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Size Structuring of Myctophids in the Northern Gulf of Mexico in the Years Following the Deepwater Horizon Oil Spill

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Thesis of
Adam Warren

Submitted in Partial Fulfillment of the Requirements for the Degree of

Master of Science
Marine Science

Nova Southeastern University
Halmos College of Arts and Sciences

August 2022

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NOVA SOUTHEATERN UNIVERSITY

HALMOS COLLEGE OF ARTS AND SCIENCES

SIZE STRUCTURING OF MYCTOPHIDS IN THE NORTHERN GULF OF
MEXICO IN THE YEARS FOLLOWING THE DEEPWATER HORIZON OIL
SPILL

By

Adam Warren

Submitted to the Faculty of
Halmos College of Arts and Sciences
in partial fulfillment of the requirements for
the degree of Master of Science with a specialty in:

Marine Science

Nova Southeastern University

September 2022

Abstract

Body size is one of the main determinants of marine ecosystem structure and is correlated with many behavioral processes such as diel vertical migration (DVM). Myctophidae, a highly abundant, speciose, and globally distributed fish family, perform diel vertical migrations between the epipelagic zone at night and the mesopelagic zone during the day with vertical distributions varying with ontogeny, and therefore body length. Understanding how DVM contributes to an ecosystem's structure is important to understanding ecosystem functioning, especially in response to anthropogenic impacts such as the *Deepwater Horizon* oil spill. The aim of this study was to investigate changes in myctophid body size in relation to their diel vertical migration distributions and species identity, using an existing and extensive myctophid dataset collected from the Gulf of Mexico during the ONSAP (2011) and DEEPEND (2015 – 2018) research programs. Using Generalized Least Squares models, patterns of fish body size were examined in relation to diel vertical migration and mesoscale environmental variables for the 12 most abundant myctophid species. All myctophid species exhibited diel vertical migration behaviors, ranging from 200 – 1000 m depth during the day and ascending to 0 – 200 m at night, and species-specific patterns were observed. Each species was grouped according to vertical distribution pattern and overall, it appeared that size does not dictate vertical distribution nor has size significantly differed between the ONSAP and DEEPEND programs. These findings help us understand the structure of deep-sea fauna and how they may change naturally or in the event of anthropogenic impacts.

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INTRODUCTION

Body size distributions of individual fish in a population can be a valuable indicator of population dynamics and ecological processes (Scott et al., 2006; Brunel and Piet, 2013) as they are commonly and easily recorded during environmental monitoring programs (Bell et al., 1985) and can be used for various purposes. For example, by examining trends in the size frequency of populations or species over time a better understanding of faunal response to ecosystem change can be developed (Izzo et al., 2016), which is valuable for developing effective conservation strategies (Chambers et al., 2013; Hobday and Evans, 2013). Examples of what fish length data can also be used for are: assess temporal change in the size and length of maturation of fishes (Heino et al., 2002); monitor ecological change and assess the performance of ecosystem management of fisheries stocks (Shin et al., 2005); and infer fishing impacts as body size determines population and community vulnerability to fishery activity (Gislason, 2003). Given the dominant role body size plays in marine ecosystems, there are compelling reasons to adopt size-based analyses (Shin et al., 2005). However, one issue that remains is that many size-structuring studies are focused on fisheries of commercially important species and the effect fisheries have on those species and ecosystems (Andersen and Beyer, 2015). There is a lack of understanding about the structure and functioning of the highly diverse mesopelagic ecosystem (the area in the water column ranging from 200 – 1,000 meters in depth), due to a historical lack of exploration and sparse data collection (St. John et al., 2016).

One of the most abundant fish families in open ocean ecosystems is Myctophidae. Myctophidae is a globally distributed family of generally small to medium (c. 2-150 mm standard length) marine fishes in mesopelagic ecosystems, consisting of 249 species in 32 genera (Staby and Salvanes, 2019; Fricke, Eschmeyer, and Van der Laan, (eds) 2022). Deep-sea trawling shows that myctophids can have extremely high biomasses, accounting for as much as 30-85% of all faunal adult and larval biomass in different ocean regions, specifically 70-85 % in the western tropical and subtropical Pacific (Muhling et al., 2007) and 30-70 % in the eastern Indian Ocean (Hidaka et al., 2003). Recent trawling estimates suggest that the total global mesopelagic fish biomass may be c. one billion tons (Lam and Pauly, 2005), though acoustic surveys suggest this figure may be far higher at c. 10-15 billion tons (Irigoien et al., 2014).

Deep-pelagic fishes comprise important functional links in oceanic ecosystems (Robison, 2009). Myctophids are a central part of most of the world's oceans, playing a key role in oceanic food webs (Gjøsaeter & Kawaguchi, 1980; Hopkins & Gartner, 1992; Tsarin, 1997). Myctophids consume herbivorous and omnivorous zooplankton (Pakhomov et al., 1996; Williams et al., 2001; Pusch et al., 2004), and are themselves consumed by oceanic top predators such as sea birds, marine mammals, and piscivorous fishes like the stomiid dragonfish (Sutton and Hopkins, 1996; Olsson & North, 1997; Pauly et al., 1998). Vertically-migrating mesopelagic fauna play a role in transferring energy through the water column by connecting the epi-, meso-, and bathypelagic habitats (Angel and Pugh, 2000; Genin, 2004; Trueman et al., 2014). The subsequent energy transfer through the water column during diel vertical migration can result in a substantial contribution to the oceanic biological carbon pump (Childress and Nygaard, 1973; Childress et al., 1980; Longhurst and Harrison, 1988; Hidaka et al., 2001; Radchenko, 2007).

An observed trend of increasing size and or advanced life history stage with depth has been reported for myctophid species (Clarke, 1973; Badcock and Merrett, 1976; Hulley, 1981). Some myctophid species spawn in mesopelagic waters and the eggs are fertilized as they rise to the surface (reviewed in Marshall, 1979). Early development happens during this ascension, and hatching occurs when the larvae reach c. 2 mm in size in epipelagic water (Gjøsæter and Tilseth, 1988). Other species spawn in the epipelagic zone where higher primary productivity leads to better conditions for rapid larval development and subsequent access to prey (Lisovenko and Prut'ko, 1987; Gartner, 1993). Post hatching, mesopelagic larval growth rates worldwide can vary between 0.05–0.40 mm-day^{-1} (Conley and Gartner, 2009; Landaeta et al., 2015; Namiki et al., 2015; Sassa and Takahashi, 2018). In the eastern Gulf of Mexico, growth rates have been estimated, varying from 0.10 mm-day^{-1} for *Notolychnus valdiviae* to 0.40 mm-day^{-1} for *Ceratoscopelus warmingii* (Conley and Gartner, 2009). Most myctophid fishes spend their 50–60-day larval stage in the epipelagic zone and do not perform diel vertical migration in this phase (Sassa et al., 2002, 2004, 2007; Moteki et al., 2009; Landaeta et al., 2015).

Myctophid species generally begin the transformation from the larval stage into a juvenile at between 9-23 mm in length depending on the species, and this transformation occurs in a short length interval that usually does not exceed 2 mm (Moser et al., 1984). Most myctophid larvae transform into juveniles as they descend from the epipelagic zone into the

mesopelagic zone to their species-specific normal daytime depth of occurrence, with average body length usually increasing with depth, suggesting ontogenic vertical migration (Loeb, 1979; Sassa and Kawaguchi, 2006). Transformation into a juvenile fish is believed to happen quickly as transforming larvae have rarely been collected from either epi- or mesopelagic zones while larvae and juveniles are more common in each zone respectively (Loeb, 1979; Kawaguchi and Mauchline, 1982). One study that captured transforming larvae of *Benthosoma suborbitale*, *Diogenichthys atlanticus*, and *Notoscopelus resplendens* in the temperate eastern North Atlantic found they were distributed deeper in the water column (500–800 m) than early-stage larvae (10–200 m) (Badcock and Merrett, 1976), while Kawaguchi and Mauchline (1982) reported a similar pattern in the same species in the subarctic eastern North Atlantic. It has been hypothesized that due to adaptations for floating, specifically the increased buoyancy from the development of a swimbladder in pre-transformation larvae causing slow sinking rates, transforming myctophids may actively swim downward rather than passively descend into the mesopelagic zone because the larger larvae and juveniles are more conspicuous to visual predators (Frost and McCrone, 1979; Sassa et al., 2007). This ontogenetic vertical migration helps aid in the survival of early transforming larvae as they begin descending from the epipelagic into the mesopelagic, where the predator density is lower (Loeb, 1979). After transformation to the juvenile stage, most myctophid species begin active diel vertical migration from the mesopelagic to epipelagic zones and continue to do so as they mature (Clarke, 1973; Badcock and Merrett, 1976).

Adult myctophid species show a wide vertical distribution in the water column, ranging from near the surface to depths around 1000 m (Badcock, 1970; Hulley, 1981; Gartner et al., 1987; Ross et al., 2010). One reason for their broad vertical range is that individual myctophids undertake diel vertical migration. The most common vertical migration pattern for myctophids is where individuals stay in the mesopelagic zone during the day to hide from visual predators and then ascend to the epipelagic zone (0–200 m depth) at night (Gjøsæter and Kawaguchi, 1980; Watanabe et al., 1999; Sutton, 2013) to feed. It has been hypothesized that the ultimate driver behind vertical migrations is predator avoidance (Pearre, 2003; Brierley, 2014) with the start of migration coinciding with decreases in light intensity at sunset (Angel & Pugh, 2000). Vertical migrators will descend into deeper, darker water during the day to avoid being hunted by visual predators (Childress, 1995) then ascend to surface waters at night when there is less light, allowing animals that would normally be easily preyed upon to feed (Wang et al., 2019).

However, the vertical extent of a fish's diel migration varies with various factors such as species identity and ontogeny (Badcock and Merrett, 1976; Staby and Salvanes, 2018), which can alter the role they play in ecological processes, circadian rhythms (Haney, 1993), and state of satiation (Bos et al., 2021) as well as external factors including light, currents (Bennett et al., 2002), lunar cycle (Alldredge and King, 1980), and food availability (Huntley and Brooks, 1982).

In terms of classifying vertical migration patterns, there is an issue that has been present for many years. The issue is that historically the terms that describe a species' vertical migration pattern have been more qualitative rather than quantitative, with different researchers using different terms to describe either similar or the same migratory behavior (Secor & Kerr, 2009). Where studies on micronektonic crustaceans refer to species who have 50% or greater of the population migrate "strong" and species that 15 – 50 % migrate "weak" (Foxton, 1970; Hopkins et al., 1994), some studies involving fishes have used the terms "full" and "partial", respectively (Badcock and Merrett, 1976; Mehner & Kasprzak, 2011; O'Malley et al., 2018. In addition, studies involving the same taxa have used different terms to describe migratory behavior. Hopkins et al., (1994) and O'Malley et al., (2018) both studied mysids, albeit in different locations, those being the Atlantic and Lake Champlain, respectively, and used different terms to describe "weak" or "partial" migratory species, i.e. species where most of the population does not migrate. Next, the very definition of those terms appear to be just as qualitative. Where one study may classify a "strong" migrator as a species where 50% or greater of the population migrates (Foxton 1970), another may consider a "complete" or "strong" migrator as any species where 99% or greater of the population migrates (Chapman et al., 2012). However, it should be noted that over time it has been observed that there is usually not a taxonomic group where all members of the population migrate, so the degree to which a study will consider a species a "complete" or "strong" migrator appears to be at the discretion of the study. Due to these variations in how species are classified regarding vertical migration patterns, the classification scheme and specific terms detailed below follows the system more commonly observed for fishes with some additions similar to those used for other taxa.

In the present study, three main categories of diel vertical migration patterns are reported for adult myctophids, describing 1) the vertical distance covered during each migration, 2) the connectivity of their daytime and nighttime ranges, and 3) the frequency of migration within a

given population. The first category recognizes three forms of migrants: strong migrants, which undertake extensive vertical movement between the mesopelagic and the epipelagic covering upward of several hundred meters; weak migrants, which undertake little vertical migration covering less than 400 meters; and non-migrants, which do not undergo any vertical migration (Collins et al., 2008; Olivar et al., 2012). A further set of patterns within this category is the connectivity of the species' vertical distribution, whether it be somewhat continuous or disconnected. Connectivity refers to how close the depths the species migrate to are relative to each other. For example, Gartner et al., (1987) observed the species *Lepidophanes guentheri* having two depth ranges at night: 75 – 155 m and 600 – 700 m, two widely separated depths, whereas the species *Hygophum taaningi* was captured between 10 – 300 m and 375 – 600 m, two very close depths with only a small gap between. The third category has been defined to describe the frequency of migration amongst adult fishes: complete migrators are populations in which a majority of individuals migrate every day; partial migrators are where only a small portion of individuals migrate each day and non-migrators do not migrate at all (Badcock and Merrett, 1976). However, both the extent and frequency of DVM varies with ontogeny and small juveniles may not undertake diel vertical migration (Clarke 1973; Badcock and Merrett 1976). For example, smaller juvenile myctophids, most notably those of the species *Ceratoscopelus warmingii* and *Lepidophanes guentheri* in the eastern Gulf of Mexico that have just completed transformation appear to remain at depth rather than migrate on a daily basis (Gartner et al., 1987).

Major differences in migration behavior may also occur between members of the same species in different geographic regions (Paxton, 1967). Gartner et al. (1987) provides evidence of this trend by observing that adult myctophids in the eastern Gulf of Mexico have distinctly smaller size ranges than same-species adults found in other tropical/subtropical areas like Hawaii. This was observed by repeatedly not being able to reach the maximum recorded size for those myctophid species or by observing a significant increase in the upper size limit of captured individuals despite using different net types and sampling methods. Another example is *Benthosema glaciale* also reaching maximum size and sexual maturity at shorter lengths in semi-enclosed basins like the Mediterranean Sea than their counterparts in open ocean areas (Gartner, 1991). Gartner (1991) suggested that the hydrography of semi-enclosed seas may provide

barriers to gene flow to the point that populations within the seas are diverging from the same species in open water.

The Gulf of Mexico is of interest for studying the properties of diverse deep-sea fish assemblages due to its unique characteristics of being a semi-enclosed sea with many mesoscale features (Biggs and Ressler, 2001; Sutton et al., 2022). Circulation patterns in the Gulf of Mexico are strongly influenced by the Loop Current and the eddies formed by it, which may entrain and transport individuals from the Caribbean Sea (Gartner et al., 1987). The offshore northern Gulf of Mexico is heavily impacted by anthropogenic impacts, but perhaps most notably by the *Deepwater Horizon* oil spill in 2010 (Sutton et al., 2022). The oil spill occurred around 60 km off the coast of Louisiana from a deep well at a depth of 1500 m and persisted for 87 days, releasing an estimated 200 million gallons of oil into the gulf, leading to concern about the effects of the oil spill on the mesopelagic fauna of the Gulf of Mexico (Beyer et al., 2016; Cook et al., 2020). As some mesopelagic fauna vertically migrate, increased exposure to the newly-released hydrocarbons throughout the water column could be possible (Cook et al., 2020). The lack of information regarding ecosystem structure and functioning makes it difficult to understand how disturbances of this magnitude affect deep-pelagic fishes and as humans continue to impact the deep pelagic ocean, knowledge of ecosystem functioning must increase because should another deep-water oil spill like the *Deepwater Horizon* oil spill occur, the direct impacts will mostly affect meso- and epipelagic ecosystems (Sutton, 2013; Sutton et al., 2020a). Given the important role mid-trophic organisms such as myctophids may play in providing ecosystem services, understanding the various vertical migration patterns of these fishes is essential to understanding regional ecosystem functioning as well as the protection of these functions through ecosystem management (Milligan and Sutton, 2020).

MATERIALS AND METHODS

DATA COLLECTION

The myctophid data used in this study were collected utilizing a 10-m^2 Multiple Opening-Closing Net and Environmental Sensing System (MOCNESS) to sample 46 locations across the northern Gulf of Mexico from January to September of 2011 during the Offshore Nekton Sampling and Analysis Program (ONSAP) (Figure 1), and a smaller subset of 22 stations in May and August in the years 2015 to 2017 during the Deep Pelagic Nekton Dynamics of the Gulf of Mexico (DEEPEND) (Figure 2) research programs (Cook et al., 2020). Two MOCNESS deployments were conducted at each sample location, centered around solar noon and midnight to allow for the observation of diel vertical migration patterns during sampling (Cook et al., 2020). The MOCNESS system was chosen for its discrete depth sampling capability, allowing for five discrete depth bands to be surveyed (Cook et al., 2020). The specific depth bands were: 1500 - 1200 m (upper bathypelagic); 1200 - 1000 m (upper bathypelagic); 1000 - 600 m (lower mesopelagic); 600 - 200 m (upper mesopelagic) and 200 - 0 m (epipelagic). The purpose of each depth band chosen was to account for the bathypelagic fauna living below the deep hydrocarbon/dispersant plume resulting from the *Deepwater Horizon* oil spill, to sample the bathypelagic fauna within the depth band occupied by the deep oil plume (1000 – 1200 m), and to sample the daytime and nighttime depths of occurrence of most vertically migrating taxa (Cook et al., 2020) following standard zonations for the pelagic ocean (Sutton, 2013).
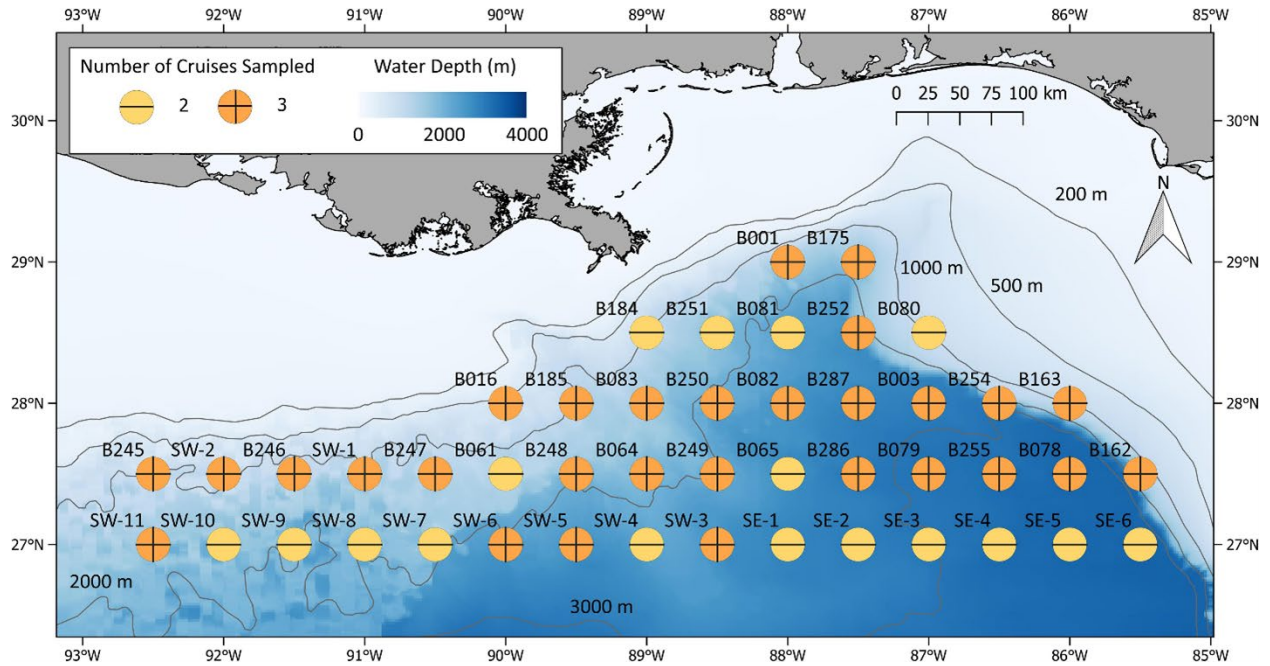
Figure 1. Map of all stations sampled during the ONSAP program (Cook et al., 2020).
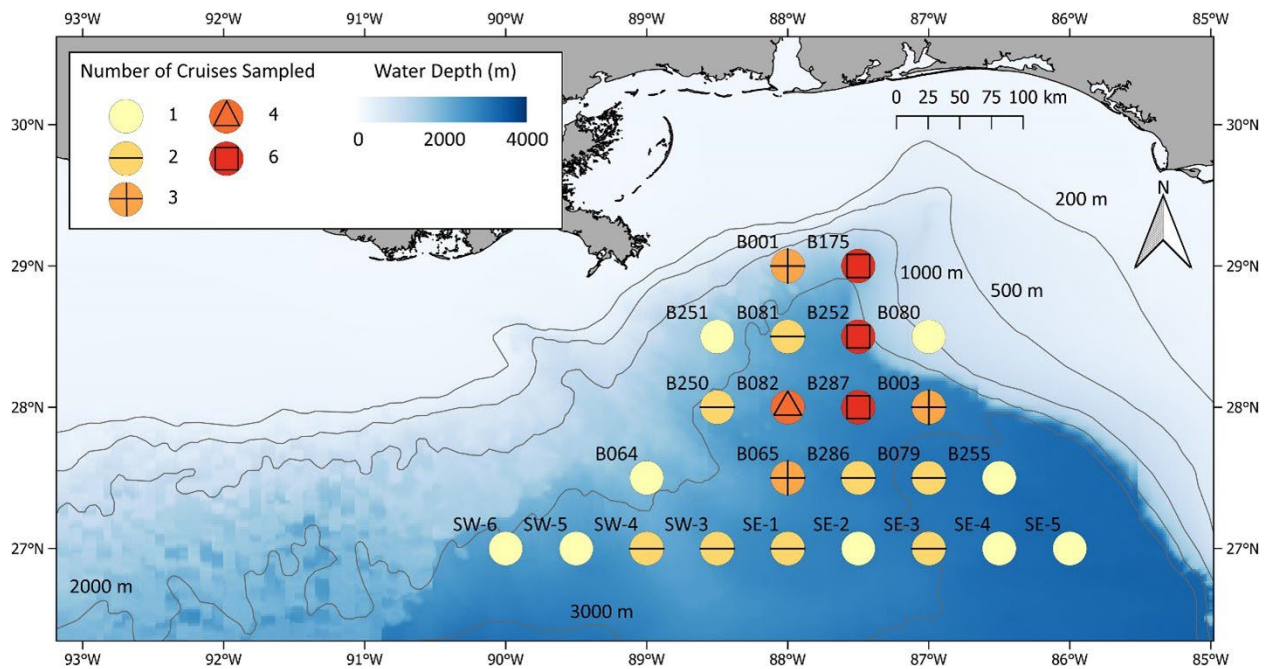
Figure 2. Map of subset of stations sampled during the DEEPEND program (Cool et al., 2020).

VERTICAL DISTRIBUTION AND MIGRATION PATTERN

The vertical distribution for each species was determined by standardized abundance, calculated by dividing the sum of the raw count of individuals by the sum of the volume of water filtered, and these data were plotted against depth with respect to the time of day captured. Due to the clear distinctions observed between species vertical distributions, in this study a strong migrator is a species that primarily vertically migrates 600 m or more and a weak migrator is a species that primarily migrates less than 600 m. For example, *Benthosema suborbitale* is primarily found in the epipelagic and upper mesopelagic, from 0 – 600 m, and will be considered a weak migrator. On the other hand, *Lampanyctus alatus* is primarily found from the epipelagic to the lower mesopelagic, ranging from 0 – 1000 m, and will be considered a strong migrator. Migration patterns were then determined by comparing the number of nighttime captures in the epipelagic to the total number of nighttime captures in all depth bins. A species was considered a complete migrator if most of the population vertically migrated and very few individuals remained at depth, and if there was a noticeable portion of individuals remaining at depth, that species was considered a partial migrator.

SIZE STRUCTURING ANALYSIS

Four quality filters were created and applied from the faunal data exploration. First, only myctophid specimens identified to species level with associated length data were included in the analysis. The species used for analysis were chosen by first selecting the ten most abundant species overall from both ONSAP and DEEPEND, then separating the overall time series by program. By doing this, the order of abundance changed to include new species as the community assemblage varied over time, introducing two new species. Second, samples taken only from Common Water were selected, as most samples from both programs came from Common Water as opposed to Arctic or Intermediate Water. This resulted in the month of July 2011 being excluded from the analysis as water mass type could not be determined from the recorded mesoscale features present (Milligan and Sutton, 2020). Third, only the depths with the highest abundances across all months were included in the statistical analysis to avoid skewing the analysis by including depths with too few samples. This was done by plotting the overall standardized abundance plots over each month and selecting the combinations of depth and month with enough specimens to analyze. If the number of months with length data for a given

depth bin was less than half of the total number of months, that depth bin was removed so the focus could be on the depths where the species mostly occurs. For example, for the species *Diaphus mollis* only the depth bins of 0 – 200 m and 200 – 600 m were selected for final analysis because of the lack of enough specimens captured in depth bins below 600 m, while for the species *Ceratoscopelus warmingii*, the depth bins of 0 – 200 m, 600 – 1000 m, and 1000 – 1200 m were chosen because of the lack of specimens captured from 200 – 600 m. There was one exception to this filter, *Hygophum benoiti*, as even though it did not meet the criteria it had a high enough abundance of samples in those few months to warrant being investigated. As an extension of this filter, if any combination of depth or time of day from each month for the remaining depth bins had less than five samples, that specific combination was removed to possibly avoid skewing the data due to net contamination. This resulted in some depth bins that were originally selected to be analyzed from the overall vertical distributions, based on standardized abundances, being removed. For example, while the depth bin covering 1000 – 1200 m for *Ceratoscopelus warmingii* had over 65 samples, spread out over each month each depth bin had anywhere between 1 – 5 samples, if any at all.

The variation in the size structuring of each species over time and at different depths depending on the time of day was then analyzed using Generalized Least Squares (GLS), a weighted linear regression model that allows for heterogeneity inherent in the data. A full GLS model was created with standard length as the dependent variable and depth bin, time of day, and month captured as the main categorical variables being tested. Additional continuous variables included were mean latitude, mean longitude, chlorophyll, distance to the coast, and distance to 200 m isobath fitted to a Gaussian distribution (Milligan and Sutton, 2020). Pairwise plots were then made to test for collinearity between variables. Distance to coast and distance to 200 m isobath were strongly collinear, as well as mean longitude and mean latitude, and resulted in distance to coast and mean latitude being removed from the model. The overall starting model became the following equation:

Standard length = depth bin + time of day + month + depth bin:time of day + chlorophyll + mean longitude + distance to 200 m isobath

Once the new model was created, backward term selection was conducted by removing one explanatory variable at a time, eventually creating each permutation possible for all

explanatory variables, and comparing the Akaike information criterion (AIC) values. Variables that caused the AIC score to increase by more than four points following removal were considered important explanatory variables and retained. During this process, most models' AIC scores varied by more than tens of points, with the simplest models having the lowest scores. Models within four AIC points of each other were validated by examining the residuals plotted vs all tested variables. If two models had similar AIC scores within 2 points but produced similar residual plots, the model with fewer variables was chosen for simplicity. This was conducted until a model with the lowest AIC score and best residuals was found. Where heteroskedasticity remained in the residuals of the selected models, the varIdent function (nlme package in R) was used with Month (*M*), Time of day (*T*), and/or Depth (D). The best model was then plotted with either one of the varIdent variables or any combination of them and the new AIC scores compared, with the model with the lowest AIC score being selected and its residual plots examined. If the residual plots were not as evenly spread as the model without the varIdent function and showed observable patterning, the model was discarded despite having the lowest AIC score. The model with the next lowest AIC score was then selected and its residuals examined for either as little observable patterns as possible or no patterns at all. This process continued as needed until the residuals showed improvement or returned to the model without the varIdent variable. The final model with its unique varIdent function are given for each species in the results section. Following model selection, the model's estimated marginal means and pairwise contrasts (EMMeans package in R) were predicted. While model selection was done using AIC scores, the significance of the variation in the estimated marginal mean lengths was determined by using a significance cutoff of p = 0.05.

ONTOGENETIC VERTICAL MIGRATION

Although life stage data were not recorded for myctophid samples captured during the ONSAP and DEEPEND programs, Gartner (1993) details the size at maturity for some myctophid species. To examine whether the observed individuals that remain at depth during the night are indeed non-migrating juveniles or a result of net contamination, the data for length at maturity for the described species in Gartner, (1993) was compared to the lengths observed in this study to determine the background of individuals remaining at depth.

RESULTS

SPECIES DATA

A total of 13,995 myctophid specimens, comprising the 12 most abundant species captured overall (Table 1), were included in the data analysis. While Table 1 lists species by their rank order of abundance, the species-specific results detailed later are in alphabetical order for clarity. Each species' abundance distributions, based on the number of samples analyzed rather than standardized abundances, were used to compare each species' vertical distribution and plots containing the specific depth bins chosen to be analyzed were included in the species-specific section of results.

Table 1. Rank order of abundance of the 12 most abundant species from two research programs in the Gulf of Mexico.

Overall (2011 – 2017)		ONSAP (2011)		DEEPEND (2015 – 2017)	
Species	Number of specimens	Species	Number of specimens	Species	Number of specimens
Lampanyctus alatus	2550	*Lampanyctus alatus*	2207	*Lampanyctus alatus*	343
Ceratoscopelus warmingii	2299	*Ceratoscopelus warmingii*	1987	*Ceratoscopelus warmingii*	312
Diaphus dumerilii	1897	*Diaphus dumerilii*	1767	*Notolychnus valdiviae*	299
Notolychnus valdiviae	1501	*Hygophum benoiti*	1274	*Benthosema suborbitale*	208
Benthosema suborbitale	1379	*Notolychnus valdiviae*	1202	*Lepidophanes guentheri*	164
Hygophum benoiti	1310	*Benthosema suborbitale*	1171	*Diaphus dumerilii*	130

Lepidophanes guentheri	1169	Lepidophanes guentheri	1005	Diaphus mollis	76
Diaphus mollis	447	Myctophum affine	397	Hygophum taaningi	43
Myctophum affine	433	Diaphus mollis	371	Notoscopelus resplendens	41
Diogenichthys atlanticus	353	Diogenichthys atlanticus	330	Hygophum benoiti	36
Hygophum taaningi	342	Hygophum taaningi	299	Myctophum affine	36
Notoscopelus resplendens	315	Notoscopelus resplendens	274	Diogenichthys atlanticus	23

SPECIES-SPECIFIC PATTERNS

BENTHOSEMA SUBORBITALE (N = 1,379; Size range: 9 – 34 mm)

Model

This species' variance was best modeled by a combination of month, depth bin, and time of day, resulting in the following final model:

$$Standard\ length_{MTD} = depth\ bin_{MTD} + time\ of\ day_{MTD} + month_{MTD} + depth$$
$bin{:}time\ of\ day_{MTD}$, varIdent = $(1|M) + (1|T) + (1|D)$.

Vertical Distribution

The majority of the species specimens were found between 200 – 600 m depth during the day and 0 – 200 m depth at night, resulting in these two depth bins being analyzed for individual lengths (Figures 3 & 4). This species exhibited a weak, continuous vertical distribution, where the depth bins the majority of individuals migrated to were adjacent to each other. Regarding migration pattern, very few specimens remained at depth only in the months of May and June of 2011 so this species is considered a complete migrator.
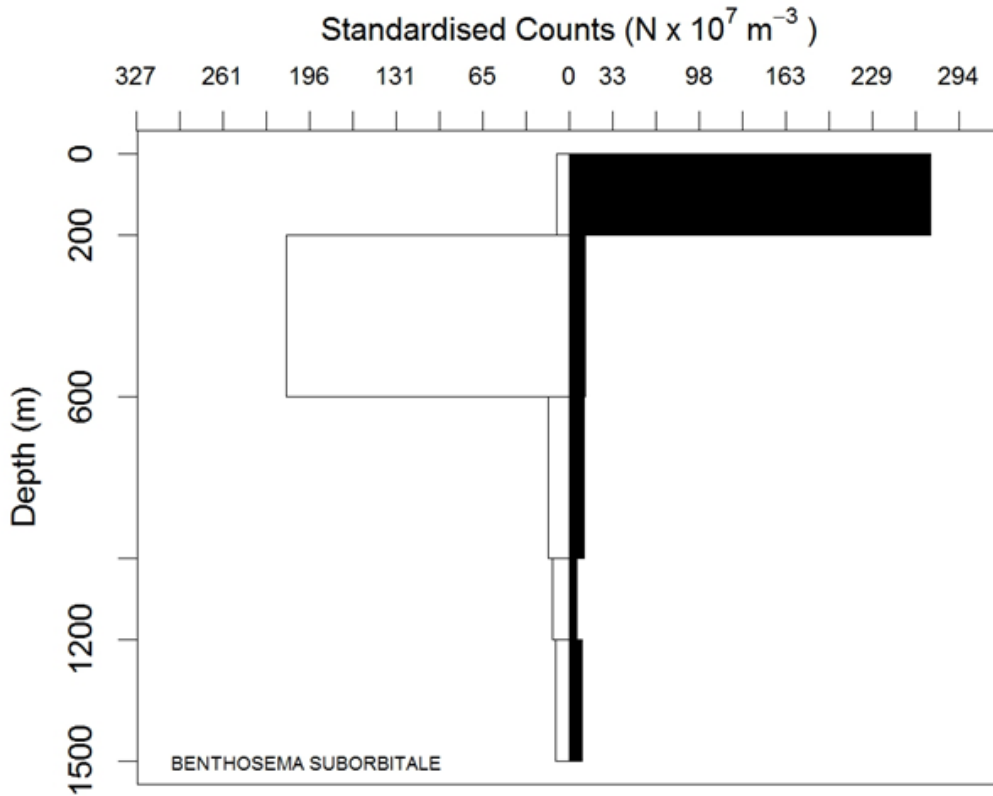
Figure 3. Diel vertical profile based on standardized abundance for *Benthosema suborbitale*.

Relationship of Size with Depth

Mean length did not vary significantly between individuals captured between 0 – 200 m at night and those captured between 200 – 600 m during the day. In the months where individuals were captured between 200 – 600 m at night, they were significantly shorter ($p < 0.05$) than those captured between 0 – 200 m at night as well as the individuals captured during the daytime at 200 – 600 m (Figure 5).

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Average lengths Across the Time Series

The species showed little significant variation in length over the course of the time series. The only significant difference in length was that individuals captured in June 2011 were significantly shorter (mean SL = 12.3 – 20.1 mm) than individuals captured in May (mean SL = 14.4 – 22.2 mm) and August 2011 (mean SL = 21.2 – 22.3 mm; $p < 0.05$) (Figure 5).

Figure 4. Time series showing estimated mean lengths with 95% confidence intervals for *Benthosema suborbitale.* Blue indicates depth bin 200 – 600 m; red indicates depth bin 0 – 200 m. The dashed line separates the months of the ONSAP and DEEPEND programs.

CERATOSCOPELUS WARMINGII (N = 2,299; Size range: 9 – 77 mm)

Model

This species' variance was best modeled by time of day, resulting in the following final model:

$$standard\ length_T = depth\ bin_T + time\ of\ day_T + month_T + depth\ bin{:}time\ of\ day_T,$$

varIdent = (1|T).

Vertical Distribution

The majority of the species specimens were found between 600 – 1000 m depth during the day and 0 – 200 m depth at night, resulting in these two depth bins being analyzed (Figures 6 and 7). This species exhibited a strong and somewhat disconnected vertical distribution, mostly skipping the depth range of 200 – 600 m and descending further to 1000 m and beyond. Regarding migration pattern, a noticeable portion of specimens remained at depth from April to September of 2011 and in May of 2017 while an even smaller portion remained in the epipelagic during the day in May and June of 2011, meaning this species is a partial migrator.
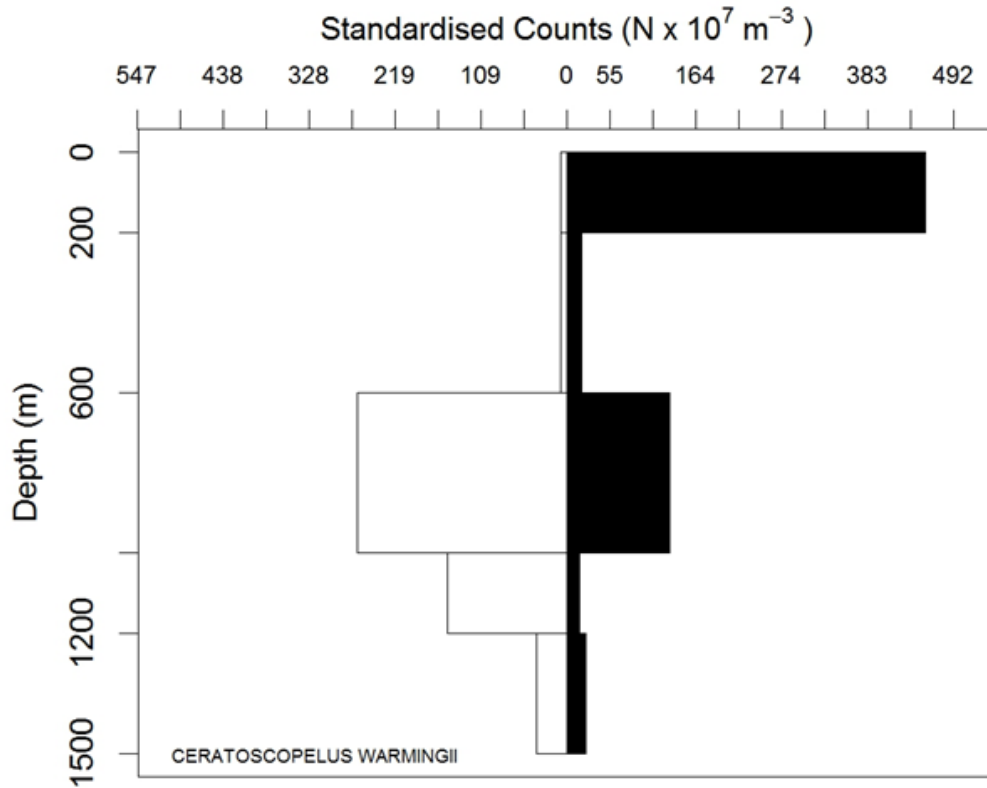
Figure 5. Diel vertical profile based on standardized abundance for *Ceratoscopelus warmingii*.

Relationship of Size with Depth

In the months where individuals were captured between 600 – 1000 m during the day and night, they were significantly shorter ($p < 0.05$) than individuals captured between 0 – 200 m. The daytime and nighttime lengths of specimens captured in the same depth bins were not significantly different (Figure 8).

Average Lengtha Across the Time Series

This species showed some significant variation in body length over the course of the time series. Starting in August 2011 and continuing into September, there was a significant increase ($p < 0.05$) in body length compared to the previous months of April, May, and June. Variations between ONSAP and DEEPEND were observed, with June 2011 (mean SL = 17.0 – 27.2 mm) being significantly shorter ($p < 0.05$) than May of 2015 (mean SL = 21.2 – 31.4 mm) and August of 2016 (mean SL = 21.4 – 31.6 mm). Lengths in September of 2011 were significantly longer (p

< 0.05) than in May 2015, 2016, and 2017, and August of 2016. No other months showed any significant difference in length (Figure 8).
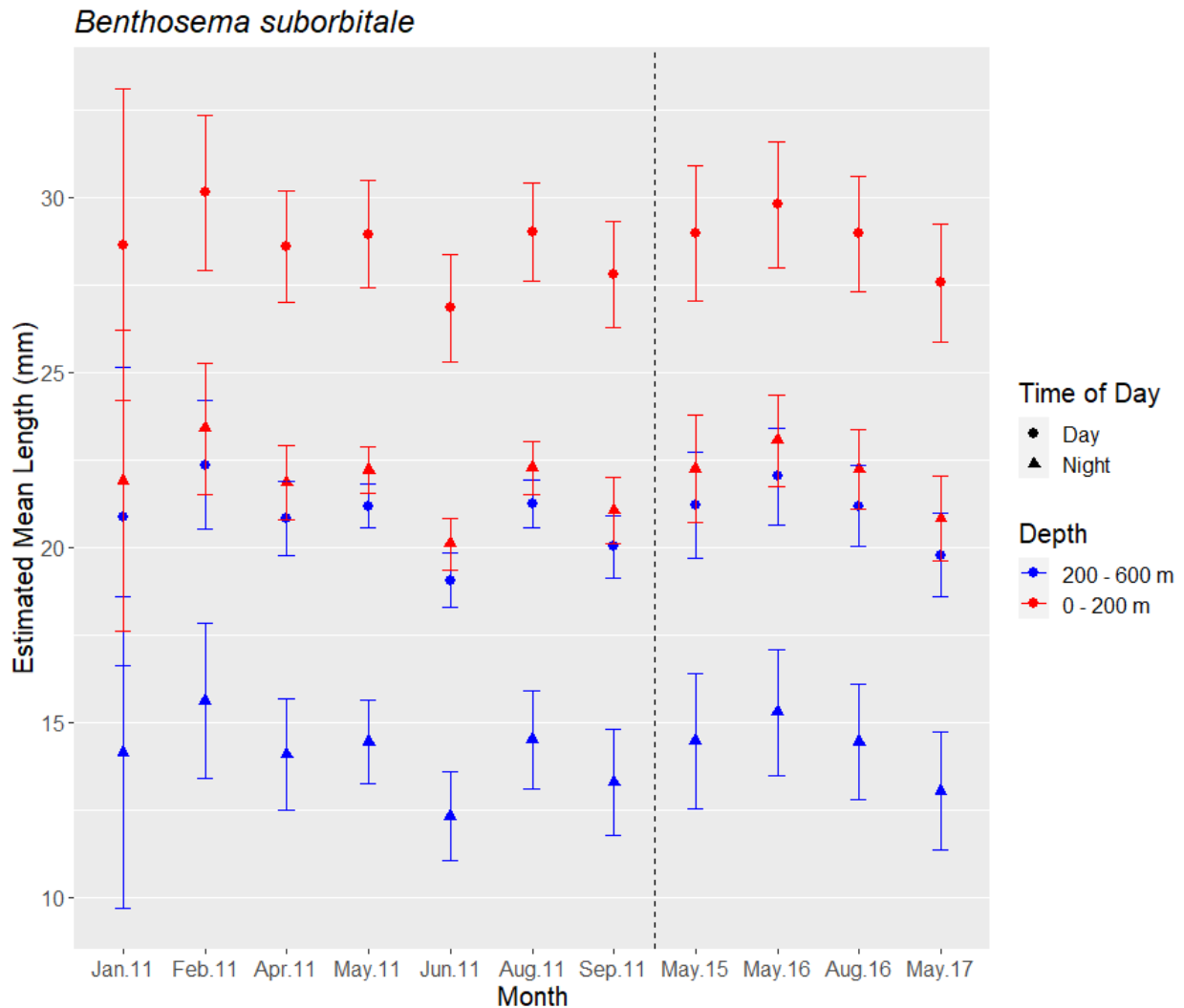

Figure 6. Time series showing estimated mean lengths with 95% confidence intervals for *Ceratoscopelus warmingii*. Black indicates depth bin 600 – 1000 m; red indicates depth bin 0 – 200 m. The dashed line separates the months of the ONSAP and DEEPEND programs.

DIOGENYCHTHYS ATLANTICUS (N = 353; Size range: 11 – 25 mm)

Model

This species' variance was homogenous and the final fitted model was:

standard length = depth bin + time of day + month + depth bin:time of day

Vertical Distribution

The of the species specimens were found between 200 – 600 m depth during the day and 0 – 200 m depth at night, resulting in these two depth bins being analyzed (Figures 9 and 10). This species exhibited a strong, continuous vertical distribution from the epipelagic to the lower mesopelagic, but due to lack of specimens the only two depth bins analyzed were the epipelagic and the mesopelagic. Regarding migration pattern, a small portion of specimens remaned at depth in May and September of 2011, so this species is considered a complete migrator.
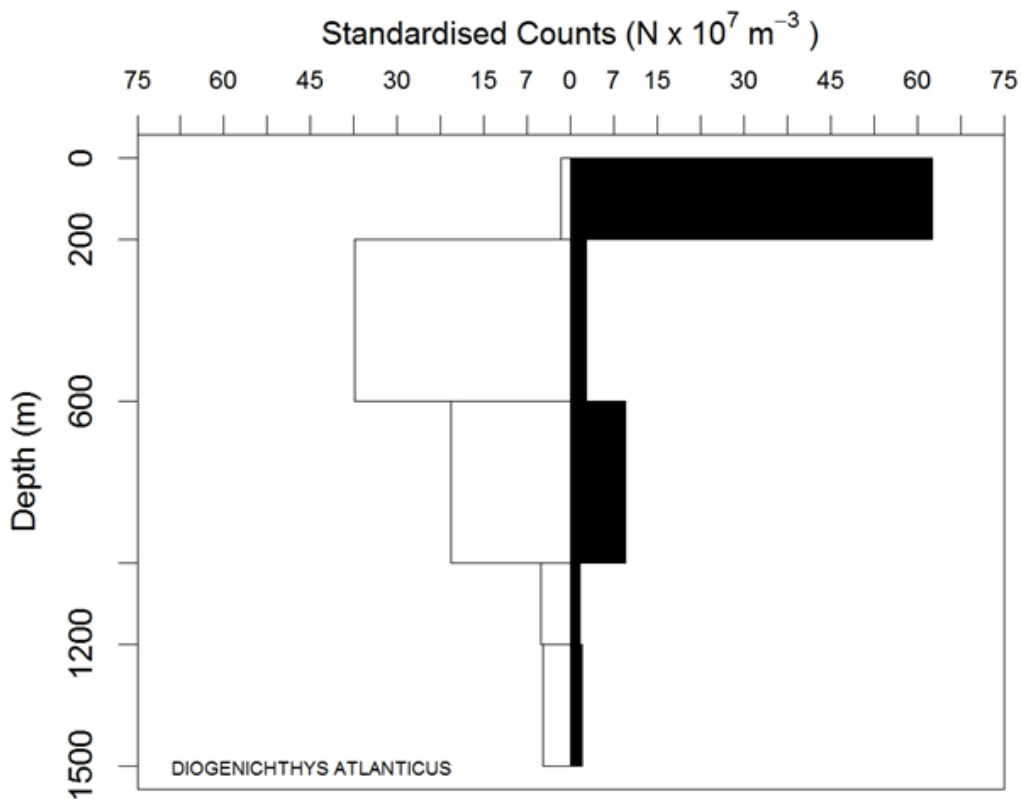
Figure 7. Diel vertical profile based on standardized abundance for *Diogenichthys atlanticus*.

Relationship of Size with Depth and Average Lengths Across the Time Series

The species showed no significant variation in length between depths at either day or
night, or over time or between ONSAP and DEEPEND (Figure 11).

Figure 8. Time series showing estimated mean lengths with 95% confidence intervals for
Diogenichthys atlanticus. Blue indicates depth bin 200 – 600 m; red indicates depth bin 0 – 200
m. The dashed line separates the months of the ONSAP and DEEPEND programs.

DIAPHUS DUMERILLI (N = 1,897; Size range: 9 – 69 mm)

Model

This species' variance was best modeled by time of day, resulting in the following final model:

$$\textit{standard length}_T = \textit{depth bin}_T + \textit{time of day}_T + \textit{month}_T + \textit{depth bin:time of day}_T,$$

varIdent = (1|T).

Vertical Distribution

The majority of the species specimens were found between 200 – 600 m depth during the day and 0 – 200 m depth at night, resulting in these two depth bins being analyzed (Figures 12 and 13). This species exhibited a weak, continuous vertical distribution, being captured between 0 – 200 m at night then migrating to between 200 – 600 m during the day. Regarding migration pattern, the portion of specimens remaining at depth was nearly nonexistent and only ocurring in May 2011, meaning the species is a complete migrator.

Figure 9. Diel vertical profile based on standardized abundance for *Diaphus dumerilii*.

Relationship of Size with Depth

Individuals captured between 200 – 600 m during the day were significantly (p < 0.05) shorter than individuals captured at night between 0 – 200 m depth across all months. In May 2011, the individuals captured between 200 – 600 m during the night were significantly longer (p < 0.05) than individuals captured during the day at the same depth but not significantly different than the individuals captued at night that migrated to 0 – 200 m. In September 2011, the individuals that were captured between 0 – 200 m during the day were significantly shorter (p < 0.05) than the individuals at night at the same depth. Those captured between 0 – 200 m during the day, however, were not significantly different than those captured between 200 – 600 m depth during the day (Figure 14).

Average Lengths Across the Time Series

The species showed some variation in lengths over time. Starting in February of 2011 there was a decline in lengths that did not become significantly lower than February (mean SL = 20.5 – 26.9 mm) until June (mean SL = 16.1 – 22.6 mm), followed by an increase in August (mean SL = 18.6 – 25.5 mm) that was significantly longer than May (mean SL = 17.0 – 23.5 mm) and June. Between ONSAP and DEEPEND, the months of April, May, June, and September of 2011 were significantly shorter (p < 0.05) than May of 2016 (mean SL = 21.7 – 28.2 mm). May of 2016 showed a significant increase in lengths compared to May in previous (mean SL in 2015 = 14.6 – 21.0 mm) and following years (2017 = 13.2 – 19.7 mm). No other months showed any significant difference in length (Figure 14).
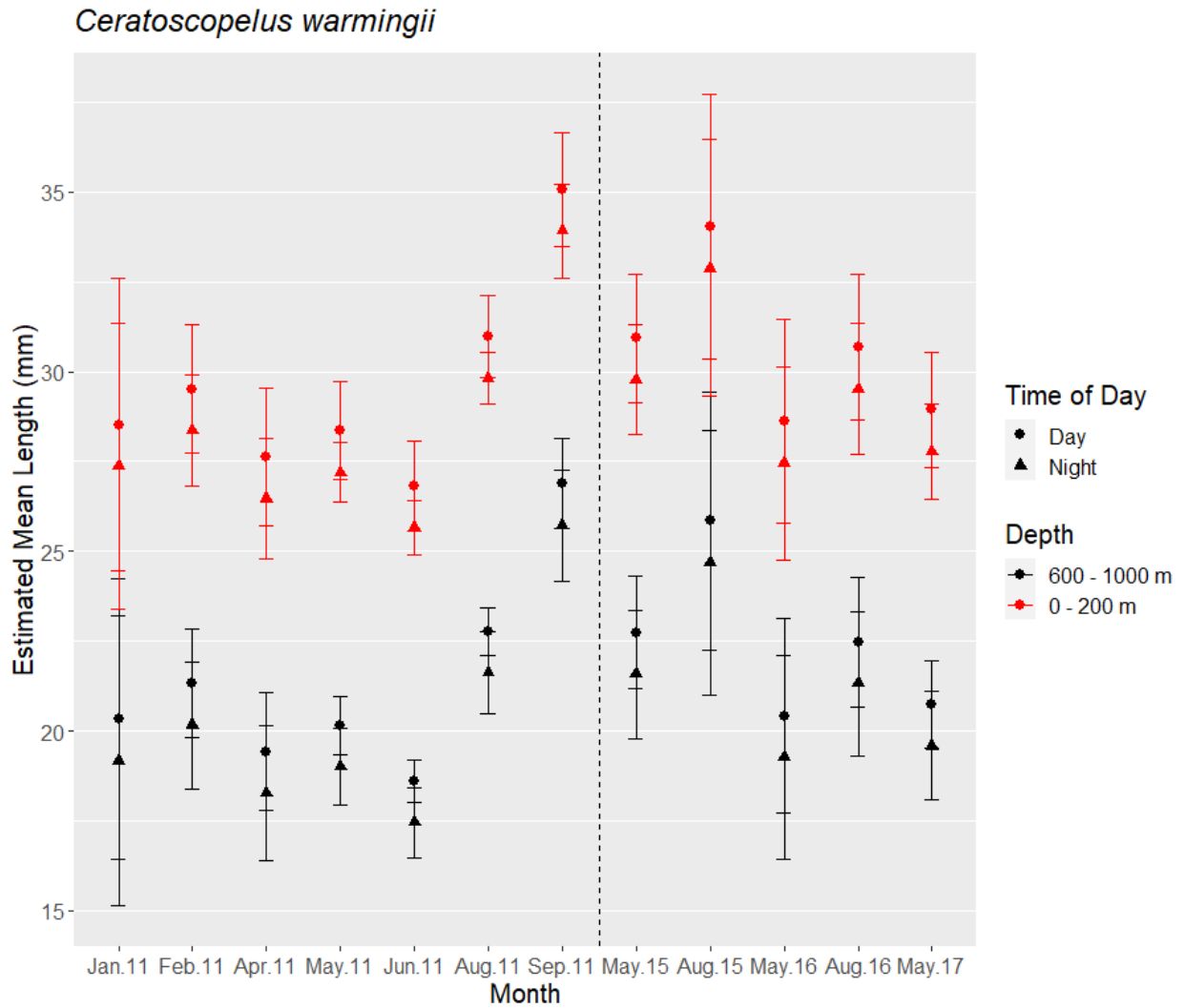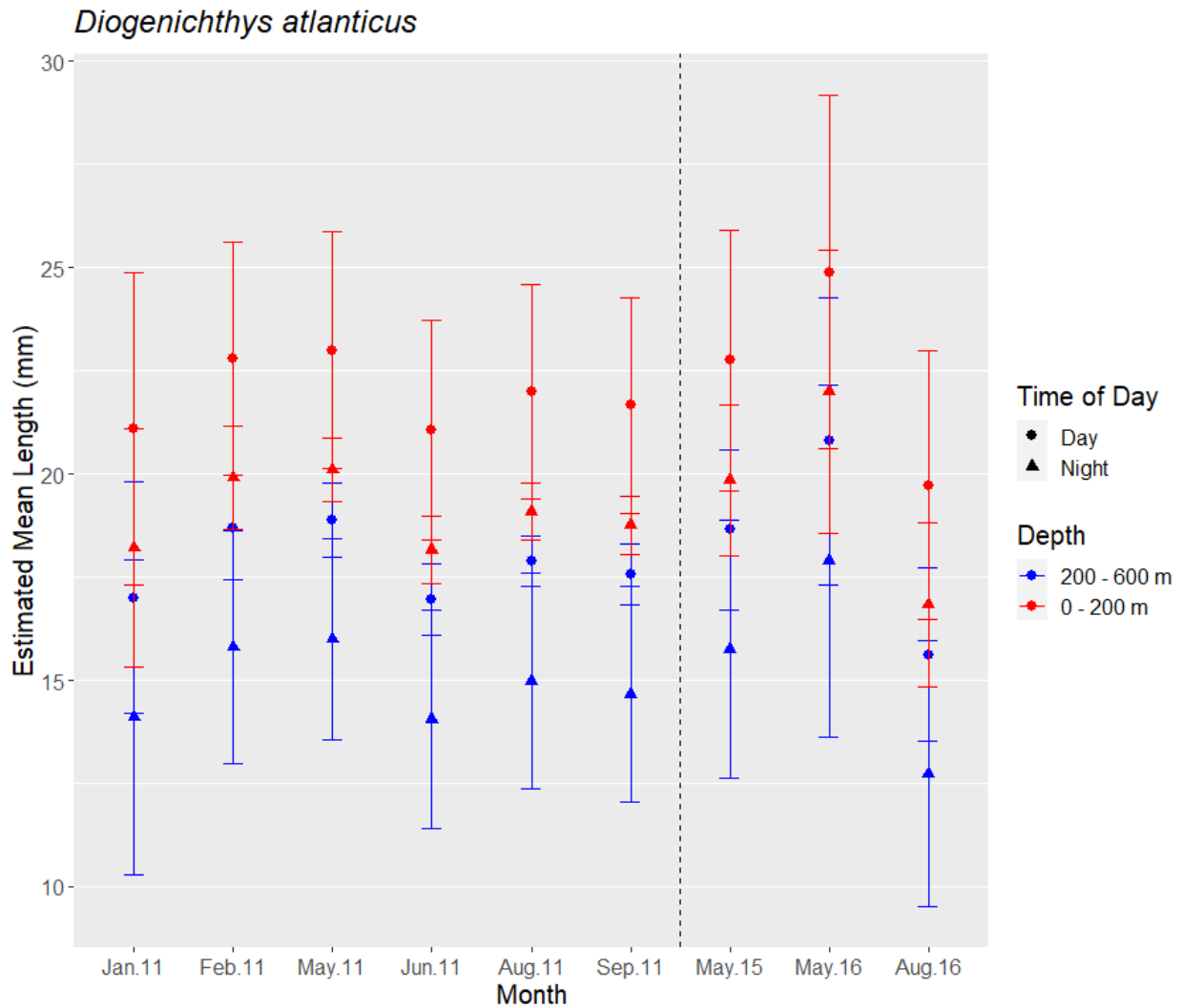
Figure 10. Time series showing estimated mean lengths with 95% confidence intervals for *Diaphus dumerilii*. Blue indicates depth bin 200 – 600 m; red indicates depth bin 0 – 200 m. The dashed line separates the months of the ONSAP and DEEPEND programs.

DIAPHUS MOLLIS (N = 447; Size range: 10 – 59 mm)

Model

This species' variance was best modeled by month, resulting in the following final model:

$$standard\ length_M = depth\ bin_M + time\ of\ day_M + month_M + depth\ bin{:}time\ of\ day_M, varIdent = (1|M).$$

Vertical Distribution

The standardized count vertical distribution indicated that a majority of the species were found between 200 – 600 m depth during the day and 0 – 200 m depth at night, resulting in these two depth bins being analyzed (Figures 15 and 16). This species exhibited a weak, continuous vertical distribution, where the depth bins the majority of individuals migrated to were adjacent to each other. Regarding migration pattern, a small portion of specimens remained at depth but only in May and August of 2011, meaning this species is a complete migrator.
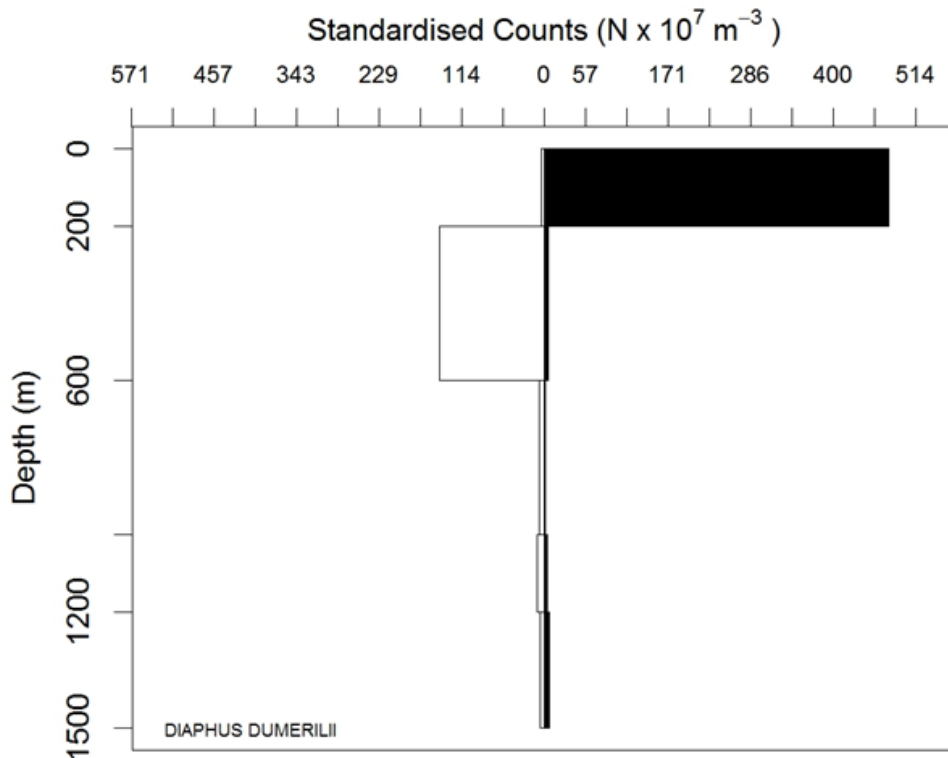

Figure 11. Diel vertical profile based on standardized abundance for *Diaphus mollis*.

Relationship of Size with Depth

Across all months, individuals captured between 200 – 600 m depth during the day were significantly shorter ($p < 0.05$) than those captured between 0 – 200 m at night. In the months where individuals were captured between 200 – 600 m during the night, they were not significantly different lengths to those captured between 0 – 200 m at night nor those captured between 200 – 600 m during the day (Figure 17).

Average Lengths Across the Time Series

This species showed little significant variation in body length over time. Starting in February, there was a decline in body length that did not become significantly different than February (mean SL = 32.0 – 51.6 mm) until September (mean SL = 18.6 – 38.2 mm) followed by a return to lengths similar to those in the first three months of 2011. No other months showed any significant difference in length (Figure 17).
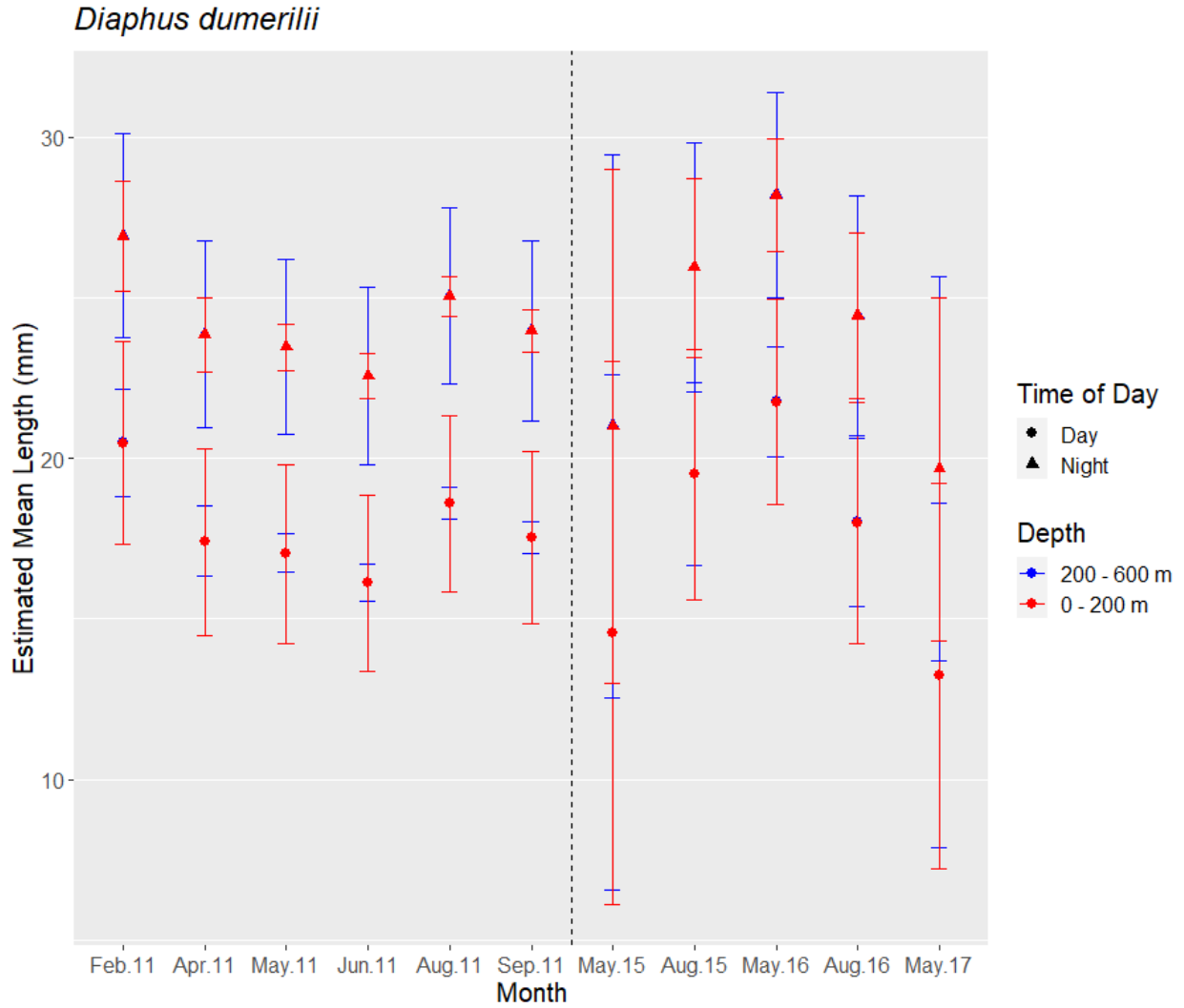
Figure 12. Time series showing estimated mean lengths with 95% confidence intervals for *Diaphus mollis*. Blue indicates depth bin 200 – 600 m; red indicates depth bin 0 – 200 m. The dashed line separates the months of the ONSAP and DEEPEND programs.

HYGOPHUM BENOITI (N = 1,310, Size range: 7 – 30 mm)

Model

This species' variance was best modeled by a combination of month, depth bin, and time of day, resulting in the following final model:

$$standard\ length_{MTD} = depth\ bin_{MTD} + time\ of\ day_{MTD} + month_{MTD} + depth$$
$$bin{:}time\ of\ day_{MTD}, \text{varIdent} = (1|M) + (1|T) + (1|D).$$

Vertical Distribution

The standardized count vertical distribution indicated that a majority of the species were found between 200 – 600 m and 600 – 1000 depth during the day, and 0 – 200 m and 600 – 1000 m depth at night, resulting in these three depth bins being analyzed (Figures 18 and 19). This species exhibited a unique strong and continuous vertical distribution, where during the day the depth bins the majority of individuals migrated to were adjacent to each other, but at night the species mostly avoided 200 – 600 m depth and were mostly captured much deeper between 600 – 1000 m. Regarding migration pattern, this species seemed to almost be a non-migrator with only a small portion migrating to shallower depths, indicating this species is a partial migrator.
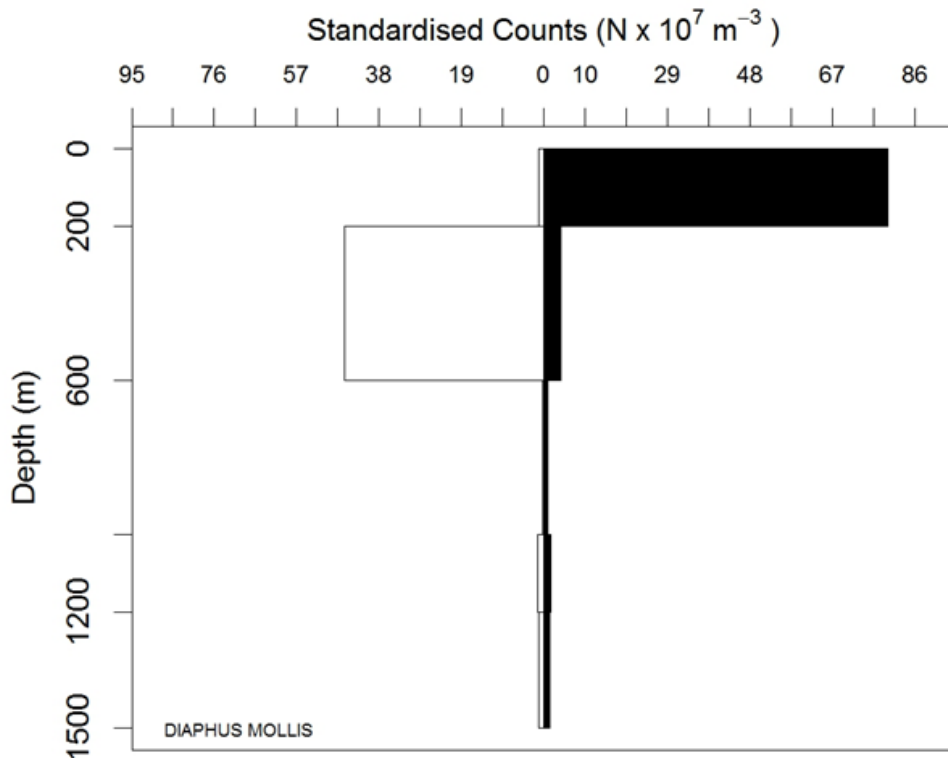
Figure 13. Diel vertical profile based on standardized abundance for *Hygophum benoiti*.

Relationship of Size with Depth

Across all months, individuals captured during the day at 200 – 600 m depth were significantly shorter ($p < 0.05$) than nighttime captures at 0 – 200 m and 600 – 1000 m. Individuals captured during the day at 600 – 1000 m were not significantly different than those captured at the same time at 200 – 600 m. At night, individuals in each depth bin were not significantly different between depth bins. Within each month, individuals captured at the same depth but at a different time of day were not significantly different (Figure 20).

Average Lengths Across the Time Series

The species showed significant variation in size across all months. After a significant decrease from May (mean SL = 13.9 – 14.9 mm) to June (mean SL = 13.0 – 14.0) ($p < 0.05$), there was a significant increase in August (mean SL = 15.8 – 16.8 mm, $p < 0.05$) followed by

another in September (mean SL = 17.0 – 17.9 mm, p < 0.05). There was a significant decrease in length between August of 2015 (mean SL = 18.8 – 19.8 mm) and a year later in August of 2016 (mean SL = 16.5 – 17.5 mm, p < 0.05), which more resembles August of 2011. Between ONSAP and DEEPEND, all months of 2011 were significantly shorter (p < 0.05) than August of 2015, and only May and June of 2011 were significantly shorter (p < 0.05) than August of 2016 (Figure 20).

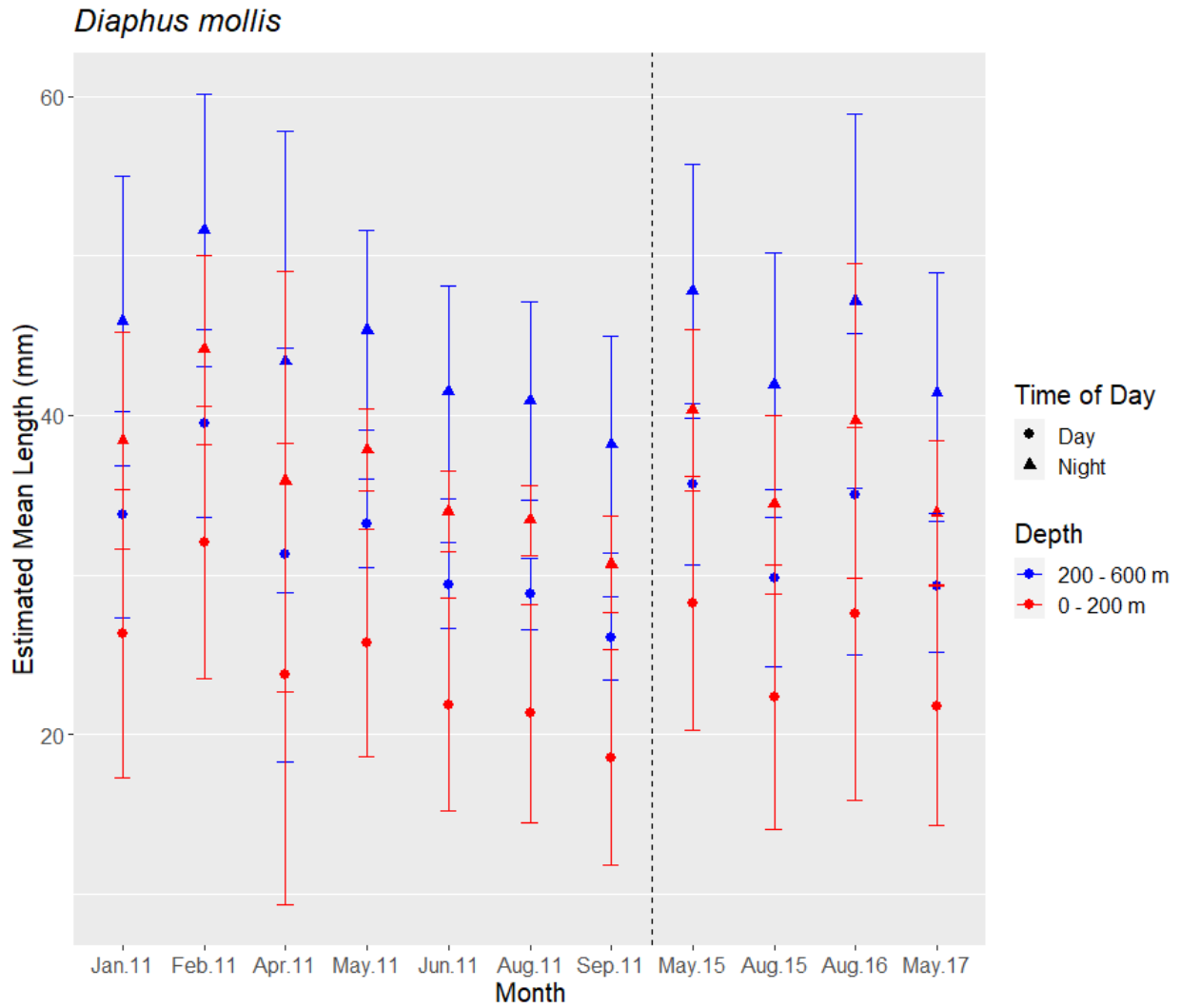Figure 14. Time series showing estimated mean lengths with 95% confidence intervals for *Hygophum benoiti.* Black indicates depth bin 600 – 1000 m; blue indicates depth bin 200 – 600 m; red indicates depth bin 0 – 200 m. The dashed line separates the months of the ONSAP and DEEPEND programs.

HYGOPHUM TAANINGI (N = 342, Size range: 9 – 48 mm)

Model

This species' variance was best modeled by a combination of month, resulting in the following final model:

$$standard\ length_M = depth\ bin_M + time\ of\ day_M + month_M + depth\ bin{:}time\ of\ day_M,\ varIdent = (1|M).$$

Vertical Distribution

The standardized count vertical distribution indicated that a majority of the species were found between 200 – 600 m and 600 – 1000 depth during the day, and 0 – 200 m and 600 – 1000 m depth at night, resulting in these three depth bins being analyzed (Figures 21 and 22). This species exhibited a strong, continuous vertical distribution resembling that of *Hygophum benoiti*, where during the day the depth bins the majority of individuals migrated to were adjacent to each other, but at night the species mostly avoided 200 – 600 m depth and were captured much deeper. The vertical distribution of the analyzed samples closely resembled that of the standardized counts. Regarding migration pattern, there was almost an even split between specimens that migrated and those that did not, with just a tiny portion of specimens occupying the depth bin between the two that were primarily occupied, meaning this species is a partial migrator. In February, May, August, and September of 2011 and August of 2016, the specimens were captured between 0 – 200 m and 200 – 600 m depth during the night, and in May, June, August, and September of 2011 and August of 2015 and May of 2016, specimens were captured between 0 – 200 m and 600 – 1000 m depth at night.
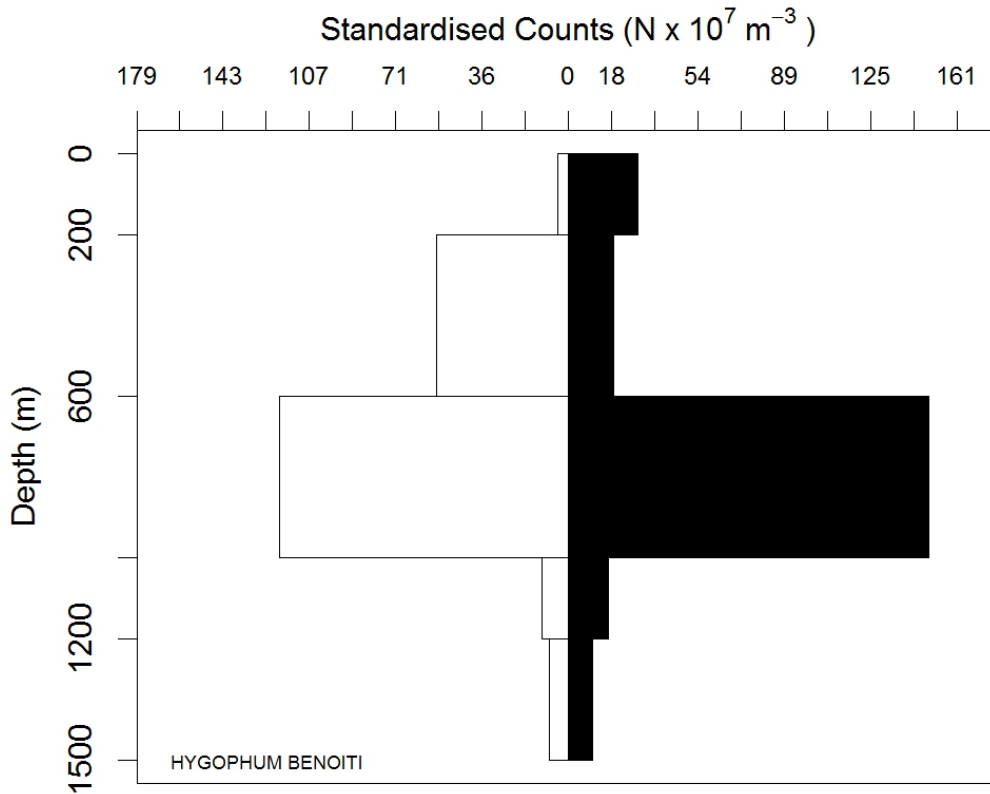
Figure 15. Diel vertical profile based on standardized abundance for *Hyhophum taaningi*.

Relationship of Size with Depth

In each month, individuals captured at 600 – 1000 m during the day were significantly longer (p < 0.05) than those found at 200 – 600 m during both day and night. Also in each month, individuals captured at 600 – 1000 m at night were significantly longer (p < 0.05) than those at 200 – 600 m at the same time. In each month, there was no significant difference between: the individuals captured at the same depth but different time of day, the individuals captured at 200 – 600 m during the day and those captured at 0 – 200 m at night, or the individuals captured at 200 – 600 m and 0 – 200 m at night (Figure 23).

Average Lengths Across the Time Series

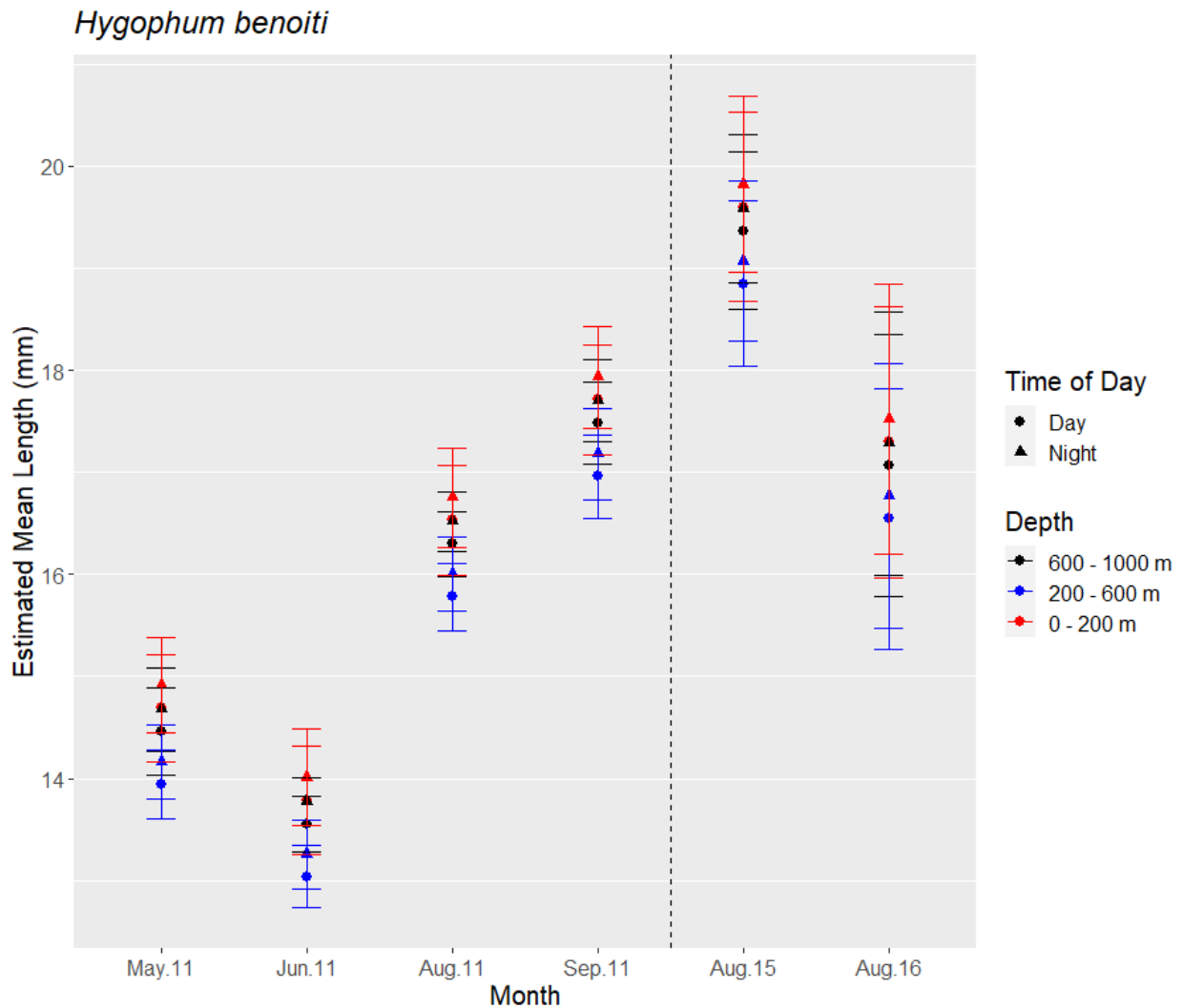No months showed any significant difference in length (Figure 23).

Figure 16. Time series showing estimated mean lengths with 95% confidence intervals for *Hygophum taaningi.* Black indicates depth bin 600 – 1000 m; blue indicates depth bin 200 – 600 m; red indicates depth bin 0 – 200 m. The dashed line separates the months of the ONSAP and DEEPEND programs.

LAMPANYCTUS ALATUS (N = 2,550, Size range: 10 – 59 mm)

Model

This species' variance was best modeled by a combination of month, depth bin, and time of day, resulting in the following final model:

$$\textit{standard length}_{MTD} = \textit{depth bin}_{MTD} + \textit{time of day}_{MTD} + \textit{month}_{MTD} + \textit{depth bin:time of day}_{MTD}, \text{varIdent} = (1|M) + (1|T) + (1|D).$$

Vertical Distribution

The standardized count vertical distribution indicated that a majority of the species were found between 200 – 600 m and 600 – 1000 depth during the day, and 0 – 200 m depth at night, resulting in these three depth bins being analyzed (Figures 24 and 25). This species exhibited a strong, continuous vertical distribution, where the depth bins the majority of individuals migrated to were adjacent to each other. Regarding migration pattern, most specimens were captured in the epipelagic while the remaining small but noticeable portion of specimens was split between the upper and lower mesopalgic, meaning this species is a partial migrator. In February, May, June, August, and September of 2011, May of 2015, and August of 2016, individuals were captured between 0 – 200 m, 200 – 600 m and 600 – 1000 m depth during the night, while in May of 2017 they were captured between 0 – 200 m and 600 – 1000 m only.
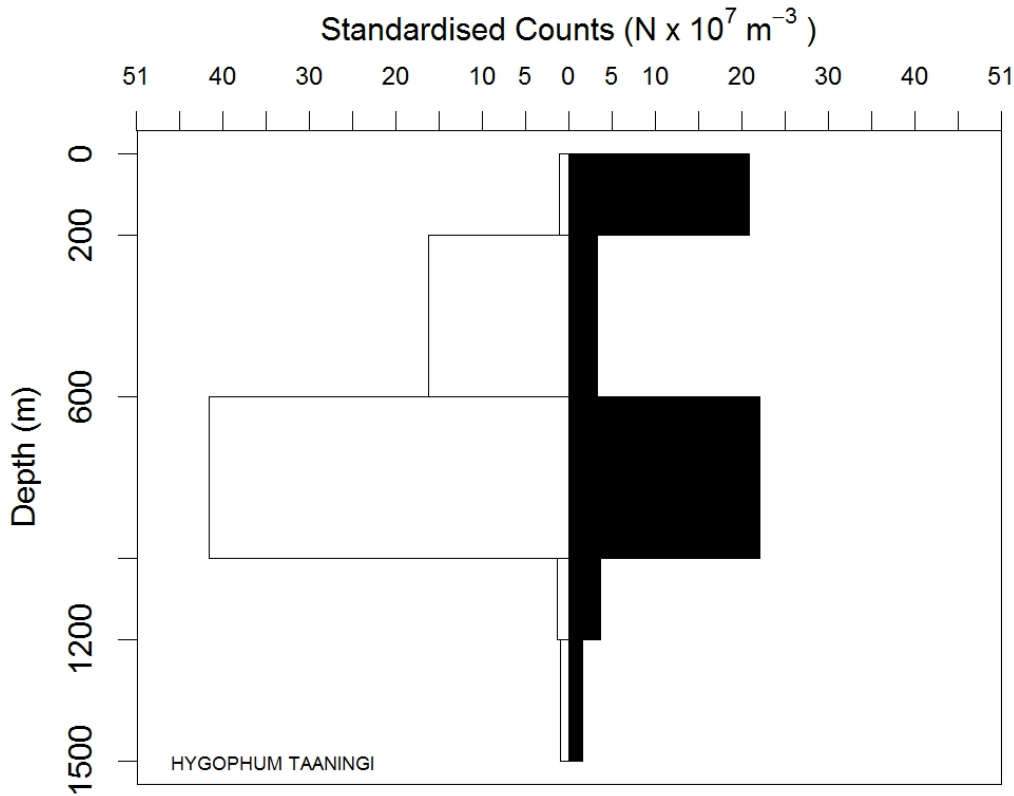
Figure 17. Diel vertical profile based on standardized abundance for *Lampanyctus alatus*.

Relationship of Size with Depth

In each month, individuals captured during the day between 600 – 1000 m depth were significantly longer ($p < 0.05$) than those captured between 200 – 600 m at the same time. In each month with nighttime captures at every depth, individuals captured between 600 – 1000 m are significantly longer ($p < 0.05$) than those captured between 200 – 600 m, but significantly shorter ($p < 0.05$) than those captured between 0 – 200 m. In each month where individuals were captured during both day and nighttime between 600 – 1000 m, individuals during the day were significantly longer ($p < 0.05$) than those at night. For individuals captured between 200 – 600 m during the day and night, the daytime individuals were significantly longer ($p < 0.05$) than those at night. In each month, individuals captured during the day between 200 – 600 m are significantly shorter ($p < 0.05$) than individuals captured between 0 – 200 m at night (Figure 26).

Average Lengths Across the Time Series

There was little significant variation in mean length over time. The species showed a significant decrease in body size ($p < 0.05$) in 2011 for the months of April (mean SL = 18.8 – 35.9 mm), May (mean SL = 18.7 – 35.8 mm), and June (mean SL = 18.3 – 35.4 mm) compared to January (mean SL = 21.1 – 38.2 mm) and February (mean SL = 23.2 – 40.3 mm) before a significant increase in August 2011 (mean SL = 22.3 – 39.4 mm) back to similar lengths before April. Between ONSAP and DEEPEND, the months of February, August, and September of 2011 had significantly longer lengths ($p < 0.05$) than May of 2017 (mean SL = 15.7 – 32.8 mm). The months of May and June of 2011 had significantly shorter lengths ($p < 0.05$) than August in both 2015 (mean SL = 25.0 – 42.1 mm) and 2016 (mean SL = 24.3 – 41.4 mm). April 2011 has significantly shorter lengths ($p < 0.05$) than just August of 2016. In May and August of the following years of 2015 – 2016, August has significantly longer individuals ($p < 0.05$) than those in May. No other months showed any significant difference in length (Figure 26).
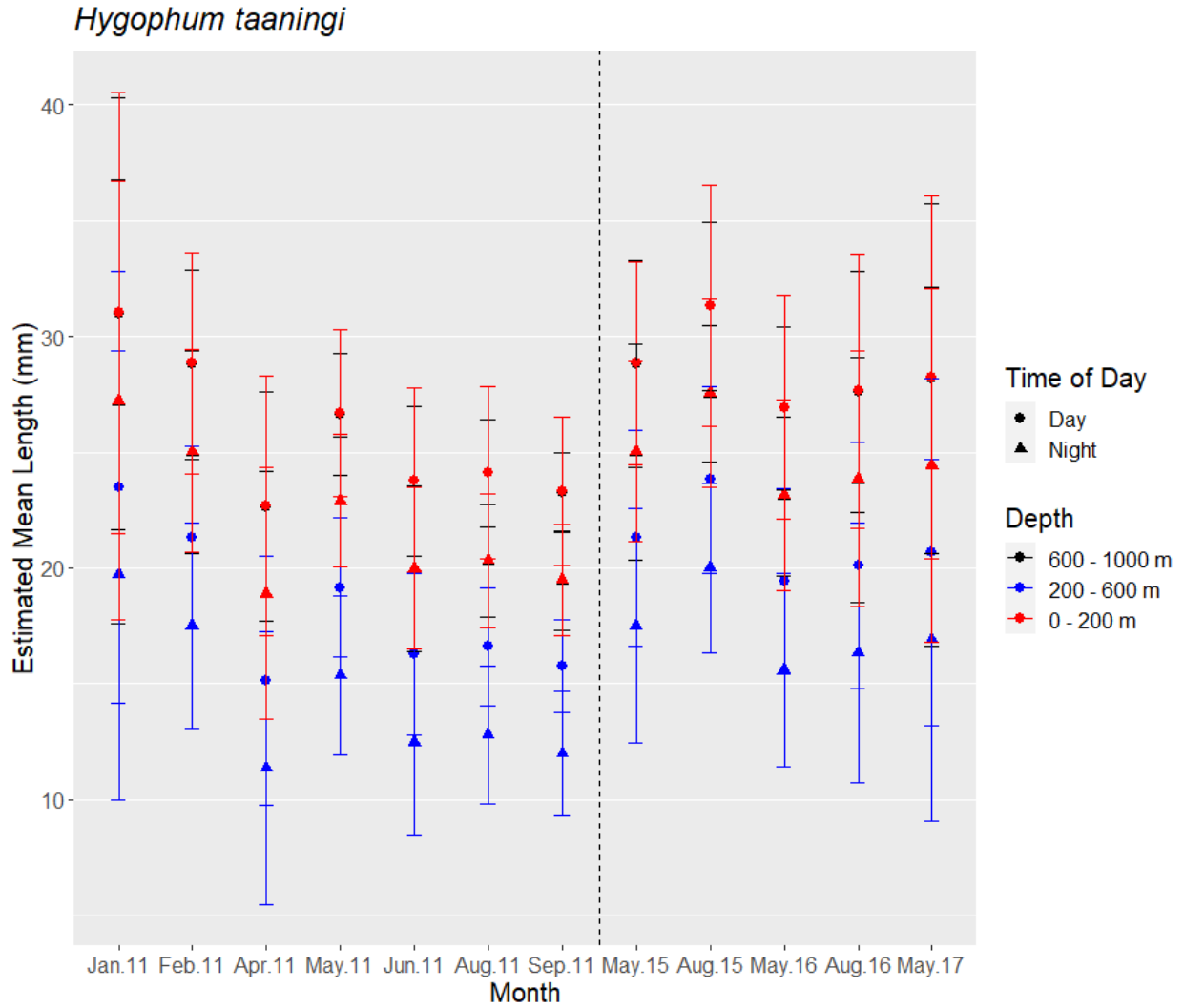
Figure 18. Time series showing estimated mean lengths with 95% confidence intervals for *Lampanyctus alatus.* Black indicates depth bin 600 – 1000 m; blue indicates depth bin 200 – 600 m; red indicates depth bin 0 – 200 m. The dashed line separates the months of the ONSAP and DEEPEND programs.

LEPIDOPHANES GUENTHERI (N = 1,169, Size range: 12 – 65 mm)

Model

This species' variance was best modeled by a combination of depth bin, resulting in the following final model:

$$\textit{standard length}_D = \textit{depth bin}_D + \textit{time of day}_D + \textit{month}_D + \textit{depth bin:time of day}_D,$$

varIdent = (1|D).

Vertical Distribution

The standardized count vertical distribution indicated that a majority of the species were found between 200 – 600 m and 600 – 1000 depth during the day, and 0 – 200 m depth at night, resulting in these three depth bins being analyzed (Figures 27 and 28). This species exhibited a strong, continuous vertical distribution, where the depth bins the majority of individuals migrated to were adjacent to each other. Regarding migration pattern, nearly all specimens were captured in the epipelagic while the very small portion of specimens remaining at depth were split between the upper and lower mesopelagic, meaning this species is a complete migrator. In May and August of 2011, individuals were captured between 0 – 200 m and 200 – 600 m depth during the night, while in June they were captured between 0 – 200 m and 600 – 1000 m only.
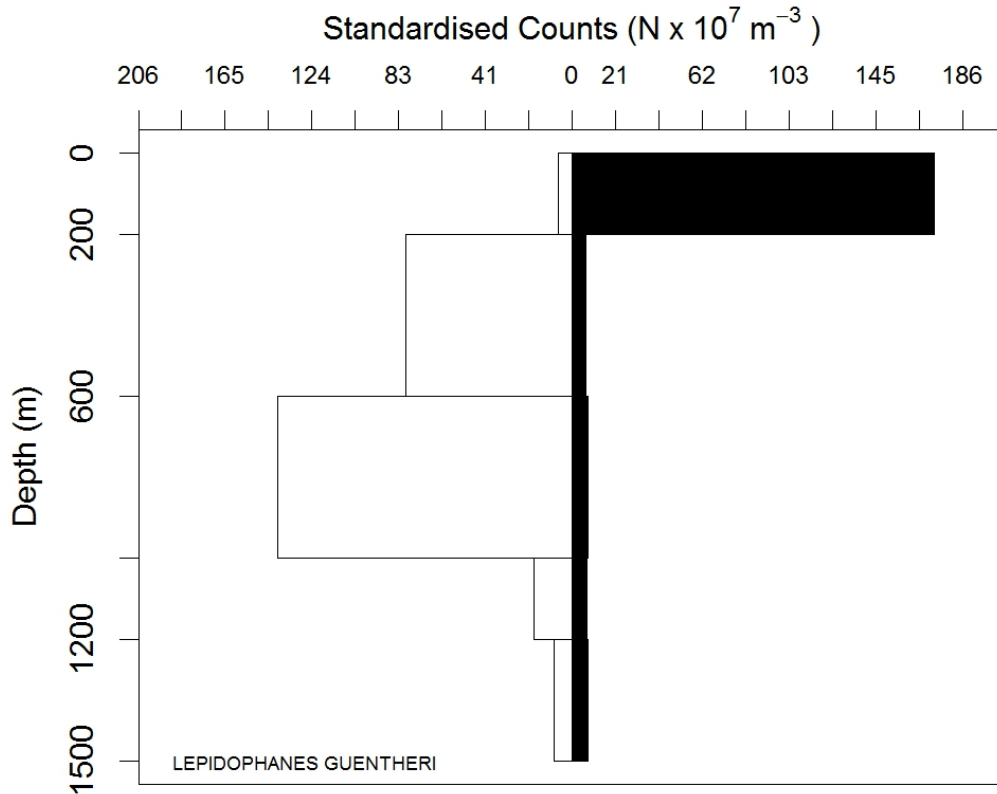
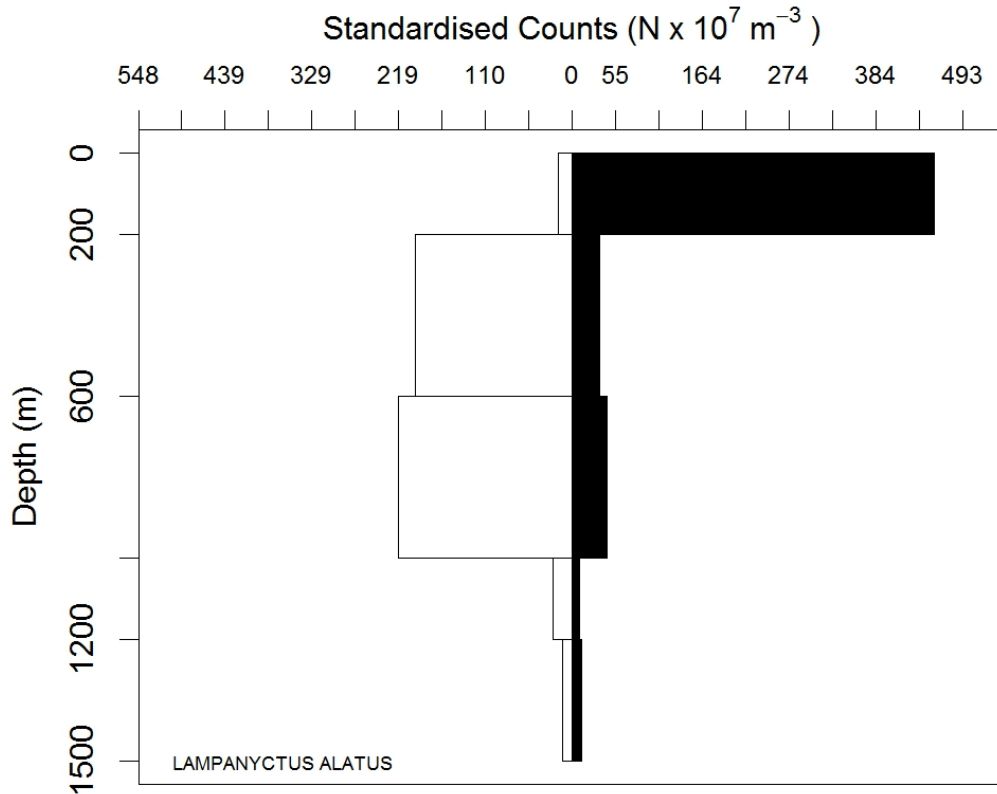Figure 19. Diel vertical profile based on standardized abundance for *Lepidophanes guentheri*.

Relationship of Size with Depth

Throughout all months, individuals captured during the day at 600 – 1000 m depth were significantly longer (p < 0.05) than those captured at the same time at 200 – 600 m depth. The daytime individuals at 200 – 600 m depth were also significantly shorter (p < 0.05) than nighttime captures at 0 – 200 m, but daytime individuals at 600 – 1000 m depth were not significantly different than those at 0 – 200 m at night. In the months with both day and night captures in the same depth range, the daytime and nighttime individuals were not significantly different. In the months where individuals remained between 200 – 600 m during the night, they were significantly shorter than those at 0 – 200 m (Figure 29).

Average Lengths Across the Time Series

Over time, there was little significant variation in body size. There was a slight insignificant increase in length over time beginning in January and going until May (mean SL = 27.5 – 49.1 mm) when there was a significant decrease ($p < 0.05$) in length into June (mean SL = 16.4 – 38.0 mm) that lasted until September. The decrease observed in June led to significantly shorter lengths ($p < 0.05$) than February (mean SL = 24.1 – 45.7 mm) and April (mean SL = 25.2 – 46.8 mm). There was a significant increase ($p < 0.05$) in length in May of 2015 (mean SL = 28.1 – 49.7 mm) followed by an insignificant decrease in August of the same year. A similar pattern was observed in 2016 where there was an insignificant decrease in lengths from May to August, both of which had insignificantly shorter lengths than the previous year. Between ONSAP and DEEPEND, the months of June and August of 2011 (mean SL = 16.6 – 38.2 mm) had significantly shorter lengths ($p < 0.05$) than August of 2015 (mean SL = 25.0 – 46.6 mm). No months showed any significant difference in length (Figure 29).
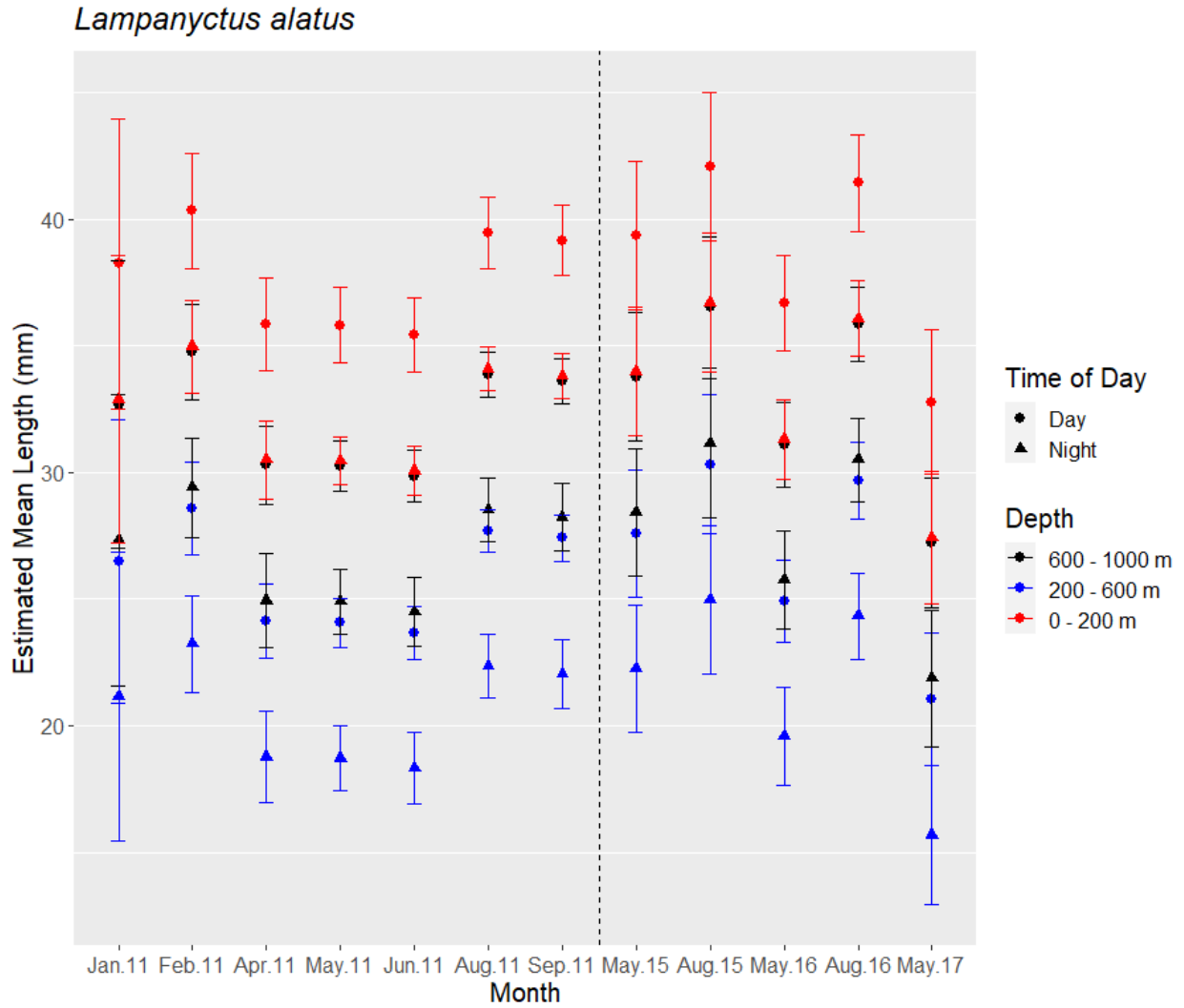
Figure 20. Time series showing estimated mean lengths with 95% confidence intervals for *Lepidophanes guentheri*. Black indicates depth bin 600 – 1000 m; blue indicates depth bin 200 – 600 m; red indicates depth bin 0 – 200 m. The dashed line separates the months of the ONSAP and DEEPEND programs.

MYCTOPHUM AFFINE (N = 433, Size range: 11 – 63 mm)

Model

This species' variance was best modeled by a combination of month, depth bin, and time of day, resulting in the following final model:

$$\textit{standard length}_{MTD} = \textit{depth bin}_{MTD} + \textit{time of day}_{MTD} + \textit{month}_{MTD} + \textit{depth bin:time of day}_{MTD}, \text{varIdent} = (1|M) + (1|T) + (1|D).$$

Vertical Distribution

The standardized count vertical distribution indicated that a majority of the species were found between 200 – 600 m and 600 – 1000 depth during the day, and 0 – 200 m and 600 – 1000 m depth at night, resulting in these three depth bins being analyzed (Figures 30 and 31). This species exhibited a strong, continuous vertical distribution similar to both *Hygophum* species analyzed, where during the day the depth bins the majority of individuals migrated to were adjacent to each other, but at night the species mostly avoided 200 – 600 m depth and were captured much deeper. Regarding migration pattern, the specimens were almost split between the epipelagic and the lower mesopelagic, with more specimens migrating to the epipelagic, meaning this species is a partial migrator. In May – September of 2011, individuals were captured between 0 – 200 m and 600 – 1000 m depth during the night.
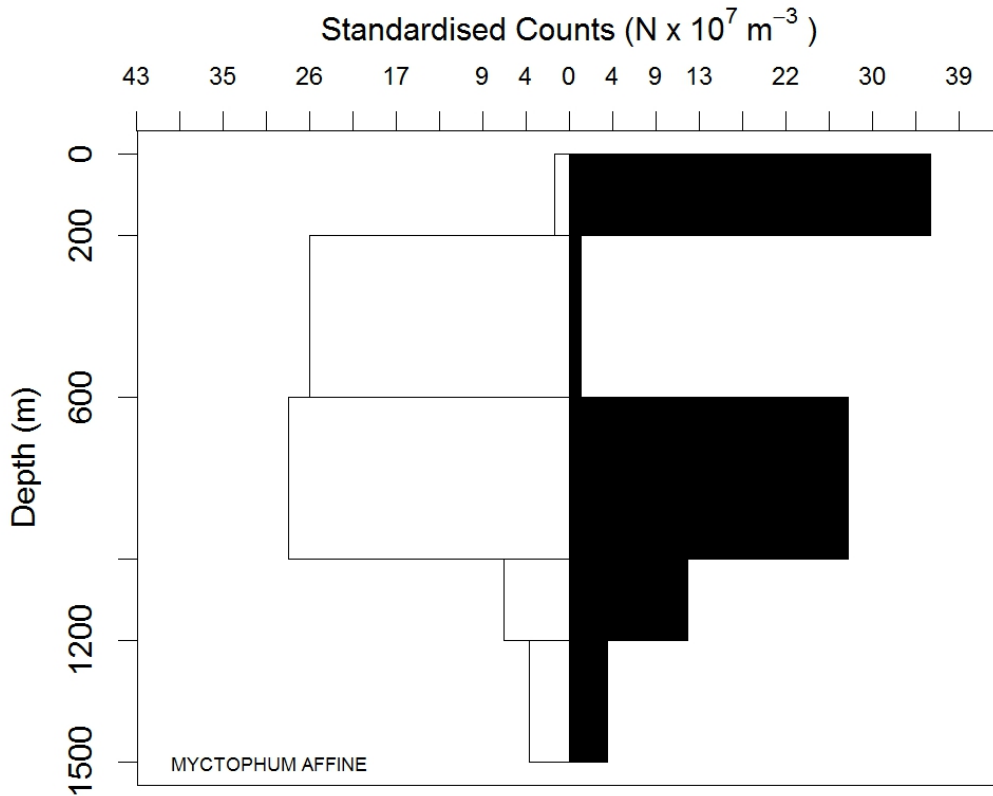
Figure 21. Diel vertical profile based on standardized abundance for *Myctophum affine*.

Relationship of Size with Depth

In each month, individuals captured during the day at 600 – 1000 m were significantly shorter (p < 0.05) than those caught at the same time at 200 – 600 m. Also, individuals captured during the day at 600 – 1000 m were significantly longer (p < 0.05) than those captured at night at the same depth. Individuals captured at 200 – 600 m during the day were not significantly different than those captured at 0 – 200 m at night. In each month, individuals captured at 600 – 1000 m at night were significantly shorter (p < 0.05) than those captured at 0 – 200 m (Figure 32).

Average Lengths Across the Time Series

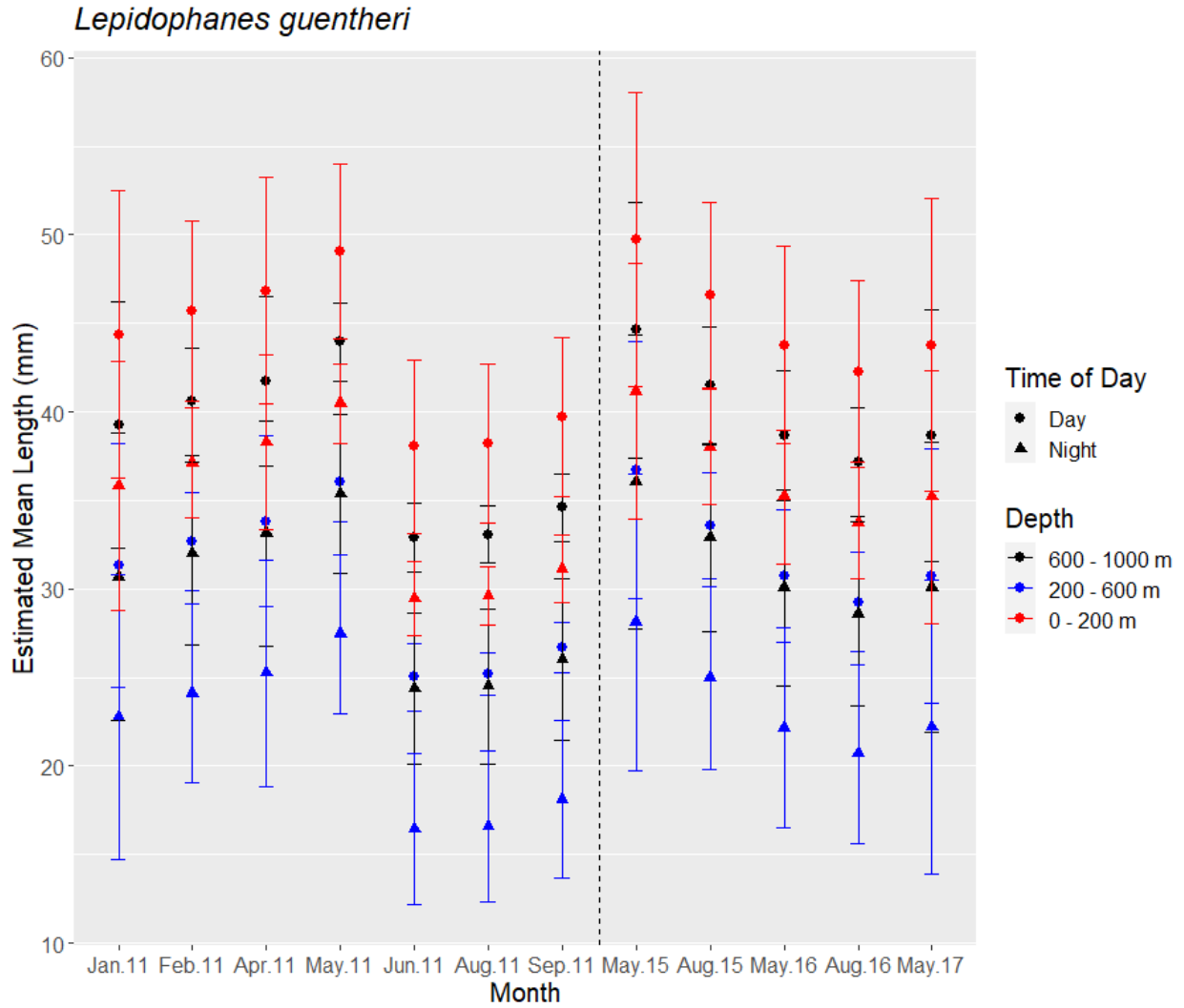No months were significantly different to each other (Figure 32).

Figure 22. Time series showing estimated mean lengths with 95% confidence intervals for *Myctophum affine.* Black indicates depth bin 600 – 1000 m; blue indicates depth bin 200 – 600 m; red indicates depth bin 0 – 200 m. The dashed line separates the months of the ONSAP and DEEPEND programs.

NOTOSCOPELUS RESPLENDENS (N = 315, Size range: 12 – 64 mm)

Model

This species' variance was best modeled by a combination of month, depth bin, and time of day, resulting in the following final model:

$$\textit{standard length}_{MTD} = \textit{depth bin}_{MTD} + \textit{time of day}_{MTD} + \textit{month}_{MTD} + \textit{depth bin:time of day}_{MTD}, \text{varIdent} = (1|M) + (1|T) + (1|D).$$

Vertical Distribution

The standardized count vertical distribution indicated that a majority of the species were found between 200 – 600 m and 600 – 1000 depth during the day, and 0 – 200 m depth at night, resulting in these three depth bins being analyzed (Figures 33 and 34). The species exhibited a strong and somewhat disconnected vertical distribution, where the depth bins a majority of individuals migrated to were not adjacent to each other but during the day ocupied adjacent depth bins. Regarding migration pattern, only a very small portion of specimens did not migrate to the epipelagic, meaning this species is a complete migrator. In April and May of 2011, individuals were captured in all three depth bins analyzed.

Figure 23. Diel vertical profile based on standardized abundance for *Notoscopelus resplendens*.

Relationship of Size with Depth

Across all months, individuals captured between 1000 – 1200 m during the day were significantly longer ($p < 0.05$) than those captured between 600 – 1000 m. Also, individuals captured between 600 – 1000 m during the day were significantly shorter ($p < 0.05$) than individuals captured between 0 – 200 m at night. In April of 2011, individuals captured between 0 – 200 m were significantly longer (mean SL = 47.0 mm, $p < 0.05$) than individuals from both 600 – 1000 m (mean SL = 25.38 mm) and 1000 – 1200 m (mean SL = 30.72 mm), with those from 1000 – 1200 m also being significantly longer ($p < 0.05$) than those from 600 – 1000 m. In May of 2011, individuals captured during the day between 600 – 1000 m and 1000 – 1200 m were significantly longer ($p < 0.05$) than individuals captured at night between the same, respective depths (Figure 35).

Average Lengths Across the Time Series

February of 2011 (mean SL = 8.57 – 46.46 mm) had significantly shorter (p < 0.05)
lengths than June (mean SL = 14.21 – 52.10 mm) and September (mean SL = 24.70 – 62.59 mm)
of 2011, and August of 2015 (mean SL = 31.38 – 69.27 mm). April of 2011 (mean SL = 9.11 –
47 mm) also had significantly shorter (p < 0.05) lengths than August of 2015. In 2015, May
(mean SL = 8.25 – 46.15 mm) had significantly shorter lengths (p < 0.05) than August. No other
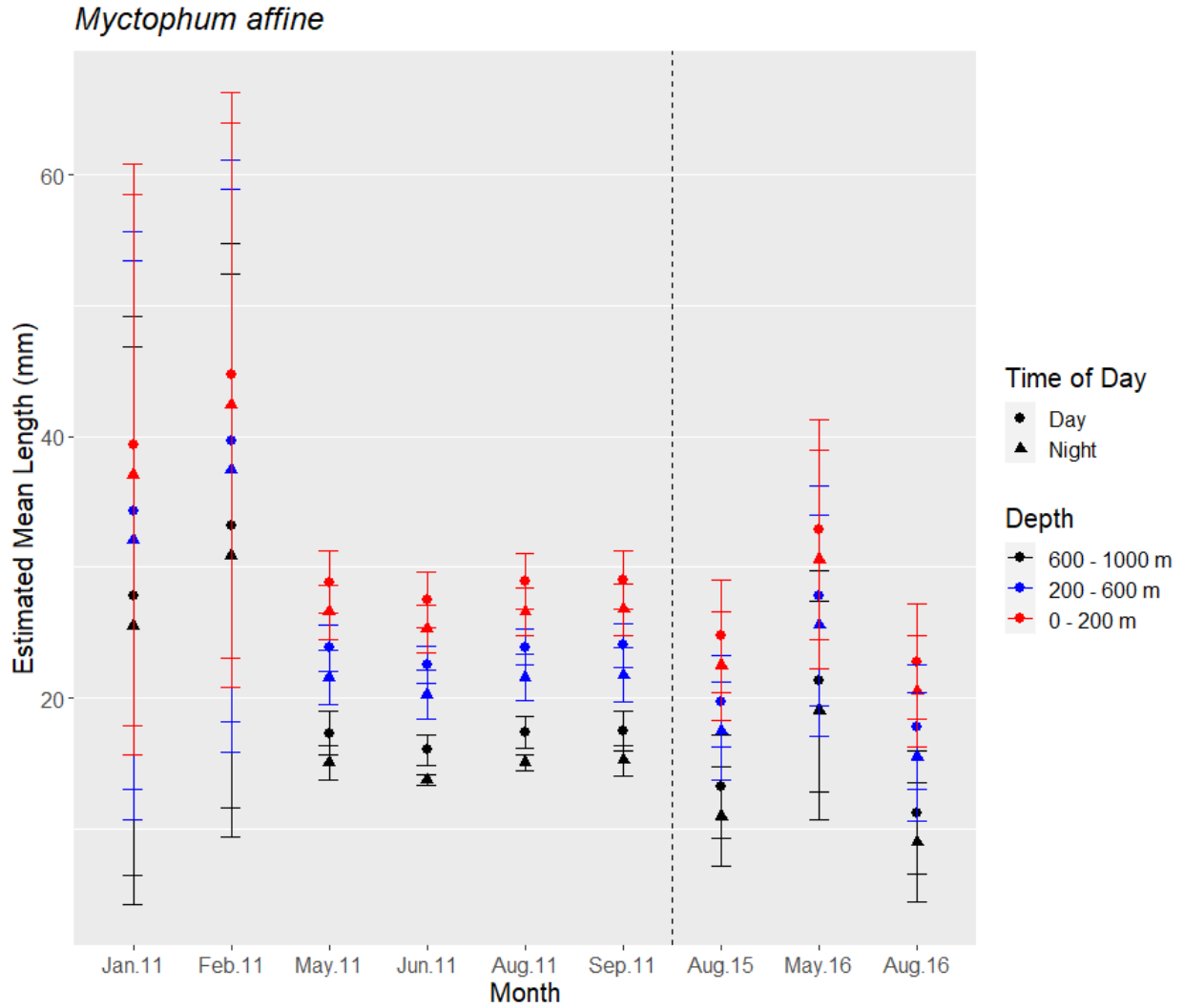months showed any significant difference (Figure 35).

Figure 24. Time series showing estimated mean lengths with 95% confidence intervals for
Notoscopelus resplendens. Black indicates depth bin 1000 – 1200 m; blue indicates depth bin

600 – 1000 m; red indicates depth bin 0 – 200 m. The dashed line separates the months of the ONSAP and DEEPEND programs.

NOTOLYCHNUS VALDIVIAE (N = 1,501, Size range: 7 – 28 mm)

Model

This species' variance was best modeled by a combination of month, depth bin, and time of day, resulting in the following final model:

standard length$_{MTD}$ = depth bin$_{MTD}$ + time of day$_{MTD}$ + month$_{MTD}$ + depth bin:time of day$_{MTD}$, varIdent = (1|M) + (1|T) + (1|D).

Vertical Distribution

The standardized count vertical distribution indicated that a majority of the species were found between 200 – 600 m depth during the day and 0 – 200 m depth at night, resulting in these two depth bins being analyzed (Figures 36 and 37). This species exhibited a weak, continuous vertical distribution, where the depth bins the majority of individuals migrated to were adjacent to each other. Regarding migration pattern, a noticeable portion did not migrate to the epipelagic throughout most of 2011, in February and from May to September, meaning this species is a partial migrator.
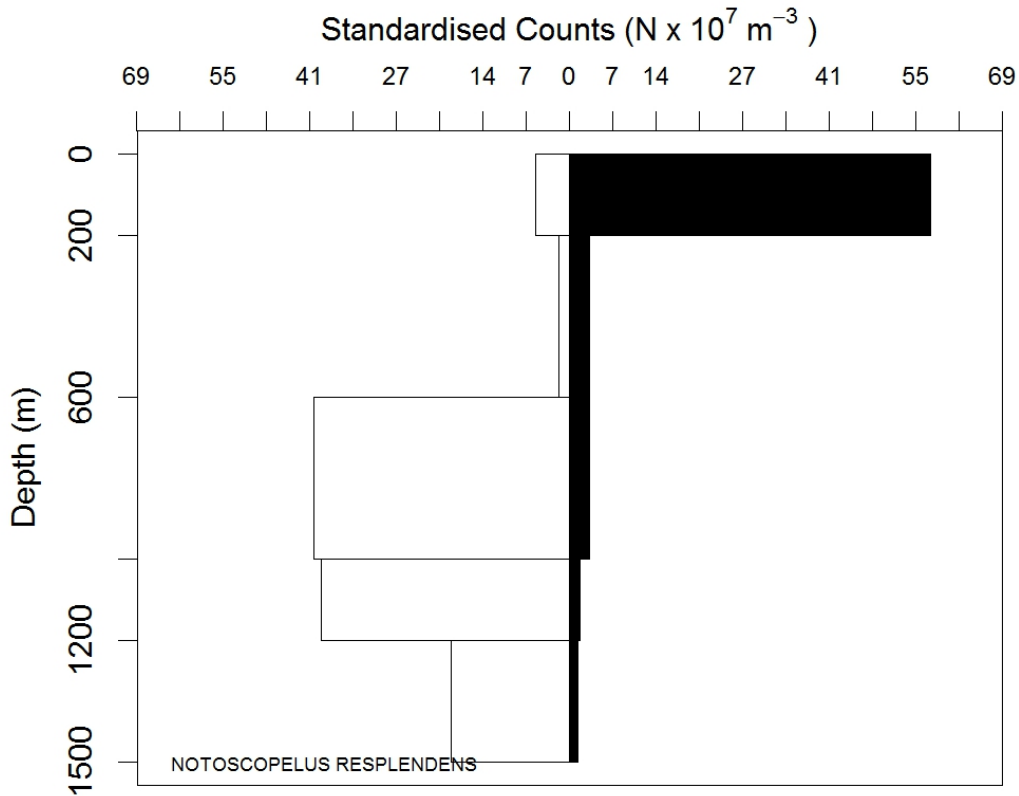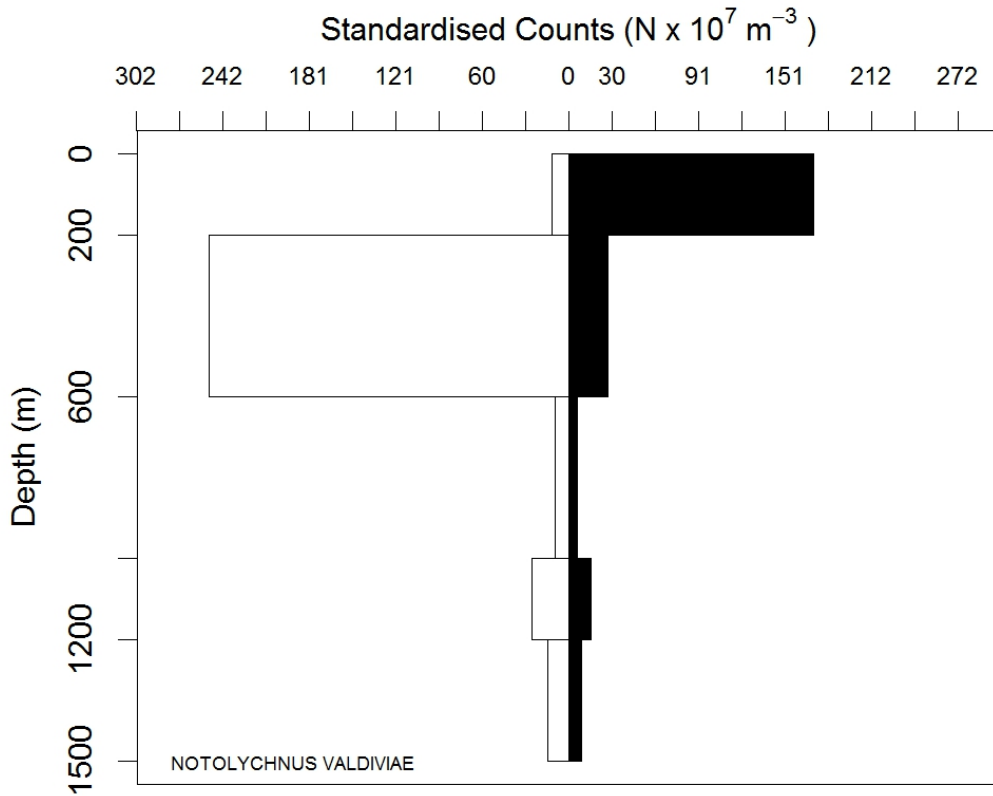
Figure 25. Diel vertical profile based on standardized abundance for *Notolychnus valdiviae*.

Relationship of Size with Depth

There was no significant difference in lengths between individuals at 200 – 600 m depth during the day and 0 – 200 m at night nor the individuals that remained at depth at night. In the months where individuals remained at depth at night, they were not significantly different than those at 0 – 200 m (Figure 38).

Average Lengths Across the Time Series

There was significant variation in mean lengths over time. Starting in January there is an insignificant increase in length until April, followed by a decrease in length that does not become significant until August. Between ONSAP and DEEPEND, May (mean SL = 18.5 – 19.0 mm) and June (mean SL = 18.1 – 18.6 mm) of 2011 had significantly shorter (p < 0.05) lengths than May of 2017 (mean SL = 19.4 – 19.9 mm), and August (mean SL = 17.5 – 18.0 mm) and

September (mean SL = 17.0 – 17.5 mm) of 2011 also had significantly shorter (p < 0.05) lengths than May of 2016 (mean SL = 19.1 – 19.6 mm) and 2017. No other months showed significant differences in lengths (Figure 38).
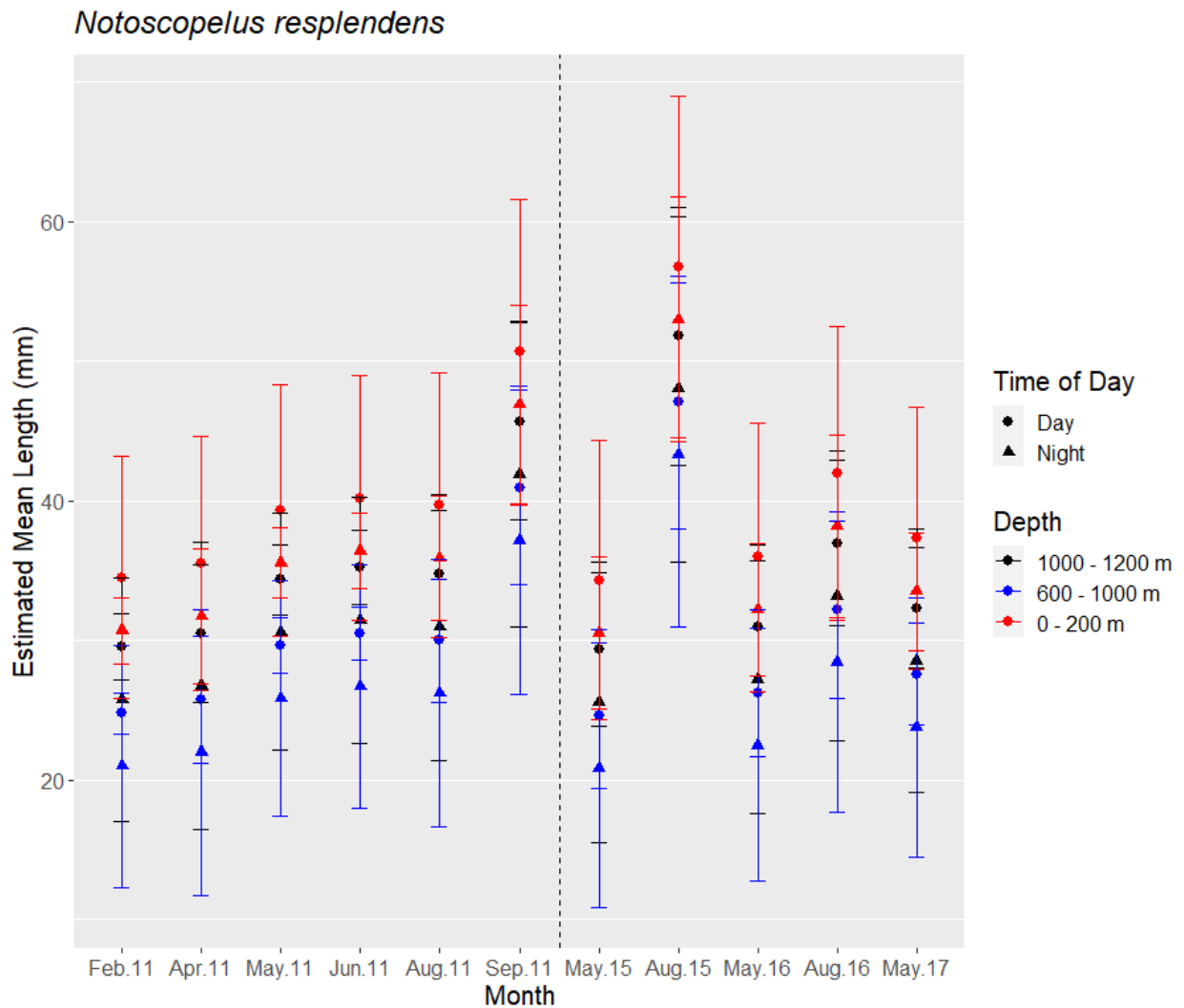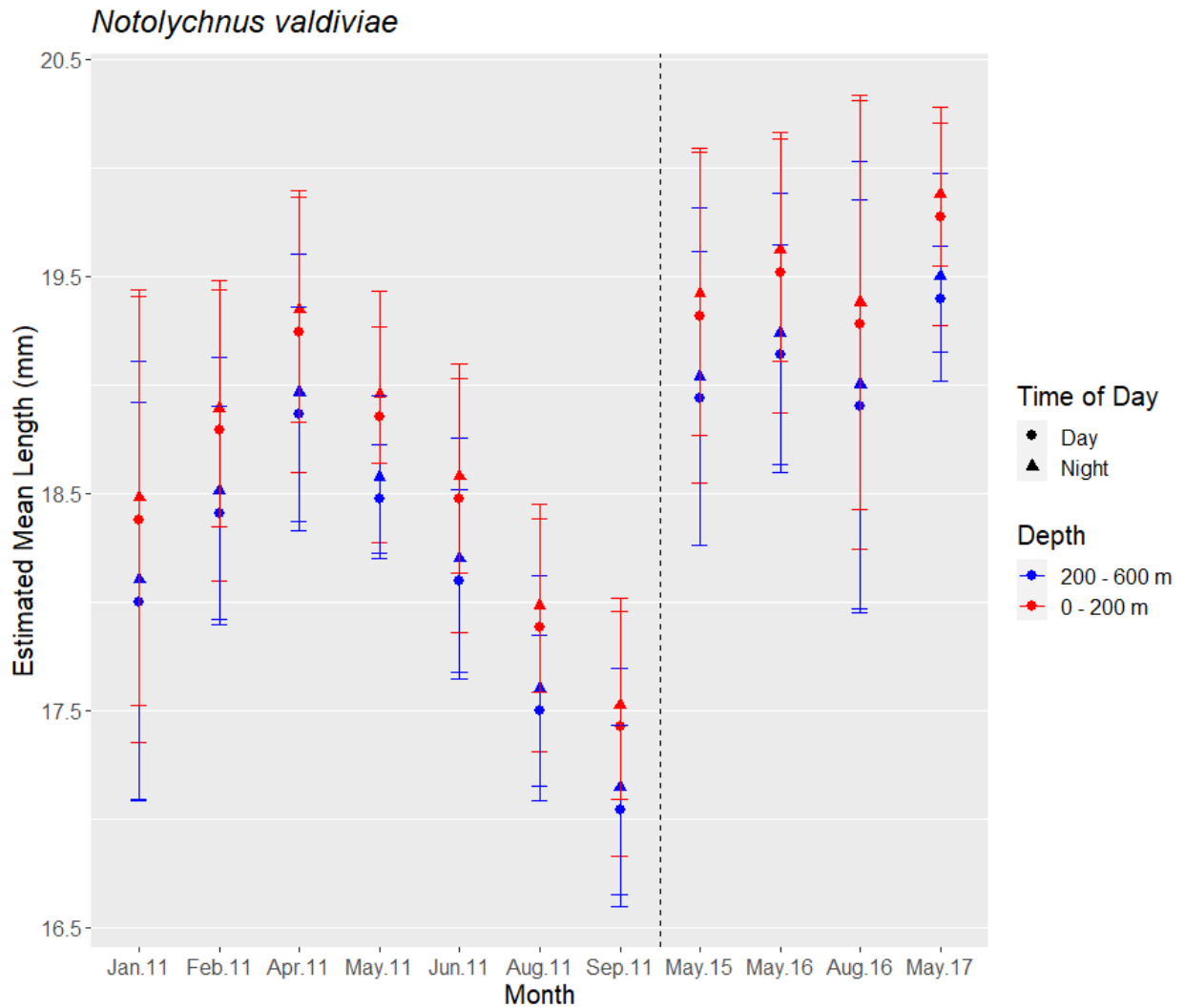

Figure 26. Time series showing estimated mean lengths with 95% confidence intervals for *Notolychnus valdiviae*. Blue indicates depth bin 200 – 600 m; red indicates depth bin 0 – 200 m. The dashed line separates the months of the ONSAP and DEEPEND programs.

LENGTH COMPARISONS TO PREVIOUS STUDIES

Table 2. Size range comparison (in mm) of selected myctophid species from this study to the same species elsewhere as well as maximum recorded size. [1] denotes measurement based on one specimen. [2] denotes measurements based on 13 samples.

Species	This study (2011 & 2015 – 2017) – Northern Gulf of Mexico	Clarke (1973) – Hawaii	Hulley (1981) – Eastern and South Atlantic	Gartner et al. (1987) – Eastern Gulf of Mexico	Ross et al. (2010) – Northern Gulf of Mexico	Maximum recorded size
Benthosema suborbitale	9 – 34	9 – 38	20 – 33	10 – 30	10 – 31	39
Ceratoscopelus warmingii	9 – 77	11 – 79	25 – 80	14 – 65	15 – 45	81
Diogenichthys atlanticus	11 – 25					27
Diaphus dumerilii	9 – 69		25 – 85	12 – 53	12 – 31	87
Diaphus mollis	10 – 59					66
Hygophum benoiti	7 – 30					55
Hygophum taaningi	9 – 48					61
Lampanyctus alatus	10 – 59		30 – 58	15 – 48	14 – 55	61
Lepidophanes guentheri	12 – 65		29 – 76	13 – 64	14 – 65	78
Myctophum affine	11 – 63		28 – 47[2]	12 – 58	13 – 45	79
Notoscopelus resplendens	12 – 64					95
Notolychnus valdiviae	7 – 28	9 – 25	19[1]	9 – 22	11 - 22	25

DISCUSSION

This study examined the changes in myctophid body size in relation to their diel vertical migration distributions and species identity over a nine-month period in 2011 and in May and August 2015 – 2107. The twelve most abundant species of the myctophid assemblage were: *Lampanyctus alatus*, *Ceratoscopelus warmingii*, *Diaphus dumerilii*, *Notolychnus valdiviae*, *Benthosema suborbitale*, *Hygophum benoiti*, *Lepidophanes guentheri*, *Diaphus mollis*, *Myctophum affine*, *Diogenichthys atlanticus*, *Hygophum taaningi*, and *Notoscopelus resplendens*.

Previous studies of myctophid fauna across the Gulf of Mexico (Gartner et al., 1987; Ross et al., 2010) reported the species *Notolychnus valdiviae*, *Ceratoscopelus warmingii*, *Lepidophanes guentheri*, *Lampanyctus alatus*, *Diaphus dumerilii*, *Benthosema suborbitale*, and *Myctophum affine* as the most abundant species with *Hygophum benoiti* and *Diaphus mollis* being uncommon and *Notoscopelus resplendens* and *Diogenychthys atlanticus* being rarer. Some changes in the order of the most abundant species were expected given that previous collections were captured from cruises in the eastern Gulf of Mexico during the summer months of 1970 - 1977 (Gartner et al., 1987) and over cold seeps scattered across the northern Gulf of Mexico in August 2009 (Ross et al., 2010). The changes in the rank order of abundance are listed (Table 2). Notably, from 1987 in the eastern Gulf of Mexico the species *Diogenichthys atlanticus* and *Notoscopelus resplendens* were not included in the top twelve species from the same study, instead replacing *Diaphus splendidus* and *Lampanyctus lineatus* in the current study. From 2010 in the northern Gulf of Mexico, *N. resplendens* replaced *D. splendidus* in the current study. While qualitatively similar, comparisons between studies regarding vertical distributions patterns may not be accurate due to various factors, mainly gear type and net size selectively fishing for certain species compared to others as fish species exist at different size ranges. As such, comparisons between studies regarding size analysis may also not be as accurate for the same reason. Thus, despite quantitative comparisons not being accurate, qualitative comparisons can be done with caution and with some caveats. While specific size comparisons may be impossible, general size trends may not be, e.g. smaller sizes of fish being found at shallower depths compared to larger individuals who remain at depth. Such qualitative comparisons can still shed light on either changing patterns or highlight the stability of species over time.

Table 3. Comparison of the rank order of abundance from multiple previous studies, in decreasing order.

Rank	Gartner et al. (1987)	Ross et al. (2010)	Present study
1	*Ceratoscopelus warmingii*	*Notolychnus valdiviae*	*Lampanyctus alatus*
2	*Notolychnus valdiviae*	*Lepidophanes guentheri*	*Ceratoscopelus warmingii*
3	*Lepidophanes guentheri*	*Benthosema suborbitale*	*Diaphus dumerilii*
4	*Lampanyctus alatus*	*Hygophum benoiti*	*Notolychnus valdiviae*
5	*Diaphus dumerilii*	*Diaphus dumerilii*	*Benthosema suborbitale*
6	*Myctophum affine*	*Myctophum affine*	*Hygophum benoiti*
7	*Benthosema suborbitale*	*Ceratoscopelus warmingii*	*Lepidophanes guentheri*
8	*Hygophum benoiti*	*Lampanyctus alatus*	*Diaphus mollis*
9	*Diaphus mollis*	*Hygophum taaningi*	*Myctophum affine*
10	*Hygophum taaningi*	*Diaphus mollis*	*Diogenichthys atlanticus*
11	*Diaphus splendidus*	*Diaphus splendidus*	*Hygophum taaningi*
12	*Lampanyctus lineatus*	*Diogenichthys atlanticus*	*Notoscopelus resplendens*

The myctophid species studied here were a split of partial migrators and complete migrators, but all species exhibited the typical diel migration pattern while varying in some aspects from other studies. The species *Diogenichthys atlanticus*, *Diaphus dumerilii*, *Diaphus mollis*, *Benthosema suborbitale*, and *Notolychnus valdiviae* were observed to be weak migrators, reaching as far down as 600 m, whereas the rest of the species, *Ceratoscopelus warmingii*, *Hygophum benoiti*, *Hygophum taaningi*, *Lampanyctus alatus*, *Lepidophanes guentheri*,

Myctophum affine, and *Notoscopelus resplendens* were strong migrators, being captured as far down as 1000 m. As stated before, any species that was observed to have very few individuals remaining at depth at night were considered to be a complete migrator, with those remaining at depth most likely being small juveniles that have not finished transforming and thus begun diel vertical migration, compared to species with an easily noticeable portion of the population remaining at depth being partial migrators. A possible explanation for individuals appearing to remain at depth during the night is that depending on the depth bin captured, some individuals were most likely in the process of vertically migrating. However, this possible reason is unlikely due to the individuals that would have migrated would have already completed doing so. The species considered complete migrators were *Benthosema suborbitale*, *Diogenichthys atlanticus*, *Diaphus dumerilii*, *Diaphus mollis*, *Lepidophanes guentheri*, and *Notoscopelus resplendens*. The rest of the species, *Ceratoscopelus warmingii*, *Hygophum benoiti*, *Hygophum taaningi*, *Lampanyctus alatus*, *Myctophum affine*, and *Notolychnus valdiviae*, were considered partial migrators. Previously, Gartner et al. (1987) reported the absence of non-migrators for the species *Lampanyctus alatus* and *Notolychnus valdiviae*, while Ross et al. (2010) and this study observed individuals remaining at depth for both species. Of the observed myctophid species, *Hygophum benoiti*, *Hygophum taaningi*, *Lampanyctus alatus*, and *Lepidophanes guentheri* exhibited the trend of increasing mean length with depth whereas *Benthosema suborbitale*, *Ceratoscopelus warmingii*, *Myctophum affine*, and *Notolychnus valdiviae* instead exhibited a decrease with increasing depth.

Overall, the myctophids showed clear groupings according to their vertical distribution patterns. Within the weak migrators, *Diogenichthys atlanticus*, *Diaphus dumerilii*, *Diaphus mollis*, *Benthosema suborbitale*, and *Notolychnus valdiviae*, a majority of each species was captured between 200 – 600 m during the day and migrated to between 0 – 200 m at night. The observed vertical distributions of *Benthosema suborbitale*, *Diogenychthys atlanticus*, *Diaphus dumerilii*, *Diaphus mollis*, and *Notolychnus valdiviae* were similar to previous observations of Gartner et al. (1987) and Ross et al. (2010) in that these species occupied the upper mesopelagic zone during the day and ascended to the epipelagic zone at night. All twelve species analyzed exhibited individuals remaining at daytime depths at night. Both *Benthosema suborbitale* and *Diaphus dumerilii* exhibited smaller individuals remaining at depth during the night, which agrees with observation from Gartner et al. (1987) and Ross et al. (2010), and these individuals

were also shorter than the observed size at maturity reported by Gartner (1993). Although individuals of *B. suborbitale* were significantly shorter than those that migrated to between 0 – 200 m, the individuals from *D. dumerilii* were not. It appears that the individuals of *B. suborbitale* that remained at depth during the night were most likely non-migrating small juveniles. However, the same cannot be said for *D. dumerilii* due to those individuals not being significantly shorter although they were below the reported size at maturity. This is evidenced by *B. suborbitale* exhibiting a significant decrease in length with depth, although these results do not agree with those of Gartner et al.,(1987) and Ross et al. (2010), who observed an increase in size with depth at smaller depth ranges. For *Notolychnus valdiviae*, Gartner (1993) recorded that most individuals below 12 mm were immature. Gartner et al. (1987) reported no non-migrators but an increase in size with depth while Ross et al. (2010) did report non-migrators but observed no size-depth trends. The observations in this study seem to agree with Ross et al. (2010) in that there was an abundance of non-migrators that showed no significant changes in length with depth. Because those non-migrators were 17.1 – 18.5 mm, well above the size at maturity reported by Gartner (1993), it cannot be concluded that they were juveniles. For *Diogenychthys atlanticus* and *Diaphus mollis*, Gartner et al. (1987) reported the presence of non-migrators. In the current study, the few individuals that remained at depth for *D. atlanticus* and *D. mollis*, four and thirteen specimens, respectively, were of similar length to those that migrated and given the lack of information about size at maturity for these species, life history stage cannot be determined. Lastly, each species had individuals captured beyond the depth ranges analyzed in this study, which agrees with observations made in Gartner et al. (1987) and Ross et al. (2010), but they were excluded from analysis because there were too few specimens to accurately model.

Two of the strong migrators, *Ceratoscopelus warmingii* and *Notoscopelus resplendens*, had similar vertical distribution patterns to the weak migrators in that they were found mostly in just two depth bins, being captured between 0 – 200 m at night but during the day mostly skipped 200 – 600 m and migrated to only 600 – 1000 m and 1000 – 1200 m, respectively. The observed vertical distributions of *Ceratoscopelus warmingii* agreed and *Notoscopelus resplendens* somewhat agreed with the observations of Gartner et al. (1987) and Ross et al. (2010) in that these species occupied the lower mesopelagic zone during the day and ascended to the epipelagic zone at night. *Ceratoscopelus warmingii* also had around 25% remaining between 600 – 1000 m during the night. For *Ceratoscopelus warmingii*, Gartner et al. (1987) reported that

the non-migrators observed were small juveniles around 15.5 mm in length, and in this study, smaller individuals ranging from 17.5 – 25.7 mm were recorded as remaining at depth. Without information regarding size at maturity, it is uncertain whether the individuals in this study could be juveniles even though the species exhibited a significant decrease in size with depth. For *Notoscopelus resplendens*, there are few published data to compare results to. Gartner et al. (1987) did not report a daytime depth range for this species whereas Ross et al. (2010) reported only two individuals at 1035 m depth, which is within the 1000 – 1200 m depth bin observed in this study, though nighttime depths from both studies agree with the depth observed here with individuals being found between 0 – 200 m. Because size at maturity is not known, life history stage cannot be estimated.

The rest of the strong migrators, *Hygophum benoiti*, *Hygophum taaningi*, *Lampanyctus alatus*, *Lepidophanes guentheri*, and *Myctophum affine* were abundant in all three depth bins sampled. *Lampanyctus alatus* and *Lepidophanes guentheri* occurred between 200 – 1000 m depth during the day and appeared to migrate to between 0 – 200 m at night. The species *Hygophum benoiti*, *Hygophum taaningi*, and *Myctophum affine* had similar vertical distributions to *Lampanyctus alatus* and *Lepidophanes guentheri* but had a large number of individuals remaining mostly between 600 – 1000 m depth at night and a few remaining between 200 – 600 m. One notable difference for *Hygophum benoiti* was that at night, more individuals were captured depth bin 600 – 1000 m than depth bin 0 – 200 m, the only species to show such a pattern. These results are similar to those observed from earlier studies in the Gulf of Mexico, particularly Gartner et al. (1987) and Ross et al. (2010), and earlier studies from other locations like the northeastern Atlantic (Badcock and Merrett, 1976). This suggests that a species' vertical distribution may be relatively stable across different regions with variances lying in smaller-scale variables.

The observed vertical distributions of the previously mentioned strong migrators, *Hygophum benoiti*, *Hygophum taaningi*, *Lampanyctus alatus*, *Lepidophanes guentheri*, and *Myctophum affine*, agree with the observations of Gartner et al. (1987) and Ross et al. (2010) in that these species occupied the upper and lower mesopelagic zone during the day and ascended to the epipelagic zone at night. For the species *Hygophum benoiti*, *Hygophum taaningi*, and *Lepidophanes guentheri*, individuals were observed to remain in the upper and lower

mesopelagic at night, mostly agreeing with observations from Gartner et al. (1987) who reported that the non-migrators were small juveniles. Size at maturity is presently unknown for both *Hygophum benoiti* and *Hygophum taaningi*, and so life history stage cannot be inferred. However, for *Hygophum taaningi*, both day and nighttime individuals exhibited a significant increase in length from 200 – 600 m to 600 – 1000 m, with significantly larger individuals occurring in epipelagic depths during both day and night. In *Lepidophanes guentheri*, Gartner, (1993) reported the species maturing around 26 mm, and with the size range of the population remaining at depth in the present study being 16.6 – 27.5 mm, it can be inferred that the individuals that remained at depth were non-migrating juveniles. In the current study, only individuals captured in multiple depth bins during the day exhibited a significant increase in size with depth whereas the individuals captured at night showed a significant decrease in size depending on the month. For *Lampanyctus alatus*, Gartner et al. (1987) observed no non-migrators but did observe an increase in size with depth. However, the current study observed roughly 25% of individuals remaining at depth at night but with no significant differences in size. The current study's results are similar to the observations of Ross et al. (2010), who captured individuals from 0 – 600 m with no apparent size-depth trends. Coupled with the noticeable abundance of individuals remaining at depth at night for the species, it can be hypothesized that these individuals were non-migrators. Gartner, (1993) reported that most, if not all, individuals longer than 30 mm were mature. Given that the individuals remaining at depth at night in the present study were 18.3 – 29.4 mm in length, it can be inferred that these individuals were small juveniles. In this study, both day and nighttime individuals exhibited a significant increase in length from 200 – 600 m to 600 – 1000 m with a significant decrease from 0 – 200 m to 200 – 600 m at night. *Myctophum affine* was unique in that the species was captured in all three depth bins with daytime depths of 200 – 600 m and 600 – 1000 m and nighttime depths of 0 – 200 m and 600 – 1000 m, so comparisons for both times of day can be made. Notably, *Myctophum affine* exhibited a significant decrease in length with depth.

There did not seem to be any correlation between the size range of different species and the vertical distribution patterns they exhibited. Smaller species such as *Benthosema suborbitale* and *Notolychnus valdiviae* exhibited the same vertical distributions as *Diaphus dumerilii*, a species that has a maximum size of 69 mm, either double or more than double that of *B. suborbitale* (34 mm) and *N. valdiviae* (28 mm), respectively. Another example are the species

Ceratoscopelus warmingii and *Hygophum benoiti* having similar vertical distributions, both reaching depths of 1000 m in the water column. However, *C. warmingii* had a maximum size of 77 mm, more than double the 30 mm maximum recorded for *H. benoiti*. It might be expected that smaller individuals would be less-likely to be captured in shallower water than larger individuals as even though there is more light present, a small body would minimize the downward projected shadow of the fish from upward-looking predators hunting for prey silhouettes (Johnsen et al., 2004). This allows the fish to remain where their prey is more abundant. All of this suggests that size alone does not dictate a species' vertical distribution in the context of this study. However, one caveat to this is that in the present study, smaller sample sizes tended to have larger confidence intervals with the predicted means, which is expected statistically, due to the lack of data the models were fitted to. While this may not directly affect mean length, it hinders our ability to accurately describe significant changes in length by increasing the possibility of Type 1 errors. For example, in *Myctophum affine* January and February of 2011 have much lower abundances than the rest of the months surveyed, including DEEPEND months. The estimated mean lengths of individuals collected during these months appear much longer than in other months but have a much wider confidence interval that overlaps the months with small intervals and in turn, a statistical program may misinterpret the lengths as not being significantly different. This is evidenced by the issue that there has been a large decline in the abundance of mesopelagic fishes since the *Deepwater Horizon* oil spill that has continued through the years (Sutton et al., 2020a), detected by both net sampling and acoustic surveys (Sutton et al., 2022). It was observed that abundances from ONSAP (2011) were higher than those of DEEPEND (2015 – 2017) (Sutton et al., 2022), and part of this study was to investigate length changes over time that may have occurred alongside the abundance decline.

Overall, the results from the present study showed no strong, consistent differences in body length between the years covered by the ONSAP and DEEPEND surveys. While there were some differences between specific months in each program depending on species identity, those differences seemed to be a result of changes that occurred over the course of individual years rather than indicative of long-term effects. Of the species that have spawning data, all spawn year-round with some species having spawning peaks in the spring and early summer months. To determine if spawning had an effect on length changing on monthly basis, if a species exhibited considerable decrease in the spring and early summer months compared to the

rest of the year it could be assumed that the decrease is due to the higher abundance of newly grown fish.

The species *Ceratoscopelus warmingii*, *Diaphus dumerilii*, *Hygophum benoiti*, *Lampanyctus alatus*, *Lepidophanes guentheri*, *Notoscopelus resplendens*, and *Notolychnus valdiviae* exhibited considerable variation in length throughout the same year. These species generally exhibited an increase in lengths in the summer months compared to those in spring. In *Ceratoscopelus warmingii*, Gartner (1993) reported a higher abundance of transforming juveniles in the spring and early summer months, which is consistent with data from the current study, in that an increase in lengths occurred between June and September of 2011. Notably, for this species, specimens collected in May had shorter lengths than those collected in August of the same year, although this difference was not significant. *Notoscopelus resplendens* exhibited an increase in lengths from February to September 2011, which may be evidence of the species acting as a batch spawner in the winter months, though this is based on data from the Canary Islands (Sarmiento Lezcano, 2016). This species also exhibited the trend of each May having shorter lengths than the August of the same year, though only in 2015 was the difference significant.

For *Hygophum benoiti*, spawning was observed to occur mostly in the spring, summer, and autumn in the Mediterranean Sea (Olivar and Palomera, 1994). However, given that this species was absent in the months before May of 2011, it is difficult to attribute the smaller sizes observed to increased abundance of recently spawned individuals. For *Lampanyctus alatus* and *Lepidophanes guentheri*, Gartner (1993) reported the species as year-round spawners. However, in the current study, both species exhibited a three-month period of decreased lengths compared to the months adjacent to those on the ends of each period, April – June 2011 and June – September 2011, respectively. This may be due to an increased abundance of smaller individuals from a spawning event or a loss of larger individuals. Notably for *L. alatus*, the May specimens of each year had shorter lengths than the August specimens of the same year, although some of these differences were not significant. However, *L. guentheri* exhibited the opposite trend where each specimen from May had longer lengths than the specimens from August of the same year. *Diaphus dumerilii*, according to Gartner (1993), was not a yearly spawner and had two batch spawning seasons in the late winter/early spring and fall. This pattern was possibly evidenced in

this study by the decrease in length starting in April 2011 that continued until it increased again in August.

Unlike the previous species, *Notolychnus valdiviae* and *Diaphus mollis* exhibited a decrease in length from the spring to summer. Gartner (1993) reported *N. valdivaie* as a yearly spawner with higher instances of spawning in the spring and early summer months. The observed decrease in lengths may be evidence of this as the newly grown individuals would be more prevalent in later months. *D. mollis* has been reported to spawn annually with peaks in the summer (Dauden-bengoa et al., 2020), which may explain the decrease observed in this species as well. The only significant variation shown by *Benthosema suborbitale* was the month of June 2011 having shorter lengths than May and August of the same year. However, this species spawns year-round according to Gartner (1993), indicating a higher abundance of newly grown fish is unlikely to be the reason behind this decrease. The species *Diogenichthys atlanticus*, *Hygophum taaningi*, and *Myctophum affine* showed no significant variation in length between any months.

While the effects of the oil released by the *Deepwater Horizon* may have affected myctophid abundances through many factors including decreased prey abundance and various effects on individual fish, it more difficult to observe whether the oil affected fish length. Observed effects of Polycyclic Aromatic Hydrocarbons (PAH) on shallow-living fishes include lethal and sub-lethal effects such as increased mortality, skeletal malformations, genetic damage, immunotoxicity, and decreased cardiac functionality (Carls et al., 1999; Incardona et al., 2004; Reynaud and Deschaux, 2006). While skeletal malformations may impact fish length, those effects would be a more readily visible change to a fish's length and attributed to short-term mortality whereas genetic damage could over time result in a gradual change in fish size. At the population level, the maximum sizes observed in this study are similar to those reported in previous studies both in the Gulf of Mexico and elsewhere, primarily the Pacific Ocean near Hawaii and Atlantic Ocean. Listed below are comparisons of the observed size ranges from four previous studies (Table 2). Of the selected species analyzed in this study, only three, *Ceratoscopelus warmingii*, *Diaphus dumerilii*, and *Myctophum affine* showed differences in maximum size captured compared to individuals of the same species found in other regions of the world. Also, *Lampanyctus alatus*, *M. affine*, and *Notolychnus valdiviae* had larger maximum

sizes recorded in this study compared to previous studies. Gartner et al. (1987) noted distinctly smaller maximum sizes for selected species compared to two previous studies (Clarke, 1973; Hulley, 1981), and noted that despite more trawling efforts the maximum sizes recorded for these species still didn't reach previous maximum sizes. Similarly, some species in the present study also did not reach near the maximum recorded size. Notably, the maximum size this study observed for *Notolychnus valdiviae* was 28 mm while the maximum recorded size was listed as 25 mm. More recent comparisons with Ross et al. (2010) and this study were included (Table 3), with the maximum size recorded provided by (Sutton et al., 2020b).

Areas of further study include studies using different sampling methods to examine a broader size range of fishes in the Gulf of Mexico. Net mesh size, for example, is known to affect the sizes of individuals that are captured (Heino et al., 2011). In the present study the smallest size measured for myctophids was 7 mm, only slightly larger than the 3 mm mesh net used to capture fish, and so there were very few larvae, transforming larvae, and juveniles, captured. Larvae are around 2 mm in size upon hatching and thus likely passed through the net mesh, but targeting these life history stages at depth may help better define patterns of ontogenetic vertical migration. However, it has been reported that identifying myctophid larvae is very difficult for some species (Sassa et al., 2004), which may reduce taxonomic resolution without additional tools (e.g. genetic studies).

Targeting narrower depth ranges, at least within the first few hundred meters of the water column, can also help more precisely define both vertical distribution and ontogenetic migration patterns in the surface waters where larvae are more present. Whereas previous studies like Gartner et al. (1987) and Ross et al. (2010) used Tucker trawls that fished horizontally at narrow discrete depths, e.g. 10 m depth bins in the first 300 m of the water column, the present study used data gathered from MOCNESS nets that were left open as the net ascended within a larger discrete depth range, e.g. 0 – 200 m, before closing. This is not a limitation, rather a sampling design choice. However, this creates a difference in depth resolution when describing a species' depth range. For example, while Gartner et al. (1987) reported the species *Benthosema suborbitale* occurring at a depth range of 400 – 600 m during the day and two distinct ranges of 50 – 105 m and 500 – 550 m at night, the present study observed the species occurring anywhere within 200 – 600 m during the day and 0 – 600 m at night, considering the individuals remaining

at depth. Even without considering those samples, the nighttime range is 0 – 200 m and still much broader than the narrower 50 – 105 m range from Gartner. Another issue the difference in depth sampling creates is that observing increases in length with depth requires enough samples at multiple different depths during the same time of day. In this study, species mentioned above that exhibited a decrease in length from 0 – 200 m to 200 – 600 m only experienced an increase in length from 200 – 600 m to 600 – 1000 m. As a result, it may be possible that the species *Benthosema suborbitale*, *Ceratoscopelus warmingii*, *Diogenichthys atlanticus*, and *Notolychnus valdiviae* also exhibited an increase in length in depths below 600 m as well but this observation was missed due to these species mostly occurring in two depth bins rather than three, as depth bins with low abundance having been excluded. This may be a possible explanation for why an increase was not observed for *Notolychnus valdiviae* when it was previously stated earlier that Gartner et al. (1987) observed an increase in size with depth. Another possible explanation is the difference between sampling procedures used by this study and Gartner et al. (1987) as stated earlier. Where Gartner, (1987) could observe size-depth trends over narrower depth ranges by discretely sampling with 10 m depth bins from 0 – 300 m, 25 m depth bins from 300 – 700 m, and 50 m depth bins from 700 – 1000 m, this study uses broad depth ranges which could aggregate across the size trends observed by Gartner. This could also determine whether trends regarding ontogenetic vertical migration are observed. Because ontogenetic vertical migration occurs by individuals growing in size as they descend to their normal daytime depth range, these changes are observed within short depth ranges rather than large ones that cover a species entire depth range. A third possibility is that these species have in fact changed patterns over time.

CONCLUSION

      This study utilized an exceptionally large dataset of deep-sea fishes to provide insight into how the deep-sea myctophid assemblage is structured in the northern Gulf of Mexico during the years following the *Deepwater Horizon* oil spill. The general conclusion from this study is that vertical distribution patterns are generally correlated with species identity rather than body size, and that although length can vary over time within a single year as well as across multiple years, it appears to have remained relatively stable despite factors such as heavily decreased abundances following a major anthropogenic environmental event like the *Deepwater Horizon* oil spill. This type of study can help refine further analyses examining temporal changes in size and how that relates to vertical distribution patterns of myctophids for a better understanding of an assemblage's population dynamics by way of species behavior.

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