, D. trispinosa, P. bispinosa*) or negative correlation for both cruises (*C. pyramidata*) (Figure 11 g, d, f, h). Therefore, the hypothesis that these species having a positive correlation of shell length to thickness for both cruises is rejected.

In 2011, 911 *C. pyramidata* shells were compared to 227 measurements used in 2015, and there was a significant difference for these shell thickness measurements ($p<0.05$) during that timeframe.

Most pteropod species were found mainly in the mid- and upper mesopelagic depths of 600 m and above. Shell length (mm) was plotted along with capture depth for five species (*C. pyramidata*, *D. trispinosa*, *P. bispinosa*, *C. columnella*, and *C. gibbosa*) to assess possible ontogenic patterns. None of the five species showed a clear ontogenic migration either up or down in the water column (Figure 10 a-e).

3.4 Discussion

3.4.1 Shell Length and Thickness

The focus of this study was to assess the correlation of shell length to thickness within several large pteropod species collected from 2011 and 2015. *Clio recurva* was the only species with a slight positive correlation for 2011 (28%) and 2015 (31%) of shell length to thickness changes. Measurements were made using a digital caliper and SEM confirmed accurate measurements but there still can be human error and digital caliper precision issues as they are measured to the hundredths place in millimeters. Shell shape and location of measurement could also account for inconsistent measurements, resulting in the rejection of the hypothesis, if shell thickness truly continues after shell growth reaches maximal length.

Overall there was a significant difference in shell thickness from 2011 to 2015 in *C. pyramidata* (n=911 in 2015, n=222, in 2015, $p<0.05$). A similar result also occurred in *C. gibbosa*, *C. uncinata*, *C. recurva*, *D. trispinosa*, and *P. bispinosa*. However, there were not significant differences found for *C. tridentata* and *D. major*. The increase in shell thickness is interesting but contradicting to other shell thickness and dissolution studies showing decreases (Maas, 2012).

There are several possible factors contributing to this increase in shell thickness in these six species, such as individual life stage when collected, length of time in preservative, shell shape and position of measurement, and possibly the depth of collection. Also, biogeochemical processes such as temperature, salinity, pH, and carbonate ion concentrations are crucial factors to interpret these results and were outside the scope of this study. These would be helpful parameters to include in future pteropod-related research.

Degradation in shell thickness can be specific to location and taxon which been observed. For example, in the Southern Ocean, *Limacina helicina antarctica* decreased and *Limacina retroversa australis* increased in shell thickness (Bednaršek et al., 2016). It is difficult to know exactly what is causing this increase in shell thickness, as pteropods are part of the pelagic midwater ecosystem and there could be many factors impacting these midwater species.

Ontogeny studies for pteropods focus on ontogenic development of the shell from the larval stage to the adult end stage (Bandel & Hemleben, 1995) but neglect possible ontogenic vertical shift patterns. None of the five pteropod species analyzed showed any habitat shift with size. Ontogenic migration is known to occur in deep-sea pteropod species, but *P. bispinosa* (found in depths > 600 m) did not exhibit this pattern (Marine Species Identification Portal, 2019).

Another pelagic snail, the heteropods, has been examined in the northern GoM for possible ontogenic shifts (Clark, 2019). Two of the five species showed an ontogenic shift upward while the other three species showed no ontogenic shift. It is interesting that the two that shifted up in the water column are larger-sized species which may indicate they inhabit deeper depths when they are of smaller size to avoid predation in the shallower depths (Clark et al., in prep). Heteropods and pteropods are important midwater molluscs as both predators and prey.

At global and local scales, 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). Therefore, pteropods are important indicators of declining habitat and OA effects. Overall, this study shows pteropods shell length is not strongly correlated to shell thickness during the four years examined and these species do not exhibit ontogenic shifts in this region. There was an increase in shell thickness found in 2015 for several species. More data is needed to fully investigate these claims and better measurement techniques would be beneficial as well such as, using SEM for shell measurements. Continued surveys during various seasons at the same sampling stations would contribute additional material to further strengthen the results found in this study.

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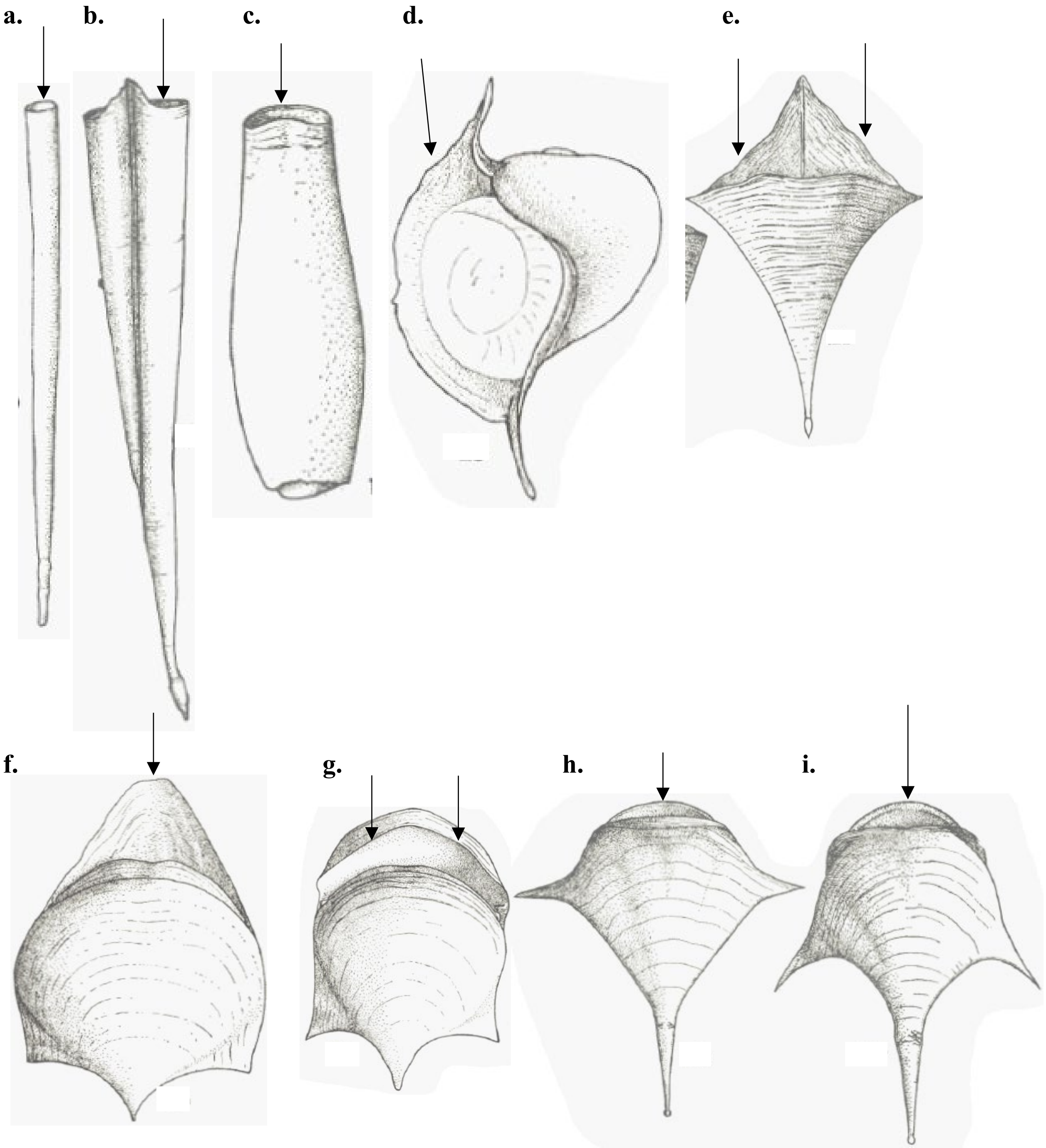
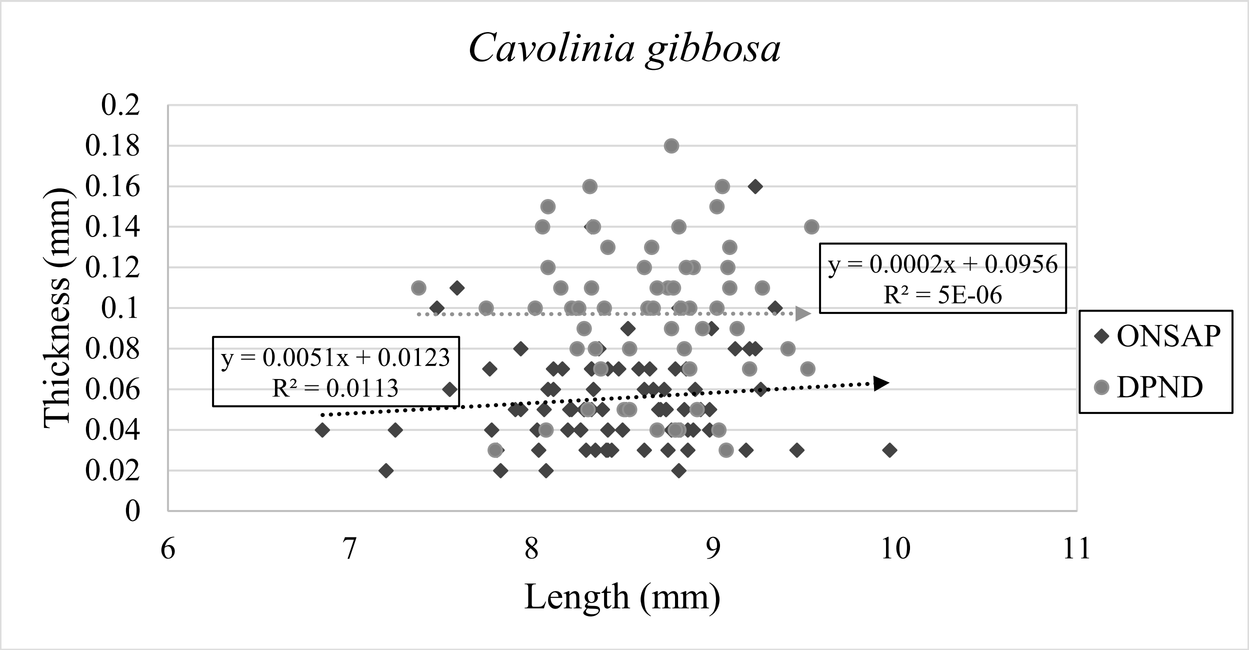
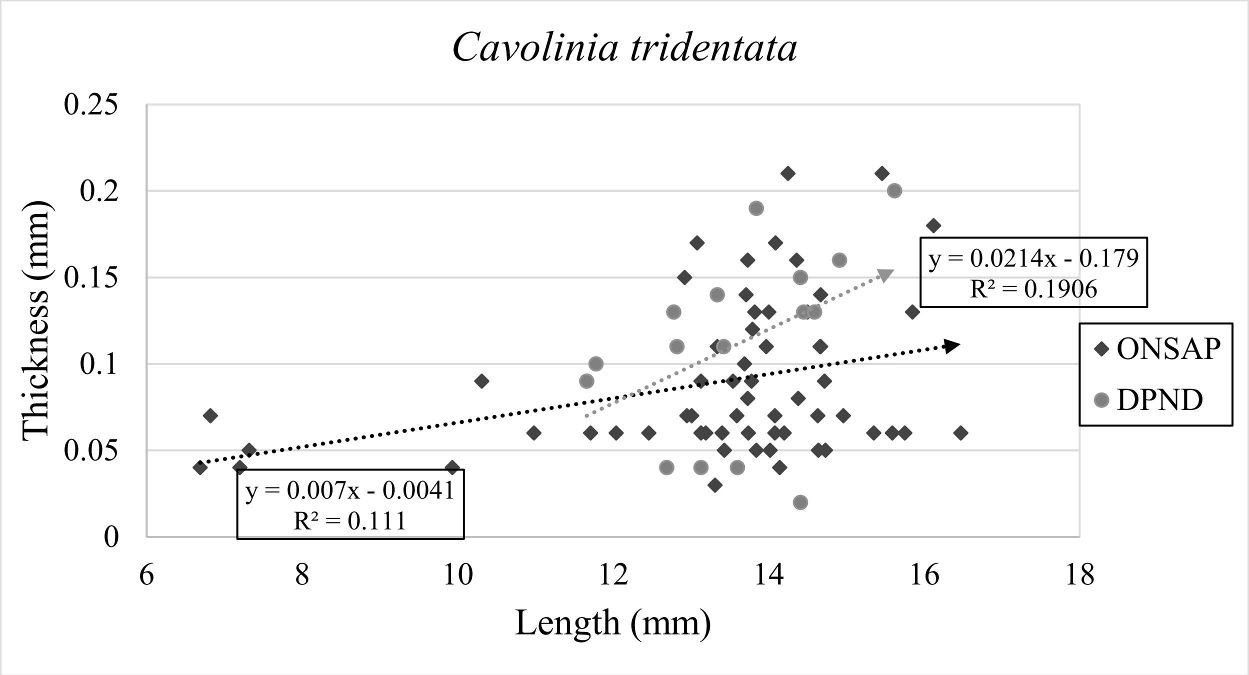


Figure 10 a-i. Nine different species from van der Spoel (1972) representing the various shell types within seven genera with arrow(s) indicating where caliper measurement were taken: **a.** *Creseis acicula* **b.** *Styliola subula* **c.** *Cuvierina columnella* **d.** *Peracle moluccensis* **e.** *Clio pyramidata* **f.** *Cavolinia tridentata* **g.** *Cavolinia uncinata* **h.** *Diacria trispinosa* **i.** *Diacria major*

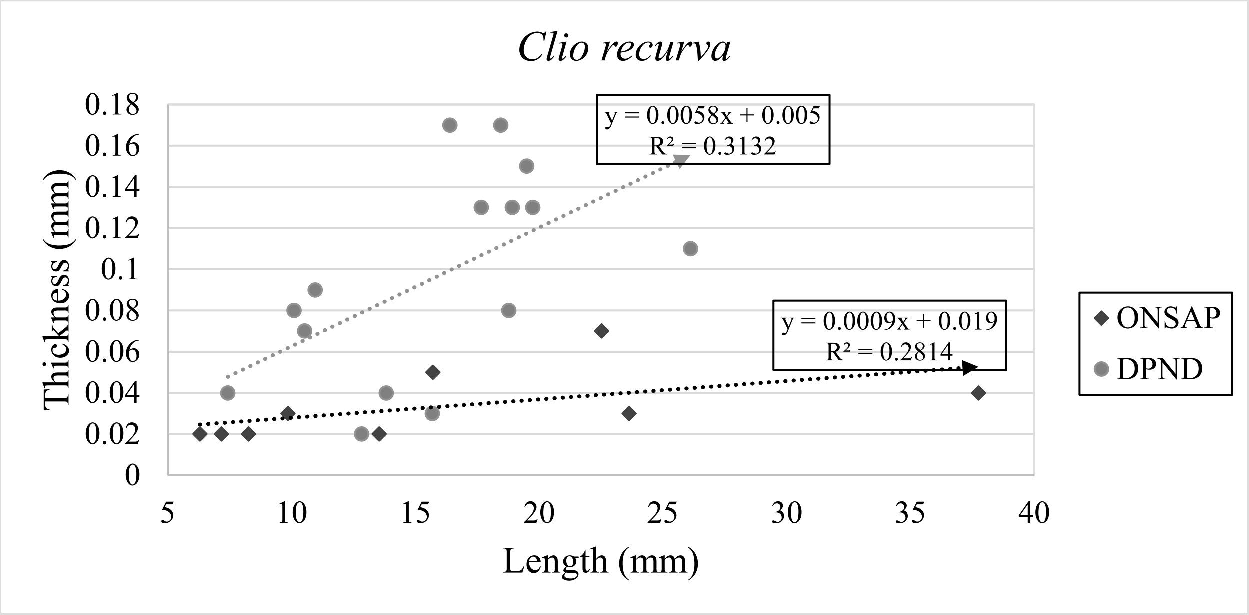
a.


Cavolinia gibbosa
Thickness (mm)
0.2
0.18
0.16
0.14
0.12
0.1
0.08
0.06
0.04
0.02
0
6
7
8
9
10
11
Length (mm)
y = 0.0002x + 0.0956
R² = 5E-06
y = 0.0051x + 0.0123
R² = 0.0113
◆ ONSAP
● DPND

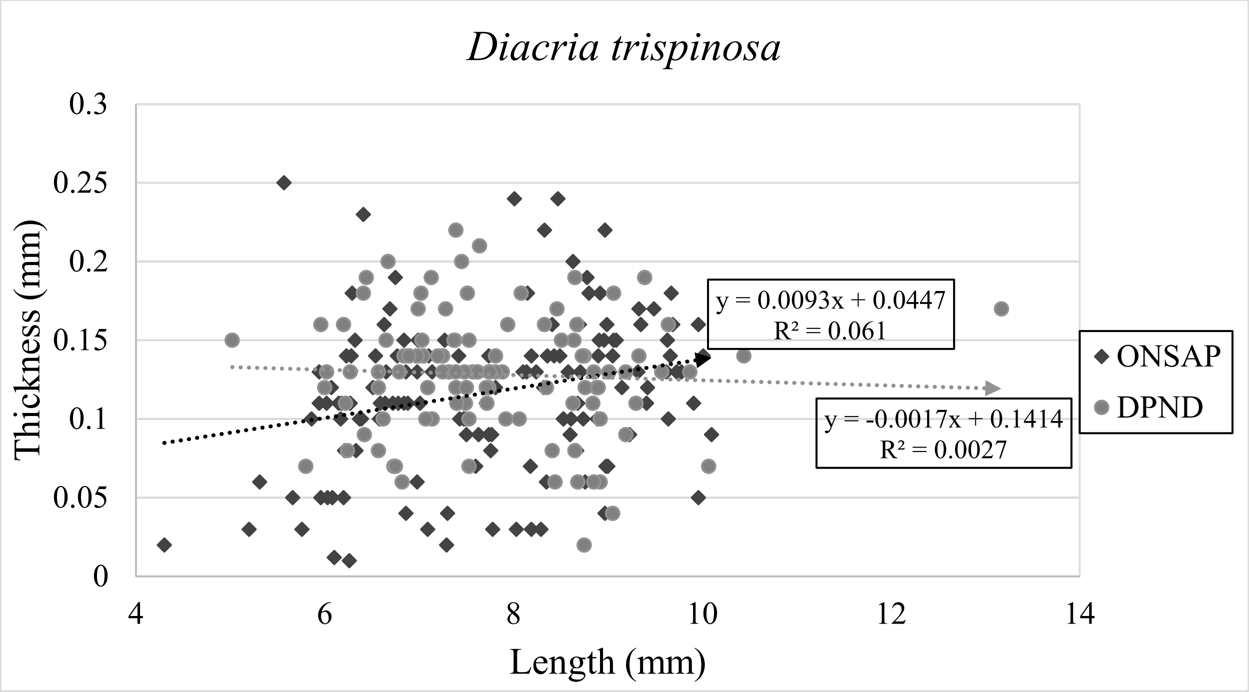
b.


Cavolinia tridentata
Thickness (mm)
0.25
0.2
0.15
0.1
0.05
0
6
8
10
12
14
16
18
Length (mm)
y = 0.0214x - 0.179
R² = 0.1906
y = 0.007x - 0.0041
R² = 0.111
◆ ONSAP
● DPND

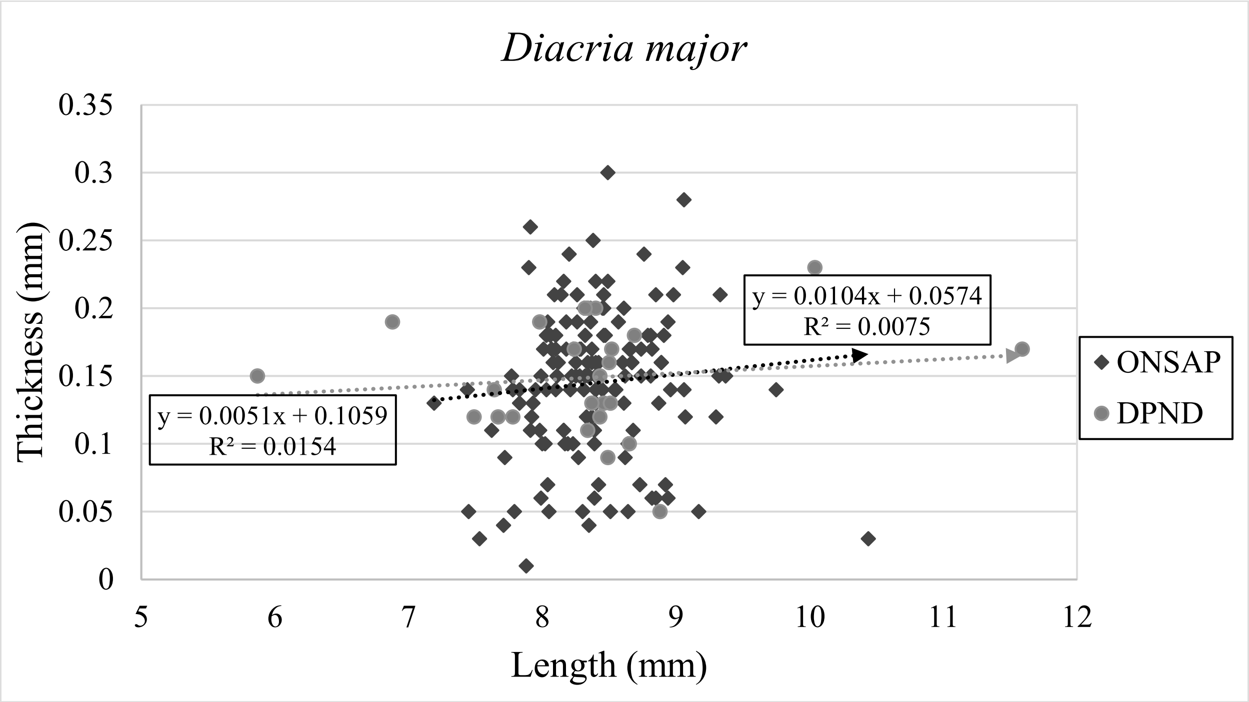
c.


Clio recurva
Thickness (mm)
0.18
0.16
0.14
0.12
0.1
0.08
0.06
0.04
0.02
0
Length (mm)
5
10
15
20
25
30
35
40
y = 0.0058x + 0.005
R² = 0.3132
y = 0.0009x + 0.019
R² = 0.2814
◆ ONSAP
● DPND

d.

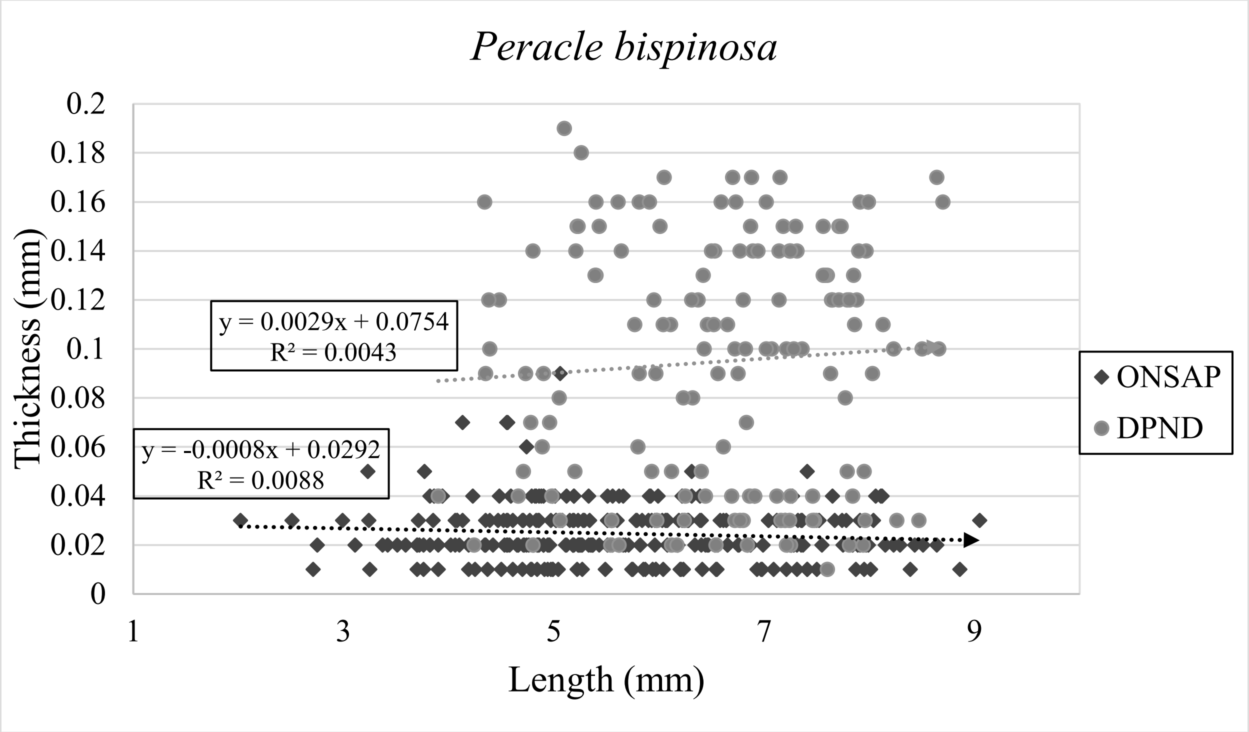

Diacria trispinosa
Thickness (mm)
0.3
0.25
0.2
0.15
0.1
0.05
0
Length (mm)
4
6
8
10
12
14
y = 0.0093x + 0.0447
R² = 0.061
y = -0.0017x + 0.1414
R² = 0.0027
◆ ONSAP
● DPND

e.



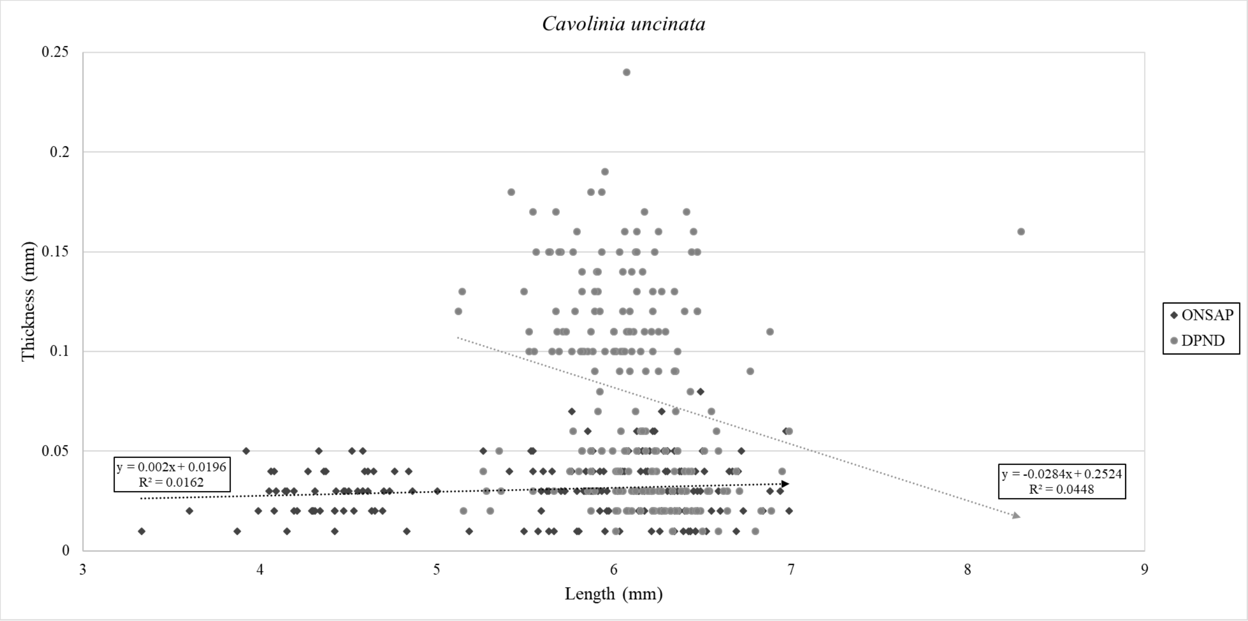
Diacria major
Thickness (mm)
0.35
0.3
0.25
0.2
0.15
0.1
0.05
0
5
6
7
8
9
10
11
12
Length (mm)
y = 0.0104x + 0.0574
R² = 0.0075
y = 0.0051x + 0.1059
R² = 0.0154
◆ ONSAP
● DPND

f.



Peracle bispinosa
Thickness (mm)
0.2
0.18
0.16
0.14
0.12
0.1
0.08
0.06
0.04
0.02
0
1
3
5
7
9
Length (mm)
y = 0.0029x + 0.0754
R² = 0.0043
y = -0.0008x + 0.0292
R² = 0.0088
◆ ONSAP
● DPND

g.



h.

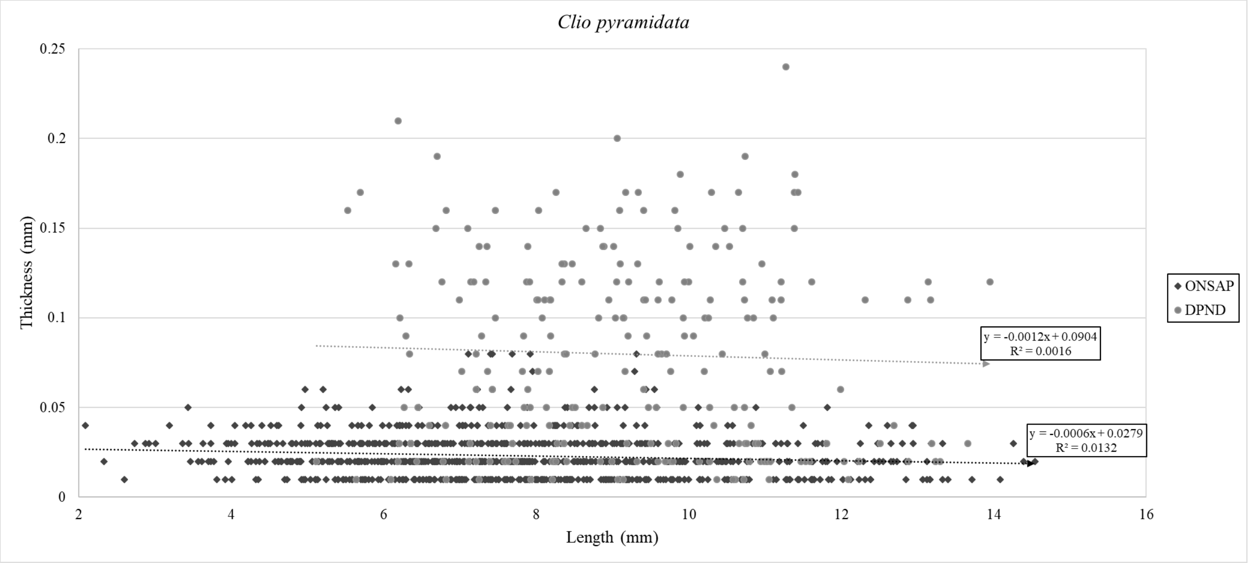
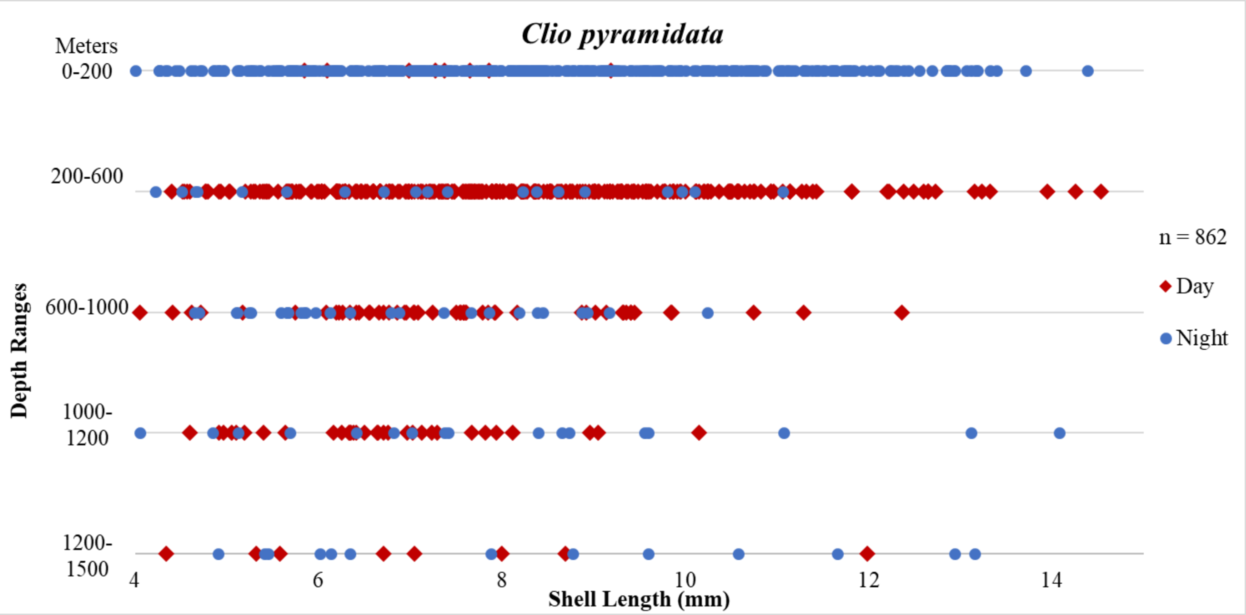
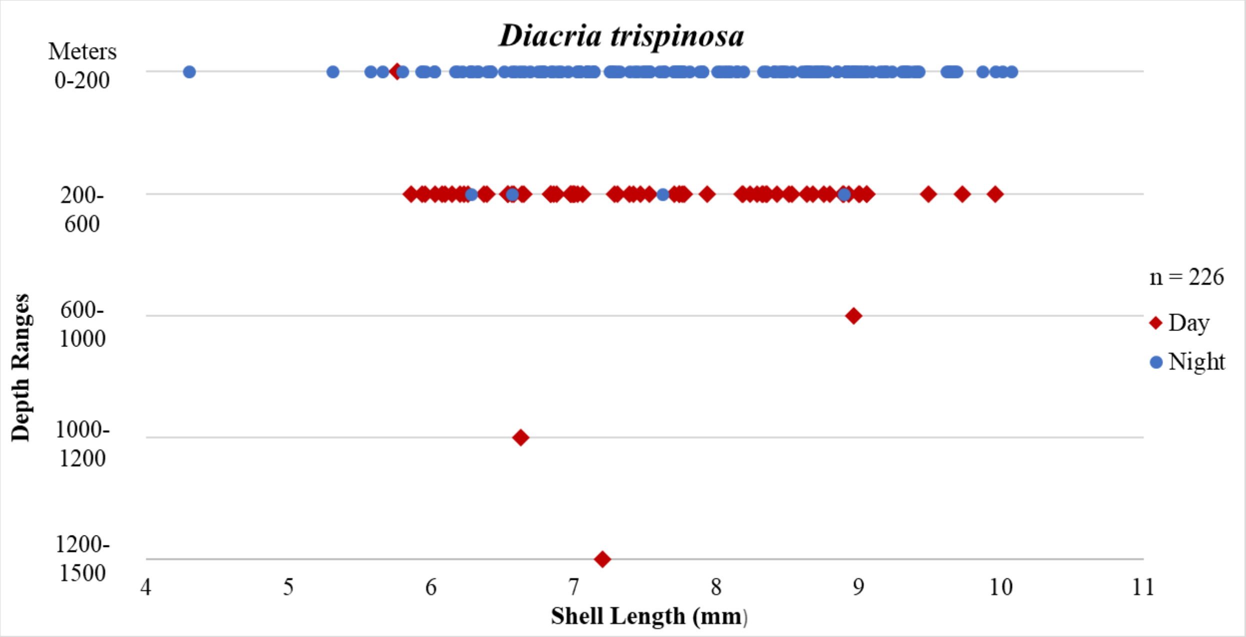


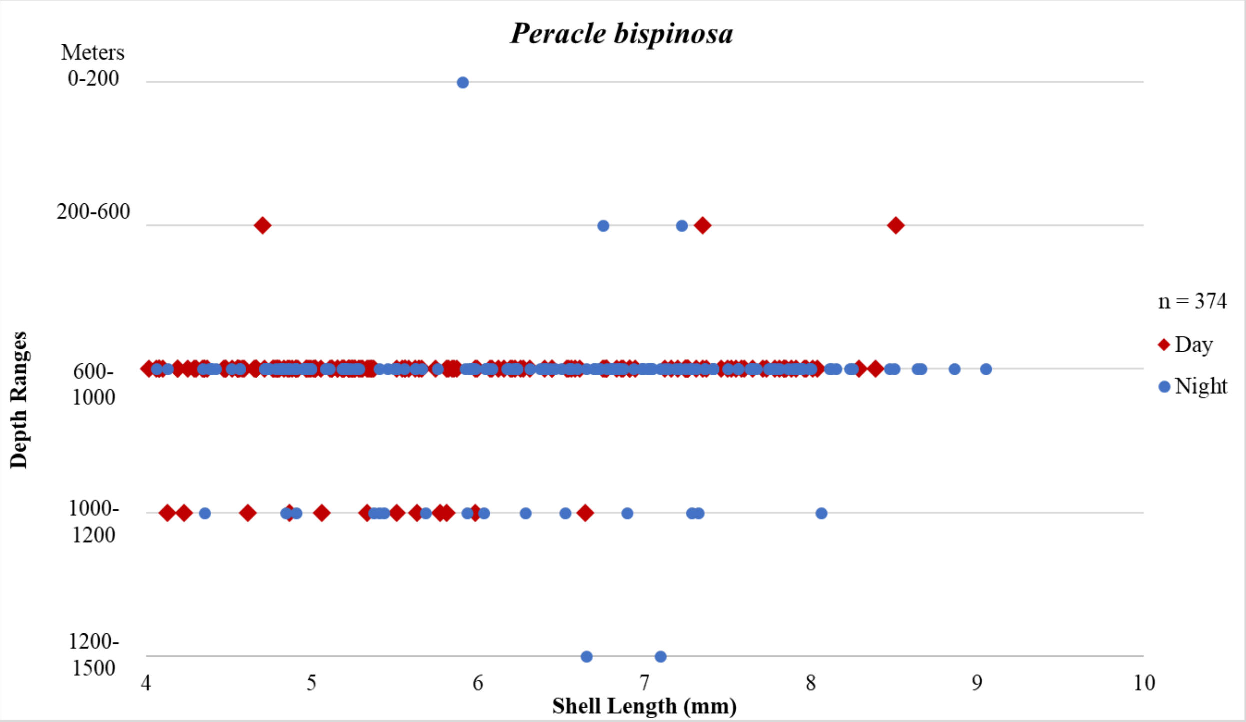
Figure 11 a-h. Correlation of shell length to thickness between 2011 (ONSAP) and 2015 (DEENPEND) for eight species. **a.** *Cavolinia gibbosa* **b.** *Cavolinia tridentata* **c.** *Clio recurva* **d.** *Diacria trispinosa* **e.** *Diacria major* **f.** *Peracle bispinosa* **g.** *Cavolinia uncinata* **h.** *Clio pyramidata* a.


Clio pyramidata
Meters
0-200
200-600
600-1000
1000-
1200
1200-
1500
Depth Ranges
4
6
8
10
12
14
Shell Length (mm)
n = 862
Day
Night

b.

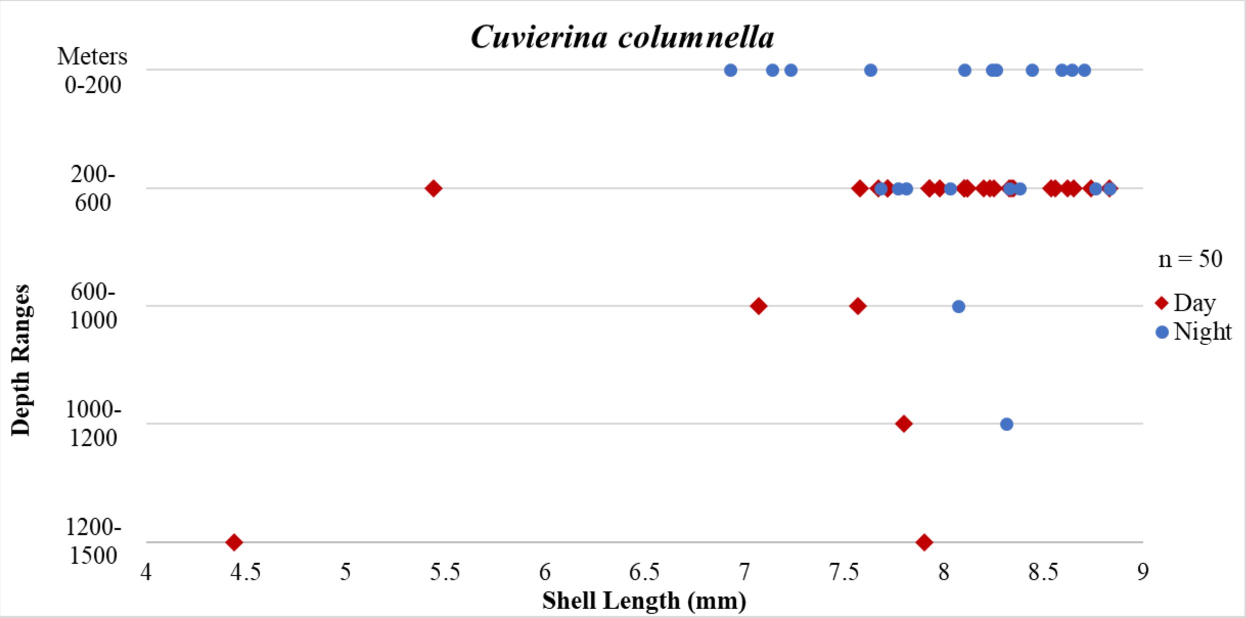

Diacria trispinosa
Meters
0-200
200-
600
600-
1000
1000-
1200
1200-
1500
Depth Ranges
4
5
6
7
8
9
10
11
Shell Length (mm)
n = 226
Day
Night

c.



Peracle bispinosa
Meters
0-200
200-600
600-1000
1000-1200
1200-1500
Depth Ranges
4
5
6
7
8
9
10
Shell Length (mm)
n = 374
Day
Night

d.



Cuvierina columnella
Meters
0-200
200-600
600-1000
1000-1200
1200-1500
Depth Ranges
4
4.5
5
5.5
6
6.5
7
7.5
8
8.5
9
Shell Length (mm)
n = 50
Day
Night

e.

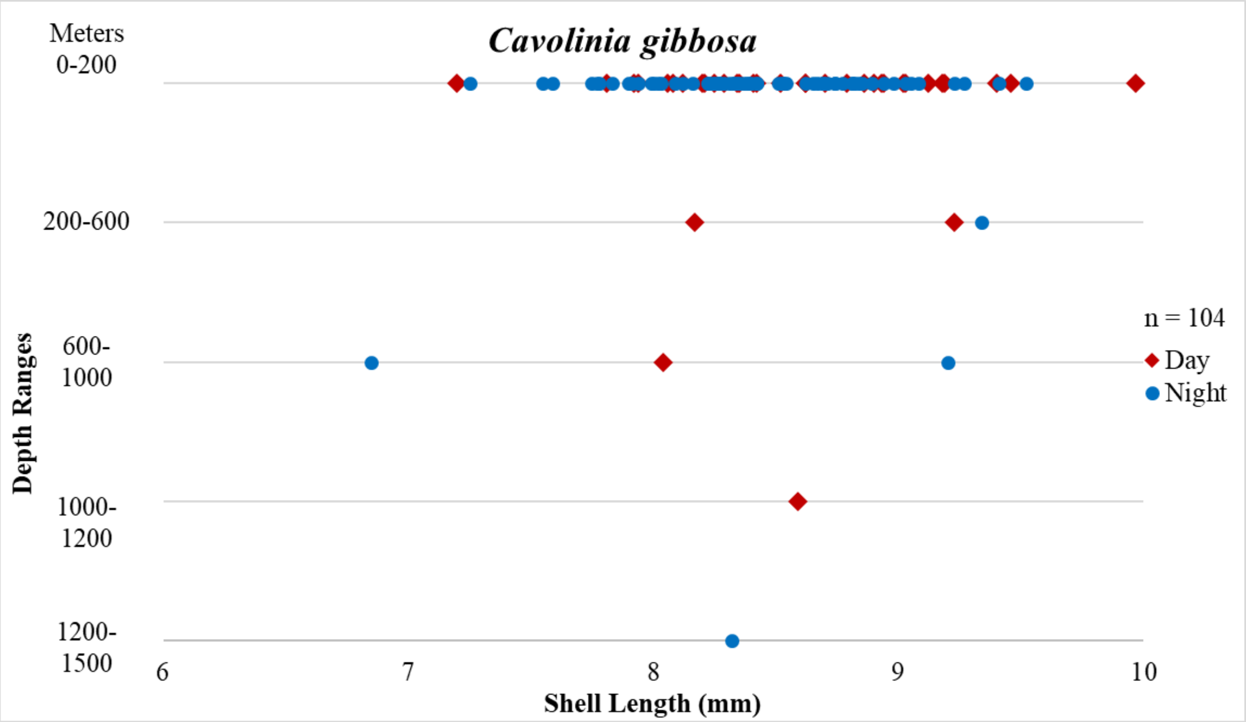
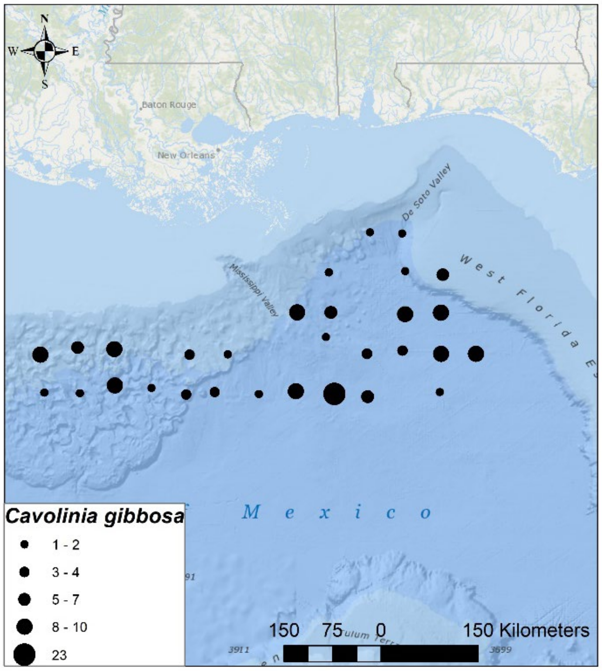


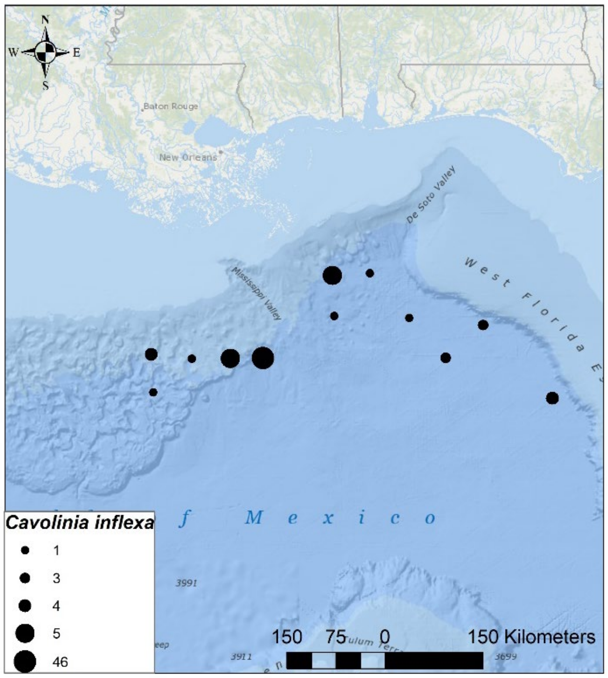
Figure 12 a-e. Pteropod shell length (mm) by depth of capture. None of the species showed an ontogenic shift. **a.** *Clio pyramidata* **b.** *Diacria trispinosa* **c.** *Peracle bispinosa* **d.** *Cuvierina columnella* **e.** *Cavolinia gibbosa*

APPENDIX A: Pteropod Distribution Maps

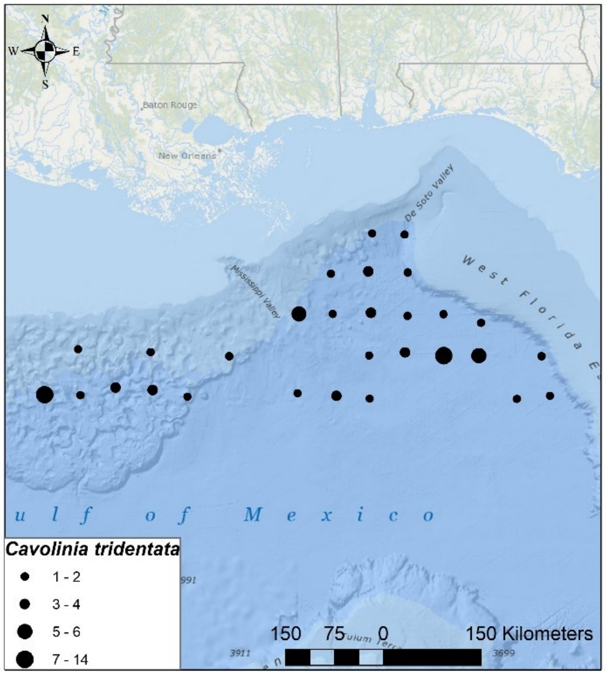
a.



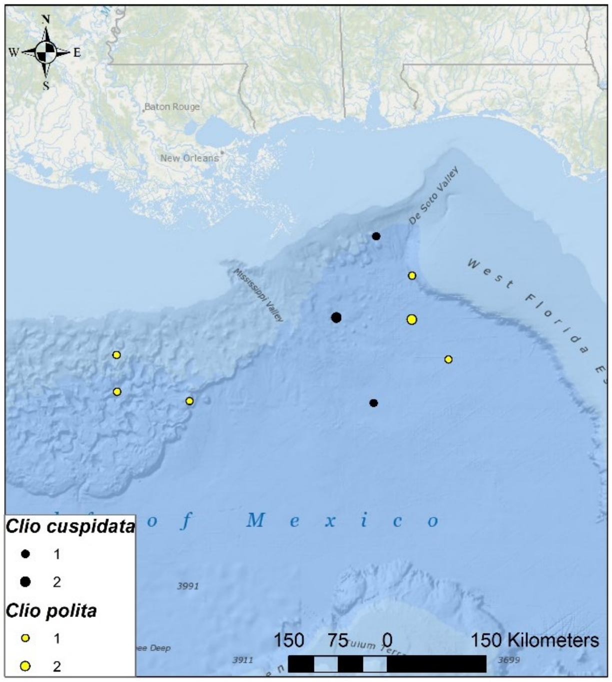
b.



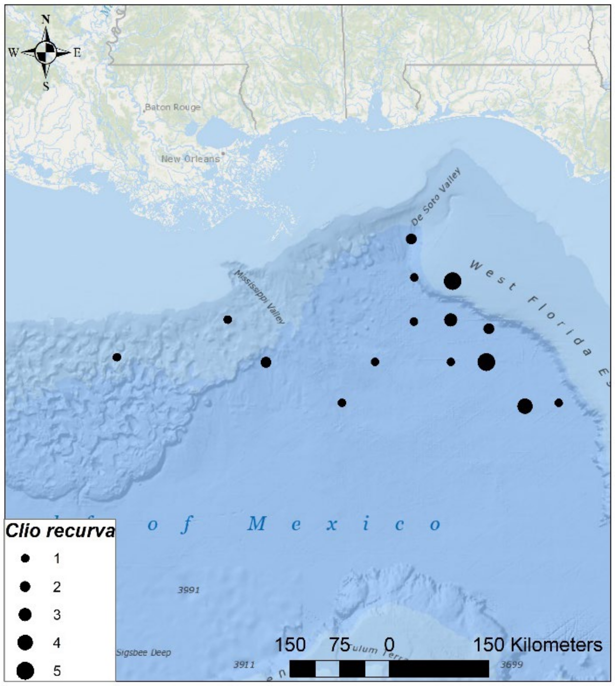
c.



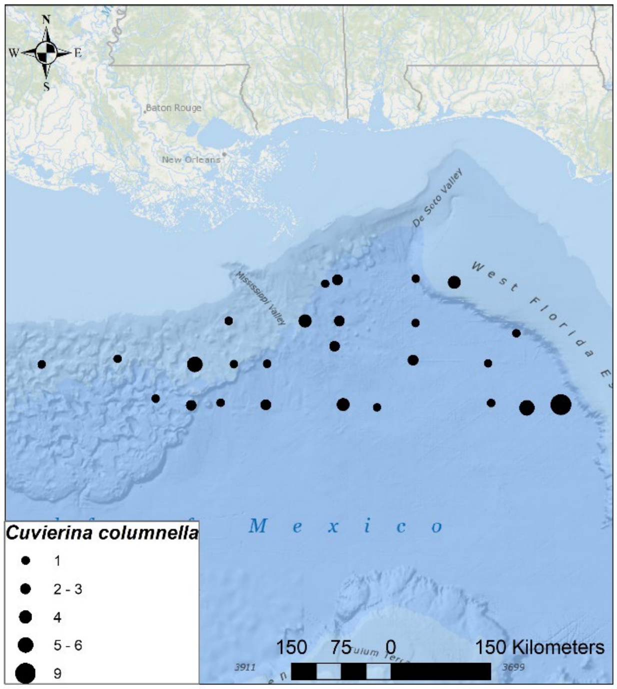
d.



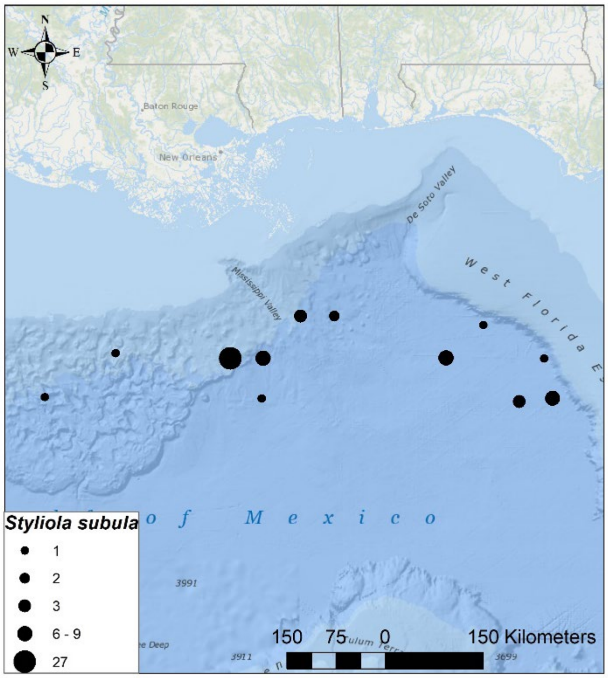
e.


N
W
E
S
Baton Rouge
New Orleans
De Soto Valley
Mississippi Valley
West Florida Es
o f M e x i c o
3991
Sigsbee Deep
3911
3699
150 75 0 150 Kilometers
Clio recurva
● 1
● 2
● 3
● 4
● 5

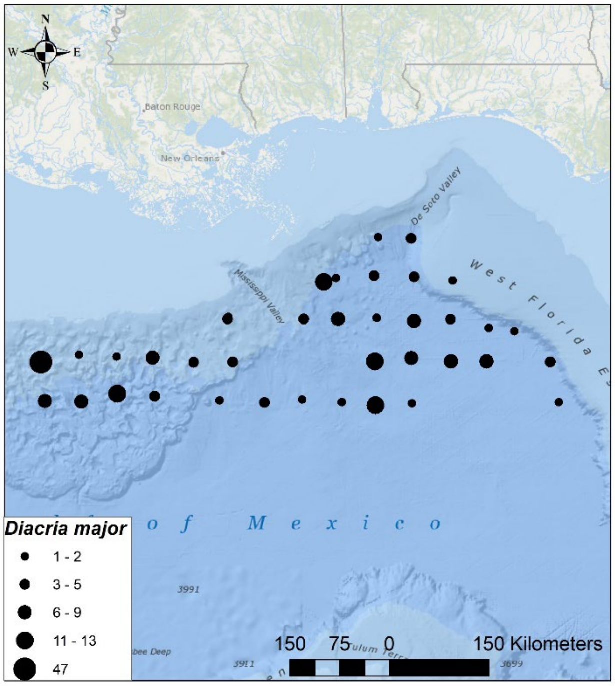
f.


N
W
E
S
Baton Rouge
New Orleans
De Soto Valley
Mississippi Valley
West Florida Es
M e x i c o
3911
3699
150 75 0 150 Kilometers
Cuvierina columnella
● 1
● 2 - 3
● 4
● 5 - 6
● 9

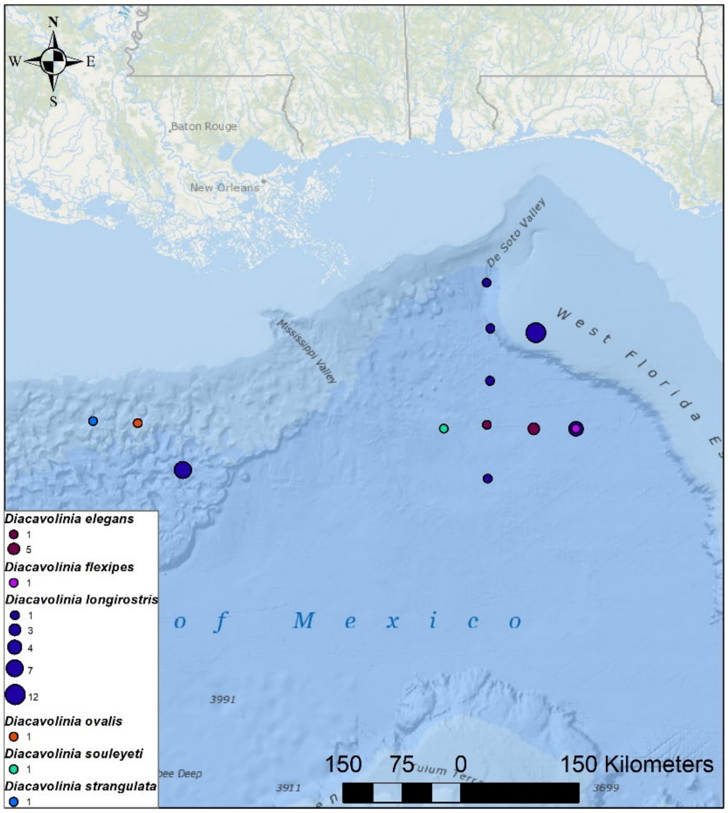
g.


N
W
E
S
Baton Rouge
New Orleans
De Soto Valley
Mississippi Valley
West Florida Es
o f M e x i c o
3991
Deep
3911
3699
150 75 0 150 Kilometers
Styliola subula
● 1
● 2
● 3
● 6 - 9
● 27

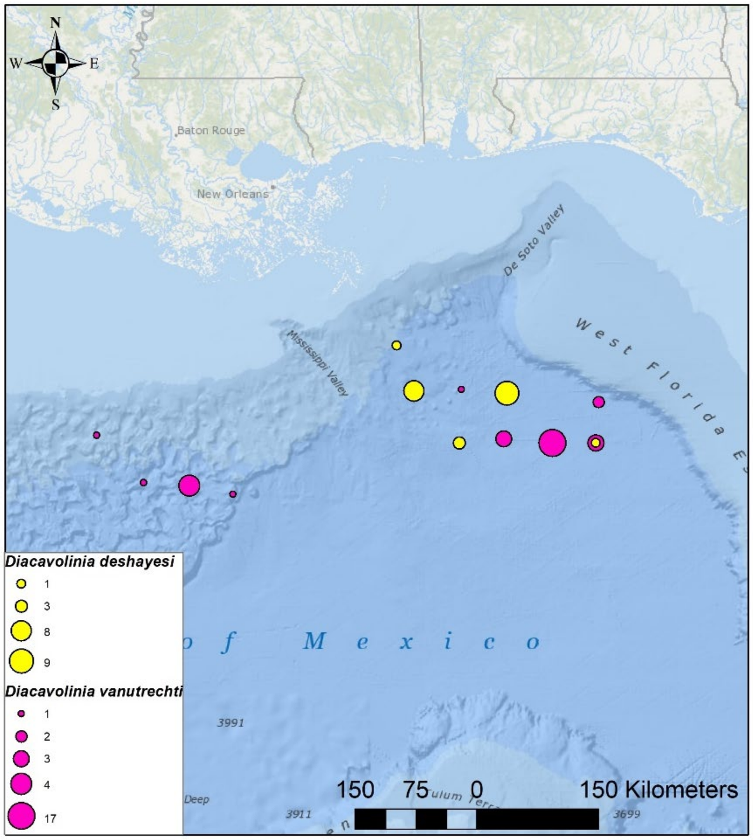
h.


N
W
E
S
Baton Rouge
New Orleans
De Soto Valley
Mississippi Valley
West Florida Es
o f M e x i c o
3991
bee Deep
3911
3699
150 75 0 150 Kilometers
Diacria major
● 1 - 2
● 3 - 5
● 6 - 9
● 11 - 13
● 47

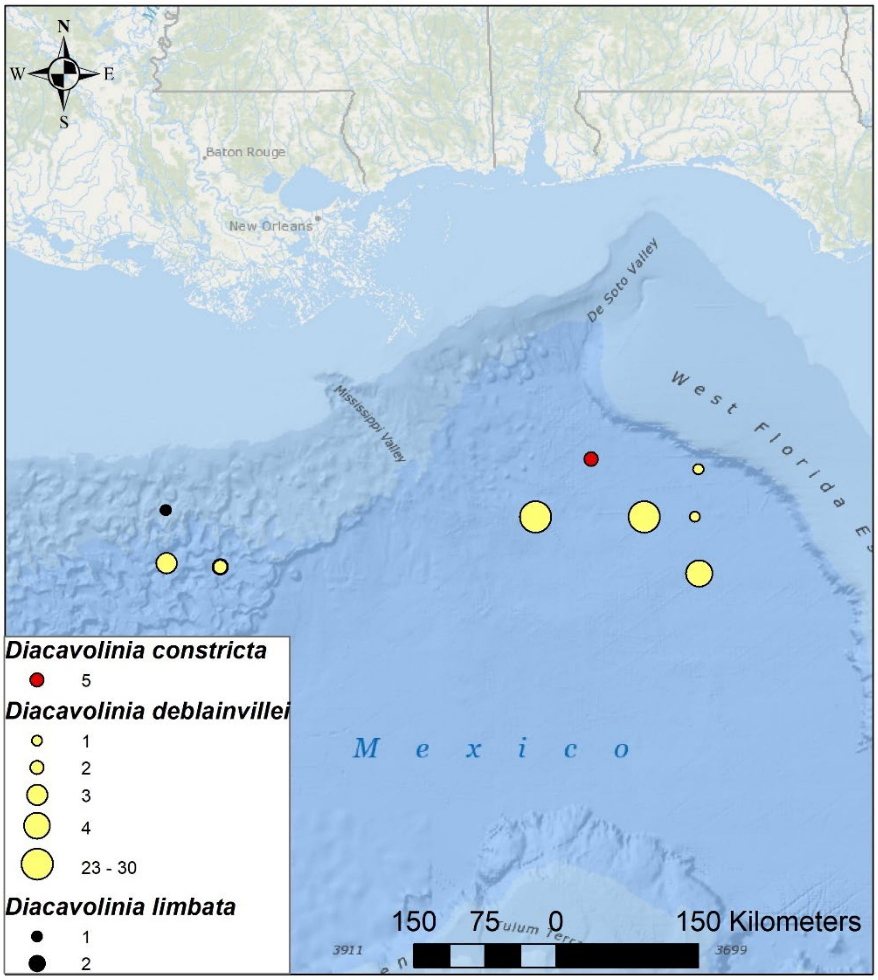
i.


N
W
E
S
Baton Rouge
New Orleans
De Soto Valley
West Florida Es
Mississippi Valley
o f Mexico
3991
ee Deep
3911
3699
150 75 0 150 Kilometers
Diacavolinia elegans
1
5
Diacavolinia flexipes
1
Diacavolinia longirostris
1
3
4
7
12
Diacavolinia ovalis
1
Diacavolinia souleyeti
1
Diacavolinia strangulata
1

j.


N
W
E
S
Baton Rouge
New Orleans
De Soto Valley
West Florida E
Mississippi Valley
of Mexico
3991
Deep
3911
3699
150 75 0 150 Kilometers
Diacavolinia deshayesi
1
3
8
9
Diacavolinia vanutrechti
1
2
3
4
17

k.



Appendix A: **a.** *Cavolinia gibbosa* **b.** *Cavolinia inflexa* **c.** *Cavolinia tridentata* **d.** *Clio cuspidata* & *Clio polita* **e.** *Clio recurva* **f.** *Cuvierina columnella* **g.** *Styliola subula* **h.** *Diacria major* **i.** *Diacavolinia elegans, D. flexipes, D. longirostris, D. ovalis, D. souleyeti, D. strangulata* **j.** *Diacavolinia deshayesi* & *Diacavolinia vanutrechti* **k.** *Diacavolinia constricta, D. deblainvillei, D. limbata*