Wiley
Journal of Applied Ichthyology
Volume 2025, Article ID 4473256, 19 pages
https://doi.org/10.1155/jai/4473256

WILEY

Research Article

Length–Weight Relationships of 68 Mesopelagic Fish Species From a Subtropical Ocean Basin

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Received 18 August 2025; Revised 17 September 2025; Accepted 30 September 2025

Academic Editor: Upali S. Amarasinghe

Wet-weight- and dry-weight-derived length–weight relationships were estimated for 68 species of mesopelagic fishes found throughout the Gulf of Mexico, 59 of which are new for the region and 28 are new globally. The length–weight relationships obtained were of good fit, with 92% of models having R^2 values above 0.90. Isometric and positive allometric growth were the most common growth models observed, which agrees with similar studies on mesopelagic fishes across various other regions. Allometric growth parameters (b) were largely within the expected range for fishes, with 76% of estimated growth parameters falling within the range 2.5–3.5. Estimates of growth form were variable across weight types and taxa, with 28 species displaying a different growth form depending on the weight type used. The shifts in growth form observed in this study were likely related to water content as the examination of the relationship between length and water content found that this relationship was significant in 22 of 28 species that exhibited a shift in growth form. Variations in relative water content in relation to length were hypothesized to reflect ontogenetic changes in body composition, driven by shifts in vertical distribution and diel vertical migration behavior. Overall, the present study represents one of the largest assemblies of length–weight relationships of mesopelagic fishes to date and will aid in regional biomass estimations of mesopelagic fishes in the Gulf of Mexico.

Keywords: deep-pelagic; Gulf of Mexico; length–weight relationships; mesopelagic; micronekton

1. Introduction

Mesopelagic fishes are classically considered those that inhabit the mesopelagic or "twilight" zone (200–1000 m) of the World's Oceans [1, 2]. Mesopelagic fishes ostensibly possess the largest biomass of all vertebrates with estimates ranging from 1 to 19.5 Gt, varying depending on the methodology (e.g., acoustic, net, or food-web-derived) [3–6]. Many mesopelagic fishes exhibit diel vertical migration (DVM) behaviors where they migrate into the epipelagic zone at dusk and then return to depth at dawn [2, 4, 7]. DVM allows access to the resource-rich epipelagic zone while simultaneously reducing mesopelagic fishes' predation risk [8, 9]. Due to mesopelagic fishes' large biomass and DVM behavior, they play critical roles in ecosystem functioning [10], biogeochemical cycling [11], and carbon sequestration [12, 13], the latter estimated to be worth as much as 300 to 900 billion USD per year globally [14].

In addition to the critical roles mesopelagic fishes play in ecosystem functioning, they also potentially represent one of the largest untapped resources on Earth [15]. Due to the growing demand for marine resources and the continued decline of traditional fisheries, mesopelagic fishes are being reexamined as a potential source of fishmeal for agriculture and aquaculture [15, 16]. Given their nearly circumglobal distribution and immense biomass [4, 5, 17], mesopelagic fisheries have been suggested as a mechanism to alleviate pressures and overexploitation of marine fisheries resources [15, 18].

Despite the significant ecosystem services mesopelagic fishes currently provide and the potential future exploitation they face, many basic biological questions remain regarding their biodiversity, biomass, biological rates, spatial and temporal distribution, and life history (e.g., age, growth, and reproduction) [1, 13, 19, 20]. Providing answers to these basic biological questions and furthering knowledge regarding the role of mesopelagic fishes in ecosystem services will aid in making informed decisions about potential mesopelagic fisheries and future offshore exploits such as deep-sea mining that may impact mesopelagic assemblages [19, 21]. One of the most prominent knowledge gaps regarding mesopelagic fishes is estimates of their biomass [20]. Species-specific estimates of biomass in particular are of importance, especially in highly speciose regions since they host a variety of species with a wide range of life histories, vertical distributions, and DVM behaviors [22]. These traits ultimately impact the specific services and the magnitude of such services mesopelagic fishes potentially provide in these regions [13, 18, 23, 24].

One method of obtaining biomass estimates of individual fishes is using length–weight relationships (LWRs), which derive biomass estimates from more easily obtained length data [25]. In addition to biomass estimation, LWRs also allow one to characterize an individual species' growth model, relative body condition, and form factor [25]. A growth model in the context of LWRs refers to the allometric relationship between length and weight which generally scales according to the cube law (isometric growth) [25]. Deviations from this pattern are referred to as allometric growth [26]. Allometric growth can be classified as either negative allometry, indicating relatively faster growth in length than in weight (e.g., elongation), or positive allometry, referring to relatively faster growth in weight than length [25, 26]. Growth models give insights into potential ontogenetic changes in the shape and/or relative condition of fishes. Despite the wide use of LWRs in fisheries ecology since the early 1900s [27], relatively few studies have been conducted on mesopelagic fishes.

The Gulf of Mexico is a semi-enclosed and subtropical ocean basin situated between the southern United States of America, Mexico, and Cuba [28]. It contains a unique mesopelagic fish assemblage characterized by greater abundance and richness than the adjacent Sargasso and Caribbean Seas [22, 29]. The Gulf of Mexico is one of the most heavily impacted bodies of water in the world, with heavy pressures from the oil and gas industry, commercial fisheries, and altered nutrient inflows with future impacts, including wind farms and future oil spills [28]. As such, understanding key ecosystem components in the Gulf of Mexico, such as the mesopelagic fish assemblage, is important for the management of its pelagic ecosystem and the services it provides. However, relatively few studies have been conducted specifically to establish LWRs of mesopelagic fishes in the Gulf of Mexico. Those that have been conducted have generated estimates from the Campeche Bank for 39 species of continental shelf and deep-pelagic fishes [30] and from the northeastern Gulf of Mexico, which includes estimates for 18 species from the family Stomiidae [31] and a single gonostomatid: *Sigmops elongatus* (Günther 1887) [32].

Over the past 15 years, the Gulf of Mexico Research Initiative (GoMRI, 2010–2015), the Deep-Pelagic Nekton Dynamics of the Gulf of Mexico Consortium (DEEPEND, 2015–2018; DEEPEND|RESTORE, 2019-present), and the Deep-Sea Benefits (DSB, 2024–2027) research programs have generated a plethora of data on the abundance, distribution, and diversity of mesopelagic fishes in the northern Gulf of Mexico [33–35]. However, due to the difficulties of obtaining accurate shipboard weights from small deep-pelagic fishes, studies based on fish biomass have yet to be attempted. Such estimates would potentially improve ecosystem, carbon transport, and species distribution modeling efforts which would help quantify the role mesopelagic fish play in the northern Gulf of Mexico. As such, the primary aim of this study was to estimate the LWRs of the most abundant species of mesopelagic fish collected in the northern Gulf of Mexico during these research programs. Multiple weight types were utilized (preserved wet weights and dry weights) in the estimation of LWRs to provide multiple ways to estimate biomass from length data, with dry weight's inclusion due to its ability to limit the impact of variable water content and to aid in the conversion to other parameters, such as biochemical metrics. Previous studies have noted differences in dry-weight- and wet-weight-derived estimates of LWRs with the relationship between length and water content possibly being the cause [36]. As such, the relationship between length and water content was investigated. In addition, we provide estimates of family-level LWRs to inform relationships where species data are not yet available, characterize species growth models, and derive species-specific water content metrics.

2. Methods

2.1. Specimen Collection. All specimens utilized in this study were collected in the northeastern Gulf of Mexico during the years 2010–2024 on several cruises conducted during four major research programs: GoMRI (2010–2015), DEEPEND (2015–2019), DEEPEND|RESTORE (2019–2024), and DSB (2024–2027). Two sampling methods were utilized across the four programs: 10-m^2 Multiple Opening and Closing Net and Environmental Sensing System (MOC10 hereafter) and a High-Speed Rope Trawl (HSRT). GoMRI collections utilized the HSRT and MOC10 sampling gear across several cruises, while DEEPEND, DEEPEND|RESTORE, and DSB cruises collected samples with only the MOC10 [37, 38]. Sample sites for both programs were selected from a series of Southeast Area Monitoring and Assessment Program (SEAMAP) stations in the northern Gulf of Mexico [37, 39]. The GoMRI surveys consisted of approximately 10 months of data collection from each station and were sampled two to three times over the entirety of the GoMRI program (Figure 1).

HSRT collections during the GoMRI program were conducted twice during the day and at night, with sample collections centered on solar noon and solar midnight,

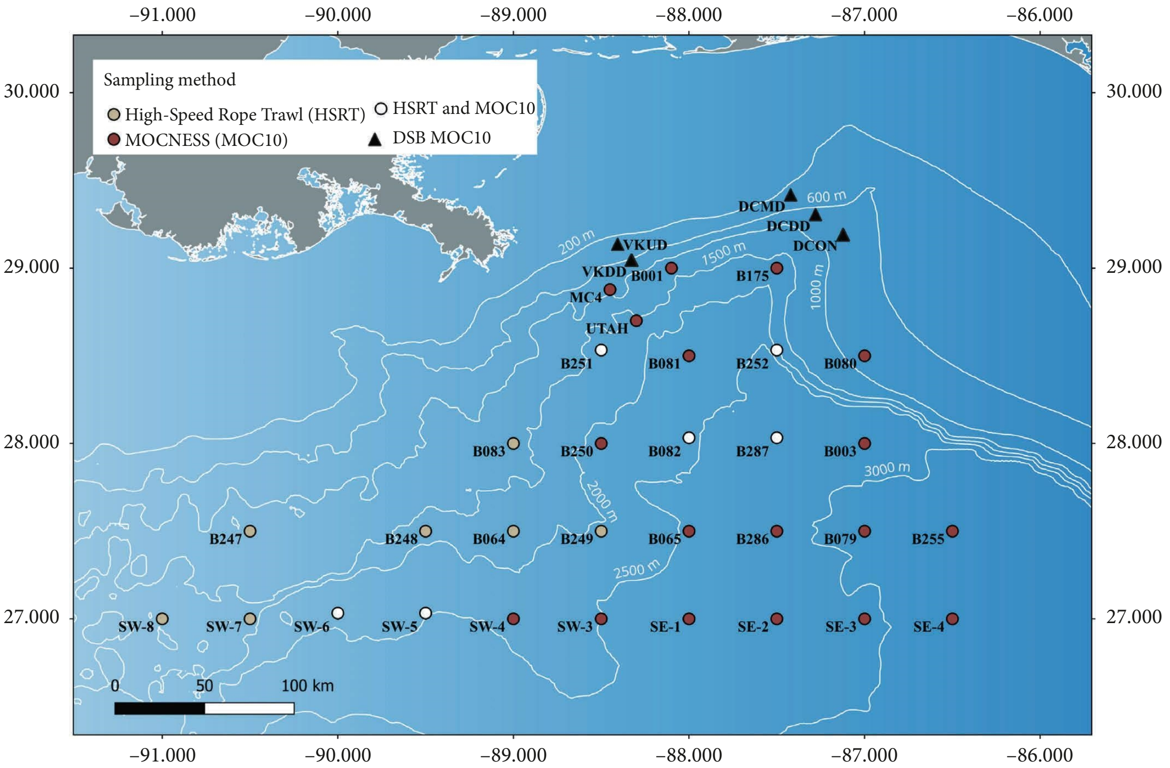

Figure 1: Map of the sites from the various research cruises in which specimens were collected, and sampling methods utilized in the Gulf of Mexico.

respectively. These GoMRI specimens were collected aboard the NOAA FSV *Pisces* [38]. The HSRT was a single large net that remained open during the entirety of trawling and fished from 0–700 m back to the surface for a shallow sample, while the second tow had a maximum depth of 1400 m [38]. The specimens from the HSRT were typically larger than those collected by the MOC10 and provided upper estimates for the LWRs.

The sampling protocols for the MOC10 sampling conducted during GoMRI and DEEPEND are described in detail in Cook et al. (2020), but we provide a brief review here. DEEPEND|RESTORE methods follow the same protocol as DEEPEND. Cruises for the DEEPEND and DEEPEND|RESTORE programs sampled a subset of the sites sampled during the GoMRI cruises (Figure 1). While GoMRI cruises focused on covering a larger portion of further offshore SEAMAP stations (Figure 1), cruises during DEEPEND field operations were more limited on time and instead focused on sampling across mesoscale oceanographic features such as the Loop Current, Loop Current–associated eddies, and the Mississippi River plume [37, 40, 41]. Stations that were chosen and sampled for the DSB cruises (Figure 1) are not a part of SEAMAP stations and instead focused on targeting mesopelagic communities along the continental slope.

Species utilized in this study were selected based on their abundance in DEEPEND and DEEPEND|RESTORE samples (Cruises DP01-DP09), their body condition (i.e., only completely intact specimens were retained), and body size (measured as standard length (SL); selected to cover a range of captured sizes). Specimens from GoMRI cruises were included in the study to ensure the LWRs included larger specimens than were captured by the MOC10. Ultimately, 68 out of 862 fish species collected during these programs occurred in high enough numbers to be included in this study (Table 1), including representatives from the families Bathylagidae, Chlorophthalmidae, Gonostomatidae, Melamphaidae, Melanonidae, Myctophidae, Omosudidae, Paralepididae, Phosichthyidae, Sternoptychidae, and Stomiidae [35]. These 68 species represent 95% of the total abundance of fishes collected over this time period and are likely to represent a substantial portion of the mesopelagic fish biomass of the Gulf of Mexico within the sampled size ranges.

2.2. Measuring Wet and Dry Weights.

Approximately 15–50 individuals per species were chosen, spanning the range of body sizes in the collections. All selected specimens had been fixed previously in 10% formalin before being transferred to 70% ethanol for long-term storage [37]. To be included in the study, specimens needed to be physically intact with minimal damage from capture and storage. If a specimen appeared to have a noticeably full stomach, they were automatically excluded from the study. Measurements to the nearest 0.1 mm were then gathered for head length, body depth, body width, and body SL for each specimen. To obtain preserved wet weight (to the nearest 0.001 g), specimens were cleared of any excess moisture and placed within a preweighed aluminum weigh boat. Each specimen was then placed in a preheated oven at 50°C where they were

Table 1: Species included in study, naming authorities for each species, and available previous LWR studies.

Taxon	Naming authority	No. of individuals in present study	Previous LWR models
Aulopiformes			
Chlorophthalmidae			
Chlorophthalmus agassizi	Bonaparte 1840	28	Northwestern Gulf of Mexico: Chi-Espinola et al. [30]; Indian EEZ: Sreedhar et al. [42]
Omosudidae			
Omosudis lowii	Günther 1887	17	Eastern Tropical North Atlantic: Czudaj et al. [43]; North Atlantic:
Paralepididae			Fock and Ehrich [44]
Lestidiops affinis	(Ege 1930)	15	Fock and Ehrich [44]
Beryciformes			
Melamphaidae			
Melamphaes simus	Ebeling 1962	15	
Scopeloberyx opisthopterus	(Parr 1933)	16	
Scopeloberyx robustus	(Günther 1887)	19	Fock and Ehrich [44]
Gadiformes			
Melanonidae			
Melanonus zugmayeri	Norman 1930	15	Tropical Brazilian Continental Shelf: Eduardo et al. [45]; Fock and Ehrich [44]
Myctophiformes			
Myctophidae			
Benthosema suborbitale	(Gilbert 1913)	57	Fock and Ehrich [44]; equatorial tropical Atlantic: López-Pérez et al. [36]
Bolinichthys photothorax	(Parr 1928)	19	Czudaj et al. [43]; López-Pérez et al. [36]
Bolinichthys supralateralis	(Parr 1928)	18	Czudaj et al. [43]; Fock and Ehrich [44]
Ceratoscopelus warmingii	(Lütken 1892)	71	Czudaj et al. [43]; López-Pérez et al. [36]
Dasyscopelus asper	(Richardarson 1845)	22	Czudaj et al. [43]
Diaphus dumerilii	(Bleeker 1856)	56	Czudaj et al. [43]; Fock and Ehrich [44]; López-Pérez et al. [36]
Diaphus lucidus	(Goode & Beane 1896)	25	
Diaphus mollis	Tåning 1928	44	Czudaj et al. [43]; Eduardo et al. [46]
Diaphus perspicillatus	(Ogilby 1898)	28	López-Pérez et al. [36]
Diaphus problematicus	Parr 1928	23	Czudaj et al. [43]; López-Pérez et al. [36]
Diaphus rafinesquii	(Cocco 1838)	23	Eastern Mediterranean sea: Badouvas et al. [47]; central Mediterranean sea: Battaglia et al. [48]; Fock and Ehrich [44]; López-Pérez et al. [36]
Diaphus splendidus	(Brauer 1904)	33	Eduardo et al. [46]
Diaphus taaningi	Norman 1930	26	
Diaphus termophilus	Tåning 1928	17	
Diogenichthys atlanticus	(Tåning 1928)	29	
Gonichthys cocco	(Cocco 1829)	17	
Hygophum benoiti	(Cocco 1838)	19	Badouvas et al. [47]; Equatorial Atlantic: Olivar et al. [49]
Hygophum hygomii	(Lütken 1892)	33	Badouvas et al. [47]; Fock and Ehrich [44]; Olivar et al. [49]
Hygophum macrochir	(Günther 1864)	26	Czudaj et al. [43]; López-Pérez et al. [36]
Hygophum reinhardtii	(Lütken 1892)	20	
Hygophum taaningi	Becker 1965	29	Czudaj et al. [43]; Eduardo et al. [46]
Lampadena luminosa	(Garman 1899)	20	
Lampanyctus alatus	Goode & Beane 1896	103	López-Pérez et al. [36]
Lampanyctus cuprarius	Tåning 1928	22	
Lampanyctus lineatus	Tåning 1928	26	Czudaj et al. [43]
Lepidophanes guentheri	(Goode & Beane 1896)	27	Czudaj et al. [43]; López-Pérez et al. [36]
Lobianchia gemellarii	(Cocco 1838)	41	Battaglia et al. [48]; Foch & Ehrich [44]
Myctophum affine	(Lütken 1892)	34	López-Pérez et al. [36]
Myctophum nitidulum	Garman 1899	20	Czudaj et al. [43]; López-Pérez et al. [36]
Notolychnus valdiviae	(Brauer 1904)	34	Czudaj et al. [43]; López-Pérez et al. [36]

Table 1: Continued.

Taxon	Naming authority	No. of individuals in present study	Previous LWR models
Notoscopelus resplendens	(Richardardson 1845)	26	Czudaj et al. [43]; López-Pérez et al. [36]
Osmeriformes			
Bathylagidae			
Dolicholagus longirostris	(Maul 1948)	25	Fock and Ehrich [44]
Stomiiformes			
Gonostomatidae			
Cyclothone acclinidens	Garman 1899	50	López-Pérez et al. [36]
Cyclothone alba	Brauer 1906	49	Chi-Espinola et al. [30]
Cyclothone braueri	Jespersen & Tåning 1926	42	Chi-Espinola et al. [30]; Fock and Ehrich [44]; Olivar et al. [49]
Cyclothone obscura	Brauer 1902	41	
Cyclothone pallida	Brauer 1902	49	Fock and Ehrich [44]; López-Pérez et al. [36]
Cyclothone pseudopallida	Mukhacheva 1964	88	Chi-Espinola et al. [30]; López-Pérez et al. [36]
Gonostoma atlanticum	Norman 1930	21	
Margrethia obtusirostra	Jespersen & Tåning 1919	19	Fock and Ehrich [44]
Sigmops elongatus	(Günther 1887)	27	Czudaj et al. [43]; Eduardo et al. [45]; Fock and Ehrich [44]; eastern Gulf of Mexico: Lancraft et al. [32]; López-Pérez et al. [36]
Zaphotias pedaliotus	(Goode & Beane 1896)	17	Eduardo et al. (2019)
Phosichthyidae			
Pollichthys mauli	(Poll 1953)	20	Fock and Ehrich [44]; Olivar et al. [49]
Vinciguerria attenuata	(Cocco 1838)	15	Czudaj et al. [43]; Fock and Ehrich [44]; López-Pérez et al. [36]
Vinciguerria nimbaria	(Jordan & Williams 1895)	19	Battaglia et al. [48]
Vinciguerria poweriae	(Cocco 1838)	21	Eduardo et al. [45]
Sternoptychidae			Czudaj et al. [43]
Argyropelecus aculeatus	Valenciennes 1850	85	Badouvas et al. [47]; Fock and Ehrich [44]; Olivar et al. [49]
Argyropelecus gigas	Norman 1930	20	
Argyropelecus hemigymnus	Cocco 1829	106	
Maurolicus weitzmani	Parin & Kobyliansky 1993	22	
Polyipnus clarus	Harold 1994	20	
Sternoptyx diaphana	Hermann 1781	29	Chi-Espinola et al. [30]; Czudaj et al. [43]; Eduardo et al. [45]; Fock and Ehrich [44]; López-Pérez et al. [36]
Sternoptyx pseudobscura	Baird 1971	37	Eduardo et al. [45]
Valenciennellus tripunctulatus	(Esmark 1871)	30	
Stomiidae			
Astronesthes macropogon	Goodyear & Gibbs 1970	16	Eastern Gulf of Mexico: Sutton & Hopkins [31]
Astronesthes nigra	Richardarson 1845	16	Fock and Ehrich [44]; Sutton & Hopkins [31]
Bathophilus pawneei	Parr 1927	17	Sutton and Hopkins [31]
Chauliodus sloani	Bloch & Schneider 1901	27	Badouvas et al. [47]; Chi-Espinola et al. [30]; Fock and Ehrich [44]; shelf break off southwest Indian EEZ: Jayaprakash et al. [50]; Sutton and Hopkins [31]
Eustomias schmidti	Regan & Trewavas 1930	15	Sutton and Hopkins [31]
Photostomias guernei	Collett 1889	18	Fock & Ehrich [44]; Sutton & Hopkins [31]
Stomias affinis	Günther 1887	29	Czudaj et al. [43]; Sutton & Hopkins [31]

Note: Study location for previous LWRs is listed with the first reference within table.

reweighed every 24 h until the specimen reached a constant dry weight (to the nearest 0.001 g). On average, it took 48–72 h for specimens to reach a consistent dry weight, with a few larger specimens requiring seven to eight days.

2.3. Data Analyses. Each specimen's SL, dry weight, and preserved wet weight were used in estimating individual species' length–weight parameters following the logarithmic form of equation (1):

$$W = aSL^{b}, \tag{1}$$

where W = wet- or dry weight (g), SL = standard length (cm), a = initial growth index (intercept), and b = allometric growth coefficient (slope).

A simple linear regression model was used to estimate the initial growth index (a) and the allometric growth coefficient (b) in R software 4.4.2 [51] utilizing the *lm()* function. To calculate family-level LWR estimates, species SL and weight data from each family with more than one represented species were pooled together and the wet- and dry-weight-derived LWRs for each family were calculated using the same methodology as used for the calculation of individual species' LWRs. A genus-level LWR was also estimated for the numerically dominant taxon *Cyclothone*, using the same methodology applied to both the family-level and individual species-level LWRs.

2.4. Test of Growth Forms. After the LWRs were estimated, each species' growth model was evaluated using the "hoCoef" test in the R package FSA [52]. The function "hoCoef" in the context of this study performed a hypothesis test to determine whether the allometric growth coefficient (b) was equal to, greater than, or less than three, where three indicates the mathematical relationship between a volume (represented by weight in the current study) and a measurement of length [52]. If a species' allometric growth coefficient was determined to not be significantly different than three, then it was determined to have isometric growth; otherwise, it was considered to exhibit negative or positive allometric growth if it was less than or greater than three, respectively.

2.5. Water Content Estimations and Relationship With Length. Water content estimations were calculated using ethanol-fixed specimens [37]. Once a dry weight was determined for each specimen, this value along with the initial preserved wet weight (g) was used to estimate the percentage of water content lost during the drying process:

$$\text{Ind.H}_2\text{O Content} = 1 - \left(\frac{\text{dry weight}}{\text{wet weight}}\right). \tag{2}$$

Utilizing this calculation and the dry-weight measurement of approximately 15–50 specimens per species, an approximate water content percentage was estimated. A water content estimation was similarly calculated at the family level by integrating the water content percentages across all confamilial species. Because water content calculations were based on ethanol-fixed specimens, values are viewed as approximations.

The correlation between SL and water content was also reported. Linear (Equation S1) or curvilinear (quadratic: Equation S2 or asymptotic: Equation S3) regressions were fitted for each species as appropriate. Where potential curvilinear relationships were suspected, corrected Akaike information criteria (AICc) was used to determine the best fitting model (Table S1). All simple linear regressions were performed using the *lm()* function and the nonlinear models using the *nls()* function within R software 4.4.2 [51].

3. Results

3.1. Species-Level LWRs. A total of 2122 specimens from 68 species were measured in this study, representing six orders and 11 families: Gonostomatidae (10 species), Melamphaidae (3 species), Myctophidae (31 species), Phosichthyidae (4 species), Sternoptychidae (8 species), and Stomiidae (7 species). One species each was studied from the remaining families (Bathylagidae, Chlorophthalmidae, Melanonidae, Omosudidae, and Paralepididae (Table 1).

All dry-weight regressions (LWR_{DW}) created in this study showed highly significant ($p < 0.01$), strong relationships between SL and dry weight, with R^2 values ranging from 0.901–0.997 (Figures 2 and 3, Table 2). The wet-weight regressions (LWR_{WW}) created in this study showed highly significant ($p < 0.01$) relationships between SL and wet weight (Table 3). R^2 values ranged from 0.625–0.995, with 59 species (87%) having an R^2 value > 0.90 (Table 3).

Allometric growth coefficient values (b) for LWR_{DW} (Figures 2 and 3, Table 2) ranged from 2.17–4.17 across species, with LWR_{WW} b values ranging from 2.12–3.68 (Table 3). The growth index (a) values for LWR_{DW} (Figures 2 and 3, Table 2) ranged from 3.52×10^{-5}–6.24×10^{-3} and ranged from 2.14×10^{-3}–6.20×10^{-2} for LWR_{WW} (Table 3). Most species represented in this study exhibited isometric growth based on LWR_{DW} (36 species; Figures 2 and 3, Table 2) and LWR_{WW} (39 species; Table 3). Positive allometric growth was the next most common growth form (LWR_{DW}: 28 species; LWR_{WW}: 16 species), with the remaining species exhibiting negative allometric growth (Figures 2 and 3, Tables 2 and 3). Additional data for each species, including SL range (cm), sample size (n), growth model, and R^2 values for both LWR_{DW} and LWR_{WW}, are shown in Tables 2 and 3, respectively.

3.2. Family Results. Out of the six families in this study that had more than one representative species, the majority of both LWR_{DW} and LWR_{WW} models exhibited either isometric or positive allometric growth (Figures 2 and 4, Tables 2 and 3). One family exhibited isometric growth for both the LWR_{DW} and the LWR_{WW} (Phosichthyidae; Figures 2 and 4, Tables 2 and 3). The family Myctophidae exhibited positive allometric growth for both the LWR_{DW} and the LWR_{WW} (Figures 2 and 4, Tables 2 and 3). The Stomiidae family was the only family to exhibit negative allometric growth, and this was true for both the LWR_{DW} and the LWR_{WW} (Figures 2 and 4, Tables 2 and 3). The remaining families for the LWR_{DW} models exhibited

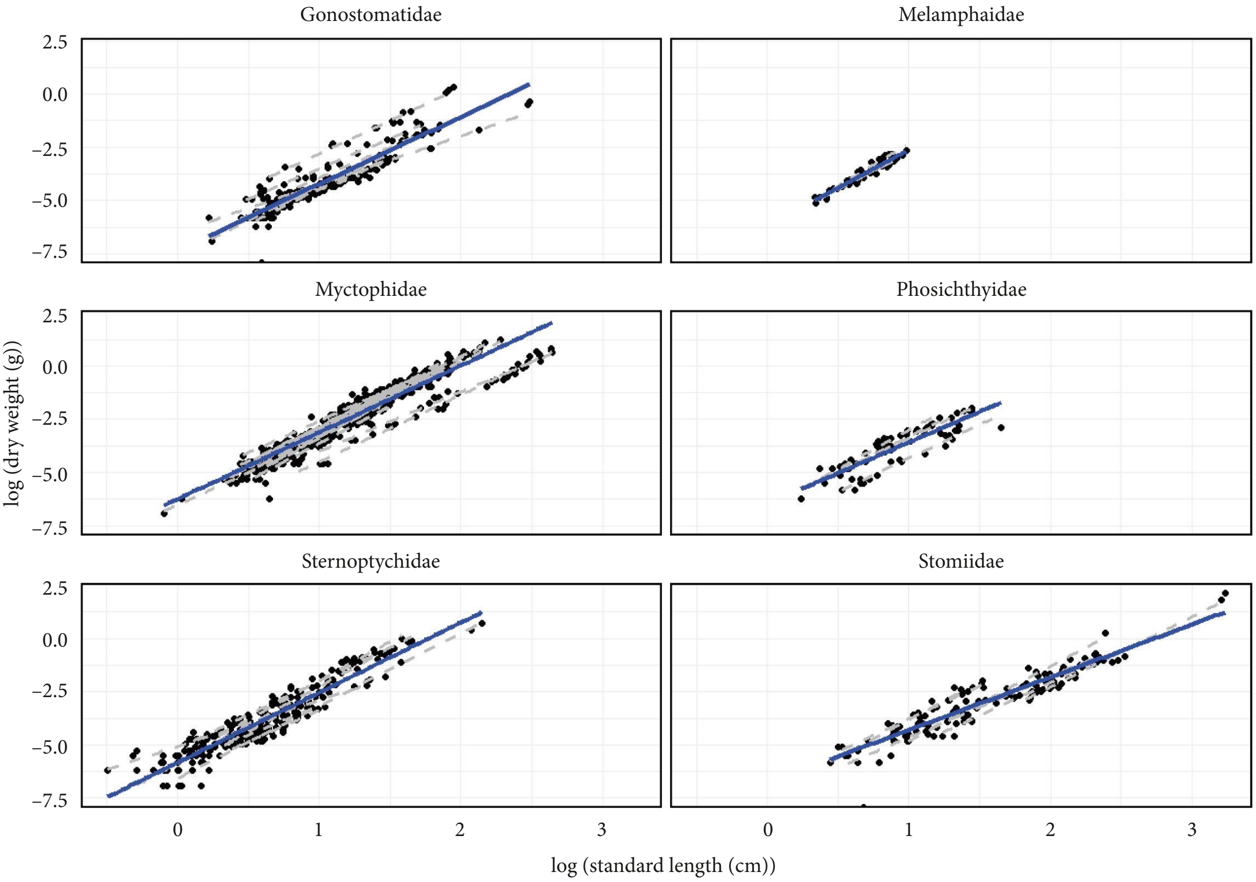

Figure 2: Standard length–dry-weight regressions for six mesopelagic fish families in the Gulf of Mexico that were represented by more than one species in the present study: Gonostomatidae (10 species), Melamphaidae (3 species), Myctophidae (31 species), Phosichthyidae (4 species), Sternoptychidae (8 species), and Stomiidae (7 species). The dashed grey lines represent the individual species length–weight regressions, while the solid blue lines represent the length–weight regression for the family as a whole.

either isometric growth (Gonostomatidae) or positive allometric growth (Melamphaidae and Sternoptychidae; Figures 2 and 4, Table 2). These families also exhibited either isometric growth (Melamphaidae and Sternoptychidae) or positive allometric growth (Gonostomatidae) for the $\mathrm{LWR}_{\mathrm{WW}}$ models (Table 3). Allometric growth coefficients (*b*) for familial $\mathrm{LWR}_{\mathrm{DW}}$ ranged from 2.49–3.58 with $\mathrm{LWR}_{\mathrm{WW}}$ *b* values ranging from 2.45–3.23 (Figures 2 and 4, Table 2). Growth index values (*a*) for $\mathrm{LWR}_{\mathrm{DW}}$ across families ranged from 6.37×10^{-4}–2.81×10^{-3}, and *a* values for the $\mathrm{LWR}_{\mathrm{WW}}$ ranged from 3.36–10^{-3}–2.87×10^{-2} (Figures 2 and 4, Tables 2 and 3). Additional data for each family, including SL ranges (cm), sample size (n), and estimated water content percentage for both $\mathrm{LWR}_{\mathrm{DW}}$ and $\mathrm{LWR}_{\mathrm{WW}}$, are shown in Tables 2 and 3, respectively.

3.3. *Differences in Species- and Family-Level LWRs.*

Species in the family Myctophidae were largely similar in terms of their LWRs except for two species: *Lampanyctus cuprarius* Tåning 1928 and *Lampanyctus lineatus* Tåning 1928 (Figure 2, Tables 2 and 3). The LWRs of *L. cuprarius* and *L. lineatus* are notably shifted downwards compared to the rest of the Myctophids (Figure 2) despite the fact that their initial growth indexes and allometric growth coefficients are largely similar to the rest of the family (Tables 2 and 3). The size ranges of *L. cuprarius* and *L. lineatus* are also comparable to the rest of the family, but they weighed relatively less overall which caused their respective LWRs to shift downward (Figure 2). Another case of this downward shift is in *Pollichthys mauli* (Poll 1953) which, in the present study, is the only species that is not a member of the genus *Vinciguerria* in the family Phosichthyidae (Figure 2). The LWR for the family Phosichthyidae shows that *P. mauli* tended to weigh relatively less than the members of the genus *Vinciguerria*, despite having a similar range of SLs which shifted its LWR downwards in comparison (Figure 2).

In the family Gonostomatidae, members of the genus *Cyclothone* and the species *Sigmops elongatus* were similar in terms of their LWRs (Figure 2). The other species of the family Gonostomatidae; *Gonostoma atlanticum* Norman 1930, *Margrethia obtusirostra* Jespersen & Tåning 1919, and *Zaphotias pedaliotus* (Goode & Beane 1896) differed compared to the general trend seen in the family (Figure 2). *Gonostoma atlanticum*, *M. obtusirostra,* and *Z. pedaliotus* were generally heavier than other members of the family which caused their LWRs to be shifted upward in comparison with *Cyclothone* spp. and *S. elongatus* (Figure 2).

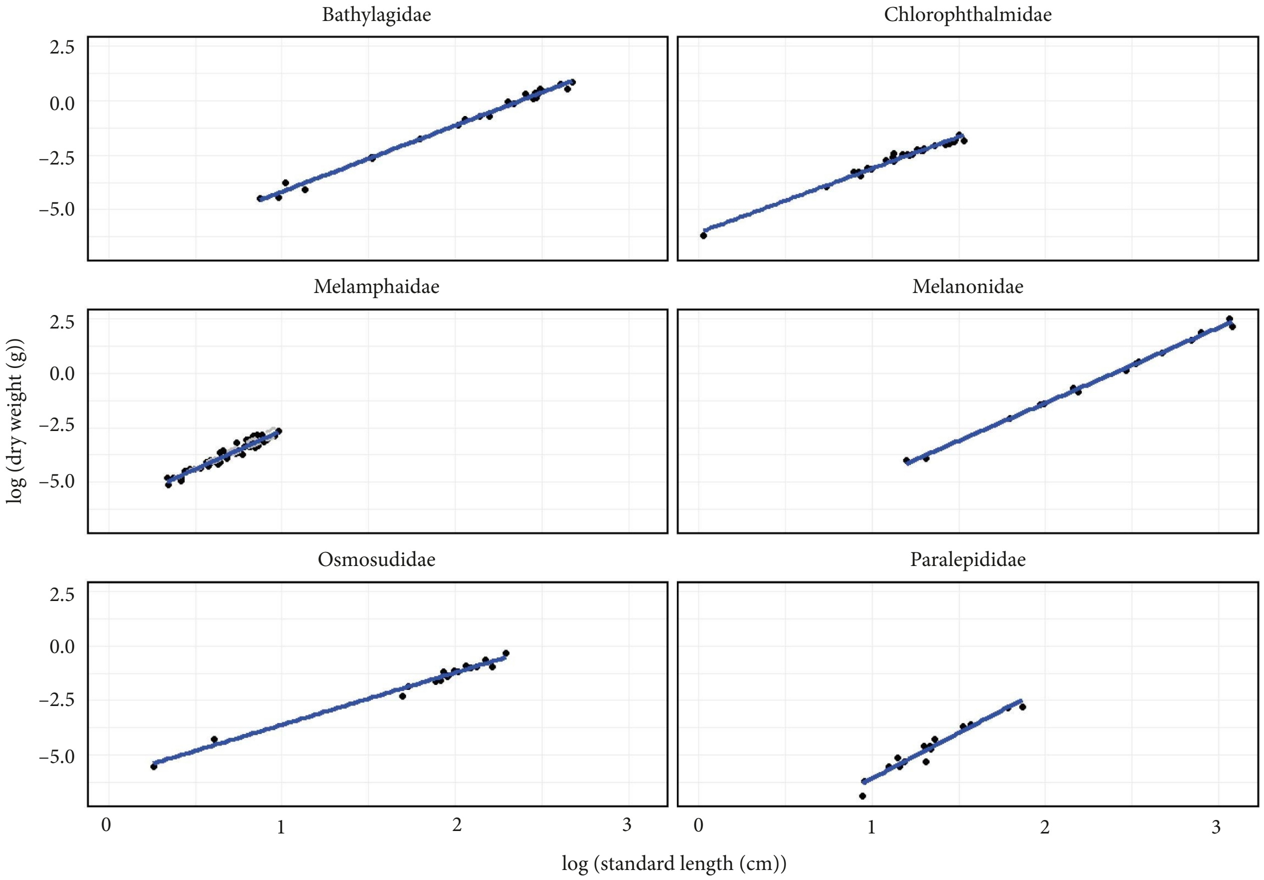

Figure 3: Standard length–dry-weight regressions for five mesopelagic fish families in the Gulf of Mexico that were represented by a single species in the present study: Bathylagidae (*Dolicholagus longirostris*), chlorophthalmidae (*Chlorophthalmus agassizi*), melanonidae (*Melanonus zugmayeri*), omosudidae (*Omosudis lowii*), and paralepididae (*Lestidiops affinis*).

Sternoptyx diaphana Hermann 1781 is the only species to show a significant departure from the family-level LWR for the family Sternoptychidae (Figure 2). This departure was the result of *S. diaphana* exhibiting a smaller allometric growth coefficient ($b_{DW} = 2.17$; $b_{WW} = 2.12$) than the other representative species (Tables 2 and 3). Additionally, it should be noted that their allometric growth coefficient fell outside the normal range for fishes (2.5–3.5; Froese, 2006) for both its wet-weight- and dry-weight-derived estimates (Tables 2 and 3).

The species-level LWRs for members of the family Stomiidae largely differed from the family-level estimate (Figure 2, Tables 2 and 3). This was due to the large differences in size and initial growth index values exhibited by the members of this taxon. For instance, many specimens of the species *Eustomias schmidti* Regan & Trewavas 1930 in this study were over 20 cm larger than the largest representatives from the species *Astronesthes nigra* Richardson 1845 and *Astronesthes macropogon* Goodyear & Gibbs 1970 which exhibit shorter SLs and lower weights than the rest of the family Stomiidae (Table 2). Additionally, the family displayed a relatively large range in initial growth indexes among its members (a_{DW}: 1.37×10^{-4} to 1.03×10^{-3}; Tables 2 and 3) which resulted in a greater "spread" in LWRs.

3.4. Water Content Estimations.

Estimated percent water content ranged from an arithmetic mean of 75.49%–90.34%, with the myctophid *Gonichthys cocco* (Cocco 1829) exhibiting the lowest value and *Cyclothone obscura* Brauer 1902 exhibiting the highest value (Table 2). Water content was also estimated for each family that had more than one representative species and exhibited a range of 78.53%–86.46% (Table 2). Water content estimates were highest within the families Stomiidae, Sternoptychidae, and Gonostomatidae, with the lowest estimates being within the family Myctophidae.

3.5. Length–Water Content Relationships.

After model selection, 62 species were modeled using a simple linear regression, three species using an exponential asymptotic model, and three species were modeled using a quadratic model (Table S1). SL was significantly linearly correlated with water content ($p < 0.05$) in 37 out of the 68 species examined (Tables S2, S3, and S4). R^2 values for significant length–water content models ranged from 0.824 (*Melamphaes simus* Ebeling 1962) to 0.138 (*Cyclothone pallida* Brauer 1902), which indicates large variations in fit between examined species (Table S2). Of the 37 significant linear models, the relationship between SL and water content was

Table 2: Length–weight parameters for analyzed specimens using specimen dry weights.

Taxon	Median SL range (mm)	n	aDW (95% CI)	bDW (95% CI)	Growth model	R^2	Mean water content
Aulopiformes							
Chlorophthalmidae							
Chlorophthalmus agassizi	39.30 (10.30–46.20)	28	2.34×10^{-3} (1.89×10^{-3}, 2.91×10^{-3})	2.94 (2.76, 3.12)	i	0.977	81.73 (77.30–84.70)
Omosudidae							
Omosudis lowii	38.40 (13.00–99.20)	17	2.44×10^{-3} (1.76×10^{-3}, 3.40×10^{-3})	2.40 (2.22, 2.57)	−a	0.982	87.99 (87.00–91.70)
Paralepididae							
Lestidiops affinis	35.65 (25.70–64.80)	15	3.52×10^{-5} (1.52×10^{-5}, 8.12×10^{-5})	4.17 (3.54, 4.79)	+a	0.938	80.53 (72.50–91.70)
Beryciformes							
Melamphaidae	35.45 (14.00–26.70)	50	2.01×10^{-3} (1.61×10^{-3}, 2.51×10^{-3})	3.58 (3.27, 3.89)	+a	0.923	82.21 (76.80–88.20)
Melamphaes simus	35.20 (14.00–26.70)	15	1.81×10^{-3} (1.38×10^{-3}, 2.37×10^{-3})	3.98 (3.59, 4.36)	+a	0.971	81.87 (77.80–88.20)
Scopeloberyx opisthopterus	32.95 (18.00–26.01)	16	2.52×10^{-3} (1.62×10^{-3}, 3.93×10^{-3})	3.18 (2.59, 3.77)	i	0.906	80.88 (76.80–82.80)
Scopeloberyx robustus	35.45 (14.50–24.50)	19	2.05×10^{-3} (1.58×10^{-3}, 2.66×10^{-3})	3.41 (3.03, 3.79)	+a	0.965	84.42 (80.80–87.50)
Gadiformes							
Melanonidae							
Melanonus zugmayeri	38.30 (33.10–216.90)	15	2.45×10^{-4} (1.18×10^{-4}, 3.25×10^{-4})	3.47 (3.35, 3.59)	+a	0.997	85.86 (82.40–89.80)
Myctophiformes							
Myctophidae	29.70 (9.10–141.00)	1002	2.00×10^{-3} (1.83×10^{-3}, 2.18×10^{-3})	3.11 (3.05, 3.18)	+a	0.912	78.53 (69.90–95.20)
Benthosema suborbitale	20.50 (14.50–30.60)	57	1.43×10^{-3} (1.24×10^{-3}, 1.65×10^{-3})	3.53 (3.36, 3.71)	+a	0.969	78.27 (74.40–86.70)
Bolinichthys photothorax	38.80 (17.60–63.50)	19	1.20×10^{-3} (9.79×10^{-4}, 1.47×10^{-3})	3.54 (3.39, 3.69)	+a	0.992	80.41 (77.60–89.90)
Bolinichthys supralateralis	37.60 (22.50–68.90)	18	1.79×10^{-3} (1.14×10^{-3}, 2.80×10^{-3})	3.29 (2.98, 3.60)	i	0.969	81.62 (78.50–84.90)
Ceratoscopelus warmingii	29.00 (18.90–60.10)	71	9.20×10^{-4} (7.94×10^{-4}, 1.07×10^{-3})	3.59 (3.45, 3.74)	+a	0.981	78.74 (74.80–83.00)
Dasyscopelus asper	42.65 (29.80–67.60)	22	1.11×10^{-3} (6.46×10^{-4}, 1.90×10^{-3})	3.75 (3.38,4.12)	+a	0.955	76.21 (70.50–84.60)
Diaphus dumerilii	24.00 (17.10–65.60)	56	2.06×10^{-3} (1.84×10^{-3}, 2.31×10^{-3})	3.18 (3.09, 3.28)	+a	0.988	77.08 (71.70–83.80)
Diaphus lucidus	36.25 (25.80–87.50)	25	1.94×10^{-3} (1.20×10^{-3}, 3.14×10^{-3})	3.35 (3.05, 3.64)	+a	0.959	76.15 (70.50–83.70)
Diaphus mollis	27.90 (17.10–52.80)	44	2.20×10^{-3} (1.75×10^{-3}, 2.78×10^{-3})	3.22 (3.05, 3.39)	+a	0.975	78.09 (74.50–80.80)
Diaphus perspicillatus	34.80 (27.90–57.50)	28	4.05×10^{-3} (2.85×10^{-3}, 5.77×10^{-3})	2.95 (2.71, 3.18)	i	0.961	77.67 (75.30–81.80)
Diaphus problematicus	33.85 (40.80–69.80)	23	3.94×10^{-3} (2.62×10^{-3}, 5.92×10^{-3})	2.90 (2.66, 3.15)	i	0.965	77.92 (74.30–81.20)
Diaphus rafinesquii	28.70 (15.90–84.20)	23	3.86×10^{-3} (2.58×10^{-3}, 5.76×10^{-3})	2.98 (2.72, 3.24)	i	0.968	78.69 (75.70–81.90)
Diaphus splendidus	38.70 (28.20–74.40)	32	1.25×10^{-3} (7.85×10^{-4}, 1.99×10^{-3})	3.45 (3.14, 3.76)	+a	0.944	78.66 (72.80–84.10)
Diaphus taaningi	51.60 (39.50–61.90)	26	2.63×10^{-3} (1.42×10^{-3}, 4.87×10^{-3})	3.15 (2.78, 3.53)	i	0.923	76.36 (73.00–79.60)
Diaphus termophilus	30.00 (18.10–38.70)	17	2.30×10^{-3} (1.78×10^{-3}, 2.97×10^{-3})	2.96 (2.71, 3.22)	i	0.974	81.89 (77.40–85.30)
Diogenichthys atlanticus	32.40 (13.80–29.80)	29	1.42×10^{-3} (1.11×10^{-3}, 1.81×10^{-3})	3.84 (3.46, 4.22)	+a	0.950	81.58 (74.80–88.90)
Gonichthys cocco	37.3 (20.00–52.30)	17	1.01×10^{-3} (7.42×10^{-4}, 1.39×10^{-3})	3.55 (3.33, 3.77)	+a	0.986	73.95 (69.90–86.70)
Hygophum benoiti	36.20 (15.00–39.80)	19	1.40×10^{-3} (9.95×10^{-4}, 1.96×10^{-3})	3.64 (3.15, 4.13)	+a	0.932	79.69 (73.50–84.60)
Hygophum hygomii	38.10 (19.60–58.80)	33	2.42×10^{-3} (1.81×10^{-3}, 3.24×10^{-3})	3.12 (2.92, 3.32)	i	0.974	80.04 (77.10–83.00)
Hygophum macrochir	42.55 (29.70–51.50)	26	4.06×10^{-3} (2.52×10^{-3}, 6.55×10^{-3})	2.75 (2.40, 3.10)	i	0.913	80.02 (78.60–83.20)
Hygophum reinhardtii	34.60 (25.40–50.00)	21	1.22×10^{-3} (7.12×10^{-4}, 2.10×10^{-3})	3.51 (3.11, 3.91)	+a	0.950	78.19 (72.10–81.70)
Hygophum taaningi	25.20 (15.60–49.90)	29	3.07×10^{-3} (2.14×10^{-3}, 3.22×10^{-3})	3.13 (2.97, 3.30)	i	0.982	77.91 (71.40–82.90)
Lampadena luminosa	38.80 (21.00–97.90)	20	1.11×10^{-3} (8.80×10^{-4}, 1.04×10^{-2})	3.49 (3.32, 3.65)	+a	0.990	81.09 (73.50–85.40)
Lampanyctus alatus	33.25 (16.30–52.10)	103	8.50×10^{-4} (5.43×10^{-4}, 1.33×10^{-3})	3.44 (3.06, 3.83)	+a	0.925	76.57 (73.90–82.70)
Lampanyctus cuprarius	29.90 (27.20–139.50)	22	1.12×10^{-3} (6.70×10^{-4}, 1.86×10^{-3})	2.79 (2.54, 3.04)	i	0.967	84.60 (80.00–88.30)
Lampanyctus lineatus	25.50 (23.50–141.00)	26	5.84×10^{-4} (4.62×10^{-4}, 7.37×10^{-4})	3.06 (2.95, 3.17)	i	0.992	84.24 (78.80–86.50)
Lepidophanes guentheri	27.00 (17.30–44.50)	27	7.99×10^{-4} (6.55×10^{-4}, 9.75×10^{-4})	3.51 (3.31, 3.72)	+a	0.981	78.88 (73.70–89.40)
Lobianchia gemellarii	43.40 (18.80–57.70)	41	1.71×10^{-3} (1.15×10^{-3}, 2.53×10^{-3})	3.52 (3.23, 3.80)	+a	0.952	77.43 (72.10–84.50)

Table 2: Continued.

Taxon	Median SL range (mm)	*n*	aDW (95% CI)	bDW (95% CI)	Growth model	R^2	Mean water content
Myctophum affine	21.80 (16.00–45.20)	34	1.06×10^{-3} (9.04×10^{-4}, 1.25×10^{-3})	3.75 (3.59, 3.91)	+a	0.985	76.47 (71.80–85.40)
Myctophum nitidulum	31.40 (21.50–68.40)	20	1.40×10^{-3} (7.90×10^{-4}, 2.48×10^{-3})	3.48 (3.07, 3.90)	+a	0.943	77.27 (70.90–82.80)
Notolychnus valdiviae	26.40 (9.10–38.50)	34	1.41×10^{-3} (1.19×10^{-3}, 1.68×10^{-3})	3.18 (2.88, 3.49)	i	0.951	76.00 (70.00–95.20)
Notoscopelus resplendens	37.65 (24.90–68.80)	26	1.77×10^{-3} (1.06×10^{-3}, 2.94×10^{-3})	3.22 (2.91, 3.53)	i	0.953	77.28 (73.80–84.70)
Osmeriformes							
Bathylagidae							
Dolicholagus longirostris	31.90 (23.90–144.80)	25	7.28×10^{-4} (5.69×10^{-4}, 9.31×10^{-4})	3.04 (2.93, 3.16)	i	0.992	86.01 (83.40–89.80)
Stomiiformes							
Gonostomatidae	29.90 (12.50–120.50)	400	6.37×10^{-4} (5.41×10^{-4}, 7.50×10^{-4})	3.04 (2.89, 3.19)	i	0.799	83.64 (67.60–93.60)
Cyclothone acclinidens	38.60 (20.50–42.60)	50	7.58×10^{-4} (5.38×10^{-4}, 1.07×10^{-3})	2.73 (2.40, 3.06)	i	0.909	86.85 (68.20–93.60)
Cyclothone alba	22.00 (12.70–27.00)	49	5.06×10^{-4} (4.23×10^{-4}, 6.07×10^{-4})	3.29 (3.07, 3.52)	+a	0.970	79.62 (73.70–87.50)
Cyclothone braueri	22.80 (15.60–25.60)	42	8.25×10^{-4} (6.27×10^{-4}, 1.08×10^{-3})	2.77 (2.40, 3.14)	i	0.905	79.30 (74.30–86.40)
Cyclothone obscura	33.60 (18.10–47.20)	41	6.02×10^{-4} (4.59×10^{-4}, 7.90×10^{-4})	2.93 (2.72, 3.14)	i	0.971	90.34 (88.00–92.60)
Cyclothone pallida	21.45 (15.80–43.60)	49	4.18×10^{-4} (3.27×10^{-4}, 5.33×10^{-4})	3.33 (3.07, 3.59)	+a	0.938	82.22 (67.60–90.90)
Cyclothone pseudopallida	22.00 (17.30–38.20)	88	1.10×10^{-3} (9.65×10^{-4}, 1.24×10^{-3})	2.32 (2.18, 2.46)	-a	0.972	83.42 (74.10–92.70)
Gonostoma atlanticum	34.60 (23.40–64.00)	21	1.12×10^{-3} (5.73×10^{-4}, 2.20×10^{-3})	2.86 (2.40, 3.31)	i	0.901	81.97 (77.90–85.60)
Margrethia obtusirostra	36.85 (19.10–70.00)	16	2.66×10^{-3} (1.97×10^{-3}, 3.59×10^{-3})	3.12 (2.91, 3.32)	i	0.986	82.08 (77.60–85.30)
Sigmops elongatus	26.50 (12.50–120.50)	27	1.50×10^{-3} (1.21×10^{-3}, 1.87×10^{-3})	2.26 (2.09, 2.44)	-a	0.965	83.00 (72.00–87.90)
Zaphotias pedaliotus	32.30 (16.20–62.70)	17	1.79×10^{-3} (1.33×10^{-3}, 2.40×10^{-3})	2.83 (2.55, 3.10)	i	0.971	80.96 (75.80–89.30)
Phosichthyidae	33.00 (12.70–52.00)	75	1.60×10^{-3} (1.09×10^{-3}, 2.33×10^{-3})	2.84 (2.45, 3.22)	i	0.744	81.95 (75.80–89.30)
Pollichthys mauli	34.10 (17.00–52.00)	20	5.69×10^{-4} (3.88×10^{-4}, 8.37×10^{-4})	3.15 (2.78, 3.52)	i	0.944	83.24 (75.80–89.30)
Vinciguerria attenuate	33.90 (16.80–42.50)	15	1.46×10^{-3} (9.70×10^{-4}, 2.19×10^{-3})	3.15 (2.79, 3.50)	i	0.963	82.70 (80.00–87.50)
Vinciguerria nimbaria	35.10 (18.70–39.80)	19	1.24×10^{-3} (7.78×10^{-4}, 1.99×10^{-3})	3.37 (2.88, 3.86)	i	0.936	81.50 (76.80–86.50)
Vinciguerria poweriae	33.10 (12.70–32.30)	21	1.29×10^{-3} (9.17×10^{-4}, 1.82×10^{-3})	3.65 (3.18, 4.11)	i	0.931	80.95 (77.30–86.40)
Sternoptychidae	31.10 (6.10–86.00)	350	2.95×10^{-3} (2.62×10^{-3}, 3.31×10^{-3})	3.29 (3.14, 3.44)	+a	0.882	85.21 (71.50–98.10)
Argyropelecus aculeatus	27.70 (7.50–43.10)	85	2.87×10^{-3} (2.53×10^{-3}, 3.24×10^{-3})	3.59 (3.36, 3.84)	+a	0.932	87.01 (75.00–98.10)
Argyropelecus gigas	34.45 (10.10–86.00)	17	1.40×10^{-3} (1.02×10^{-3}, 1.91×10^{-3})	3.42 (3.14, 3.70)	+a	0.977	88.62 (83.60–97.40)
Argyropelecus hemigymnus	35.50 (14.40–29.00)	106	2.06×10^{-3} (1.54×10^{-3}, 2.76×10^{-3})	3.59 (3.19, 3.99)	+a	0.938	82.78 (81.10–90.80)
Maurolicus weitzmani	27.90 (13.90–25.90)	22	2.70×10^{-3} (2.15×10^{-3}, 3.39×10^{-3})	2.75 (2.37, 3.13)	i	0.916	80.90 (74.20–85.10)
Polyipnus clarus	32.70 (13.40–48.80)	20	3.53×10^{-3} (2.89×10^{-3}, 4.31×10^{-3})	3.67 (3.43, 3.91)	+a	0.982	82.56 (71.50–87.60)
Sternoptyx diaphana	35.50 (6.10–40.1)	29	6.24×10^{-3} (5.34×10^{-3}, 7.30×10^{-3})	2.17 (1.91,2.44)	-a	0.922	89.49 (81.50–94.10)
Sternoptyx pseudobscura	29.90 (11.20–52.30)	37	5.72×10^{-3} (4.59×10^{-3}, 7.14×10^{-3})	3.16 (2.96, 3.37)	i	0.965	88.26 (86.10–91.70)
Valenciennellus tripunctulatus	31.80 (14.70–28.40)	21	1.77×10^{-3} (1.35×10^{-3}, 2.32×10^{-3})	2.96 (2.57, 3.35)	i	0.904	78.08 (75.80–88.40)
Stomiidae	30.60 (17.00–46.10)	128	1.11×10^{-3} (8.66×10^{-4}, 1.43×10^{-3})	2.49 (2.33, 2.64)	-a	0.894	86.45 (80.00–92.60)
Astronesthes macropogon	36.80 (17.00–46.10)	16	1.03×10^{-3} (7.06×10^{-4}, 1.51×10^{-3})	3.10 (2.79, 3.40)	i	0.969	86.43 (85.00–89.50)
Astronesthes niger	32.55 (15.60–39.20)	15	6.25×10^{-4} (3.59×10^{-4}, 1.09×10^{-3})	3.56 (2.98, 4.13)	i	0.927	87.35 (80.20–92.50)
Bathophilus pawneei	32.75 (27.20–108.70)	17	2.34×10^{-4} (9.98×10^{-5}, 5.49×10^{-4})	3.53 (2.96, 4.09)	i	0.917	88.98 (86.10–92.60)
Chauliodus sloani	32.00 (17.70–101.10)	22	5.54×10^{-4} (4.02×10^{-4}, 7.61×10^{-4})	2.85 (2.62, 3.08)	i	0.969	85.42 (80.00–90.00)
Eustomias schmidti	78.30 (62.10–253.60)	15	1.37×10^{-4} (6.30×10^{-5}, 2.97×10^{-4})	3.31 (2.97, 3.64)	i	0.970	89.59 (87.40–91.30)
Photostomias guernei	57.00 (46.70–101.50)	18	6.79×10^{-4} (2.83×10^{-4}, 1.63×10^{-3})	2.76 (2.31, 3.21)	i	0.907	86.25 (83.50–88.50)
Stomias affinis	23.65 (19.70–107.30)	25	3.69×10^{-4} (2.34×10^{-4}, 5.82×10^{-4})	2.92 (2.68, 3.16)	i	0.965	83.41 (81.00–86.40)

Note: n: sample size, R^2: coefficient of determination. Growth models: +a: positive allometry ($b > 3$), −a: negative allometry ($b < 3$), and i: isometry ($b = 3$). Estimated mean water content percentage and range for each study species and family.

Abbreviation: SL, standard length.

Table 3: Length–weight parameters for analyzed specimens using specimen preservative wet weights.

Taxon	Median SL range (mm)	*n*	aWW (95% CI)	bWW (95% CI)	Growth model	R^2
Aulopiformes						
Chlorophthalmidae						
Chlorophthalmus agassizi	39.30 (10.30–46.20)	28	1.49×10^{-2} (1.09×10^{-2}, 2.03×10^{-2})	2.81 (2.55, 3.07)	i	0.948
Omosudidae						
Omosudis lowii	38.40 (13.00–99.20)	17	2.59×10^{-2} (1.98×10^{-2}, 3.39×10^{-2})	2.27 (2.13, 2.24)	-a	0.987
Paralepididae						
Lestidiops affinis	35.65 (25.70–64.80)	15	3.84×10^{-4} (1.82×10^{-4}, 8.11×10^{-4})	3.62 (3.07, 4.18)	+a	0.934
Beryciformes						
Melamphaidae	35.45 (14.00–26.70)	50	1.93×10^{-2} (1.58×10^{-2}, 2.36×10^{-2})	2.84 (2.56, 3.12)	i	0.902
Melamphaes simus	35.20 (14.00–26.70)	15	1.92×10^{-2} (1.51×10^{-2}, 2.44×10^{-2})	3.02 (2.68, 3.36)	i	0.963
Scopeloberyx opisthopterus	32.95 (18.00–26.01)	16	1.79×10^{-2} (1.08×10^{-2}, 2.96×10^{-2})	2.78 (2.11, 3.45)	i	0.850
Scopeloberyx robustus	35.45 (14.50–24.50)	19	1.76×10^{-2} (1.37×10^{-2}, 2.26×10^{-2})	2.99 (2.63, 3.36)	i	0.957
Gadiformes						
Melanonidae						
Melanonus zugmayeri	38.30 (33.10–216.90)	15	2.69×10^{-3} (1.95×10^{-3}, 3.73×10^{-3})	3.29 (3.15, 3.42)	+a	0.995
Myctophiformes						
Myctophidae	29.70 (9.10–141.00)	1002	9.58×10^{-3} (8.88×10^{-3}, 1.04×10^{-2})	3.08 (3.04, 3.16)	+a	0.925
Benthosema suborbitale	20.50 (14.50–30.60)	57	9.03×10^{-3} (8.04×10^{-3}, 1.01×10^{-2})	3.15 (3.01, 3.29)	+a	0.973
Bolinichthys photothorax	38.80 (17.60–63.50)	19	6.79×10^{-3} (5.05×10^{-3}, 9.13×10^{-3})	3.47 (3.24, 3.69)	+a	0.983
Bolinichthys supralateralis	37.60 (22.50–68.90)	18	1.20×10^{-2} (7.69×10^{-3}, 1.87×10^{-2})	3.14 (2.84, 3.45)	i	0.968
Ceratoscopelus warmingii	29.00 (18.90–60.10)	71	5.06×10^{-3} (4.41×10^{-3}, 5.80×10^{-3})	3.44 (3.31, 3.57)	+a	0.982
Dasyscopelus asper	42.65 (29.80–67.60)	22	5.20×10^{-3} (2.74×10^{-3}, 9.88×10^{-3})	3.68 (3.24,4.12)	+a	0.935
Diaphus dumerilii	24.00 (17.10–65.60)	56	9.29×10^{-3} (8.49×10^{-3}, 1.02×10^{-2})	3.16 (3.08, 3.23)	+a	0.993
Diaphus lucidus	36.25 (25.80–87.50)	25	1.96×10^{-2} (1.31×10^{-2}, 2.96×10^{-2})	2.83 (2.58, 3.08)	i	0.956
Diaphus mollis	27.90 (17.10–52.80)	44	9.58×10^{-3} (7.52×10^{-3}, 1.22×10^{-2})	3.26 (3.08, 3.44)	+a	0.973
Diaphus perspicillatus	34.80 (27.90–57.50)	28	2.54×10^{-2} (1.78×10^{-2}, 3.64×10^{-2})	2.73 (2.49, 2.96)	−a	0.954
Diaphus problematicus	33.85 (40.80–69.80)	23	2.66×10^{-2} (1.65×10^{-2}, 4.30×10^{-2})	2.66 (2.37, 2.95)	−a	0.943
Diaphus rafinesquii	28.70 (15.90–84.20)	23	2.10×10^{-2} (1.43×10^{-2}, 3.08×10^{-2})	2.88 (2.63, 3.12)	i	0.969
Diaphus splendidus	38.70 (28.20–74.40)	32	9.03×10^{-3} (5.71×10^{-3}, 1.43×10^{-2})	3.17 (2.86, 3.47)	i	0.936
Diaphus taaningi	51.60 (39.50–61.90)	26	1.81×10^{-2} (1.18×10^{-2}, 2.77×10^{-2})	2.86 (2.60, 3.12)	i	0.954
Diaphus termophilus	30.00 (18.10–38.70)	17	1.65×10^{-2} (1.28×10^{-2}, 2.13×10^{-2})	2.70 (2.44, 2.95)	−a	0.970
Diogenichthys atlanticus	32.40 (13.80–29.80)	29	1.51×10^{-2} (1.16×10^{-2}, 1.96×10^{-2})	2.78 (2.37, 3.19)	i	0.895
Gonichthys cocco	37.3 (20.00–52.30)	17	7.51×10^{-3} (5.42×10^{-3}, 1.04×10^{-2})	3.09 (2.85, 3.32)	i	0.981
Hygophum benoiti	36.20 (15.00–39.80)	19	8.41×10^{-3} (6.37×10^{-3}, 1.11×10^{-2})	3.35 (2.95, 3.75)	i	0.945
Hygophum hygomii	38.10 (19.60–58.80)	33	1.25×10^{-2} (9.04×10^{-3}, 1.72×10^{-2})	3.10 (2.88, 3.32)	i	0.967
Hygophum macrochir	42.55 (29.70–51.50)	26	2.38×10^{-2} (1.64×10^{-2}, 3.44×10^{-2})	2.63 (2.36, 2.90)	−a	0.942
Hygophum reinhardtii	34.60 (25.40–50.00)	21	5.51×10^{-3} (2.81×10^{-3}, 1.08×10^{-2})	3.53 (3.03, 4.03)	+a	0.924
Hygophum taaningi	25.20 (15.60–49.90)	29	1.22×10^{-2} (9.42×10^{-3}, 1.57×10^{-2})	3.12 (2.91, 3.32)	i	0.972
Lampadena luminosa	38.80 (21.00–97.90)	20	8.33×10^{-3} (6.68×10^{-3}, 1.04×10^{-2})	3.24 (3.09, 3.39)	+a	0.990
Lampanyctus alatus	33.25 (16.30–52.10)	103	4.28×10^{-3} (3.15×10^{-3}, 5.81×10^{-3})	3.30 (3.04, 3.57)	+a	0.960
Lampanyctus cuprarius	29.90 (27.20–139.50)	22	6.48×10^{-3} (3.75×10^{-3}, 1.12×10^{-2})	2.85 (2.58, 3.11)	i	0.964
Lampanyctus lineatus	25.50 (23.50–141.00)	26	3.09×10^{-3} (2.52×10^{-3}, 3.77×10^{-3})	3.15 (3.06, 3.25)	+a	0.995
Lepidophanes guentheri	27.00 (17.30–44.50)	27	5.05×10^{-3} (3.80×10^{-3}, 6.70×10^{-3})	3.22 (2.93, 3.52)	i	0.956
Lobianchia gemellarii	43.40 (18.80–57.70)	41	1.31×10^{-2} (9.39×10^{-3}, 1.82×10^{-2})	3.13 (2.89, 3.36)	i	0.957

Table 3: Continued.

Taxon	Median SL range (mm)	n	aWW (95% CI)	bWW (95% CI)	Growth model	R^2
Myctophum affine	21.80 (16.00–45.20)	34	6.28×10^{-3} (5.62×10^{-3}, 7.02×10^{-3})	3.41 (3.30, 3.52)	+a	0.992
Myctophum nitidulum	31.40 (21.50–68.40)	20	9.58×10^{-3} (5.72×10^{-3}, 1.61×10^{-2})	3.16 (2.79, 3.54)	i	0.944
Notolychnus valdiviae	26.40 (9.10–38.50)	34	7.53×10^{-3} (6.49×10^{-3}, 8.74×10^{-3})	2.77 (2.51, 3.04)	i	0.953
Notoscopelus resplendens	37.65 (24.90–68.80)	26	1.23×10^{-2} (9.62×10^{-3}, 1.57×10^{-2})	2.95 (2.80, 3.09)	i	0.987
Osmeriformes						
Bathylagidae						
Dolicholagus longirostris	31.90 (23.90–144.80)	25	6.82×10^{-3} (5.33×10^{-3}, 8.73×10^{-3})	2.92 (2.80, 3.03)	i	0.991
Stomiiformes						
Gonostomatidae	29.90 (12.50–120.50)	400	3.36×10^{-3} (2.89×10^{-3}, 3.92×10^{-3})	3.24 (3.10, 3.38)	+a	0.836
Cyclothone acclinidens	38.60 (20.50–42.60)	50	3.99×10^{-3} (1.15×10^{-3}, 1.05×10^{-2})	3.18 (2.25, 4.11)	i	0.625
Cyclothone alba	22.00 (12.70–27.00)	49	4.60×10^{-3} (3.89×10^{-3}, 5.44×10^{-3})	2.53 (2.32, 2.74)	−a	0.957
Cyclothone braueri	22.80 (15.60–25.60)	42	5.64×10^{-3} (3.91×10^{-3}, 8.14×10^{-3})	2.31 (1.82, 2.81)	−a	0.786
Cyclothone obscura	33.60 (18.10–47.20)	41	1.16×10^{-2} (8.88×10^{-3}, 1.52×10^{-2})	2.44 (2.23, 2.65)	−a	0.960
Cyclothone pallida	21.45 (15.80–43.60)	49	3.69×10^{-3} (2.91×10^{-3}, 4.68×10^{-3})	2.88 (2.63, 3.13)	i	0.923
Cyclothone pseudopallida	22.00 (17.30–38.20)	88	4.24×10^{-3} (2.63×10^{-3}, 6.82×10^{-3})	2.85 (2.34, 3.37)	i	0.789
Gonostoma atlanticum	34.60 (23.40–64.00)	21	6.29×10^{-3} (3.26×10^{-3}, 1.21×10^{-2})	2.86 (2.41, 3.30)	i	0.905
Margrethia obtusirostra	36.85 (19.10–70.00)	16	2.10×10^{-2} (1.56×10^{-2}, 2.81×10^{-2})	2.88 (2.68, 3.08)	i	0.985
Sigmops elongatus	26.50 (12.50–120.50)	27	6.63×10^{-3} (5.60×10^{-3}, 7.83×10^{-3})	2.54 (2.41, 2.68)	−a	0.984
Zaphotias pedaliotus	32.30 (16.20–62.70)	17	1.13×10^{-2} (8.80×10^{-3}, 1.46×10^{-2})	2.64 (2.41, 2.88)	−a	0.976
Phosichthyidae	33.00 (12.70–52.00)	75	1.12×10^{-2} (8.10×10^{-3}, 1.55×10^{-2})	2.60 (2.28, 2.93)	i	0.771
Pollichthys mauli	34.10 (17.00–52.00)	20	$5.5.4 \times 10^{-3}$ (4.64×10^{-3}, 6.60×10^{-3})	2.69 (2.52, 2.86)	−a	0.984
Vinciguerria attenuata	33.90 (16.80–42.50)	15	1.07×10^{-2} (7.94×10^{-3}, 1.45×10^{-2})	2.93 (2.67, 3.20)	i	0.976
Vinciguerria nimbaria	35.10 (18.70–39.80)	19	1.18×10^{-2} (8.03×10^{-3}, 1.73×10^{-2})	2.79 (2.39, 3.18)	i	0.937
Vinciguerria poweriae	33.10 (12.70–32.30)	21	8.74×10^{-3} (6.35×10^{-3}, 1.20×10^{-2})	3.30 (2.86, 3.73)	i	0.967
Sternoptychidae	31.10 (6.10–86.00)	350	2.46×10^{-2} (2.15×10^{-2}, 2.82×10^{-2})	3.10 (2.92, 3.28)	i	0.831
Argyropelecus aculeatus	27.70 (7.50–43.10)	85	2.58×10^{-2} (2.26×10^{-2}, 2.94×10^{-2})	3.34 (3.09, 3.59)	+a	0.915
Argyropelecus gigas	34.45 (10.10–86.00)	17	1.87×10^{-2} (1.56×10^{-2}, 2.24×10^{-2})	3.04 (2.88, 3.21)	i	0.990
Argyropelecus hemigymnus	35.50 (14.40–29.00)	106	2.23×10^{-2} (1.46×10^{-2}, 3.42×10^{-2})	3.04 (2.45, 3.62)	i	0.834
Maurolicus weitzmani	27.90 (13.90–25.90)	22	1.32×10^{-2} (9.87×10^{-3}, 1.76×10-2)	2.90 (2.42, 3.38)	i	0.882
Polyipnus clarus	32.70 (13.40–48.80)	20	3.51×10^{-2} (2.99×10^{-2}, 4.12×10^{-2})	2.99 (2.80, 3.19)	i	0.982
Sternoptyx diaphana	35.50 (6.10–40.1)	29	6.20×10^{-2} (5.45×10^{-2}, 7.07×10^{-2})	2.12 (1.90, 2.34)	−a	0.942
Sternoptyx pseudobscura	29.90 (11.20–52.30)	37	5.60×10^{-2} (4.52×10^{-2}, 6.93×10^{-2})	3.03 (2.84, 3.23)	i	0.964
Valenciennellus tripunctulatus	31.80 (14.70–28.40)	21	1.10×10^{-2} (8.01×10^{-3}, 1.50×10^{-2})	2.73 (2.28, 3.18)	i	0.858
Stomiidae	30.60 (17.00–46.10)	128	8.95×10^{-3} (6.84×10^{-3}, 1.17×10^{-2})	2.45 (2.29, 2.61)	−a	0.877
Astronesthes macropogon	36.80 (17.00–46.10)	16	9.04×10^{-3} (5.81×10^{-3}, 1.41×10^{-2})	2.96 (2.61, 3.31)	i	0.956
Astronesthes niger	32.55 (15.60–39.20)	15	1.10×10^{-2} (5.53×10^{-3}, 2.17×10^{-2})	2.73 (2.02, 3.44)	i	0.828
Bathophilus pawneei	32.75 (27.20–108.70)	17	2.14×10^{-3} (1.06×10^{-3}, 4.30×10^{-3})	3.53 (3.07, 3.99)	+a	0.943
Chauliodus sloani	32.00 (17.70–101.10)	22	4.72×10^{-3} (3.32×10^{-3}, 6.70×10^{-3})	2.69 (2.44, 2.95)	−a	0.959
Eustomias schmidti	78.30 (62.10–253.60)	15	1.05×10^{-3} (4.84×10^{-4}, 2.28×10^{-3})	3.41 (3.07, 3.75)	+a	0.971
Photostomias guernei	57.00 (46.70–101.50)	18	4.82×10^{-3} (2.34×10^{-3}, 9.92×10^{-3})	2.78 (2.41, 3.16)	i	0.936
Stomias affinis	23.65 (19.70–107.30)	25	2.19×10^{-3} (1.40×10^{-3}, 3.42×10^{-3})	2.93 (2.70, 3.16)	i	0.966

Note: n: sample size, R^2: coefficient of determination. Growth models: +a: positive allometry ($b > 3$), −a: negative allometry ($b < 3$), and i: isometry ($b = 3$).
Abbreviation: SL, standard length.

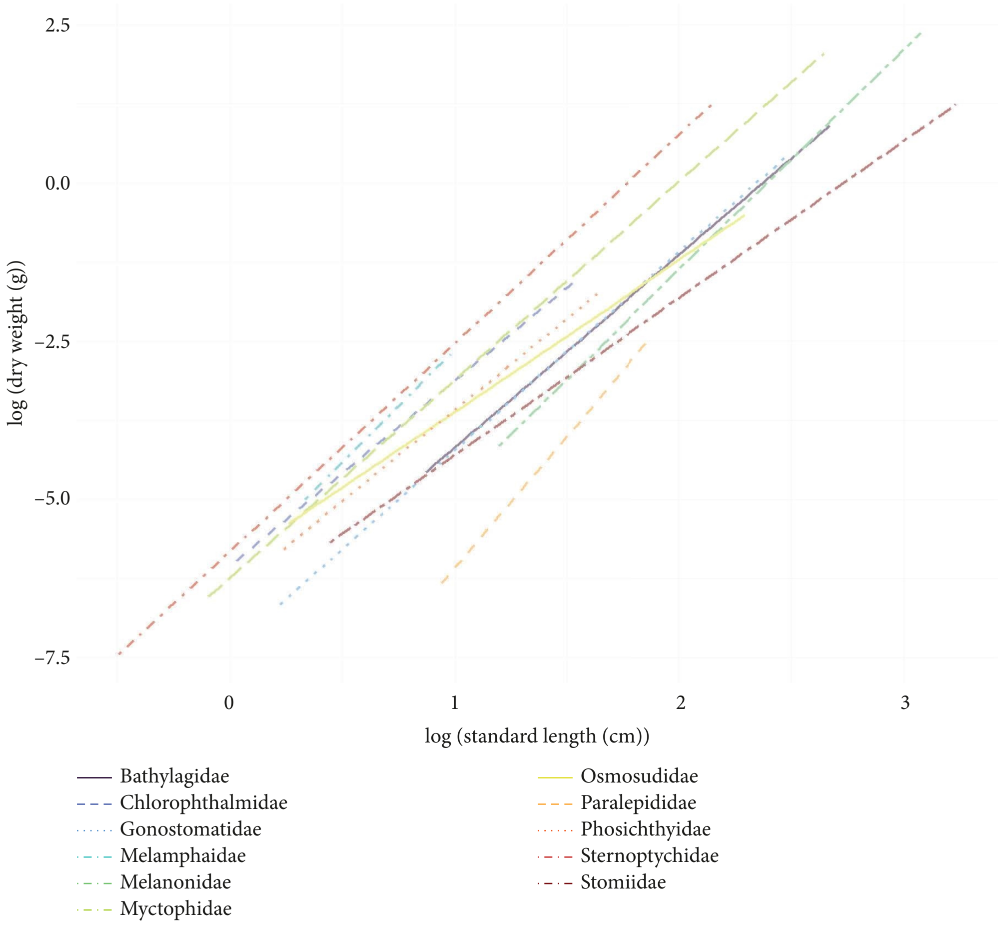

Figure 4: Family-level standard length–dry-weight regressions for 11 mesopelagic fish families in the Gulf of Mexico.

negative in 35 and positive in two, indicating that the relationship between SL and water content is largely negative across examined species (Table S2, S3, and S4).

In the curvilinear models, the water content of *Sigmops elongatus* and *Eustomias schmidti* displayed a positive relationship with SL, with the models reaching an asymptote at 87.2% and 90.4%, respectively (Figure 5; Table S3). The water content of *Benthosema suborbitale* (Gilbert 1913) displayed a negative relationship with SL and reached an asymptote at 77.2% (Figure 5; Table S3). In all three models, the horizontal asymptote (*Asym*) was significant ($p < 0.05$; Table S4). The intercept term was only significant in the *S. elongatus* model, and the natural logarithm of the rate constant (lrc) was only significant in the *B. suborbitale* model (Table S4). The three species modeled using quadratic regressions *Diaphus dumerilii* (Bleeker 1856), *Gonichthys cocco*, and *Dolicholagus longirostris* (Maul 1948) were represented by upward-facing parabolas which first dipped to a minimum water content before increasing with SL (Figure 5; Table S3). All quadratic model parameters (b_0, b_1, and b_2) were significant ($p < 0.05$; Table S3) in all three species models. Additionally, SL exhibited no relationship with water content within 20 species, indicating that water content remained consistent across size classes in these taxa (Table S2).

4. Discussion

The present study provides both wet-weight- and dry-weight-derived LWRs for 68 species of mesopelagic fishes in the Gulf of Mexico, 59 of which are new for the region and 28 of which are not listed in FishBase records globally [53]. The obtained LWRs were generally of good fit, with 59 wet-weight-derived models and all 68 of the dry-weight-derived models having R^2 values above 0.90. Wet-weight- and dry-weight-derived estimates of allometric growth coefficients (b) were largely within the expected range for fishes, with 76% of estimated growth parameters falling within the range 2.5–3.5 [25]. The largest deviations from this range occurred in the paralepidid *Lestidiops affinis* Ege 1930 ($b_{DW} = 4.17$), the melamphaid *Melamphaes simus* ($b_{DW} = 3.98$), and the myctophid *Diogenichthys atlanticus* (Tåning 1928) ($b_{DW} = 3.84$), indicating relatively faster increases in weight than length as the individuals grow.

Deviations from the expected range in allometric growth coefficients are rare but seen in nature, such as the case of the Blackfin Icefish *Chaenocephalus aceratus* (Lönnberg 1906), which is due to a change in its body form as it grows [25]. Similar changes may also occur in *L. affinis, M. simus*, and *D. atlanticus*. However, *Lestidiops affinis* was also noted to have extreme positive allometric growth ($b > 3.5$) in a previous study [43] which suggests that this may be

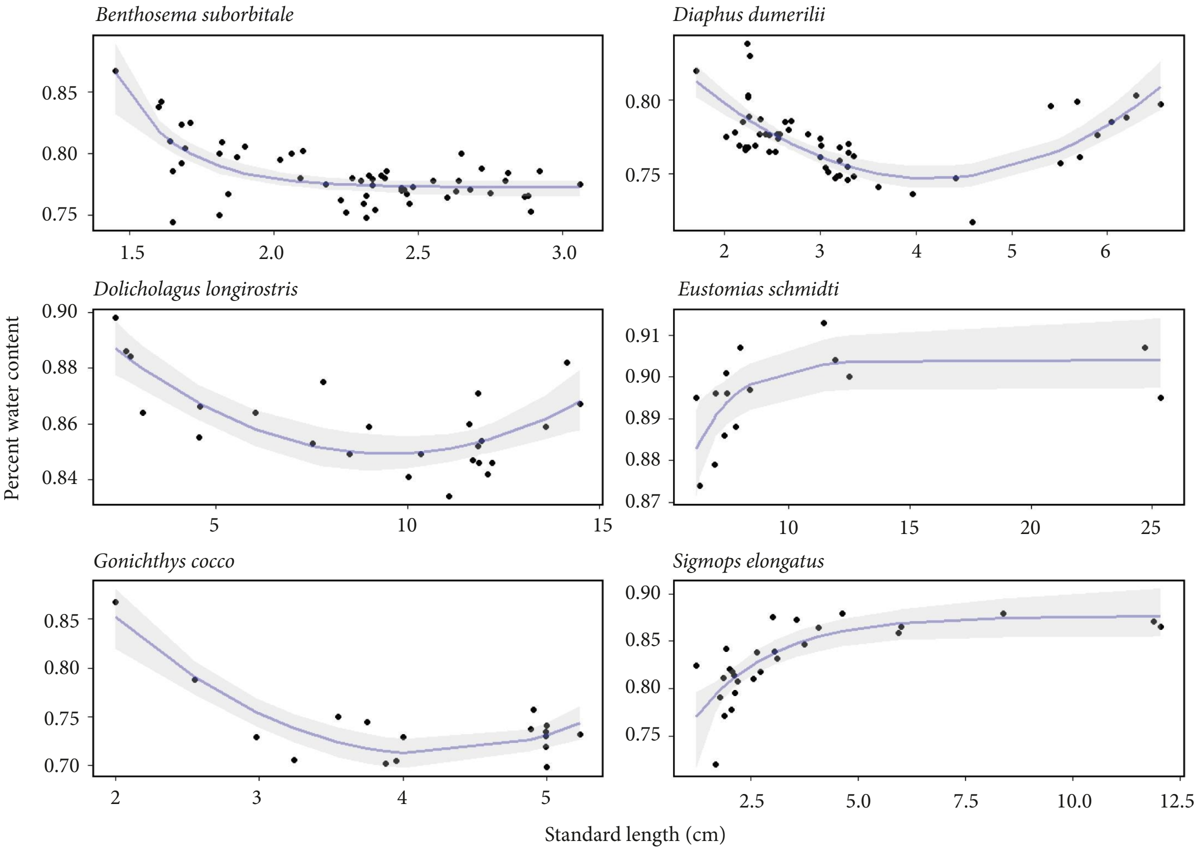

Figure 5: Standard length–water content nonlinear regressions for six dominant mesopelagic fish species in the Gulf of Mexico: *Benthosema suborbitale*, *Diaphus dumerilii*, and *Gonichthys cocco* (myctophidae); *Dolicholagus longirostris* (bathylagidae); *Eustomias schmidti* (stomiidae); and *Sigmops elongatus* (gonostomatidae).

characteristic of this taxon. Repeated length–weight studies in the Gulf of Mexico and elsewhere would likely help confirm these hypotheses.

Species-specific LWR parameter values were generally comparable to those obtained in other regions, such as the northern Atlantic [44], tropical Atlantic [36, 43], Indian Ocean [50], Mediterranean [47, 49], and the western [30] and eastern Gulf of Mexico [31, 32]. Broad similarities in LWRs across ocean basins and environmental conditions suggest that LWR parameter values are characteristic features of many mesopelagic fish species [36, 54]. These broad similarities suggest that LWRs from across regions may help inform such research in potentially understudied ocean basins, such as the Indian and Pacific Oceans. Further research would help to refine these LWR parameter values, given that few taxa have multiple LWRs, and would help fill data gaps on unstudied mesopelagic species.

Differences in LWR parameter values between the present study and other ocean basins such as the Atlantic and Mediterranean did not follow specific patterns. For instance, the wet-weight-derived allometric growth coefficient for the stomiid *Chauliodus sloani* Bloch & Schneider 1901 in the present study was similar to that obtained in the Mediterranean (2.69 vs. 2.78) [47] but differed from the value obtained in the tropical Atlantic (2.69 vs. 3.35) [36]. However, for the myctophid *Diaphus rafinesquii* (Cocco 1838), the presented wet-weight allometric growth coefficient was similar to the value obtained in the tropical Atlantic (2.88 vs. 2.85) [36] but largely differed from those obtained in the northern Atlantic (2.88 vs. 3.43) [44] and Mediterranean (2.88 vs. 3.52) [47]. The Gulf of Mexico potentially hosting a smaller size range of mesopelagic fishes [55] and a differing oceanographic regime may explain the differences, especially given temperature's potential role in altering LWRs [56]. Additionally, recent evidence of distinct genetic subpopulations of cosmopolitan mesopelagic fish species [57] and factors such as individual nutritional condition, gonadal mass, and gut contents all potentially influence LWRs and explain these regional differences [36, 53, 58].

In comparison with previous studies conducted in the Gulf of Mexico, the LWRs reported here largely agreed with past estimates [30–32], although only nine of the 68 species analyzed (*Chlorophthalmus agassizi* Bonaparte 1840, *Cyclothone alba* Brauer 1906, *Cyclothone braueri* Jespersen & Tåning 1926, *Cyclothone pseudopallida* Mukhacheva 1964, *Chauliodus sloani, Photostomias guernei* Collett 1889, *Stomias affinis* Günther 1887, *Sternoptyx diaphana,* and *Sigmops elongatus*) had previously been reported. The most notable differences in LWRs occurred within the wet-weight-derived allometric growth coefficients of *S. diaphana* and *C. sloani* when compared to the values collected in the western Gulf of Mexico [30]. The eastern and western Gulf of Mexico differ in their oceanographic signatures with the eastern Gulf of Mexico being dominated by the Loop Current and the highly productive outflow from the Mississippi River [59], so it is possible that differing oceanographic conditions may have given rise to the discrepancies observed in the LWRs as small-scale regional differences in mesopelagic fish growth patterns have been observed previously [43]. However, in these cases, specific methodological differences between the present study and Chi-Espínola et al. (2023) may better explain these discrepancies, particularly given that the differences were only observed in the wet-weight and not dry-weight data. In the case of *C. sloani*, for example, Chi-Espínola et al. (2023) examined a larger size range than that of the present study. Differences may have also arisen due to differences in preservation strategies as Chi-Espínola et al. (2023) used frozen specimens rather than ethanol preservation as used in the present study. Ethanol fixation is known to impact both fish weight and length, with the biggest impact being a reduction in body weight due to dehydration [60–63]. Still, the LWRs of the other seven species were very similar despite differences in size ranges and preservation strategies, so it is unclear why these discrepancies existed in only these two species.

Isometric and positive allometric growth were the most common growth models observed, which agreed with similar studies on mesopelagic fishes [30, 36, 43, 47]. This trend was primarily driven by members of the family Myctophidae due to the high numbers of species analyzed from that family, with only *Diaphus termophilus* Tåning 1928 and *Hygophum macrochir* (Günther 1864) exhibiting negative allometric growth (Tables 2 and 3). Positive allometric growth in the highly migratory taxa like myctophids may be indicative of relatively greater increases in muscle accumulation as an animal grows, which is necessary for DVM. In contrast, nonmigratory species (e.g., *Cyclothone* spp.) had the most frequent instances of negative allometric growth and are generally known to possess reduced skeletal and muscular mass than their migrating counterparts [64]. Differences in DVM behavior may also explain intragenus differences in growth forms. For instance, *Lampanyctus cuprarius* and *Lampanyctus lineatus* both display isometric growth, asynchronous migration, and deeper daytime depth distributions than *Lampanyctus alatus* Goode & Beane 1896, which exhibits positive allometric growth and is considered a synchronous migrator [55]. However, potential connections between growth form and DVM behavior are largely speculative at present given the counterexamples (e.g., *H. macrochir* exhibiting DVM behavior despite its negative allometric growth) and lack of conclusive evidence in prior studies of LWRs.

Estimates of growth form varied between wet and dry weights, with 28 species displaying a different growth form depending on the weight type used. Similar to López-Pérez et al. (2020), the changes in growth form largely occurred as an increase in allometric growth coefficients in dry-weight-derived estimates (24 species; Figures 2 and 3, Table S2), but decreases in allometric growth coefficients between wet-weight- and dry-weight-derived estimates were also observed within four species: the gonostomatid *C. pseudopallida*, the myctophid *Lampanyctus lineatus*, and the stomiids *Bathophilus pawneei* Parr 1927 and *Eustomias schmidti.* While the LWR parameters will obviously vary depending on the weight measured, this finding highlights that the weight type measured may also affect how a species' growth form is characterized, depending on the taxa. This further implies that future research may benefit from adopting a standardized preservation and weighing approach, such as the use of eviscerated dry weights described by López-Pérez et al. (2020), to account for potential differences caused by these practices.

The relationship between an individual's body length and water content appeared to explain the change in growth form between wet- and dry-weight-derived LWRs in 22 of the 28 species (22 of 28) that exhibited a shift in growth form. Overall, the relationship between body length and water content was significant in 43 species with 36 of these relationships being negative (i.e., larger individuals contained less water in their tissues), four being positive, and three being quadratic (Table S2). A negative relationship between length and water content shifts allometric growth coefficients upward due to the relative differences in dry weights between size classes. That is, smaller individuals with relatively higher water content have relatively lower dry weights than their larger counterparts and thus cause the slope of the length-dry-weight regression to shift upward in comparison with the wet-weight estimate, resulting in a higher allometric growth coefficient. Additionally, these relative differences in water content between size classes may explain many of the "extreme" allometric growth parameters obtained as 23 out of the 32 allometric growth parameters outside of the typical range found in fishes (2.5–3.5) were dry-weight-derived estimates.

The observed decrease in water content with growth agrees with previous observations from other fish species, including some mesopelagic ones [65–67]. This decrease in water content is generally associated with lipid and muscle accumulation with body size, as lipid and muscle content are known to be inversely related to water content in many fish species [65, 67, 68]. This trend may also be partly due to ontogenetic shifts in life history, such as changes in vertical distribution or DVM behavior, which may come with body compositional changes. Additionally, many myctophids and members of the genus *Cyclothone* possess air-filled swim bladders as juveniles and young adults that either regress or become lipid-invested as adults [69, 70]. In order to compensate for the associated loss of buoyancy, many species incorporate lipids and a reduced skeletal mass, which likely also alters their body mass and relative water content [64].

Significant positive length–water content regressions were observed in the myctophid *L. lineatus*, the gonostomatids *C. pseudopallida* and *S. elongatus,* and the stomiid *E. schmidti* which goes against the general negative length–water content trend seen in fishes (Figure 5; Tables S2 and S4) and may also be due to changes in vertical distribution or DVM behavior. For instance, *L. lineatus* and *S. elongatus* convert from synchronous to asynchronous migrators at larger sizes [32, 55]. Fishes residing at deeper depths often possess higher water content and lower muscle and lipid mass which coupled with reduced DVM may lead to increased metabolic efficiency in these low-energy environments [64, 71, 72]. The positive length–water content regression for *C. pseudopallidus* may reflect increased metabolic efficiency, but it could also be related to buoyancy as its swim bladder volume grows slower than its overall size [70]. Thus, the increased water content may help offset the potential buoyancy loss with growth. However, it should be noted that this trend was not seen in other *Cyclothone* species despite similarities in swim bladder morphologies. Ultimately, further studies of body composition are required to confirm these hypotheses, especially since the strength of these interactions was highly variable within and between species.

Quadratic relationships between water content and length were also noted. In the case of the myctophid *Diaphus dumerilii,* the vertex of this relationship (~45–50 mm; Figure 5) seemed to coincide with the size at which they are reported to reach sexual maturity (~52 mm) [73]. Thus, the asymptotic relationship may indicate a shift in body composition away from muscle and lipid accumulation to gonadal development. Additionally, *D. dumerilii* have been hypothesized to transition to a nonmigratory, benthopelagic habitat at larger size classes, so the increase in water content may be a response to this transition, perhaps due to the lower metabolic demands [73]. *Gonichthys cocco* and *Dolicholagus longirostris* also exhibited a similar trend, but the lack of life history data for these species makes confirming this hypothesis difficult.

5. Conclusion

The present study constitutes one of the most comprehensive analyses of LWRs in mesopelagic fishes to date, estimating wet- and dry-weight regressions for 68 species and potentially reporting novel global records for 28. Along with the LWRs, the growth form designations, estimated water contents, and length–water content regressions presented add to the limited literature on the allometry and general biology of mesopelagic fishes. Given the large uncertainties in mesopelagic fishes' biomass and role in ecosystem functioning, we expect that the results will help refine regional biomass estimates of mesopelagic fishes, and through ecosystem, carbon transport, and species distribution modeling efforts, this work will ultimately aid in quantifying mesopelagic fishes' role in the Gulf of Mexico.

Data Availability Statement

Data are publicly available through the Gulf of Mexico Research Initiative Information & Data Cooperative (GRIIDC) at https://data.gulfresearchinitiative.org. A DOI number for the dataset is included (https://doi.org/10.7266/d9xnhqa3).

Disclosure

The content is solely the responsibility of the authors and does not necessarily represent the official views of the Gulf Research Program of the National Academies of Sciences, Engineering, and Medicine.

Conflicts of Interest

The authors declare no conflicts of interest.

Author Contributions

Ian M. Areford led/conducted/contributed to the data collection, data analyses, preparation of all figures and tables, and wrote the first draft of the manuscript. Sidney R. Trimble contributed to data collection/data analyses/preparation of all tables/specimen selection. Tracey T. Sutton and April B. Cook primarily conducted specimen collection, Tracey T. Sutton provided the specimens, and all taxonomic identifications used in the project. Rosanna J. Milligan devised the project and supervised Ian M. Areford and Sidney R. Trimble through the data collection process. All authors contributed to the manuscript revisions.

Funding

This work was, in-part, supported by the Deep-Sea Benefits: Outcomes of Mesophotic and Deep Benthic Community Restoration (PID #350) project, which was selected by the Open Ocean Trustee Implementation Group (Resolution #OO-2023-017) to restore natural resources injured by the 2010 Deepwater Horizon oil spill, with grant funding through the University of Miami Cooperative Institute of Marine and Atmospheric Science award NA21OAR4050472-T3-01S004 to Nova Southeastern University. This research was additionally supported in part by research funded by the National Oceanic and Atmospheric Administration's RESTORE Science Program (ROR-https://ror.org/0042xzm63) under award NA24NOSX451C0002-T1-01 to Nova Southeastern University. Research reported in this work was also supported by an Early-Career Research Fellowship from the Gulf Research Program of the National Academies of Sciences, Engineering, and Medicine awarded to Rosanna J. Milligan. Additional funding for Sidney R. Trimble was provided by a President's Faculty Research and Development Grant from Nova Southeastern University.

Acknowledgments

The authors would like to thank all the scientists and crew from the R/V *Meg Skansi*, FSV *Pisces*, and R/V *Point Sur*, who contributed to the sample collection efforts detailed here, and also thank Hannah Johnson, Manuel Ploner, Megan Laskowski, Alianna Jones, and Si'ron Davis for their help collecting the morphometric data detailed in this work.

Supporting Information

Additional supporting information can be found online in the Supporting Information section. *(Supporting Information)*

Equation S1 describes standard length–water content equation used when the relationship was linear.

Equation S2 describes standard length–water content equation used when an exponential asymptotic model was used.

Equation S3 describes standard length–water content length equation used when a quadratic model was used.

Tables S1: Nonlinear standard length–water content AICc scores used in model selection.

Table S2: Standard length–water content linear regression parameters.

Tables S3: Standard length–water content quadratic model coefficients.

Table S4: Standard length–water content asymptotic model coefficients.

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