

# Length–weight relationships of 55 mesopelagic fishes from the eastern tropical North Atlantic: Across- and within-species variation (body shape, growth stanza, condition factor)

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## Abstract

We present estimates of length–weight relationships (LWRs) of 55 mesopelagic fish species of 13 taxonomic families based on data collected in the eastern tropical North Atlantic (ETNA) in March/April 2015. Our data include novel records for 19 species, while for 25 species LWRs are based on the most robust sample sizes, and for 21 species they are based on the most representative size ranges available up to now. In 31 species, body lengths were within the maximum range of body lengths recorded in the area, with new records of maximum lengths for 13 species. Most values for  $b$  fell between 2.5 and 3.5 with a mean exponent  $b$  of 3.08 (median 3.12) and a mean  $a$  of 0.0172 (median 0.0113). Body shape as covariate ('elongated', 'fusiform' and 'short-deep') strongly determined the variation in  $\log a$  as a function of parameter  $b$ . For the mesopelagic fish species investigated, the form factor  $a_{3.0}$  indicated a significant increase of median  $a_{3.0}$  from 'elongated' to 'fusiform' to 'short-deep' body shapes. Large variability existed in parameter  $b$  between species of the same taxonomic family. Isometric growth was indicated in only nine species, whereas a positive allometry was suggested in 22 species. Using segmented regression analysis, we investigated ontogenetic variation in LWRs in 30 species. Of these, 20 species showed a breakpoint in LWR, whereby nearly equal numbers exhibited an increase or a decrease in slope following the breakpoint. Seven out of nine species showed significant regional variation in the slope of the relationship of the relative condition factor  $K_{rel}$  vs. body length between two or more regions of the ETNA [eastern and western part of the oxygen minimum zone (LO-E, LO-W), northern and central equatorial region (EQ-N, EQ-C)]. A conspicuous pattern was an increase in  $K_{rel}$  with body size in the LO-E (in six out of eight species), whereas in the LO-W and the equatorial regions the majority of species showed a related decrease. These findings support the idea that growth patterns in mesopelagic fishes in tropical regions show species-specific ecological niche and life-history adaptations that are finely tuned to small-scale regional environmental conditions. Comparison of our data with those of other studies emphasises that, regarding the small adult sizes of many mesopelagic

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fish species, estimates of LWR parameters are strongly influenced by sampled size distributions.

#### KEYWORDS

body shape, condition, eastern tropical Atlantic, length–weight relationships, mesopelagic zone, ontogeny, oxygen minimum layer

## 1 | INTRODUCTION

Harvesting of the large, hitherto mostly untapped, mesopelagic fish biomass resource is increasingly considered a realistic option (Hidalgo & Browman, 2019; Olsen *et al.*, 2020; Prelezo & Maravelias, 2019; Standal & Grimaldo, 2020). At present, mesopelagic fish species are all unregulated species subject to no fisheries regulations (Standal & Grimaldo, 2020). Besides questions regarding regulatory mechanisms and economic viability, management of mesopelagic fish species is hampered by the lack of a sound biological knowledge base. Biomass estimates of mesopelagic fishes are currently connected to different sources of uncertainty associated with fish swimbladder volume, length distribution, species morphology, community composition and spatio-temporal variability related to these factors (see Hidalgo & Browman, 2019 and references therein). In addition, basic biological parameters related to growth, maturation and regional and seasonal variability in condition are currently missing for most mesopelagic fish species (Sarmiento-Lezcano *et al.*, 2018, 2020). Collecting regionally extensive biological data is more easily conducted in temperate and boreal ecosystems where few mesopelagic fish species dominate (Grimaldo *et al.*, 2020). On the contrary, in the equatorial regions that host a large diversity in mesopelagic fish species, capturing the full suite of the species community and its respective biological parameters constitutes a challenge. Because the mesopelagic fish community is an important component of global trophic and carbon cycles (*e.g.*, Klevjer *et al.*, 2016), with individual species likely constituting key components (*e.g.*, Eduardo *et al.*, 2020b), improving our knowledge on biological characteristics of individual species is an essential prerequisite prior to any exploitation (Hidalgo & Browman, 2019).

Length–weight relationships (LWRs) are used to estimate biomass based on more easily obtained length distributions, to determine species' growth patterns and to identify spatio-temporal variation in population condition and fitness (Froese, 2006). Across-species variation exists regarding body shape, life-history patterns and habitat. Within-species variation in LWRs can be due to sex, maturity stage and recent feeding history. Depending on the season, the geographic population and annual differences in environmental conditions, LWRs in individual species can vary substantially (Froese, 2006), but sampling gear and methodology also impact the size ranges sampled and, consequently, their size-based parameters (Gartner *et al.*, 1989; Harrison, 1967; Heino *et al.*, 2011; Jamieson *et al.*, 2006; Kaartvedt *et al.*, 2012; Kashkin & Parin, 1983; Pearcy, 1983). LWRs in mesopelagic fish species have been reported in comparatively few studies

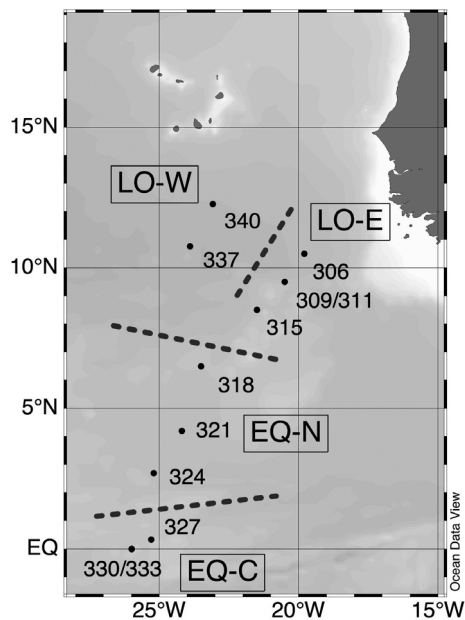
(Battaglia *et al.*, 2010; Eduardo *et al.*, 2019, 2020a; Grimaldo *et al.*, 2020; Jiang *et al.*, 2017; López-Pérez *et al.*, 2020; Olivar *et al.*, 2013; Sarmiento-Lezcano *et al.*, 2018; Slayden, 2020; Wang *et al.*, 2018). Studies are not always comparable due to differences in preservation strategies employed that further affect LWR estimates. Relative body condition is an important indicator of individual or population physiological and nutritional status, which can be interpreted in terms of energy reserves, but also with respect to life-history parameters, for example reproduction and growth (Gubiani *et al.*, 2020; Jakob *et al.*, 1996). Due to generally limited sample sizes in mesopelagic fish studies, spatio-temporal variation in LWRs and relative condition has only rarely been explored (López-Pérez *et al.*, 2020). Differences in LWRs related to development phases or growth stanzas, which have been demonstrated in other pelagic fish species, remain, as yet, unexplored (Froese, 2006).

Based on a comparatively extensive dataset, the present study reports LWRs of 55 mesopelagic fish species from the eastern tropical North Atlantic, covering both vertically migrant and nonmigrating species of 13 different taxonomic families. We investigated (a) across-species variation in LWRs related to taxonomic level and body shape, and (b) within-species variation in LWRs by considering different growth stanza and regional variation in condition factors between subregions in the two ecoregions #26 'Mauritania/Cape Verde' and #27 'Tropical and West Equatorial Atlantic' (Sutton *et al.*, 2017).

## 2 | MATERIALS AND METHODS

### 2.1 | Biological sample collection and processing

Fish samples were collected between 23 March and 2 April 2015 during cruise WH383 on the *FRV Walther Herwig III* at 10 stations in the eastern tropical North Atlantic between 0–12°N and 20–26°W (Figure 1). A pelagic midwater trawl ('Aalnet', Engel Netze, Bremerhaven, Germany, 16 × 30 m mouth opening, length 150 m including multiple opening-closing devices, 260 meshes by 180 cm stretched mesh size at front, cod end 20 mm stretched mesh-opening, 1.8 mm inlet sewn into last 1 m of cod end, see British Columbia midwater trawl modification; Harrison, 1967) was used that sampled three discrete depth strata between 45 and 680 m (for details see Czudaj *et al.*, 2021). Depending on the size of the total catch, we preserved either subsamples or the total catch in 4% formaldehyde–seawater solution (buffered with sodium-tetraborate), and identified and measured them onboard and in the laboratory in Steedman sorting fluid



**FIGURE 1** Stations in the eastern low-oxygen (LO-E), western low-oxygen (LO-W), northern equatorial (EQ-N) and central equatorial (EQ-C) regions of the eastern tropical North Atlantic sampled in this study

(Steedman, 1976). A minor portion of samples was preserved frozen at  $-30^{\circ}\text{C}$ . Fish specimens were identified by consulting regional identification keys (Bigelow *et al.*, 1964; Carpenter & De Angelis, 2016a,b; Nafpaktitis *et al.*, 1977; Whitehead *et al.*, 1986) and FishBase (Froese & Pauly, 2022). We measured and weighed fishes to the nearest 0.01 mm and 0.01 g (0.1 g in a few cases).

## 2.2 | Data analysis

All analyses were conducted in the statistical computing package R (version 1.4.1106; R Core Team, 2020) using the packages ‘tidyverse’ (Wickham, 2019), ‘reshape’ (Wickham, 2007), ‘ggpubr’ (Kassambara, 2019) and those specified with the analyses. We estimated LWRs according to the equation  $TW = a \times SL_b$ , where TW is the body weight in grams, SL is the standard length in centimetres,  $a$  is the intercept and  $b$  is the allometric coefficient (Keys, 1928). Using the logarithmic form of this LWR, we fitted mean regional LWRs for each species with sample sizes  $\geq 25$  specimens per region, based on all data available. We excluded individual outliers and singular extreme values at the minimum/maximum end of the size range. We also included data for four species with sample availability  $< 25$ , but a fairly representative size range covered and with no reference data available in the literature so far. We investigated across-species variation in LWRs by first looking at the frequency distribution of mean  $\log a$  and mean exponent  $b$  for the 55 species included in our study. We evaluated the growth pattern in the species examined and whether it was isometric ( $b = 3$ ) or allometric ( $b < 3$ ,  $b > 3$ ) in our study region during the respective time of our sampling. For this purpose we used the ‘hoCoef’ test of the R package ‘FSA’, which performs a hypothesis test

that a linear model parameter is equal to a specific value (Ogle *et al.*, 2019). We looked at the relationship to taxonomic level and explored the influence of body shape on the parameters of the LWR. For this purpose, we predetermined three groups of body shapes, *i.e.*, ‘short-deep’, ‘fusiform’ and ‘elongated’ (categories according to Froese, 2006), which we assigned to each species based on information available in FishBase (Froese & Pauly, 2022). In cases with no information available in FishBase, we assigned a similar morphology as in other family members (marked with brackets in Table 1). We reassigned the gonostomatid *Diplophos taenia* Günther 1873 from ‘eel-like’ to ‘elongated’ because of the lack of further ‘eel-like’-shaped species in our analysis. In the particular case of the myctophid *Electrona risso* (Cocco 1829), which is described as ‘elongated’ in FishBase based on a reference that refers to young stages only (Moser, 1996), we reassigned it as ‘fusiform’ considering its rather deep adult body shape compared to other myctophids. We estimated linear regressions for each of the groups and analysed significant differences in the intercept and slope between them using an ANCOVA with  $\log a$  as response variable,  $b$  as continuous covariate and ‘body shape’ as categorical covariate. We further looked at the form factor  $a_{3.0}$  and its applicability as an indicator of body shape in mesopelagic fishes. The form factor  $a_{3.0} = 10^{\log a - S(b - 3)}$  is the value that coefficient  $a$  would have if exponent  $b$  was 3.0 (Froese, 2006), where  $S$  is the slope of the regression of  $\log a$  vs.  $b$ . Here, we used the across-species slope of  $S = 1.358$  based on a dataset of 1223 fish species presented in Equation 17 by Froese (2006). This was chosen for better comparability between studies and because of its greater generality compared to our comparatively more limited dataset. We used Akaike information criterion (AIC) model selection to distinguish among two models that differed in the respective body shape assignments of three questionable species as identified by the form factor. We further investigated within-species variation in LWRs by first examining growth stanza in LWRs of 30 mesopelagic fish species with sufficiently available size ranges and size distributions sampled using segmented regression analysis (R package ‘segmented’; Muggeo, 2003, 2008, 2016, 2017). In addition, we explored regional variation in a species’ condition in nine species with sufficient data to compare at least two regions among the eastern low-oxygen (LO-E), western low-oxygen (LO-W), northern equatorial (EQ-N) and central equatorial (EQ-C) regions. In this analysis, we excluded regions (a) with sample sizes  $< 30$  and (b) with sample sizes  $> 30$ , but unrepresentative size distributions. We explored regional variation in a species’ condition *via* a double-logarithmic plot of the relative condition factor  $K_{\text{rel}}$  vs. standard length (cm) and an ANCOVA with ‘region’ as covariate comparing  $K_{\text{rel}}$  correcting for body size (SL). We checked the underlying assumptions of normality using a Shapiro–Wilk test and of homoscedasticity using a Bartlett and a Levene test (Zuur & Ieno, 2015). Significant deviation from homogeneity of variance was indicated in many pairwise comparisons, but in all cases the ratio between the smallest and largest variance of the residuals was  $< 4$ , which according to the rule of thumb given in Zuur and Ieno (2015) suggests sufficient homogeneity.  $K_{\text{rel}} = W / a \times SL^b$  (Le Cren, 1951) compares the weight of an individual with the average weight predicted from the corresponding parameters  $a$  and  $b$  of a LWR, which we calculated for each species in different regions. Le Cren’s (1951) relative condition factor  $K_{\text{rel}}$  allows us to compare the

**TABLE 1** Estimated parameters and descriptive statistics of length–weight relationships of 55 mesopelagic fish species of the eastern tropical North Atlantic based on data of the WH383 cruise

Family	Species	Body shape	Max SL lit. (cm)	N	SL (cm)	TW (g)	log $\alpha$ and 95% CI log $\alpha$	b and 95% CI b	b Std. error	R <sup>2</sup>	P value allom. growth
Bathylagidae	<i>Bathylagoides argyrogaster</i> (Norman 1930)	nm elong	11.0	122	3.3–12.0	0.3–11.6	0.0057 (0.0047–0.0069)	3.145 (3.043–3.245)	0.051	0.969	0.01
Caristiidae	<i>Platyberyx opalescens</i> Zugmayer 1911	nm deep	11.5	10	2.2–13.9	0.6–123.0	0.0603 (0.0401–0.0907)	2.855 (2.599–3.111)	0.111	0.987	0.23
Diretmidae	<i>Diretmus argenteus</i> Johnson 1864	nm deep	11.1	447	2.2–7.6	0.6–21.3	0.0755 (0.0691–0.0825)	2.769 (2.716–2.823)	0.027	0.959	0.00
Diretmidae	<i>Diretmoides pauciradiatus</i> (Woods 1973)	nm deep	14.0	55	2.5–11.8	0.7–58.4	0.0670 (0.0586–0.0767)	2.739 (2.661–2.816)	0.039	0.989	0.00
Gonostomatidae	<i>Diplophos taenia</i> Günther 1873	dm (elong)	20.0	139	4.9–14.7	0.1–5.1	0.0009 (0.0008–0.0011)	3.257 (3.186–3.328)	0.036	0.984	0.00
Gonostomatidae	<i>Gonostoma denudatum</i> Rafinesque 1810	dm elong	14.0	79	3.0–14.4	0.1–16.6	0.0030 (0.0026–0.0035)	3.245 (3.183–3.306)	0.031	0.993	0.00
Gonostomatidae	<i>Sigmops elongatus</i> (Günther 1878)	nm elong	27.5	32	9.9–20.6	2.8–31.9	0.0020 (0.0013–0.0030)	3.177 (3.014–3.340)	0.080	0.981	0.03
Gonostomatidae	<i>Zaphotias pedaliotus</i> (Goode & Bean 1896)	nm elong	7.2	478	1.8–7.8	0.1–3.4	0.0097 (0.0082–0.0115)	2.819 (2.725–2.914)	0.048	0.878	0.00
Melamphidae	<i>Melamphaes polylepsis</i> Ebeling 1962	nm fusi	7.3	273	3.6–7.9	0.9–11.1	0.0205 (0.0177–0.0237)	3.026 (2.935–3.117)	0.046	0.940	0.58
Melamphidae	<i>Melamphaes typhlops</i> (Lowe 1843)	nm fusi	7.8	32	3.4–7.7	0.8–11.4	0.0167 (0.0129–0.0215)	3.184 (3.020–3.348)	0.080	0.981	0.03
Melamphidae	<i>Scopelogadus mizolepis</i> (Günther 1878)	nm fusi	9.4	280	3.7–9.3	0.6–15.2	0.0072 (0.0065–0.0081)	3.440 (3.379–3.501)	0.031	0.978	0.00
Myctophidae	<i>Benthosema suborbitalis</i> (Gilbert 1913)	dm fusi	3.9	58	2.0–3.3	0.1–0.6	0.0091 (0.0065–0.0129)	3.355 (3.021–3.689)	0.167	0.876	0.04
Myctophidae	<i>Bolinichthys indicus</i> (Nafpaktitis & Nafpaktitis 1969)	dm (fusi)	4.5	63	1.9–4.6	0.1–1.3	0.0125 (0.0010–0.0157)	3.132 (2.958–3.305)	0.087	0.955	0.13
Myctophidae	<i>Bolinichthys photothorax</i> (Parr 1928)	dm fusi	7.3	57	4.1–6.9	0.9–5.5	0.0121 (0.0092–0.0161)	3.115 (2.943–3.287)	0.086	0.959	0.19
Myctophidae	<i>Bolinichthys supralateralis</i> (Parr 1928)	am elong	11.7	65	2.7–10.5	0.3–18.8	0.0118 (0.0103–0.0136)	3.189 (3.116–3.264)	0.037	0.992	0.00
Myctophidae	<i>Ceratospilus warmingii</i> (Lütken 1892)	dm elong	8.1	430	1.7–7.4	0.06–5.3	0.0093 (0.0087–0.0098)	3.213 (3.178–3.248)	0.018	0.987	0.00
Myctophidae	<i>Dasy Scopelus asper</i> (Richardson 1845)	dm elong	7.2	250	2.5–6.8	0.2–5.1	0.0080 (0.0072–0.0090)	3.379 (3.317–3.441)	0.031	0.979	0.00
Myctophidae	<i>Diaphus brachycephalus</i> Täning 1928	dm fusi	6.0	189	1.8–5.3	0.1–3.3	0.0209 (0.0183–0.0238)	3.025 (2.940–3.111)	0.043	0.963	0.56
Myctophidae	<i>Diaphus dumerilii</i> (Bleeker 1856)	dm fusi	6.5	512	2.2–6.5	0.2–3.6	0.0184 (0.0170–0.0200)	2.825 (2.773–2.877)	0.027	0.957	0.00
Myctophidae	<i>Diaphus fragilis</i> Täning 1928	dm elong	9.9	112	3.0–8.2	0.4–8.6	0.0174 (0.0159–0.0190)	2.953 (2.903–3.002)	0.025	0.992	0.06
Myctophidae	<i>Diaphus holti</i> Täning 1918	dm (fusi)	7.0	36	3.1–7.0	0.5–5.8	0.0186 (0.0140–0.0246)	2.984 (2.814–3.153)	0.083	0.973	0.85
Myctophidae	<i>Diaphus lucidus</i> (Goode & Bean 1896)	dm elong	11.8	44	4.3–9.8	1.3–14.9	0.0187 (0.0157–0.0223)	2.901 (2.811–2.991)	0.045	0.990	0.03
Myctophidae	<i>Diaphus mollis</i> Täning 1928	dm fusi	6.6	102	2.1–5.8	0.1–3.0	0.0173 (0.0155–0.0193)	2.988 (2.909–3.066)	0.040	0.983	0.76
Myctophidae	<i>Diaphus perspicillatus</i> (Ogilby 1898)	dm fusi	7.1	108	3.2–6.2	0.6–4.2	0.0219 (0.0192–0.0250)	2.881 (2.795–2.966)	0.043	0.976	0.01
Myctophidae	<i>Diaphus vanhoefeni</i> (Brauer 1906)	dm (fusi)	4.2	338	1.4–3.6	0.05–0.8	0.0213 (0.0183–0.0247)	2.744 (2.609–2.880)	0.069	0.824	0.00
Myctophidae	<i>Electrona risso</i> (Cocco 1829)	lm elong	8.2	979	3.1–8.4	0.8–16.1	0.0341 (0.0323–0.0360)	2.875 (2.844–2.906)	0.016	0.971	0.00
Myctophidae	<i>Hygophum macrochir</i> (Günther 1864)	dm (fusi)	6.0	342	1.3–5.7	0.02–2.8	0.0111 (0.0104–0.0120)	3.244 (3.195–3.293)	0.025	0.980	0.00
Myctophidae	<i>Hygophum taaningi</i> Becker 1965	dm (fusi)	6.1	734	1.2–5.9	0.03–2.9	0.0151 (0.0143–0.0159)	3.033 (2.996–3.070)	0.019	0.973	0.08
Myctophidae	<i>Lampanyctus ater</i> Täning 1928	am elong	13.0	60	12.3–18.1	11.3–36.3	0.0050 (0.0028–0.0088)	3.082 (2.878–3.288)	0.102	0.939	0.42
Myctophidae	<i>Lampanyctus isaacsii</i> Wisner 1974	am (elong)	13.3	862	2.3–15.8	0.1–26.7	0.0038 (0.0034–0.0042)	3.248 (3.200–3.295)	0.024	0.954	0.00
Myctophidae	<i>Lampanyctus lineatus</i> Täning 1928	am elong	23.5	74	6.1–17.0	1.0–30.9	0.0022 (0.0018–0.0028)	3.370 (3.271–3.469)	0.050	0.984	0.00

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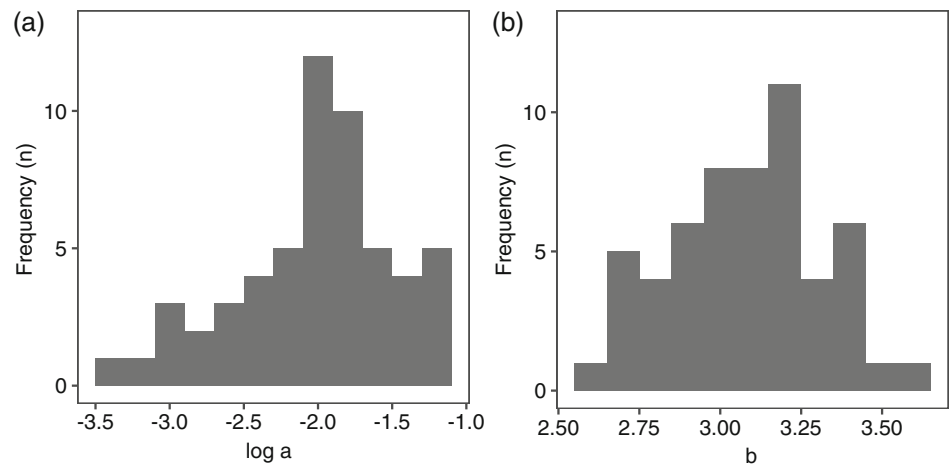
TABLE 1 (Continued)

Family	Species	Body Migr shape	Max SL lit. (cm)	N	SL (cm)	TW (g)	log $\alpha$ and 95% CI log $\alpha$	b and 95% CI b	b Std. error	R <sup>2</sup>	P value allom. growth
Myctophidae	<i>Lampanyctus nobilis</i> Täning 1928	dm elong	12.4	338	1.8–12.0	0.1–15.4	0.0071 (0.0066–0.0076)	3.095 (3.056–3.134)	0.020	0.987	0.00
Myctophidae	<i>Lampanyctus tenuiformis</i> (Brauer 1906)	pm elong	15.3	108	4.4–15.2	0.7–40.1	0.0084 (0.0070–0.0102)	3.117 (3.036–3.199)	0.041	0.982	0.01
Myctophidae	<i>Lepidophanes guentheri</i> (Goode & Bean 1896)	dm elong	7.8	795	2.4–7.7	0.1–4.4	0.0081 (0.0076–0.0088)	3.099 (3.055–3.142)	0.022	0.961	0.00
Myctophidae	<i>Lobianchia doffeini</i> (Zugmayer 1911)	dm fusi	5.0	110	2.4–4.9	0.3–2.2	0.0322 (0.0268–0.0386)	2.614 (2.475–2.753)	0.070	0.928	0.00
Myctophidae	<i>Myctophum nitidulum</i> Garman 1899	dm fusi	8.3	17	1.7–7.3	0.1–5.5	0.0109 (0.0092–0.0129)	3.129 (3.029–3.229)	0.047	0.996	0.01
Myctophidae	<i>Notosopelus resplendens</i> (Richardson 1845)	dm elong	9.5	628	1.6–9.3	0.05–9.9	0.0113 (0.0108–0.0117)	3.045 (3.026–3.063)	0.010	0.994	0.00
Myctophidae	<i>Symbolophorus veranyi</i> (Moreau 1888)	dm fusi	12.0	18	4.1–11.6	0.8–21.3	0.0142 (0.0097–0.0207)	2.978 (2.792–3.164)	0.088	0.985	0.80
Nomeidae	<i>Cubiceps gracilis</i> (Lowe 1843)	NA	18.0	29	6.6–12.5	3.8–30.1	0.0069 (0.0048–0.0099)	3.346 (3.170–3.523)	0.087	0.982	0.00
Opisthroctidae	<i>Opisthroctus soleatus</i> Vaillant 1888	nm (fusi)	10.5	25	3.6–7.4	1.8–11.9	0.0454 (0.0328–0.0628)	2.809 (2.600–3.018)	0.101	0.970	0.07
Paralepididae	<i>Lestidiops affinis</i> (Ege 1930)	nm (elong)	11.2	27	4.1–9.6	0.1–1.6	0.0005 (0.0004–0.0007)	3.573 (3.399–3.750)	0.085	0.985	0.00
Paralepididae	<i>Lestidiops joyakari</i> (Boulenger 1889)	nm elong	10.0/20.0	25	7.6–15.1	0.6–6.3	0.0006 (0.0003–0.0011)	3.439 (3.171–3.707)	0.130	0.967	0.00
Paralepididae	<i>Lestolepis intermedia</i> (Poey 1868)	nm elong	22.0/33.8	61	9.8–17.8	1.0–5.9	0.0013 (0.0008–0.0020)	2.944 (2.772–3.116)	0.086	0.951	0.52
Phosichthyidae	<i>Ichthyococcus ovatus</i> (Cocco 1838)	nm fusi	6.0	43	3.5–8.5	0.7–8.4	0.0253 (0.0211–0.0304)	2.663 (2.555–2.770)	0.053	0.984	0.00
Phosichthyidae	<i>Vinciguerra nimbaria</i> (Jordan & Williams 1895)	dm fusi	5.3	460	1.9–5.5	0.05–2.1	0.0065 (0.0059–0.0071)	3.250 (3.184–3.316)	0.034	0.954	0.00
Platyroctidae	<i>Searsia koefoedi</i> Parr 1937	nm (fusi)	15.0	68	5.5–14.3	1.4–33.4	0.0034 (0.0026–0.0043)	3.453 (3.352–3.555)	0.051	0.986	0.00
Sternoptychidae	<i>Argyropelecus affinis</i> Garman 1899	lm deep	8.4	1076	1.5–7.8	0.04–10.4	0.0155 (0.0147–0.0164)	3.163 (3.129–3.197)	0.017	0.969	0.00
Sternoptychidae	<i>Argyropelecus gigas</i> Norman 1930	lm deep	12.0	98	2.6–9.4	0.3–24.1	0.0144 (0.0128–0.0163)	3.268 (3.195–3.341)	0.037	0.988	0.00
Sternoptychidae	<i>Argyropelecus sladeni</i> Regan 1908	lm deep	7.0	499	2.3–8.3	0.4–13.2	0.0333 (0.0314–0.0354)	2.897 (2.859–2.936)	0.020	0.978	0.00
Sternoptychidae	<i>Polyipnus polli</i> Schultz 1961	nm deep	5.0	71	2.4–4.5	0.7–3.5	0.0586 (0.0407–0.0843)	2.659 (2.356–2.962)	0.152	0.814	0.03
Sternoptychidae	<i>Sternoptyx diaphana</i> Hermann 1781	nm deep	5.5	271	1.4–5.0	0.1–6.9	0.0763 (0.0733–0.0900)	2.673 (2.565–2.782)	0.055	0.900	0.00
Stomiidae	<i>Astronesthes richardsoni</i> (Poey 1852)	am elong	15.9	65	2.3–17.2	0.1–32.9	0.0038 (0.0033–0.0044)	3.179 (3.108–3.248)	0.035	0.992	0.00
Stomiidae	<i>Chauliodus schmidtii</i> Ege 1948	am (elong)	23.0	250	5.0–22.3	0.3–32.2	0.0013 (0.0010–0.0016)	3.231 (3.148–3.315)	0.042	0.959	0.00
Stomiidae	<i>Chauliodus sloani</i> Bloch & Schneider 1801	am elong	30.0	71	8.0–24.8	1.2–42.6	0.0008 (0.0005–0.0016)	3.355 (3.143–3.568)	0.107	0.934	0.00
Stomiidae	<i>Chauliodus</i> spp.	am (elong)	30.0	73	3.0–25.6	0.1–53.1	0.0021 (0.0016–0.0027)	3.043 (2.952–3.135)	0.046	0.984	0.35
Stomiidae	<i>Stomias affinis</i> Günther 1887	am elong	20.0	11	5.2–18.0	0.3–14.4	0.0010 (0.0006–0.0019)	3.318 (3.070–3.565)	0.109	0.989	0.02

Note: Migr, migration behaviour according to literature references (dm, diel migrator >300 m vertical range; lm, limited migration amplitude of <300 m vertical range; am, asynchronous/partial migrator, where part of the population migrates every night or the whole of the population migrates at different daytimes (e.g., bimodal); nm, nonmigrator); body shape: deep, short-deep; fusi, fusiform; elong, elongated, brackets indicate that no FishBase entry was available or the species was reassigned; Max SL lit. cm, maximum reported standard length (cm) in the area; N, sample size; SL (cm), size ranges (standard length in cm) analysed in the present study; TW (g), weight range (total weight g) analysed; log  $\alpha$  and 95% CI log  $\alpha$ , intercept of log-log LWR (cm, g) and 95% confidence interval; b and 95% CI b, regression coefficient b and 95% confidence interval; b std. error, standard error of b; R<sup>2</sup>, coefficient of determination; P value allometric growth <0.05 indicates significant departure from isometric growth. Bold font indicates new maximum sizes for a species.



**FIGURE 2** Frequency distribution of (a) mean log  $a$  (binwidth 0.2) and (b) mean exponent  $b$  (binwidth 0.1) based on 55 records (measured in centimetres and grams) of mesopelagic species of the eastern tropical North Atlantic during cruise WH383



condition of different specimens from the same sample, independent of length, but dependent on the same underlying LWR. Although the investigated species showed in many cases significant variation in LWRs between different regions, no subpopulation structure on the scales of our study regions is known in the investigated species. Therefore, and to facilitate comparison with existing studies, we present results using  $K_{rel}$  in the present study in favour of relative weight ( $W_{rel}$ ) in relation to mean weight, which was recommended by Froese (2006) for across-population studies with differing underlying LWRs.

### 3 | RESULTS

Based on a total of 12,597 individual length and weight measurements (Supporting Information Figure S1), we estimated LWRs of 55 species of mesopelagic fishes belonging to 13 families (Table 1). Species of the family Myctophidae were most numerous in our study (27 species), followed by the families Sternoptychidae (five species), Stomiidae (four species) and Gonostomatidae (four species). Functionally, diel migrators and nondiel migrators (asynchronous, limited, partial and nonmigrators) were covered in equal parts. The number of analysed individuals ranged from 10 to 1076 specimens, with 50% of the species having 98 or more individuals analysed each. In 31 species, body lengths were within the maximum range of body lengths recorded in the area, with new records for maximum lengths for 13 species: *Argyroleucus sladeni* Regan 1908, *Astronesthes richardsoni* (Poey 1852), *Bathylagoides argyrogaster* (Norman 1930), *Bolinichthys indicus* (Nafpaktitis & Nafpaktitis 1969), *Zaphotias pedaliotus* (Goode & Bean 1896), *E. risso*, *Gonostoma denudatum* Rafinesque 1810, *Ichthyococcus ovatus* (Cocco 1838), *Melamphaes polylepis* Ebeling 1962, *Lampanyctus ater* Täning 1928, *Lampanyctus isaaci* Wisner 1974, *Platyberyx opalescens* Zugmayer 1911 and *Vinciguerria nimbaria* (Jordan & Williams 1895).

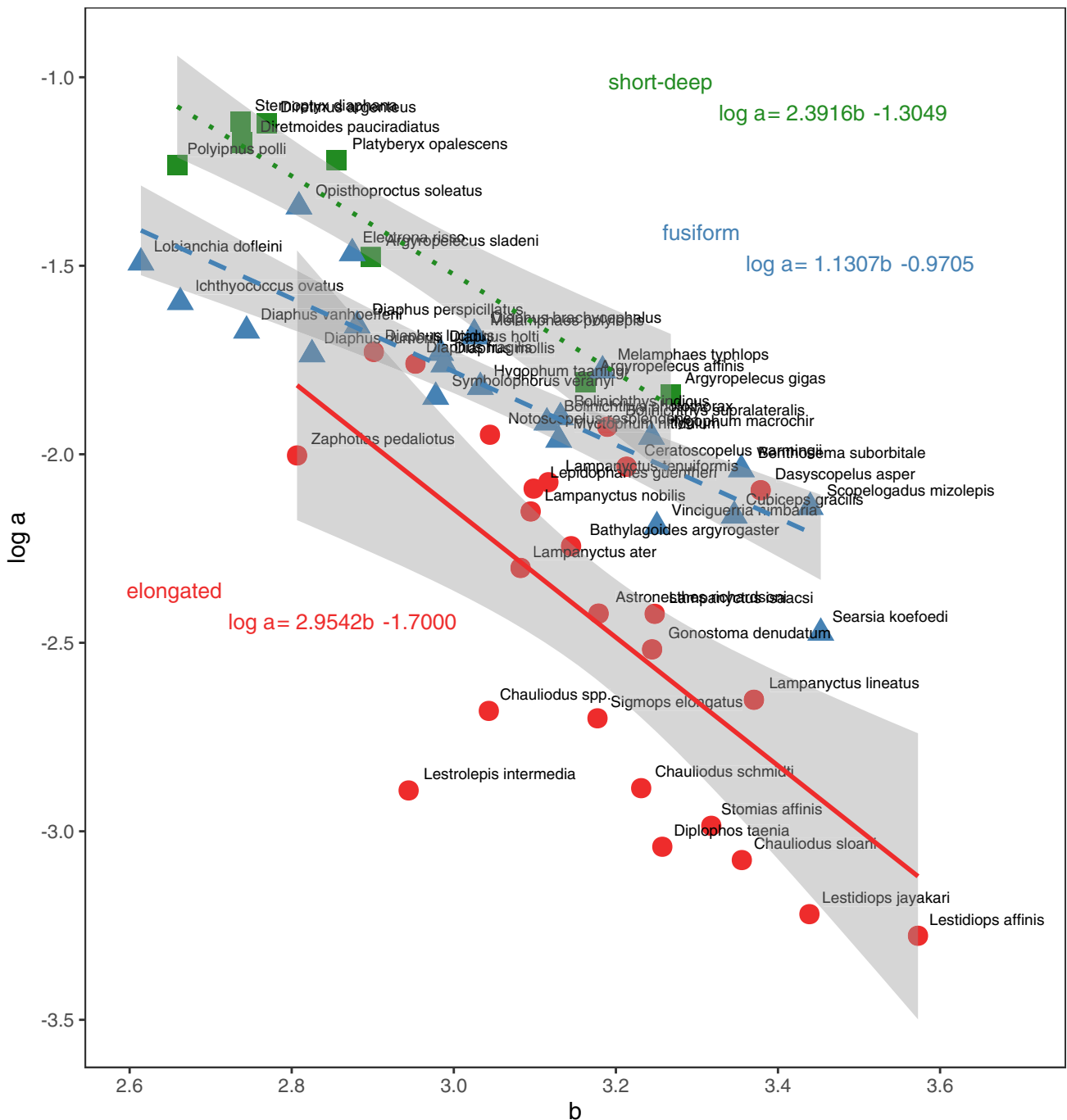
#### 3.1 | Across-species variation in LWRs

The frequency distribution of mean log  $a$  for the 55 species analysed in this study showed a slightly left-skewed distribution and a mean

$a$  of 0.0172 (median 0.0113; Shapiro–Wilk test  $P < 0.001$ ; Figure 2a). The frequency distribution of mean  $b$  showed a roughly normal distribution (Shapiro–Wilk test  $P > 0.5$ ). Most values for  $b$  fell between 2.5 and 3.5, and the mean exponent  $b$  was 3.08 (median 3.12; Figure 2b).

#### 3.1.1 | Body shape and form factor $a_{3,0}$

Body shape as covariate ['elongated' (n: 25), 'fusiform' (n: 23) and 'short-deep' (n: 8)] strongly determined the variation in log  $a$  as a function of parameter  $b$  (Figure 3; residual std. error: 0.27 on 50 d.f., multiple  $R^2 = 0.78$ , adj.  $R^2 = 0.76$ ,  $F_{(5,50)} = 35.7$ ,  $P < 0.001$ , AIC ( $k=2$ ) = 18.12). Neither slopes nor intercepts differed significantly between the different body shape groups (difference between 'elongated' and 'fusiform', intercept  $P = 0.141$ , slope  $P = 0.066$ ). For the mesopelagic fish species investigated, the form factor  $a_{3,0}$  indicated a significant increase of median  $a_{3,0}$  from 'elongated' to 'fusiform' to 'short-deep' body shapes [median 0.0066 (elongated), 0.0174 (fusiform), 0.0314 (short-deep)], whereby roughly upper and/or lower quartiles overlapped between the different body shape groups (Figure 4a). Also related to sampled species numbers, most taxonomic families showed a similar form factor  $a_{3,0}$ , with the notable exception of species of the family Myctophidae and, less so, the family Sternoptychidae, which occupied a comparatively wide range (Figure 4b). In the elongated body shape group, species with an exceptionally large form factor  $a_{3,0}$  were the myctophids *Dasyscopelus asper* (Richardson 1845), *Bolinichthys supralateralis* (Parr 1928) and *Ceratoscopelus warmingii* (Lütken 1892, Figure 4c). Overlap in the form factor between the 'fusiform' and 'short-deep' body shapes was due to comparatively high form factors  $a_{3,0}$  in the myctophid *Benthosema suborbitale* (Gilbert 1913), the melamphids *Melamphaes typhlops* (Lowe 1843) and *Scopelogadus mizolepis* (Günther 1878), as well as the opisthotroctid *Opisthoproctus soleatus* (Vaillant 1888), all characterized as fusiform, as well as a comparatively low form factor  $a_3$  in the short-deep-shaped sternoptychid *Polyipnus polli* Schultz 1961. When reassigning the most questionable overlapping species based on their form factor  $a_{3,0}$  (*D. asper*, *B. supralateralis*, *C. warmingii* as 'fusiform' instead of 'elongated'), the fit of the previous model improved considerably (Supporting Information Figure S2; residual std. error 0.22 on 50 d.f., multiple  $R^2 = 0.85$ , adj.



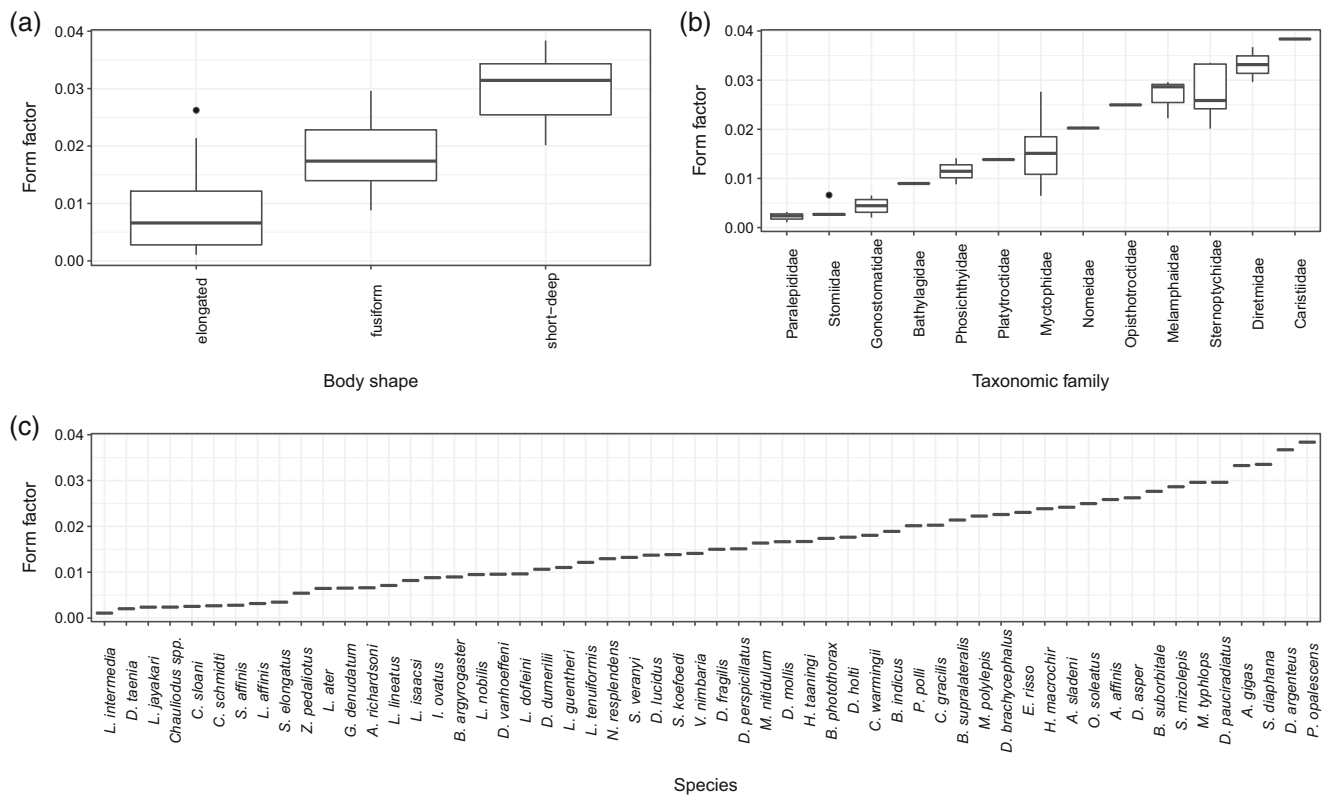
**FIGURE 3** Scatter plot of mean  $\log a$  (SL) over mean  $b$  for 55 mesopelagic species with information on body shape. Body shape: ●, elongated; ▲, fusiform; ■, short-deep

$R^2 = 0.84$ ,  $F_{(5,50)} = 58.5$ ,  $P < 0.001$ ,  $AIC = -4.56$ ) and the difference in the intercept and slope between 'elongated' and 'fusiform' became significant (intercept  $P = 0.012$ , slope  $P = 0.003$ ).

### 3.1.2 | Parameter $b$

At the taxonomic level, large variability existed in parameter  $b$  between species of the same taxonomic family (Table 1 and Figure 3). In only nine out of the 55 species analysed, isometric growth was very likely in our

study region [ $P > 0.05$ , excluding five species: three species with limited samples sizes ( $\leq 25$ ) and two species with a limited size range analysed]. These included four species of the genus *Diaphus*, two species of the genus *Bolinichthys*, the myctophid *Hygophum taaningi* Becker 1965, the melamphaid *M. polylepis* and the stomiid *Chauliodus* spp. In 13 species, the lower (CI 2.5%) and upper confidence interval (CI 97.5%) of parameter  $b$  were lower than 3.0, suggesting negative allometric growth. The species with lowest values for mean  $b$  (2.6–2.8) were the nonmigrators *P. polli* (Sternoptychidae), *I. ovatus* (Phosichthyidae), *Sternoptyx diaphana* Hermann 1781 (Sternoptychidae), *Diretmus argenteus* Johnson 1864



**FIGURE 4** Distribution of form factor  $a_{3,0}$  for 55 mesopelagic species related to (a) body shape, (b) taxonomic family and (c) species. Form factor calculated from Equation 2 using across-species slope of  $S = -1.358$  based on 1223 fish species presented in equation 17 in Froese (2006)

(Diretmidae), *Diretmoides pauciradiatus* (Woods 1973) (Diretmidae), *O. soleatus* (Opisthroctidae) and *Z. pedaliotus* (Gonostomatidae), but also the migratory myctophids *Lobianchia doleini* (Zugmayer 1911), *Diaphus vanhoeffeni* (Brauer 1906) and *Diaphus dumerilii* (Bleeker 1856). On the contrary, 22 species (excluding seven species, six species with biased size ranges and one with limited sample availability) had a value of  $b$  with an upper and lower confidence interval limit larger than 3.0, suggesting positive allometric growth. Excluding species with potentially limited size ranges analysed [i.e., the paralepidids *Lestidiops affinis* (Ege 1930) and *Lestidiops jakakari* (Boulenger 1889), the myctophid *B. suborbitale* and the stomiid *Chauliodus sloani* Bloch & Schneider 1801], highest values for mean parameter  $b$  (3.25–3.45) were encountered in the nonmigrators *Searsia koefoedi* Parr 1937 (Platyroctidae), *S. mizolepis* (Melamphidae), *Cubiceps gracilis* (Lowe 1843) (Nomeidae), *Argyropelecus gigas* Norman 1930 (Sternoptychidae), *G. denudatum* (Gonostomatidae), *D. taenia* (Gonostomatidae), but also the diel migrators *D. asper* (Myctophidae) and *V. nimbaria* (Phosichthyidae), *Lampanyctus lineatus* Täning 1928 (asynchronous migrator at larger sizes) and *L. isaacsi* (asynchronous migrator at larger sizes, both Myctophidae).

## 3.2 | Within-species variation in LWRs

### 3.2.1 | Growth stanza

Using segmented regression analysis we investigated breakpoints in the LWRs of 30 mesopelagic fish species with sufficiently available size

ranges and size distributions sampled (Table 2). No breakpoint was estimated in 10 species; in nine species parameter  $b$  was larger before the breakpoint, whereas in 11 species it was smaller. Of 12 species with available estimates for size at first maturity (Froese & Pauly, 2022; Sarmiento-Lezcano *et al.*, 2018), six species had estimated breakpoints at smaller body sizes compared to size at first maturity, whereas in three species each this was at larger or at equal sizes.

### 3.2.2 | Condition

In seven of the nine species in which we investigated regional variation in relative condition  $K_{rel}$ , we observed significant regional differences in the relationship of  $K_{rel}$  with increasing body sizes (Figure 5 and Table 3). In six out of eight species sampled in the eastern low-oxygen region (LO-E), we observed an increase in relative condition from small to large specimens. At a station level, in five out of eight species (including the myctophid *L. isaacsi* not shown in Figure 5), the north-eastern-most stations 306 and/or 309 had a steeper slope in the increase in relative condition compared to other stations. On the contrary, in all other regions, relative condition decreased from small to large specimens in the majority of species (LO-W, 3 decreasing vs. 1 increasing/1 stagnant; EQ-N, 5 decr. vs. 1 incr./1 stagn.; EQ-C, 4 decr. vs. 3 incr./1 stagn.).

The sternoptychid *Argyropelecus affinis* Garman 1899 differed significantly in the slope of the relationship of  $K_{rel}$  vs. standard length (SL) between all stations, most pronounced in comparison to LO-E,



TABLE 2 Growth stanza in LWRs of 30 mesopelagic fish species of the eastern tropical North Atlantic

Family	Species	Max SL	SL first mat (L50)	n	Range SL	Break-point SL	St. err.1	Slope 1	Std. err.	CI (95%) J_u	CI (95%) J_u	Slope 2	Std. err.	CI (95%) J_u	CI (95%) J_u	Diff.
BAT	<i>Bathylagoides argyrogastrer</i>	11.0	NA	122	3.3–12.0	7.9	0.095	3.209	0.090	3.030	3.387	2.923	0.259	2.410	3.436	-0.29
DIR	<i>Diretrus argenteus</i>	11.1	NA	447	2.2–7.6	5.1	0.014	2.931	0.048	2.837	3.025	2.410	0.087	2.239	2.581	-0.52
GSTO	<i>Zaphotias pedaliotus</i>	7.2	NA	475	1.8–7.8	5.3	0.020	2.411	0.101	2.213	2.610	3.177	0.104	2.973	3.381	0.77
GSTO	<i>Diplaphos taenia</i>	20.0	NA	139	4.9–14.7	7.3	0.032	3.577	0.131	3.317	3.837	3.103	0.073	2.958	3.249	-0.47
MEL	<i>Melamphaes polylepis</i>	7.3	NA (4.0)	270	3.6–6.6	5.3	0.013	2.819	0.072	2.677	2.960	3.479	0.157	3.170	3.788	0.66
MEL	<i>Scopelogadus mizolepis</i>	9.4	NA (4.6)	280	3.7–9.3	7.2	0.011	3.582	0.045	3.494	3.671	2.634	0.180	2.280	2.988	-0.95
MYC	<i>Bolnichthys supralateralis</i>	11.7	9.0	63	4.1–10.5	n.e.										0.00
MYC	<i>Ceratoscopelus warmingii</i>	8.1	4.4	428	1.7–7.4	n.e.	0.018									0.00
MYC	<i>Dasy Scopelus asper</i>	7.2	6.5	250	2.5–6.8 (ir)	5.6	0.009	3.572	0.043	3.487	3.657	2.541	0.126	2.293	2.789	-1.03
MYC	<i>Diaphus brachycephalus</i>	6.0	3.8	189	1.8–5.3 (ir)	4.0	0.019	3.297	0.076	3.148	3.446	2.729	0.079	2.574	2.885	-0.57
MYC	<i>Diaphus dumerilii</i>	6.5	4.7	512	2.2–6.5	4.5	0.025	2.931	0.053	2.826	3.035	2.665	0.067	2.534	2.797	-0.27
MYC	<i>Diaphus fragilis</i>	9.9	5.8	112		n.e.										0.00
MYC	<i>Diaphus mollis</i>	6.6	3.0	101		n.e.										0.00
MYC	<i>Diaphus perspicillatus</i>	7.1	5.4	107		n.e.										0.00
MYC	<i>Electrona risso</i>	8.2	5.9 (5.6)	975	3.4–8.4	4.7	0.026	2.673	0.090	2.497	2.849	2.933	0.025	2.885	2.981	0.26
MYC	<i>Lampanyctus isaacsi</i>	13.3	11.0	856	5.0–15.8	11.1	0.005	3.642	0.038	3.567	3.717	2.369	0.102	2.169	2.570	-1.27
MYC	<i>Lampanyctus lineatus</i>	23.5	15.2	74	6.1–17.0	8.9	0.028	2.797	0.209	2.380	3.214	3.512	0.068	3.377	3.647	0.72
MYC	<i>Lampanyctus nobilis</i>	12.4	11.2	335	2.8–12.0	5.7	0.038	2.960	0.063	2.836	3.084	3.217	0.041	3.137	3.297	0.26
MYC	<i>Lampanyctus tenuiformis</i>	15.3	12.3	107	5.6–15.3 (ir)	9.6	0.026	3.395	0.105	3.186	3.603	2.793	0.095	2.603	2.982	-0.60
MYC	<i>Lepidophanes guentheri</i>	7.8	4.7	787	2.4–7.7	n.e.										0.00
MYC	<i>Lobianchia dofleini</i>	5.0	3.1	110		n.e.										0.00
MYC	<i>Notoscopelus resplendens</i>	9.5	5.6–6.0	628	1.6–9.3	5.8	0.036	3.111	0.021	3.070	3.153	2.902	0.044	2.817	2.988	-0.21
MYC	<i>Vinciguerra nimbaria</i>	5.3	3.4	444	1.9–5.0	n.e.										0.00
PHO	<i>Ichthyococcus ovatus</i>	6.0	NA	43		n.e.										0.00
SEA	<i>Searsia koefoedi</i>	15.0	NA	68	5.5–14.3	12.3	0.023	3.389	0.061	3.267	3.511	4.131	0.540	3.053	5.210	0.74
STE	<i>Argyroleucus affinis - LO-E</i>	8.4	NA	406		n.e.										0.00
STE	<i>Argyroleucus affinis - LO-W, EQ-N, EQ-C</i>	8.4	NA	670	2.5–7.8	4.2	0.020	2.857				3.188				0.33
STE	<i>Argyroleucus gigas</i>	12.0	NA	93	3.2–9.4	n.e.										0.00

TABLE 2 (Continued)

Family	Species	Max SL	SL first mat (L50)	n	Range SL	Break-point SL	St. err.1	Slope 1	Std. err.	CI (95%) <sub>l</sub>	CI (95%) <sub>u</sub>	Slope 2	Std. err.	CI (95%) <sub>l</sub>	CI (95%) <sub>u</sub>	Diff.
STE	<i>Argyropelecus sladeni</i>	7.0	NA	409	2.3–7.8	3.9	0.020	3.219	0.093	3.036	3.402	2.815	0.033	2.752	2.879	–0.40
STO	<i>Astronesthes richardsoni</i>	15.9	NA	64	2.8–17.2	7.2	0.075	3.024	0.093	2.838	3.210	3.441	0.111	3.219	3.664	0.42
STO	<i>Chauliodus schmidti</i>	23.0	15.5	250	5.0–22.3	12.6	0.040	2.993	0.105	2.786	3.200	3.411	0.091	3.232	3.590	0.42
STO	<i>Chauliodus schmidti/sloani</i> spp.	30.0	NA	390	5.0–25.6	12.6	0.050	3.002	0.090	2.825	3.180	3.302	0.062	3.181	3.423	0.30

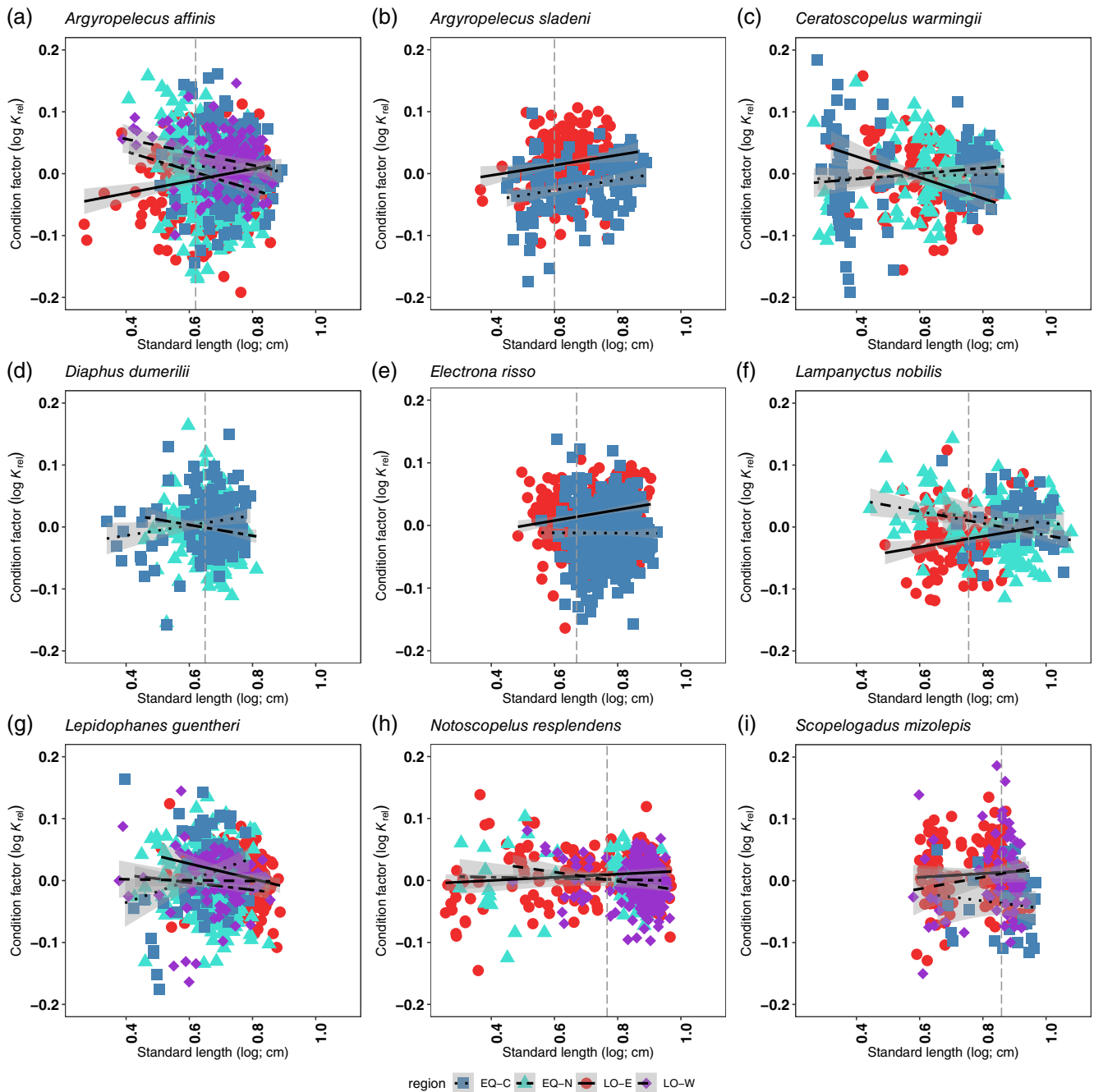
Note: Max SL, maximum reported standard length (cm) in the area; SL first mat (L50), body size (SL, cm) at first maturity based on data from FishBase (L50 estimates, unpublished data); N, sample size; Range SL, size ranges (standard length in cm) analysed in the present study (ir = interrupted); Breakpoint SL, estimated breakpoint by segmented regression analysis (cm); Std. err., standard error; Slope 1/2, parameter b of slope 1/2; CI (95%)<sub>l</sub>/CI (95%)<sub>u</sub>, lower/upper confidence interval of parameter b; Diff., difference between slope 1 and slope 2.

except for the difference northern equatorial region (EQ–N) vs. western low-oxygen region (LO–W; Figure 5a and Table 3). At small body sizes, *A. affinis* showed highest relative condition in the LO–W and EQ–N, and lowest in the LO–E. At large body sizes, relative condition was highest in the LO–E and LO–W, and lowest in the EQ–N. The sternoptychid *A. sladeni* had significantly better relative condition in the LO–E compared to the EQ–C at all body sizes (Figure 5b), increasing from small to large specimens in both regions, with a similar slope. The myctophid *C. warmingii* differed significantly in the slope of the relationship of  $K_{rel}$  vs. SL between the LO–E compared to the EQ–C and EQ–N regions, which were comparable. Relative condition in *C. warmingii* showed a slight increase in the EQ–N and EQ–C regions with increasing body sizes, whereas it decreased considerably in the LO–E (Figure 5c). The slope of the relationship of  $K_{rel}$  vs. SL increased in the myctophid *D. dumerillii* at EQ–C stations, whereas it decreased at EQ–N stations. Considering a comparable size range and removing individual outliers did not change this result (Figure 5d). The myctophid *E. risso* differed significantly in slope of  $K_{rel}$  vs. SL between the LO–E and EQ–C regions, and whereas relative condition increased from small to large specimens in the LO–E, it remained stagnant at an overall lower level at the EQ–C stations (Figure 5e). The myctophid *Lampanyctus nobilis* Tåning 1928 significantly differed in its slope of the relationship of  $K_{rel}$  vs. SL only between the LO–E and EQ–N regions. Relative condition was lower in small specimens in the LO–E compared to the EQ–N, and comparable at larger sizes (Figure 5f). The myctophid *Lepidophanes guentheri* (Goode & Bean 1896) differed significantly in its slope of the relationship of  $K_{rel}$  vs. SL between the LO–E and both the EQ–C and the EQ–N. In the EQ–C only, the slope of the relationship of  $K_{rel}$  vs. SL increased from small to large specimens, whereas it decreased in the other regions, most pronounced in the LO–E (Figure 5g). The myctophid *Notoscopelus resplendens* (Richardson 1845) differed significantly in the slope of the relationship of  $K_{rel}$  vs. SL only between the LO–E and the LO–W. Relative condition in this species increased slightly with increasing body sizes in the LO–E, remained stagnant in the EQ–N, whereas a decrease was suggested in the LO–W, based on predominantly larger specimens sampled (Figure 5h). The melamphaid *S. mizolepis* did not differ significantly in the slope of the relationship of  $K_{rel}$  vs. SL among regions. Relative condition increased in the LO–E and LO–W regions from small to large specimens, whereas a decrease was indicated in the EQ–C region (Figure 5i).

## 4 | DISCUSSION

### 4.1 | Across-species variation in LWRs of mesopelagic fishes from the eastern tropical North Atlantic

The present study presents estimates of LWRs of 55 mesopelagic fish species with novel records for 19 species. To the best of the authors' knowledge, for 25 species these LWRs are based on the most robust sample sizes and for 21 species they are based on the most



**FIGURE 5** Log-log plot of the relative condition factor ( $K_{rel}$ ) vs. standard length (cm) calculated from length-weight relationships (LWRs) of the species (a) *Argyropelecus affinis*, (b) *Argyropelecus sladeni*, (c) *Ceratoscopelus warmingii*, (d) *Diaphus dumerilii*, (e) *Electrona risso*, (f) *Lampanyctus nobilis*, (g) *Lepidophanes guentheri*, (h) *Notoscopelus resplendens* and (i) *Scopelogadus mizolepis* (Table 3). Geographic regions are indicated by linetype, symbol and colour (EQ-C, dotted line, dark-blue square; EQ-N, two-dashed line, turquoise triangle; LO-E, solid line, red circle; LO-W, dashed line, violet diamond). If present, vertical dashed grey line indicates breakpoint in the LWR estimated by segmented regression analysis (cf. Table 2)

representative size ranges reported up to now (Battaglia *et al.*, 2010; Eduardo *et al.*, 2019, 2020a; Jiang *et al.*, 2017; López-Pérez *et al.*, 2020; Olivar *et al.*, 2013; Sarmiento-Lezcano *et al.*, 2018; Slayden, 2020; Wang *et al.*, 2018). In 31 species, body lengths were within the maximum range of body lengths recorded in the area, with new records of maximum lengths for 13 species. Of these, due to the large discrepancy to known maximum size, *Lampanyctus ater* possibly is a misidentified *L. lineatus*.

Our study confirms the earlier observed influence of body shape on the parameters of LWRs in fishes in general and mesopelagic fishes in particular (Froese, 2006; López-Pérez *et al.*, 2020). Compared to findings by López-Pérez *et al.* (2020), who used a different approach and assigned the same body shape on a family level, results from the present study equally show the steepest slope in ‘elongated’ species, but also a comparatively steeper slope in as ‘short-deep’ assigned species. The respective assignment of body shape to each species is

**TABLE 3** Regional comparison of length–weight relationship parameters and pairwise statistical significance tests (ANCOVA, *P* value) of regional differences in the slope of the relationship of  $K_{rel}$  with increasing body size (SL) in nine species between four different regions (EQ–C, EQ–N, LO–E, LO–W; Fig. 1) in the eastern tropical North Atlantic

Species	Region	N	SL range	log <i>a</i> (cm, g)	<i>b</i>	Adj. <i>R</i> <sup>2</sup>	ANCOVA <i>P</i> value		
							EQ–N	LO–E	LO–W
<i>Argyropelecus affinis</i>	EQ–C	165	3.2–7.8	0.0166	3.1324	0.9482	<b>0.04</b>	<b>0.001</b>	<b>0.02</b>
<i>Argyropelecus affinis</i>	EQ–N	369	2.6–6.9	0.0199	2.9939	0.9474		<b>&lt;0.0001</b>	0.17
<i>Argyropelecus affinis</i>	LO–E	406	1.5–7.2	0.0130	3.2697	0.9803			<b>&lt;0.0001</b>
<i>Argyropelecus affinis</i>	LO–W	137	2.5–7.3	0.0194	3.0568	0.9818			
<i>Argyropelecus sladeni</i>	EQ–C	142	2.8–7.8	0.0279	2.9800	0.9875		0.06	
<i>Argyropelecus sladeni</i>	LO–E	283	2.3–7.3	0.0307	2.9793	0.9681			
<i>Ceratoscopelus warmingii</i>	EQ–C	122	1.7–7.1	0.0092	3.2188	0.9897	0.43	<b>0.04</b>	
<i>Ceratoscopelus warmingii</i>	EQ–N	155	1.8–7.4	0.0088	3.2570	0.9884		<b>0.0004</b>	
<i>Ceratoscopelus warmingii</i>	LO–E	128	2.1–6.9	0.0121	3.0107	0.9693			
<i>Diaphus dumerilii</i>	EQ–C	152	2.2–6.2	0.0165	2.9061	0.9579	<b>0.0007</b>		
<i>Diaphus dumerilii</i>	EQ–N	360	2.9–6.5	0.0209	2.7376	0.9348			
<i>Electrona risso</i>	EQ–C	525	3.6–8.4	0.0333	2.8716	0.9756		<b>&lt;0.0001</b>	
<i>Electrona risso</i>	LO–E	323	3.1–8.0	0.0308	2.9601	0.9854			
<i>Lampanyctus nobilis</i>	EQ–C	55	4.7–11.4	0.0080	3.0545	0.9798	0.22	0.07	
<i>Lampanyctus nobilis</i>	EQ–N	143	2.8–12.0	0.0087	2.9975	0.9874		<b>&lt;0.0001</b>	
<i>Lampanyctus nobilis</i>	LO–E	135	3.1–9.2	0.0059	3.1857	0.9834			
<i>Lepidophanes guentheri</i>	EQ–C	98	2.5–6.2	0.0063	3.2782	0.9598	<b>0.0001</b>	<b>&lt;0.0001</b>	0.09
<i>Lepidophanes guentheri</i>	EQ–N	426	2.7–7.1	0.0089	3.0283	0.9478		<b>0.02</b>	0.51
<i>Lepidophanes guentheri</i>	LO–E	151	3.2–7.7	0.0102	2.9760	0.9735			0.07
<i>Lepidophanes guentheri</i>	LO–W	112	2.4–7.2	0.0082	3.0917	0.9757			
<i>Notoscopelus resplendens</i>	EQ–N	63	2.0–8.7	0.0115	3.0356	0.9937		0.30	0.42
<i>Notoscopelus resplendens</i>	LO–E	208	1.8–9.3	0.0112	3.0636	0.9963			<b>0.007</b>
<i>Notoscopelus resplendens</i>	LO–W	331	2.9–9.2	0.0129	2.9712	0.9816			
<i>Scopelogadus mizolepis</i>	EQ–C	31	4.5–9.3	0.0075	3.3758	0.9718		0.39	0.27
<i>Scopelogadus mizolepis</i>	LO–E	154	3.9–8.9	0.0070	3.4708	0.9815			0.72
<i>Scopelogadus mizolepis</i>	LO–W	72	3.8–8.6	0.0061	3.5348	0.9679			

Note: Significant differences highlighted in bold.

crucial to the obtained parameters in this analysis. Since FishBase is a broadly accepted reference base for fish data, we used the morphological information given there for all but one species to have an accepted base of morphological characterization not affected by subjective interpretations, even though some morphological assignments in FishBase seemed questionable to us [e.g., the species *D. asper*, *B. supralateralis*, *C. warmingii*, *Diaphus fragilis* Tåning 1928, *Diaphus lucidus* (Goode & Bean 1896) are all assigned elongated in FishBase, although there are no obvious differences in body shape compared to the majority of other *Bolinichthys* spp. and *Diaphus* spp., which are assigned as fusiform in FishBase]. The form factor  $a_{3.0}$  proved to be reasonably suitable as an indicator of body shape in our analysis and supported reassignment of the myctophid species *D. asper*, *B. supralateralis*, and *C. warmingii* from ‘elongated’ to ‘fusiform’, which resulted in a pronounced improvement in model fit. However, as illustrated, for example, by a high form factor in the obviously not short-deep-shaped myctophid *B. suborbitale*, due to general overlap in the

form factor  $a_{3.0}$  between the different body shape groups, it may not be used as a sole indicator of body shape, as was pointed out earlier (Froese, 2006).

Considering only robust estimates based on the most representative sample sizes and size ranges from our data, in only nine out of 55 species was isometric growth indicated, whereas in the majority of species positive allometric growth was most likely. Highest values for mean parameter *b* (3.25–3.45) and increased likelihood of significant positive allometry ( $b > 3.0$ ) were encountered in the nonmigrators *S. koefoedi* (Platyroctidae), *S. mizolepis* (Melamphidae), *C. gracilis* (Nomeidae) and *A. gigas* (Sternoptychidae), but also in myctophids with known nonmigratory behaviour at larger sizes (*L. lineatus*, *L. isaacsi*), as well as in diel migratory species of the genus Gonostomatidae (*G. denudatum*, *D. taenia*). On the one hand, this could be related to the fact that larger specimens are simply thicker (Froese, 2006). On the other hand, heavier large-sized specimens could also indicate the onset of spawning in some species. Although

not examined systematically, we observed mature individuals with ripe eggs in the species *L. isaacsi* and *S. koefoedi* during random sampling. Values for  $b$  were significantly lower than 3.0 (indication of negative allometry) for the nonmigratory species *I. ovatus* (Phosichthyidae), *S. diaphana* (Sternoptychidae), *D. argenteus* (Diretmidae), *D. pauciradiatus* (Diretmidae), *Z. pedaliotus* (Stomiidae) and *E. risso* (Myctophidae), but also for the migratory myctophids *D. dumerilii* and *Diaphus perspicillatus* (Ogilby 1898). Whereas in some species with  $b < 3.0$ , sampling effects may be responsible [limited sample size in *O. soleatus* (Opisthopteroctidae) and *P. polli* (Sternoptychidae); bias towards larger size ranges in *L. dofleini* and *D. vanhoeffeni* (Myctophidae)], in other species this indication of negative allometry could equally be related to life-history patterns. In our sample area, the large-sized specimens of these species might have had already spawned, and were therefore thinner and more slender. In *D. dumerilii*, available data indicate a lifespan of only 1–2 years and post-spawning body regression would be expected in this case (Gartner, 1991). This idea is further supported by a decrease in condition at mean length for *D. dumerilii* in larger body sizes at stations 321 and 324.

## 4.2 | Within-species variation in LWRs

The analysis of breakpoints in LWRs using segmented regression analysis indicated variable patterns in the 30 species observed, unrelated to taxonomy or migration behaviour. This suggests species-specific ontogenetic variation in growth patterns at young and mature life stages, which is likely related to each species' strategy for niche separation and increasing competitive advantage at particular life stages. In the species *E. risso*, *L. lineatus*, *L. nobilis*, *L. tenuiformis*, *Chauliodus schmidti* Ege 1948 and *D. asper*, for which estimates for size at first maturity or  $L_{50}$  (length at which 50% of the fish are mature) were available (FishBase and unpublished data), the breakpoint estimate was smaller compared to size at first maturity. While the available data for size at first maturity may not be representative for our study region, this observation suggests important changes in these species' body shapes, and likely ecology, already prior to maturity. This could be related to ontogenetic changes in the vertical ecological habitat of these fishes, with accompanying changes in feeding ecology and physiology that affect body proportions. The species *N. resplendens*, *D. dumerilii* and *L. isaacsi* matched in breakpoint to size at first maturity. The former two decreased thereafter, which is in line with the hypothesis that *D. dumerilii* possibly had already spawned in the area. In *N. resplendens*, off the Canary Islands, spawning activity was observed from January to April, which would fit the same idea (Sarmiento-Lezcano *et al.*, 2018). An increase in slope following the breakpoint in *L. isaacsi* is in line with the random observation that the species was just prior to the spawning event during our sampling period.

We observed significant differences in relative condition  $K_{rel}$  between two or more regions in most species analysed. This indicates a tight connection between individual species population's fitness and/or its life-history strategy, and regional environmental

conditions (Figure 5 and Table 3). We observed the strongest increase in relative condition with increasing body sizes in the eastern low-oxygen region (LO-E) in the majority of species analysed, particularly at the north-eastern-most stations 306 and 309. An exceptional influence of increased productivity from the Mauritanian upwelling region and special conditions due to the oxygen minimum zone have already been suggested to influence trophic, community and size structure of mesopelagic communities in this area (Czudaj *et al.*, 2020, 2021; Fock *et al.*, 2019). On the contrary, the observed decrease in relative condition in the majority of species of the EQ-N indicates profound variation in overall life-history patterns and/or food supply between the two regions. The EQ-N region is influenced by the eastward flowing Northern Intermediate Countercurrent (NICC) at about 2°N and the North Equatorial Countercurrent (NECC) between c. 3 and 10°N (Stramma *et al.*, 2003, 2005, 2008), offering more oligotrophic conditions fuelled intermittently by equatorial upwelling. The most pronounced regional variations in overall relative condition were obvious in the limited migratory species *A. affinis*, *A. sladeni*, *E. risso* and *S. mizolepis*. The latter three species showed overall better condition in the LO-E, where large abundances of these species were caught at depths coinciding with the core depth of the OMZ (c. 400 m). At these depths, trophic and community analyses suggested pronounced vertical structuring, thereby possibly providing increased feeding opportunities on enhanced zooplankton biomass at biogeochemical boundary layers (Czudaj *et al.*, 2020, 2021). *A. affinis* exhibited comparatively lower relative condition compared to the other three species in the LO-E, suggesting lower competitive advantage under more productive conditions. The species shows the rare adaptation of having yellow lenses, which enables increased visual acuity and contrast, but likely also has further particular functional importance for this species, possibly offering competitive advantage under more oligotrophic tropical conditions (Somiya, 1976), where we caught the species in larger abundances. Overall, these regional variations in relative condition support the notion of complex mesopelagic fish communities in tropical regions that are finely tuned to small-scale regional environmental conditions and show a high degree of ecological niche and life-history adaptation on temporal and spatial scales (Hopkins & Gartner, 1992).

## 4.3 | Sampling effects

Compared to LWR estimates presented by López-Pérez *et al.* (2020), who sampled in the same region at the same time predominantly smaller size ranges compared to our study (comparisons based on wet-weight estimates given in their supplementary information), in 12 out of 18 species, which did not correspond in their underlying size range between the two studies, the resulting parameter  $b$  and the corresponding conclusion of growth pattern differed between the two studies, whereas in two species with a comparable size range sampled, the results were similar. These comparisons match similar



findings by López-Pérez *et al.* (2020) in comparing their own LWR estimates with those presented by Fock and Ehrich (2010) (The latter were, however, estimated by various modi and in their majority not empirically measured, but derived from already-published LWRs.). In the present study, in nine out of 10 species comparisons, in which López-Pérez *et al.* (2020) reported smaller size ranges compared to our study, the resulting parameter *b* and corresponding growth pattern were more positive based on the smaller size ranges. Our results for parameter *b* were comparable to those presented by Eduardo *et al.* (2019) from oceanic islands of the Southwestern Tropical Atlantic in the six species sampled in both studies, for which sampled size ranges were overall comparable. These comparisons demonstrate that regarding the small adult sizes of many mesopelagic fish species, estimates of LWR parameters and corresponding conclusions on growth patterns are strongly influenced by sampled size distributions and size ranges. On the other hand, compared to the study by Eduardo *et al.* (2020) from the western tropical Atlantic, in three out of five species with comparable size ranges [*D. argenteus* (Diretmidae), *Hygophum taaningi* (Myctophidae) and *D. taenia* (Gonostomatidae)], larger differences in the parameter *b* existed. In that regard, it is impossible to disentangle possible variation caused by geographic differences in population structure and different preservation strategies employed between the two studies [4% formaldehyde in the present study vs. 4% formaldehyde/70% alcohol solution in the studies by Eduardo *et al.* (2019, 2020)]. Although all specimens have been measured preserved in 4% formaldehyde in the present study, the metric analyses were conducted by different people, which could be another possible source of variation in our data. Individual sampling routines, e.g., regarding blotting and the batch size of fishes processed at one time, leaving individual fishes for varying times drying in air, could be influential in small-sized fish species. Additionally, the time span of preservation varied between a couple of days to several months, which possibly accounted for some additional variation observed in our data. In the present study, comparatively large standard errors in the species *B. suborbitale*, *L. ater*, *P. polli* and *C. sloani* indicate that the size ranges were not sufficient for a robust LWR estimate, despite a reasonable sample size ( $N > 25$ ). In the myctophid *L. guentheri*, the strong deviation in LWR at station 318 from all other stations, despite the large sample size ( $N = 322$ ), was possibly influenced by an unrepresentative size distribution. Overall, we acknowledge that the sampled size ranges in our study lack the smaller post-larval and transformation stages that would allow them to be fully representative for a given species. To achieve this, the combined use of two gear types is imperative, which is an operationally and logistically challenging, but valuable, approach to increase our understanding of the biology of mesopelagic fishes.

#### AUTHOR CONTRIBUTIONS

SC and HF conceived the study; SC identified the major part of fish samples; SC and HF analysed the data; SC wrote the first draft of the manuscript; HF and CM critically reviewed the manuscript. This Research was funded by the EU Seventh Framework Programme, Project PREFACE, grant agreement number 603521, and HF further

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## SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.

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