Journal of Sea Research 199 (2024) 102501

Contents lists available at ScienceDirect

# Journal of Sea Research

journal homepage: www.elsevier.com/locate/seares

# Dynamic oceanographic influences on zooplankton communities over the northern Gulf of Mexico continental shelf

Hui Liu [a,*], Jillian Gilmartin [a], Michelle Zapp Sluis [a], Toru Kobari [b], Jay Rooker [a,c], Hongsheng Bi [d], Antonietta Quigg [a]

[a] Department of Marine Biology, Texas A&M University at Galveston, Galveston, TX, USA
[b] Aquatic Sciences, Faculty of Fisheries, Kagoshima University, Kagoshima, Japan
[c] Department of Ecology and Conservation Biology, Texas A&M University, College Station, TX, USA
[d] University of Maryland Center for Environmental Science, Solomons, MD, USA

ARTICLE INFO

*Keywords:*
Zooplankton
Oceanographic processes
Gulf of Mexico
Loop current
Climate change

ABSTRACT

Dynamic influences of ocean processes on distribution, abundance, and diversity of zooplankton communities were studied over the continental shelf in the northern Gulf of Mexico (GoM) from 2015 to 2017. Zooplankton sampling was conducted on four summer cruises in the northcentral GoM. Sampling was designed in waters potentially influenced by the Loop Current (LC) and/or Mississippi River discharge to assess the impacts of these two mesoscale features on the abundance and diversity of zooplankton. During the three-year study, the LC displayed distinct spatial-temporal variations in penetration and occurrence in the northern GoM. Environmental conditions (i.e., sea surface temperature, salinity, and dissolved oxygen) varied between months and years sampled, and were significantly different among cruises (ANOVA, $p < 0.001$). The majority of zooplankton consisted of calanoid copepods (65% ± 7.2%, mean ± SD), while non-copepod taxa were primarily chaetognaths, polychaetes, tunicates, and ostracods (23 ± 9.2%). Species abundance and diversity of zooplankton were significantly correlated with sea surface temperature, salinity, and dissolved oxygen ($p < 0.05$). Canonical correspondence analysis displayed significant associations between mesoscale features and dominant zooplankton groups among cruises and by taxa (Monte Carlo Permutation Test, $p < 0.001$). In addition, non-metric multidimensional scaling indicated that zooplankton assemblages were distinct, likely caused by Mississippi River plumes during the study period. As one of the few efforts to examine zooplankton dynamics at a low taxon level over the GoM continental shelf regarding the impact of mesoscale features, this study revealed seasonal (i.e. summer) and spatial patterns in distribution, abundance, and diversity of zooplankton communities subjected to the dynamic physicochemical conditions in the northern GoM, which will continue in a changing climate.

## 1. Introduction

The Gulf of Mexico (GoM) is ecologically productive and economically important, providing the nation critical ecosystem services (Fodrie and Heck Jr, 2011) and lucrative fisheries (Adams et al., 2004; Liu et al., 2017a). Physically, the GoM is highly dynamic and primarily driven by a variety of hydrographic processes. The Loop Current (hereafter LC) and Mississippi River discharge are major physical processes affecting spatial-temporal patterns in water properties, phytoplankton, zooplankton, and ichthyoplankton communities in the GoM (Wormuth et al., 2000; Liu and Dagg, 2003; Coleman et al., 2004; Williams et al., 2015). The LC associated cold and warm core eddies are common mesoscale features that are often present between 25°N and 27°N and 86°W and 88°W in the GoM (Lindo-Atichati et al., 2012). When the LC penetrates farther north, offshore water masses, along with the residing planktonic organisms, are transported into the northern and often western GoM (Biggs, 1992; Dorado et al., 2012; Williams et al., 2015; Gilmartin et al., 2020). In addition, the Mississippi River discharge is another major contributor shaping the biophysical characteristics of the northern GoM ecosystem (Dagg and Breed, 2003; Quigg et al., 2011). The nutrient rich freshwater discharge triggers phytoplankton blooms and subsequent shifts in the zooplankton community (Lohrenz et al.,

* Corresponding author.
*E-mail address:* liuh@tamug.edu (H. Liu).

https://doi.org/10.1016/j.seares.2024.102501
Received 22 March 2024; Received in revised form 18 April 2024; Accepted 21 April 2024
Available online 23 April 2024

2008; Quigg et al., 2011; Li and Liu, 2022). Therefore, interacting regions between the LC front and the Mississippi River plume provide optimal habitats for various marine organisms, which influence the community structure of phytoplankton, zooplankton, and eventually upper trophic level organisms.

One central issue in oceanography is to understand physicochemical and biological processes that regulate the dynamics and distribution of marine living resources in the ocean. Owing to their sheer abundance and vital ecological roles, zooplankton are critical to the function of marine ecosystems and widely considered as sentinels for changing ocean conditions in response to natural and anthropogenic disturbances (Liu et al., 2015; Liu et al., 2021). Considering that mesoscale features, such as eddies, retain planktonic organisms from the origin waters as they meander (Biggs, 1992), it is noteworthy to study the presence and extent of the LC and eddies associated with this feature interacting with zooplankton distribution, abundance, and diversity in this highly dynamic ecosystem. Moreover, biophysical interactions that affect distribution, abundance, and species composition of zooplankton are highly informative to trophodynamics and fisheries production in the ocean. For example, frontal zones of eddies and mesoscale features induced by the LC are often associated with increased zooplankton, ichthyoplankton, and nekton abundance (Williams et al., 2015; Zimmerman and Biggs, 1999; Rooker et al., 2012, 2013; Cornic and Rooker, 2021). Additionally, potential aggregations of plankton that occur along frontal boundaries supply prey items to higher trophic levels and influence the distribution and abundance of predators, including gelatinous organisms (McClatchie et al., 2012; Greer et al., 2018), seabirds (Schneider, 1990), larval fishes (Cornic and Rooker, 2018; Meinert et al., 2020), teleosts including billfishes and tunas (Teo and Block, 2010), sea turtles (Aleksa et al., 2018), and marine mammals (Davis et al., 2002; Naganobu et al., 2006).

The importance of dynamic ocean conditions to zooplankton has been widely recognized within scientific communities (Keister et al., 2009; Batchelder et al., 2013; Kürten et al., 2019). In general, zooplankton in the northern GoM consist of assorted assemblages of copepods, chaetognaths, larvaceans, jellyfishes, and various meroplanktonic larvae (Checkley Jr et al., 1992; Hopkins, 1982; Ortner et al., 1989; Gilmartin et al., 2020; Liu et al., 2021; Li and Liu, 2022). A growing body of literature has advanced the understanding of zooplankton dynamics in relation to changing environmental conditions, such as hypoxia (Elliott et al., 2012; Roman et al., 2012), exposure to crude oil (Carassou et al., 2014; Almeda et al., 2013), mesoscale oceanographic processes (Liu and Dagg, 2003; Dorado et al., 2012; Gilmartin et al., 2020), and jellyfish bloom dynamics (Li and Liu, 2022). While research has highlighted the underlying physical impact of the LC on nutrients, plankton, and primary productivity in the GoM (Biggs, 1992; Hamilton et al., 1999; Lohrenz et al., 2008; Quigg et al., 2011), the current understanding of the LC and Mississippi River discharge induced environmental variations to zooplankton communities in the GoM remains limited (e.g., Biggs and Ressler, 2001; Färber Lorda et al., 2019; Hopkins, 1982) relative to other large marine ecosystems in U.S. waters of the Atlantic Ocean and Pacific Ocean.

Here, we expand the recent effort on chaetognaths (Gilmartin et al., 2020) and jellyfish dynamics (Li and Liu, 2022) to zooplankton communities and investigate zooplankton response to the ocean conditions in the northern GoM. A hypothesis of this study is that the LC along with its associated mesoscale features (eddies) and the Mississippi River plume jointly influence zooplankton abundance and community structure in the northern GoM, leading to changes in the occurrence and dominance of coastal versus oceanic species that are attributed to the Mississippi River discharge and the LC, respectively. The present study is designed to contribute to an improved understanding of the environmental conditions and physical processes that regulate zooplankton dynamics and explore how these changes may potentially influence ecosystem functions of the northern GoM in the light of changing climate.

## 2. Methods

### 2.1. Sampling

Sampling was carried out in an area to cover a wide range of zooplankton communities responding to oceanographic conditions within potential domain of the LC and Mississippi River discharge over the northcentral GoM continental shelf (Fig. 1). Zooplankton were collected using a 50-cm diameter, 202 μm mesh plankton net with a digital flowmeter (SEA-GEAR MF-315) mounted in the center of the net frame that was towed vertically through the upper 100 m of the water column during daylight hours. Upon retrieval zooplankton samples were preserved in 5% buffered formaldehyde/seawater solution for further processing in the laboratory.

Zooplankton sampling was conducted aboard the *R/V Blazing Seven* in July 2015, June 2016 and July 2016, and aboard the *R/V Pelican* in July 2017. Sea surface temperature (SST), salinity and dissolved oxygen (DO) were recorded at each collection site using a YSI model 650 MDS attached to 6920 V2 Multiparameter Water Quality Sonde. One net tow and associated environmental measurements were conducted at each site along two transect lines (northern transect near Mississippi River discharge and southern transect close to the LC domain) from approximately 26.5 to 28.0°N latitude and 88.0 to 94.0°W longitude (Fig. 1).

In addition to data collection aboard each vessel, sea surface height (SSH) anomaly was extracted from the Copernicus Marine Environmental Monitoring Service (https://marine.copernicus.eu/) to determine the location of LC fronts and associated eddies during the time frame in which samples were collected (Fig. 2). Once the LC and associated eddies were identified, the nearest distance from each sampling site to the edge of the frontal boundary was calculated based on the 20 cm SSH contour using the Spatial Analyst toolbox in ArcGIS. Then, the calculated distance to the LC front was used to separate zooplankton samples within an interval of 20 nm from the frontal region (e.g., 0–20 nm, 20–40 nm, 40–60 nm etc.).

Zooplankton samples were processed according to the protocol in Liu et al. (2017b) by rinsing the samples with freshwater, then pouring the sample into a graduated beaker to determine the settled volume. Samples were diluted to between 5 and 10 times of the settled volume and sub-sampled with a 5- or 10-ml piston pipette. Subsamples representing 10–40% of total samples were sorted and enumerated to species or genera where possible (Boltovskoy et al., 1999; Johnson and Allen, 2012) under a motorized stereomicroscope (Leica M205C). Identifying sub-adults of copepods was challenging, thus specimens were simply enumerated and grouped to genera or higher taxonomic levels when possible. Zooplankton abundance was calculated as individuals per $m^{-3}$ (ind. $m^{-3}$) and expressed as the mean value and standard deviation (mean ± SD) were provided.

### 2.2. Data analysis

Principal component analysis (PCA) was conducted to classify the major environmental factors driving the ocean conditions on each cruise. Since all cruises were conducted in the same region during the summer, PCA was analyzed by site locations separated by their position either in the northern transect or southern transect. Linear discriminate analysis (LDA) was performed to identify differences in PCA ordinations for each cruise using the *ade4* package in R and the *randtest* package was used to determine statistical significance of the differences in LDA between transects using Monte-Carlo permutation tests (Dray and Dufour, 2007).

Shannon diversity index ($H'$) was calculated to represent the zooplankton diversity of each sample using the following equation:

$$H' = \sum_{i=1}^{s} p_i ln p_i$$

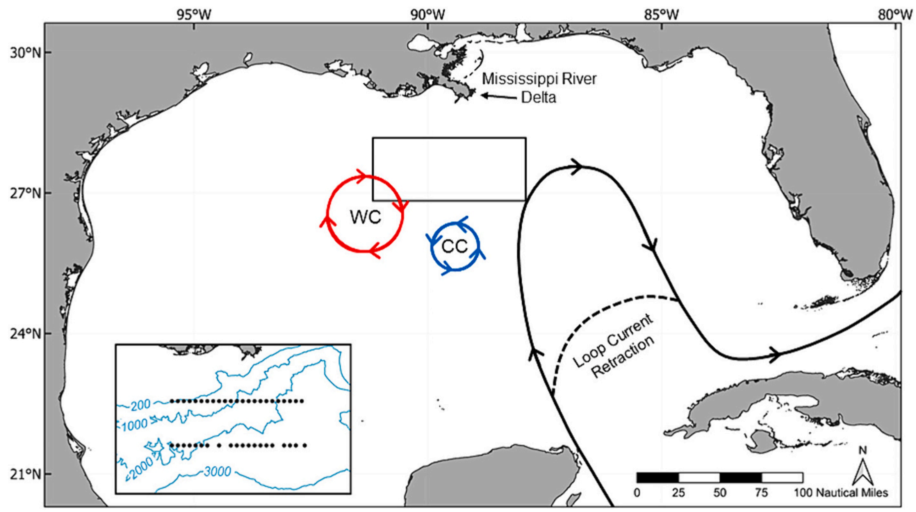


**Fig. 1.** Transects and stations of zooplankton sampling in the northern Gulf of Mexico. WC: warm core eddy; CC: cold core eddy.

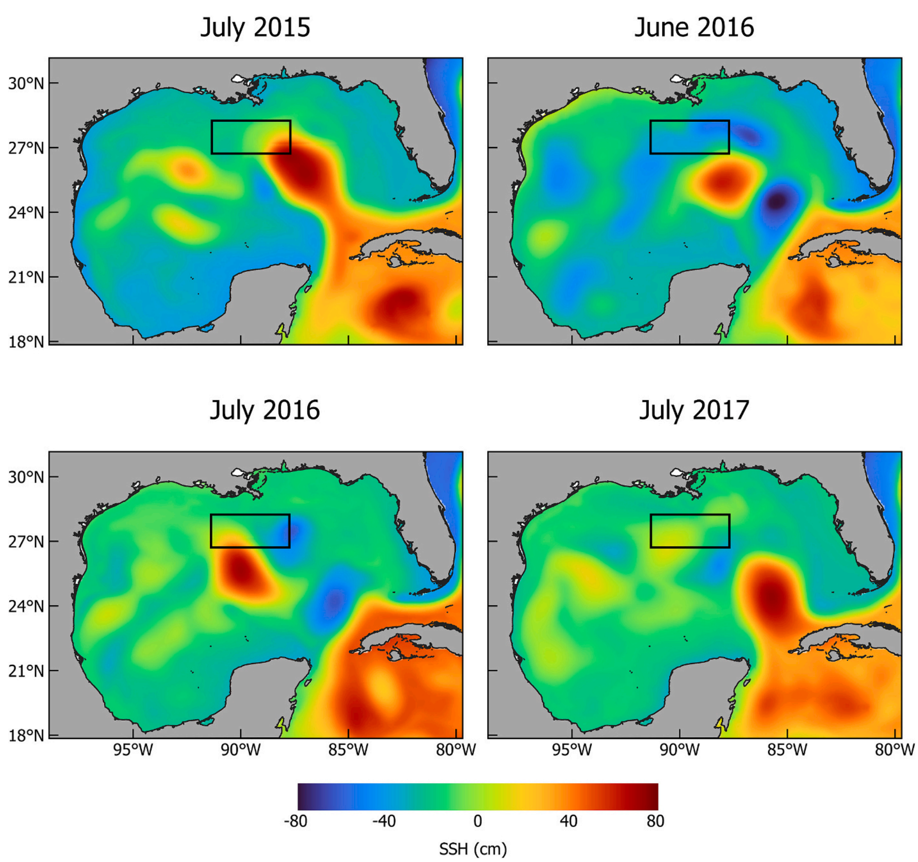


**Fig. 2.** Locations of the Loop Current represented as Sea Surface Height (SSH) during the study period in the northern Gulf of Mexico. Higher SSH represents the warm cores and anticyclonic eddies. Low SSH indicates the cold cores and cyclonic eddies. Black boxes indicate the region for each sampling cruise performed during the study period.

where $p$ is the proportion (n/N) of a particular taxon (n) divided by the total number of individuals (N), and $s$ is the number of taxa. Pearson correlation analyses were performed to examine relationships between zooplankton abundance, $H'$ and environmental factors. Differences in $H'$ were analyzed based on their distance to the LC front.

Zooplankton abundance and sampling sites in relation to physical and biological factors were further explored using canonical correspondence analysis (CCA) (Ter Braak, 1986). This type of correspondence analysis adds linear regressions between the canonical axes and uses external environmental factors to constrain the ordination of sampling sites. To visualize the CCA results, an ordination plot is developed with the zooplankton community structure of each site represented by points and environmental factors by arrows. Dominant patterns in zooplankton communities regarding environmental parameters are jointly displayed by the CCA to identify differences in the impact of environmental factors (e.g., salinity, SST, and DO) between cruises. The Bray-Curtis similarity matrix was used for spatial grouping of locations in different cruise collections. The Monte Carlo permutation test was conducted to test the significance of the axes at $\alpha = 0.01$. Zooplankton assemblages were further examined with nonmetric multidimensional scaling (NMDS) to explore the spatial-temporal patterns of zooplankton communities during the study period. The NMDS is used to reveal compositional variations across time (e.g., samples from four cruises in the northcentral GoM) by overlaying individual species on the sample space. Both CCA and NMDS were performed using the *vegan* package in R (Oksanen et al., 2007). All statistical analyses were performed using R Statistical Software (v4.1.2; R Core Team, 2021).

## 3. Results

### 3.1. Dynamic oceanographic processes in the northern Gulf of Mexico

The intrusion of the LC and associated eddies into the northern GoM based on SSH data indicated pronounced variation during the three-year sampling period (Fig. 2). Strong penetration of the LC occurred in July 2015 with the northernmost frontal region at approximately 28.5°N. During the sampling cruise in June 2016, a warm core eddy detached from the main LC circulation, occurring southeast of the sampling area, whereas in July 2016 a warm core eddy propagated southwest of the sampling region along with a cold core eddy occurring east of the study area. In July of 2017, the northern extend of the LC front remained at ~25°N and was in the process of expanding farther north. Sampling sites in July 2015 and 2016 remained inside of the direct influence of the LC and associated eddies (Fig. 2). In the vicinity of the sampling area, SST was warmer in July 2015 and July 2016 than that in June 2016 and July 2017 (Fig. S2). Influences of Mississippi River discharge appeared obvious in the sampling area in July 2015, June 2016 and July 2016, especially at sites along the northern transect in the study area (Fig. S1).

Environmental variables reflected the broad ocean conditions varying seasonally and interannually (Fig. 3). In July of 2015 and 2016, mean SST (30.5 ± 0.91 and 30.6 ± 0.64) and salinity (31.2 ± 5.92 and 33.1 ± 2.42) were not significantly different between the years (*t*-test, $p > 0.05$), but SST was different between months (June vs. July) in 2016 ($p < 0.001$). While salinity was slightly higher in June 2016 (33.9 ± 1.22) compared to July 2016 (33.1 ± 2.42), the difference was not significant between months ($p > 0.05$). The lowest salinity of 18.0 in the sampling region occurred in July 2015 on the northern transect close to the Mississippi River plume, whereas the highest salinity (37.5) was observed in July 2017 at sites on the southern transect close to the LC frontal zone. DO was significantly different in July between 2015 and 2016 (t-test, $p < 0.001$), and was significantly different between June and July in 2016 ($p < 0.001$).

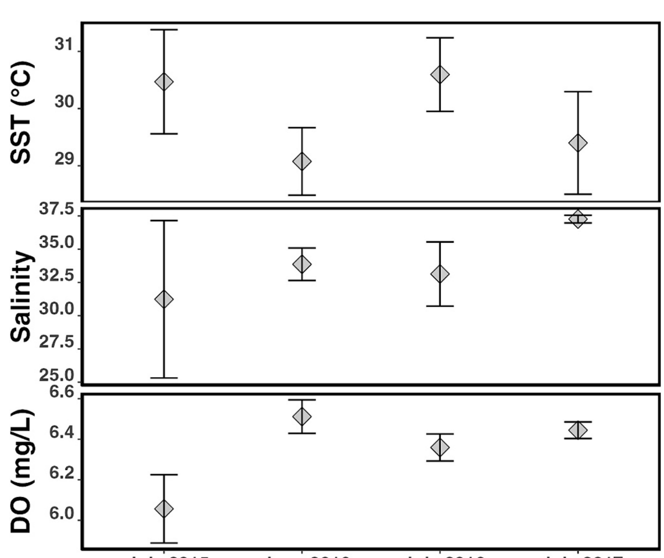


**Fig. 3.** Sea Surface Temperature (SST), salinity and dissolved oxygen (DO) (mean ± SD) during the sampling periods.

The PCA biplots disclosed seasonal differences in environmental conditions among sampling sites in the northern GoM (Fig. 4). The LDA showed all factors investigated being statistically significant between the separated northern and southern transects (Monte-Carlo permutation tests, $p < 0.001$), except July 2017 ($p = 0.465$). A complete separation of the PCA positioning occurred in June 2016 with the northern transect largely associated with higher SST and the southern transect associated with higher salinity, which reflects the relatively distant frontal zone of the LC as seen in Fig. 2.

### 3.2. Abundance, distribution, and species composition of zooplankton

Zooplankton abundance was highly variable in the northern GoM with higher abundance occurred in July 2016 and July 2017 (Fig. 5). Regarding proximity of sampling sites to LC frontal regions, higher zooplankton abundance was observed at sites far removed from the frontal zone (Fig. 6). In June 2016 and July 2017, the LC front was further than 40 nm of all sampling sites (see Fig. 2). The lowest zooplankton abundance was observed in July 2015, exhibiting relatively lower abundance than all the other cruises across the same distance range (Fig. 6). Considering heterogeneity, the number of zooplankton taxa per sample ranged from 25 to 38, and $H'$ ranged between 1.45 and 3.10. While $H'$ varied among the cruises, it was not significantly different (ANOVA, $p > 0.05$) (Fig. 7). With all cruises considered, zooplankton assemblages across the northern transect were relatively less diverse than those in the southern transect.

Overall, miscellaneous zooplankton taxa were observed in the northern GoM during the study period (Table S1), including 26 genera/species of copepods, as well as chaetognaths, fish larvae, and other non-copepod taxa. Mean zooplankton abundance was significantly different among cruises (ANOVA, $p < 0.001$) with the highest abundance in July 2017 (1798 ± 73 ind./$m^3$) and lowest in July 2015 (808 ± 59 ind./$m^3$) (Fig. 8). While copepod contributions (i.e. percentages) to zooplankton abundance differed among cruises and seasons ranging between 53% and 71% (65% ± 7.2%), dominant coastal and oceanic species identified in the samples included: *Acartia* spp., *Candacia simplex*, *Centropages furcatus*, *Clausocalanus* spp., *Eucalanus* spp., *Oncaea venusta*, *Oithona*

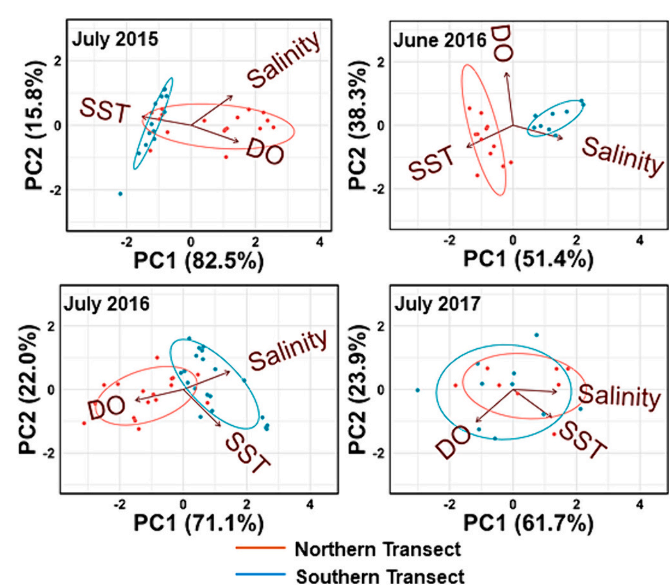


**Fig. 4.** Principal Component Analysis (PCA) ordinations of environmental factors in summer (July 2015, June 2016, July 2016, July 2017) in the northern Gulf of Mexico.

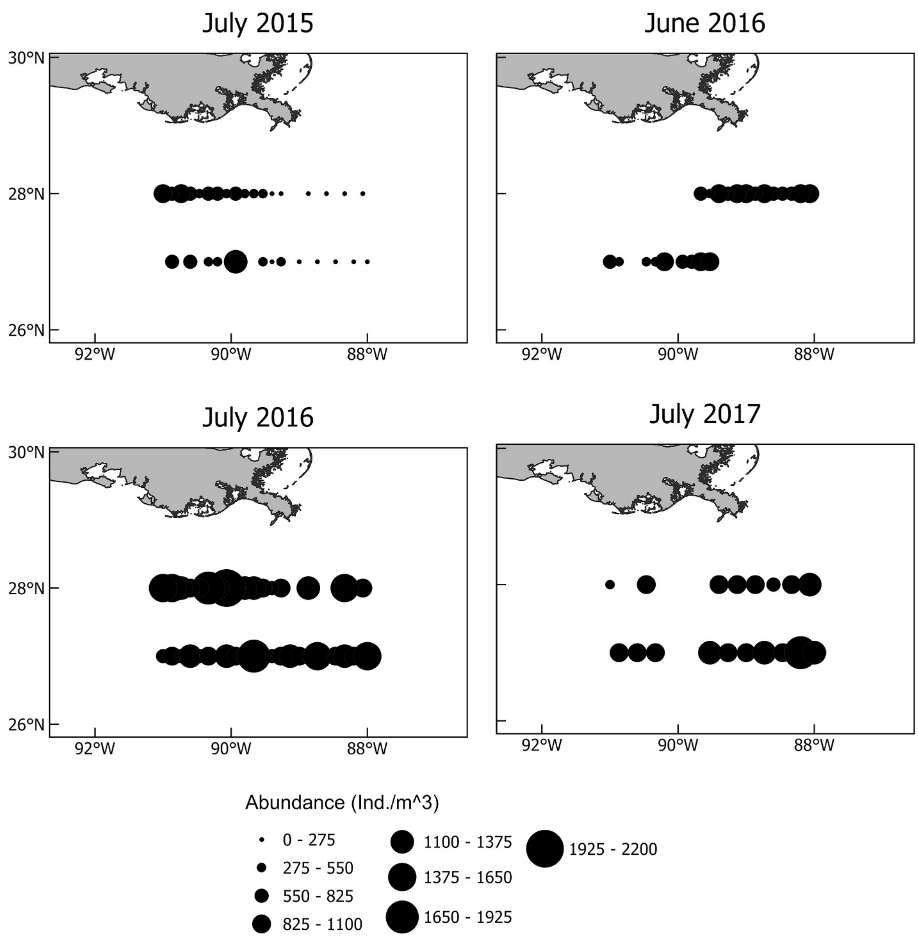


**Fig. 5.** Zooplankton abundance in summer months (July 2015, June 2016, July 2016, July 2017) in the northern Gulf of Mexico.

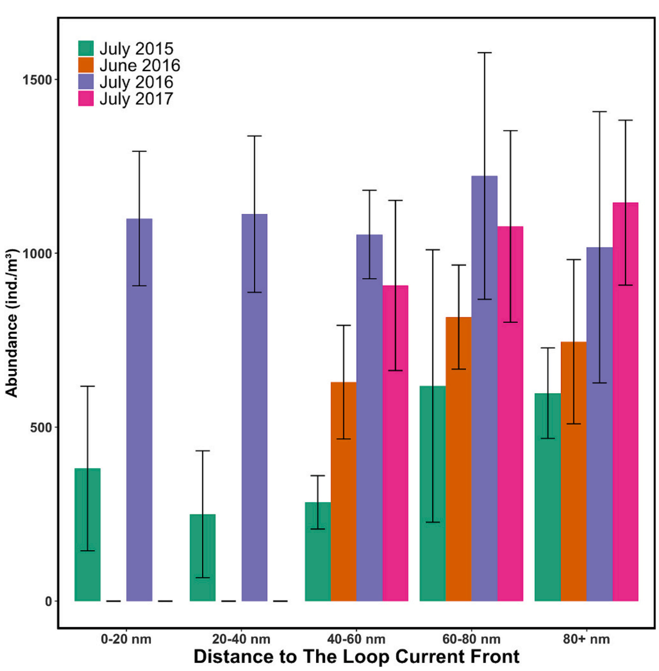


**Fig. 6.** Zooplankton abundance classified by distance to the Loop Current front in July 2015, June 2016, July 2016, and July 2017 in the northern Gulf of Mexico.

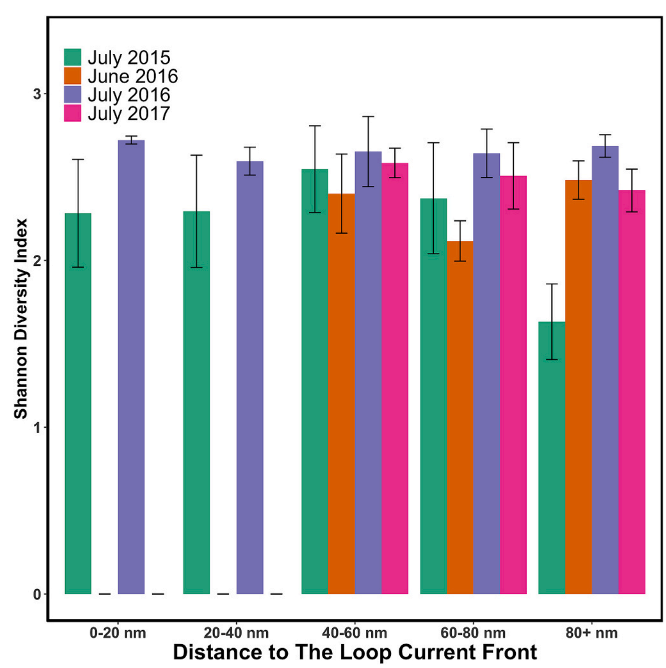


**Fig. 7.** Shannon diversity ($H'$) of zooplankton grouped by distance to the Loop Current front in July 2015, June 2016, July 2016, and July 2017 in the northern Gulf of Mexico.

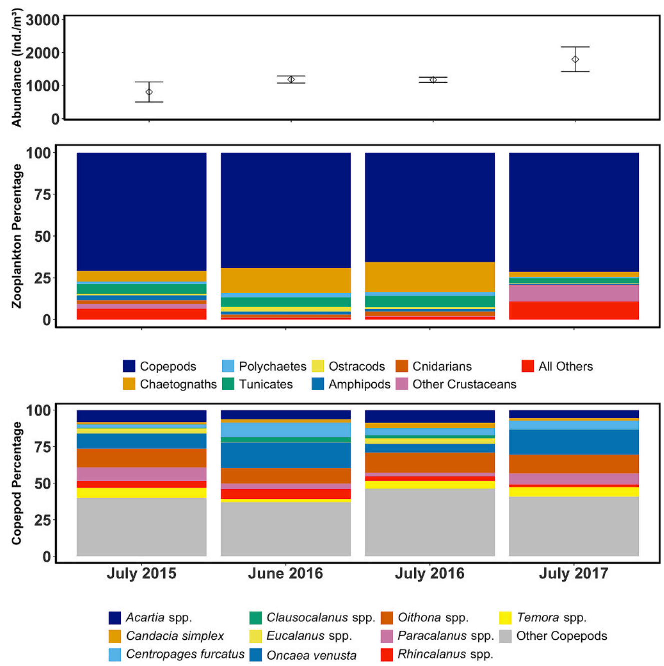


**Fig. 8.** Zooplankton total abundance, percent abundance per taxon group, and percent abundance for copepods during the study periods in the northern Gulf of Mexico.

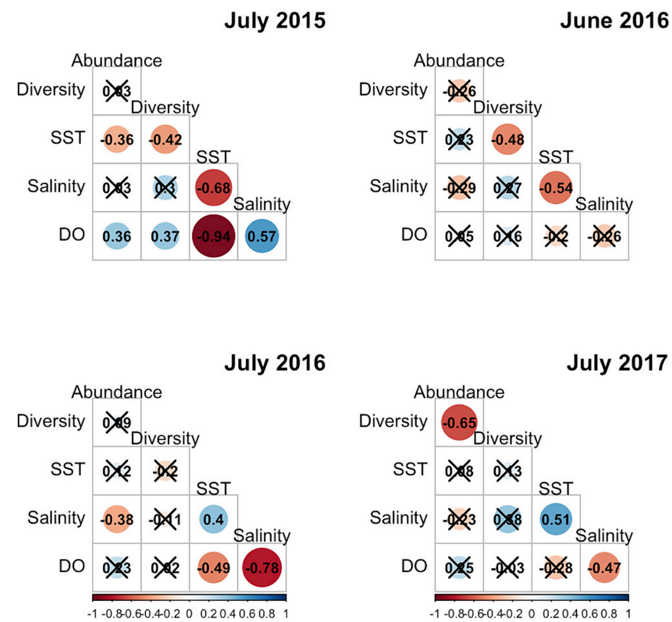


**Fig. 9.** Correlation analyses for zooplankton abundance and Shannon diversity with SST, salinity and DO during the study period. Only significant Pearson correlation coefficients are shown ($p < 0.05$). Color bars represent correlation coefficients.

spp., *Paracalanus* spp., *Temora* spp., and *Rhincalanus rostifrons*. Non-copepod taxa, including chaetognaths, polychaetes, tunicates, and ostracods, accounted for 7.1% and 32% (23% ± 9.2%) of the zooplankton abundance (Fig. 8). Interestingly, a few species tended to dominate the abundance when considering the distance to the LC frontal zone. In July 2015, regions 80 nm away from the frontal area with the highest abundance had the lowest diversity that was dominated by a few cosmopolitan species: *Oithona* spp., *Oncaea venusta,* and *Temora* spp.

### *3.3. Zooplankton and oceanographic conditions*

Both abundance and $H'$ of zooplankton were significantly correlated with SST, salinity, and DO (Fig. 9). Four cruises exhibited varying relationships between environmental factors and abundance and $H'$, possibly due to the impact of dynamic ocean conditions during the study period (Fig. 2 and Figs. S1&S2). In July 2015 abundance and diversity were negatively correlated with SST and positively correlated with DO. In June 2016, only $H'$ was negatively correlated with SST, whereas abundance was negatively correlated with salinity in July 2016.

CCA biplots disclosed the ordination among taxa and stations in relation to physical and biological factors during the study (Fig. 10). Taxon-environmental associations were statistically significant (Monte Carlo Permutation Test, $p < 0.001$), indicating that species tend to reside in specific water masses. The response of zooplankton to environmental factors was variable among taxonomic groups, also varying in the same region between years. For instance, *Candacia simplex* showed strong associations with low salinity in July 2016 but higher salinity in July 2017, likely due to the far extent of Mississippi River outflow in 2016 compared to that in 2017 (Fig. S1). Few cosmopolitan copepods were present during all cruises and appeared highly abundant, such as *Paracalanus* spp. and *Oncaea venusta*. The CCA biplot showed that most species tend to be near the center of the plot, indicating a wide tolerance of these dominant species to environmental conditions in the region. *Acartia* spp., typically associated with coastal waters with low salinity, exhibited negative relationships with salinity. Similarly, *Rhincalanus rostifrons*, an oceanic species associated with higher salinity, showed strong relationships with higher salinity across multiple cruises.

The NMDS ordinations indicated the presence of two distinct zooplankton groups during the study period (Fig. 11). The first group represents zooplankton assemblages in July 2016, while the second group consists of zooplankton assemblages in July 2015, June 2016 and July 2017. Additionally, species were dominated by coastal taxa (e.g., *Acartia* spp., cnidarians, polychaete larvae) in the first group and oceanic species (e.g. *Rhincalanus* spp., *Eucalanus* spp., *Oithona* spp., and *Candacia* spp.) in the second group. These patterns may indicate that zooplankton assemblages tend to be distinctive in the study area between the northern and southern transects since two areas are subjected to relative influences from the Mississippi River discharge and the LC, respectively.

## 4. Discussion

### *4.1. Zooplankton dynamics in the northern Gulf of Mexico*

In the northern GoM, the main mesoscale features impacting biophysical interactions of plankton communities are related to the LC circulation and Mississippi River outflow (Dagg and Breed, 2003). Spatial and temporal variations of diverse zooplankton assemblages reported in the present study show associations with the ocean conditions observed across the sampling periods. The environmental variability disclosed in the PCA is echoed on the SSH maps (Fig. 2), exhibiting distinct groupings of zooplankton assemblages among cruises, which appear linked to the dynamic nature of mesoscale features in the northern GoM. The first sampling year in 2015 was noted particularly as an unusual period of the LC, as circulation and associated eddies were so strong that they forced the historic period of oil and gas downtime, with water current speeds recorded as high as 4 knots (Perry et al., 2016). During this period, distinctive zooplankton community structure and low abundance were observed in the vicinity of the LC region, which was largely related to the unusual strength of the LC circulation.

Anticyclonic (warm core) features in the ocean are often considered as biological deserts with localized low nutrient waters (Bakun, 2006). However, the northern GoM is physically dynamic and often influenced not only by the LC circulation but also the Mississippi River plume where

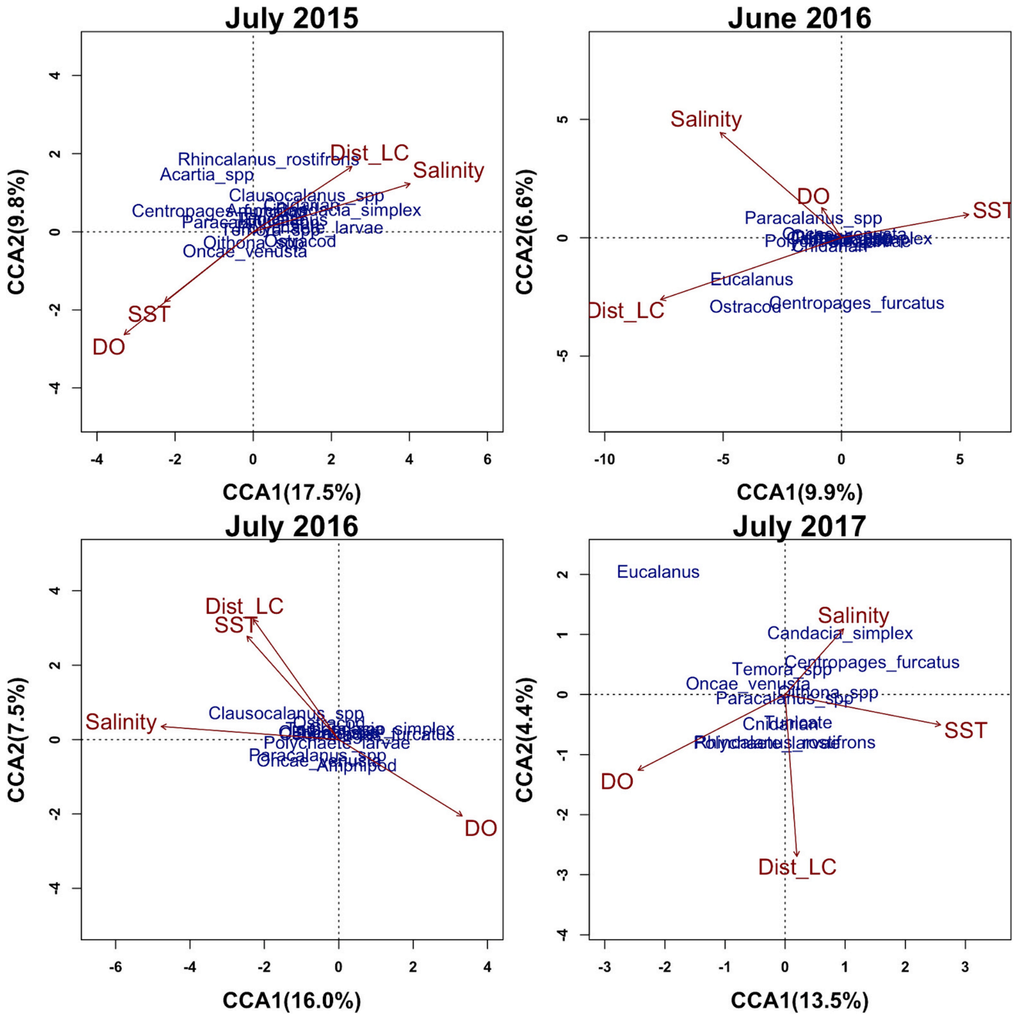


**Fig. 10.** Conical Correlation Analysis (CCA) ordinations between zooplankton abundance and environmental variables (SST, salinity and DO) during the study period in the northern Gulf of Mexico.

higher nutrient loadings are present near the surface (Dagg and Breed, 2003). Therefore, trophodynamics in this region are more complex when attempting to hypothesize and interpret the responses of zooplankton communities to ocean conditions. During periods when the LC is at its farthest northern extent, oligotrophic, saline oceanic water interacts with higher nutrient, low salinity water from the Mississippi River to provide a unique environment for diverse zooplankton assemblages that reflect the relatively higher diversity index at sampling sites in July 2015 and July 2016 close to the LC frontal zone (Fig. 7).

The present study revealed noticeable differences in zooplankton community composition between years in offshore waters of the northern GoM in relation to ocean conditions induced by eddies and freshwater outflow. The variability in zooplankton abundance among years in the same region also reflect source water conditions, as well as the influence of entrainments from the shelf, which varied considerably in terms of zooplankton taxa and their abundance. A recent study (Szczepanski, 2019) reported the relative contribution of various zooplankton taxa in the offshore waters of Louisiana and Mississippi, north of our study region. Coincidently they found that calanoid copepods dominate the zooplankton community in summer months, with chaetognaths, cnidarians, and tunicates additionally contributing to zooplankton assemblages. Significant contributions of chaetognaths in zooplankton assemblages were reported in the northern GoM with lower abundance near the LC front and higher abundance closer to the Mississippi River plume (Gilmartin et al., 2020). Therefore, zooplankton assemblages tend to differ between these two oceanographic features in the northern GoM.

Our findings indicate that zooplankton communities in the northern GoM are generally composed of both coastal and offshore species (Table S1), and the species composition changes with varying mesoscale physical impacts. Analyses of biotic and abiotic factors in the present study exhibited that annual variations of zooplankton in the northern GoM are affected by ocean conditions associated with mesoscale features. In summer 2015, during the most northern extent of the LC, decreased overall zooplankton abundance was observed closest to the LC front, and the community structure shifted to oceanic species (*Oithona* spp., and *Temora* spp.) that are typically found at higher salinities and lower food concentrations. Additionally, neritic species (*Acartia* spp.) were present in the offshore region of the GoM, signifying the strong influence of freshwater inflow from the Mississippi River on zooplankton communities. Of non-copepod taxa, chaetognaths displayed the highest abundance, which is consistent with a recent study by Gilmartin et al. (2020). Moreover, the vital role of copepods as major prey contributing to the higher abundance of chaetognaths has been reported in other regions (Baier and Terazaki, 2005; Baier and Purcell, 1997; Pearre Jr, 1982). Analyses indicated that differences in environmental factors, as well as the timing and region of the cruise, had significant impacts on the species presence and relationships among taxa. These differences in time and space are probably linked to external physical processes, such as the location and strength of mesoscale

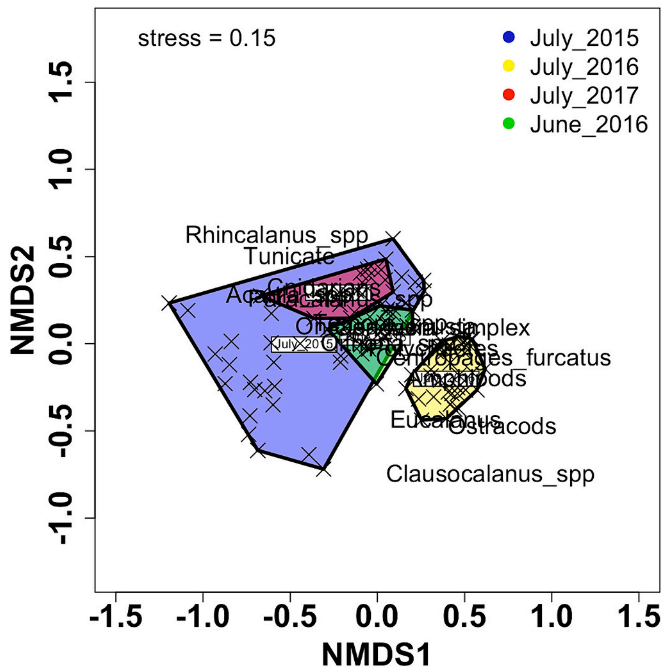


**Fig. 11.** Nonmetric multidimensional scaling (NMDS) for spatial ordinations of zooplankton assemblages during the study period in the northern Gulf of Mexico.

features induced by the LC and freshwater inflow from the Mississippi River that might alter zooplankton diets (e.g., Dorado et al., 2012).

Hot spots of biological productivity in the northern GoM have been studied through observations (Biggs and Ressler, 2001) and mechanistic modeling (Li and Liu, 2022). The impact of mesoscale features on the distribution and abundance of fish larvae has been well recognized in this region (Lindo-Atichati et al., 2012; Rooker et al., 2012, 2013). It has been reported that higher abundance of ichthyoplankton in frontal zones is largely attributed to hydrographic convergence (Grimes and Finucane, 1991). Specifically, this pattern has been observed in the northern GoM (Cornic and Rooker, 2018; Richards et al., 1993; Rooker et al., 2013), with some of these studies occurring in the same region as the present study. Lower zooplankton abundance near frontal zones observed in the present study suggests that the mesoscale structures may not only influence abundance and distribution of zooplankton taxa, but also cause potential shifts in their trophic roles within the pelagic community with implications for the transfer efficiencies of carbon and nitrogen in the pelagic food web (Liu et al., 2014; Coyle et al., 2019).

### 4.2. Oceanographic impacts on zooplankton

A recent study highlighted the dynamic variability in zooplankton abundance, diet, and trophic position in relation to mesoscale features in the GoM (Shropshire et al., 2020), finding that mesoscale oceanographic features significantly contributed to the biogeochemistry and food web structure of the GoM. In the southern GoM, pteropod abundance was reported to be associated with the LC eddy circulation, even in regions farther south of the LC itself (López-Arellanes et al., 2018). Another study about the influence of oceanographic features on ichthyoplankton distribution in the southern GoM reported that the mesoscale circulation, mixing processes and freshwater discharge, are key determinants of community structure (Sanvicente-Añorve et al., 2000). While similar research is limited in the northern GoM, consistent results exist in the present study that fluctuations in the Mississippi River inflow and the position of the LC front appeared the main drivers in shaping zooplankton community structure across the study region.

Environmental heterogeneity in open waters is often attributed to water column mixing due to winds, mesoscale oceanographic circulations, as well as river discharge (Meier and Kauker, 2003; Savenkoff et al., 1997). In addition, fronts, eddies, and upwelling zones significantly influence the spatial distribution of zooplankton communities (Lee and Park, 2002). This has been observed in the Indian Ocean, where spring inter-monsoon induced shifts in the environment allowed for shifts in copepod and larvacean community structure (Li et al., 2017). Physical aggregations of zooplankton driven by surface currents contribute to higher zooplankton abundance along frontal regions (Maravelias and Reid, 1997; Wade and Heywood, 2001; Albaina and Irigoien, 2004; Coyle, 2005; Gómez-Gutiérrez et al., 2007), which is different from our findings in the northern GoM. Possible causes of low zooplankton abundance near the frontal zone include relative low zooplankton abundance in oligotrophic waters within anticyclonic features such as the LC. Cold and warm core eddies influenced zooplankton in the present study, as abundance and distribution of zooplankton taxa have shown to shift regarding proximity to these mesoscale features with species-specific relationships in the northern GoM. In addition, eddy age plays an important role in influencing the community structure of zooplankton (Mackas and Galbraith, 2002; Mackas et al., 2005). These studies found that as eddies age, the community structure of zooplankton shifts from abundant species dominating to less abundant species dominating. This is likely due to alterations in vertical mixing during the eddy lifetime, which causes weakened upwelling leading to the reduced nutrient supply to sustain the plankton communities or diminished hydrographic convergence to lessen aggregation of zooplankton in the eddy. While studies assessing the effect of eddy age on zooplankton dynamics remain scarce in the northern GoM, including the eddy age in the future research could improve the mechanistic understanding of zooplankton communities regarding mesoscale physical processes in the dynamic GoM ecosystem.

### 4.3. Relevance to ecosystems and fisheries in the light of climate change

Findings in the present study are relevant to understanding zooplankton taxa that are associated with the dynamic regions and hot spots of zooplankton secondary production for larval fishes of commercially important species. Ocean conditions at the boundary of the LC support high abundance of zooplankton by either advection of nutrients or replenish new primary production through physical processes occurring around the boundary (Rathmell, 2007). Larval fish survival depends on timing and presence of primary and secondary production. Commercially valuable fish, such as bluefin tuna in the GoM, tend to spawn near frontal regions of the LC between April and June annually (Muhling et al., 2011). Adult bluefin tuna cannot tolerate waters above a maximum temperature limit, and thus the location and timing of the LC circulation significantly affects their spawning in the northern GoM. Additionally, the abundance of bluefin tuna is higher in or near cyclonic eddies (Teo and Block, 2010), which could be related to the possible zooplankton aggregation in these areas. This speculation is worthy of further test, especially considering the recent finding that Atlantic bluefin tuna larvae in the GoM have the capacity to switch from active to passive selection of zooplankton prey due to physical processes (Shiroza et al., 2021). As one of lucrative fisheries in the northern GoM, red snapper displays distinctive stock dynamics between the eastern and western GoM divided by the Mississippi River outflow plume (Liu et al., 2017a). In general, variations in population dynamics of fish stocks could be driven by differences in food resources, physiological tolerances, predation, mortality, and oceanographic processes. Population growth and morphometrics of red snapper vary significantly off Alabama and Louisiana from those off Texas, and red snapper residing in the waters off Texas reach smaller maximum sizes at faster rates and have a consistently lower total weight at age than their siblings off Alabama and Louisiana (Fischer et al., 2004). It is interesting to link the finding of distinct zooplankton assemblages in the northern GoM to population dynamics and stock assessment of fishes because information on the zooplankton community structure in the spawning regions would help to gain insight on the trophic dynamics and recruitment of bluefin tuna and red snapper in terms of match-mismatch (Cushing, 1974) with the prey availability and subsequent implications for fisheries production in the northern GoM.

The GoM appears to be trending toward a warmer and windier ecosystem since the mid-90s with increasing evidence of climate driven reorganization of this large marine ecosystem (Karnauskas et al., 2015). Due to the dynamic nature of the GoM, studies addressing mesoscale biophysical interactions of zooplankton regarding the consequences of changing climate to the GoM ecosystem warrant further attention. The mesoscale vertical mixing near the ocean surface in the GoM has shown implications for carbon cycling and heat storage, which is a central theme of research on climate change and carbon budget (Justic et al., 1997). Shifts in zooplankton community structure under projected climate scenarios could disrupt carbon cycling in this region (Bracco et al., 2019), therefore continued climate research with linkage to zooplankton dynamics is imperative in the GoM region. The present study highlights the potential that with the strengthening or weakening of the physical circulations in relation to climate change, potential substantial responses could occur from the zooplankton community residing in the fronts and eddies with significant implications to this large marine ecosystem.

In conclusion, the present study attempted to examine the influence of physical processes (i.e., the LC, eddies, fronts, and freshwater inflow) on distribution, abundance and diversity of zooplankton communities in offshore waters of the northern GoM. Our findings indicate that zooplankton community composition and abundance are significantly influenced by the variation in mesoscale processes of the LC fronts and associated eddies, as well as the freshwater inflow of the Mississippi River. Mesoscale impacts on zooplankton community structure are highly variable across years surveyed in the northern GoM resulting in the spatiotemporal interaction of zooplankton and mesoscale features. It is highly recommended to continue research across full seasons and extensive regions integrating observations using advanced sampling technology (Bi et al., 2022) and modeling approaches (Li and Liu, 2022 & 2023) to fully understand the mechanistic impacts of mesoscale features on zooplankton in the northern GoM.

Supplementary data to this article can be found online at https://doi.org/10.1016/j.seares.2024.102501.

## CRediT authorship contribution statement

**Hui Liu:** Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Jillian Gilmartin:** Writing – original draft, Visualization, Investigation, Formal analysis, Data curation. **Michelle Zapp Sluis:** Writing – review & editing, Formal analysis. **Toru Kobari:** Writing – review & editing. **Jay Rooker:** Writing – review & editing. **Hongsheng Bi:** Writing – review & editing, Investigation. **Antonietta Quigg:** Writing – review & editing.

## Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests:

Hui Liu reports financial support was provided by Texas A&M University. None If there are other authors, they declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

## Data availability

Data will be made available on request.

## Acknowledgments

We acknowledge the crew of the *R/V Blazing Seven* and the *R/V Pelican* for the logistical support at sea. We thank the scientists and graduate students of Texas A&M University at Galveston who contributed to the sample collection, especially, Dr. Maëlle Cornic, Dr. Qing Yang, Corinne Meinert, and Jason Mostowy. Sampling of this study was made possible by the grant awarded to JR from the Gulf of Mexico Research Initiative (Deep Pelagic Nekton Dynamics consortium). This was a study partially supported by National Science Foundation under NSF grant OCE-1760463.

## References

Adams, C.M., Hernandez, E., Cato, J.C., 2004. The economic significance of the Gulf of Mexico related to population, income, employment, minerals, fisheries and shipping. Ocean Coast. Manag. 47, 565–580.
Albaina, A., Irigoien, X., 2004. Relationships between frontal structures and zooplankton communities along a cross-shelf transect in the Bay of Biscay (1995 to 2003). Mar. Ecol. Prog. Ser. 284, 65–75.
Aleksa, K.T., Sasso, C.R., Nero, R.W., Evans, D.R., 2018. Movements of leatherback turtles (*Dermochelys coriacea*) in the Gulf of Mexico. Mar. Biol. 165, 158. https://doi.org/10.1007/s00227-018-3417-9.
Almeda, R., Wambaugh, Z., Wang, Z., Hyatt, C., Liu, Z., Buskey, E.J., 2013. Interactions between zooplankton and crude oil: toxic effects and bioaccumulation of polycyclic aromatic hydrocarbons. PLoS One 8, e67212.
Baier, C.T., Purcell, J.E., 1997. Trophic interactions of chaetognaths, larval fish, and zooplankton in the South Atlantic bight. Mar. Ecol. Prog. Ser. 146, 43–53.
Baier, C., Terazaki, M., 2005. Interannual variability in a predator–prey interaction: climate, chaetognaths and copepods in the southeastern Bering Sea. J. Plankton Res. 27, 1113–1125.
Bakun, A., 2006. Wasp-waist populations and marine ecosystem dynamics: navigating the “predator pit” topographies. Prog. Oceanogr. 68, 271–288.
Batchelder, H.P., Daly, K.L., Davis, C.S., Ji, R., Ohman, M.D., Peterson, W.T., Runge, J.A., 2013. Climate impacts on zooplankton population dynamics in coastal marine ecosystems. Oceanography 26 (4), 34–51.
Bi, H., Song, J., Zhao, J., Liu, H., Cheng, X., Wang, L., Cai, Z., Benfield, M., Otto, S., Goberville, E., Keister, J., Yang, Y., Yu, X., Cai, J., Ying, K., Gonversi, A., 2022. Temporal characteristics of plankton indicators in coastal waters: high-frequency data from PlanktonScope. J. Sea Res. 189, 102283.
Biggs, D.C., 1992. Nutrients, plankton, and productivity in a warm-core ring in the western Gulf of Mexico. J. Geophys. Res. Oceans 97, 2143–2154.
Biggs, D.C., Ressler, P.H., 2001. Distribution and abundance of phytoplankton, zooplankton, ichthyoplankton, and micronekton in the Deepwater Gulf of Mexico. Gulf of Mexico Science 19 (1).
Boltovskoy, D., Gibbons, M.J., Hutchings, L., Binet, D., 1999. General biological features of the South Atlantic. South Atlantic Zooplankton 1, 1–42.
Bracco, A., Liu, G., Sun, D., 2019. Mesoscale-submesoscale interactions in the Gulf of Mexico: from oil dispersion to climate. Chaos, Solitons Fractals 119, 63–72.
Carassou, L., Hernandez, F.J., Graham, W.M., 2014. Change and recovery of coastal mesozooplankton community structure during the Deepwater horizon oil spill. Environ. Res. Lett. 9 (12), 124003.
Checkley Jr., D.M., Uye, S., Dagg, M.J., Mullin, M.M., Omori, M., Onbe, T., Zhu, M.Y., 1992. Diel variation of the zooplankton and its environment at neritic stations in the Inland Sea of Japan and the north-West Gulf of Mexico. J. Plankton Res. 14 (1), 1–40.
Coleman, F.C., Baker, P.B., Koenig, C.C., 2004. A review of Gulf of Mexico marine protected areas: successes, failures, and lessons learned. Fisheries 29, 10–21.
Cornic, M., Rooker, J.R., 2018. Influence of oceanographic conditions on the distribution and abundance of blackfin tuna (*Thunnus atlanticus*) larvae in the Gulf of Mexico. Fish. Res. 201, 1–10.
Cornic, M., Rooker, J.R., 2021. (2021) temporal shifts in the abundance and preferred habitats of yellowfin and bigeye tuna larvae in the Gulf of Mexico. J. Mar. Syst. 217, 103524.
Coyle, K.O., 2005. Zooplankton distribution, abundance and biomass relative to water masses in eastern and central Aleutian Island passes. Fish. Oceanogr. 14, 77–92.
Coyle, K.O., Hermann, A.J., Hopcroft, R.R., 2019. Modeled spatial-temporal distribution of production, chlorophyll, iron and nitrate on the northern Gulf of Alaska shelf relative to field observations. Deep-Sea Res. II 165, 163–191.
Cushing, D.H., 1974. The natural regulation of fish populations. In: Harden Jones, F.R. (Ed.), Sea Fisheries Research. Elek Science, London, UK, pp. 399–412.
Dagg, M.J., Breed, G.A., 2003. Biological effects of Mississippi River nitrogen on the northern Gulf of Mexico—a review and synthesis. J. Mar. Syst. 43, 133–152.
Davis, R.W., Ortega-Ortiz, J.G., Ribic, C.A., Evans, W.E., Biggs, D.C., Ressler, P.H., Cady, R.B., Leben, R.R., Mullin, K.D., Würsig, B., 2002. Cetacean habitat in the northern oceanic Gulf of Mexico. Deep-Sea Res. I Oceanogr. Res. Pap. 49, 121–142.
Dorado, S., Rooker, J.R., Wissel, B., Quigg, A., 2012. Isotope baseline shifts in pelagic food webs of the Gulf of Mexico. Mar. Ecol. Prog. Ser. 464, 37–49. https://doi.org/10.3354/meps09854.
Dray, S., Dufour, A.B., 2007. The ade4 package: implementing the duality diagram for ecologists. J. Stat. Softw. 22 (4), 1–20.

Elliott, D.T., Pierson, J.J., Roman, M.R., 2012. Relationship between environmental conditions and zooplankton community structure during summer hypoxia in the northern Gulf of Mexico. J. Plankton Res. 34, 602–613.

Färber Lorda, J., Athié, G., Camacho Ibar, V., Daessle, L., Molina, O., 2019. The relationship between zooplankton distribution and hydrography in oceanic waters of the southern Gulf of Mexico. J. Mar. Syst. 192, 28–41.

Fischer, A.J., Baker Jr., M.S., Wilson, C.A., 2004. Red snapper (*Lutjanus campechanus*) demographic structure in the northern Gulf of Mexico based on spatial patterns in growth rates and morphometrics. Fish. Bull. 102, 593–603.

Fodrie, F.J., Heck Jr., K.L., 2011. Response of coastal fishes to the Gulf of Mexico oil disaster. PLoS One 6, e21609.

Gilmartin, J., Yang, Q., Liu, H., 2020. Seasonal abundance and distribution of chaetognaths in the northern Gulf of Mexico: the effects of the loop current and Mississippi River plume. Cont. Shelf Res. 203, 104146.

Gómez-Gutiérrez, J., Martínez-Gómez, S., Robinson, C.J., 2007. Influence of thermo-haline fronts forced by tides on near-surface zooplankton aggregation and community structure in Bahía Magdalena, Mexico. Mar. Ecol. Prog. Ser. 346, 109–125.

Greer, A.T., Chiaverano, L.M., Luo, J.Y., Cowen, R.K., Graham, W.M., 2018. Ecology and behaviour of holoplanktonic scyphomedusae and their interactions with larval and juvenile fishes in the northern Gulf of Mexico. ICES J. Mar. Sci. 75 (2), 751–763. https://doi.org/10.1093/icesjms/fsx168.

Grimes, C.B., Finucane, J.H., 1991. Spatial distribution and abundance of larval and juvenile fish, chlorophyll and macrozooplankton around the Mississippi River discharge plume, and the role of the plume in fish recruitment. Mar. Ecol. Prog. Ser. 75, 109–119.

Hamilton, P., Fargion, G., Biggs, D., 1999. Loop current eddy paths in the western Gulf of Mexico. J. Phys. Oceanogr. 29, 1180–1207.

Hopkins, T.L., 1982. The vertical distribution of zooplankton in the eastern Gulf of Mexico. Deep Sea research part a. Oceanogr. Res. Papers 29, 1069–1083.

Johnson, W.S., Allen, D.M., 2012. Zooplankton of the Atlantic and Gulf Coasts: A Guide to their Identification and Ecology. The Johns Hopkins University Press, pp. 1–452.

Justic, D., Rabalais, N.N., Turner, R.E., 1997. Impacts of climate change on net productivity of coastal waters: implications for carbon budgets and hypoxia. Clim. Res. 8 (3), 225–237.

Karnauskas, M., Schirripa, M.J., Craig, J.K., Cook, G.S., Kelble, C.R., Agar, J.J., Black, B. A., Enfield, D.B., Lindo-Atichati, D., Muhling, B.A., Purcell, K.M., Richards, P.M., Wang, C., 2015. Evidence of climate-driven ecosystem reorganization in the Gulf of Mexico. Glob. Chang. Biol. 21 (7), 2554–2568. https://doi.org/10.1111/gcb.12894.

Keister, J., Peterson, W., Pierce, S., 2009. Zooplankton distribution and cross-shelf transfer of carbon in an area of complex mesoscale circulation in the northern California current. Deep-Sea Res. I Oceanogr. Res. Pap. 56, 212–231.

Kürten, B., Zarokanellos, N.D., Devassy, R.P., El-Sherbiny, M.M., Struck, U., Capone, D. G., Schulz, I.K., Al-Aidaroos, A.M., Irigoien, X., Jones, B.H., 2019. Seasonal modulation of mesoscale processes alters nutrient availability and plankton communities in the Red Sea. Prog. Oceanogr. 173, 238–255.

Lee, C., Park, C., 2002. Coastal upwelling of the East Sea and zooplankton distribution. In: Proceedings of the Spring Meeting of the Korean Society of Oceanography, pp. 9–11.

Li, C., Liu, H., 2022. Exploring cosmopolitan jellyfish (*Aurelia* spp.) bloom dynamics and ecological implications in subtropical waters with mechanistic dynamic modeling. J. Mar. Syst. 228, 103705 https://doi.org/10.1016/j.jmarsys.2022.103705.

Li, C., Liu, H., 2023. (2023) comparative ecosystem modelling of dynamics and stability of subtropical estuaries under external perturbations in the Gulf of Mexico. ICES J. Mar. Sci. 0, 1–16. https://tinyurl.com/2p8nvd4r.

Li, K., Yin, J., Tan, Y., Huang, L., Li, G., 2017. Diversity and abundance of epipelagic larvaceans and calanoid copepods in the eastern equatorial Indian Ocean during the spring inter-monsoon. Indian J. Geo Marine Sci. 46, 1371–1380.

Lindo-Atichati, D., Bringas, F., Goni, G., Muhling, B., Muller-Karger, F.E., Habtes, S., 2012. Varying mesoscale structures influence larval fish distribution in the northern Gulf of Mexico. Mar. Ecol. Prog. Ser. 463, 245–257.

Liu, H., Dagg, M., 2003. Interactions between nutrients, phytoplankton growth, and micro- and mesozooplankton grazing in the plume of Mississippi River. Mar. Ecol. Prog. Ser. 258, 31–42.

Liu, H., Fogarty, M.J., Hare, J.A., Hsieh, C.-h., Glaser, S.M., Ye, H., Deyle, E., Sugihara, G., 2014. Modeling dynamic interactions and coherence between marine zooplankton and fishes linked to environmental variability. J. Mar. Syst. 131, 120–129.

Liu, H., Bi, H., Peterson, W.T., 2015. Large-scale forcing of environmental conditions on subarctic copepods in the northern California current system. Prog. Oceanogr. 134, 404–412.

Liu, H., Karnauskas, M., Zhang, X., Linton, B., Porch, C., 2017a. Forecasting dynamics of red snapper (*Lutjanus campechanus*) in the U.S. Gulf of Mexico. Fish. Res. 187, 31–40.

Liu, H., Zhang, X., Yang, Q., Zuo, T., Quigg, A., 2017b. Mesozooplankton dynamics in relation to environmental factors and juvenile fish in a subtropical estuary of the Gulf of Mexico. J. Coast. Res. 335, 1038–1050.

Liu, H., Gilmartin, J., Li, C., Li, K., 2021. Detection of time varying pulsed event effects on estuarine pelagic communities with ecological indicators after catastrophic hurricanes. Ecol. Indic. 123, 107327.

Lohrenz, S.E., Redalje, D.G., Cai, W.-J., Acker, J., Dagg, M., 2008. A retrospective analysis of nutrients and phytoplankton productivity in the Mississippi River plume. Cont. Shelf Res. 28, 1466–1475.

López-Arellanes, H., Funes-Rodríguez, R., Flores-Coto, C., Zavala-García, F., Espinosa-Fuentes, M., 2018. Comparison of pteropod assemblages and their relationship with environmental variables in the southern Gulf of Mexico. J. Molluscan Stud. 84, 386–396.

Mackas, D.L., Galbraith, M.D., 2002. Zooplankton distribution and dynamics in a North Pacific eddy of coastal origin: I. Transport and loss of continental margin species. J. Oceanogr. 58 (5), 725–738.

Mackas, D.L., Tsurumi, M., Galbraith, M.D., Yelland, D.R., 2005. Zooplankton distribution and dynamics in a North Pacific Eddy of coastal origin: II. Mechanisms of eddy colonization by and retention of offshore species. Deep-Sea Res. II Top. Stud. Oceanogr. 52 (7–8), 1011–1035.

Maravelias, C.D., Reid, D.G., 1997. Identifying the effects of oceanographic features and zooplankton on prespawning herring abundance using generalized additive models. Mar. Ecol. Prog. Ser. 147, 1–9.

McClatchie, S., Cowen, R., Nieto, K., Greer, A., Luo, J.Y., Guigand, C., Demer, D., Griffith, D., Rudnick, D., 2012. Resolution of fine biological structure including small narcomedusae across a front in the Southern California bight: fine biological structure across a front. J. Geophys. Res. Oceans 117. https://doi.org/10.1029/2011JC007565.

Meier, H.M., Kauker, F., 2003. Modeling decadal variability of the Baltic Sea: 2. Role of freshwater inflow and large-scale atmospheric circulation for salinity. J. Geophys. Res. Oceans 108.

Meinert, C.R., Clausen-Sparks, K., Cornic, M., Sutton, T.T., Rooker, J.R., 2020. Taxonomic richness and diversity of larval fish assemblages in the oceanic Gulf of Mexico: links to oceanographic conditions. Front. Mar. Sci. 7, 579.

Muhling, B.A., Lee, S.K., Lamkin, J.T., Liu, Y., 2011. Predicting the effects of climate change on bluefin tuna (*Thunnus thynnus*) spawning habitat in the Gulf of Mexico. ICES J. Mar. Sci. 68 (6), 1051–1062.

Naganobu, M., Nishiwaki, S., Yasuma, H., Matsukura, R., Takao, Y., Taki, K., Hayashi, T., Watanabe, Y., Yabuki, T., Yoda, Y., 2006. Interactions between oceanography, krill and baleen whales in the Ross Sea and adjacent waters: an overview of Kaiyo Maru-JARPA joint survey in 2004/05. J. Cetacean Res. Manag. 10, 438–439.

Oksanen, J., Kindt, R., Legendre, P., O'Hara, B., Stevens, M.H.H., Oksanen, M.J., Suggests, M., 2007. The vegan package. Community Ecology Package 10, 631–637.

Ortner, P.B., Hill, L.C., Cummings, S.R., 1989. Zooplankton community structure and copepod species composition in the northern Gulf of Mexico. Cont. Shelf Res. 9, 387–402.

Pearre Jr., S., 1982. Feeding by Chaetognatha: aspects of inter-and intra-specific predation. Mar. Ecol. Prog. Ser. 7, 33–45.

Perry, R.L., Leung, P.T., Zwissler, C., Bouchard, R., Hervey, R., Fiorentino, L., Sharma, N., Martin, K., Howden, S., Kirkpatrick, B., 2016. Collaborative observational and operational oceanography to improve 2015 and 2016 loop current forecasting in the Gulf of Mexico, OCEANS 2016 MTS/IEEE Monterey. IEEE 1–8.

Quigg, A., Sylvan, J.B., Gustafson, A.B., Fisher, T.R., Tozzi, S., Ammerman, J.W., 2011. Going west: nutrient limitation of primary production in the northern Gulf of Mexico and the importance of the Atchafalaya River. Aquat. Geochem. 17, 519–544. https://doi.org/10.1007/s10498-011-9134-3.

R Core Team, 2021. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Rathmell, K., 2007. The Influence of the Loop Current on the Diversity, Abundance, and Distribution of Zooplankton in the Gulf of Mexico. Graduate Theses and Dissertations. University of South Florida. https://digitalcommons.usf.edu/etd/2334.

Richards, W., McGowan, M., Leming, T., Lamkin, J., Kelley, S., 1993. Larval fish assemblages at the loop current boundary in the Gulf of Mexico. Bull. Mar. Sci. 53, 475–537.

Roman, M.R., Pierson, J.J., Kimmel, D.G., Boicourt, W.C., Zhang, X., 2012. Impacts of hypoxia on zooplankton spatial distributions in the northern Gulf of Mexico. Estuar. Coasts 35, 1261–1269.

Rooker, J.R., Simms, J.R., Wells, R.D., Holt, S.A., Holt, G.J., Graves, J.E., Furey, N.B., 2012. Distribution and habitat associations of billfish and swordfish larvae across mesoscale features in the Gulf of Mexico. PLoS One 7 (4), e34180.

Rooker, J.R., Kitchens, L.L., Dance, M.A., Wells, R.D., Falterman, B., Cornic, M., 2013. Spatial, temporal, and habitat-related variation in abundance of pelagic fishes in the Gulf of Mexico: potential implications of the Deepwater horizon oil spill. PLoS One 8, e76080.

Sanvicente-Añorve, L., Flores-Coto, C., Chiappa-Carrara, X., 2000. Temporal and spatial scales of ichthyoplankton distribution in the southern Gulf of Mexico. Estuar. Coast. Shelf Sci. 51, 463–475.

Savenkoff, C., Vézina, A.F., Gratton, Y., 1997. Effect of a freshwater pulse on mesoscale circulation and phytoplankton distribution in the lower St. Lawrence estuary. J. Mar. Res. 55, 353–381.

Schneider, D.C., 1990. Seabirds and fronts: a brief overview. Polar Res. 8, 17–21.

Shiroza, A., Malca, E., Lamkin, J.T., Gerard, T., Landry, M.R., Stukel, M.R., Laiz-Carrión, R., Swalethorp, R., 2021. Active prey selection in developing larvae of Atlantic bluefin tuna (*Thunnus thynnus*) in spawning grounds of the Gulf of Mexico. J. Plankton Res. https://doi.org/10.1093/plankt/fbab020.

Shropshire, T.A., Morey, S.L., Chassignet, E.P., Bozec, A., Coles, V.J., Landry, M.R., Swalethorp, R., Zapfe, G., Stukel, M.R., 2020. Quantifying spatiotemporal variability in zooplankton dynamics in the Gulf of Mexico with a physical–biogeochemical model. Biogeosciences 17, 3385–3407.

Szczepanski, A.A., 2019. Copepod-microplankton dynamics in the northern gulf of mexico. Master's Thesis. North Carolina State University. https://www.proquest.com/dissertations-theses/copepod-microplankton-dynamics-northern-gulf/docview/2384839450/se-2, 65 Pages.

Teo, S.L., Block, B.A., 2010. Comparative influence of ocean conditions on yellowfin and Atlantic bluefin tuna catch from longlines in the Gulf of Mexico. PLoS one 5 e10756. pmid:20526356.

Ter Braak, C.J., 1986. Canonical correspondence analysis: a new eigenvector technique for multivariate direct gradient analysis. Ecology 67, 1167–1179.

Wade, I.P., Heywood, K.J., 2001. Acoustic backscatter observations of zooplankton abundance and behaviour and the influence of oceanic fronts in the Northeast Atlantic. Deep-Sea Res. II Top. Stud. Oceanogr. 48, 899–924.

Williams, A.K., McInnes, A.S., Rooker, J.R., Quigg, A., 2015. Changes in microbial plankton assemblages induced by mesoscale oceanographic features in the northern Gulf of Mexico. PLoS One 10, e0138230.

Wormuth, J.H., Ressler, P.H., Cady, R.B., Harris, E.J., 2000. Zooplankton and micronekton in cyclones and anticyclones in the Northeast Gulf of Mexico. Gulf of Mexico Science 18 (1), 23–34.

Zimmerman, R.A., Biggs, D.C., 1999. Patterns of distribution of sound-scattering zooplankton in warm-and cold-core eddies in the Gulf of Mexico, from a narrowband acoustic Doppler current profiler survey. J. Geophys. Res. Oceans 104, 5251–5262.