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An Ecological Assessment of the Deep-Pelagic Fish Genus Cyclothone (Gonostomatidae; Stomiiformes), Possibly the World's Most Abundant Fishes, in the Gulf of Mexico

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TABLE OF CONTENTS

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ABSTRACT:

The fish genus *Cyclothone* is considered the most abundant vertebrate taxon on Earth. Despite this assertion, very few detailed ecological studies of this genus exist for any site in the World Ocean, largely due to the lack of expertise (and willingness) to identify specimens from existing sample sets. This study will provide a species-level description of the abundance, vertical distribution, and size structuring of the genus *Cyclothone* in the Gulf of Mexico, a hyper-diverse, deep-pelagic ecosystem that is increasingly impacted by anthropogenic disturbances. As the putative most-abundant fishes in the ecosystem, this characterization is critically needed for a holistic understanding of the deep Gulf of Mexico as an integrated ecosystem. Data were collected during ONSAP and DEEPEND cruises from 2011 – 2021 using MOCNESS trawls from the surface to 1500 m depth.

In this study, the most abundant *Cyclothone* species was *C. pallida* (55.3%), with seven other species each contributing 14 to <0.1% to the total assemblage. Most *Cyclothone* occurred between 600 and 1000 m depth. Light-colored species were primarily found above the 600-m benchmark depth: *C. alba* (200 – 600 m), *C. braueri* (200 – 600 m) and *C. pseudopallida* (200 – 1000 m). Below the 600-m mark, *C. pallida* and *C. acclinidens* were most abundant until another benchmark at 1000 m. Below 1000 m, the dominant species was *C. obscura*. All *Cyclothone* species were non-vertically migrating, with no vertical distribution differences between the day and night trawls. This study is the first documentation of *C. microdon* in the Gulf of Mexico.

KEY WORDS:

Gulf of Mexico, *Cyclothone*, abundance, vertical distribution, species composition

Introduction

The open ocean, the region beyond the continental shelf break that encompasses the pelagic environment, can be classified into zones based on depth and other key abiotic features (Koppelmann & Frost 2008) and comprises upwards of 90% of oceanic environments such as the Gulf of Mexico (GoM) (Sutton et al. 2022). The epipelagic zone is the uppermost, photic layer of the ocean, from the surface to 200 m depth (Sutton 2013). The epipelagic zone is the largest, in terms of area, and most productive zone of the open ocean (Lewallen et al. 2011). The mesopelagic zone, sometimes referred to as the twilight zone, is one of the least understood zones of the ocean (Webb et al. 2010, Sutton et al. 2017b), but accounts for 31% of the total volume of the GoM (Fisher et al. 2016). Available light trends from 1% of surface irradiance at 200 m to 0% at ~1000 m (Costello & Breyer 2017), leaving enough solar light penetration within the mesopelagic zone for a solar cycle pattern to be present but not enough light to support primary production (Sutton 2013). Below 1000 m depth is the bathypelagic zone, characterized by the absence of solar light, low temperatures, and very low amounts of available nutritional resources such as particulate organic carbon (Danovaro et al. 2014). Cumulatively, the meso- and bathypelagic zones represent the largest living space on Earth and account for over 90% of the total volume of the World Ocean (Priede 2017). The deep sea, the pelagic ocean past the depth of the continental shelf, is characterized by high hydrostatic pressure, limited light, and extremely limited food supply. These extremes exist in the form of vertical gradients that influence the biological activity of the ocean (Leroy & Parthiot 1998, Robinson et al. 2010). Research has documented variables, such as chlorophyll concentration, temperature, and salinity, affecting the community composition of mesopelagic and bathypelagic fishes as deep-sea process such as vorticity were found to be influenced by surface factors that established vertical gradients (Fock et al. 2004). Bathymetry and level of the water column have also been documented to be important factors for the structuring of the mesopelagic fauna of the Mediterranean during trawls using various nets such as modified commercial trawls and MOCNESS trawls (Olivar et al. 2012)

The pelagic ocean is a dynamic system where there are no exact boundaries between communities (Sutton 2013). The intermediate-sized organisms termed “micronekton” (actively moving organisms 2-20 cm in length), are a highly important and abundant component of the pelagic ocean, including teleost, crustaceans, mysidaceans, and cephalopods, (Broduer et al. 2005, Sutton et al. 2021). The epipelagic zone is dominated by specialized fishes that have limited connections with the deeper depths as they mainly live in shallow waters, larval and juvenile fishes, fishes that dive to deep depths, and migrating fishes at night (Merrett & Roe 1974, Roe 1984, Hopkins et al. 1996, Sutton 2013). The mesopelagic zone is a common habitat for reflective and bioluminescent vertical migrators within the upper limits of the zone (Denton et al. 1985) and less reflective, less robust fishes within the lower extent of the mesopelagic zone (Salvanes & Kristofersen 2001, Sutton 2013). Vertical migration is done by organisms to increase food availability and decrease predation driven by numerous factors, such as light levels (Brierley 2014). The mesopelagic and bathypelagic zones also host a numerous amount of non-vertical migrators that permanently reside at deeper depths. Vertical distributions are influenced by food availability, light levels, and mobility that cause organisms to have specific physical adaptations to survive within various conditions.

Cyclothone are classified within the class Actinopterygii, order Stomiiformes, family *Gonostomatidae*, and exhibit a cosmopolitan distribution (McEachran & Fechhelm 1998, Nelson et al. 2016). The genus *Cyclothone* now contains 15 recognized species (Fricke et al. 2021), with seven species of *Cyclothone* currently reported from the Gulf of Mexico: *Cyclothone acclinidens, Cyclothone alba, Cyclothone obscura, Cyclothone pallida, Cyclothone pseudopallida*, *Cyclothone parapallida*, and *Cyclothone braueri* (McEachran & Fechhelm 1998, Ross et al. 2010). While there have been many species descriptions within scientific literature of the genus, it was only in the past 40 years that scientists became confident in the taxonomy (Jordan & Evermann 1905, Jespersen 1926, Badcock 1981, Larson et al. 2013, Burton & Lea 2019, Carneiro et al. 2019, Sutton et al. 2020). Previously, studies have not focused on *Cyclothone* as they are described as weak bodied and typically damaged beyond identification within high-volume, open, and knotted mesh trawls (Thompson & Kenchington 2017). These fishes are typically discussed at the genus level and not the species level because of difficulty in identifying *Cyclothone* to genus without substantial expertise (Halliday & Scott 1969, Robinson et al. 2010).

Cyclothone are elongate, slender, and are among the smallest fishes at maturity found within the open ocean (Maynard 1982, McEachran & Fechhelm 1998, Sutton et al. 2010). *Cyclothone* species exhibit a light to dark body coloration gradient at the species level (Bigelow et al. 1964, Maynard 1982). Most fishes within the order Stomiiformes, including *Cyclothone* species, possess photophores (Tchernavin 1953, O'Day 1973) in species-specific patterns (Bigelow et al. 1964, Coad 2019). Bioluminescence is commonly utilized in fishes as a means of communication, a method to attract a mate, attract prey, and avoid predators as light is created by the organisms in an aphotic environment (Lawry 1974, Mensinger & Case 1990, Widder 2010). *Cyclothone* utilize ventral and eye photophores (except *C. obscura*) to counterilluminate, diminishing body silhouette by matching the amount of downwelling light (Davis et al. 2020). The mouth of *Cyclothone* is horizontally set with numerous small teeth present along both the upper and lower jaw (Moyle & Cech 1996). It is possible that the neotenic morphology (the retention of juvenile features into adulthood) of *Cyclothone* has allowed for the genus to become numerically dominant (Maynard 1982). *Cyclothone* never develop spines, unlike many other pelagic fishes, and stay relatively small through their whole life (Sutton & Hopkins 1996a), reducing the energy required to develop.

Cyclothone are zooplanktivores that feed on nauplii, copepods, ostracods, euphausiids and other zooplankton (DeWitt Jr 1972, Mauchline & Gordon 1985, Drazen & Sutton 2017). *Cyclothone* have developed a mouth like other pelagic predators, though much smaller in size, to take advantage of resting migratory organisms as a main food source (Childress & Nygaard 1973). A diet study sampling fishes from The Gully, a submarine canyon off Nova Scotia, characterized *Cyclothone microdon* as feeding on relatively few prey types (mainly calanoid copepods and conchoeciinid ostracods), with infrequent feeding (most stomachs were empty) and low prey numbers per meal (Thompson & Kenchington 2017). *Cyclothone* have been found to feed during the day (Hopkins & Sutton 1998), allowing them to utilize the increased number of vertical migrators found at depth during the day as food resources since zooplankton can vertically migrate to approximately 400 – 500 m depth (NOAA, 2021).

Cyclothone feeding suggests that species within the genus have evolved to optimize prey consumption and energy expenditures, relying on chance or infrequent prey encounters (Maynard 1982, Thompson & Kenchington 2017). Decreasing the required caloric intake likely allows for species to thrive in food-poor environments. Metabolic energy requirements are in part a function of prey consumption and activity, because higher predation leads to more movements and thus a higher caloric intake needed to sustain survival, thus smaller deep-sea fishes such as *Cyclothone* must balance the cost of avoiding predators and obtaining food, whilst lowering metabolic rate to thrive in the deep-sea habitat (Seibel & Drazen 2007).

The genus *Cyclothone* is described as the most abundant vertebrate taxon on Earth (Marshall 1979, Sabates 1990, Cuttitta et al. 2004) and in midwater sampling with nets, they are usually the most common taxon. For example, in The Gully submarine canyon (Western North Atlantic), *Cyclothone* were caught within all IYGPT trawls below 250 m and two-thirds of trawls above 250 m (Thompson & Kenchington 2017).

As currently understood, *Cyclothone* species do not undergo diel vertical migration (Andersen & Sardou 1992, Watanabe et al. 1999), unlike other bioluminescent species that do undergo diel vertical migration to feed in epipelagic waters at night and escape predation by returning to meso- or bathypelagic water during the day (Sutton 2013, Richards et al. 2020). Although adult *Cyclothone* species are not known to vertically migrate on a diel basis, ontogenic migration, with juveniles residing shallower than adults, may vertically structure *Cyclothone* populations (Priede 2017). For example, in the Northeast Atlantic *Cyclothone* larvae occur primarily between the surface to 50 m (Zelck 1993). The development of photophores and pigmentation coincides with the downward migration of each species (Badcock & Merrett 1976, Salvanes & Kristofersen 2001), as photophores and pigementation are utalized for survival within deeper waters. The majority of *Cyclothone* adults occur within the mesopelagic and bathypelagic zones (Table 1).

Table 1. Summary of the global vertical distribution of *Cyclothone* species.

Species	**Pacific**	**Atlantic**	**Other Regions as Specified**	**Citations**
Cyclothone acclinidens	300 – 1900 m; Maximum abundance: 600 – 700 m	500 – 800 m (Equatorial Atlantic)		Smith & Laver 1981 Olivar et al. 2017
Cyclothone alba	300 – 500 m; Maximum abundance: 350 m	300 – 500 m (Equatorial Atlantic) 200 – 500 m (Mid-North Atlantic)		Miya & Nemoto 1986a Olivar et al. 2017 Sutton 2013
Cyclothone pallida	400 m to 1000 m (Sagami Bay);	400 – 700 m (Eastern North Atlantic);		Miya & Nemoto 1986b Maynard 1982 Badcock & Merrett 1977 McClain et al. 2001

	600 – 1300 m (Hawaii)	500 – 700 m (Bahamas); 500 – 600 m (Equatorial Atlantic); 500 – 800 m (Mid-North Atlantic)		Olivar et al. 2017 Sutton 2013
Cyclothone pseudopallida		400 – 500 m (Equatorial Atlantic)		Olivar et al. 2017
Cyclothone braueri		400 – 600 m (Equatorial Atlantic); 200 – 800 m (Mid-North Atlantic)	200 - 550 m (Mediterranean)	Olivar et al. 2017 Laval et al. 1989 Sutton 2013
Cyclothone parapallida	0-1650 (Equatorial Pacific)	400 – 800 m (Equatorial Atlantic)		Ross et al. 2010 Miya 1994
Cyclothone microdon		500 - >1500 m (North Atlantic); 200 – 800 m (Mid-North Atlantic)	500 – 2000 m (Southern Ocean)	Moteki et al. 2009 Moteki et al. 2011 Badcock & Merrett 1976 Sutton 2013
Cyclothone obscura		> 1000 m (Gulf of Mexico)	> 1500 m (Sagami Bay)	Miya & Nemoto 1986a Richards et al. 2020

Given the predominance of this genus in open ocean ecosystems worldwide, knowledge of the abundance and distribution of *Cyclothone* within the Gulf of Mexico (GoM) is integral to our understanding of that ecosystem. The GoM is a semi-enclosed, marginal sea of the Atlantic Ocean with a central basin depth of 3500 m and many dynamic topographical features (Liu et al. 2011). In the Gulf of Mexico and open-ocean ecosystems globally, deep-pelagic micronekton are a direct link between top predators and lower trophic levels. Likewise, zooplankton consumption by micronekton is an important component of carbon sequestration, as micronekton are very abundant and transfer the carbon into the lower zones of the ocean where it remains (Sutton & Hopkins 1996b, Durgham et al. 2014, Sutton et al. 2021). As a prey taxon, *Cyclothone* has been documented in the diets of dragonfishes (Sutton & Hopkins 1996a), decapod Crustacea (Roe 1984), and anglerfishes (Hopkins et al. 1996). Understanding the ecology and abundance of prey could give insight into the health of their predator taxon as resource abundance would be better understood. The goal of this study therefore is to provide a comprehensive ecological assessment of *Cyclothone* given their importance to the GoM ecosystem. Detailed descriptions of *Cyclothone* vertical distributions are available world-wide, but these are lacking in the GoM. Species-specific resolution of *Cyclothone* is a foundational step towards a comprehensive understanding of the structure of the deep-pelagic ichthyofaunal assemblage of the GoM. In this study the assemblage composition, abundance, vertical distribution, and size distributions of *Cyclothone* species will be presented.

The specific aims of this thesis are to: 1) provide a quantitative, species-level characterization of the genus *Cyclothone* in the GoM, 2) quantitatively characterize the vertical distribution of the species regarding influences of depth, solar cycle, and water mass, 3) determine whether any portion of the assemblage undertakes diel vertical migrations, and 4) investigate size structuring of individual species.

2. Materials and Methods

2.1. Sample Collection and Processing

Following the *Deepwater Horizon* oil spill (DWHOS) in 2010, two research programs were created to investigate the impacts of the spill: ONSAP (Offshore Nekton Sampling and Analysis Program) and DEEPEND (Deep Pelagic Nekton Dynamics of the Gulf of Mexico). Both programs were multidisciplinary in nature to achieve a new perspective of the GoM regarding composition, connectivity, drivers, and variability of oceanic micronektonic species and the environment (Boswell et al. 2020, Easson et al. 2020, Timm et al. 2020).

The NOAA-funded ONSAP program occurred from 2010 to 2015 as part of the DWHOS Natural Resource Damage Assessment, with sample collection occurring from 2010 to 2011. The ONSAP consisted of survey sites across a 47-station grid sampled by the M/V *Meg Skansi* (Table 2, Figure 1). The DEEPEND Consortium, from 2015 to this writing, has conducted eight cruise surveys to date on the R/V *Point Sur*. DEEPEND sample sites included a subset of the ONSAP sample locations.

Table 2. Sampling programs providing samples and data for this study, listed in chronological order.

Research Program	Research Vessel	Abbreviation	Duration
ONSAP	*Meg Skansi*	MS 6	01/28/2011 – 03/30/2011
	Meg Skansi	MS 7	04/14/2011 – 06/30/2011
DEEPND	*Point Sur*	DP01	05/01/2015 – 05/08/2015
	Point Sur	DP02	08/08/2015 – 08/21/2015
	Point Sur	DP03	04/30/2016 – 05/14/2016
	Point Sur	DP04	08/05/2016 – 08/19/2016
	Point Sur	DP05	05/01/2016 – 05/11/2017
	Point Sur	DP06	07/19/2018 – 08/02/2018
	Point Sur	DP07	04/24/2021 – 05/06/2021
	Point Sur	DP08	07/25/2022 – 08/08/2022

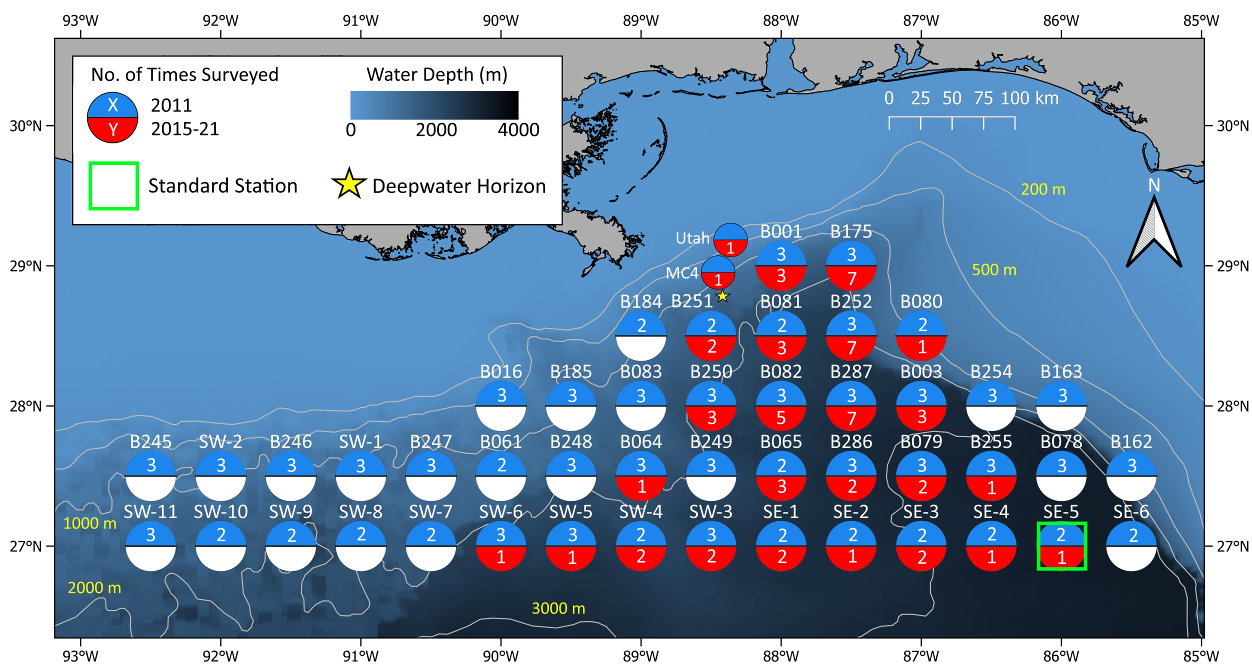

Figure 1. Sample sites from the ONSAP and DEEPEND sampling programs across the Gulf of Mexico. Numbers in blue represent sample sites from the ONSAP cruises and red represents sites from the DEEPEND surveys. Figure from Cook et al. (2020).

Samples were collected with a Multiple Opening Closing Net and Environmental Sensing System (MOCNESS) (Wiebe et al. 1985) with a 10-m^2 mouth size and six nets (mesh size of 3 mm) during all trawls utalized in this research (Figure 2). Each trawl net was numbered according to the order each net was triggered (N0, N1, N2, N3, N4, and N5; Table 3).

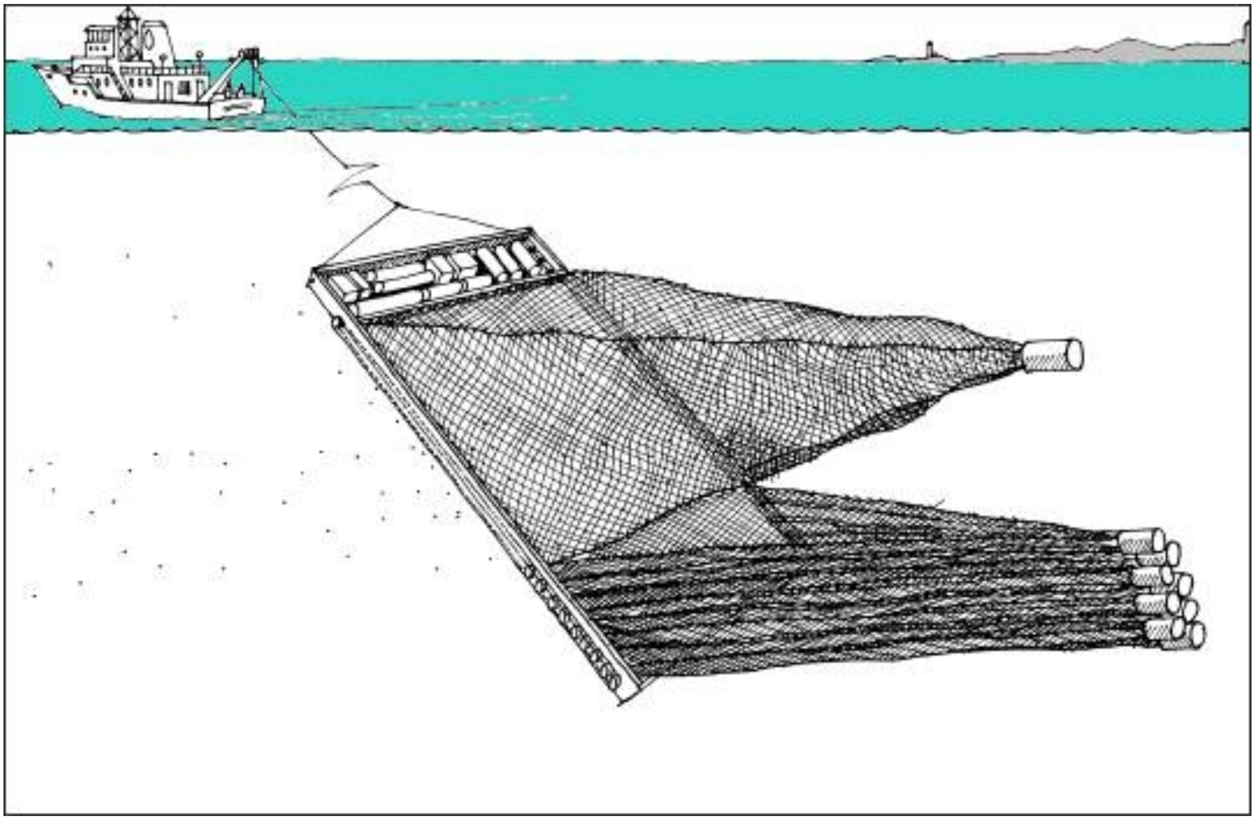

Figure 2. Representation of the MOCNESS equipment utilized for the sample collection during ONSAP and DEEPEND cruises (https://www.omao.noaa.gov/find/media/images/diagram-mocness-net)

Table 3. MOCNESS sampling depths during ONSAP and DEEPEND cruises.

Bin Number	Depth Range
0	Surface – 1500 m
1	1500 – 1200 m
2	1200 – 1000 m
3	1000 – 600 m
4	600 – 200 m
5	200 m – surface

2.2. Specimen Processing

During ONSAP, samples were fixed in 10% formalin at sea. Initial taxonomic identification was completed to the genus level (*Cyclothone*) at the Oceanic Ecology Lab at Nova Southeastern University (NSU). *Cyclothone* samples were not identified to the lowest possible taxa as it was not focus of the ONSAP program as time and expertise were limited. During DEEPEND, the majority of *Cyclothone* were identified to species at sea, and any unidentified *Cyclothone* samples were brought back to NSU for further identification. Once samples arrived at NSU, samples were transferred to a 70% ethanol: water solution.

2.3. Specimen Selection

A total of 540 quantitative trawl samples formed the basis of this study. Data were obtained from 38,287 individuals collected from quantitative samples in the GoM from 2011 to 2021. These samples (Table 4) spanned the 47-station grid presented in Figure 1. Samples were considered quantitative if nets fished within standard depth strata and the flow meter accurately indicated volume filtered by the net. Net 0s were not used in this thesis as those nets fished across several depth bins. Samples collected during MS8 were not incorporated into this study as they were not located at NSU. Additionally, samples had to have a water mass assigned to them to be used for analysis. Lastly, only full deployments (all 5 day/night pairs quantitative) were included in this study.

Table 4. Sample locations for sets of full deployment trawls utilized for analysis of the *Cyclothone* assemblage in the Gulf of Mexico.

MS6	MS7	DP01	DP02	DP03	DP04	DP05	DP06	DP07
B249	B249	B175	B079	B079	B175	B175	B252	B287
SW-6	SW-6	B252	B287	B175	B287	B287		B081
B254	B254		SW-3	B081	SW-5	B081		B252
B078	B079		SE-3	SE-4	SW-3	B252		B082
B255	B081		SW-4	B252	SE-3			
B079	B162		SE-1	SE-5	B252			
B175	SE-6		B286		SW-4			
B287	SW-5				SE-1			
B081	SW-3				SE-2			
	SE-4				B065			
	SE-3							

2.4. Species Identification

Specimens were examined using a Zeiss stereomicroscope (Carl Zeiss™ STEMI 2000-C). External pigmentation, the number and position of photophores, and teeth were the physical attributes utilized following a key created by Ashley Marranzino (2016). For the purposes of this thesis, a DEEPEND database search was conducted and the samples that were already identified to species were not reevaluated during this study but incorporated into the data analysis.

Following the original methods of the DEEPEND Consortium used during ONSAP and DEEPEND collection, species identifications were first documented on data collection sheets and then transferred to the electronic database. Additional data collected during the identification process included wet weight (g) and standard length (mm) of up to 25 individuals of each species per net sample (Table 5). Weight was obtained using a mass balance scale to the nearest hundredth gram and standard length was measured using a standard ruler to the nearest millimeter. For 2011 ONSAP samples, standard length measurements occurred after they were identified to species during the lab processing portion of this thesis. The DEEPEND sample measurements were taken during the identification process that immediately followed sample collection aboard the ship. For this thesis, a search of the DEEPEND database was conducted to obtain the *Cyclothone* standard lengths for samples previously measured during DEEPEND sample collection.

Table 5. Numbers of *Cyclothone* measured for size distribution analysis, presented by depth range.

	Species (Number Measured)					
Depth Range (m)	*acclinidens*	*alba*	*braueri*	*obscura*	*pallida*	*pseudopallida*
0-200	6	17	19	39	142	51
200-600	31	1203	1090	47	1145	1258
600-1000	740	120	104	395	2293	999
1000-1200	89	63	57	1203	1569	89
1200-1500	42	110	74	1730	658	94
Total	908	1513	1344	3414	5807	2491

Outliers were identified as measurements found to be unrealistic or improperly recorded and were removed from analysis. Likewise, outliers were also identified and removed when assessing histograms of each species size range as well as during analysis of residual plots of GLMs. Normality was visually assessed using histograms.

2.5. Species Abundance and Vertical Distribution

The standardized abundance of *Cyclothone* was calculated by dividing specimen counts by volume filtered (m^3) for each net and multiplying by 10^6 (for graphical clarity) following Cook et al. (2020). Volume filtered (m^3) was determined at sea via a magnetically sensing Tsurumi-Seiki-Kosakusho flowmeter attached to the MOCNESS.

To classify the abundance of *Cyclothone* a DAFOR scale was utilized regarding the percent standard abundance of each species following Hearnshaw and Hughey (2010).

Table 6. Species abundance categories based on a DAFOR scale regarding abundance of each species in context of the genus.

Species Abundance Percentage	DAFOR term	Abbreviation
51 – 100%	Dominant	D
31% – 50%	Abundant	A
16 – 30%	Frequent	F
6 – 15%	Occasional	O
1 – 5%	Rare	R
0%	Absent	X

Johnston et al. used a method utilizing sea surface height and temperature at depth to classify water sampled and each type was then assigned to samples using during this study (2019). The GoM can be divided into three different water masses, Loop Current-origin water (LCOW), Gulf Common Water (CW), and mixed water (MIX). Of the samples utalized in this study, a total of 275 samples were collected from Common Water and 100 samples from Loop Current Water.

Cyclothone vertical distributions per species collected in Common Water and Loop Current water masses were plotted and analyzed using R Software (R Core Team 2022). Double-sided histograms of standardized abundance for each species and size class per depth were created to identify vertical distributions including the presence or absence of vertical migration.

Individuals were classified as non-migratory if abundances across solar cycle were consistent. Samples were categorized by solar cycle (day or night) based on collection times relative to the time of sunset and sunrise. To determine the effect of solar cycle on overall frequency of occurrence of *Cyclothone* in trawl samples in the GoM, percentages of trawls catching at least one *Cyclothone* individual were determined out of the total number of trawls investigated.

2.6. GLM Analysis

Standardized abundance was modeled using the "MASS" package (Venables & Ripley 2002) in R software (version 4.2.1, R Core Team 2022) through a series of negative binomial generalized linear models (GLMs) comparing every combination of the predictor variables (depth bin, solar cycle, water mass, sampling period (MS versus DP)) for each *Cyclothone* species. GLMs were used to analyze the abundance and distribution of each *Cyclothone* species due to the low number of zeros, times in which a net did not catch a *Cyclothone* individual, in the dataset . When comparing the AIC scores of a Poisson distribution model to that of a negative binominal model, the negative binomial had a lower score. Thus, negative binomial distribution models were used to assess the significance of the explanatory variables and their interactions regarding *Cyclothone* counts, as those models had the lowest AIC score when compared to the Poisson models. The GLMs investigated patterns from the entire sample depth range (0 – 1500 m) were investigated during the GLM analysis. Volume was assigned to offset the response variable 'Counts' to standardized for sampling effort across all trawls. The following equation represents the full model created to test each possible explanatory variable and their interactions for the vertical distribution of each species (*C. acclinidens*, *C. alba*, *C. braueri*, *C. obscura*, *C. pallida*, and *C. pseudopallida*):

$$\text{Counts} = \text{Depth x Solar Cycle x Sampling Period x Water Mass} + \text{Offset log(Volume)}.$$

Term selection for the Minimum Adequate Model was determined by the p-values provided by the anova() function and conducted by backwards selection of variables and interactions regarding the simpler model's AIC score in comparison to the AIC score of the full model to produce a model of variables and interactions that together best explain the data. Residual plots were used to validate models. The "emmeans" package (Lenth 2023) in R studio was utalized to interpret important variable interactions. The "emmip" function was used to visualize the trends between significant variables.

Another GLM was performed to determine if there is a relationship between standard length, depth, and sampling period using the methods detailed above. Only samples collected in depth bins that represented at least 5% abundance of the species were included in this analysis. Log-normal models were created for each species, as the AIC value was lower than that of a Gaussian model and had residual plots that showed stronger linearity, normality, and homogeneity of the data. The full model created to examine length versus the explanatory variables and their interactions for each species is represented by the following equation:

Standard length = Depth x Solar Cycle x Sampling Period x Water Mass.

Term selection for the Minimum Adequate Model was determined by the p-values provided by the anova() function and conducted by backwards selection of variables and interactions regarding the simpler model's AIC score in comparison to the AIC score of the full model to produce a model of variables and interactions that together best explain the data. Residual plots were used to validate models. The "emmeans" package (Lenth 2023) in R studio was utilized to interpret important variable interactions. The "emmip" function was used to visualize the trends between significant variables.

2.7. Species Size Categorization

Single fixed factor (Model I) ANOVA tests were run for each species in their selected depths bins to determine if length was significantly different between species. Additionally, to determine how *Cyclothone* can be categorized by size, a parametric multiple comparisons test (Tukey test) was conducted using the "multcompView" package (Graves et al. 2019) in R software.

3. Results

A total of 249,787 *Cyclothone* were collected during the ONSAP (205,939 individuals) and DEEPEND (43,848 individuals) surveys, of which 40,296 met the criteria for this analysis (ONSAP = 26,118 and DEEPEND = 14,178). From that subset, 38,286 were identified to the species level (ONSAP = 24,135 and DEEPEND = 14,178) (Table 7). Eight species of *Cyclothone* were identified within this subset of ONSAP and DEEPEND data (Figure 3).

Table 7. Number of *Cyclothone* individuals per species collected during both ONSAP and DEEPEND sampling periods used in data analysis.

	ONSAP	**DEEPEND**
Lowest Taxonomic Identification	N	
Cyclothone pallida	13,409	7,778
Cyclothone obscura	3,539	1,810
Cyclothone pseudopallida	2,490	1,970
Cyclothone acclinidens	1,720	945
Cyclothone alba	1,594	887
Cyclothone braueri	1,377	785
Cyclothone parapallida	6	1
Cyclothone microdon	0	2
Total	**24,135**	**14,178**

Figure 3. *Cyclothone* species of the northern and eastern Gulf of Mexico: A. *Cyclothone alba*, B. *Cyclothone braueri*, C. *Cyclothone pseudopallida*, D. *Cyclothone parapallida*, E. *Cyclothone pallida*, F. *Cyclothone acclinidens*, G. *Cyclothone obscura*, and H. *Cyclothone microdon*. All images by Danté Fenolio, courtesy of DEEPEND.

Quantitative abundance measures, standardized by volume filtered, are presented in Table 8 along with each species DAFOR category. Primary species were *Cyclothone acclinidens*, *C. alba*, *C. braueri*, *C. obscura*, *C. pallida*, and *C. pseudopallida* as they made up the majority of the *Cyclothone* population within the GoM. *Cyclothone microdon* and *C. parapallida* were secondary species because they were deemed rare because of their low abundances. The *Cyclothone* assemblage in the selected samples in the 0 – 1500 m depth range was dominated by *C. pallida* (55.3%) (Figure 6). *Cyclothone. Obscura* (14%), *C. pseudopallida* (11.6%), *C.* acclinidens (7%), *alba* (6.5%), and *C. braueri* (5.6%) were occasional species. *Cyclothone microdon* (0.01%) and *C. parapallida* (0.02%) were rare in the Gulf of Mexico (GoM).

Table 8. Total specimen counts (N) and standardized abundance of *Cyclothone* from 0-1500 m depth in the Gulf of Mexico and attributed DAFOR category.

Lowest taxonomic identification	**N**	**Standardized Abundance (Ind. 10^{-6} m^{-3})**	**DAFOR Category**
Cyclothone pallida	21,187	192.2	Dominant
Cyclothone obscura	5,349	48.5	Occasional
Cyclothone pseudopallida	4,434	40.2	Occasional
Cyclothone acclinidens	2,664	24.2	Occasional
Cyclothone alba	2,481	22.5	Occasional
Cyclothone braueri	2,162	19.6	Occasional
Cyclothone parapallida	7	0.06	Rare
Cyclothone microdon	2	0.02	Rare
TOTAL	38,286	347.28	

At least one *Cyclothone* individual was collected in 93.6% of ONSAP and DEEPEND trawl samples. (Table 9). *Cyclothone* frequency of occurrence was nearly identical in day and night samples, with a 0.1% difference.

Table 9. Percent frequency of occurrence of *Cyclothone* in trawl samples in the Gulf of Mexico.

Solar Cycle		
Day	Night	Day & Night Combined
93.5%	93.6%	93.6%

3.1. Vertical Distribution

Abundances were best predicted by different explanatory variables and their interaction with AIC values of a more simplistic model reflecting (Minimum Adequate Model, MAM) (Table 10). All p-values of the selected terms were found to be significant (Table 11). Non-investigated variables are also responsible for the distribution of *Cyclothone*, as R^2 values show the selected models do not fully explain all the data (Table 10).

Table 10. Minimum Adequate Model Negative Binominal GLM investigating which variables and their interaction best explain the abundance of *Cyclothone* in the Gulf of Mexico with AIC comparison to the full model.

Species	Minimum Adequate Model (MAM)	MAM AIC	Full Model AIC	R^2
Cyclothone acclinidens	Counts = Depth + Depth : Sampling Period + Depth : Watermass + offset(log(Volume)	1275.503	1297.141	0.655
Cyclothone alba	Counts = Depth + Sampling Period + Depth : Watermass + offset(log(Volume)	1299.496	1341.733	0.563
Cyclothone braueri	Counts = Depth + Sampling Period + Watermass + Solar Cycle : Water mass + Depth : Watermass + Solar Cycle : Watermass + offset(log(Volume)	1123.645	1151.247	0.649
Cyclothone obscura	Counts = Depth + Solar Cycle + Sampling Period + Watermass + Depth : Watermass + offset(log(Volume)	2805.397	2830.813	0.563
Cyclothone pallida	Counts = Depth + Sampling Period + Watermass + Depth : Watermass + offset(log(Volume)	3902.362	3941.170	0.657
Cyclothone pseudopallida	Counts = Depth + Solar Cycle + Sampling Period + Watermass + Solar Cycle : Sampling Period + Depth : Watermass + offset(log(Volume)	1800.544	1838.674	0.694

Table 11. ANOVA p-value results from a Minimum Adequate Model Negative Binominal GLM investigating which variables and their interaction best explain the abundance of *Cyclothone* in the Gulf of Mexico.

Cyclothone acclinidens	
Depth	< 0.001
Depth : Sampling Period	< 0.001
Depth : Water mass	0.013
Cyclothone alba	
Depth	< 0.001
Sampling Period	< 0.001
Depth : Water mass	< 0.001
Cyclothone braueri	
Depth	< 0.001
Sampling Period	< 0.001
Water mass	0.029
Depth : Solar Cycle	0.010
Depth : Water mass	0.025
Watermass : Solar Cycle	0.034
Cyclothone obscura	
Depth	< 0.001
Solar Cycle	0.004
Sampling Period	< 0.001
Water mass	< 0.001
Depth : Watermass	< 0.001
Cyclothone pallida	
Depth	< 0.001
Sampling Period	< 0.001
Water mass	0.002
Depth : Watermass	< 0.001
Cyclothone pseudopallida	
Depth	< 0.001
Solar Cycle	0.003
Sampling Period	< 0.001
Water mass	< 0.001
Solar Cycle : Sampling Period	0.006
Depth : Water mass	< 0.001

Depth was an important model factor for all species. The genus *Cyclothone* (all species combined) occurred in maximum abundance between 600 and 1000 m depth (Table 12). *Cyclothone* abundance was lowest in the 0 – 200 depth range. However, species-specific depth patterns were apparent (Figure 4). The dominant species, *Cyclothone pallida*, occurred throughout the 0 – 1500 m depth range sampled but was most abundant within the 600–1000 m depth bin (7,486 Ind. 10^{-6} m^{-3}, 58 % of species total abundance, Table 13). *Cyclothone alba* was most abundant between 200 – 600 m (1,095 Ind. 10^{-6} m^{-3}, 86 % of species total abundance, Table 13), with fewer individuals in other sampled depth ranges. *Cyclothone braueri* was most abundant between 200 – 600 m depth (1143 Ind. 10^{-6} m^{-3}, 87 % percent of species total abundance, Table 13), with minimal occurrences in other depth bins. *Cyclothone pseudopallida* was most prevalent between 200 – 600 m (1635 Ind. 10^{-6} m^{-3}, 61 % of species total abundance, Table 13) and 600 – 1000 m (899 Ind. 10^{-6} m^{-3}, 34 % of species total abundance, Table 13) depths. *Cyclothone acclinidens* was most concentrated between 600 – 1000 m (1392 Ind. 10^{-6} m^{-3}, 88 % of species total abundance, Table 13). *Cyclothone obscura* was most abundant between 1200 – 1500 m (1,553 Ind. 10^{-6} m^{-3}, 46 % of species total abundance, Table 13) and 1000 – 1200 m (1428 Ind. 10^{-6} m^{-3}, 43 % of population, Table 13).

Table 12. Percent by depth bin of overall vertical distribution of primary species of *Cyclothone* in the Gulf of Mexico.

Depth (m)	Percent *Cyclothone* Abundance (%)
0 - 200	0.84
200 - 600	28.47
600 - 1000	47.01
1000 - 1200	16.08
1200 - 1500	7.60

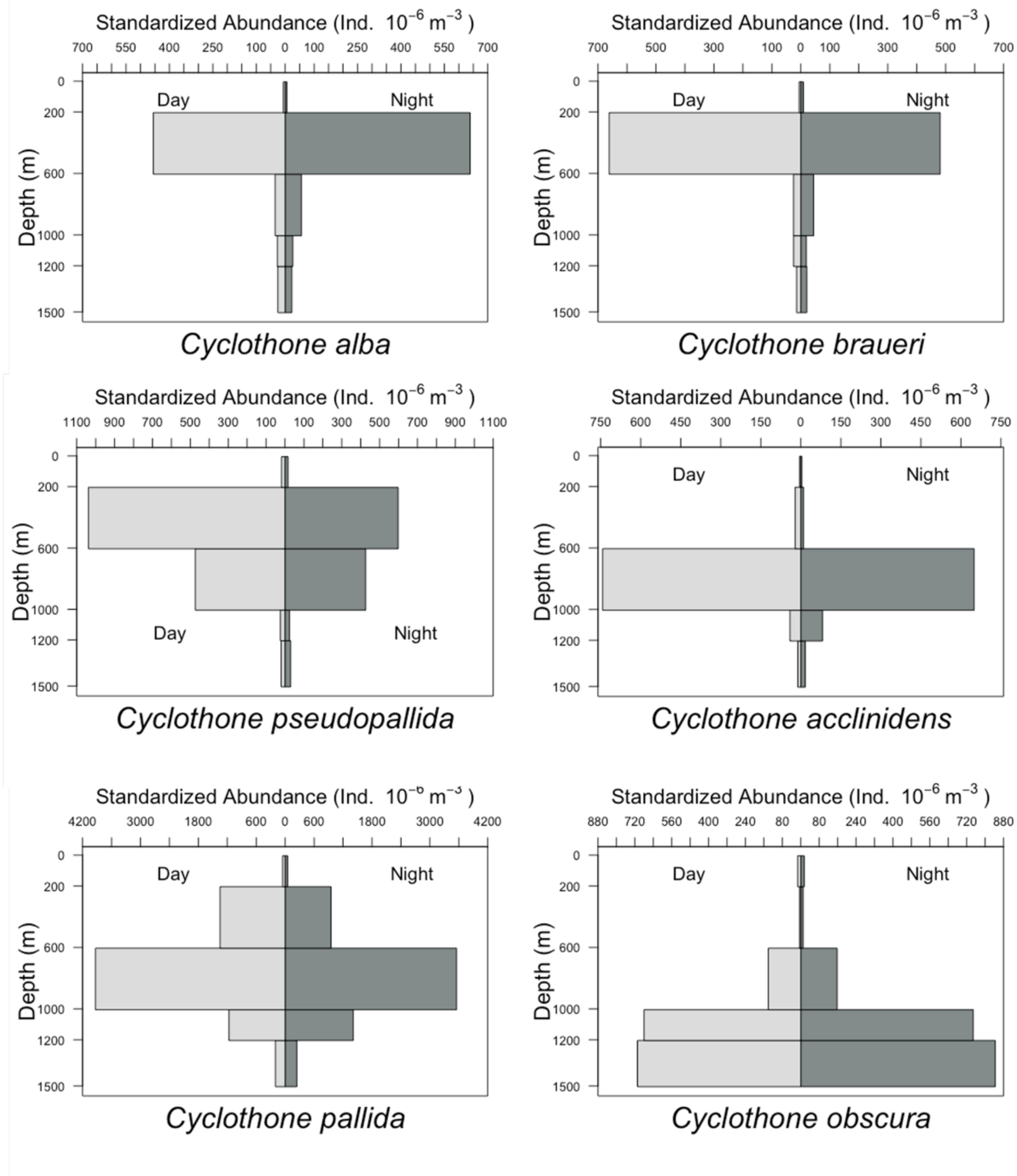

Figure 4. Diel vertical distributions of *Cyclothone* species in the Gulf of Mexico from the surface to 1500 m depth.

Table 13. Percent of total abundance by depth for each primary species of *Cyclothone* in the Gulf of Mexico.

Depth (m)	*Cyclothone alba*	*Cyclothone braueri*	*Cyclothone pseudopallida*	*Cyclothone pallida*	*Cyclothone acclinidens*	*Cyclothone obscura*
0 - 200	0.84	1.12	1.32	0.81	0.58	0.87
200 - 600	86.04	87.31	60.79	17.62	1.93	0.48
600 - 1000	6.22	5.46	34.17	58.08	88.05	9.05
1000 - 1200	3.62	3.43	1.85	20.06	7.7	43.13
1200 - 1500	3.28	2.68	1.87	3.43	1.74	46.47

The two rare species, *C. microdon* and *C. parapallida,* had low occurrences (N = 2 and N = 7, respectively). Distribution patterns for *C. parapallida* and *C. microdon* are presented (Figure 5) but will not be discussed further due to sample size limitation.

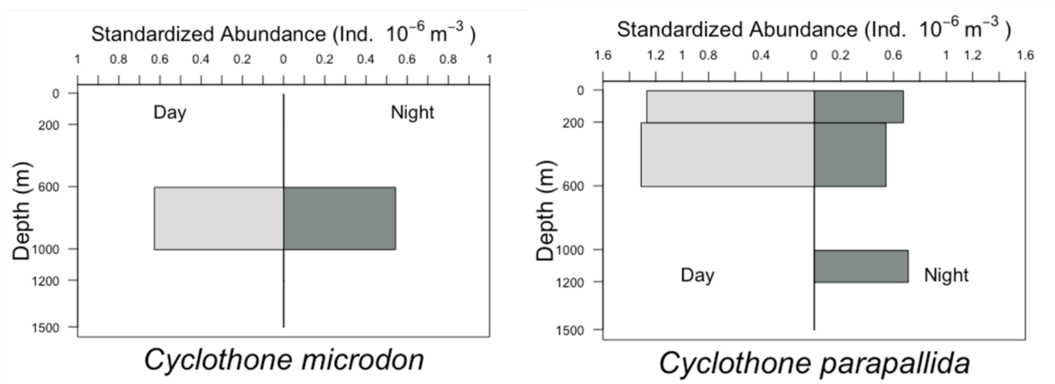

Figure 5. Diel vertical distributions of *Cyclothone parapallida* and *Cyclothone microdon* in the Gulf of Mexico.

An interaction between solar cycle and depth was found to be important when modeling the distribution of *C. braueri* (Table 10). *Cyclothone braueri* decreased in abundance within 200 – 600 m and 1000 – 1500 m across day and night sampling and is expected to increase slightly within night sampling between 600 – 1000 m (Figure 6).

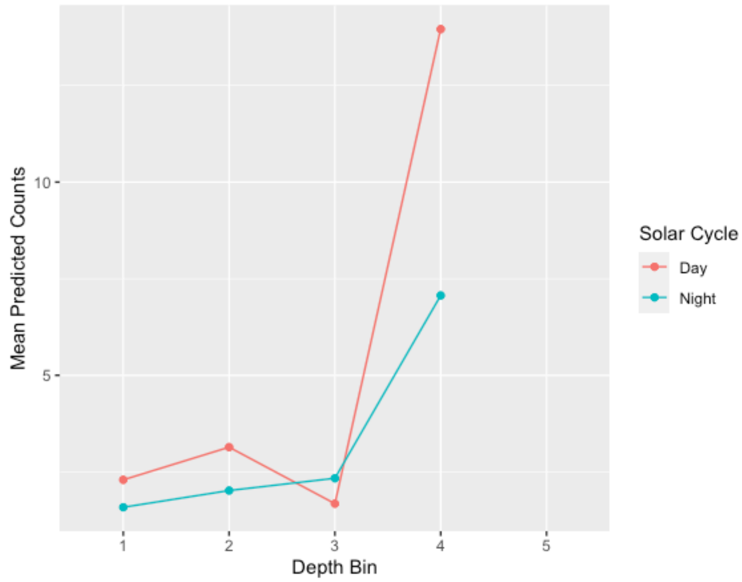

Figure 6. Prediction plot describing the modeled relationship of solar cycle interacting with depth for *Cyclothone braueri*. Depth bin 5 (0 – 200 m) prediction was not completed as there were no *C. braueri* caught within that depth across all sampling variables.

Water mass was a significant term for modeling *C. braueri*, *C. obscura*, *C. pallida*, and *C. pseudopallida* (Table 11). Standardized abundance for *Cyclothone* was higher in Common Water than Loop Current Water (Figure 7). *Cyclothone* exhibited vertical distributions within Loop Current Water deeper than that of Common Water (Figure 7, Figure 8). Within Loop Current Water *C. alba*, *C. braueri*, and *C. pseudopallida* occurred in greater abundances within Common Water depths during the day than at night. *Cyclothone braueri* abundance within water mass was affected by solar cycle (Figure 9). An increased amount of *C. braueri* is expected within Common Water during the day.

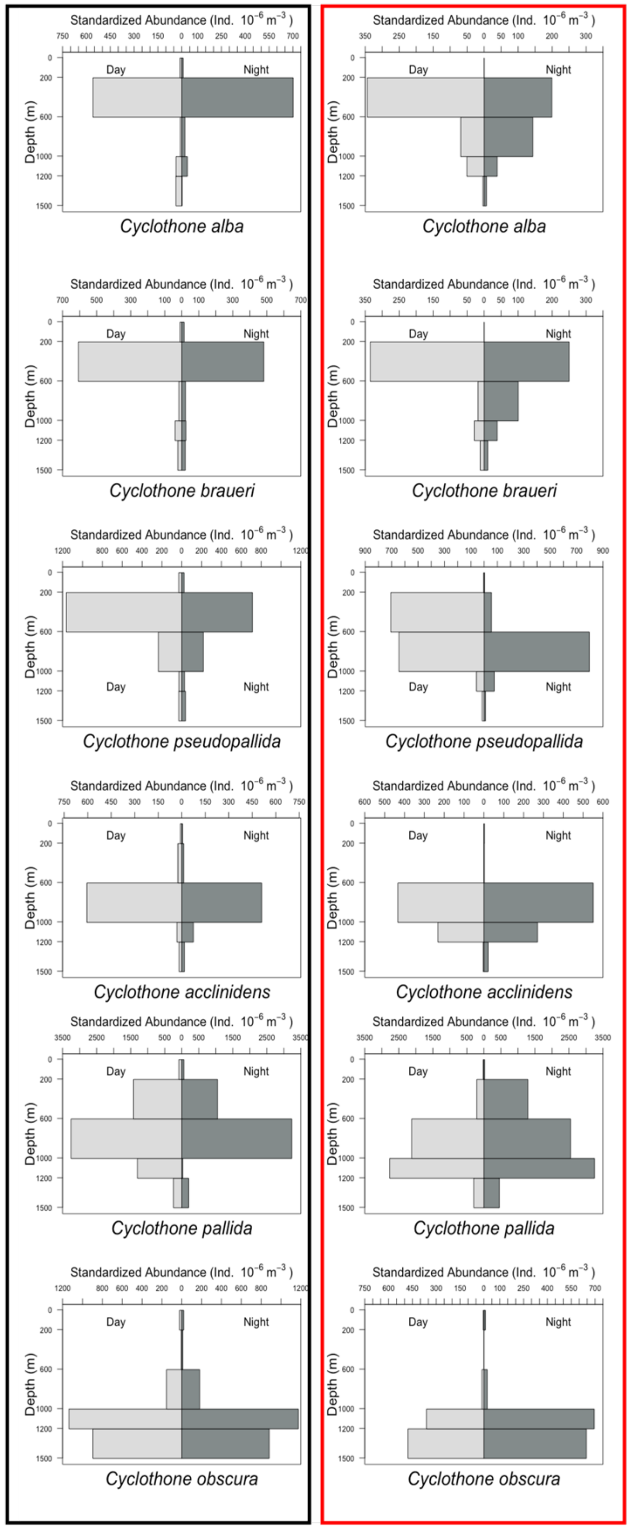

Figure 7. Diel vertical distributions of *Cyclothone* species in the Gulf of Mexico plotted by water mass, Common Water (black) and Loop Current Water (red).

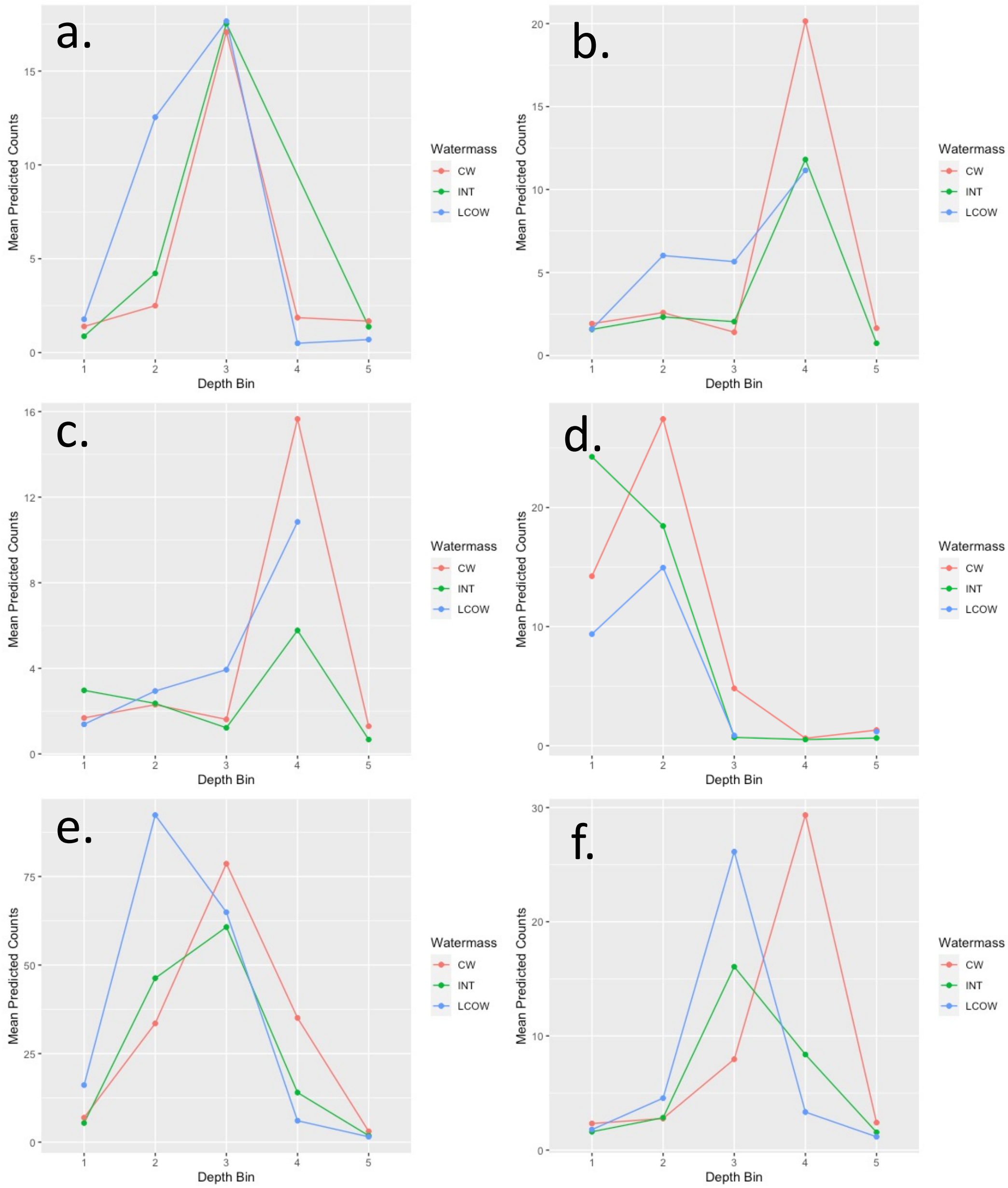

Figure 8. Prediction plot describing the modeled relationship of depth (depth bins) interacting with water mass for *Cyclothone*. a. *Cyclothone acclinidens*, b. *Cyclothone alba*, c. *Cyclothone braueri*, d. *Cyclothone obscura*, e. *Cyclothone pallida*, and f. *Cyclothone pseudopallida*

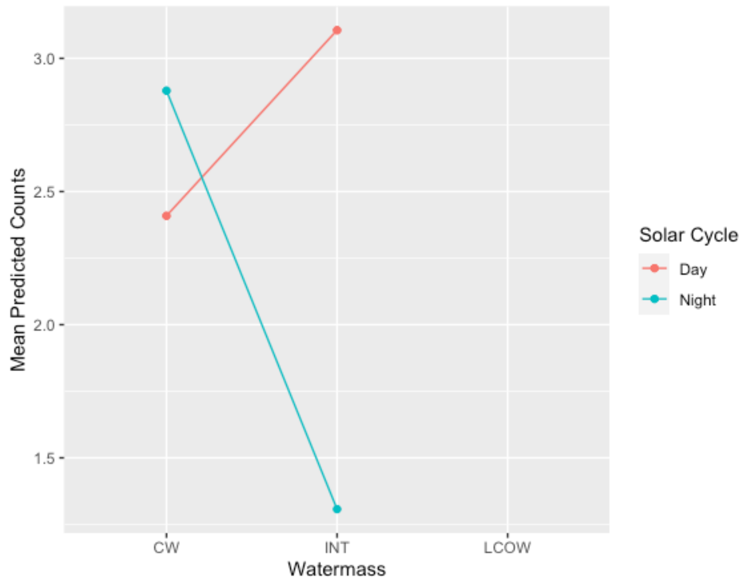

Figure 9. Prediction plot describing the modeled relationship of solar cycle interacting with water mass for *Cyclothone braueri*. Loop Current Water (AR) prediction is absent as there were no *C. braueri* caught within all factor levels of the variables depths during day and night trawls in AR water.

Models for all species except *C. acclinidens* retained the variable sampling period (Table 10). Over the duration of the 10-year sampling program, each species was found within previously reported (ONSAP) depth ranges during the subsequent research sampling program (DEEPEND) (Figure 10), however, *Cyclothone* standardized abundance (Ind. 10^{-6} m^{-3}) across both day and night sampling trawls from 0 – 1500 m decreased by 56% over the sampling period (ONSAP and DEEPEND), from 175,949 to 77,415 (Table 14). *Cyclothone obscura* experienced the largest decrease at 74%. *Cyclothone pallida* had the next highest percent decrease over the sampling period at 56%. *Cyclothone braueri* decreased by 51%. Both *C. alba* and *C. acclinidens* decrease by 52%. *Cyclothone pseudopallida* had the smallest change in total standard abundance over the sampling period (30%).

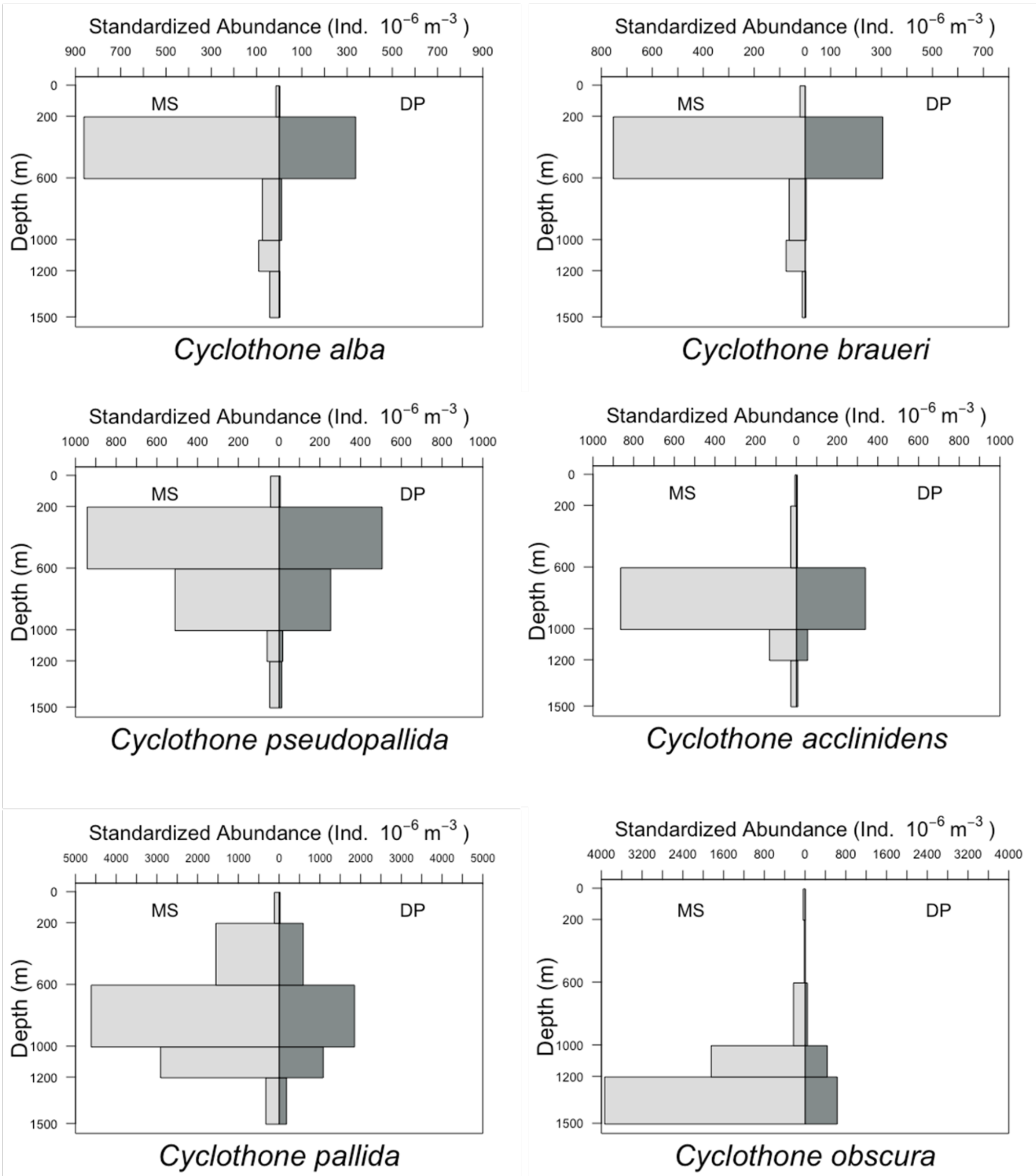

Figure 10. Standardized abundance (Ind. 10^{-6} m^{-3}) of combined day and night sampling of *Cyclothone* in the Northern Gulf of Mexico as a function of sampling program (MS = ONSAP and DP = DEEPEND).

Table 14. Change in standard abundance of *Cyclothone* over the sampling period.

Species	Total Standard Abundance MS	DP	Percent Change
Cyclothone obscura	32,881.59	8,537.10	-74
Cyclothone pallida	96,555.90	42,947.27	-56
Cyclothone acclinidens	11,027.89	5,311.45	-52
Cyclothone alba	10,481.38	5,023.55	-52
Cyclothone braueri	9,048.11	4,446.69	-51
Cyclothone pseudopallida	15,901.44	11,131.86	-30
Total	175896.307	77397.9695	-56

Cyclothone acclinidens standardized abundance decreased with depth across sampling periods (Figure 11), as shown by the interaction of depth and sampling period being a retained variable in the minimum adequate model (Figure 10).

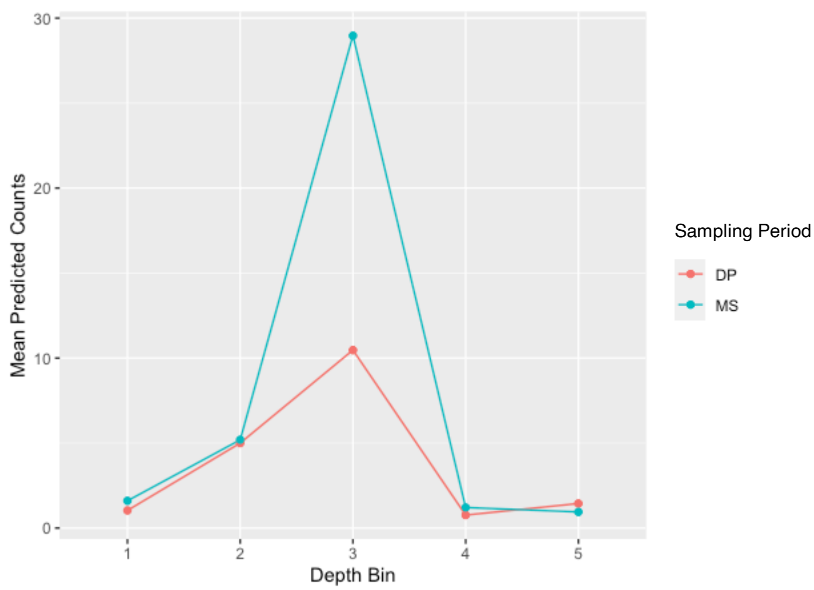

Figure 11. Prediction plot describing the modeled relationship of depth (depth bins) interacting with sampling period for *Cyclothone acclinidens*.

Cyclothone pseudopallida standardized abundance was partially explained by the interaction of solar cycle and sampling period (Table 10). *Cyclothone pseudopallida* standardized abundance is predicted to decrease between trawls during the day and night for both sampling programs (Figure 12).

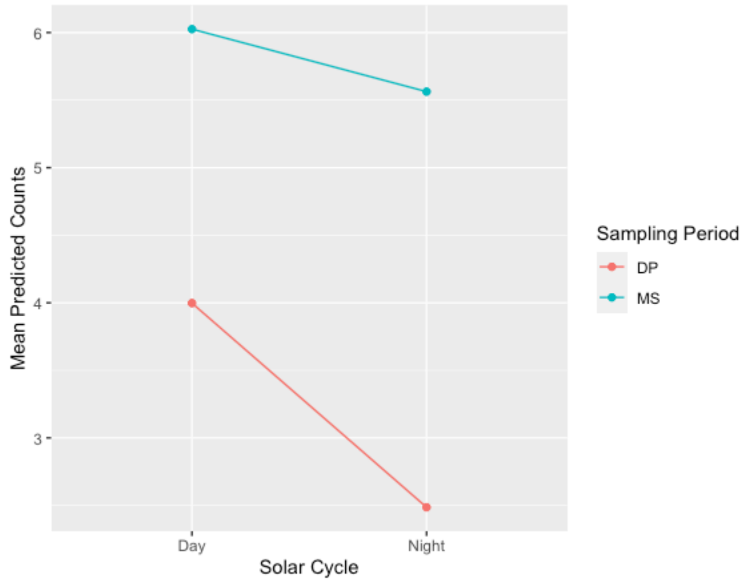

Figure 12. Prediction plot describing the model factor of solar cycle interacting with sampling period for *Cyclothone pseudopallida*.

3.2. *Cyclothone* Size Variation

Cyclothone specimens collected during the two sampling programs ranged in size from 8 mm to 61 mm (SL), with the majority of *Cyclothone* specimens collected between 20-40 mm SL (Table 15, Figure 13). *Cyclothone obscura* exhibited the largest range (8 – 61 mm) of sizes and the largest measured individual (61 mm), while the smallest range (8 mm – 32 mm) was from *C. alba*. *Cyclothone braueri*, *C. pseudopallida*, and *C. obscura* lengths were normally distributed, while *C. alba*, *C. pallida*, and *C. acclinidens* exhibited a bimodal distribution (Figure 14).

Table 15. Standard length (mm) measurements of *Cyclothone* species in the Gulf of Mexico, including minimum, maximum, mean, and standard deviation.

	Standard Length Measurements (mm)		
Species	**Minimum**	**Maximum**	**Mean**
Cyclothone obscura	8	61	32 (+/- 11)
Cyclothone acclinidens	13	50	30 (+/- 5)
Cyclothone pallida	10	60	29 (+/- 9)
Cyclothone pseudopallida	10	50	29 (+/- 6)
Cyclothone alba	8	32	22 (+/- 4)
Cyclothone braueri	10	41	22 (+/- 3)

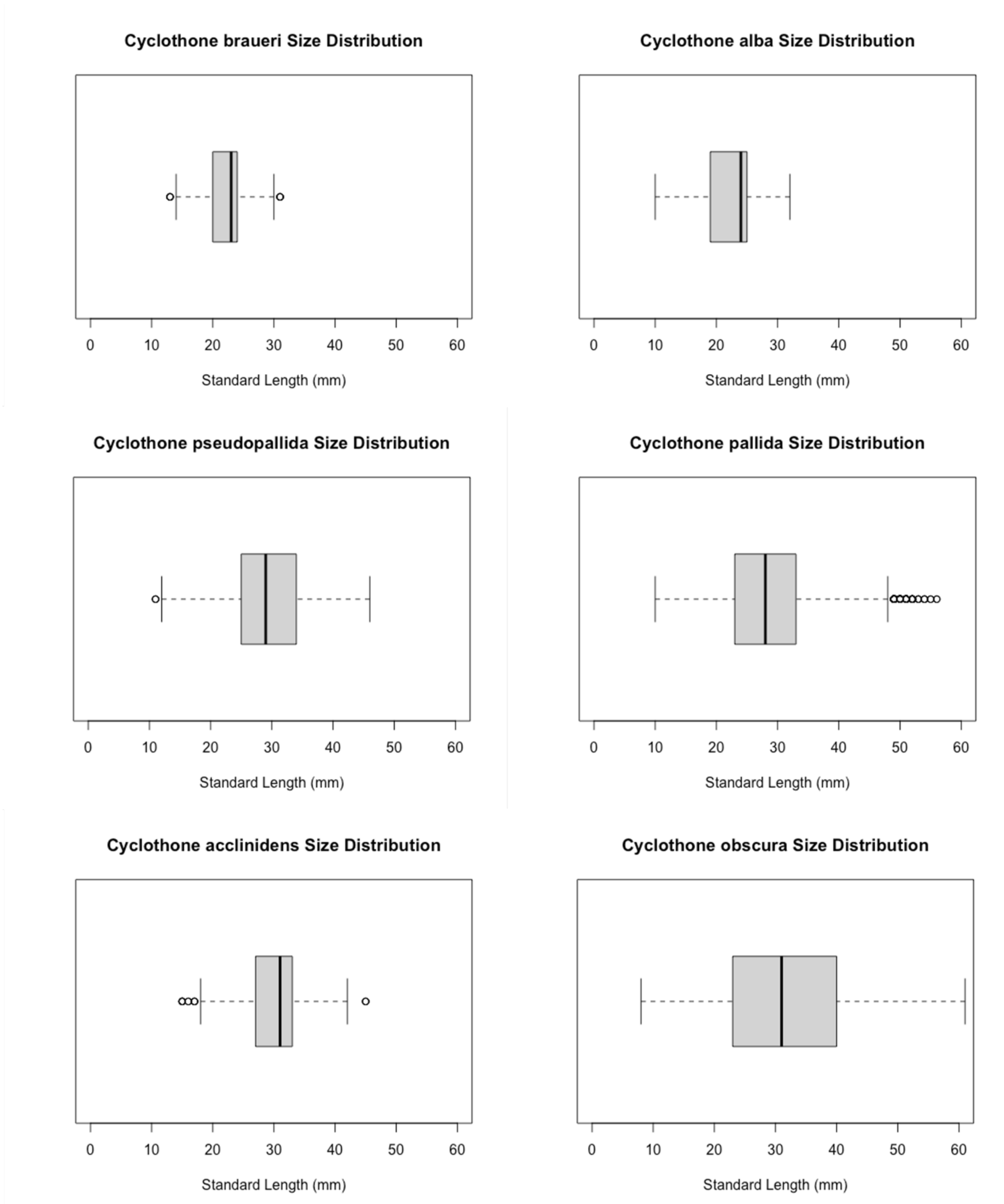

Figure 13. Standard length distributions of *Cyclothone* species collected in the Gulf of Mexico.

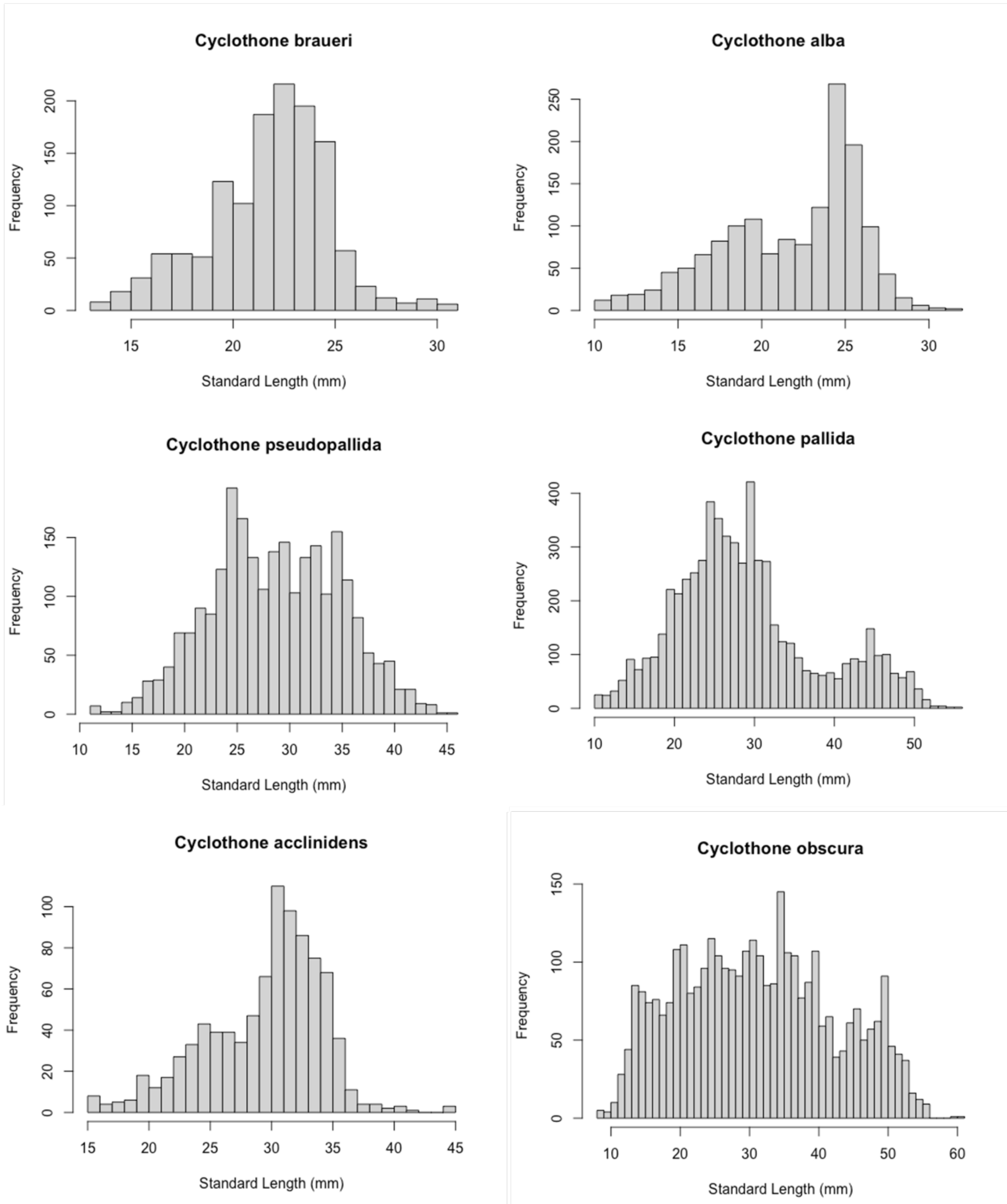

Figure 14. Size-frequency distributions of *Cyclothone* species collected in the Gulf of Mexico.

ANOVA results indicated significant differences in the standard lengths of *Cyclothone* species. *Cyclothone braueri* and *C. alba* had the smallest average lengths (22 mm and 22 mm, respectfully). The largest species was *C. obscura* (averaged 32 mm). The remaining species (*C. pallida*, *C. acclinidens*, and *C. pseudopallida*) all had intermediate average lengths (29 mm, 30 mm, and 29 mm, respectively). A Tukey test (Table 16) confirmed that there were three size groups of *Cyclothone* species. Group A, the smallest-bodied, comprised *C. alba* and *C. braueri*, Group B, the largest-bodied, comprised *C. obscura*, and Group C, the intermediate-sized species, comprised *C. pallida*, *C. acclinidens*, and *C. pseudopallida*.

Table 16. Results from a Tukey test for the interactions between *Cyclothone* species to determine different size classes.

Interaction	p-value
C. alba – C. acclinidens	< 0.001
C. braueri – C. acclinidens	< 0.001
C. obscura – C. acclinidens	< 0.001
C. pallida – C. acclinidens	0.453
C. pseudopallida – C. acclinidens	0.086
C. braueri – C. alba	0.999
C. obscura – C. alba	< 0.001
C. pallida – C. alba	< 0.001
C. pseudopallida – C. alba	< 0.001
C. obscura – C. braueri	< 0.001
C. pallida – C. braueri	< 0.001
C. pseudopallida – C. braueri	< 0.001
C. pallida – C. obscura	< 0.001
C. pseudopallida – C. obscura	< 0.001
C. pseudopallida – C. pallida	0.598

Size variations were best predicted by different explanatory variables and their interaction with AIC values of a more simplistic model reflecting (Minimum Adequate Model, MAM) (Table 17). All p-values of the selected terms were found to be significant (Table 18). Non-investigated variables are also responsible for the distribution of *Cyclothone*, as R^2 values show the selected models do not fully explain all the data (Table 17).

Table 17. Minimum Adequate Model Negative Binominal GLM investigating which variables and their interaction best explain the size structure of *Cyclothone* in the Gulf of Mexico with AIC comparison to the full model.

Species	Minimum Adequate Model (MAM)	MAM AIC	Full Model AIC	R^2
Cyclothone acclinidens	Standard length = Water mass + Period + Water mass: Depth : Solar Cycle + Sampling Period :Depth : Solar Cycle	-4086.799	-4079.310	0.063
Cyclothone alba	Standard length = Depth + Water mass + Sampling Period + Sampling Period : Solar Cycle	-2886.731	-2878.264	0.132
Cyclothone braueri	Standard length = Water mass + Period + Depth : Water mass + Depth : Sampling Period + Depth : Solar Cycle + Depth : Water mass : Sampling Period + Depth : Water mass : Solar Cycle	-3266.688	-3269.252	0.122
Cyclothone obscura	Standard length = Depth + Water mass + Sampling Period + Solar Cycle + Depth : Water mass + Depth : Sampling Period + Water mass : Sampling Period + Depth : Water mass : Sampling Period : Solar Cycle	-3921.169	-3921.169	0.366
Cyclothone pallida	Standard length = Depth + Water mass + Sampling Period + Solar Cycle + Depth : Water mass + Water mass : Sampling Period + Depth : Solar Cycle + Water mass : Solar Cycle	-7127.629	-7116.092	0.158
Cyclothone pseudopallida	Standard length = Depth + Water mass + Sampling Period + Solar Cycle + Depth : Water mass + Sampling Period : Solar Cycle	-4696.350	-4697.058	0.208

Table 18. ANOVA p-value results from a Minimum Adequate Model Log-Normal GLM investigating which variables and their interaction best explain the standard length of *Cyclothone* in the Gulf of Mexico.

Cyclothone acclinidens	
Water mass	< 0.001
Sampling Period	< 0.001
Water mass : Depth : Solar Cycle	0.007
Sampling Period : Depth : Solar Cycle	0.016
Cyclothone alba	
Depth	0.002
Water mass	< 0.001
Sampling Period	< 0.001
Sampling Period : Solar Cycle	0.002
Cyclothone braueri	
Water mass	< 0.001
Sampling Period	< 0.001
Water mass : Depth	< 0.001
Sampling Period : Depth	< 0.001
Depth : Solar Cycle	< 0.001
Water mass : Sampling Period : Depth	< 0.001
Water mass : Depth : Solar Cycle	0.002
Cyclothone obscura	
Depth	< 0.001
Water mass	< 0.001
Sampling Period	< 0.001
Solar Cycle	0.004
Depth : Water mass	< 0.001
Depth : Sampling Period	< 0.001
Water mass : Sampling Period	< 0.001
Depth : Water mass : Sampling Period : Solar Cycle	< 0.001
Cyclothone pallida	
Depth	< 0.001
Water mass	< 0.001
Sampling Period	< 0.001

Solar Cycle	0.002
Depth : Water mass	< 0.001
Water mass : Sampling Period	< 0.001
Depth : Solar Cycle	0.004
Water mass : Solar Cycle	0.017
Cyclothone pseudopallida	
Depth	< 0.001
Water mass	< 0.001
Sampling Period	< 0.001
Solar Cycle	0.004
Depth : Water mass	0.007
Sampling Period : Solar Cycle	0.022

All species except for *C. acclinidens* and *C. braueri* had models that contained depth as an important factor for standard length (Figure 15). As depth decreased size of *Cyclothone* increased.

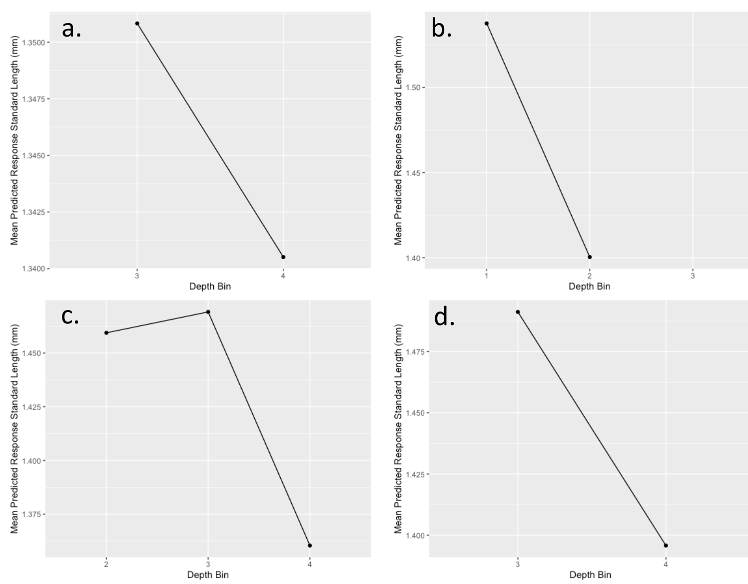

Figure 15. Prediction plot describing the model factor of depth interacting for a. *Cyclothone alba,* b. *Cyclothone obscura*, c. *Cyclothone pallida*, and d. *Cyclothone pseudopallida*.

Boxplots of size sizes of each species in their primary depth bins are presented in Figure 16. *Cyclothone alba* was mainly concentrated between 200 – 600 m and 600 – 1000 m. *Cyclothone alba* collected from 200 – 600 m averaged a standard length of 23 mm. Those from 600 – 1000 m had a higher average standard length of 22 mm. *Cyclothone braueri* was concentrated in depths between 200 – 600 m and 6000 – 1000 m. Standard length of *C. braueri* varied depending on depth. Average size of *C. braueri* within 200 – 600 m was 22 mm and between 600 – 1000 m was 21.5 mm. *Cyclothone pseudopallida* were on average the largest within 600 – 1000 m with mean lengths of 32 mm. *C. pseudopallida* between 200 – 600 m averaged 27 mm in standard length. *Cyclothone pallida* were largest between 1000 – 1200 m and 600 – 1000 m, with average lengths of 29 and 31 mm. Between 200 – 600 m *C. pallida* averaged 27 mm. *Cyclothone obscura* had highest standardized abundances between 1200 – 1500 m, 1000 – 1200 m, and 600 – 1000 m. Average standard length for *C. obscura* was 23 mm between 600 – 1000 m, 27 mm between 1000 – 1200 m, and 36 mm 1200 – 1500 m. *Cyclothone acclinidens* averaged 31 mm between 1000 – 1200 m and 31 mm between 600 – 1000 m.

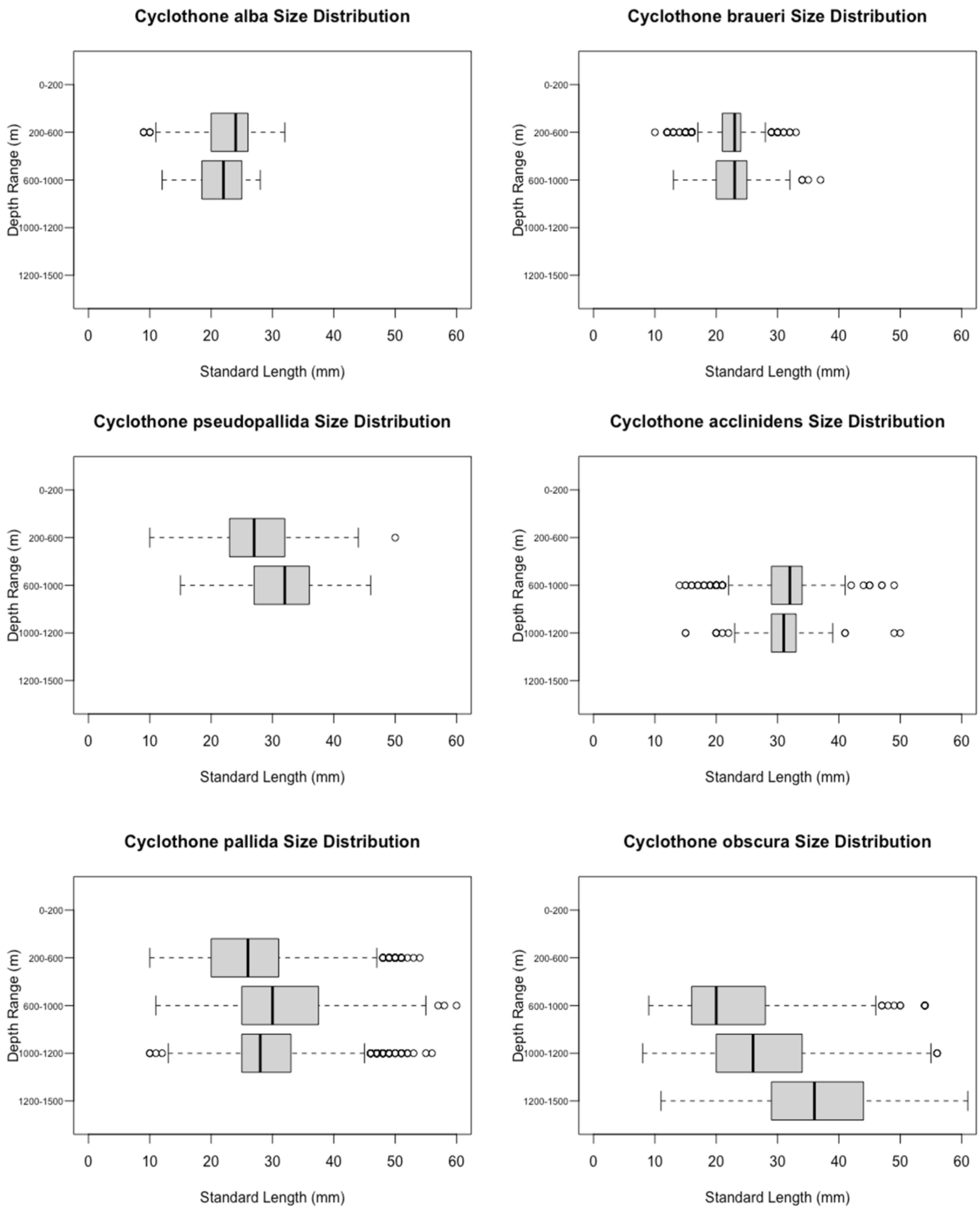

Figure 16. Size distribution of *Cyclothone* species in the Northern Gulf of Mexico as a function of depth. Represented depth bins contained at least 5 % of the overall abundance of each species.

Watermass was an important component of all models for size of *Cyclothone* (Table 17). *Cyclothone acclinidens*, *C. alb*a, *C. pallida*, and *C. pseudopallida* were smaller within Loop Current Water (AR) than Common Water (CW) (Figure 17). Figure 17 also demonstrates that *C. braueri* and *C. obscura* are larger within Loop Current Water than Common Water.

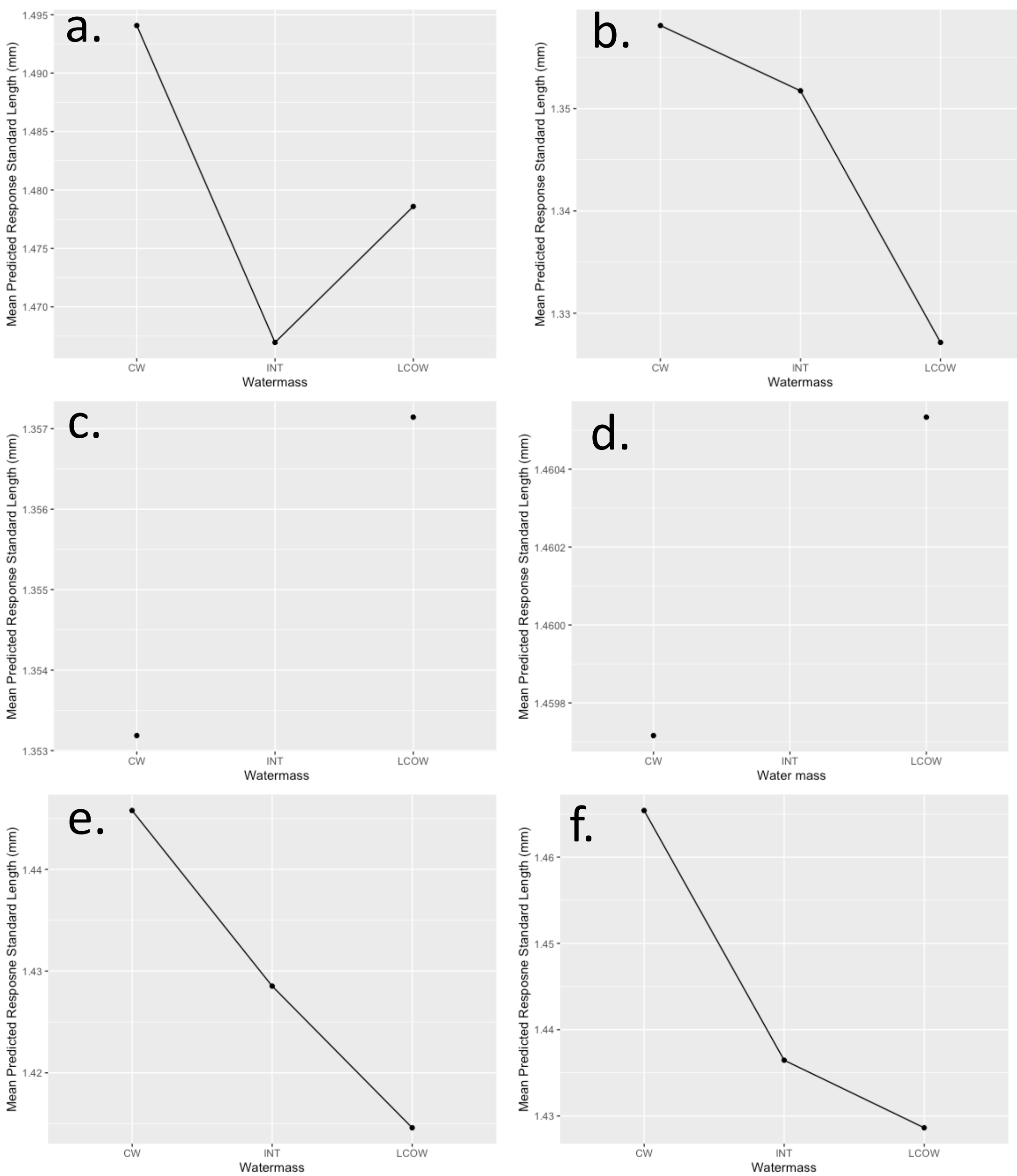

Figure 17. Prediction plot describing the model factor water mass for, a. *Cyclothone acclinidens*, b. *Cyclothone alba*, c. *Cyclothone braueri*, d. *Cyclothone obscura*, e. *Cyclothone pallida*, and f. *Cyclothone pseudopallida.* AR represents Loop Current Water, CW represents Common water, and INT represents Intermediate Water.

The interaction between depth and water mass was an important factor for the models explaining the standard length of *C. braueri*, *C. obscura*, *C pallida*, and *C. pseudopallida* (Table 17). Size decreased across depth for each water mass, but standard length was typically smaller within each depth for Loop Current water when compared to the same depth in Common Water (Figure 18). *Cyclothone braueri* within depth bin 3 (600 – 1000 m) does not follow the trend, as individuals in Loop Current water were larger than those found in Common Water. As well, *C. obscura* within depth bin 3 (600 – 1000 m) were also on average longer in Loo Current water than Common Water.

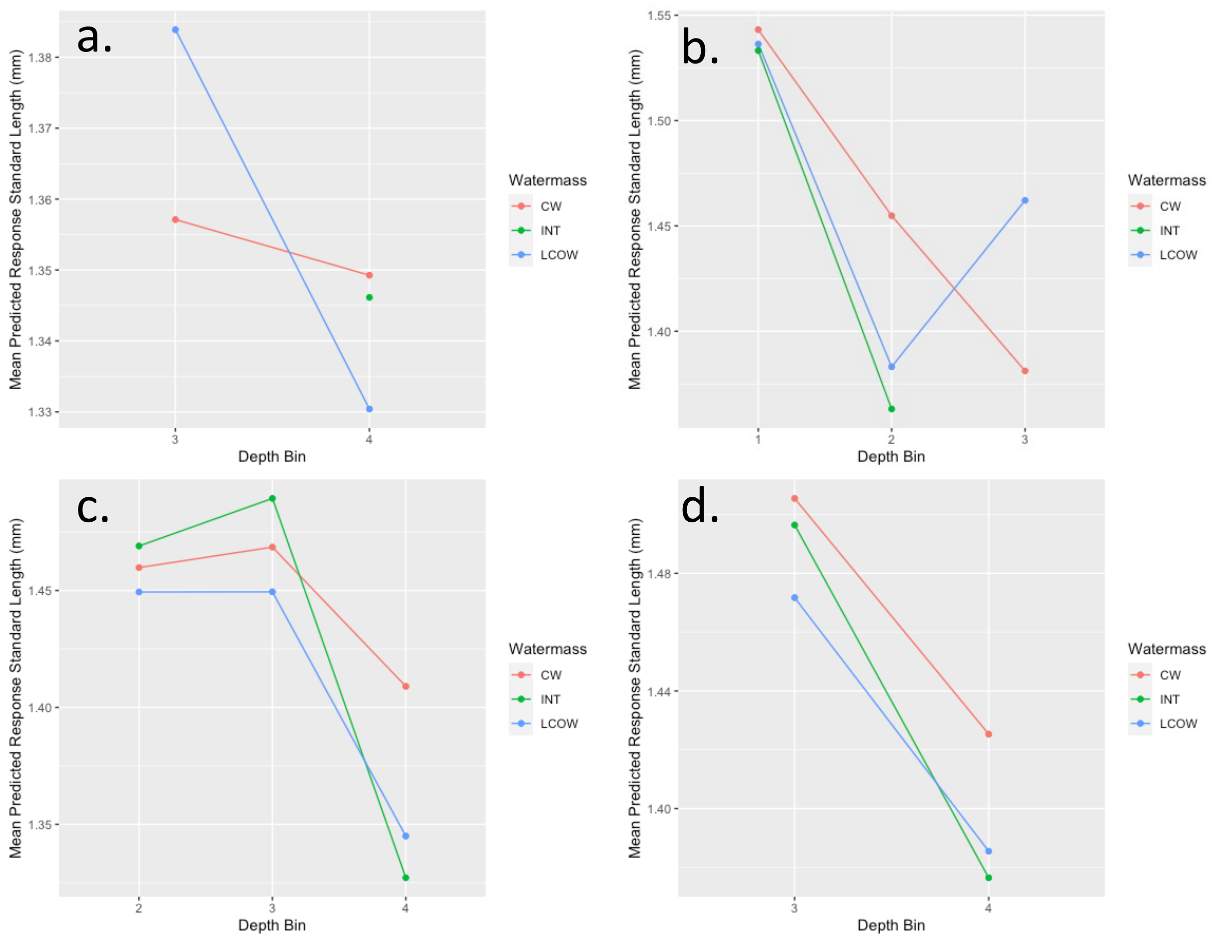

Figure 18. Prediction plot describing the model interaction for depth and water mass for, a. *Cyclothone braueri*, b. *Cyclothone obscura*, c. *Cyclothone pallida*, and d. *Cyclothone pseudopallida*.

The interaction between water mass and sampling period was retained in the minimum adequate model for *C. obscura* and *C. pallida* (Table 17). *Cyclothone obscura* decreased in standard length from Loop Current water to Common water during DEEPEND and increased during ONSAP (Figure 18). *Cyclothone pallida* increased in standard length from Loop Current water to Common water during both sampling programs (Figure 19).

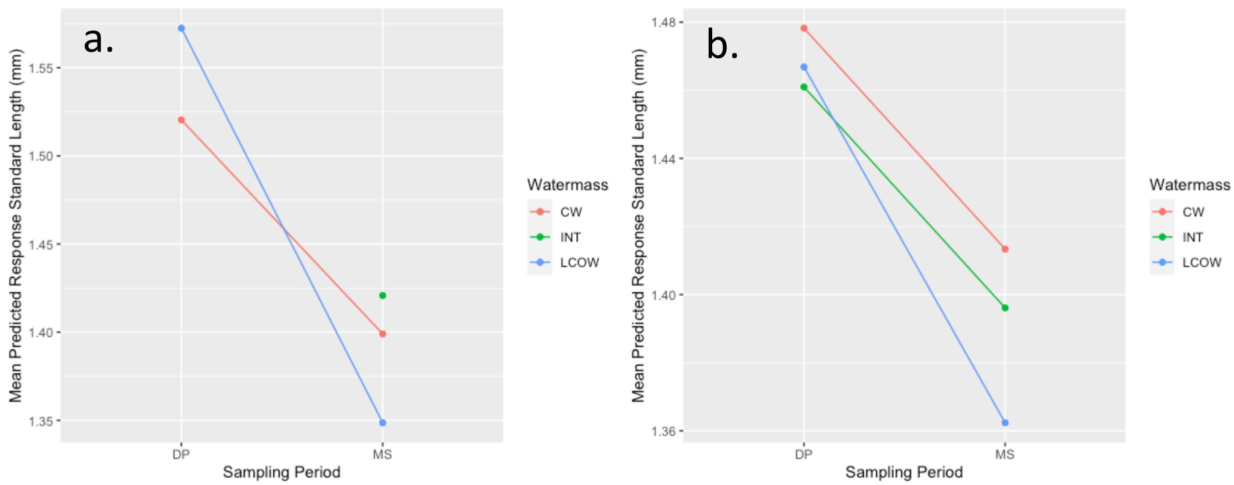

Figure 19. Prediction plot representing the model interaction for water mass and sampling period for, a. *Cyclothone obscura* and b. *Cyclothone pallida*.

The interaction between water mass and solar cycle was only retained within the minimum adequate model for *C. pallida* (Table 17). Standard length within Loop Current water was higher during night trawls than day and Common Water standard lengths were higher during the day (Figure 20).

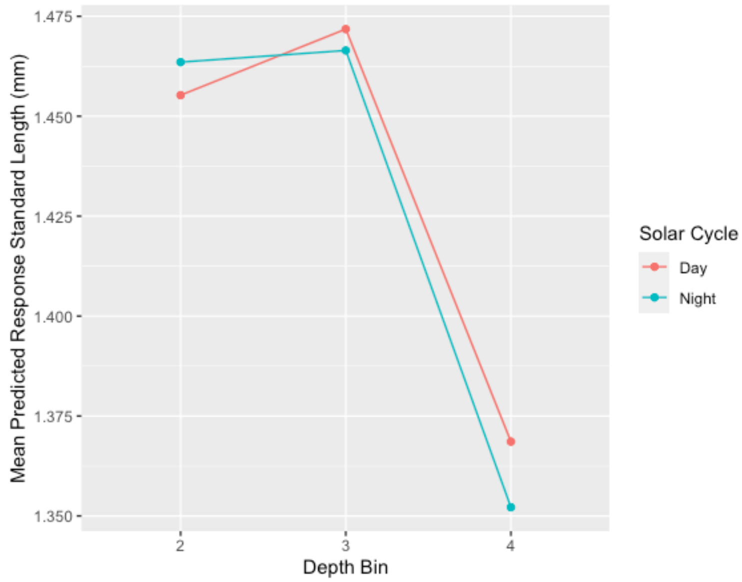

Figure 20. Prediction plot representing the model interaction for water mass and solar cycle for *Cyclothone pallida*.

Sampling period was a retained factor for all *Cyclothone* (Table 17). The general trend was that *Cyclothone* were smaller during ONSAP (MS) samples compared to DEEPEND (DP) samples (Figure 21). Average standard length of *Cyclothone* during ONSAP sampling was 27 mm and during DEEPEND sampling *Cyclothone* averaged 31 mm.

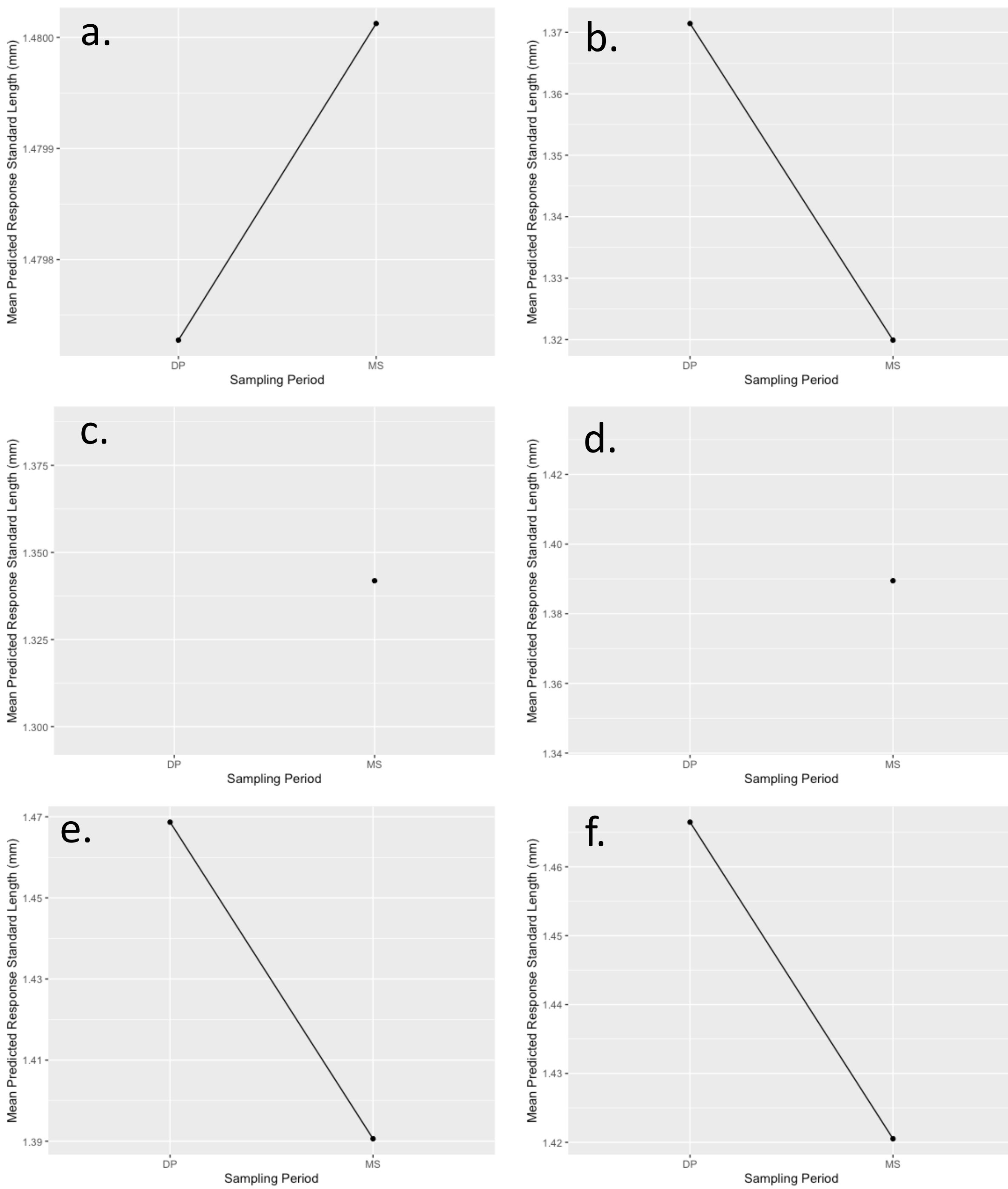

Figure 21. Prediction plot describing the model of the factor sampling period for, a. *Cyclothone acclinidens*, b. *Cyclothone alba*, c. *Cyclothone braueri*, d. *Cyclothone obscura*, e. *Cyclothone pallida*, and f. *Cyclothone pseudopallida.* Absent samples within each factor of the variables sampled inhibited values from being predicted.

The interaction between sampling period and depth was found to be an important factor for *C. braueri* and *C. obscura* (Table 17). The average standard length for each species increased with depth across the sampling period (Figure 22).

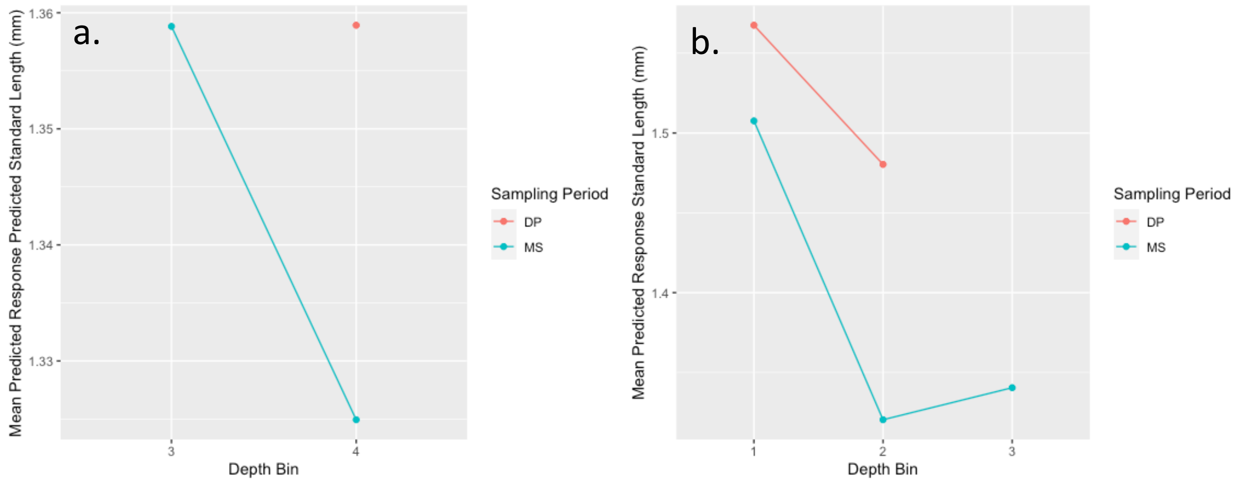

Figure 22. Prediction plot describing the model interaction for depth and sampling period for, a. *Cyclothone braueri*, b. *Cyclothone obscura*. Absent samples within each factor of the variables sampled inhibited values from being predicted.

Solar Cycle was a factor that was retained for *C. obscura*, *C. pallida*, and *C. pseudopallida* (Table 17). *Cyclothone* caught during the day were on average larger than those caught at night (Figure 23).

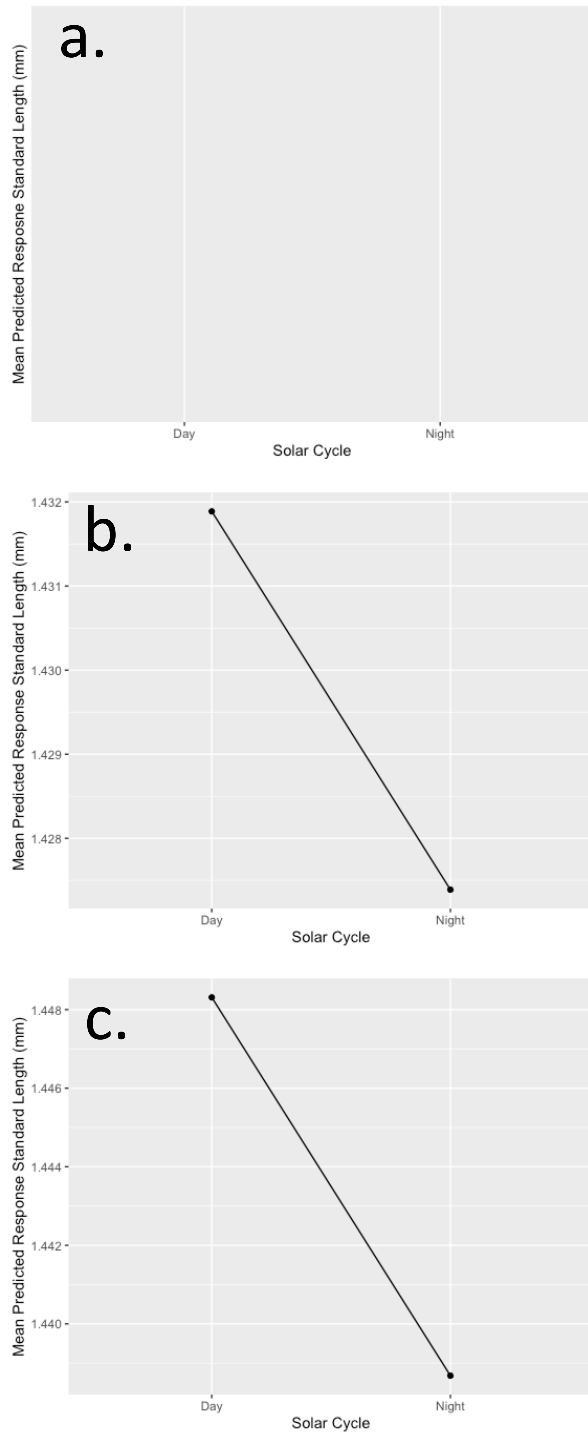

Figure 23. Prediction plot describing the model factor solar cycle for, a. *Cyclothone obscura*, b. *Cyclothone pallida*, c. *Cyclothone pseudopallida*. Absent samples within each factor of the variables sampled inhibited values from being predicted.

The interaction between solar cycle and sampling period was important for *C. alba* and *C. pseudopallida* (Table 17). *Cyclothone pseudopallida* standard length during DEEPEND and ONSAP both decreased across day and night samples, but *Cyclothone alba* size during ONSAP was negatively correlated to solar cycle and positively correlated during DEEPEND sampling. (Figure 24).

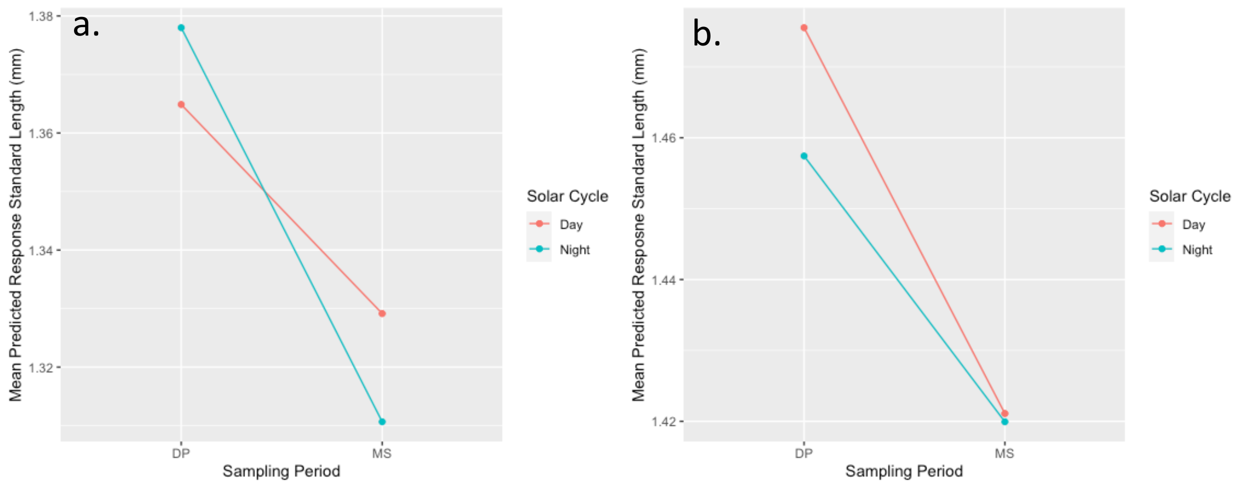

Figure 24. Prediction plot describing the model interaction of solar cycle and sampling period for, a. *Cyclothone alba* and b. *Cyclothone pseudopallida*.

The interaction between solar cycle and depth was important for the model explaining standard lengths of *C. braueri* and *C. pallida* (Table 17). Standard length of *C. braueri* increased across day to night within 200 – 600 m depth and standard lengths of *C. pallida* increased across day to night within 600 – 1000 m and 200 – 600 m depth (Figure 25).

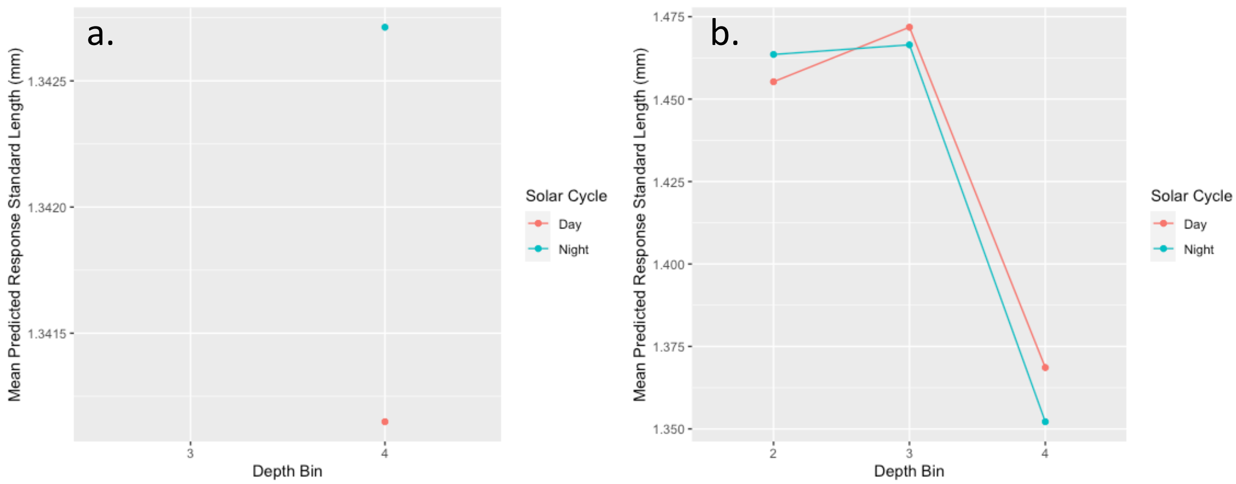

Figure 25. Prediction plot describing the model interaction of solar cycle and depth for, a. *Cyclothone braueri* and b. *Cyclothone pallida*.

The interaction between all variables (depth, solar cycle, water mass, and sampling period) was retained for *C. obscura* (Table 17). Standard length varied depending on the interaction of the four variables (Figure 26).

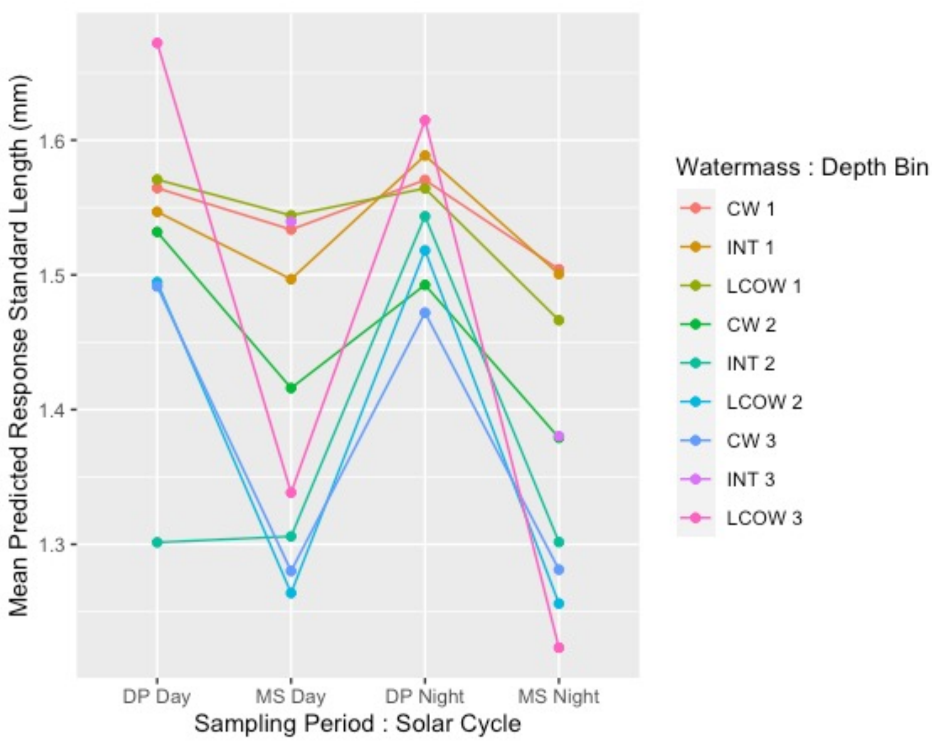

Figure 26. Prediction plot describing the model interaction of depth, water mass, sampling period, and solar cycle for *Cyclothone obscura.*

4. Discussion

Eight species of the genus *Cyclothone* were collected in in the Gulf of Mexico (GoM), with six species comprising the bulk of the assemblage. One species, *Cyclothone pallida*, was dominant, and the remaining primary species were occasional (*C. obscura* and *C. pseudopallida*, *C. alba*, *C. braueri*, and *C. acclinidens*). *Cyclothone microdon* and *C. parapallida* were rare. *Cyclothone parapallida* has been recorded in the GoM once before by Ross et al. (2010). However, it appears that this is the first study to document *C. microdon* in the GoM. The presence of *C. microdon* outside of its typical habitat range (Atlantic Ocean, Indian Ocean, and Pacific Ocean) could be due to the Loop Current, pushing infrequent individuals from their known distribution into the GoM (Olson 1991).

All species of *Cyclothone* have been reported to inhabit specific depth ranges (Badcock and Merrett 1977). That said, in the GoM there was overlap between species (Figure 27). *Cyclothone* were stratified by coloration and depth. Above 600 m the dominant species were the lighter – colored species (*C. alba* and *C. braueri*). Between 600 – 1000 m the *Cyclothone* assemblage was dominated by *C. pallida*, *C. acclinidens*, and *C. pseudopallida*. Beneath 1000 m the primary *Cyclothone* species was the large, dark species *C. obscura*. The species richness maximum for deep-pelagic fauna typically occurs around 1000 m depth (Angel 1993, Leathwick et al. 2006, Priede et al. 2010). Abundances of *Cyclothone* species of the GoM followed suit, as the 600 – 1000 m sampling bin was the most diverse.

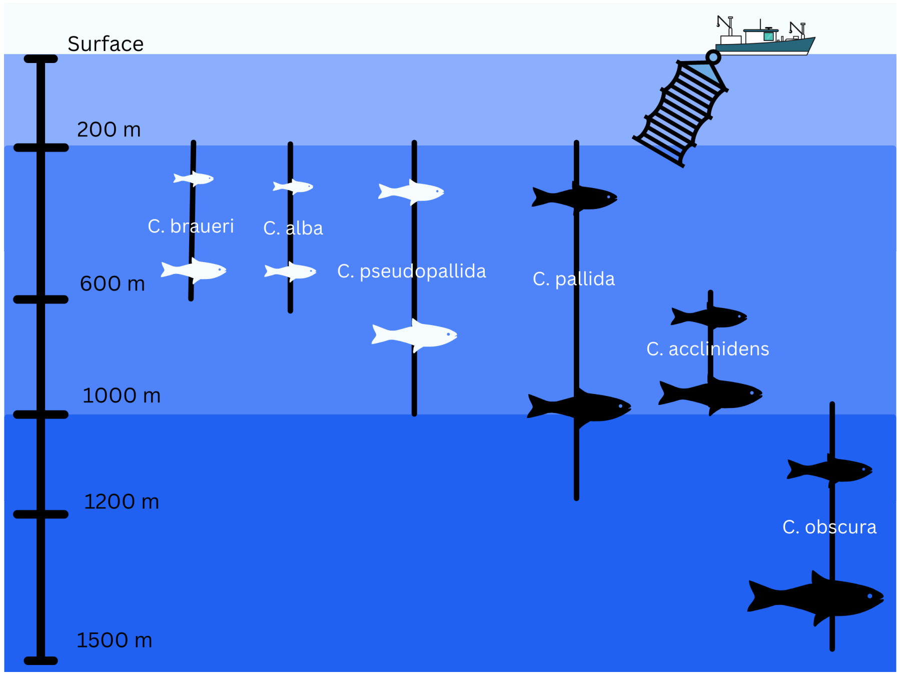

Figure 27. Vertical distributions of *Cyclothone* species found in the Gulf of Mexico. Size of fish is relative to the general size increases with depth trend. Color of fish represents if the species is a light are dark species of *Cyclothone*.

Typically, lighter-colored species are found at shallower depths than darker species (Murray et al. 1912, Marshall 1979, Salvanes & Kristofersen 2001). For example, lighter species of *Cyclothone* (*C. alba*, *C. braueri*, and *C. signata*) dominated upper depths in the Pacific, while darker species (*C. acclinidens*, *C. ataria*, *C. microdon*, and *C. pallida*) dominated deeper waters (Miya & Nemoto 1991). Crypsis, the utilization of color to become difficult to detect from others, is an important adaptation for organisms that have many predators (Ruxton et al. 2004). *Cyclothone* use crypsis (Uiblein et al. 2003) to survive in the harsh deep-sea ecosystem as darker species will be better hidden in darker waters. Minimal coloration in the shallows likely reduces visual predation in ample light environments. Utilizing the lack of solar light within the aphotic zone can be advantageous as organisms are able to camouflage themselves in an environment that has no physical structures. The vertical distribution of *Cyclothone* from this study in the GoM follows this pattern of lighter species in more illuminated waters and dark species in areas that lack solar light. Head photophores were found on all *Cyclothone*, with body photophores being found on all species except *C. obscura*. *Cyclothone* use their photophores to assist with counter illumination to be less noticeable from below against any downwelling light (Davis et al. 2020). All species with body photophores were found within shallow water with higher concentrations of light. *Cyclothone obscura* was the deepest living species and never developed body photophores, probably because developing photophores would be energetically wasteful since the amount of light penetrating their depth range is minimal.

Diel vertical migration (DVM) is a specific form of vertical migration, where fauna rise to shallower depths at night to feed, then return to deeper water during the day to avoid predation (Brierley 2014, Bos et al. 2021). Previous studies have found various species of *Cyclothone* within the same depths across the entire solar cycle (Ross et al. 2010, Gloeckler et al. 2018). There were not enough shifts in overall vertical distribution in relation to solar cycle to demonstrate that *Cyclothone* participate in DVM in the GoM. Any small difference in vertical distribution may be due to partial migrations, as small subsets of larger *Cyclothone* individuals have previously been recorded to undergo limited upward migration (Miya & Nemoto 1987). Additionally, the slight change in abundances depending on time of day could be due to rates of activity. *Cyclothone* have been found to feed during the day (Hopkins & Sutton 1998). Species such *as C. acclinidens* are like larger pelagic predators, in that they have periods of rest and digestion after periods of heavy food consumption (DeWitt & Cailliet 1972).

Species of *Cyclothone* found in the GoM using the 3-mm MOCNESS trawls within 0 – 1500 m can be broken down into three size classes. The size class structure follows the same pattern of light to dark. Smaller and lighter *Cyclothone* species were found in shallow water, whereas larger and darker species were found deeper. Increased size with depth has been seen in teleosts as a possible explanation of response to reproductive strategy, feeding behavior, and morphology (Smith and Brown 2002). This pattern of larger species residing deeper is consistent with findings of positive correlations between depth and size of *Cyclothone* and other pelagic species (Macpherson & Duarte 1991, McClain et al. 2001). *Cyclothone* may increase in size with increasing depth as their body structure may allow them to live in harsher environments (Miya & Nishida 1996). *Cyclothone* are slender fishes, and their body shape would allow them to move through the water easier at depth (increased pressure). Larger fishes are going to have more tissue to store energy within and could thus go longer without food sources. Throughout development *Cyclothone* gas bladder will change from being air-filled sacs to more fluid filled and body tissues will be comprised of higher concentrations of water to assist with neutral buoyancy and pressure at depths (Peña et al. 2023).

A historical trend is that larger individuals of a single species are found in deeper waters than that of their smaller counterparts (Macpherson & Duarte 1991, Coad 2019). *Cyclothone* and other meso/bathy- pelagic fishes typically demonstrate ontogenic migration, with larvae and juvenile fishes living in the epipelagic that will descend to deeper depths as they mature (Sutton 2013). *Cyclothone pseudopallida*, *C. alba*, and *C. atraria* have been reported to separate by depth at different life history stages (smaller-shallower and larger-deeper) (Miya & Nemoto 1991). Presumably smaller (younger) fish of a species inhabit shallower depths where zooplankton densities are higher, an important consideration for faster growth at smaller sizes. Deep-pelagic fishes typically have decreased metabolic rates as they reach deeper depths, as described in Childress' visual-interaction hypothesis (Torres et al. 1979, Torres & Somero 1988, Drazen & Seibel 2007). This hypothesis links predator prey interactions to vision and light (Childress 1995). Deep-sea fishes have a lower need for impulsive movements caused by visual detection of predators because there are limited light sources available, and they thus do not primarily rely on visual cues for movement (Sutton 2013). Fishes within deeper waters will thus utilize other methods of predator avoidance such as photophores or other senses. Food resources generally decline rapidly with increasing depth (Haedrich 1996). The reduced need for energy used for predator avoidance leaves more energy to be allocated for growth, allowing for deeper *Cyclothone* species that encounter fewer predators to grow the largest. *Cyclothone* are also not going of offer much caloric reward to predators given feeding effort, as *Cyclothone* are small, oily, and heavily dispersed (Norse 2005).

It has been noted that juvenile *Cyclothone* have been caught within all depth ranges sampled and not just in the epipelagic zone (McClain et al. 2001). Larval forms of *C. atraria* were found in the species' upper depth range (< 800 m), but not solely in the epipelagic zone (Miya & Nemoto 1987). In the GoM there was a statistically significant pattern of standard length increasing with depth across the depth bins sampled for all *Cyclothone*. Length distributions suggest a that there is a size vertical distribution between *Cyclothone*. However, to know if *Cyclothone* larvae and juveniles of each species live within the epipelagic zone, a finer mesh net would be needed to fully investigate the potential ontogenic migration pattern of *Cyclothone* in the GoM as the nets in this study would only collect individuals larger than the mess (3 mm).

Mesopelagic communities can be influenced by various water masses and current, such as warm core Gulf Stream rings that form in the Northern Atlantic (Craddock et al. 1992). The Loop Current within the GoM brings larvae, pelagic fishes, plant materials, and heat into the eastern portion of the GoM (Pequegnat et al. 1990). The Loop Current is a variable system that changes location and creates eddies throughout the GoM over time (Liu et al. 2011). Loop Current water is known to create areas of downwelling (Johnston et al. 2019). Areas of downwelling with increased dissolved oxygen and nutrients could cause fishes to inhabit deeper depths as resources are more plentiful at deeper depths. Surface waters within downwelling regions are less productive and do not offer high levels of resources. Loop Current waters could oxygenate the deeper water enough to create the downward shift in vertical distributions seen within Loop Current water. When plotted by water mass, vertical distributions of each species exhibited a downward shift in depth within Loop Current waters. Furthermore, Loop Current water is associated with decreased abundances of pelagic species (Wells et al. 2017). *Cyclothone* abundances within Loop Current water followed this trend as they were much lower than abundances within Common Water.

5. Conclusions

Cyclothone is a numerically dominant genus in the deep-pelagic northern and eastern Gulf of Mexico (GoM) and may be the most abundant fish taxon in the entire GoM ecosystem. *Cyclothone* ubiquity is evidenced by the finding that at least one *Cyclothone* individual was collected in 94% of all trawls conducted over a 10-year period. The lack of overall changed in vertical distribution in relation to solar cycle confirmed that *Cyclothone* do not vertically migrate in the GoM. There were two clear vertical "landmarks" in the depth distribution of *Cyclothone* in the GoM based on the vertical sampling resolution of this study: 1) 600 m, where a transition occurred in light-colored and dark-colored species (living above and below this depth, respectively), and 2) 1000 m, where a transition occurred from the dominant deep-mesopelagic species (*C. pallida* and *C. acclinidens*) to a truly bathypelagic species (*C. obscura*). *Cyclothone* species vary significantly in size and can be classified as small (*C. alba*, and *C. braueri*), medium (*C. pallida*, *C. acclinidens*, and *C. pseudopallida*) and large (*C. obscura*), with larger individuals of a species residing in deeper water than smaller individuals.

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