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Submitted in Partial Fulfillment of the Requirements for the Degree of

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Marine Science

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HALMOS COLLEGE OF ARTS AND SCIENCES

Variability in the vertical distributions of mesopelagic fishes: effect of body size, season, and sampling strategy on the characterization of diel vertical migration

By

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Submitted to the Faculty of Halmos College of Arts and Sciences in Partial

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ABSTRACT

Diel vertical migration, or DVM, is defined as the large-scale changes in the depth distribution of a species or an assemblage with respect to the time of day. DVM is the largest active movement of biomass on Earth, driven by the need for food balanced against predator avoidance and metabolic constraints. Asynchronous diel vertical migration, in the context of this study, refers to the phenomenon where only a portion of a species' population migrates upwards at night while others remain at depth. The extent that factors such as temporal variation, ontogenic variation, and methodological variation explain this migratory pattern is the focus of this study. Data for five numerically dominant mesopelagic fishes species (four lanternfishes, *Benthosema suborbitale, Ceratoscopelus warmingii, Lampanyctus alatus*, and *Lepidophanes guentheri*, and one bristlemouth, *Sigmops elongatus*) were analyzed from two extensive deep-pelagic research programs in the Gulf of Mexico. A size-depth relationship, with larger individuals in a population residing deeper during daytime, was clearly apparent for four of the five species examined, and likely applied to the fifth. Two species, *L. guentheri* and *B. suborbitale*, were synchronous, or near-synchronous vertical migrators. The remaining three species were asynchronous migrators whose diel migration fidelity appeared tied primarily to size. In the two asynchronously migrating lanternfishes the largest size class migrated daily while the smallest migrated least, while the pattern was opposite in the bristlemouth, *S. elongatus*. A possible ecological explanation for these patterns is presented based on fluid mechanics theory. Given the importance of diel vertical migrators in the global sequestration of carbon via the biological pump, and the increasing sophistication of individual-based models of carbon flux, quantifying the variability in DVM and AVM behavior is essential, as these values drive the models. Quantifying this variability will greatly enhance the accuracy (and likely precision) of carbon flux models, which are vitally important in a rapidly changing deep ocean subjected to increasing human disturbance.

Keywords: asynchronous vertical migration, mesopelagic, carbon sequestration

INTRODUCTION

Open-ocean ecosystems are primarily structured vertically (Angel, 1989; Herring, 2002; Sutton, 2013), and a key component of that structure is vertical migration, regarded as the largest synchronous movement of biomass on Earth (Bollens and Frost, 1989). The open-ocean water column (pelagic) fauna exhibits Multiple patterns of vertical migration are utilized by. During the ubiquitous form, known as diel vertical migration (DVM), populations migrate simultaneously to surface waters at night and return to greater depths prior to sunrise (Marshall, 1954). Reverse diel vertical migration is a rarer variant of this pattern, whereby animals descend at dusk to avoid migrating predators that feed in the epipelagic at night (Ohman et al., 1983).

Regarding the vertical movements of the oceanic fauna, there are several recognized types of behavior. In contrast to the aforementioned vertical migrators, some deep-pelagic animals (those living below 200 m during daytime) do not migrate vertically; these are called "non-migrators" (Loose and Dawidowicz, 1994). In between these patterns, some species have been classified as 'weak migrators,' with some individuals of a population migrating while others do not. Sutton and Hopkins (1996) termed this behavior 'asynchronous vertical migration' (AVM), which is the subject of this thesis. AVM is a pattern of migration where a population resides within the mesopelagic layer (200 – 1000 m) or deeper during daylight and at night the population divides, with some individuals migrating upwards while some individuals remain at depth. AVM differs from the vertical migration behavior described by Lampert (1989), 'variable speed migration,' which is a form of diel vertical migration where all individuals migrate daily, but with varying velocity and direction.

One aspect rarely examined in AVM species is body size. Juveniles of a species may migrate more frequently than the adults, as the juveniles require more energy per unit mass to devote to growth and development (Herring, 2002). The contrary could also be said, that since juveniles need to expend more energy on growing, they might not be able to afford the energetic costs of migration. While the energetic cost of migration for juveniles would be higher due to Reynold's number environment (the relationship between organismal size, frictional forces, and inertial forces), the amount of biomass consumed during feeding may be enough to balance their energy budgets. In contrast, adults of some species may migrate more frequently than juveniles owing to a more favorable Reynold's number environment.

For those taxa classified as asynchronous vertical migrators, it should not be assumed that the proportion of migrants is constant on a diel basis, since the observed pattern of AVM is potentially a function of pooling data when plotting vertical distributions. For example, Figure 1 from Sutton and Hopkins (1996) was based on pooled data that were acquired over the course of several decades, obfuscating inferences about shorter-term temporal, spatial and/or ontogenetic cycles. To illustrate this point with a simplistic example, if a species migrates in unison in odd-numbered months, and not at all on even-numbered months, the resulting t-plot of a year's worth of pooled data might suggest that 50% of the population migrated on a diel basis, when in fact, the migration was perfectly synchronous, just not on a diel basis. Seasonal changes may be one such driver. Most pelagic ecosystems undergo some form of seasonality driven by changes in temperature and/or weather, with concomitant changes in primary and secondary productivity (i.e., food resources for vertically migrating organisms). The latter factor is often tied to reproductive cycles, and thus size distributions within oceanic populations.

This study draws upon one of the largest vertically resolved deep-pelagic datasets in existence to examine variability in diel migration as a function of population size structure and of season. Vertical distribution analyses was conducted on five numerically dominant mesopelagic fish species in the Gulf of Mexico, first as whole units (i.e., all data pooled per species over several years) and then as treatments (size classes and seasons) to provide an in-depth examination of the mechanics of diel vertical migration in mesopelagic fishes.
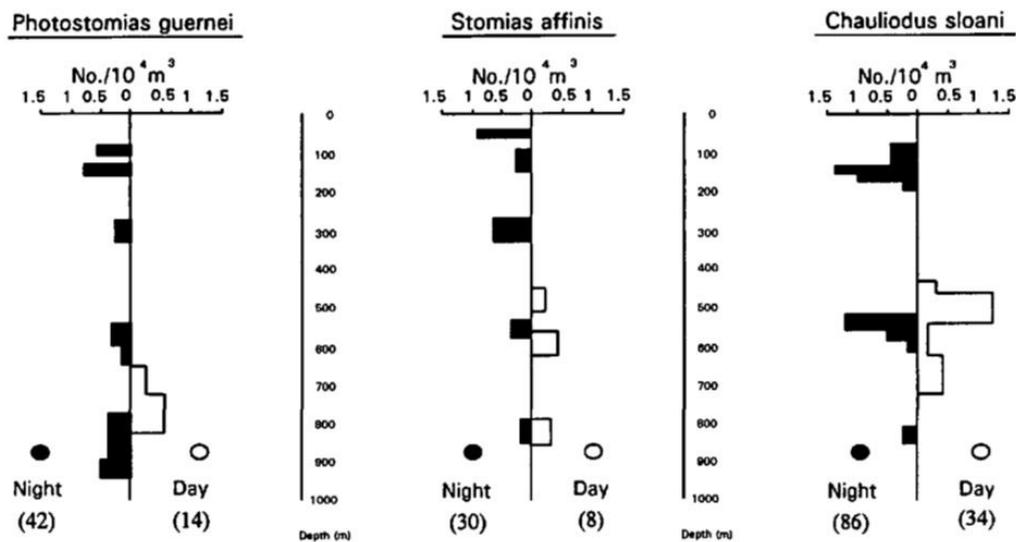

Figure 1. Vertical distribution of three dragonfish (Stomiidae) species from the Gulf of Mexico, with sample size in parentheses. After Sutton and Hopkins, 1996.

AIM OF STUDY

The aim of this study is to analyze the diel vertical distributions of a suite of dominant mesopelagic fishes with respect to data aggregation (all seasons and size classes combined, as is generally presented in the literature), size classes within species' populations, and season to identify the underlying sources of variation in diel vertical migration fidelity. In other words, do composite vertical distributions generated using pooled data across size classes reflect those of individual ontogenic stages (smaller vs larger individuals within a population)? Likewise, do vertical distributions change on seasonal scales? And if so, do these sources of variation explain asynchronous patterns of vertical migration we see in many (or most) migrating species? It is possible that since vertical distribution patterns are frequently derived from data taken over long periods of time and over wide geographic locations, the graphical representation of these pooled data may portray ratios of migratory and non-migratory sub-elements within migrators' populations that never locally exist at any time or place. Or, conversely, vertical migration patterns within a species may be highly conserved over the course of an individual's lifetime and over the seasonal variation experienced within a year (i.e., the behaviors are 'hardwired'). Ecological modeling efforts can then be based on these ecological units (i.e., whole populations or subpopulations) to create more accurate depictions of energy flow through pelagic systems.

SIGNIFICANCE OF STUDY

The "ladder of migration" concept, developed by Vinogradov (1962), depicts overlapping interactions between vertical migrators and non-migrators within the epipelagic, mesopelagic, and bathypelagic zones. The connectivity of these three zones is a key element of the pelagic ocean (Angel, 1989; Cook et al., 2013). This connected food supply corresponds with the active transport of carbon via feeding in surface waters and then descending to depth, where the carbon is excreted and settled (Figure 2). Such activity is crucial to deep-sea communities, as the supply of particulate organic matter decreases exponentially with depth (Vinogradov, 1968).
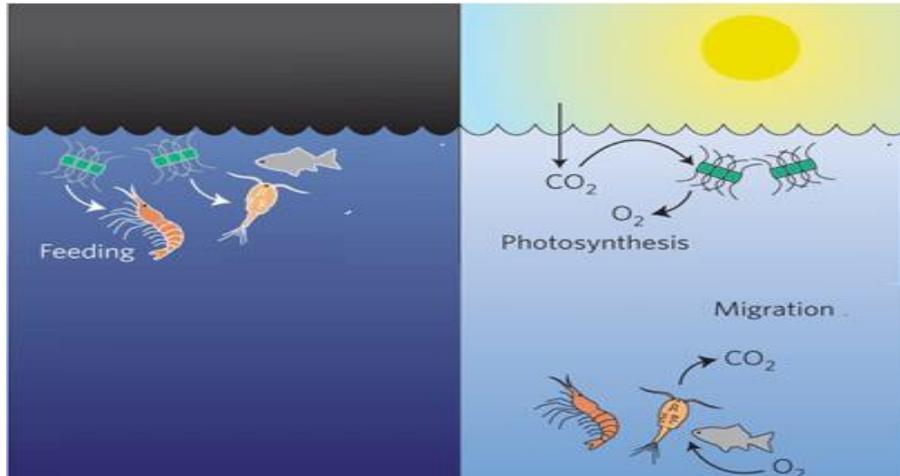
Figure 2. Feeding at night in the epipelagic (left) is shown for contrast in depths with the same populations during the day (right). After Huang (2014).

The biological pump facilitates the transport of photosynthetically produced biological materials, and thus sequestration of carbon, from the atmosphere to the interior of the ocean and seafloor (Volk and Hoffert, 1985; Longhurst and Harrison, 1989; Longhurst, 1991; Passow and Carlson, 2012; Figure 3). Through vertical migration, migrant planktivorous and piscivorous fishes, notably within the mesopelagic, are a major source of carbon transport (Brierly, 2014; Wang et al., 2019). Within the Gulf of Mexico (GoM), species of the families of Myctophidae, Sternoptychidae and Gonostomatidae consume 21%, 27% and 14% of prey biomass, respectively (primarily zooplankton), amounting to 2.5-4.3 kg C km^{-2} within the top 1000 m of the GoM daily (Hopkins et al., 1996). After this paper was published, new evidence was presented that showed that previous midwater fish estimates based on midwater trawls were underestimated, and that the midwater fish fauna likely influence the biological pump even more (Kaartvedt et al. 2009; Kaartvedt et al., 2012; Irigoien et al., 2014).

Organic carbon and nutrients consumed by these fishes are "pumped" into ocean depths because of nighttime feeding in the epipelagic and daytime residence and excretion in the mesopelagic (Longhurst and Harrison, 1989; Longhurst, 1991; Ducklow et al., 2001), and through death and sinking of zooplankton consumers. This pumping has profound effects on marine ecosystems by redistributing oxygen, nutrients and fixed carbon to deep-pelagic, deep-demersal, and deep-benthic organisms that would not have access otherwise (Levin, 2003; Rex et al., 2006; Sperling et al., 2014).
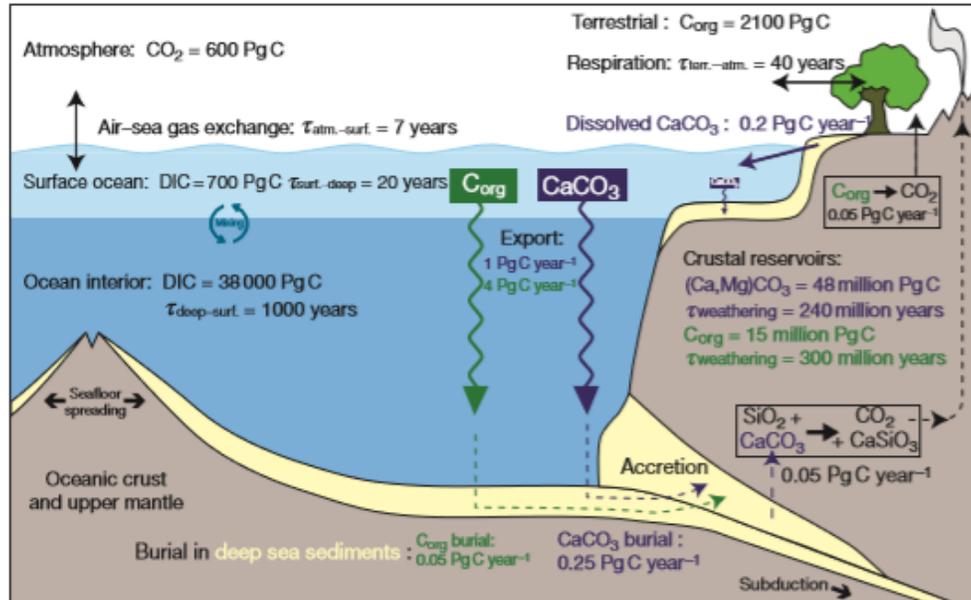
Figure 3. A simplified view of the preindustrial carbon cycle (Hain et al., 2014).

This study provides the most extensive investigation to date into the size- and season-structured dynamics of vertical migration, including the potential drivers of asynchronous vertical migration, a phenomenon that undoubtedly affects the scaling of the open ocean's biological pump on a global basis. Findings presented herein will improve the accuracy of increasingly sophisticated individual- and trait-based modeling of carbon flux in the deep-pelagic ocean.

METHODS

As a first step, vertical distribution patterns of the dominant mesopelagic fish species in the northern Gulf of Mexico were examined to determine target species of this study. This step elucidated a range of vertical migration patterns upon which to base further investigation. Data for these investigations were collected during the Offshore Nekton Sampling and Analysis Program (ONSAP) and the Deep Pelagic Nekton Dynamics of the Gulf of Mexico (DEEPEND) research consortium (Table 1; Sutton et al., 2020; Cook et al., 2020; Milligan and Sutton, 2020). ONSAP was implemented as part of the Natural Resource Damage Assessment procedure to assess the impacts of the *Deepwater Horizon* oil spill and to develop basic knowledge of pelagic fauna in the Gulf of Mexico. The DEEPEND Consortium was established to expand on ONSAP research of

the pelagic ecosystem in the northern Gulf of Mexico. Four numerically-dominant lanternfishes (Myctophidae), *Benthosema suborbitale*, *Ceratoscopelus warmingii, Lampanyctus alatus, Lepidophanes guentheri,* and the biomass-dominant bristlemouth (Gonostomatidae) species *Sigmops elongatus* were selected for analysis based on their presumed ecological importance in the mesopelagic Gulf of Mexico and the adequacy of data for detailed investigations.

Vertical distributions were examined using aggregated data and apportioned by size class and season (Spring, Summer, and Fall). Spring included February, March, and April, Summer included May, June, and July, and Fall included August and September. The remaining Winter season, including January, October, November, and December, were omitted as sampling was not conducted during these months.

Sampling and specimen handling/curation.

The three ONSAP cruise series and six DEEPEND cruises utilized a 10-m^2 MOCNESS (Multiple Opening/Closing Net and Environmental Sensing System; Wiebe et al., 1985) with a mesh size of 3 mm (Burdett et al., 2017; Judkins et al., 2017) as the primary sampling unit.

Table 1. The collection date ranges and years for the two data sources (ONSAP and DEEPEND) used in this study.

Collection Program	Research Vessel	Cruise ID	Month(s)	Year
ONSAP	*Meg Skansi*	MS6	January 28th – March 30th	2011
ONSAP	*Meg Skansi*	MS7	April 14th – June 30th	2011
ONSAP	*Meg Skansi*	MS8	July 18th – September 30th	2011
DEEPEND	*Point Sur*	DP01	May 1st – May 8th	2015
DEEPEND	*Point Sur*	DP02	August 8th – August 21st	2015
DEEPEND	*Point Sur*	DP03	April 30th – May 14th	2016
DEEPEND	*Point Sur*	DP04	August 5th – August 19th	2016
DEEPEND	*Point Sur*	DP04	May 1st – May 11th	2017
DEEPEND	*Point Sur*	DP06	July 19th -August 2nd	2018

The MOCNESS nets can be opened and closed in a sequential series to sample discrete-depth intervals (Wiebe et al., 1985). Discrete-depth intervals during MOCNESS sampling encompassed the epipelagic, upper mesopelagic, lower mesopelagic, upper bathypelagic, and mid-bathypelagic zones (Table 2). Net sampling occurred twice a day at each sampling station, once during daylight (0900h – 1500h) and once during the night (2100h – 0300h). Only stations where day and night samples were obtained consecutively were included in these analyses.

Table 2. Discrete depth intervals taken during cruises aboard the research vessels *Meg Skansi* and *Point Sur* in the Gulf of Mexico.

Net #	0	1	2	3	4	5
Starting Depth	Surface	1500 m	1200 m	1000 m	600 m	200 m
Ending Depth	1500 m	1200 m	1000 m	600 m	200 m	Surface

During ONSAP, whole samples were fixed in a mixture of 10% buffered formalin and 90% seawater onboard. During DEEPEND, specimens collected were initially processed by scientific personnel aboard the vessel and identified to the lowest possible taxonomic level. Samples were fixed onboard and later transferred to a mixture of 70% ethanol:30% water. Further identification and quantitative analyses of all samples were conducted by members of the Oceanic Ecology Laboratory at Nova Southeastern University in Dania Beach, Florida. Quantitative analyses included specimen enumeration, batch weighing, and standard-length measurement (the distance from the most anterior part of the fish, being the snout or mouth, to the end of the hypural bone located before the caudal fin).

Size class and seasonal variation analysis

Size-frequency distributions of target taxa were plotted to determine if there were natural inflection points in population structure indicating peaks in abundance of individuals of a given length and thus serve as a base for structuring size classes. Vertical distribution plots were then constructed for each size class to determine if greater numbers of specific size classes migrate more regularly than others. The main issue associated with determining the size classes of the species included in this study is the size at transition from juvenile to adult life stages. Since the transition size for many or most taxa is not known, Gaussian mixed models were used to cluster specimen groups based on size. These mixed models were based on probabilities in normally distributed subpopulations within an overall population. Vertical distribution plots were generated for the size classes discriminated in this manner for each species.

As with size classes, vertical plots of paired day-night trawl data were constructed from cruises conducted seasonally. One caveat present in this analysis is that differences in catch rates over different seasons could affect plots due to the increased graphical importance of individual

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specimens during low-catch periods. This consideration was integrated into graphical interpretation when necessary.

RESULTS

Vertical distributions using aggregated data.

      Analysis of vertical distribution plots generated with aggregated data (all times and size classes) suggested that of the five species examined here, two (*Benthosema suborbitale* and *Lepidophanes guentheri*) classify as synchronous vertical migrators (Fig. 4a, b) and three (*Lampanyctus alatus, Ceratoscopelus warmingii*, and *Sigmops elongatus*) as asynchronous (Fig. 4c-d). Of the former two, *B. suborbitale* displayed a daytime maximum of abundance in the upper mesopelagic zone (between 200-600 m), while *L. guentheri* appeared evenly divided between the upper and lower (600-1000 m) mesopelagic zones during daytime. In both species, all but a miniscule fraction of individuals from size classes sampled in this study migrated into the epipelagic zone at night.

      Of the asynchronous vertical migrators, *Sigmops elongatus* exhibited the shallowest daytime distribution (primarily upper mesopelagic, with a smaller portion in the lower mesopelagic), *Lampanyctus alatus* occurred somewhat deeper during daytime (population evenly divided between the upper and lower mesopelagic), and *Ceratoscopelus warmingii* occurred deepest, with a substantial fraction occurring below 1000 m (i.e., bathypelagic distribution). Of the latter two myctophid species, nighttime depth distributions were bimodal, with most of the non-migrating portion occurring in the lower mesopelagic zone. The nighttime distribution of *S. elongatus* was unimodal (primarily epipelagic), but with a substantial portion occurring in the upper mesopelagic zone, suggesting limited upward migration of daytime-lower-mesopelagic occupants, non-migration of daytime-upper-mesopelagic occupants, or a combination of the two.
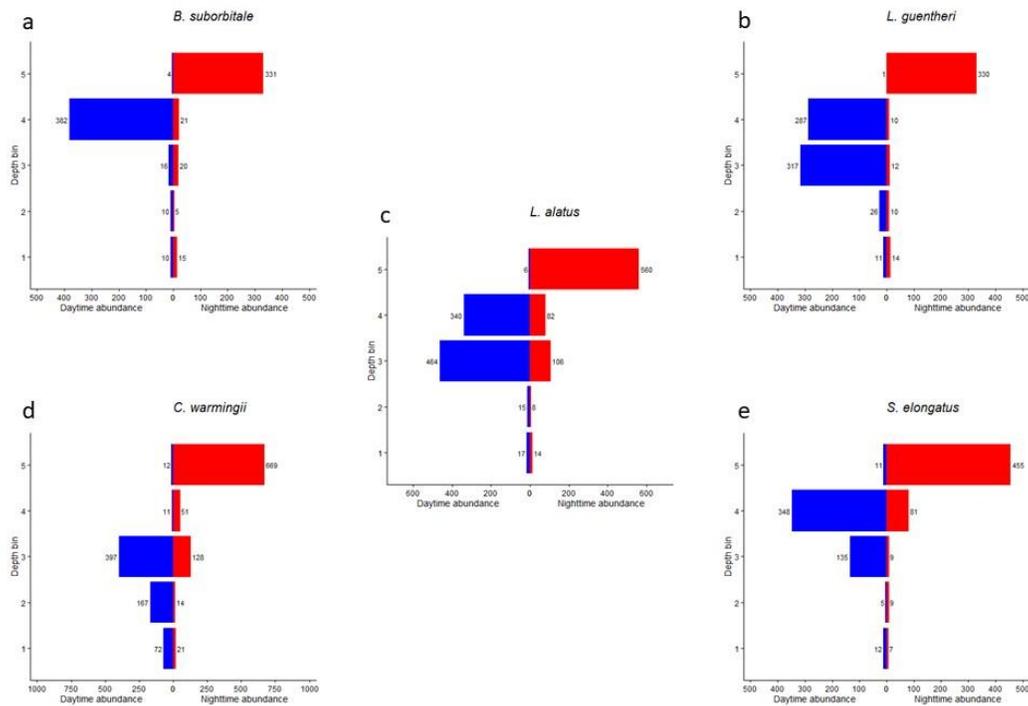
Figure 4. Diel vertical distributions of five numerically dominant mesopelagic fishes in the Gulf of Mexico: a) *Benthosema suborbitale* (Myctophidae); b) *Lepidophanes guentheri* (Myctophidae); c) *Lampanyctus alatus* (Myctophidae); d) *Ceratoscopelus warmingii* (Myctophidae); and e) *Sigmops elongatus* (Gonostomatidae). Abundances = no. individuals per 10^5 m^3.

Size-frequency distributions of target species.

Size-frequency histograms were generated for the five target taxa (Figure 5). Size distributions ranged from unimodal to bimodal to multimodal, with *B. suborbitale* demonstrating four size-frequency peaks. This number was chosen for all species for consistency. The overall size range of the five species varied greatly (10-35 mm SL for *B. suborbitale* versus 10 - >200 mm SL for *S. elongatus*), which affected the size-class interval range for each of the species.
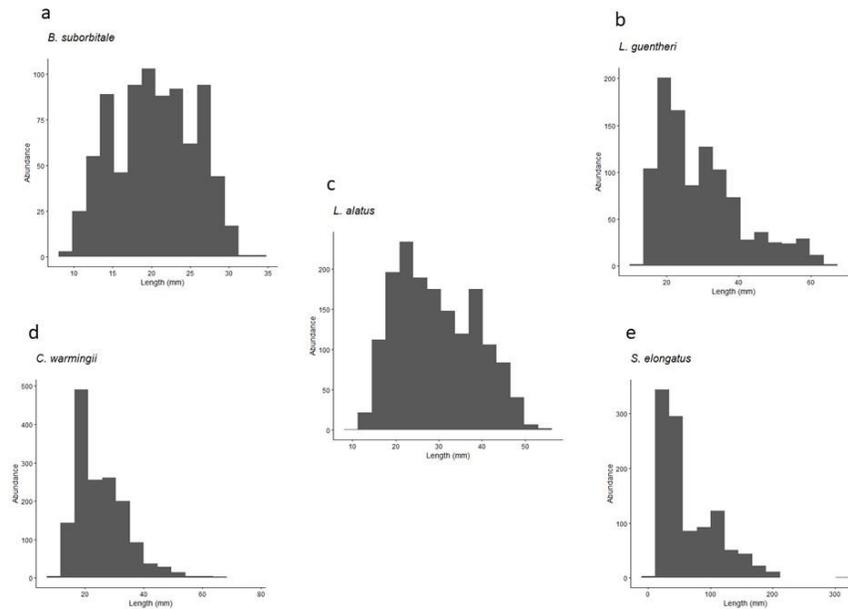
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Figure 5. Size-frequency distributions of five numerically dominant mesopelagic fishes in the Gulf of Mexico: a) *Benthosema suborbitale* (Myctophidae); b) *Lepidophanes guentheri* (Myctophidae); 3) *Lampanyctus alatus* (Myctophidae); *Ceratoscopelus warmingii* (Myctophidae); and e) *Sigmops elongatus* (Gonostomatidae).

Patterns of diel vertical migration as a function of size.

The two lanternfish species exhibiting the highest degree of diel migration fidelity, *B. suborbitale* and *L. guentheri,* also exhibited very little size-based differentiation in diel vertical migration patterns (Figures 6, 7). This was particularly manifest in the deeper-dwelling *L. guentheri*, as patterns of depth distributions and vertical migration habits were mirrored by all size classes (Figure 6a-d). This pattern was also exhibited by *B. suborbitale,* with the exception of a small non-migrating element at night in the 15-18 mm size class (Figure 7b). The depth distribution of *L. guentheri* appeared to be size-structured, with larger individuals occurring deeper during daytime, but all size classes converged in the epipelagic zone at night (Figure 6a-d). The size-depth relationship of *B. suborbitale* was not apparent (Figure 7a-d) but may have been obfuscate by the wide depth ranges sampled in this study (i.e., segregation within the epipelagic at night and upper mesopelagic during daytime would not be discernable).
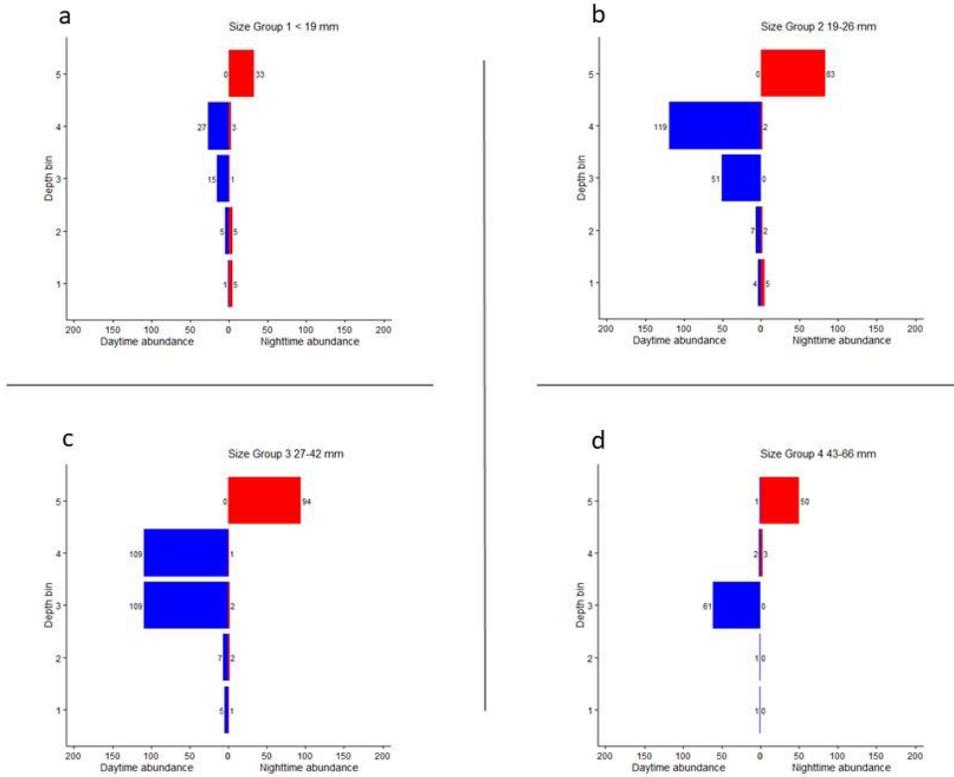
Figure 6. Diel vertical distributions of four size classes of *Lepidophanes guentheri* (Myctophidae) in the Gulf of Mexico: a) < 19 mm SL; b) 19-26 mm SL; c) 27-42 mm SL; d) 43-66 mm SL. Abundances = no. individuals per 10^5 m^3.
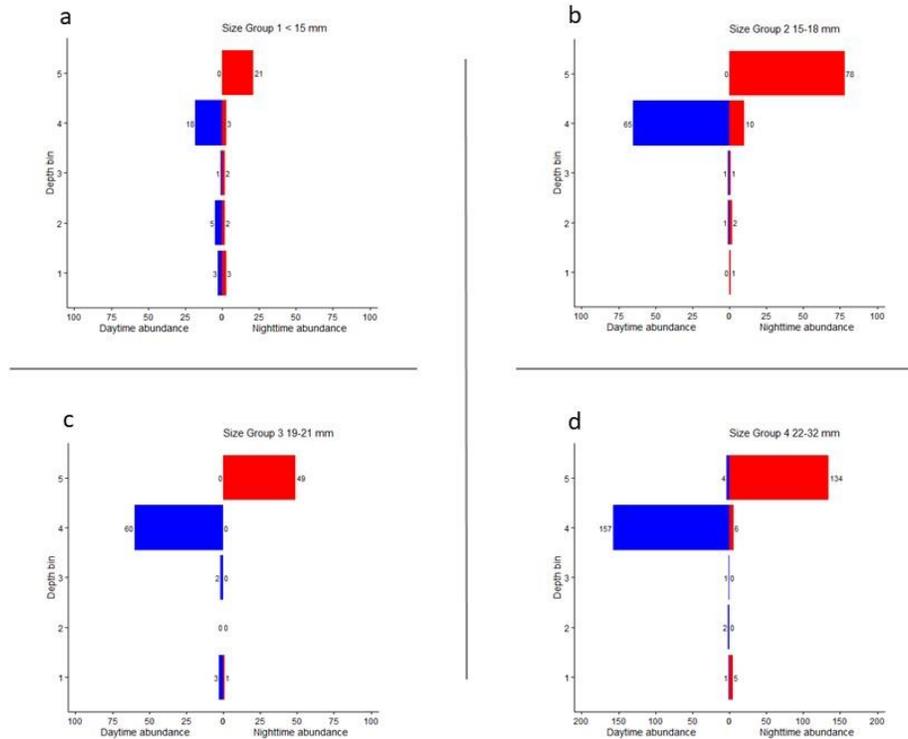
Figure 7. Diel vertical distributions of four size classes of *Benthosema suborbitale* (Myctophidae) in the Gulf of Mexico: a) < 15 mm SL; b) 15-18 mm SL; c) 19-21 mm SL; d) 22-32 mm SL. Abundances = no. individuals per 10^5 m^3.

Among the asynchronous migrators, size-differentiated vertical distribution and migration was readily apparent, with each species showing a unique pattern. The species with the shallowest overall daytime distribution, *S. elongatus*, exhibited near-complete migration synchronicity among the smallest individuals collected (Figure 8a), with increasing tendency for non-migration and/or limited migration as body length increased (Figure 8b-d). The largest size class appeared to undertake migration from the lower to the upper mesopelagic zone at night (Figure 8d).
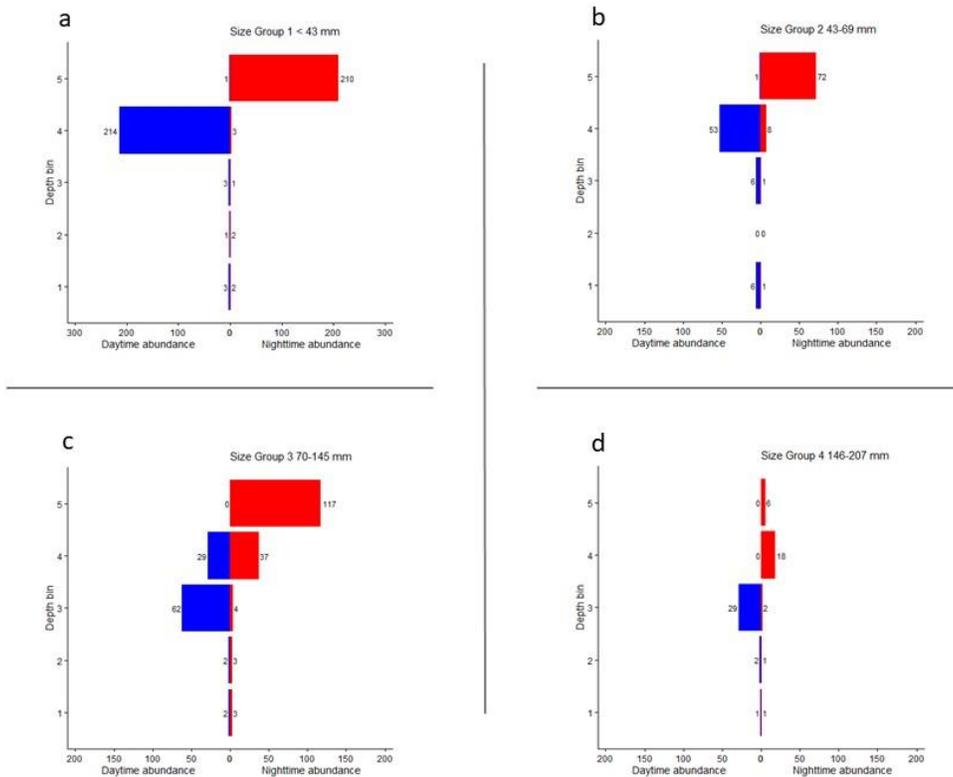
Figure 8. Diel vertical distributions of four size classes of *Sigmops elongatus* (Gonostomatidae) in the Gulf of Mexico: a) < 43 mm SL; b) 43-69 mm SL; c) 70-145 mm SL; d) 146-207 mm SL. Abundances = no. individuals per 10^5 m^3.

The migration patterns of the remaining two species, *L. alatus* and *C. warmingii*, exhibited a reciprocal form of asynchrony, with the smallest individuals migrating least (Figures 9a, 10a) and the largest exhibiting near-synchronous diel vertical migration (Figures 9d, 10d). The distributions of *C. warmingii* were remarkable in that the two largest size classes provided clear evidence of diel vertical migration by fishes residing in the bathypelagic zone (Figure 10c, d).
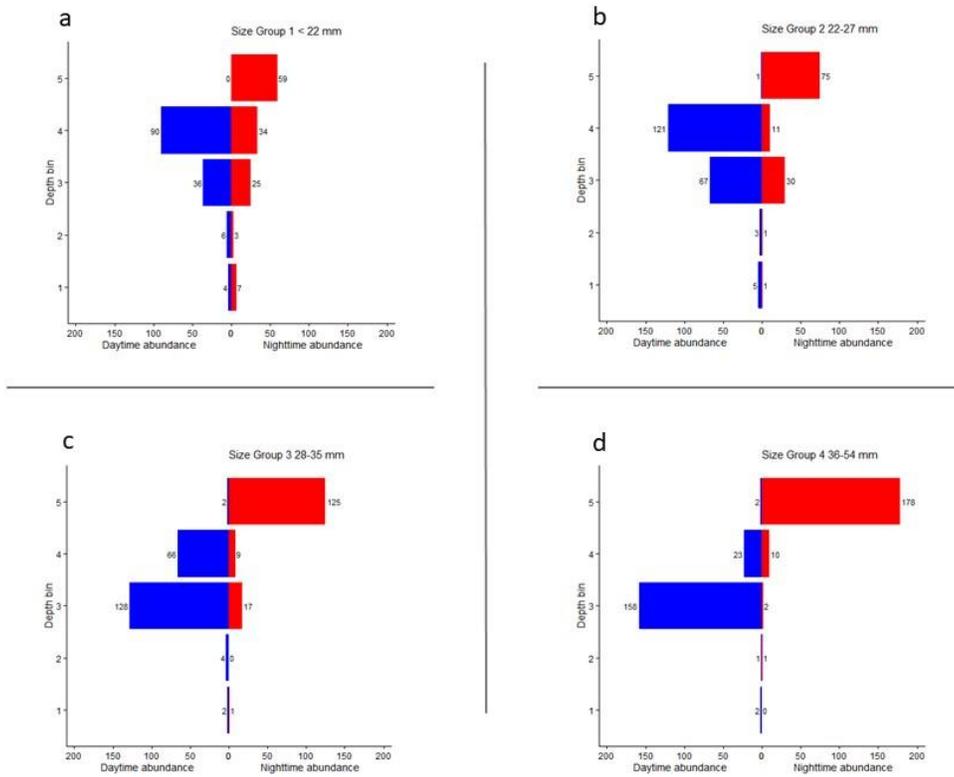
Figure 9. Diel vertical distributions of four size classes of *Lampanyctus alatus* (Myctophidae) in the Gulf of Mexico: a) < 22 mm SL; b) 22-27 mm SL; c) 28-35 mm SL; d) 36-54 mm SL. Abundances = no. individuals per 10^5 m^3.
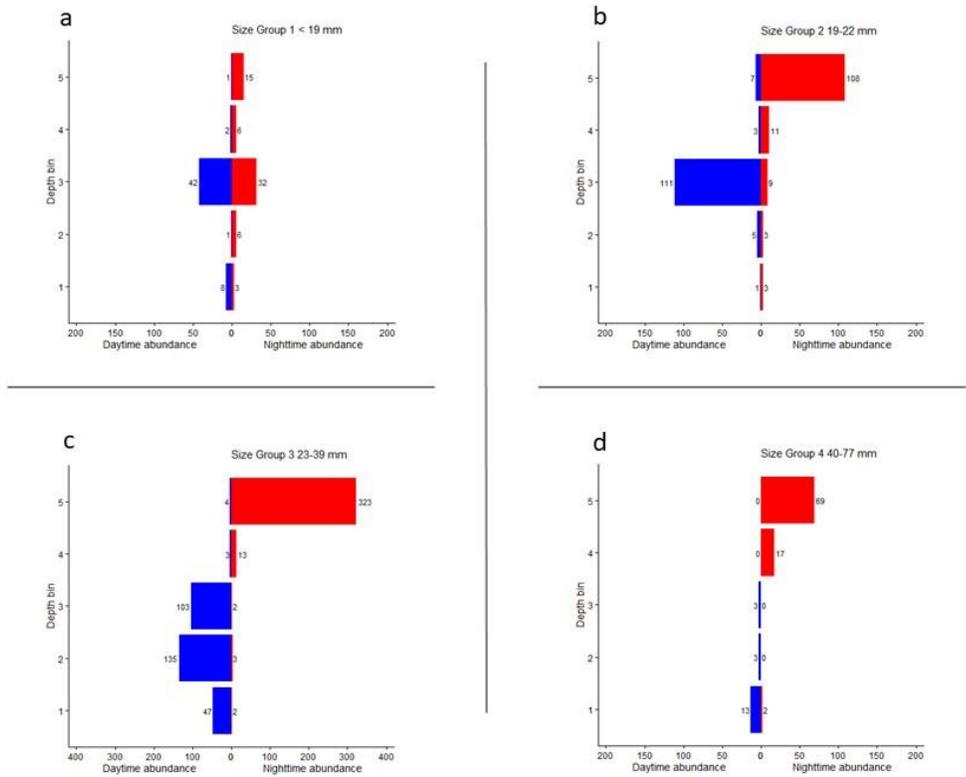
Figure 10. Diel vertical distributions of four size classes of *Ceratoscopelus warmingii* (Myctophidae) in the Gulf of Mexico: a) < 19 mm SL; b) 19-22 mm SL; c) 23-39 mm SL; d) 40-77 mm SL. Abundances = no. individuals per 10^5 m^3.

Diel vertical distribution as a function of season.

  As with size, the synchronously migrating lanternfishes *B. suborbitale* and *L. guentheri* exhibited no signs of seasonal variation in diel vertical migration behavior (Figure 11), though the pattern was somewhat obfuscated by lower overall catches in Autumn for both species (Figure 11c). Very few individuals were collected below 200 m at night during any season.
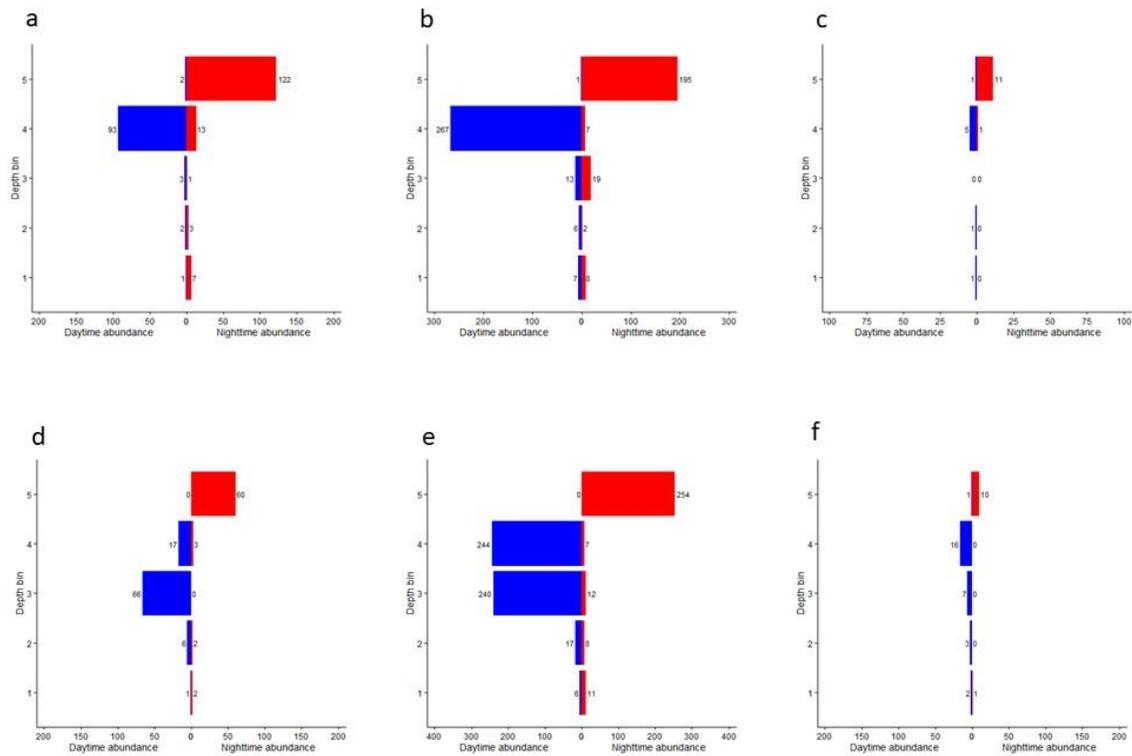

Figure 11. Seasonal vertical distributions of the lanternfishes *Benthosema suborbitale* (a. Spring; b. Summer, c. Autumn) and *Lepidophanes guentheri* (d. Spring, e. Summer, f. Autumn) in the Gulf of Mexico. Abundances = no. individuals per 10^5 m^3.

Seasonal variation in vertical distributions of the asynchronous migrators was also not readily apparent (Figures 12, 13), at least for Spring and Summer. Diel vertical migrations appeared synchronous in Autumn, but this interpretation is tempered by overall lower catch numbers relative to Spring and Summer. Given the potential for a seasonal change in migratory behavior, this finding at the very least provides impetus for more detailed seasonal study of these species.
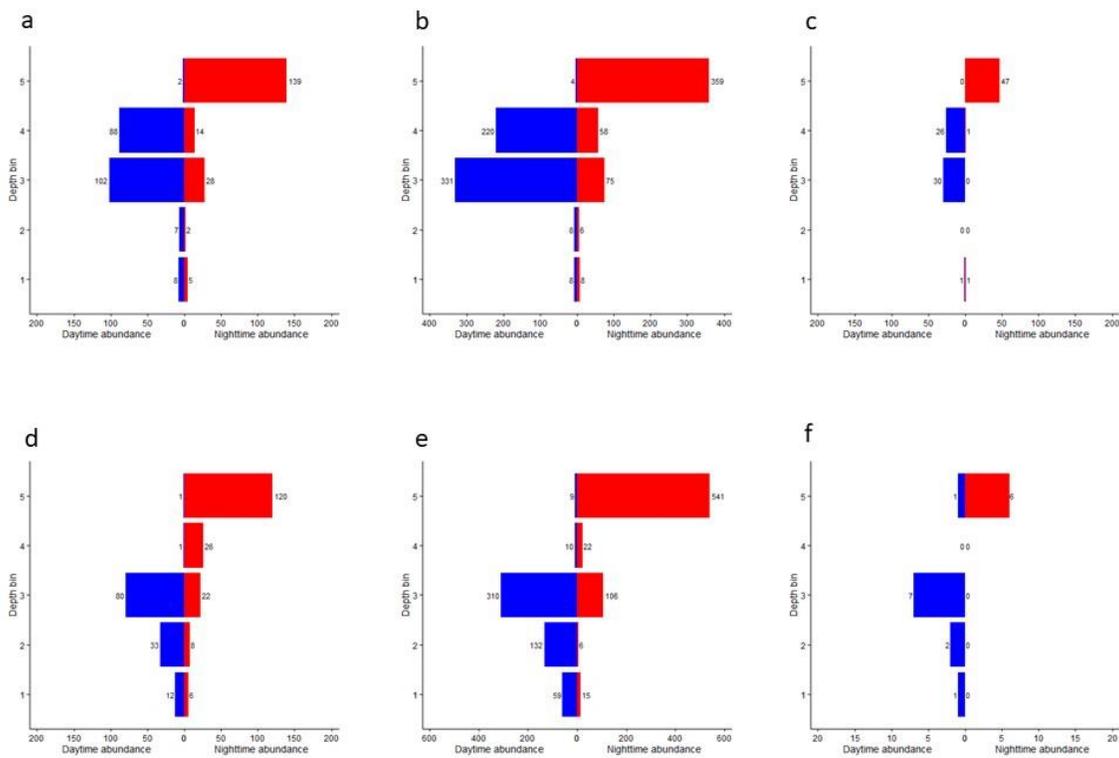

Figure 12. Diel vertical distributions as a function of season of *Lampanyctus alatus* (a. Spring; b. Summer, c. Autumn) and *Ceratoscopelus warmingii* (d. Spring, e. Summer, f. Autumn). Abundances = no. individuals per 10^5 m^3.
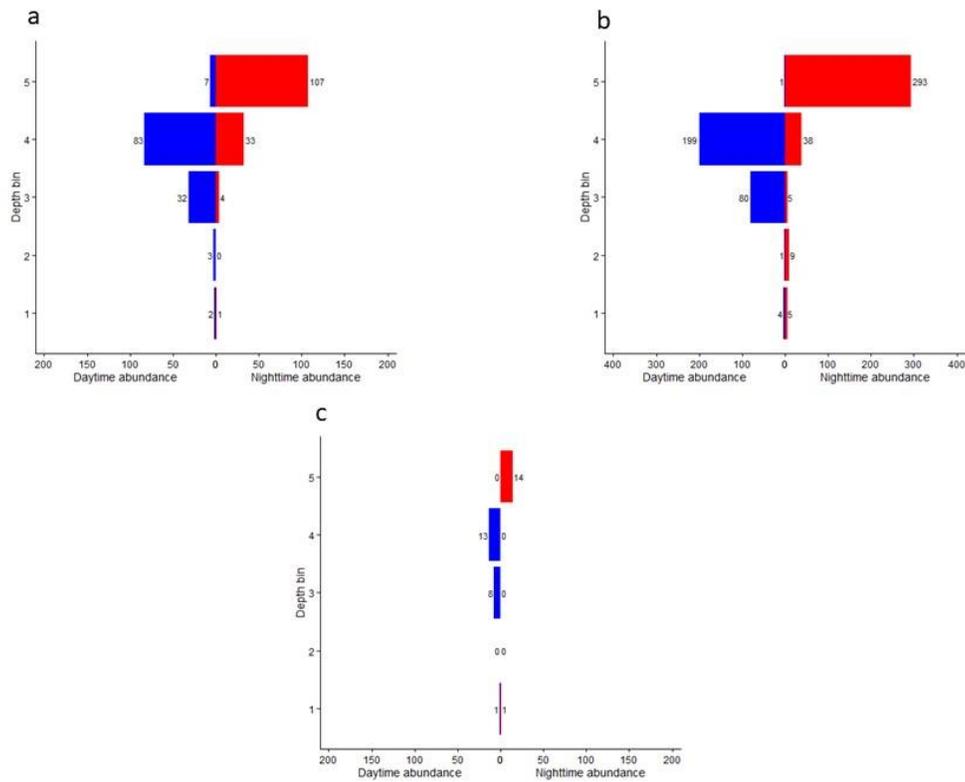
Figure 13. Diel vertical distribution as a function of season of *Sigmops elongatus* (a. Spring; b. Summer, c. Autumn). Abundances = no. individuals per 10^5 m^3.

DISCUSSION

Overall, vertical distributions based on aggregated data for the five species treated in this study agree well with published reports, specifically from studies previously conducted in the Gulf of Mexico. The most detailed examinations prior to this one were those of Gartner et al. (1987; Myctophidae), Lancraft et al. (1988, *Sigmops elongatus*, then referred to as *Gonostoma elongatum*), and Hopkins et al. (1996). These publications were elements of an extensive series of papers from Thomas Hopkins' multi-decadal program investigating the mesopelagic fauna of a single oceanic station in the eastern GoM, "Standard Station" (27˚N, 86˚W). Standard Station was one of 47 stations sampled in the current study. Sampling at Standard Station by Hopkins' program was conducted with a single-net, opening/closing midwater trawl (Tucker Trawl) with smaller mouth area (3.2 or 6.5 m^2) and cod-end mesh size (0.505 mm) than the MOC10 used in this study

(10 m^2, 3 mm, respectively. Hopkins, Gartner, and Lancraft et al. fished at 25-m depth intervals night and day from the surface to 1000 m. Thus, the vertical resolution of their study was higher, while this study was conducted to greater depths (1500 m).

Despite the limited depth resolution of this study compared to previous GoM surveys, four of the five species exhibited a 'bigger-deeper' trend in vertical distribution during daytime. The lone outlier, *B. suborbitale*, may also show the same pattern *within* the depth zones sampled here, as has been shown for this species with finer-vertical-resolution sampling in the Sargasso Sea (Karnella (1987). The bigger-deeper trend in daytime distribution can be considered a mesopelagic fish maxim (Sutton, 2013, and references therein), and has been corroborated for all five species treated herein by other studies (Clarke, 1978; Badcock and Merrett, 1976; Hulley, 1986; Gartner et al, 1987; Karnella, 1987; Lancraft et al, 1988; Hulley, 1990; Hopkins et al., 1996).

Of the synchronously migrating lanternfish, *Lepidophanes guentheri*, Gartner et al. (1987) reported daytime catches as shallow as 400 m, with an abundance maximum between 650-800 m, and catches primarily in the top 200 m, in good agreement with the distribution reported here (Figure 4b). This distribution is consistent with reports of this species from the Sargasso Sea (Karnella, 1987) and the eastern tropical Atlantic (Hulley, 1990). No evidence of bimodal depth distributions at night is presented in any of these studies.

The daytime vertical distributions of the lanternfish *Benthosema suborbitale* in the GoM reported by Gartner et al. (1987) and by Karnella (1987) for this species in the Sargasso Sea are identical to this study (well defined distribution between 400-600 m). However, Gartner et al. reported a bimodal nighttime distribution, with a migratory group between 50 and 100 m and a non-migratory group at daytime depths, which was not found in this study, nor was it reported by Hulley (1986) or Mundy (2005) for *B. suborbitale* in the Indian and Pacific Oceans, respectively. Regarding GoM distributions, it is unlikely that myctophid vertical behavior differs between Standard Station and the rest of the ONSAP/DEEPEND sampling grid due to high three-dimensional dispersion (Milligan and Sutton, 2020). It is more likely that size-of-capture differences between the studies accounted for the disparity in the accounts of vertical distribution and migration for the same species in the same location. In this study, and in that of Karnella (1987), a very small fraction of the *B. suborbitale* population (three specimens in the Karnella study) were collected below 200 m at night. All three of the Karnella (1987) specimens were very small individuals (juveniles, 11-12 mm). Clarke (1978) and Badcock and Merrett (1976) reported

that juvenile *B. suborbitale* (10-12 mm) were non-migratory off Hawaii and the Northeast Atlantic, respectively. Thus, the mesh size used in Gartner et al. (1987) (0.505 mm versus 3.0 mm in this study) is the likely reason; they sampled a smaller size fraction of this fish than that of 'standard' midwater trawling, and this size fraction migrates the least.

Daytime vertical distributions reported in Gartner et al. (1987) and this study of the lanternfish *Lampanyctus alatus* are in close agreement. However, nighttime distributions reported by Gartner et al. (1987) did not include evidence for members of the population remaining at depth at night, a finding that was quite clear in this study. Non-migrants were found in the 22-27- and 28-35 mm size classes, so it is less likely that mesh size was the primary determinant; individuals in these sizes should be retained fully by 3-mm mesh. Karnella (1987) presented evidence for asynchronous migration by *L. alatus* in the Sargasso Sea, albeit with very limited data.

Direct vertical distribution comparisons between this study and Gartner et al. (1987) regarding the lanternfish *Ceratoscopelus warmingii* are hindered by the lack of sampling below 1000 m depth in the latter study. This study and those of Karnella (1987) in the Sargasso Sea and Hulley (1984) in the eastern Atlantic clearly show that the species occurs well into the bathypelagic zone during daytime. That said, all studies indicate that this species has a broad daytime vertical distribution with a maximum in abundance between 600-1000 m, and that most of the population migrates into the epipelagic zone at night. Gartner et al. did not find evidence of asynchronous migration as did this study, Hulley (1984), and Karnella (1987).

Close concordance was observed between the vertical distribution results of this study and those of Lancraft et al. (1988) for the gonostomatid *Sigmops elongatus* in the GoM. The latter study reported daytime distributions centered between 425 – 725 m, a much finer resolution than that in the present study (mainly 200-600 m, with a lesser fraction between 600 – 1000 m). Their study reported a nighttime maximum between 25-325 m depth, again a more highly resolved version of 0-200 m abundance maximum with a portion between 200-600 m. Neither study in the Gulf reported a bimodal nighttime distribution, as has been reported for this species in the eastern tropical Atlantic (Quéro et al., 1990).

Diel vertical migration as a function of body size and season.

A comparison of this study with that of Gartner et al. (1987) demonstrated the effect of sampling strategy, specifically mesh size of the trawl used, on the characterization of diel vertical

migration in mesopelagic fishes. By extension, this also demonstrates the relationship between body size and vertical migration habit. The diel vertical distribution of the lanternfish *B. suborbitale* demonstrates both cases: post-larvae/juveniles do not vertically migrate while subadults and adults migrate strongly.

The diel vertical distributions of the two of the remaining three lanternfishes, *C. warmingii* and *L. alatus*, show the same general pattern: larger individuals migrate strongly while smaller individuals are less apt to migrate on a diel basis. The trend in the fourth lanternfish species, *L. guentheri*, shows that while this size-based diel vertical migration fidelity may be the rule among lanternfishes, some species appear to be synchronous vertical migrators throughout their post-larval life. Of the size-dependent migrating species, it is possible that there is a tipping point in size, related to Reynold's number dynamics, in which migration is 'easier' for larger individuals, and thus more cost-effective. Reynold's numbers are expressed by the equation $R = \rho L U \mu$, which relates the ratio of frictional to inertial forces to distance (in this case, animal size) and speed, as related to movement through a fluid. At small Reynold's numbers, which are experienced by smaller fishes, viscous (frictional) forces dominate; i.e., water is more like molasses. At larger Reynold's numbers, which are experienced by larger fishes, inertial forces dominate; i.e., water is more like alcohol. This relationship may explain, at least in part, why larger fishes migrate while smaller do not. Detailed biophysical modeling would be needed to further investigate this hypothesis.

Analysis of the diel vertical distribution of *S. elongatus* in the GoM reveals a contrasting pattern; larger individuals are less apt to migrate than smaller, or if they do vertically migrate, they do not go as far, stopping in the upper mesopelagic zone instead of continuing to the epipelagic. As *S. elongatus* is substantially larger than the lanternfishes examined here (e.g., the smallest size class of *S. elongatus* [< 43 mm] includes individuals that would be placed in the largest size class of the other four species), it is possible that Reynold's number considerations do not dictate migratory behavior. In the case of this species, it is possible that metabolic needs and feeding selectivity are the primary drivers. Smaller fishes have higher weight-specific metabolic demands than larger (Urbina and Glover, 2013), and take smaller prey (Hopkins et al., 1996), which are digested faster (Sutton and Hopkins, 1996). Thus, smaller fishes need to eat more often, and thus may be motivated to migrate more frequently to meet these needs.

Regarding the possibility that aggregating data across seasons delivers an asynchronous trend in species that migrate synchronously, but not on a diel cycle, there was no evidence for this possibility in these data, though seasonal changes in absolute abundance certainly affect vertical distribution plots. At small sample sizes, proportions of migrating and non-migrating fractions are highly affected by relatively low numbers of individuals. Size-dependent migration fidelity appeared to be a much more important driver of asynchronous vertical migration.

Given the importance of diel vertical migrators in the global sequestration of carbon via the biological pump, and the increasing sophistication of individual-based models of carbon flux, quantifying the variability in DVM and AVM behavior is essential, as these values drive the models. Quantifying this variability will greatly enhance the accuracy (and likely precision) of carbon flux models, which are vitally important in a rapidly changing deep ocean subjected to increasing human disturbance.

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