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The Deep-Pelagic Sergestid Shrimp Assemblage in the Gulf of Mexico in the vicinity of the Deepwater Horizon Oil Spill

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Erik W. Hine

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HALMOS COLLEGE OF ARTS AND SCIENCES

The Deep-Pelagic Sergestid Shrimp Assemblage in the Gulf of Mexico in the vicinity of the *Deepwater Horizon* Oil Spill.

By

Erik Hine

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Abstract

This thesis focuses on the geographical (near-slope vs. offshore) and temporal analyses (2011 – 2018) of the Sergestidae assemblage, the crustacean family with the fourth highest total biomass, in the Gulf of Mexico near the location of the *Deepwater Horizon* oil spill. The abundance and biomass of the assemblage were analyzed to determine if statistical differences were present between the near-slope and offshore environments. In addition, this study analyzed the vertical distributions of sergestid species in the epipelagic, mesopelagic, and bathypelagic zones to determine the extent of the migratory behavior of these species. Lastly, the abundance and biomass in the offshore environment between 2011 and 2018 were analyzed. There are no data on the sergestid assemblage in this area before the oil spill, so 2011 served as a contaminated baseline against which data from 2015-2018 samples were compared. The results of this study demonstrate that the sergestid biomass at near-slope stations was significantly higher than at offshore stations. In addition, the temporal analysis shows that the sergestid assemblage decreased significantly in abundance and biomass between 2011 and 2015-2018. Both the geographical and the temporal results provide data that are crucial for future study efforts and trends pertaining to these species.

Key words: *Sergia*, *Sergestes*, Photophores, Mesopelagic, Temporal, Vertical Distribution

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Introduction

About 95% of Earth's underwater realm, including that of the Gulf of Mexico (GOM), has been vastly under-explored by humans (Hopkins *et al.* 1994; Charette and Smith 2010). The target Sergestidae species in this study are largely found (during the day) in the mesopelagic (200-1000 m) and bathypelagic (1000-4000 m) zones in the GOM (Flock and Hopkins 1992; Felder *et al.* 2009). These zones are considered the deep sea, which is defined as depths deeper than 200 m (Marshall 1954). The family Sergestidae consists of economically and ecologically important crustaceans found in marine ecosystems globally, although most individual species are typically restricted to a single ocean (Vereshchaka *et al.* 2014). This family of crustaceans plays an important role in the trophic structure of ecosystems as these crustaceans primarily prey upon euphausiids, copepods, phytoplankton, fishes and protists (Flock and Hopkins 1992), and are themselves food sources for cephalopods, cetaceans, midwater fishes and epipelagic fishes as well as targets of large filter feeding predators such as whale sharks and baleen whales (Donaldson 1975; Hopkins *et al.* 1994; Rohner *et al.* 2015). Sergestidae is in the suborder Dendrobranchiata, consisting of 15 genera (Vereshchaka 2000, 2009). Originally described as one genus because of similar characters, "*Sergia*" and "*Sergestes*" became two separate genera due to differences in features including the presence of organs of Pesta in "*Sergestes*" and dermal photophores in "*Sergia*" (Farfante and Kensley 1997; Judkins and Kensley 2008; Vereshchaka *et al.* 2014). However, this "two-genus" classification changed in Vereshchaka *et al.* 2014 and there are now 15 genera, 12 of which (19 species) were examined in this study. Species in this study originally described as "*Sergia*" include: *Phorcosergia grandis*, *Challengerosergia hansjacobi*, *Robustosergia regalis*, *Robustosergia robusta*, *Gardinerosergia splendens*, *Challengerosergia talismani*, *Sergia tenuiremis* and *Phorcosergia wolffi* (Table 2). Species in this study originally described as "*Sergestes*" are: *Eusergestes arcticus*, *Parasergestes armatus*, *Sergestes atlanticus*, *Deosergestes corniculum*, *Cornutosergestes cornutus*, *Neosergestes edwardsii*, *Deosergestes henseni*, *Deosergestes paraseminudus*, *Allosergestes pectinatus*, *Allosergestes sargassi*, and *Parasergestes vigilax* (Table 3). For simplicity, "*Sergia*" and "*Sergestes*" will be used to discuss the species groups listed in Tables 2 and 3.

Background on Sergestidae

Sergestids in the eastern GOM are more prevalent in shallower depths than other regions such as the western North Atlantic near Bermuda (Hopkins *et al.* 1994). This may be because light does not penetrate as deep into the water column in the GOM compared to the region near Bermuda with clearer oceanic water (Flock and Hopkins 1992; Hopkins *et al.* 1994). Light availability decreases with depth, therefore unique strategies for predator avoidance are necessary in the deep sea compared to predator avoidance strategies of organisms residing in shallower depths where more light is present (Johnsen 2002). Sergestids use a variety of predator avoidance strategies including small size, semitransparent body (with or without red chromatophores - Figure 1), counter-illumination using photophores or organs of Pesta (Foxton and Roe 1974; Vestheim and Kaartvedt 2009) and vertical migrations.

Most sergestids are diel vertical migrators, meaning they live at deep depths during the day and migrate upwards towards the surface at night to feed (Hopkins and Sutton 1998). This migratory behavior is closely related to sergestids' feeding habits (Foxton and Roe 1974; Donaldson 1975). Nearly all sergestid species have increased feeding behavior at night, primarily because prey abundance decreases with depth, although daytime feeding still occurs to a lesser extent (Foxton and Roe 1974; Donaldson 1975; Omori 1975). Diel migratory behavior allows sergestid species to feed in higher risk (i.e. greater predator pressure) shallow waters where prey are more abundant because they are less visible at night and allows them to avoid visual predators during the day in darker, deeper waters (Chiou *et al.* 2003; Hays 2003).

Background on "*Sergia*"

The genus "*Sergia*" was established by Stimpson (1860) and the first species described was *Sergia remipes* (Vereshchaka 2000; Vereshchaka 2017). "*Sergia*" was later separated into eight genera with 28 species and eight of those species are included in this study (Vereshchaka 2000; Vereshchaka *et al.* 2014). For simplicity's sake, this group will be referred to as the "*Sergia"* group throughout this thesis. Species of "*Sergia*" are classified based on structure: position and number of dermal photophores, structure of petasma, presence of an ocular papilla, presence of a hepatic spine and articulation of the first maxilliped endopod (Yaldwyn 1957; Vereshchaka 2000). The complicated male copulatory organ known as the petasma, only found in sexually mature stages, is the most important feature for identification purposes since other morphological features such as spines do not differ much between species (Vereshchaka 2000), and photophores fade after long term storage in fixatives. The *"Sergia"* species have a smooth carapace and abdomen, and small rostrum. Unique dermal/antennal photophores of varying abundances and locations (with or without lens) are found in all species in the GOM, except for *Sergia tenuiremis*. "*Sergia"* species can be both half-red (Figure 1) or all-red and do not possess organs of Pesta as in the original genus "*Sergestes"* (Vereshchaka 2000; Guzman 2002).

Figure 1: *Sergia* sp. with red chromatophores and semitransparent coloring (credit: Dante Fenolio)

"Sergia" are found in temperate and tropical waters of the Atlantic, Pacific, and Indian oceans. Their vertical distribution is typically in the upper 1000 m and most species are primarily found in the lower mesopelagic (500-1000 m) throughout the day (Flock and Hopkins 1992), with vertical migrations into the epipelagic zone (0-200 m) occurring after sunset (Flock and Hopkins 1992; Vereshchaka 2000; Vestheim and Kaartvedt 2009). These migrations can be

several hundred meters in locations such as the eastern GOM, northern Atlantic and western Mediterranean (Flock and Hopkins 1992; Froglia and Gramitto 2000). However, *Sergia splendens* (now known as *Gardinerosergia splendens*) a common species that was analyzed in this project, has been shown to migrate as much as 825 m off Bermuda (Donaldson 1975). Most "*Sergia*" species in the eastern GOM have been found in the lower half of the epipelagic zone (100-200 m) at night but *Sergia filica* and *Sergia robusta* (now known as *Robustosergia robusta)* were found in the mesopelagic zone (400-700 m) at night (Flock and Hopkins 1992). A focus of the current study was to determine the depth range of the sergestid assemblage in the northeastern GOM and to categorize which species are strong, weak, or non-vertical migrators.

"*Sergia*" primarily prey on crustaceans such as copepods, ostracods and euphausiids but noncrustaceans, such as chaetognaths, coelenterates, pteropods and protozoans were also preyed upon (Flock and Hopkins 1992). Interestingly, *Gardinerosergia splendens* and *Robustosergia robusta* both have an evenly distributed diet of crustaceans and noncrustaceans, feeding on coelenterates proportionately more than other "*Sergia*" species (Flock and Hopkins 1992).

Background on "*Sergestes*"

The genus "*Sergestes*" was created by Krøyer (1855) and the first species described was *Sergestes atlanticus* by H. Milne-Edwards in 1830 (Cardoso and Tavares 2006; Vereshchaka 2009). "*Sergestes*" is now separated into seven genera containing 36 species (Vereshchaka 2009); 11 of these species were included in this study. For simplicity's sake, this group will be referred to as the "*Sergestes"* group throughout this thesis.

"*Sergestes*" are semitransparent organisms that possess a modified gastrohepatic gland which forms luminescent organs of Pesta, while lacking the dermal photophores found in most "*Sergia*" species (Omori 1975; Judkins and Kensley 2008). The function of the organs of Pesta is to hide the body from predators below by replacing the light blocked by the body so precisely that the silhouette disappears, a process known as counter-illumination (Warner *et al.* 1979; Latz and Case 1992). "*Sergestes*" exhibit slight variations in most morphological characters (Omori 1975; Vereshchaka 2009) and as with *"Sergia",* the petasma is the best characteristic to distinguish the difference species but is only found in sexually mature males. "*Sergestes*" have red chromatophores scattered throughout the body and the variance of color observed in

Eusergestes arcticus (formerly *Sergestes arcticus)* which are substantially less red above 100 m depth than below 200 m depth, suggests that this species may be able to adjust these chromatophores for predation avoidance, but this has not been verified (Vestheim and Kaartvedt 2009). Semitransparent "*Sergestes*" have been observed to migrate closer to the surface than those that are not semitransparent (Omori 1975; Vereshchaka 2009).

The vertical distribution of mature "*Sergestes*" is usually restricted to above 700 m but a few species are found at depths of 900-1000 m (Omori 1975; Vereshchaka 2009). Overall, most mature "*Sergestes*" stages vertically migrate into the epipelagic zone at night and return to 400-700 m during the day in the eastern GOM (Flock and Hopkins 1992). The smaller sized crustaceans are typically found in shallower water during the day than larger sized individuals consistent with DeRobertis' model that predicts that smaller organisms should ascend in to surface waters earlier and descend later compared to larger organisms (Flock and Hopkins 1992; De Robertis 2002). Since "*Sergestes*" continuously feed throughout the day in two separate water layers (epipelagic and mesopelagic), this group increases the diversity of available ecological niches (Omori 1975; Roe 1984; Vereshchaka 2009).

"*Sergestes*" highest feeding activity occurs between sunset and 3-4 hours before sunrise and have a varied diet that is dependent on size (Vereshchaka 2009). In the eastern GOM, the smaller species such as *Allosergestes pectinatus* (formerly *Sergestes pectinatus*), *Allosergestes sargassi* (formerly *Sergestes sargassi*) and *Sergestes atlanticus* commonly feed on copepods and ostracods, while the larger species such as *Deosergestes corniculum* (formerly *Sergestes corniculum*) and *Deosergestes henseni* (formerly *Sergestes henseni*) feed on chaetognaths, euphausiids, decapods and fish (Foxton and Roe 1974; Vereshchaka 2009). Mesopelagic fishes, commercial fishes and basking sharks are known predators of "*Sergestes,*" demonstrating that "*Sergestes*" play an integral role in the pelagic food web (Mutoh and Omori 1978; Vereshchaka 2009). Considering the potential importance of "*Sergestes*" in the GOM, another goal of this study was to categorize the extent to which they vertically migrate and their overall abundance.

Background on the Gulf of Mexico/DWHOS

The GOM, one of the world's largest and deepest marine basins, is connected to the Atlantic Ocean via the Yucatan Channel and the Straits of Florida (Oey *et al.* 2005). The width of the GOM from east to west is about 1,000 miles and the U.S. shoreline is over 17,000 miles in length, making this a major US marine ecosystem (Gore 1992; Felder and Camp 2009). The GOM reaches a maximum depth of around 3800 m and is rich in marine life and natural resources, making this basin a unique study site (Lynch and Pollock 1958). The GOM is a region of high marine biodiversity that should be conserved for economic and ecological reasons (Gore 1992; Felder and Camp 2009).

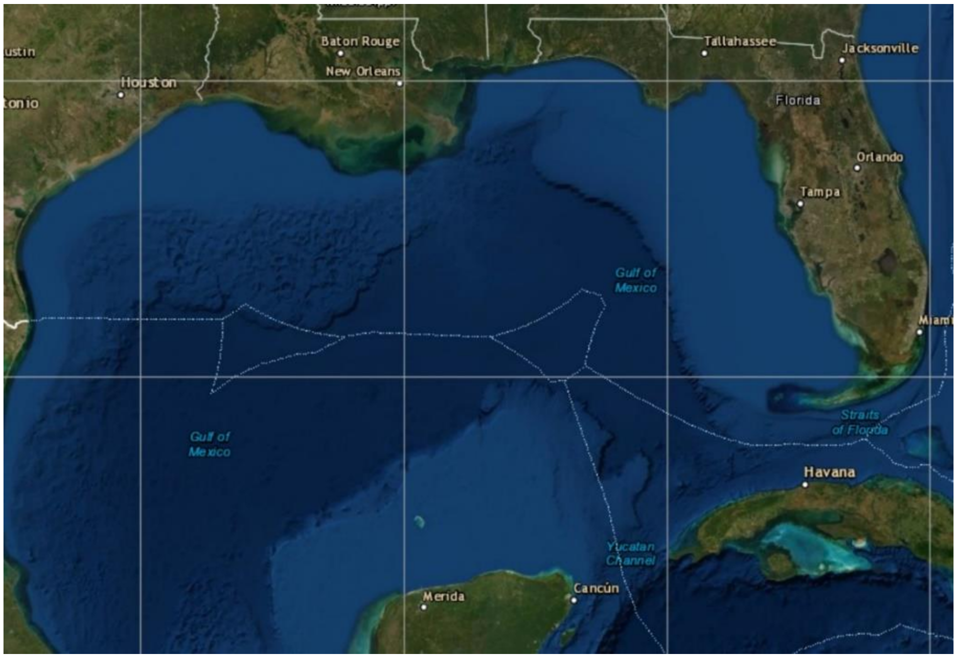


Figure 2: Satellite image of the Gulf of Mexico (NOAA 2019)

Oceanic water from the Atlantic Ocean flows through the Yucatán Channel into the GOM and then exits through the Straits of Florida, creating the Gulf Stream. The Loop Current has numerous effects on the eastern GOM, such as bringing pelagic organisms into the GOM as well as forming warm-water eddies that can penetrate down the water column (Pequegnat *et al.* 1990; Oey *et al.* 2005). The Loop current gradually dissipates and mixes with the surrounding water mass known as the Gulf Common Water (CW), which is also identified by the absence of the Subtropical Underwater water mass (Johnston *et al.* 2019). The current study focuses on samples taken in the northern and eastern GOM where the Loop Current was present, but this study is restricted to only CW stations.

***Deepwater Horizon* Oil Spill**

The *DWHOS* released 6.7 x 10^5 mT of oil in the GOM at a depth of 1480 m from April, 2010 until September, 2010 (Abbriano *et al.* 2011). A subsurface oil plume was present between 900 m and 1300 m, which are within the daytime depths ranges of several sergestid species (Vereshchaka 2000, 2009; Romero *et al.* 2018). Oil from the spill rose to the surface but a portion of the oil sank by mixing with solids and remained at deep depths in the water column (Ramseur 2010). As a result, the mesopelagic food web of the GOM was contaminated with high levels of oil by sinking oil particle aggregates and organisms came in direct contact with the plume (Romero *et al.* 2015; Romero *et al.* 2018). The *DWHOS* may have impacted the sergestid assemblage in the northern GOM but there are no baseline data on sergestid biomasses and abundances for this region before the oil spill. Although no pre-spill data are available, this research seeks to determine if temporal changes are present in the sergestids assemblage over time after the spill. Data samples from 2011 were considered a contaminated baseline against which to compare data from cruises conducted between 2015 and 2018.

<u>Methods: Study Sites</u>

Samples were collected during a series of cruises from multiple stations in the northern Gulf of Mexico (Figure 3): the Offshore Nekton Sampling and Analysis Program (ONSAP) cruises in 2011 using the M/V *Meg Skansi* (MS6, 7 and 8) and the Deep Pelagic Nekton Dynamics (DEEPEND) cruises in 2015-2018 (DP01-DP06), using the RV *Point Sur*, both directed by Dr. Tracey Sutton. These samples were collected using the Multiple Opening and Closing Net and Environmental Sensing System (MOCNESS) (Wiebe *et al.* 1976) which consisted of six nets, five of which fished at discrete depth ranges (Table 1), twice per 24 hour period (Sutton *et al.* 2020).

Table 1: MOCNESS net sampling depths for each cruise.

Net Number	Depth Codes
1	1200-1500 m
2	1000-1200 m
3	600-1000 m
4	200-600 m
5	0-200 m

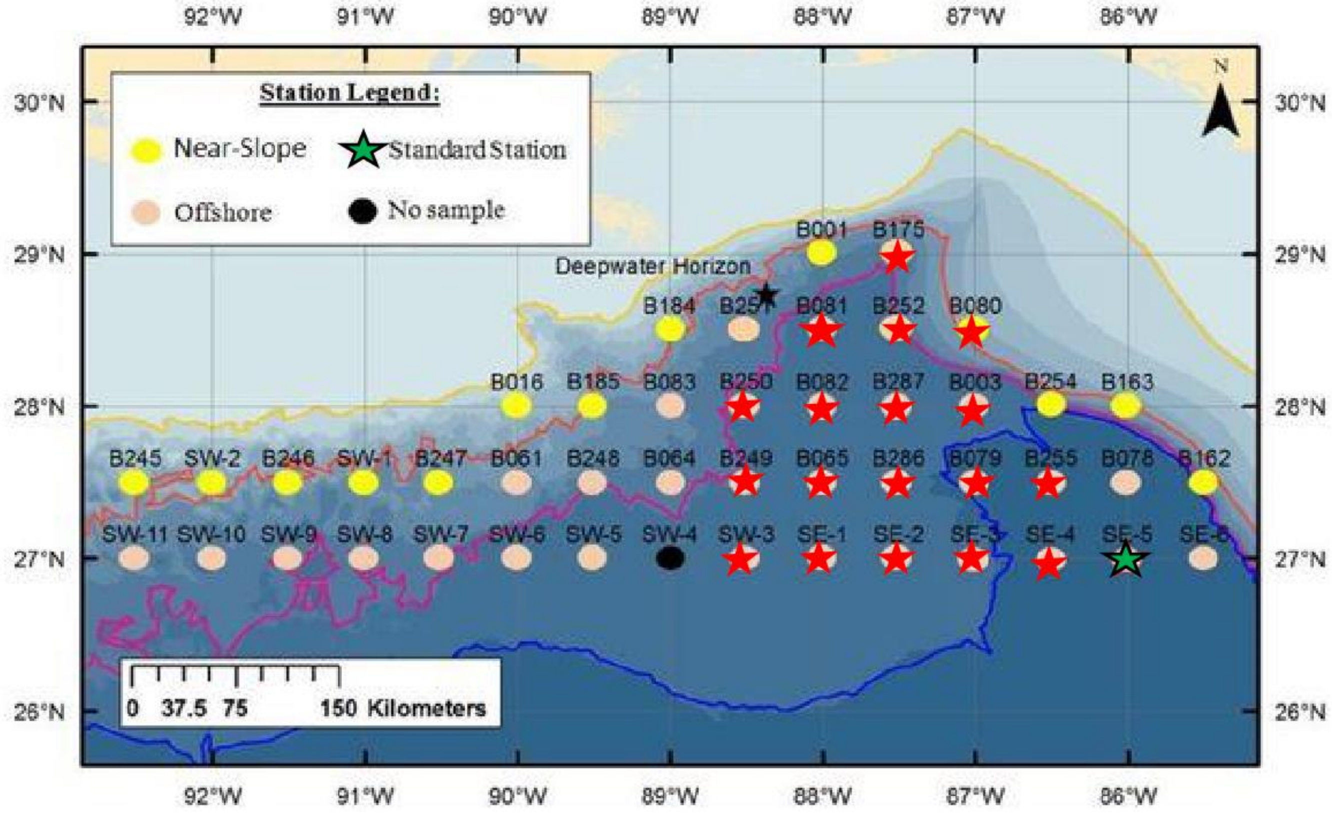


Figure 3: Map of stations sampled with MOCNESS, showing near-slope stations in yellow and offshore stations in pink. All the stations were sampled on the ONSAP cruises; DEEPEND cruise sampling stations are marked with red stars. The black star indicates the site of the *Deepwater Horizon* oil spill and the green star indicates the Standard Station (Nichols 2018).

Methods – sampling and analysis

After each trawl, the samples were sorted into major taxonomic groups and stored in 10% formalin in seawater on shipboard. Back at the lab, they were identified to species or lowest possible taxonomic level with Vereshchaka's (2000, 2009) taxonomic keys. "*Sergestes* "and "*Sergia*" belong to the same family, but due to substantial differences in biomass, abundance, and physiological characteristics between the two, the genera were separated for the analyses in this study. The "*Sergia"* are generally larger in size, have a deeper depth distribution and, while not all are bioluminescent, those that are possess dermal photophores. The "*Sergestes"* are generally smaller in size, have shallower depth distributions and all possess bioluminescent organs of Pesta. The carapace length of each identified specimen was measured using digital calipers (Fisher Scientific digital caliper, Model No. FB70250) to the nearest 0.01 mm, and the wet mass of each species group was measured to the nearest 0.01g using a digital scale (P-114 balance, Denver Instruments). Day and night abundances for species with a large enough sample size (> 50 individuals) to analyze vertical migrations were standardized by the volume filtered for each trawl. These standardized abundances of each species were then converted into percentages of the total catch per station to determine the percentage of the species present at each depth range (Burdett *et al.* 2017). The species were then further categorized into groups based on their percent of the total abundance. The groups are as follow: 1) dominant species consisted of ≥ 10% of the total abundance 2) abundant species consist of 1-9.99% of the total abundance and 3) rare species consist of < 1% of the total abundance (after Burdett *et al.* 2017). Species were also categorized as strong vertical migrators (SVM) if more than 50% of individuals migrated into shallower waters at night, weak vertical migrators (WVM) if 15-49% of individuals migrated, and non-vertical migrators (NVM) if less than 15% of individuals migrated daily (Burdett *et al.* 2017).

One of the goals of this study was to describe the overall assemblage and to determine if differences in near-slope vs. offshore abundance and biomass were present, as was found for the oplophorids (Burdett *et al.* 2017) and euphausiids (Frank *et al.* 2020). Only the MS7 data were analyzed, to be consistent with these earlier studies. Near-slope stations were defined as stations landward of the 1000-m isobath and offshore stations are on the ocean side of the 1000-m isobath (Burdett *et al.* 2017). Statistical tests (see below) were used to determine if statistically significant differences were present in abundances and/or biomasses between the two sites.

In addition, data from the ONSAP cruises in 2011 (MS7 and MS8) were analyzed with respect to data from the DEEPEND cruises in 2015-2016 (DP01-04) to determine if there were significant temporal differences in abundances and biomass between one year after the oil spill and 5-7 years post spill. Spring and Fall data sets from 2011 were not significantly different from each other and therefore were combined to form a one-year dataset. Similarly, spring and fall data sets from 2015 and 2016 were not significantly different from each other and were also combined. As there was not an August 2017 cruise to provide a yearly dataset for 2017, May 2016 was compared to May 2017, and August 2016 data were analyzed with respect to August 2018 data to determine if there were further temporal changes in the assemblage. Temporal analysis of individual species was conducted to compare abundance and biomass from 2011 to 2015-16 but further individual species comparisons after 2016 were not conducted.

Statistical Analysis - near-slope vs. offshore data

The Shapiro-Wilk test demonstrated that the data were not normally distributed; therefore, non-parametric Mann-Whitney *U* tests were conducted to determine if significant differences between the abundance and biomass of near-slope vs. offshore stations was present.

Statistical Analysis – temporal data

The temporal analysis of abundance and biomass was conducted using a Kruskal-Wallis test since the data was continuous but not normally distributed according to the Shapiro-Wilk test. Sergestid species were included for this part of the study if they contributed to 99% of the species abundance (after Fine 2016). Due to the larger size and deeper depth distribution of the "*Sergia*" group than the "*Sergestes"* group, separate analyses were conducted to determine if these differences correlated to larger or smaller declines in the respective groups. Only offshore stations which were identified as common water stations (Johnston *et al.* 2019) with quantifiable volumes were used for this analysis comparison because 1) significant differences were present in samples collected from loop current stations vs. common water stations in the oplophorid assemblage analysis (Nichols 2018) and 2) all the DEEPEND stations were offshore common water stations (Johnston *et al.* 2019).

Sergestidae Near-slope vs. Offshore Abundance/Biomass

Results

During the *Meg Skansi* 7 research cruise in 2011 (April 20 – June 29), a total of 6148 specimens from the family Sergestidae were collected. Seventeen sergestid species made up 99% of the total abundance with 13 categorized as dominant or uncommon and the remaining four species categorized as rare. Tables 2 and 3 show the former names and the current names, which will be used throughout this thesis.

Table 2: Known species of "*Sergia*" in GOM (WoRMS 2020).

Previous Species Name	Accepted Species Name
Sergia grandis (Sund, 1920)	*Phorcosergia grandis* (Vereshchaka, Olesen, & Lunina, 2014)
Sergia hansjacobi (Vereshchaka, 1994)	*Challengerosergia hansjacobi* (Vereshchaka, Olesen, & Lunina, 2014)
Sergia regalis (Gordon, 1939)	*Robustosergia regalis* (Vereshchaka, Olesen, & Lunina, 2014)
Sergia robusta (Smith, 1882)	*Robustosergia robusta* (Vereshchaka, Olesen, & Lunina, 2014)
Sergia splendens (Sund, 1920)	*Gardinerosergia splendens* (Vereshchaka, Olesen, & Lunina, 2014)
Sergia talismani (Barnard, 1946)	*Challengerosergia talismani* (Vereshchaka, Olesen, & Lunina, 2014)
Sergia tenuiremis (Krøyer, 1855)	*Sergia tenuiremis* (Krøyer, 1855)
Sergia wolffi (Vereshchaka, 1994)	*Phorcosergia wolffi* (Vereshchaka, Olesen, & Lunina, 2014)

Table 3: Known species of "*Sergestes*" in GOM (WoRMS 2020).

Previous Species Name	Accepted Species Name
Sergestes arcticus (Krøyer, 1855)	*Eusergestes arcticus* (Judkins & Kensley, 2008)
Sergestes armatus (Krøyer, 1855)	*Parasergestes armatus* (Judkins & Kensley, 2008)
Sergestes atlanticus (H. Milne Edwards, 1830)	*Sergestes atlanticus* (H. Milne Edwards, 1830)
Sergestes corniculum (Krøyer, 1855)	*Deosergestes corniculum* (Judkins & Kensley, 2008)
Sergestes cornutus (Krøyer, 1855)	*Cornutosergestes cornutus* Vereshchaka, Olesen, & Lunina, 2014)
Sergestes edwardsii (Krøyer, 1855)	*Neosergestes edwardsii* (Judkins& Kensley, 2008)
Sergestes henseni (Ortmann, 1893)	*Deosergestes henseni* (Judkins& Kensley, 2008)
Sergestes paraseminudus (Crosnier & Forest, 1973)	*Deosergestes paraseminudus* (Judkins & Kensley, 2008)
Sergestes pectinatus (Sund, 1920)	*Allosergestes pectinatus* (Judkins & Kensley, 2008)
Sergestes sargassi (Ortmann, 1893)	*Allosergestes sargassi* (Judkins & Kensley, 2008)
Sergestes vigilax (Stimpson, 1860)	*Parasergestes vigilax* (Judkins & Kensley, 2008)

Overall, "*Sergestes*" contributed to 64% of the total abundance while "*Sergia*" made up 36% (Figure 4A). Because they were larger, the "*Sergia*" made up 66% biomass, while the smaller "*Sergestes*" contributed to 34% of the total (Figure 4B).

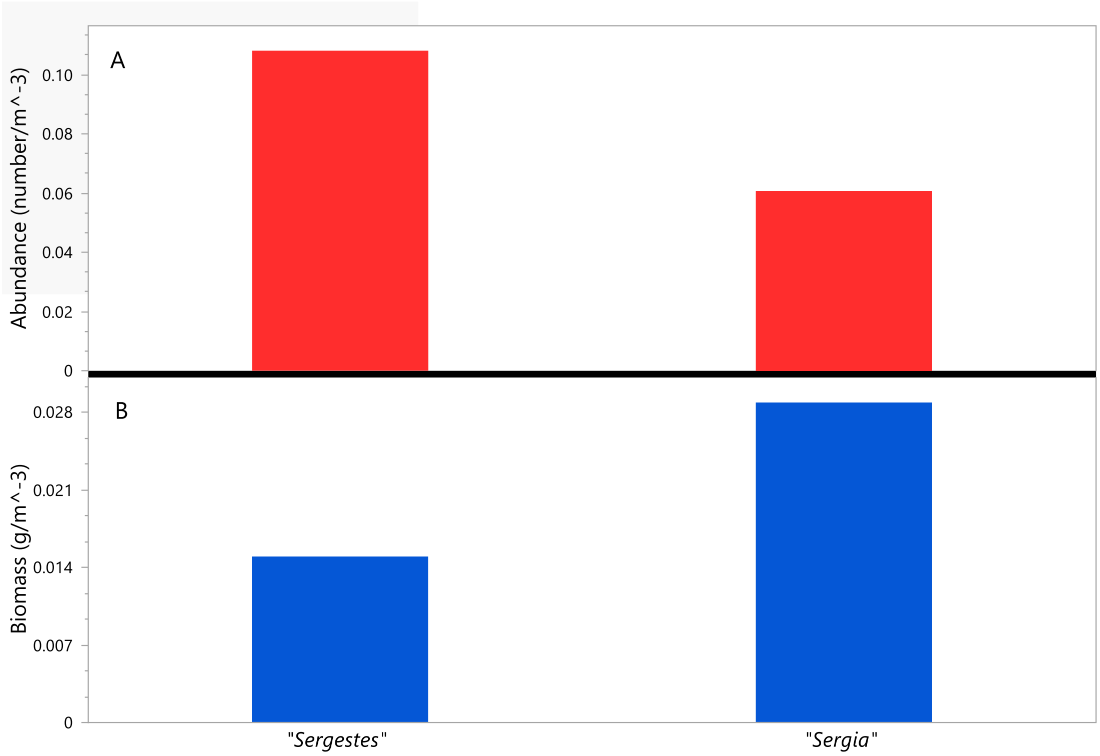


Figure 4: "*Sergestes*" and "*Sergia*" total abundance (A) and total biomass (B) of specimens collected during *Meg Skansi* 7.

"Sergia" Species Abundance

Seven "*Sergia*" species (2224 specimens) were collected during *Meg Skansi* 7. *Gardinerosergia splendens* (67.6%), *Sergia tenuiremis* (17.6%) and *Robustosergia regalis* (formerly *Sergia regalis* - 11.2%) were in the dominant classification, making up 96% of the total "*Sergia*" abundance. *Phorcosergia grandis* (formerly *Sergia grandis* - 2.0%) was the only species categorized as uncommon while the three remaining species were categorized as rare: *Robustosergia robusta* (0.9%), *Challengerosergia talismani* (formerly *Sergia talismani* - 0.7%) and *Phorcosergia wolffi* (formerly *Sergia wolffi* - 0.03%).

“Sergestes” Species Abundance

Ten “*Sergestes*” species (3924 specimens) were collected during *Meg Skansi* 7. *Allosergestes pectinatus* (formerly *Sergestes pectinatus* - 42.0%), *Sergestes atlanticus* (12.4%) and *Neosergestes edwardsii* (formerly *Sergestes edwardsii* - 11.3%) were the three dominant species and contributed to 66% of the total abundance of the “*Sergestes*” assemblage. Six species were in the uncommon classification: *Deosergestes henseni* (formerly *Sergestes henseni* - 9.8%), *Allosergestes sargassi* (formerly *Sergestes sargassi* - 9.2%), *Parasergestes vigilax* (formerly Sergestes vigilax - 6.6%), *Deosergestes corniculum* (formerly *Sergestes corniculum* - 3.4%), *Parasergestes armatus* (formerly *Sergestes armatus* - 2.7%), *Cornutosergestes cornutus* (formerly *Sergestes cornutus* - 2.5%), while *Deosergestes paraseminudus* (formerly *Sergestes paraseminudus* - 0.02%) was the only rare species.

“Sergia” Biomass

Robustosergia regalis (30.9%), *Gardinerosergia splendens* (30.4%) and *Sergia tenuiremis* (27.0%) accounted for 88.33% of the total biomass. *Robustosergia regalis* made up only 11.2% of the total “*Sergia*” abundance but 30.94% of the total biomass, the greatest total biomass percentage of any “*Sergia”* species due to large size of individual specimens. Two of the remaining four species, *Phorcosergia grandis* (6.8%) and *Robustosergia robusta* (4.2%) were uncommon in terms of abundance, but they were typically larger than the other “*Sergia”* species, resulting in a relatively larger contribution to the overall biomass, making up 11% of the total biomass combined. *Challengerosergia talismani* (0.6%) and *Phorcosergia wolffi* (0.06%) were uncommon species in terms of abundance, and this is reflected in their low overall contribution to the biomass of the “*Sergia*” assemblage.

“Sergestes” Biomass

Deosergestes henseni (33.5%), *Allosergestes pectinatus* (23.9%), *Sergestes atlanticus* (11.6%), and *Deosergestes corniculum* (10.1%) were the four dominant species in terms of total biomass, accounting for 79.1% of the total biomass. *Deosergestes henseni,* the species with the highest percentage of the biomass due to its slightly larger size, was only the fourth most abundant species in the “*Sergestes”* assemblage. *Sergestes atlanticus* is the only species that ranked in the top three in both total abundance and total biomass (second in abundance and third in biomass). The remaining six "*Sergestes*" species represented 20.9% of the total biomass with each species contributing to 6% or less. *Allosergestes sargassi* (6.0%), *Neosergestes edwardsii* (4.6%), *Parasergestes armatus* (4.4%) and *Parasergestes vigilax* (4.2%) were all abundant species, ranking as the fifth through eighth most abundant species respectively. *Neosergestes edwardsii*, was the third highest in terms of abundance but only ranked as sixth in terms of biomass. *Cornutosergestes cornutus* (1.5%) and *Deosergestes paraseminudus* (0.3%) were the lowest two species in terms of biomass.

Near-slope vs. Offshore Sergestidae Assemblage Comparisons

The total abundance at 16 near-slope stations were analyzed with an intrastation variance of 7.99 x 10^{-8} m^{-3} and 29 offshore stations with a variance of 6.12 x 10^{-8} m^{-3} (Appendix 1). The mean abundance in the near-slope stations vs. the offshore stations (1.23 x 10^{-4} m^{-3} vs. 1.07 x 10^{-5} m^{-3}, p = .0594) was not significantly different (Figure 5A), while the mean biomass was significantly higher in near-slope stations vs. the offshore stations (2.59 x 10^{-4} m^{-3} vs. 3.52 x 10^{-5} m^{-3}, p=.0219) (Figure 5B).

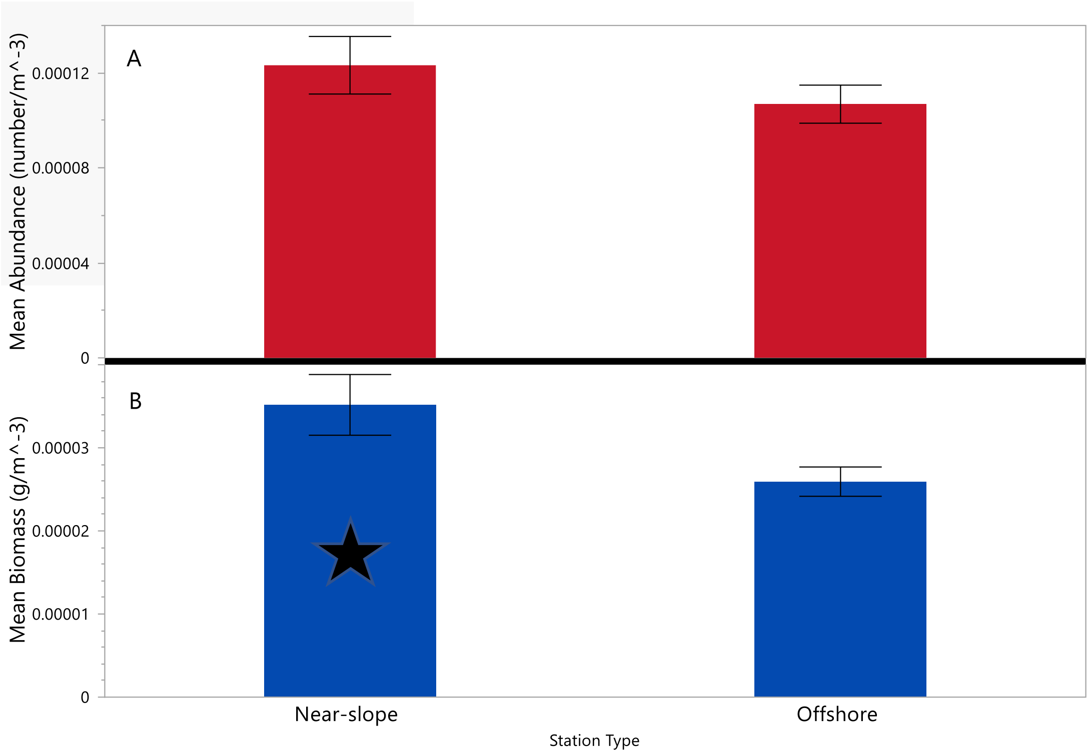


Figure 5: Sergestidae Near-slope vs. Offshore abundance (A) and biomass (B). Black star indicates a statistically significant difference. Bars represent the standard error of the mean.

"Sergia" and "Sergestes" Near-slope vs. Offshore Abundance/Biomass Comparisons

Both the mean abundance and mean biomass of the "*Sergestes"* assemblage were not significantly different in the near-slope stations compared to the offshores stations (1.28×10^{-4} m^{-3} vs. 1.20×10^{-4} m^{-3} , 2.21×10^{-5} m^{-3} vs. 1.41×10^{-5} m^{-3} respectively), as shown in Figures 6A and 7A ($p = 0.3327$ for abundance, p =0 .6005 for biomass). The "*Sergia*" mean abundance was not significantly different (Figure 6B; $p = 0.0519$) at near-slope stations than offshore (1.17×10^{-4} m^{-3} vs. 8.82×10^{-5} m^{-3}), while the biomass was significantly higher at the near-slope stations (Figure 7B; $p = 0.0349$) compared to offshore stations (5.39×10^{-5} g/m^{-3} vs. 4.27×10^{-5} g/m^{-3}).

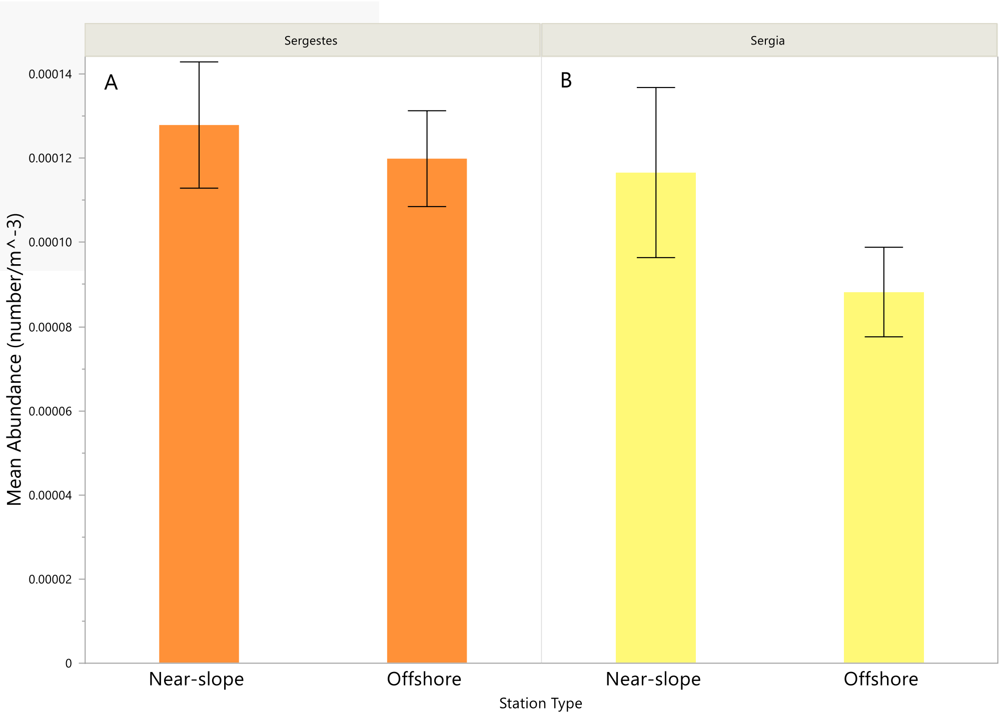


Figure 6: Mean abundance comparison of A) "*Sergestes"* and B) *"Sergia"* at near-slope vs. offshore stations. Bars represent the standard error of the mean.

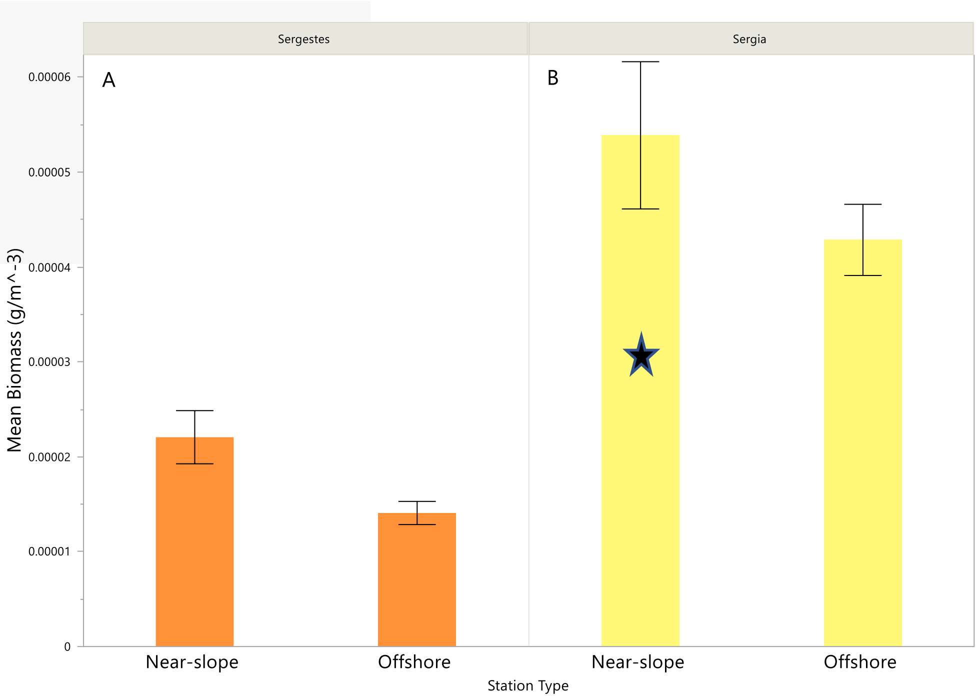


Figure 7: Mean biomass comparison of A) "*Sergestes"* and B) *"Sergia"* at near-slope vs. offshore stations. Black star indicates that "*Sergia*" at near-slope stations had a significantly higher biomass than "*Sergia*" at offshore stations. Bars represent the standard error of the mean.

The “*Sergestes”* species had a similar structure at near-slope stations and offshore stations in terms of species abundance ranks (Figure 8). *Allosergestes pectinatus* was found to be the most abundant at both near-slope and offshore stations by far, but the remaining “*Sergestes*” species were more evenly distributed. Overall, the “*Sergestes*” species abundances were not significantly different at offshore and near-slope stations, but only *Neosergestes edwardsii* did have a significantly higher abundance at offshore stations.

The two dominant species in terms of biomass were *Deosergestes henseni* and *Allosergestes pectinatus*, making up 65.16 % of the total near-slope biomass (Figure 9). Of the two previously mentioned species, only the biomass of *Allosergestes pectinatus* was significantly higher (p=.0151). Due to its large size and large carapace lengths, *Deosergestes corniculum* was a dominant species in terms of biomass at offshore stations while making up less than 4% of the total abundance. Similar to the abundance, “Sergestes” species biomasses were not significantly different at offshore and near-slope stations, except for *Allosergestes pectinatus* (significantly higher at near-slope stations) and *Neosergestes edwardsii* (significantly higher at offshore stations).

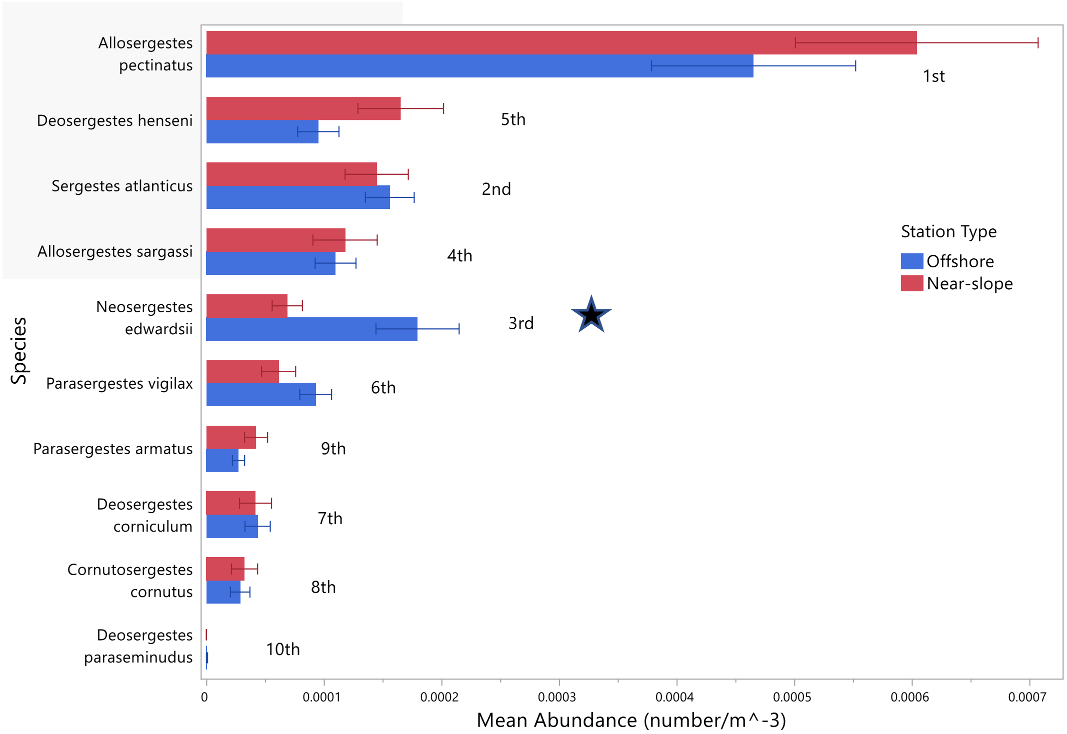


Figure 8: Mean abundance (n/m^{-3}) comparison of “*Sergestes”* species at near-slope vs. offshore stations. Black star represents a statistically significant difference. Species are ordered by abundance at near-slope stations.

Numbers next to the offshore data indicate species ranks for that location. Bars represent the standard error of the mean.

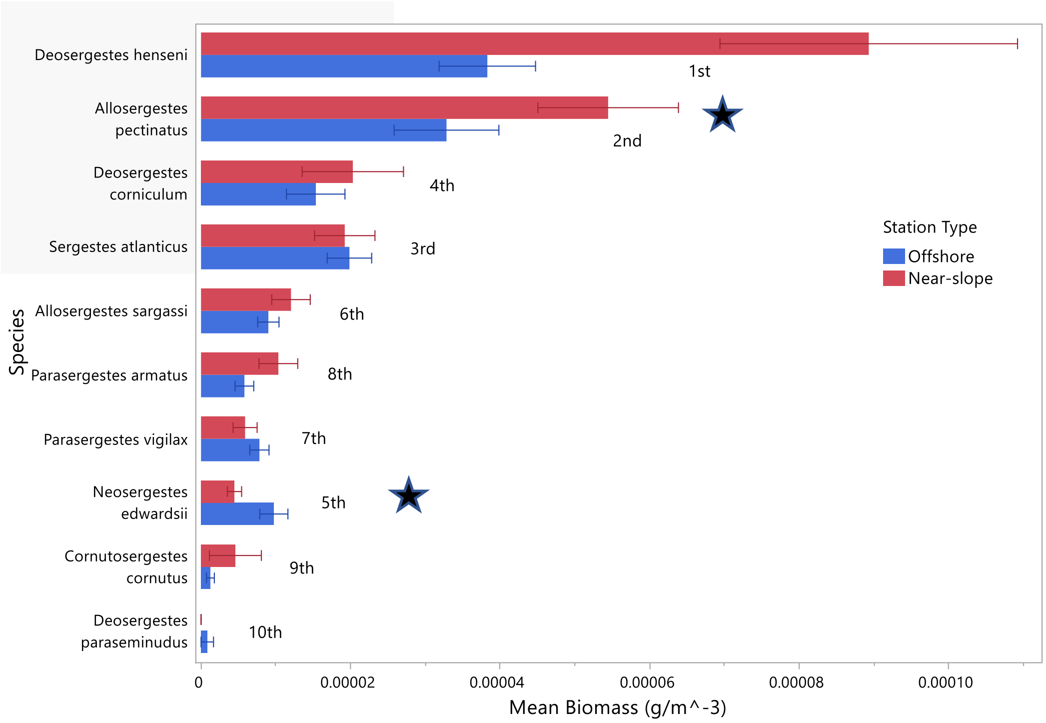


Figure 9: Mean biomass (g/m^{-3}) comparison of "*Sergestes*" species at near-slope vs. offshore stations. Black star represents a statistically significant difference. Species are ordered by abundance at near-slope stations. Numbers next to the offshore data indicate species ranks for that location. Bars represent the standard error of the mean.

In the "*Sergia*" group, the dominant species at both the near-slope and offshore stations were, in order of abundance, *Gardinerosergia splendens*, *Sergia tenuiremis*, *Robustosergia regalis* and *Phorcosergia grandis*, all of which were not significantly different at near-slope vs. offshore stations (Figure 10). Out of the other three, less abundant species, only *Challengerosergia talismani* significantly more abundant at offshore stations than near-slope.

The two dominant species in terms of overall biomass, *Sergia tenuiremis* and *Robustosergia regalis* were not significantly different between the two station types (Figure 11). The species that ranked third in overall biomass, *Gardinerosergia splendens*, had the highest biomass at the offshore stations but only the third highest biomass at near-slope stations. The remaining species (*P. grandis, R. robusta* and *P. wolffi*) only made up a small percentage of the total biomass and were not found to be significantly different at offshore and near-slope stations. Consistent with the abundance analysis, *Challengerosergia talismani* was the only species to have a significantly greater biomass at offshore stations although these original values were relatively small compared to other species (Wilcoxon, p = .0120). As with the "*Sergestes*" group, the species that contributed heavily to the total biomass of "*Sergia*" (*Sergia tenuiremis* and *Robustosergia regalis*) were both found to have greater biomasses at near-slope stations while the rest of the "*Sergia*" species which contributed much less to the total biomass were found to have greater biomasses at offshore stations.

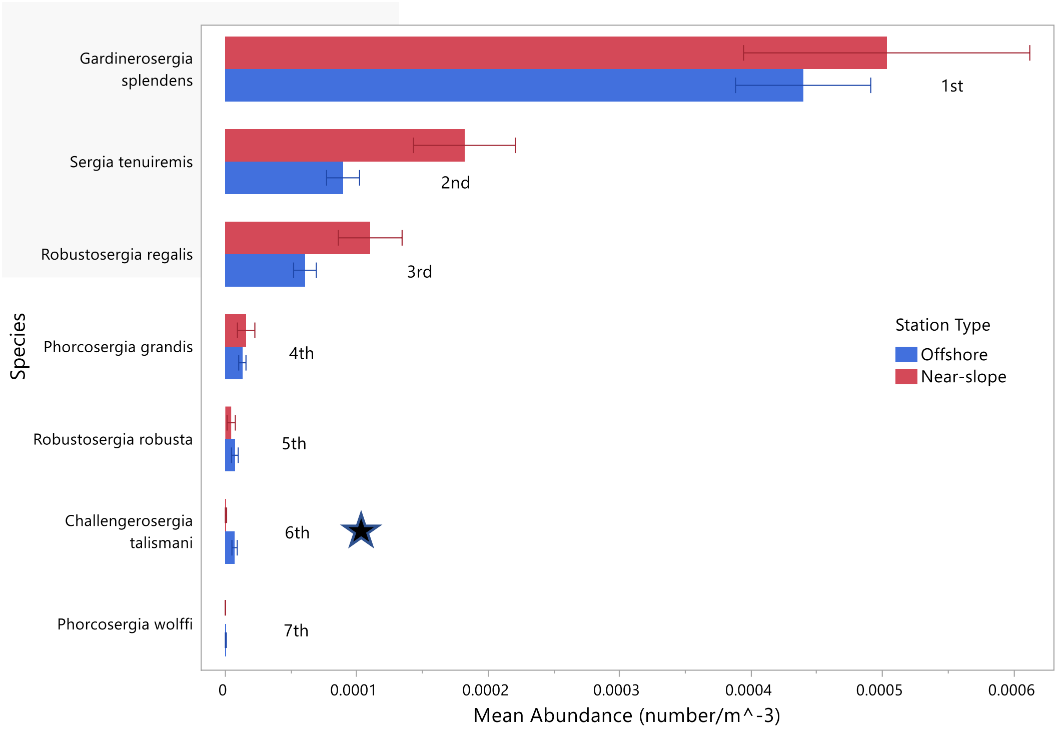


Figure 10: Mean abundance comparison of "*Sergia*" species at near-slope vs. offshore stations. Species are ordered by abundance at near-slope stations. Numbers next to the offshore data indicate species ranks for that location. Black star represents a statistically significant difference. Bars represent the standard error of the mean.

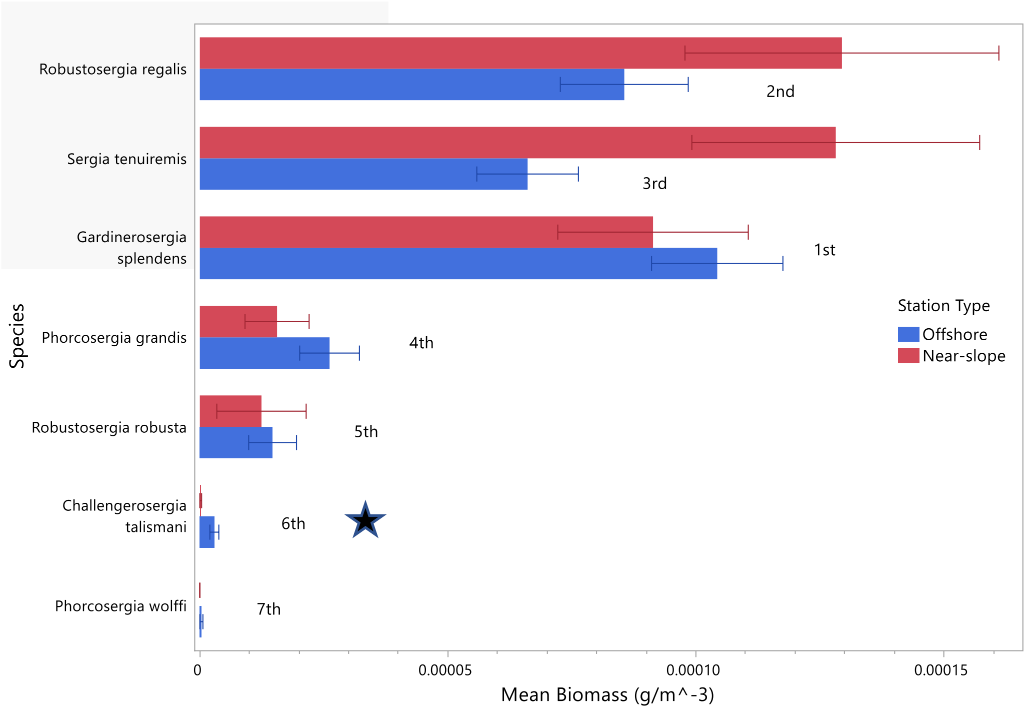
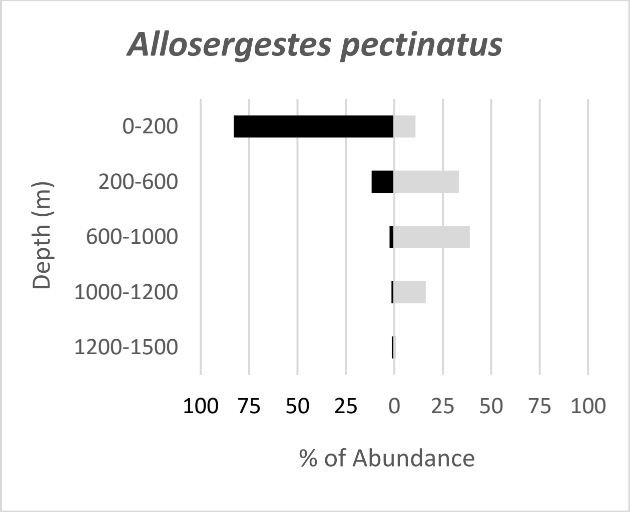
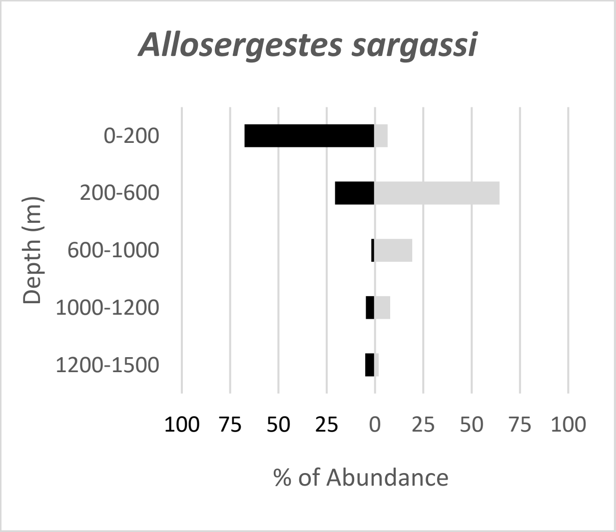


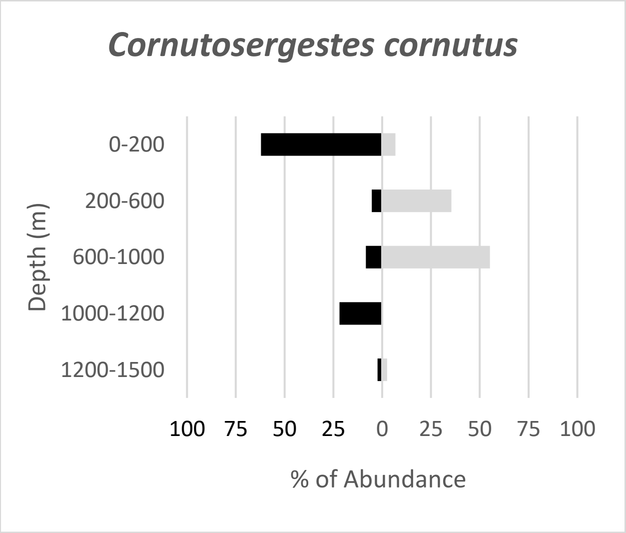
Figure 11: Mean biomass comparison of "*Sergia*" species at near-slope vs. offshore stations. Species are ordered by abundance at near-slope stations. Numbers next to the offshore data indicate species ranks for that location. Black star represents a statistically significant difference. Bars represent the standard error of the mean.

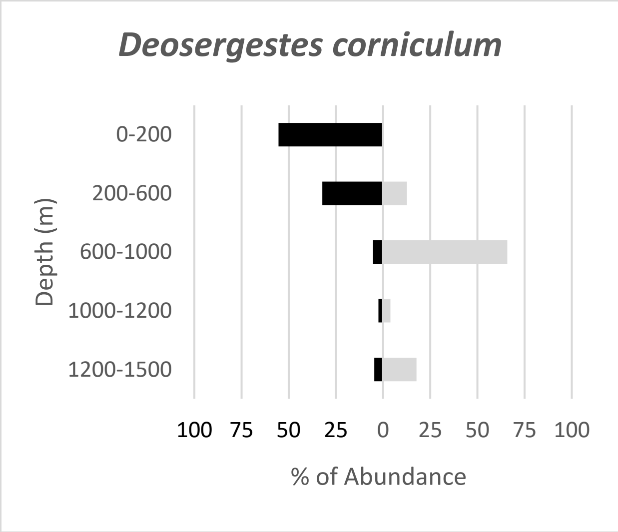
Sergestidae Vertical Distribution

Of the 13 Sergestidae species that were categorized as dominant or uncommon, all were categorized as strong vertical migrators (SVM - defined as >50% of the population ascending to shallower waters at night) (Figure 12). Of the nine dominant SVM species, *Allosergestes sargassi*, *Neosergestes edwardsii*, *Parasergestes vigilax* and *Cornutosergestes cornutus* spent the daytime in the mesopelagic zone, while *Gardinerosergia splendens*, *Sergestes atlanticus*, *Allosergestes pectinatus*, *Deosergestes corniculum* and *Deosergestes henseni* had daytime depth ranges covering portions of both the mesopelagic and bathypelagic zones. The larger species, *Robustosergia regalis* and *Phorcosergia grandis* limited their nocturnal migrations to the mesopelagic zones, all having greater than 65% of individuals in the upper mesopelagic zone at night and greater than 65% of individuals in the lower mesopelagic zone during the day (rarely found in the bathypelagic zone). *Robustosergia robusta* and *Sergia tenuiremis* had larger daytime ranges than the previous two "*Sergia*" species mentioned, with ~ 40% in lower mesopelagic and ~ 25% in the bathypelagic zone during the day; both species migrated into the upper mesopelagic zone at night. Except for the four aforementioned species, the rest of the species migrated to the epipelagic during the day, but oddly, three species (*A. sargassi D. corniculum,* and *S. atlanticus*) had a small percentage of individuals that migrated down into the bathypelagic at night.

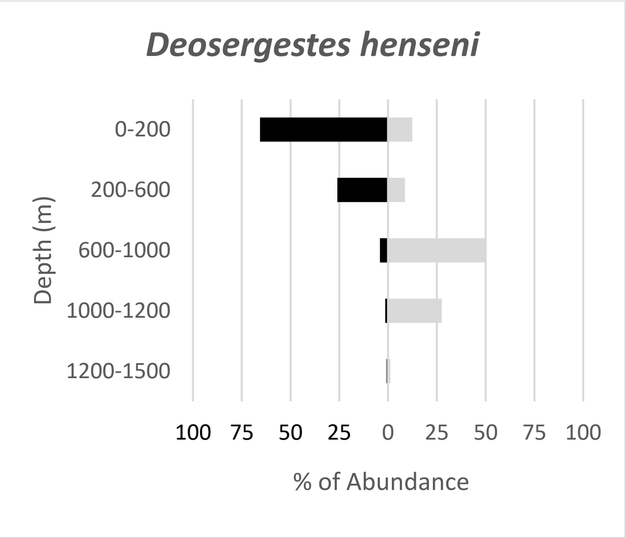




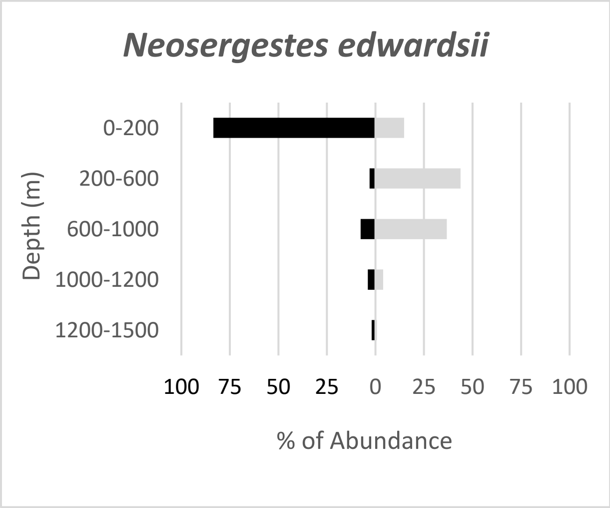




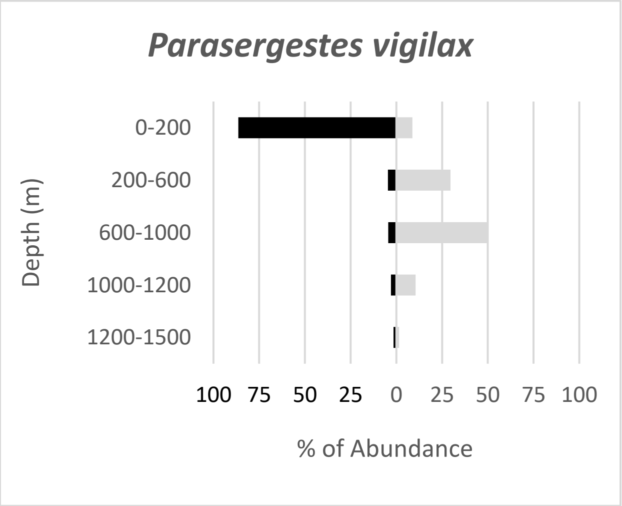
Deosergestes corniculum



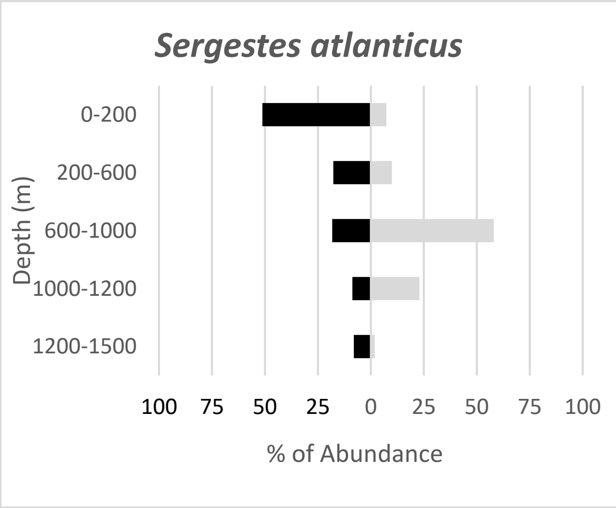
Deosergestes henseni



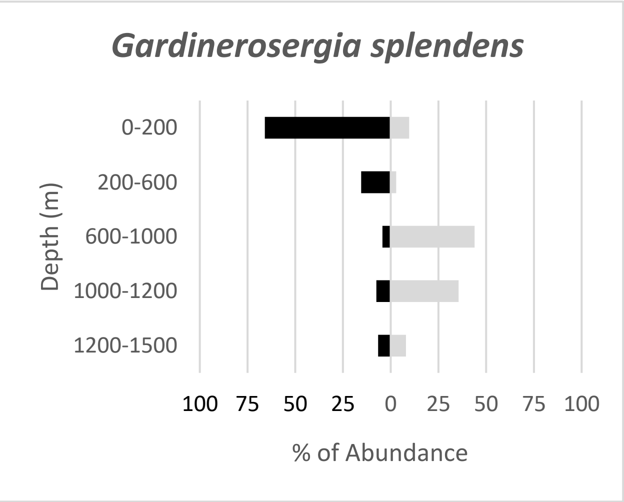
Neosergestes edwardsii



Parasergestes vigilax



Sergestes atlanticus



Gardinerosergia splendens

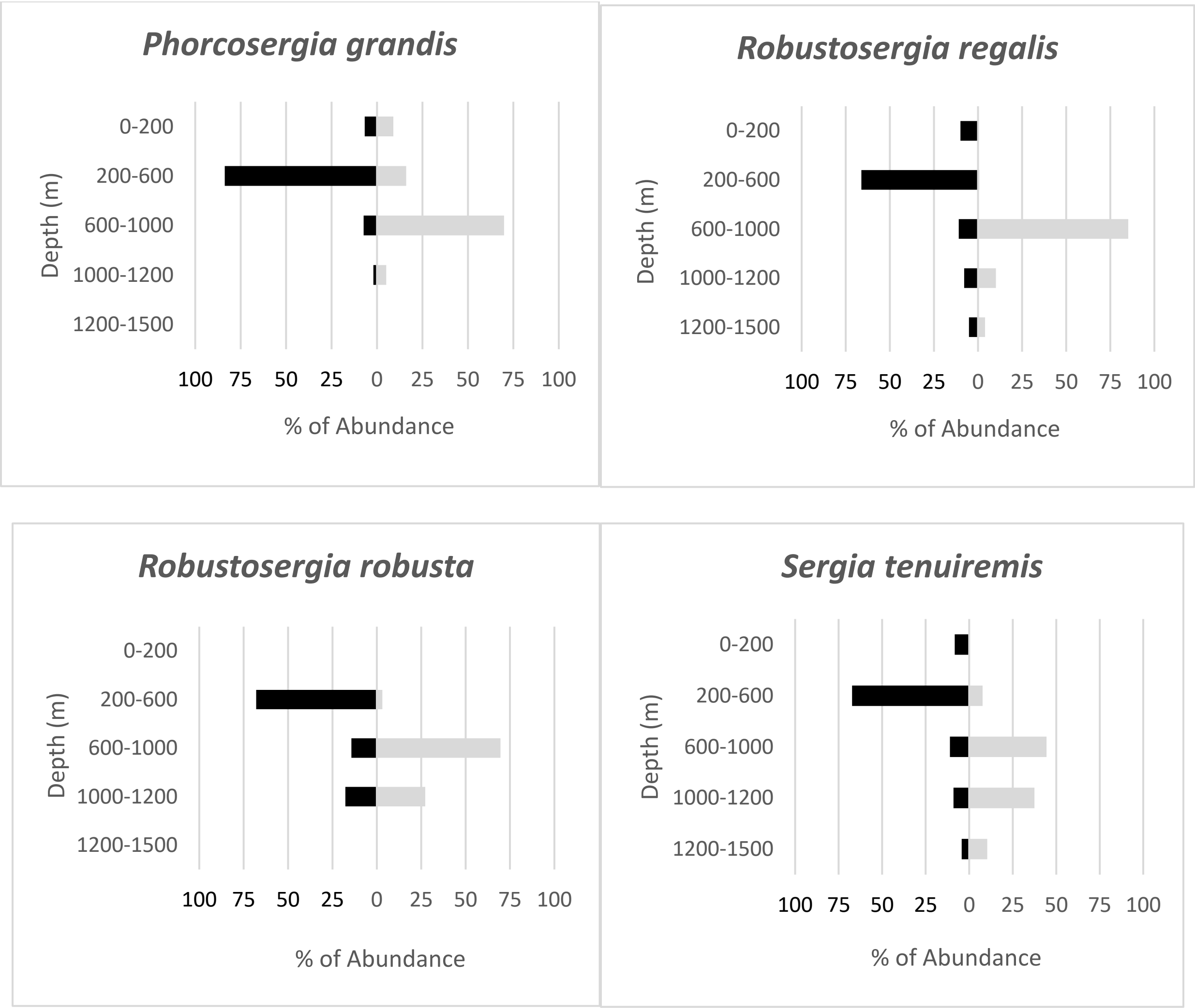


Figure 12: Vertical Distribution of "*Sergestes*" and "*Sergia*" species collected from 0-1500m. Black bars represent night abundances and gray bars represent day abundances. Graphs are sorted in alphabetical order by "*Sergestes*" group then "*Sergia*" group.

There were not enough data for the three rare species (*Deosergestes paraseminudus*, n=19, *Phorcosergia wolffi*, n=11 and *Challengerosergia talismani*, n=26) to draw conclusions about their migratory behavior. The depth ranges for these species are shown in Table 4.

Table 4: Vertical distribution data for rare sergestid species in the GOM.

Species	***Depth (m)***	***% of Total Abundance***	
		Night	***Day***
Deosergestes paraseminudus (n=19)	0-200	29.89%	0.0%
	200-600	70.11.%	5.35%
	600-1000	0.0%	19.09%
	1000-1200	0.0%	75.56%
	1200-1500	0.0%	0.0%
Phorcosergia wolffi (n=11)	0-200	77.58%	0.0%
	200-600	19.81%	0.0%
	600-1000	2.61%	80.52%
	1000-1200	0.0%	19.48%
	1200-1500	0.0%	0.0%
Challengerosergia talismani (n=26)	0-200	0.0%	0.0%
	200-600	18.55%	0.0%
	600-1000	81.45%	82.86%
	1000-1200	0.0%	17.14%
	1200-1500	0.0%	0.00%

Discussion

Sergestidae Assemblage Abundance

The two dominant species in this study in terms of abundance (*Gardinerosergia splendens* and *Allosergestes pectinatus*) each contributed more than double the total abundance of any other species and accounted for 51% of the total abundance of sergestids. Flock and Hopkins (1992) found that these same species were the most abundant species at their Standard Station location (station SE-5 in the current study – see Figure 3) 30 years ago, accounting for 53% of the total. The two aforementioned species have remained as the most dominant species over time even after the presence of human induced stressors, suggesting that they may adjust to changes better than other sergestids. Additionally, *Gardinerosergia splendens* has a broad diet and does not overlap niches with other sergestid species in the GOM, which could contribute to the continued dominance of his species. Conversely, *Allosergestes pectinatus* has a more specific diet comprised of mostly Candiciidae and Metridiidae copepods which only overlaps with the diets of relatively uncommon species diets (*A. sargassi* and *S. curvatus*) so the competition could be low for this niche as well (Flock and Hopkins 1992). *Sergestes atlanticus* and *Deosergestes henseni* were also relatively abundant species making up 16.5% of the total together, consistent with the Flock and Hopkins data (14.2%). While the current study found *Deosergestes paraseminudus* and *Challengerosergia talismani* to be rare species, Flock and Hopkins found both to be relatively abundant species. *Deosergestes paraseminudus* was found to have a similar diet to very abundant sergestid species, so inter specific competition along with the impact of the *DWHOS* could be a potential explanation for this assemblage change (Flock and Hopkins 1992).

Sergestidae plays an integral part in the trophic structure of the GOM and had the 3rd greatest total biomass in the order Decapoda in the GOM, only behind Oplophoridae and Benthesicymidae respectively (Burdett *et al.* 2017). In this study, *Gardinerosergia splendens, Robustosergia regalis, Sergia tenuiremis* and *Deosergestes henseni* were the four species that contributed most to the total biomass in descending order. Flock and Hopkins also found that *Gardinerosergia splendens* and *Deosergestes henseni* ranked in the top four in biomass, combining for about half of the total biomass. However, *Deosergestes paraseminudus* and

Robustosergia robusta were their other two species to round out the top four contributors for biomass but both species only made minor contributions to the total biomass in the current study. *Sergia filictum* was their species with the fifth highest total biomass, a species that was not found during this current study. *Robustosergia regalis* and *Sergia tenuiremis* were the other two species in the top four in this study but *Robustosergia regalis* was not observed and *Sergia tenuiremis* ranked last in biomass in the Flock and Hopkins study.

Offshore vs. Near-slope Assemblage Comparisons

Overall, there was not a significant difference between near-slope and offshore abundance but the biomass at the near-slope stations was significantly higher than at the offshore stations. The significantly higher biomass was likely driven by the "*Sergia*" group considering 1) there were no significant differences in biomass between near-slope and offshore stations for the "*Sergestes*" group 2) the "*Sergia"* group had a significantly higher biomass at near-slope stations compared to offshore and 3) the "*Sergia"* group has individuals larger in size than the "*Sergestes"* group. When looking at individual species, *Robustosergia regalis* and *Sergia tenuiremis,* both of which are generally large sized species, did not have significantly different biomass values at near-slope and offshore stations. *Gardinerosergia splendens* was by far the most abundant species at both near-slope and offshore stations but no significant differences were found between the two locations for this species. Substantially higher variance in sergestid abundance at near-slope stations compared to offshore was likely due to fewer near-slope stations sampled along with a higher mean abundance at near-slope stations. This substantially higher variance may explain the differences among species abundances, as suggested by Burdett (2016) for the Oplophoridae.

It appears that the two groups are structured in similar ways considering few significant differences at the species level were found in terms of abundance. Burdett *et al*. (2017*)* who also analyzed MS7 samples, reported similar results for the Oplophoridae, with only three oplophorid species (*Acanthephyra stylorostratis, A. purpurea,* and *Systellaspis debilis*) being significantly more abundant at near-slope stations while two oplophorid species (*Hymenodora gracilis* and *Janicella spinicauda*) had significantly higher abundances offshore.

There are few studies comparing offshore and near-slope assemblages, but Reid *et al.* (1991) studied the mesopelagic-boundary distribution of fishes, squids, and shrimps off Hawaii. That study indicated that individual species known as boundary species may only inhabit a narrow zone above the upper slope of continents, islands, and seamounts. The crustacean boundary community differed noticeably from the oceanic community with greater biomass values at "boundary" stations compared to "oceanic" stations. Reid *et al.* (1991) sampled three "boundary" bottom isobath stations (BIS) at 500, 250 and 100 m, while the current study characterized a near-slope station to be on or landward of the 1000-m isobath (per Burdett *et al.* 2017), a similar significantly greater biomass was present at the near-slope stations vs. the oceanic stations. In Reid *et al.* (1992) study, *Sergia fulgens* was characterized as one of the most abundant "boundary" species with a significantly greater abundance at the 500 m BIS compared to the "oceanic" 800 m BIS where very few individuals were caught. Reid *et al.* (1991) suggested that *Sergia fulgens* plays a crucial role when it comes to the interaction of neritic and oceanic ecosystems. While abundance between near-slope and offshore stations for the most abundant species were analyzed, none of these differences were statistically significant, which may be due to the higher variance at the near-slope stations due to a smaller sample size (see above) and further sampling may produce "boundary" species of sergestids as well. As with the biomass values for sergestids in this current study, Burdett *et al.* (2017) reported that a majority of the oplophorid species were higher in terms of biomass at near-slope stations. compared to offshore stations and Frank *et al.* (2020) reported the same for the Euphausiidae. A study by Daly *et al.* (2021) also showed the zooplankton abundances were highest in their near shore stations and decreased off shelf. As these zooplankton are major prey for the crustacean species in the aforementioned studies, as well as the sergestids in the current study, this could provide an explanation for the distribution differences seen in the micronektonic crustaceans.

Sergestidae Vertical Distribution

All the dominant and abundant sergestid species in this study were found to be strong vertical migrators, with nine species migrating to the epipelagic and four migrating to the upper mesopelagic (200-600m). All eight "*Sergestes*" species (which tend to be smaller) were found to migrate to the epipelagic, compared to only one of five "*Sergia*" species. This vertical separation of sergestid shrimp species, also reported by Foxton (1972), provides further support that

Sergestidae species of different sizes may have different depth distributions, allowing similar species to coexist by reducing competition (Foxton 1972; Donaldson 1975). Flock and Hopkins (1992) also found that most of the sergestids in their study were diel vertical migrators, with most "*Sergia*" found deeper during the day than "*Sergestes*," attributing this difference due to "*Sergia*" being larger in size and having an "all-red" coloration. Size-depth trends of average size increasing with depth are known to occur in fishes and other micronektonic groups (Foxton 1972; Flock and Hopkins 1992). Flock and Hopkins (1992) determined that at least 50% of each species' populations, except for *Robustosergia robusta* and *Sergia filictum*, were found in the epipelagic zone at night. Those results differ from the results reported here in that the majority of the *Phorcosergia grandis, Sergia tenuiremis* and *Robustosergia regalis* species populations migrated to the upper mesopelagic at night, with only a very small percentage in the epipelagic. Compared to the "*Sergestes*,", these deeper nighttime migration depths by the larger-bodied "*Sergia*" support the hypothesis of De Robertis (2002), who suggested that larger-bodied organisms will not migrate as shallow as smaller-bodied species and will start their ascent later and their descent earlier compared to smaller-bodied organisms. The larger-bodied species are more easily seen and therefore more vulnerable to predation, so their migration patterns ensure that they will be at lower light levels than the smaller, less visible, species.

Temporal Analysis of Abundance and Biomass

Results

A total of 7345 Sergestidae samples were examined and used for statistical analysis, collected from the ONSAP (MS7 & 8, both in 2011) and DEEPEND (DP01-04 – 2015 and 2016) cruises. The Sergestidae assemblage declined significantly in abundance and biomass by 30.5% (Kruskal-Wallis, p = 0.0018) and 34.1% (Kruskal-Wallis, p = 0.0028) respectively, between 2011 to 2015 (Figure 13A & 13B). Additionally, the mean abundance (Kruskal-Wallis, p = 0.0002) decreased significantly by 26.8% and the biomass decreased by 43.1% (Kruskal-Wallis, p = 0.0006) from 2011 to 2016. There were no significant differences in abundance (Kruskal-Wallis, p = 0.2744) or biomass (Kruskal-Wallis, p = 0.3204) from 2015 to 2016.

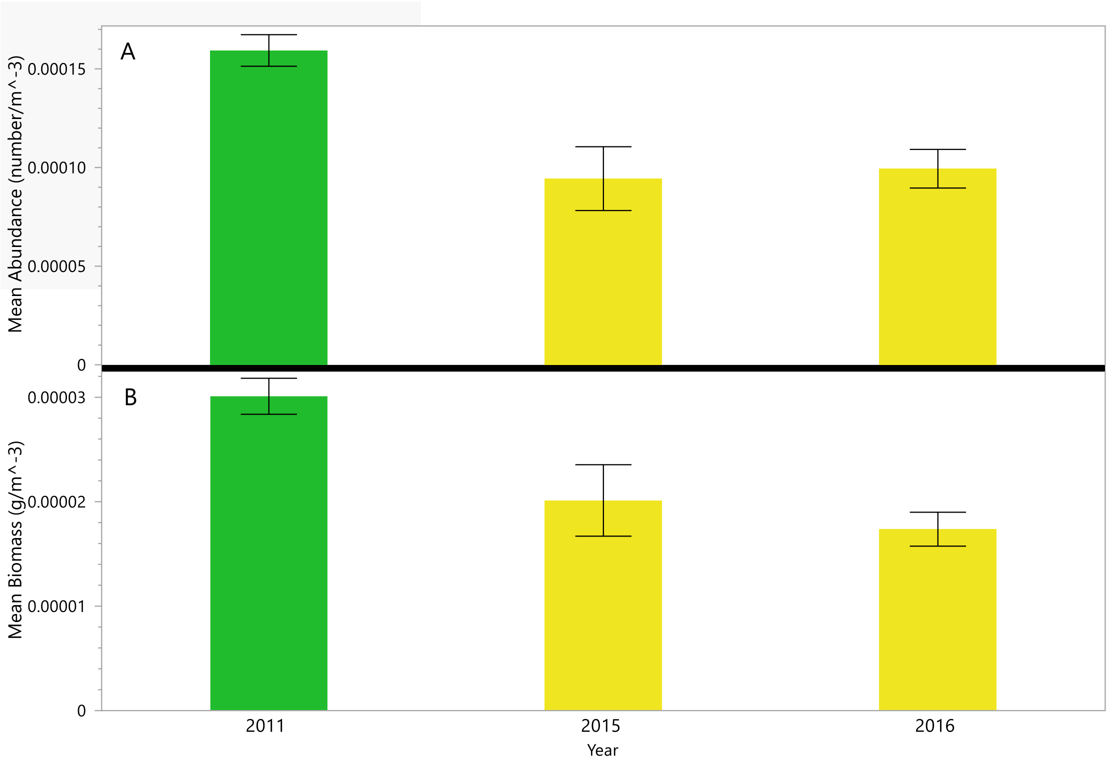


Figure 13: Sergestidae assemblage mean abundance (A) and mean biomass (B) during 2011 and 2015-2016 in chronological order. Bars represent the standard error of the mean.

Both abundance and biomass were significantly lower in May 2017 than May 2016 (Kruskal-Wallis, p = 0.0225 and 0.0217, respectively), with a 12.1% decline in abundance and a 23.9 % decline in biomass (Figure 14A &14B). However, the differences between the between August 2016 and August 2018 were not significantly different (Figure 15A & 15B) for either abundance (Kruskal-Wallis, p = 0.5948) or biomass (Kruskal-Wallis, p = 0.9021).

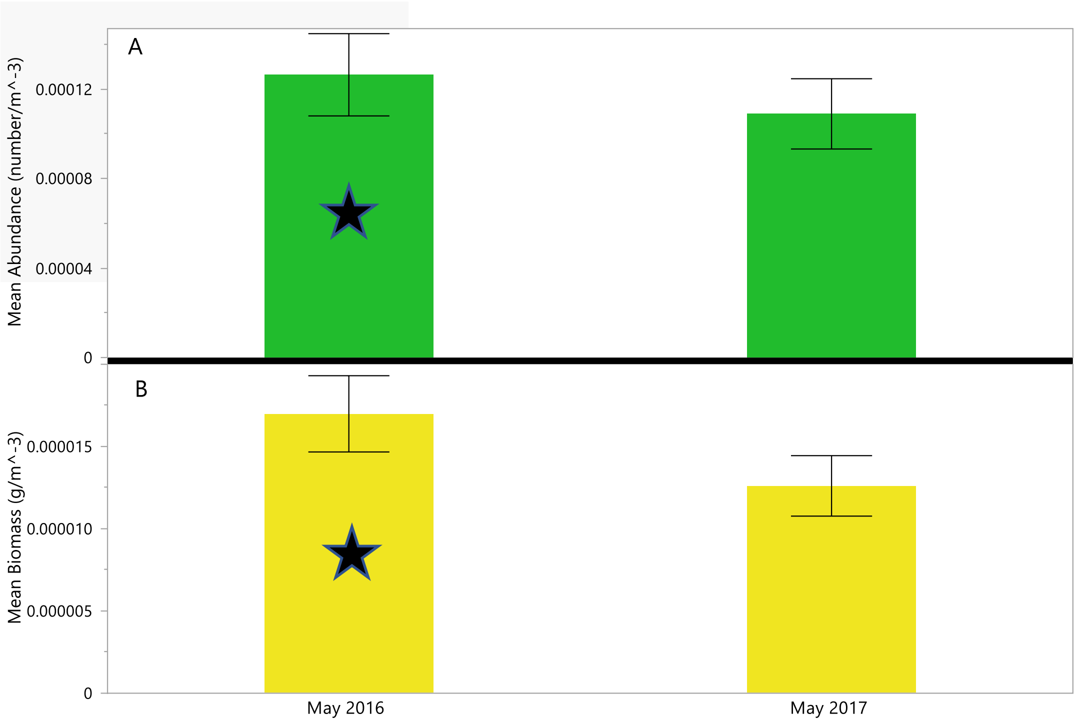


Figure 14: Sergestidae assemblage mean abundance (A) and mean biomass (B) during May 2016 and May 2017. Black star indicates a statistically significant difference. Bars represent the standard error of the mean.

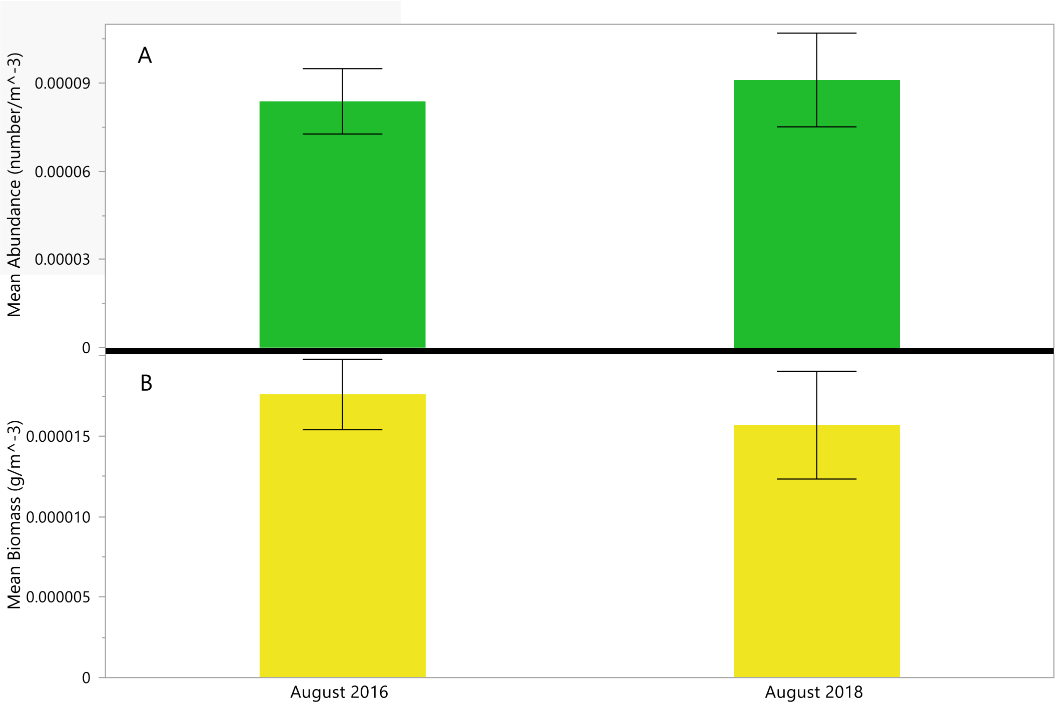


Figure 15: Sergestidae assemblage mean abundance (A) and mean biomass (B) during August 2016 and August 2018. No significant differences were found. Bars represent the standard error of the mean.

The “*Sergia*” group mirrored the Sergestidae assemblage data, with significant declines in both abundance (33.0 %, Kruskal-Wallis, p = 0.014)) and biomass (37.7 %, , Kruskal-Wallis, p = 0.009) from 2011 to 2015 and from 2011 and 2016 (abundance – 48.9 %, Kruskal-Wallis, p < 0.001; biomass – 46.5%, Kruskal-Wallis, p < 0.001), with no significant changes in either parameter between 2015 and 2016 (Figure 16A & 16B).

The “*Sergestes*” group also mirrored the entire sergestid assemblage with both abundance and biomass declining significantly - 39.7% (Kruskal-Wallis, p = 0.002) and 24.4% (Kruskal-Wallis, p = 0.0047) respectively between 2011 to 2015. Between 2011 and 2016, the decreases in abundance and biomass were again statistically significant - 20.8% (Kruskal-Wallis, p < 0.001). and 35.8% (Kruskal-Wallis, p < 0.001) respectively. There were no significant changes in either parameter between 2015 to 2016 (Figure 17A &17B).

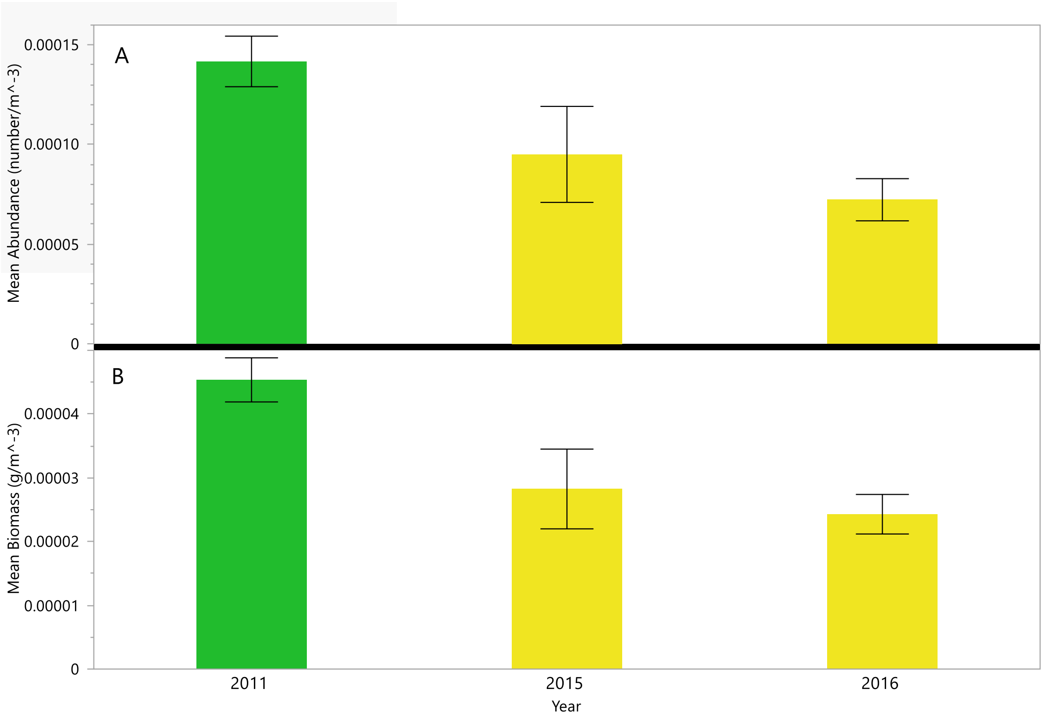


Figure 16: “*Sergia”* assemblage mean abundance (A) and mean biomass (B) during 2011 and 2015-2016 in chronological order from ONSAP and DEEPEND cruises. Bars represent the standard error of the mean.

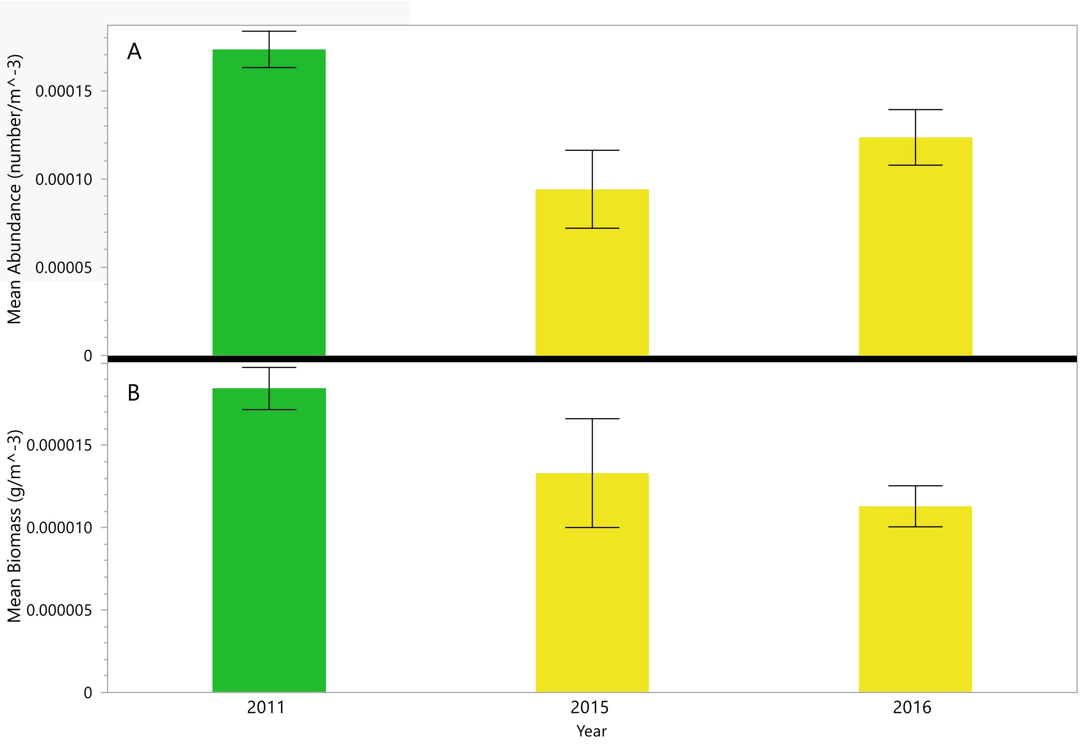


Figure 17: "*Sergestes*" assemblage mean abundance (A) and mean biomass (B) during 2011 and 2015-2016 in chronological order from ONSAP and DEEPEND cruises. Bars represent the standard error of the mean.

"*Sergia*" Species Temporal Analysis

There were no significant differences between the 2015 and 2016 DEEPEND data, therefore these were combined for the purpose of species comparisons to the 2011 ONSAP data. The abundance of three of the four most abundant "*Sergia*" species decreased significantly between 2011 to 2015-2016 while *Sergia tenuiremis*, the third highest in both abundance and biomass did not decrease significantly. *Gardinerosergia splendens*, the most abundant species for ONSAP decreased significantly in abundance by 33.3% while the biomass did not decrease significantly (Table 5 & 6). Two larger sized species, *Robustosergia regalis* and *Robustosergia robusta*, suffered the greatest biomass decline of any species, with significant decreases of 73% and 80% respectively.

Table 5: Temporal comparisons of mean abundance from “*Sergia*“ species between 2011 to 2015-16 in order from ONSAP abundance highest to lowest. Asterisks represent statistically significant differences.

	MEAN ABUNDANCE (n/m^{-3})			
SPECIES	***ONSAP***	***DEEPEND***	***p-value***	***% CHANGE***
Gardinerosergia splendens	4.74E-04	3.16E-04	0.0295**	-33.34%
Robustosergia regalis	8.80E-05	4.35E-05	0.0198**	-50.94%
Sergia tenuiremis	8.53E-05	5.51E-05	0.0896	-35.43%
Robustosergia robusta	4.81E-05	1.72E-05	0.0167**	-64.27%
Phorcosergia grandis	2.72E-05	2.77E-05	0.6055	+1.66%
Challengerosergia talismani	1.87E-05	2.87E-05	0.9526	+53.85%
Challengerosergia hansjacobi	5.59E-06	2.11E-05	0.0467**	+278.08%

Table 6: Temporal comparisons of mean biomass from “*Sergia*“ species between 2011 to 2015-16 in order from ONSAP biomass highest to lowest. Asterisks represent statistically significant differences.

	MEAN BIOMASS (g/m^{-3})			
SPECIES	***ONSAP***	***DEEPEND***	***p-value***	***% CHANGE***
Robustosergia regalis	9.38E-05	2.52E-05	0.0062**	-73.09%
Gardinerosergia splendens	8.04E-05	6.56E-05	0.4649	-18.45%
Sergia tenuiremis	6.89E-05	4.51E-05	0.0896	-34.59%
Robustosergia robusta	5.51E-05	1.12E-05	0.0066**	-79.60%
Phorcosergia grandis	2.17E-05	2.01E-05	0.4834	-7.16%
Challengerosergia talismani	2.06E-06	5.37E-06	0.8534	+160.73%
Challengerosergia hansjacobi	6.36E-07	3.67E-06	0.0437**	+478.45%

“*Sergestes*” Species Temporal Analysis

All the “*Sergestes*” species exhibited a decrease in terms of abundance and biomass from 2011 to 2015-16 with four of these species - *Allosergestes sargassi*, *Neosergestes edwardsii*, *Deosergestes henseni*, and *Parasergestes vigilax* - showing statistically significant declines for each parameter (Table 7 & 8), with the largest decline seen in *Parasergestes vigilax*.

Table 7: Temporal comparisons for mean abundance from "*Sergestes*" species between 2011 to 2015-16 in order from ONSAP biomass highest to lowest. Asterisks represent a significant difference with a p-value less than 0.05.

	MEAN ABUNDANCE (n/m^{-3})			
SPECIES	***ONSAP***	***DEEPEND***	***p-value***	***% CHANGE***
Allosergestes pectinatus	4.18E-04	3.31E-04	0.3717	-20.86%
Allosergestes sargassi	2.25E-04	1.19E-04	0.0063**	-47.37%
Neosergestes edwardsii	2.23E-04	1.66E-04	0.0017**	-25.32%
Deosergestes henseni	1.33E-04	7.52E-05	0.0312**	-43.30%
Sergestes atlanticus	1.20E-04	1.04E-04	0.1700	-13.48%
Parasergestes vigilax	1.19E-04	4.62E-05	0.007**	-61.29%
Deosergestes corniculum	7.45E-05	6.67E-05	0.4847	-10.39%
Parasergestes armatus	6.82E-05	3.34E-05	0.4499	-51.02%
Cornutosergestes cornutus	2.10E-05	0	0.3431	-100%

Table 8: Temporal comparisons for mean biomass from "*Sergestes*" species between 2011 to 2015-16 in order from ONSAP biomass highest to lowest. Asterisks represent a significant difference with a p-value less than 0.05.

	MEAN BIOMASS (g/m^{-3})			
SPECIES	***ONSAP***	***DEEPEND***	***p-value***	***% CHANGE***
Deosergestes corniculum	3.69E-05	2.50E-05	0.2255	-32.33%
Deosergestes henseni	3.63E-05	2.03E-05	0.0430**	-44.02%
Allosergestes pectinatus	2.65E-05	1.52E-05	0.3602	-42.90%
Allosergestes sargassi	1.48E-05	8.50E-06	0.0153**	-42.74%
Sergestes atlanticus	1.26E-05	7.93E-06	0.1578	-37.28%
Parasergestes armatus	1.11E-05	8.78E-06	0.6470	-20.59%
Neosergestes edwardsii	8.86E-06	6.61E-06	0.0038**	-25.42%
Parasergestes vigilax	8.81E-06	2.98E-06	0.0014**	-66.18%
Cornutosergestes cornutus	3.15E-06	0	0.3433	-100%

Discussion

The results show a significant decline in sergestid abundance and biomass between 2011, one year after the *DWHOS,* and 2015-2017 (4-6 years after the spill). Since no pre-spill data were available, the 2011 data are a contaminated baseline, and therefore, normal biological variability must be considered as well as the impacts from the *DWHOS*. However, Rooker *et al.* (2013) conducted a temporal analysis of fish larvae populations, and found that, while larval abundances were lower in 2010 (right after the *DWH*OS) relative to three years before the oil spill, these changes were not statistically significant, and suggest that this small decrease may fall within natural variability. In the current study, the significant declines in both abundance and biomass of over 30%, with no evidence of recovery to 2011 levels seven years after the oil spill, suggest that natural variability is not a likely explanation.

Micronektonic crustaceans are vulnerable to deep-water oil plumes, as they possess a large surface area relative to their volume and a large gill surface area through which oil can enter (Knap *et al.* 2017). The recent study by Knap *et al*. (2017) also indicated that deep-sea crustaceans showed a high sensitivity to 1-MN, a chemical found in petroleum leading to toxic effects and mortality after as little as 24 hours of exposure. The sergestids could have been residing in depths with high hydrocarbon and oil dispersant concentrations that potentially hinder neural function and motor activity. Furthermore, the presence of polycyclic aromatic hydrocarbons (PAHs), a substance found in crude oil that is easily taken up into the cell membrane of invertebrates such as shrimp, has been shown to reduce swimming capacity, impair feeding and increase mortality in euphausiid crustaceans under controlled laboratory studies (Arnberg *et al.* 2017).

LaSpina (2020) found that the euphausiid assemblage declined substantially from 2011-2016 in the GOM (La Spina 2020). This decrease in the euphausiid assemblage could be linked to the decrease in the Sergestidae assemblage as euphausiids are known to be a crucial component of the sergestid diet (Judkins and Fleminger 1972; Donaldson 1975). Nichols (2018) also found that the oplophorid abundance and biomass declined significantly 2011-2017. Both studies were in the same area as this current study, which indicates the significant decline of crustacean micronekton has occurred in the vicinity of the *DWHOS.*

Li *et. al* (2019) studied the potential impact of the *DWHOS* on primary productivity in the northern GOM using satellite remote sensing of chlorophyll-*a* (Chl-*a*) concentrations, which is an indicator for primary productivity in the ocean. This study revealed a multi-year reduction of primary productivity and decreased concentrations of Chl-*a* from 2011 to 2014 compared to pre-spill levels, which were thought to be correlated to long-term effects from the *DWHOS* (Li *et al.* 2019). This decrease in Chl-*a* levels also implies that the food availability for sergestids was also much lower during this time. However, Chl-*a* levels returned to pre-spill levels by 2015, but no recovery in the sergestid assemblage has occurred as of 2018 (the last dataset in this analysis). In addition, a study on zooplankton in the northeastern GOM following the oil spill found that the abundance of zooplankton during the oil spill (in the spring of 2010) was not significantly different from abundances in the following two years (Daly *et al.* 2021). They suggested that the oil spill may have had short-term, local effects on the zooplankton populations that could not be detected with their sampling techniques, but that overall, there were no large adverse effects on the zooplankton community. They suggested that if there was high mortality due to oil, the high fecundity and short generation times of the zooplankton, together with connectivity with other regions, would have enabled them to rapidly return to normal levels. This assumption is supported by the results of a study on zooplankton off the coast of Alabama (Carassou *et al.* 2014). There was a decline in abundance for a short period of time after the *DWHOS* but there was a rapid recovery shortly thereafter, but they also noted that zooplankton tend to have very patchy distributions, and this could have been normal biological variability. This kind of resiliency has not been seen in the micronektonic species such as the sergestids in this study, which showed a significant decrease between 2011 and 2015, with no signs of recovery up to the last sampling series in 2018.

When estimating the mean biomass of sergestid shrimp off Southwestern Taiwan, Wu *et al.* (2010) found a decline from 4207 to 2640 tons from 1997-2008, suggesting that the maximum sustainable yield (MSY) had been surpassed due to overfishing by commercial fisheries. This may be what is happening with the sergestid assemblage in the Gulf of Mexico, due to a presumed (an uncontaminated baseline is not available) decline after the oil spill. Regardless of what the levels were before the oil spill, the >30% decline in the four years after the oil spill, with no evidence of recovery, is greater, and of a longer duration, than what one would expected from "natural" biological variability, and suggests that the Sergestidae population may have fallen below the threshold of ecological resilience (Wu and Hu 2020), thus preventing the populations from rebounding. While both the "*Sergestes*" and "*Sergia*" groups decreased significantly in abundance and biomass, the decline within the larger "*Sergia*" was greater than the smaller "*Sergestes"* possibly due to the inability to maintain sufficient food intake levels necessary to sustain larger-bodied species. Small-bodied species are hypothesized to dominate at lower food supply and higher temperatures while large-bodied species would dominate at lower temperatures and higher food supply (Feniova *et al.* 2013). The impact of the *DWHOS* cannot be fully quantified but it is important to note that understanding the effect on pelagic shrimp such as sergestids is important since they are a major trophic link between deep-water and shallow-water ecosystems (Knap *et al.* 2017).

Conclusion

Understanding anthropogenic events and how they impact deep-sea community is critical to assess the status of oceanic ecosystems. Micronektonic crustaceans such as sergestids make up a substantial amount of the epi- and mesopelagic micronekton biomass in the eastern GOM and support upper trophic levels of the ecosystem (Hopkins *et al.* 1994; Fisher *et al.* 2016). All sergestid species in this study were found to be strong vertical migrators, suggesting that they contribute substantially to the transport of organic matter and may act as a vital trophic link in the GOM. The results of this study showed that there was a significant decline in sergestid abundance and biomass between 2011-2016, with no signs of recovery as recently as August 2018, which may eventually have long-lasting impacts on upper trophic levels. This study also emphasized the importance of separating near-slope and offshore samples for analyses, as the Sergestidae biomass was significantly higher at near-slope stations, likely driven by the "*Sergia*" group which contributed much more to the overall biomass. Considering that no pre-spill data were available, it is imperative to understand normal Sergestidae population variability in the GOM in order to accurately access impacts of anthropogenic events such as the *DWH*OS.

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Appendix 1

Appendix 1: Sergestidae abundance at stations from *Meg Skansi* 7

Sergestidae Near-slope vs. Offshore Abundance Table by Station

Near-slope Station	Abundance(n/m^-3)	Offshore Station	Abundance(n/m^-3)
B001	0.001341	B003	0.003208
B016	0.002464	B061	0.006054
B080	0.003609	B064	0.004954
B162	0.003768	B065	0.001416
B163	0.003018	B078	0.001711
B175	0.003454	B079	0.003820
B184	0.004299	B081	0.002692
B185	0.002171	B082	0.006734
B245	0.003537	B083	0.003143
B246	0.01004	B248	0.005265
B247	0.008922	B249	0.008225
B251	0.02753	B250	0.009334
B252	0.001303	B255	0.006285
B254	0.003881	B286	0.002410
SW-1	0.009453	B287	0.004236
SW-2	0.003030	SE-1	0.000638
		SE-2	0.001092
		SE-3	0.001987
		SE-4	0.001800
		SE-5	0.003066
		SE-6	0.006690
		SW-3	0.002506
		SW-5	0.004334
		SW-6	0.003778
		SW-7	0.001598
		SW-8	0.001018
		SW-9	0.001627
		SW-10	0.000713
		SW-11	0.001388

Near-slope	Offshore
Mean = 1.23 x 10^{-4} m^{-3}	Mean = 1.07 x 10^{-4} m^{-3}
Variance = 7.99 x 10^{-8} m^{-3}	Variance = 6.12 x 10^{-8} m^{-3}