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Nathan A. La Spina Nova Southeastern University

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Thesis of Nathan A. La Spina

Submitted in Partial Fulfillment of the Requirements for the Degree of

Master of Science M.S. Marine Biology

Nova Southeastern University Halmos College of Natural Sciences and Oceanography

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A Temporal Analysis of the Euphausiid Assemblage in the Gulf of Mexico after the *Deepwater Horizon* Oil Spill, with Notes on Seasonal Reproduction

By Nathan Andrew LaSpina

Submitted to the Faculty of Nova Southeastern University Halmos College of Natural Sciences and Oceanography in partial fulfillment of the requirements for the degree of Master of Science with a specialty in:

Marine Biology

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Abstract

A Temporal Analysis of the Euphausiid Assemblage in the Gulf of Mexico after the *Deepwater Horizon* Oil Spill, with Notes on Seasonal Reproduction

This thesis presents the results of the first multi-year study on the euphausiid assemblage in the vicinity of the *Deepwater Horizon* oil spill (DWHOS), covering depths down to 1000 m. There are no data on the euphausiid assemblage from this region prior to the oil spill; therefore, the data in this study were analyzed with respect to year (samples collected in 2011 vs. those collected between 2015 – 2016), and season (May vs. August) to determine if any trends were present. These results presented here show a statistically significant decrease in both abundance and biomass between 2011 and 2015 – 2016, indicating that the assemblage has been declining since 2011, along with a continued decline from May 2016 to May 2017. Seasonal effects were also present, as abundance and biomass were statistically higher in May than in August in both 2011 and 2016. In addition, the percentage of gravid females of the grouped species, *Nematoscelis atlantica/microps*, was also higher in May for both years, but only statistically significant in 2016. This seasonal variability may possibly be linked to food availability as a result of seasonal phytoplankton blooms. The information presented here will act as a reference point for future studies in the Gulf of Mexico (GOM), to aid in understanding how the euphausiid assemblage responds to anthropogenic events.

Key words: Euphausiidae, Pelagic Crustaceans, Seasonality, *Deepwater Horizon* Oil Spill.

Introduction

Euphausiids constitute about 40% of the biomass within the world's oceans and are important to the diets of many higher trophic level consumers (Simard *et al.* 1986; Pillar and Stuart 1988; Kinsey and Hopkins 1994; Dalpadado and Skjoldal 1996; Nicol and Endo 1997; Castellanos and Morales 2009; Kaplan *et al.* 2013). A number of whale species, including blue (*Balaenoptera musculus*), minke (*Balaenoptera acutorostrata*), fin (*Balaenoptera physalus*), humpback (*Megaptera novaeangliae*), Bryde's (*Balaenoptera brydei*), and sei whales (*Balaenoptera borealis*) all rely on euphausiids to sustain themselves (Strickland *et al.* 1970; Schoenherr 1991). Many other animals such as fishes (Robinson 2000; Jayalakshmi *et al.* 2011), seabirds (Deagle *et al.* 2007), seals (Bradshaw *et al.* 2003), squid (Cargnelli *et al.* 1999), and humans harvest euphausiids as a source of food as well (Nicol and Endo 1999). Because euphausiids are so widely distributed and play such a vital role in many regional food webs, a reduction in their numbers could be detrimental to many higher trophic level species.

Of the 86 documented species of euphausiids, 34 can be found in the GOM (Castellanos and Morales 2009; Felder and Camp 2009). Euphausiids are classified as either zooplankton or micronekton, depending on their size and current life history phase. Larval phase individuals, which are in the zooplankton phase of their life, are typically less than five mm in length, while mature adults of many species are considered micronekton (Brinton 1962; Brinton *et al.* 1999). Euphausiids typically live about two to three years in the wild; however, laboratory results suggest that some species of euphausiids that live near Antarctica, such as *Euphausia superba*, can live for 11 years (Einarsson 1945; Mackintosh 1972; Ikeda 1985).

There have been previous studies on the euphausiid assemblage in the GOM, but none that reach the geographical or temporal range of the work presented in this thesis. Gasca *et al*. (2001) completed work on the spatial distribution of these animals within the photic zone, at depths of only $0 - 200$ m, in the southern part of the Gulf, while Kinsey and Hopkins (1994) collected data on the diet of euphausiids, from the surface waters down to 1000 m, during the summer months of 1975 – 1977, at one location in the northeastern Gulf that they referred to as Standard Station (Kinsey and Hopkins 1994; Gasca *et al.* 2001). In 2016, Fine and Frank described the euphausiid assemblage in the northern GOM following the DWHOS, but this study was limited to data collected from April – June of 2011 (Fine 2016; Frank *et al.* 2020). One of their primary finding was that euphausiid abundance and biomass were significantly higher at

slope stations, stations on the landward size of the 1000 m isobath, than offshore stations, stations on the ocean side of the 1000 m isobath, (Figure 1). For this reason, only samples associated with offshore sites were used in the study presented in this thesis.

The location of this study is of particular interest because it is the site of the 2010 *Deepwater Horizon* oil spill (DWHOS). The DWHOS is the largest aquatic oil spill in U.S. history, releasing nearly five million barrels of Louisiana Sweet Crude oil from a leak that occurred at 1500 m depth (Abbriano *et al.* 2011; McNutt *et al.* 2012). The effects of the oil spill on deep-sea crustaceans remain difficult to determine because no baseline data are available for this region prior to the oil spill (Fine 2016; Burdett *et al.* 2017; Nichols 2018). However, the abundance of four fish taxa larvae declined in 2010 compared to the three years before the oil spill, which may have resulted from a detrimental effect of oil and dispersants, although natural inter-annual variability cannot be discounted as the basis of the decline (Rooker *et al.* 2013). Another study examined near-slope mesozooplankton communities, for which pre-spill baseline data were available, and hypothesized that it was highly plausible that the DWHOS was the reason for the initial decline in zooplankton densities, which included euphausiid protozoea (Carassou *et al.* 2014). However, Carassou *et al*. (2014) only examined zooplankton within the top 200 m of near-slope waters off the coast of Louisiana. Regardless of the cause, increased mortality amongst euphausiids may be detrimental to the stability of the local marine ecosystem. The modelling study of Kaplan *et al*. (2013) showed that when euphausiids along the California coast are harvested to 40% of unfished levels, the result would be a reduction in abundance of more than 20% for nearly one-third of all other groups within their food web. The major goal of this thesis was to determine whether there was a temporal change in the assemblage in the vicinity of the *DWHOS,* incorporating data from samples collected from offshore stations, in both May and August of 2011, 2015, 2016, as well as May 2017, from 1000 m to the surface, with consideration given to seasonal variations that may skew the results.

Materials and Methods

Euphausiids were analyzed from samples collected on two cruises onboard the M/V *Meg Skansi* (as part of the ONSAP studies) in 2011 and five cruises onboard the R/V *Point Sur* in 2015 – 2017, conducted by the Deep Pelagic Nekton Dynamics of the GOM (DEEPEND) consortium, both directed by Dr. Tracey Sutton (Table 1). Samples were collected with a $10-m^2$ MOCNESS trawl (Wiebe *et al.* 1985), which entailed deploying five nets to open and close at five discrete depth ranges (Table 2), twice per 24-h period (four to six-hour deployment with each launch), at every station visited. During each trawl, conductivity-temperature-depth equipment (CTD) continuously recorded temperature and salinity (as a function of conductivity), along with the corresponding depth. Net contents were sorted and stored in a 10% formalinseawater mixture. Many more stations were sampled on the *Meg Skansi* cruises in 2011 (n=46) than on the DEEPEND cruises ($n=23$) between 2015 – 2017. Since all stations sampled on the DEEPEND cruises (DP01 – DP05) were offshore stations, and because the offshore assemblage was statistically different from the near-slope assemblage (Fine 2016; Frank *et al.* 2020), only offshore stations were included in this analysis (Figure 1). MS7 and MS8 were both 3-month long cruises, so only data collected in May on the MS7 cruise and August on the MS8 cruise were used to overlap with the two week-long DEEPEND sampling efforts. Samples were labelled with the cruise name, sample location identification number, along with the month, year, depth, and time of day they were collected on. Samples were then brought back to the Deep-Sea Biology Laboratory at Nova Southeastern University and euphausiids were identified to the lowest taxonomic level possible using the comprehensive key, Baker et al. (1990). After identification, total body lengths were measured using a digital caliper (Fisher Scientific digital caliper, Model No. FB70250) and the weight of each species group was measured to the nearest 0.01g using a digital balance (P-114 balance, Denver Instruments). Processed samples were stored in 50% ethanol and kept for future study.

Table 1. – Cruise name and month of data collection at sea. MS7 and MS8 cruises each lasted 72 days in 2011 while DP01 – DP05 each took no more than two weeks to complete.

***Only samples from May and August from the M/V** *Meg Skansi* **cruises (MS7-8) were used. See justification above.**

Table 2. – Net number and depth range of MOCNESS sampling protocol for every cruise. *Only nets 5 – 3 were used (see justification below).

Some species were grouped together due to the apparent discrepancies between observed characteristics of certain individual specimens and species descriptions (Fine 2016). As described by Fine (2016), the key characteristic that distinguishes *Nematoscelis atlantica* from *Nematoscelis microps* are the 5 – 6 setae on the propodus of the first thoracic; *N. microps* has 8 – 9 setae (Baker *et al.* 1990). Because more than 90% of all specimens identified possessed seven setae, those individuals that possessed between $5 - 9$ setae were grouped together as *Nematoscelis atlantica/microps*. *Thysanopoda obtusifrons* and *Thysanopoda aequalis* were also grouped together due to the often-indistinguishable level of antennular lappet coverage on the antennular peduncle. Lastly, the distinguishing characteristic between *Thysanopoda acutifrons* and *Thysanopoda orientalis* was the morphology of the reproductive organ in sexually mature adult males (Baker *et al.* 1990), and many of the individuals used in this study were immature males or possibly mature females. Therefore, these two species were also grouped together as *Thysanopoda acutifrons/orientalis*, as per Fine (2016).

Statistical Analysis

Total abundance and biomass, per cubic meter of seawater filtered from each station, were analyzed with respect to the month and year of sample collections. May and August samples from each year were compared to determine if there were seasonal differences in the assemblage. Data from 2015 were only used in figures and for descriptive statistics on seasonal differences due to a sample size considered too low for reliable statistical analysis (McDonald 2009). May 2017 was also left out of the analysis on seasonality and only used in figures and for descriptive statistics as well, as no cruise was conducted in August 2017. Due to seasonal differences in abundance, yearly temporal comparisons were only completed for years in which samples were collected in both May and August. Temporal analyses first compared 2011, or ONSAP cruises, with DEEPEND years 2015 and 2016 where both May and August samples were available. May 2017 was compared with May 2016 to assess any possible changes to the assemblage in the final year of this study. The work presented here was restricted to the top 1000 m of the water column due to lack of a sufficient number of viable nets (nets with usable flow data) from $1000 - 1200$ m and $1200 - 1500$ m (See Appendix III.) and because only one euphausiid species, *Bentheuphausia amblyops,* had a daytime depth range with a population maximum below 1000 m. By restricting the analyses to nets $3 - 5$ the number of usable stations

increased substantially. For example, restricting the depth ranges to $0 - 1000$ m, rather than $0 -$ 1500 m, increased the number of viable stations from n=3 to n=6 for the May 2011 *Meg Skansi* cruise dataset. This allowed for the inclusion of the May 2011 data to the statistical analyses as the minimum sample size threshold is 5 (McDonald 2009). Statistics were performed using the computer software program JMP. Testing for normality is unreliable for very small sample sizes (Öztuna *et al.* 2006), therefore, non-parametric tests, which do not assume a normal distribution, were used to analyze the results presented here: the Wilcoxon rank sum test, the Kruskal-Wallis test and the post hoc multiple comparisons test (Everitt and Skrondal 2010). The post hoc multiple comparisons test was conducted using the Benjamini-Hochberg procedure to decrease the rate of a false discovery.

Figure 1. – Bathymetric diagram of the stations that were sampled within the GOM, with red stars indicating stations used in this study. The yellow star indicates the location of the *Deepwater Horizon* **oil platform [Adapted from (French-McCay** *et al.* **2011)].**

Results

Seasonal effects on the assemblage abundance, biomass, and reproduction

Data collected from 22,224 specimens were examined and only the most abundant species, defined as those species that made up 99% of the total abundance in this study (Fine 2016), were used for statistical analyses. A Kruskal-Wallis test indicated that significant differences were present between the seasons, in terms of both abundance ($χ2(3) = 24.785$, p < 0.001) and biomass (γ 2(3) = 25.246, p < 0.001). A post hoc multiple comparisons test showed that abundance was significantly higher in May than in August for 2011 ($Z = -2.248$, $p = 0.024$) and 2016 ($Z = -2.388$, $p = 0.017$). Biomass was also statistically higher in May for both 2011 (Z) $= -2.396$, $p = 0.017$) and 2016 (Z = -2.388 , $p = 0.017$). The sample size for May and August 2015 samples were too small for statistical analysis, but as with the other years, there were more euphausiids present in May than in August (Figure 2 & 3).

A total of 1,085 females bearing eggs (henceforth called gravid females) were identified, and of these, 95% were *Nematoscelis atlantica/microps*. The remaining 5% were identified as *Euphausia gibboides*, *Nematoscelis tenella*, *Stylocheiron abbreviatum, Stylocheiron carinatum* and *Stylocheiron maximum*. *Nematoscelis tenella* gravid females (n=36) were all caught in August 2011. Counts of other gravid females, identified as either *Euphausia gibboides*, *Stylocheiron abbreviatum, Stylocheiron carinatum* and *Stylocheiron maximum*, ranged between 0 – 3 individuals each season. Such low numbers could not be included in the statistical analysis of the seasonality of reproduction for each species considered gravid; the analysis was therefore limited to *Nematoscelis atlantica/microps*. Individual specimens equal to, or larger than, the length of the smallest gravid *Nematoscelis atlantica/microps* female (10.44 mm) were deemed sexually mature. Results showed significant differences between May and August were present (Kruskal-Wallis test, γ 2(3) = 13.393, p = 0.004). The percentage of the sample population found to be gravid in May 2011 was higher than the levels in August 2011, 11.3% and 8.2%, respectively, however the post hoc analysis was inconclusive $(Z = -1.918, p = 0.055)$. There was, however, a statistically higher proportion of gravid females in May than August in 2016, 20.6% vs. 11.1%, respectively, $(Z = -2.270, p = 0.023, Figure 4)$. While the sample size from May and August 2015 were too small for statistical analysis, there were substantially more gravid females in May than in August, with both the maximum and minimum percentages found in this study occurring in 2015 (32% and 2.5%, in May and August, respectively).

Figure 2. – Seasonal comparisons of mean assemblage abundance. Bars are the standard deviation of the mean. Gray plots were excluded due to low sample size while the May 2017 plot was excluded due to a lack of August 2017 data. Matching colors indicate data that were compared, and a black star signifies a statistically higher standardized abundance in May of 2011 and 2016.

Figure 3. – Seasonal comparisons of mean assemblage biomass. Bars are the standard deviation of the mean. Gray plots were excluded due to low sample size while the May 2017 plot was excluded due to a lack of August 2017 data. Matching colors indicate data that were compared, and a black star signifies a statistically higher standardized biomass in May of 2011 and 2016.

Figure 4. – Mean percentages of the *N. atlantica/microps* **sample population that was gravid. Bars are the standard deviation of the mean. Matching colors indicate the data were compared. Gray plots were excluded due to low sample size. A black star signifies a statistically significant higher percentage of gravid females in May than August 2016.**

Temporal effects on the assemblage abundance, biomass, and mean total length

Results from a Kruskal-Wallis test on the most abundant species showed differences in the assemblage parameters were present between the different years in terms of abundance $(\chi^2)^2$ $= 18.724$, p < 0.001) and biomass (χ 2(2) = 18.962, p < 0.001). The post hoc analysis revealed a statistically significant decline in the mean abundance (69.1%, $Z = -2.585$, $p = 0.010$) and biomass (57.0%, $Z = -2.350$, $p = 0.019$), between 2011 to 2015. In addition, mean abundance in 2016 was 75.6% lower than the mean abundance in 2011 ($Z = -4.060$, $p < 0.001$) and mean biomass was 75.3% lower ($Z = -4.060$, $p < 0.001$). No significant difference was found between 2015 and 2016 for abundance $(Z = 0.0, p = 1.0)$ or biomass $(Z = -1.479, p < 0.139)$ (Figure 5 and 6). May 2016 and May 2017 were also compared, and the Wilcoxon rank sum test indicated the assemblage abundance decline of 28.1% was statistically significantly (γ 2(1) = 5.633, p = 0.018); biomass also declined by 14.7%, but this change was not statistically significant (γ 2(2) = 1.20, p $= 0.273$).

With no significant difference between 2015 and 2016, the two DEEPEND cruises were then combined and treated as a single dataset and compared with the ONSAP data for individual species comparisons. Every species defined as abundant experienced a decline between the ONSAP and DEEPEND cruises and, for 15 of these species, this decline was statistically significant in terms of at least one parameter (Appendix I.). *Thysanopoda tricuspidata* was the only abundant species without significant changes, in abundance (Wilcoxon, $\chi(1) = 0.511$, p = 0.475) or biomass (Wilcoxon, χ 2(1) = 0.2269, p = 0.634), while also remaining within the top 99% most abundant species throughout the ONSAP and DEEPEND cruises. *Thysanopoda tricuspidata* was considered one of the nine most abundant taxa, meaning it was one of the few species to be caught in abundance during every cruise. The most abundant species of this study, *Nematoscelis atlantica/microps* accounted for nearly 47% of the entire assemblage abundance in 2011 and 37% in the $2015 - 2016$ dataset, being four times more abundant than the $2nd$ most abundant species, *Euphausia gibboides*. Like most species, *Nematoscelis atlantica/microps* significantly decreased in abundance between 2011 to $2015 - 2016$, by 77.3% (Wilcoxon, χ 2(1) $= 16.393$, p < 0.001) and biomass by 84.4% (Wilcoxon, χ 2(1) = 15.756, p < 0.001), (Table 3). Assemblage mean total length (MTL) also declined significantly between ONSAP to DEEPEND (Wilcoxon, γ 2(1) = 18.842, p < 0.001) and changes between each year of sampling were only examined for the most abundant taxa as they were the few species caught each year. All the most abundant taxa showed the same trend: a decrease in MTL between 2011 – 2015, followed by an increase between 2015 – 2016 samples (Figure 8). A post hoc analysis showed that for seven out of nine species, this decrease in MTL between 2011 – 2015 was highly significant, while significant increases in MTL between 2015 – 2016 were apparent for six of the nine most abundant taxa (Appendix II.). *Nematobrachion sexspinosum* was the only species that did not show any significant changes in MTL (post hoc, $Z = -0.907$, $p = 0.364$, $2011 - 2015$; $Z = 1.327$, $p = 0.185$, 2015 – 2016).

Figure 5. – Temporal comparisons of mean assemblage abundance. Bars are the standard deviation of the mean. There was no statistically significant difference between 2015 and 2016. A black star signifies a statistically higher standardized abundance between 2011 and both 2015 and 2016.

Figure 6. – Temporal comparisons of mean assemblage biomass. Bars are the standard deviation of the mean. There was no statistically significant difference between 2015 and 2016. A black star signifies a statistically higher standardized biomass between 2011 and both 2015 and 2016.

Figure 7. – Species that constituted 99% of the assemblage abundance. Bars are the standard deviation of the mean. Black stars indicate a species that was classified as abundant only during the ONSAP cruises. A white star indicates a species was classified as abundant only during the DEEPEND cruises (2015 & 2016).

Table 3. – Mean abundance and biomass, by species. $(\sigma \overline{x})$ signifies the standard deviation. **Data collected from 2015 and 2016 regarded as a single DEEPEND dataset (See justification above).**

Figure 8. – Mean total length for most abundant species. Significant differences between both 2011 – 2015, and 2015 – 2016, are signified with a red star. Species with no significant differences between 2011 – 2015, but a significant increase from 2015 – 2016 are represented with a black star, while species that experienced a significant decrease from 2011 – 2015 and no significant change in length between 2015 – 2016 are signified with a white star. Bars are the standard deviation of the mean.

Discussion

Seasonal variability and reproduction

The results presented here indicate that there is a seasonal effect on the abundance and biomass of the euphausiid assemblage, with significantly higher values in the spring for each of the years analyzed. Such differences may be linked to phytoplankton production and food availability (Willason and Cox 1987). Phytoplankton blooms in the Gulf are driven by seasonal, nutrient rich, freshwater discharge and reach peak abundance between December to February (Kinsey and Hopkins 1994; Li *et al.* 2019), after which their numbers diminish by the end of summer (Müller‐Karger *et al.* 1991; Dagg 1995; Li *et al.* 2019). Phytoplankton, as well as copepods which come to graze on the phytoplankton, are essential components to the euphausiid diet and euphausiid mortality may increase as food becomes less available (Kinsey and Hopkins 1994; Dagg 1995; Gislason and Astthorsson 1995). As May is closer to the peak of the bloom than August, the higher abundance in May could be correlated with this bloom.

In terms of seasonal reproduction, *Nematoscelis atlantica/microps* was the only species with enough data for an analysis and the results here, along with the work completed by Fine (2016), indicates this species prefers to spawn in the spring, possibly in response to the springtime bloom. Euphausiid reproduction is complicated because it varies by species, and even among members of the same species, so it is difficult to make predictions about how often a species reproduces in a region where little data are available (Mauchline and Fisher 1969; Siegel 2000). For example, *Thysanopoda acutifrons* are only known to breed in May within the North Atlantic, while for *Meganyctiphanes norvegica*, breeding varies with latitude in this region (Einarsson 1945). These differences in breeding preferences may due to the timing, duration and magnitude of phytoplankton blooms around the world, events which have been observed to coincide with euphausiid spawning times (Pillar and Stuart 1988; Dalpadado and Skjoldal 1996; Nicol and Endo 1997). All euphausiids within the GOM are either tropical or subtropical species and may reproduce seasonally as peak phytoplankton production in the GOM occurs earlier in the year. No conclusions regarding the preferred spawning time of the remaining 17 species could be made due to either low numbers or a complete lack of gravid females.

Temporal changes in the assemblage

Species were considered abundant if they constituted 99% of the total assemblage abundance and rare if they were in the remaining 1% (Fine 2016). In May 2011 alone (from the MS7 samples), of the 27 species collected over the course of this study, 13 species were considered abundant while 14 were either absent from this sample period (meaning that they were present in the subsequent samples) or considered rare. Fine (2016), which included all three months of MS7 sample collections, listed 16 species as abundant and 15 rare. *Euphausia mutica*, *Stylocheiron elongatum* and *Stylocheiron maximum*, considered abundant in Fine (2016), were rare species in May 2011 from the work presented here. This apparent disparity is the result of our slightly divergent methodologies for selecting data for analyses. The euphausiid individuals collected for Fine (2016) came from samples collected between April – June 2011 with samples depths ranging from $0 - 1500$ m, whereas the analysis presented here used data solely from May of the MS7 cruise and depths of $0 - 1000$ m (see justification in methods).

Although significant declines in the assemblage abundance and biomass occurred between 2011, one year after the oil spill, and 2015 – 2016, five to six years after the oil spill, they cannot be directly attributed to the DWHOS. Since there were no pre-spill data on the assemblage available, it is difficult to assess whether the decline is part of normal biological variability or is a direct result of the spill. It should be noted, however, that large scale die-offs of zooplankton, which included larval stage euphausiids, occurred following the 1979 Ixtoc-1 oil spill, which released 3.1 million barrels of oil into the shelf waters of the southern GOM. After this spill, there was a reduction in biomass by a factor of four, relative to pre-spill levels (Próo *et al.* 1986). Some species of euphausiids have displayed limited swimming capacity, impaired feeding ability and increased mortality due to prolonged exposure to dissolved hydrocarbons under laboratory conditions (Arnberg *et al.* 2017; Knap *et al.* 2017). Knap *et al.* (2017) also showed that, of all the crustaceans tested, euphausiids were among the most sensitive to the toxicity of the hydrocarbon used in that study. Although it's uncertain how long the oil from the DWHOS was in contact with the euphausiid assemblage in the GOM, computer modelling results indicated it could have taken at least 100 days before more than 50% of the oil exited the model's domain extent (Weisberg *et al.* 2011). Laboratory results showed it only took 24-hours of exposure time to reach a lethal concentration of the hydrocarbon 1-methylnaphthalene and prompt mortality in several euphausiid species (Knap *et al.* 2017).

In addition, copepods and phytoplankton, common constituents of the euphausiid diet, may have also experienced a decline in their abundance from the effects of the DWHOS. In 2012, 2 years after the spill, laboratory results on samples taken from near-shore GOM locations indicated that mesozooplankton (mostly comprised of copepods) mortality peaked at 96% and was found to increase with oil concentration (Almeda *et al.* 2013). In addition, satellite data from 2001 to 2017 on Chlorophyll-*a* (Chl-*a*) concentration in the GOM, a proxy for the level of primary productivity, noted a substantial decrease in 2011 which remained low until 2014, relative to pre-spill years. Chl-*a* then returned to pre-spill values in 2015 (Li *et al.* 2019). This appears to coincide with the change in MTL of the most abundant taxa observed in this study; a significant decline occurred between 2011 to 2015 and was followed by an increase in MTL which, in some species, exceeded 2011 values. It may be possible that, as their food source became scarcer, the carrying capacity of that region could no longer support larger individuals, but once phytoplankton density values increased, larger individuals could once again be supported.

Although MTL increased, both assemblage abundance and biomass declined through 2016 despite a renewal of a major source of food. This continued downward trend between May 2016 and May 2017 may relate to a maximum sustainable yield (MSY). This is a term used in fisheries science and is the theorized limit of exploitation for a commercially viable population

of fish. Once this limit is exceeded, the number of reproductive individuals in the population is not high enough to replace the individuals that have been removed, meaning that the population cannot sustain itself, and the associated fishery then crashes. The Orange Roughy (*Hoplostethus atlanticus*) is a commercially harvested deep-sea fish that is vulnerable to overexploitation, inpart due to its low fecundity, a common trait among many deep-sea species (Koslow *et al.* 2000; Lack *et al.* 2003). Due to its high vulnerability, for *Hoplostethus atlanticus* the MSY is removable of 30% of the biomass; beyond this point the assemblage population is no longer be considered sustainable. Given that the euphausiid assemblage declined by nearly 76% between 2011 and 2016, and continued to decline into 2017, it may too have reached a point in its biomass levels where the return to a more stable assemblage population is uncertain. All euphausiids within the GOM are tropical and sub-tropical species, which means they have relatively low fecundity, or egg count, especially when compared to the Antarctic euphausiid species, *Euphausia superba*, which possess between 310 – 800 eggs per female (Mauchline and Fisher 1969; Mauchline 1980; Kinsey and Hopkins 1994). Estimates for some species found in the GOM rarely exceed 100 eggs per female (Roger 1976; Mauchline 1980). Koslow *et al*. (2000) also surmises low fecundity may dampen the resiliency of a species. For example, *Stylocheiron carinatum* and *Stylocheiron longicorne* experienced significant declines between 2011 and 2015, so much so that *Stylocheiron longicorne* was rarely caught in DEEPEND samples, while *Stylocheiron carinatum* was never observed again after May 2011. Both species of this genus are estimated to have no more than 16 eggs per female (Roger 1976). In contrast, *Thysanopoda tricuspidata*, a species with similar abundance levels as the two *Stylocheiron* species in 2011, did not experience a statistically significant decline in abundance or biomass and, and this species carried hundreds of eggs. Euphausiid species with higher fecundity may be more resilient to significant reductions in their abundance than those with lower fecundity. Therefore, the effects of intrinsically low fecundity, an intermittent lack of food and likely exposure to hydrocarbon compounds in the water column, may all be important factors to consider when attempting to determine the causes of the decline observed in the euphausiid assemblage of the northern GOM, following the DWHOS.

The full consequences of this decline to the ecology of the Gulf are unknown; however, analogies may be drawn from a computer model that simulated the over exploitation of euphausiids off the coast of California (Kaplan *et al.* 2013). Their results indicated that

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predators, specifically various species of fish and whales, experienced declines of near 20%. In the GOM, a significant decline occurred amongst the myctophids and gonostomatids (Sutton *et al.* in review), which specialize on krill (Hopkins *et al.* 1996) and would likely experience significant impacts from the decline in the euphausiids. Other species which rely on euphausiids as a food source may have also experienced significant declines, but more study is needed.

Conclusions

The results from this study on the euphausiid assemblage in the northern GOM revealed a significant reduction in abundance and biomass between 2011 to $2015 - 2016$, along with a continuation of this decline into May 2017. Although these findings could not be directly attributed to the DWHOS due to a lack of information prior to the spill, the data collected for this thesis did give insight into how the assemblage fluctuated years after a major oil spill. The statistically significant decline in abundance between May 2016 to May 2017 suggests that the euphausiid assemblage of the northern GOM may have been reduced to such an extent that a rise in their numbers may take many years. Seasonality, particularly as it relates to food availability, was also identified as an important factor to include in any temporal analysis on the euphausiid assemblage. It likely affects the reproductive cycle of many euphausiid species, including the most abundant species in this study, *Nematoscelis atlantica/microps*. These results presented here add some empirical support to the hypothesis that the initial change in the euphausiid assemblage between $2011 - 2015$ was due to an acute stressor such as an oil spill, rather than normal temporal variability in the assemblage.

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Appendices:

Appendix I.

Test statistic (χ2), DF = 1, P-value and percent (%) decline between ONSAP – DEEPEND (2015 & 2016).

Appendix II.

2011 – 2015 2015 – 2016 Species Z-score P-value Z-score P-value *Euphausia gibboides* -5.824 < 0.001 4.186 < 0.001 *Nematobrachion boopis* 1 2.353 0.019 3.176 0.002 *Nematobrachion flexipes* \vert -7.232 \vert < 0.001 | 1.931 | 0.053 *Nematobrachion sexspinosum* -0.907 0.364 1.327 0.185 *Nematoscelis atlantica/microps* \vert -8.987 \vert < 0.001 \vert 5.293 \vert < 0.001 *Stylocheiron abbreviatum* -6.501 < 0.001 2.434 0.015 *Thysanopoda acutifrons/orientalis* | -1.920 | 0.055 | 2.710 | 0.007 *Thysanopoda aequalis/obtusifrons* -8.434 < 0.001 3.435 0.001 *Thysanopoda tricuspidata* $\begin{array}{|l} \hline \end{array}$ -3.081 0.002 1.120 0.263

Test statistic (Z) and P-value of change in MTL of most abundant taxa between 2011 – 2015 and 2015 – 2016. *Results with P-values of 0.05 were inconclusive.

Appendix III.

Sample data from ONSAP (2011) and DEEPEND (2015 – 2017) cruises in the Gulf of Mexico

*****Abbreviations: Cycle = Time of day (Day = D, Night = N); Water type (Common water = CW)

