Mesopelagic fish communities of the tropical North Atlantic: Spatial and temporal patterns in composition and structure

Dissertation

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“*The ocean is full of surprises, particularly for those who make up their minds too quickly.*”

(N.B. Marshall, 1954)

SUMMARY

The tropical North Atlantic is a region affected by pronounced natural climate variability on multiple spatio-temporal scales, in interplay with environmental effects due to anthropogenic warming. In its eastern part, an oxygen minimum zone (OMZ) is expanding, while in addition, intensive commercial fishing effort on tuna and small pelagic fish species such as *Sardinella spp*. occurs; with potential consequences for the structure of pelagic communities and food webs. To be able to assess and monitor these changes, one essential aspect is to increase our current knowledge on mesopelagic fish communities and their functional ecology under different environments. The mesopelagic zone hosts huge biomass of mesopelagic fishes that vertically migrate and interact in the food web with other micronekton organisms, and, thereby, contribute importantly to global marine trophic and biogeochemical cycles. Global large-scale studies demonstrated regional variation in daytime main sound scattering layer (SSL) related to regional environmental characteristics. The accompanying regional variation in the vertical mesopelagic fish community structure and its relative contribution to ecological functioning remain, however, poorly investigated.

I conducted the present thesis as part of the EU FP7-Environment project Enhancing Prediction of tropical Atlantic Climate and its Impacts (PREFACE), which aimed to improve our understanding of the functioning of the tropical Atlantic climate, its predictability, and, as part of Work Package 12 (‚Environmental and anthropogenic pressures on pelagic ecosystems and fisheries'), its impacts on pelagic ecosystems and fisheries. Within this framework, we conducted a comprehensive study on abundances, biomass, vertical distribution patterns, size distributions and community and trophic structure of mesopelagic fishes and other micronekton organisms, which were collected during two surveys in 2014 (WH375) and 2015 (WH383) in the eastern North Atlantic. Additional data included in this thesis in article 2 was collected during cruise WH373 in the Southern Sargasso Sea. The study further includes a historical dataset which we compiled from surveys conducted during the period 1966–79 by the Thünen Institute of Sea Fisheries (Fock and Czudaj 2015).

The thesis is organised over a general introduction, three main chapters and a synoptic discussion. **Chapter I** (**articles 1, 2**) investigated the biogeographic composition of mesopelagic fish communities constituting sound scattering layers in three ecoregions of the tropical North Atlantic: 'Mauritania/Cape Verde' (ER 26), 'Tropical and West Equatorial Atlantic' (ER 27) and 'Central North Atlantic' (ER 24). Results from **articles 1 and 2** confirm biogeographic variation between the three ecoregions in the taxonomic composition of daily migratory fish communities sampled in the epipelagic layer during night-time. Contrary, greater spatial uniformity in non-diel migratory fish communities sampled in SSLs at mesopelagic depths conforms with the lower variability in the biotic and abiotic environment at greater depths. Our analysis thereby supports the notion that depth occurrence and migration behaviour are important factors of biogeographic distribution patterns in mesopelagic fish species. In addition, **articles 1 and 2** add detailed data regarding two poorly investigated regions in terms of mesopelagic fish community composition and hydroacoustic SSLs, i.e. the southern part of ER 26, including the OMZ, and the Southern Sargasso Sea (ER 24). Both regions are boundary zones between the tropical and the subtropical Atlantic and therefore important study regions to monitor possible future biogeographical shifts in mesopelagic fish species distributions. Our data for ER 26 and ER 27 suggest that in regions with high seasonal variability, biogeographic boundaries seasonally diverge from static lines based on mean annual oceanographic characteristics.

Chapter II (**articles 1–3**) investigated regional variation in the functional community composition and the hydroacoustic and trophic structure of mesopelagic fishes in the tropical Atlantic. Our results from **article 1** emphasise the important contribution of non-diel migratory fishes to tropical SSLs in terms of abundances and species. Because these mostly swimbladderless species remain undetected in hydroacoustic studies operating at 38 kHz, this raises an important unknown regarding their quantitative contribution to mesopelagic fish biomass and, thereby, their possible contribution to ecosystem fluxes. The increase in relative weighting of the rather large-sized myctophids *L. isaacsi, L. ater, L. lineatus* and *L. tenuiformis,* when using biomass instead of abundances in our community analyses (**article 1),** is further indicative of the potentially important functional roles of these large-sized species for ecosystem functioning. Hydroacoustic profiles (38 kHz) investigated in **articles 1 and 2** showed strong variation in the formation, amplitude and backscattering strength of SSLs between the three ERs, as well as between eastern and western oxygen minimum zone (OMZ) stations in ER 26. This implies a concomitant regional gradient in migration amplitude of the underlying mesopelagic community, which seemed to be particularly reduced in ER 26. Based on clustering and nMDS ordination (**Article 1**), as well as using stable isotope analysis (**Article 3**), simultaneous regional differences in mesopelagic fish functional community composition and trophic structure were indicated between ER 26 and ER 27, but also between the eastern and the western OMZ region, in agreement with the observed hydroacoustic patterns. The results from these analyses overall supported the hypothesis of vertically restructured mesopelagic communities and food webs in the eastern OMZ compared to the other regions. On the one hand, community analysis indicated increased mixing between diel migrators and non-diel migrators in ER 26 compared to ER 27. On the other hand, our analysis indicated also differences in the vertical ecology of generally deeper occurring non-diel migratory and predatory members of the mesopelagic fish community in ER 26, especially in the eastern OMZ. These results are in line with an influence of upwelling conditions, while in addition, increased vertical biogeochemical gradients due to the presence of the OMZ could be partly influential, which our analysis was not able to disentangle.

In **Chapter III** we used size-based indicators to investigate regional and temporal variability in mesopelagic fish communities of the eastern Atlantic. **Article 4** presents length-weight relationships (LWRs) of 55 mesopelagic fish species with novel records for 19 species. In addition we provide rare data on ontogenetic variation in LWRs and spatial variation in relative condition in mesopelagic fishes. Whereas in the eastern OMZ the majority of analysed species showed the strongest increase in relative condition from small to large specimens, this was opposite in the northern part of the equatorial region, which suggests distinctive variability in life history patterns and/or food supply on rather small scales in these biogeographic boundary regions. In **article 5** we demonstrate seasonal changes in length-frequency distributions (LFD) in the more northern located subtropical region with smaller maximum sizes and increases in younger size classes in summer compared to spring. But also in the OMZ compared to the equatorial region, larger overall abundances of smaller size classes and smaller maximum sizes were observed. These results could either be indicative of regional variation in life history patterns or alternatively, they could be related to higher oxygen demands in the OMZ region, since low-oxygen conditions favour smaller sizes due to advantageous body-mass-oxygen consumption ratios. Overall results from this regional analysis of size structure (**articles 4 and 5**) supported the observation of pronounced variation in mesopelagic fish community structure between the equatorial and the OMZ region identified also in **articles 1 and 3**. In **article 5**, we further we studied long-term changes in mesopelagic communities of the eastern North Atlantic between the periods 1966–79 and 2014/2015, using size-based indicators at the species (size class structure, extreme values and LFDs) and the community level (relative community LFD and biomass size distributions). Size-based indicators proved overall suitable to disentangle sampling from environmental effects; suggesting an environmental impact on mesopelagic size structure between the two investigated periods.

By using a comparative approach on spatio-temporal scales and a broad suite of sampling and analysis methods, this thesis provides an integrative view of mesopelagic fish communities and their functional structure in the tropical North Atlantic under varying environmental characteristics. The study presented here gives crucial ecological insights regarding the biogeographic composition of mesopelagic SSLs under different environmental conditions (**articles 1, 2**), the vertical and functional community composition, hydroacoustic and trophic structure of mesopelagic fishes under different productivity and oxygen environments (**articles 1–3**), and regional and temporal variation in relative condition and size structure (**articles 4, 5)** that overall importantly increase our current understanding of mesopelagic communities in the tropical Atlantic.

ZUSAMMENFASSUNG

Der tropische Nordatlantik ist von einer ausgeprägten natürlichen Klimavariabilität auf mehreren räumlich-zeitlichen Skalen im Zusammenspiel mit Umwelteffekten durch anthropogene Erwärmung betroffen. Im östlichen Teil breitet sich eine Sauerstoffminimumzone aus, während zusätzlich intensiver kommerzieller Fischfang auf wichtige Fischarten wie Thunfisch und kleine pelagische Fischarten wie *Sardinella spp.* betrieben wird; mit möglichen Folgen für die Struktur der Artengemeinschaften und Nahrungsnetze. Ein wichtiger Aspekt, um diese Veränderungen im pelagischen Ökosystem bewerten und überwachen zu können, ist, unser Wissen über mesopelagische Fischarten und ihrer funktionalen Ökologie unter verschiedenen Umweltbedingungen zu erweitern. Die mesopelagische Zone beherbergt eine große Biomasse von mesopelagischen Fischen und anderen Mikronekton-Organismen, die vertikal wandern und im Nahrungsnetz interagieren, und hierdurch wesentlich zu globalen marinen trophischen und biogeochemischen Kreisläufen beitragen. Globale Studien zeigten regionale Unterschiede in der Tiefe der Hauptschallstreuschicht bei Tag, hervorgerufen durch spezifische regionale Umweltbedingungen. Damit einhergehende Unterschiede in der vertikalen Struktur der mesopelagischen Fischgemeinschaften und ihrem jeweiligem funktionalem Ökosystembeitrag sind allerdings nur unzureichend untersucht.

Ich habe die vorliegende Dissertation im Rahmen des EU FP7-Environment-Projekts “Enhancing Prediction of Tropical Atlantic Climate and its Impacts” (PREFACE) durchgeführt, welches darauf abzielte, unser Verständnis der Funktionsweise des tropischen atlantischen Klimas, unsere Vorhersagemöglichkeiten und, als Teil des Arbeitspakets 12 (‚Umwelt- und anthropogene Einflüsse auf pelagische Ökosysteme und Fischereien'), seine Auswirkungen auf pelagische Ökosysteme und Fischereien zu verbessern. In diesem Rahmen führten wir eine umfassende Studie zu Abundanzen, Biomasse, vertikalen Verteilungsmustern, Größenverteilungen, Fischgemeinschaften und der trophischen Struktur mesopelagischer Fische und anderer Mikronekton-Organismen durch, die 2014 und 2015 während zweier Forschungsfahrten gesammelt wurden. Die Studie umfasst außerdem einen historische Datensatz, der beruhend auf Expeditionen des Thünen-Instituts für Seefischerei im Zeitraum 1966–79 zusammengestellt wurde (Fock und Czudaj 2015).

Die Arbeit gliedert sich in eine allgemeine Einführung, drei Hauptkapitel und eine synoptische Diskussion. **Kapitel I (Artikel 1, 2)** untersucht die biogeografische Zusammensetzung von mesopelagischen Fischgemeinschaften, aus welchen sich die Schallstreuschichten in drei Ökoregionen des tropischen Nordatlantiks zusammensetzen: ‘Mauretanien/Kap Verde’ (ER 26), ‘Tropischer and West-äquatorialer Atlantik’ (ER 27) and ‘Zentral-nördlicher Atlantik’ (ER 24). Die Ergebnisse aus **Artikeln 1 und 2** bestätigten die biogeografischen Unterschiede zwischen den drei Ökoregionen hinsichtlich der taxonomischen Zusammensetzung der täglich wandernden Fischgemeinschaften, die nachts in der epipelagischen Schicht beprobt werden. Im Gegensatz dazu beobachteten wir eine größere räumlichen Einheitlichkeit in der biogeografischen Zusammensetzung der nicht täglich vertikal migrierenden Fischgemeinschaften in Schallstreuschichten in mesopelagischen Tiefen, welches in Einklang mit der geringeren Variabilität in der biotischen und abiotischen Umwelt steht. Unsere Analyse unterstützt hiermit die Idee, dass Tiefenvorkommen und Migrationsverhalten wichtige Faktoren biogeographischer Verbreitungsmuster bei mesopelagischen Fischarten sind. Darüber hinaus liefern **Artikel 1 und 2** detaillierte Daten zu zwei bisher unzureichend untersuchten Regionen bezüglich der Zusammensetzung mesopelagischer Fischgemeinschaften und der hydroakustischen Schalstreuschichten, nämlich den südlichen Teil von ‘Mauretanien/Kap Verde’ (ER 26), einschließlich der Sauerstoffminimumzone, und die südliche Sargassosee (ER 24). Beide Regionen sind Grenzzonen zwischen dem tropischen und dem subtropischen Atlantik und daher wichtige Studienregionen, um mögliche zukünftige biogeographische Verschiebungen in mesopelagischen Fischartenverteilungen zu überwachen. Unsere Daten für ER 26 und ER 27 unterstützen die Idee, dass in Regionen mit hoher saisonaler Variabilität biogeografische Grenzen saisonal von statischen Linien abweichen, die auf mittleren jährlichen ozeanografischen Eigenschaften basieren.

Kapitel II (Artikel 1–3) untersuchte regionale Unterschiede in der Zusammensetzung der funktionellen Gemeinschaft und der hydroakustischen sowie trophischen Struktur von mesopelagischen Fischgemeinschaften im tropischen Atlantik. Unsere Ergebnisse aus **Artikel 1** heben nicht täglich vertikal migrierende Fische als wichtige Komponente tropischer

Schallsteuschichten hervor. Da diese meist schwimmblasenlosen Arten in hydroakustischen Studien bei 38 kHz unentdeckt bleiben, wirft dies eine wichtige Unbekannte hinsichtlich ihres quantitativen Beitrags zur mesopelagischen Fischbiomasse, und damit ihres möglichen Beitrags zu Ökosystemflüssen auf. Die Zunahme der relativen Gewichtung der recht großwüchsigen Myctopidenarten *L. isaacsi*, *L. ater*, *L. lineatus* und *L. tenuiformis* bei der Verwendung von Biomasse anstatt Abundanzen als grundlegende Variable in unseren Gemeinschaftsanalysen (**Artikel 1**) ist ein weiterer Hinweis auf die potenziell bedeutende funktionelle Rolle großer Arten in mesopelagischen Ökosystemen. Die in **Artikel 1 und 2** untersuchten hydroakustischen Profile (38 kHz) zeigten starke Unterschiede in der Zusammensetzung, der vertikalen Tiefe und der Rückstreustärke der Schallstreuschichten zwischen den drei ERs, sowie zwischen den Stationen der östlichen und westlichen Sauerstoffminimumzone (OMZ) in ER 26. Dies impliziert einen gleichzeitigen regionalen Gradienten im vertikalen Migrationsumfang der zugrunde liegenden mesopelagischen Gemeinschaft, die in ER 26 besonders reduziert zu sein schien. Basierend auf Clustering und nMDS-Ordination (**Artikel 1**), sowie unter Verwendung von stabiler Isotopenanalyse (**Artikel 3**) zeigen die Ergebnisse dieser Studien regionale Unterschiede in der Zusammensetzung der funktionellen Gemeinschaft mesopelagischer Fische und der trophischen Struktur zwischen ER 26 und ER 27, aber auch zwischen der östlichen und der westlichen Sauerstoffminimum-Region, in Übereinstimmung mit den beobachteten hydroakustischen Mustern. Die Ergebnisse dieser Analysen unterstützen insgesamt die Hypothese von vertikal umstrukturierten mesopelagischen Gemeinschaften und Nahrungsnetzen in der östlichen Sauerstoffminimumzone im Vergleich zu den anderen Regionen. Einerseits deutete die Gemeinschafts-Analyse auf eine verstärkte Vermischung zwischen täglich vertikal migrierenden und nicht täglich vertikal migrierenden Fischen in ER 26 im Vergleich zu ER 27 hin. Andererseits zeigte unsere Analyse auch Unterschiede in der vertikalen Ökologie von im Allgemeinen tiefer vorkommenden, nicht täglich vertikal migrierenden und räuberischen Mitgliedern der mesopelagischen Fischgemeinschaft in ER 26, insbesondere in der östlichen OMZ. Diese Ergebnisse stehen im Einklang mit einem Einfluss der Auftriebsbedingungen, während zusätzlich erhöhte vertikale biogeochemische Gradienten aufgrund des Vorhandenseins der Sauerstoffminimumzone teilweise einen Einfluss auf die vertikale Nahrungsverfügbarkeit haben könnten.

In **Kapitel III** haben wir größenbasierte Indikatoren verwendet, um die regionale und zeitliche Variabilität in mesopelagischen Fischgemeinschaften des Ostatlantiks zu untersuchen. **Artikel 4** präsentiert Längen-Gewichts-Beziehungen (LWRs) von 55 mesopelagischen Fischarten mit neuen Daten für 19 Arten. Zudem analysieren wir in einem selten durchgeführten Ansatz ontogenetische Variationen bei LWRs und räumliche Variationen der 'relative condition' bei mesopelagischen Fischen. Während in der östlichen Sauerstoffminimumzone die Mehrheit der analysierten Arten die stärkste Zunahme des 'relatvie condition' von kleinen zu großen Exemplaren zeigte, war dies im nördlichen Teil der Äquatorregion umgekehrt. Dies deutet auf eine ausgeprägte Variabilität in Lebenszyklen und/oder der Nahrungsversorgung auf eher kleinräumigen Skalen in diesen biogeografischen Grenzregionen hin. In **Artikel 5** zeigen wir saisonale Veränderungen der Längen-Häufigkeits-Verteilungen (LFD) in der nördlich gelegenen subtropischen Region, wobei kleinere Maximalgrößen und Zunahmen an jüngeren Größenklassen im Sommer im Vergleich zum Frühjahr beobachtet wurden. Aber auch in der OMZ zeigten sich im Vergleich zur Äquatorregion größere Gesamthäufigkeiten kleinerer Größenklassen, sowie kleinere Maximalgrößen. Diese Ergebnisse könnten entweder auf regionale Unterschiede in den Lebenszyklusmustern hinweisen oder alternativ mit einem höheren Sauerstoffbedarf in der ersteren Region zusammenhängen, da sauerstoffarme Bedingungen aufgrund vorteilhafterer Körpermasse-Sauerstoffverbrauchsverhältnisse kleinere Größen begünstigen. Die Gesamtergebnisse dieser regionalen Analyse der Größenstruktur (**Artikel 4 und 5**) unterstützten die Beobachtung ausgeprägter Unterschiede in der Struktur mesopelagischer Fischgemeinschaften zwischen der äquatorialen und der OMZ-Region, die auch in den **Artikeln 1 und 3** identifiziert wurden. Größenbasierte Indikatoren erwiesen sich insgesamt als geeignet, um die Probennahme von Umweltauswirkungen analytisch zu entkoppeln; und wiesen auf einen relevanten Einfluss der veränderten Umweltbedingungen auf die Größenstruktur mesopelagischer Fische zwischen den zwei untersuchten Perioden hin.

Durch die Verwendung eines vergleichenden Ansatzes auf räumlich-zeitlichen Skalen und einer breiten Palette von Probenahme- und Analysemethoden bietet diese Arbeit eine integrative Sicht auf mesopelagische Fischgemeinschaften und ihre funktionelle Struktur im tropischen Nordatlantik unter verschiedenen Umweltbedingungen. Die hier vorgestellte Studie gibt entscheidende ökologische Einblicke in die biogeographische Zusammensetzung mesopelagischer Schalstreuschichten unter unterschiedlichen Umweltbedingungen (**Artikel 1, 2**), die vertikale und funktionale Zusammensetzung der Fischgemeinschaften, die hydroakustische und trophische Struktur mesopelagischer Fische unter verschiedenen Produktivitäts- und Sauerstoffumgebungen (**Artikel 1–3**), sowie regionale und zeitliche Unterschiede in der ‘relative conditon’ und Größenstruktur (**Artikel 4, 5**), die insgesamt unser aktuelles Verständnis mesopelagischer Gemeinschaften in dieser Studienregion unter dem Einfluss von Umweltveränderungen bedeutend erweitern.

OUTLINE OF PUBLICATIONS

ARTICLE 1

Community structure of mesopelagic fishes constituting sound scattering layers in the eastern tropical North Atlantic

Stephanie Czudaj, Rolf Koppelmann, Christian Möllmann, Matthias Schaber, Heino O. Fock

SC and HF conceived the study; SC identified the major part of fish samples with contributions from HF; SC compiled the literature review of functional groups and core depth ranges; SC and HF analysed the environmental and fish community data; MS contributed and analysed the hydroacoustic data; SC wrote the first draft of the manuscript; RK, CM, MS and HF critically reviewed the manuscript.

Published in Journal of Marine Systems, Vol. 224. https://doi.org/10.1016/j.jmarsys.2021.103635.

ARTICLE 2

Distribution and diel vertical migration of mesopelagic fishes in the Southern Sargasso Sea – Observations through hydroacoustics and stratified catches

Lasse Marohn, Matthias Schaber, Marko Freese, Jan Dag Pohlmann, Klaus Wysujack, Stephanie Czudaj, Tina Blancke, Reinhold Hanel

LM and MS conceived and designed the research and analysed the data; LM, MF, JP, KW, SC and RH conducted morphological species identification; MF and JP analysed CTD and SST data; TB made genetic analyses; All authors contributed to manuscript writing and read and approved the manuscript.

Published in Marine Biodiversity. https://doi.org/10.1007/s12526-021-01216-6.

ARTICLE 3

Spatial variation in the trophic structure of micronekton assemblages from the eastern tropical North Atlantic in two regions of differing productivity and oxygen environments

Stephanie Czudaj, Anette Giesemann, Henk-Jan Hoving, Rolf Koppelmann, Florian Lüskow, Christian Möllmann, Heino O. Fock

SC, HF and RK conceived the study; SC identified the fish samples; SC compiled the literature review of functional groups and core depth ranges; SC created lab routines and prepared the samples for stable isotope analysis (SIA); AG performed SIA; SC and HF analysed the environmental and SIA data; SC wrote the first draft of the manuscript; AG, HJH, RK, FL, CM and HF critically reviewed the manuscript.

Published in Journal of Deep-Sea Research I, Vol. 163. https://doi.org/10.1016/j.dsr.2020.103275.

ARTICLE 4

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

Stephanie Czudaj, Heino O. Fock, Christian Möllmann

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.

Published in Journal Fish of Biology. https://doi.org/10.1111/jfb.15068.

ARTICLE 5

Size structure changes of mesopelagic fishes and community biomass size spectra along a transect from the equator to the Bay of Biscay collected in 1966-1979 and 2014-2015

Heino O. Fock and Stephanie Czudaj

HF conceived the study; HF and SC identified the fish samples; HF and SC compiled historical database; HF analysed the data; HF wrote the first draft of the manuscript; HF critically reviewed the manuscript.

Published in ICES Journal of Marine Science. https://doi.org/10.1093/icesjms/fsy068.

Further Publication (not included in this thesis):

An integrative assessment combining deep-sea net sampling, in situ observations and eDNA analysis identifies Cabo Verde as a cephalopod biodiversity hotspot in the Atlantic Ocean

Véronique Merten, Till Bayer, Thorsten B. H. Reusch, Oscar Puebla, Janina Fuss, Julia Stefanschitz, Alexandra Lischka, Helena Hauss, Philipp Neitzel, Uwe Piatkowski, Stephanie Czudaj, Bernd Christiansen, Anneke Denda and Henk-Jan T. Hoving

H-JH conceived the study; VM, H-JH, TB, TR, and OP planned the study; VM, JS, and JF conducted the lab work; AL, UP, SC, HH, BC, AD, and H-JH contributed the data; VM and H-JH analysed the data; VM and H-JH wrote the manuscript; TB, TR, OP, JF, JS, AL, HH, UP, SC, BC, and AD critically reviewed the manuscript. All the authors contributed to the article and approved the submitted version.

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GENERAL INTRODUCTION

Vertical ecology of mesopelagic fishes

Mesopelagic fishes in the micronekton size range (between c. 2 to 20 cm) form an important component of the mesopelagic ecosystem (Irigoien et al., 2014; Kaartvedt et al., 2012; Koslow et al., 1997), which encompasses an estimated 20–30 % of the total global ocean volume (Proud et al., 2017; Reygondeau et al., 2018). The depth interval between 200–1000 m is commonly accepted to delimit the mesopelagic zone, although this static view oversimplifies the regionally more heterogenous environmental and biological conditions encountered across ocean basins (Priede, 2017; Reygondeau et al., 2018). Although physical, biogeochemical and zoological perspectives each have their own definition, in general, the mesopelagic zone is characterised in terms of light levels as the interim zone between the sunlit epipelagic layer, where irradiance levels are sufficient to drive photosynthesis, and the dark bathypelagic and abyssal depths, where light is too low for vision to operate (below 1% of surface light levels). As pressure increases with increasing depth, the level of disturbance decreases and offers increasingly stable environmental conditions regarding temperature, salinity, dissolved oxygen concentration and nutrient profiles (Robinson et al., 2010; Sutton, 2013). These changes in the physical environmental largely drive vertical mesopelagic fish community composition and its structure. Clearly a vertical succession of specific species assemblages is demonstrated in form and function of fishes taken below 200 m (Marshall, 1979). Physiological variations regarding sensory organs (eyes, olfactory organs, lateral line systems, photophores), modes of camouflage (body colour and shape, photophores) and organismal organisation (swimbladder presence, skeleton, musculature, central nervous system, gill system) reflect adaptations to the requirements of the different vertical ecological niche dimensions (Marshall, 1979). These species assemblages occurring at different depths are vertically connected by their ultimate reliance on food from the sunlit epipelagic layers where photosynthesis takes place (e.g. Drazen and Sutton, 2017; Priede, 2017; Fig. 1).

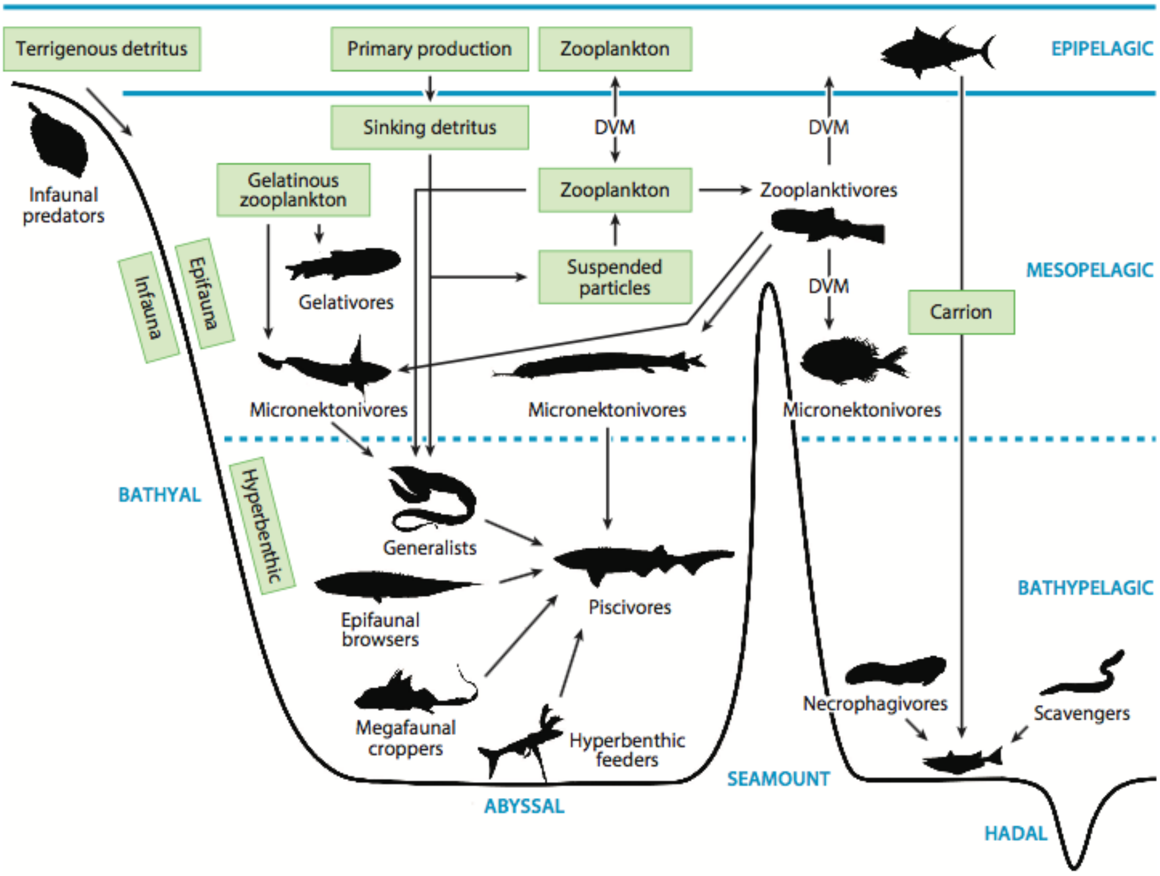

Fig. 1

Trophic diagram illustrating the various sources of food for fishes (boxes) and the primary feeding guilds. (from Drazen and Sutton, 2017)

Meso- and bathypelagic fishes may access this primary food source by active vertical migration to productive surface layers or by preying upon surface migrators in the so-called “ladder of vertical migrations” (Merrett and Roe, 1974; Vinogradov, 1962). Alternatively, they may rely upon a complimentary food web which has its base in sinking partially degraded organic material, i.e. fecal pellets, detritus, suspended and slowly sinking material (Drazen and Sutton, 2017; Gloeckler et al., 2018; Hannides et al., 2013; Koppelmann et al., 2009; Romero-Romero et al., 2019). Feeding guilds in mesopelagic fish species encompass zooplanktivores, gelativores, micronektonivores and piscivores (Drazen and Sutton, 2017). Feeding preferences in zooplanktivores vary on a size-gradient from species relying predominantly on small-sized copepods to those with a mixed crustacean diet, and others preferring non-crustacean zooplankton prey, including gelatinous zooplankton and invertebrates (Hopkins et al. 1996). The relative contribution of micronektonivores increases with increasing depth, whereby species show varying preferences for fishes, cephalopods and/or large decapods. Physiological adaptations for feeding at greater depths where prey becomes rare includes a large mouth (Ebeling and Cailliet, 1974) and the capacity to swallow prey that is larger than the predator, thereby ignoring classic predator:prey size ratios. Overall, omnivory is widespread in the mesopelagic (Drazen and Sutton, 2017), but pronounced niche partitioning has been demonstrated (Hopkins & Gartner 1992, Mauchline & Gordon 1986) including variations in feeding plasticity between specialists and generalists that may change opportunistically, as well as forced by competition pressure (Watanabe and Kawaguchi 2003). Via this vertical ecological structuring, mesopelagic fishes actively transport organic carbon and other bio-minerals between surface and mesopelagic layers, which makes them an important component of the 'biological carbon pump' (Ariza et al., 2015; Choy, 2013; Hernández-León et al., 2019; Robinson et al., 2010; Saba et al., 2021).

Rather than a simple dichotomy between migrators and non-migrators, migration behaviour is a complex phenomenon that evolved as a means of niche diversification (Marshall, 1979). Different modes exist among species and particular life cycle stages, that vary in vertical extent, depth ranges, community coherence, daytimes and modes (Hopkins et al., 1996; Pearre, 2003; Sutton, 2013). In many mesopelagic fish species life history patterns involve larval stages in surface waters, that later descent to depth layers characteristic for the adult population (Badcock and Merret, 1976; Dove et al., 2021; Moser, 1996). The majority of species of the families Myctophidae, Gonostomatidae, Phosichthyidae, Sternoptychidae have gas-filled swimbladders and perform active nocturnal diel vertical migrations to near surface layers as adult specimens (Davison, 2011; Sutton, 2013). Together with other resonant mesopelagic organisms, e.g. crustaceans and siphonophores (Barham, 1963; Davison, 2011; Proud et al., 2019; Stanton et al., 1998), they form conspicuous sound scattering layers (SSLs) at mesopelagic depths that can be detected using hydroacoustic methods. Migration amplitude and other structural characteristics of SSLs were shown to vary on global scales (Bianchi and Mislan, 2016; Klevjer et al., 2016). This implies concomittant regional variation in the mesopelagic community composition and its functional and trophic structure (Klevjer et al., 2016), but few studies have addressed the underlying biological components of SSLs, especially in a comparative approach (Ariza et al., 2016; Badcock, 1970; Currie et al., 1969; Foxton, 1970). Migration amplitude and migration behaviour in mesopelagic fishes are largely driven by irradiance levels (Aksnes et al., 2017; Langbehn et al., 2019; Melle et al., 2020; Røstad et al., 2016). Light penetration is foremost governed by productivity in surface layers due to increased turbidity from increased particulate organic matter and is, therefore, deepest in oligotrophic gyral systems and shallowest in upwelling areas. In addition, a pronounced relationship to subsurface oxygen levels was demonstrated, whereby shallower migration amplitudes were observed in oxygen minimum zones (OMZ; Bianchi et al., 2013a; Klevjer et al., 2016; Netburn and Anthony Koslow, 2015). It was suggested that this was due to interacting dynamics between the mesopelagic community and the OMZ, which produces vertical gradients of particular biogeochemical conditions (Bianchi et al., 2013a). These biogeochemical gradients increase niche opportunities and attract biological life, as shown for the OMZ of the eastern tropical Pacific where zooplankton aggregations were observed at specific boundary layers (Maas et al., 2014; Williams et al., 2014; Wishner et al., 2013). The responses of micronekton organisms remained hitherto unexplored and were speculated to vary between either, attraction, due to increased feeding opportunities, shelter from higher-aerobic predators (Stramma et al., 2012, 2010), or avoidance, when critical oxygen levels fall below a certain threshold (Ekau et al., 2010). Because OMZs are predicted to expand globally and thereby impact mesopelagic ecosystem functioning, an increased understanding of the biological processes is needed.

Mesopelagic fish communities of the tropical North Atlantic

Species compositions and their spatial distribution patterns are comparatively well described in the Atlantic. In the eastern and central part of the tropical North Atlantic studies reported species diversity (Backus et al., 1965; Hanel and John, 2015), investigated general biogeographic and vertical patterns (Kinzer and Schulz, 1988, 1985; Kobyliansky et al., 2010; Krefft, 1976, 1974; Olivar et al., 2017), biogeographic distribution patterns focussing on the families Myctophidae (Backus et al., 1977; Hulley, 1981; Nafpaktitis et al., 1977), and Stomiidae (Porteiro, 2005), the contribution of migratory mesopelagic fishes to neuston fish assemblages (Olivar et al., 2016) and distribution of larval stages

(Dove et al., 2021). In the western part, a regional focus was on the Sargasso Sea (Backus et al., 1970, 1969; Hulley and Krefft, 1985; Jahn and Backus, 1976; Sutton et al., 2010), and the western equatorial region (Backus et al., 1970). Functioning and structure of the communities have received much less attention, foremost restricted to individual species. Regarding this, feeding in mesopelagic fishes has been explored in several studies, mostly in the eastern equatorial region (De Alwis and Gjøsaeter, 1988; Duka, 1987; Kinzer, 1982; Kinzer and Schulz, 1988, 1985; Tkach, 1988, 1987a, 1987b).

Mesopelagic species communities and their functional structure are assumed to be relatively consistent in regions that show similar environmental and productivity characteristics (Angel, 1997; Krefft, 1974). The physical environment strongly determines physiological processes and each species shows a specific tolerance towards e.g. temperature, pressure, light intensity, dissolved oxygen concentration and food availability (Marshall, 1979). In addition, competitive interaction and exclusion strongly co-determine distribution patterns (Marshall, 1979). Moreover, previous work strongly suggests that species have very close adaptations to use surface and midwater currents throughout their life histories as means to maintain their population in the right environment (Sassa et al., 2004, 2002). Based on distribution patterns in either, mixed mesopelagic fish species (Backus et al., 1970, 1977; Badcock and Merret, 1977; Krefft, 1974) or specifically myctophid communities (Hulley, 1981; Hulley and Krefft, 1985), mesopelagic biogeographic classification schemes were proposed. These schemes were largely based on collections obtained with gear only able to sample the smaller size-spectra of the mesopelagic community (10-foot IKMT, RMT8). It is expected that species' distribution patterns change throughout life histories and that larger-sized deeper occurring non-migratory species vary in their distribution patterns from shallower species (Badcock and Merret, 1976). Krefft (1976, 1974), based on data collected with the large commercial midwater trawl Engel MT-1600, has overall confirmed the biogeographic boundaries derived based on smaller gear, but also indicated wider distribution patterns in meso- and bathypelagic species, however with specialized patterns. In the present study we use the classification presented by Sutton et al. (2017) that is based on an integrated approach combining physical parameters (water masses, OMZs, temperature extremes and surface water productivity) and taxonomic expertise (Fig. 2). Other classifications based on acoustic (Backus and Craddock, 1977; Proud et al., 2017) or biogeochemical characteristics (Reygondeau et al., 2018) give stronger emphasis to the vertical dimension and indicate more varying characteristics in deeper mesopelagic depth layers. All of these schemes reflect the strong influence of surface processes on mesopelagic communities by largely corresponding with the ecological biogeography based on surface primary productivity (Longhurst, 2007).

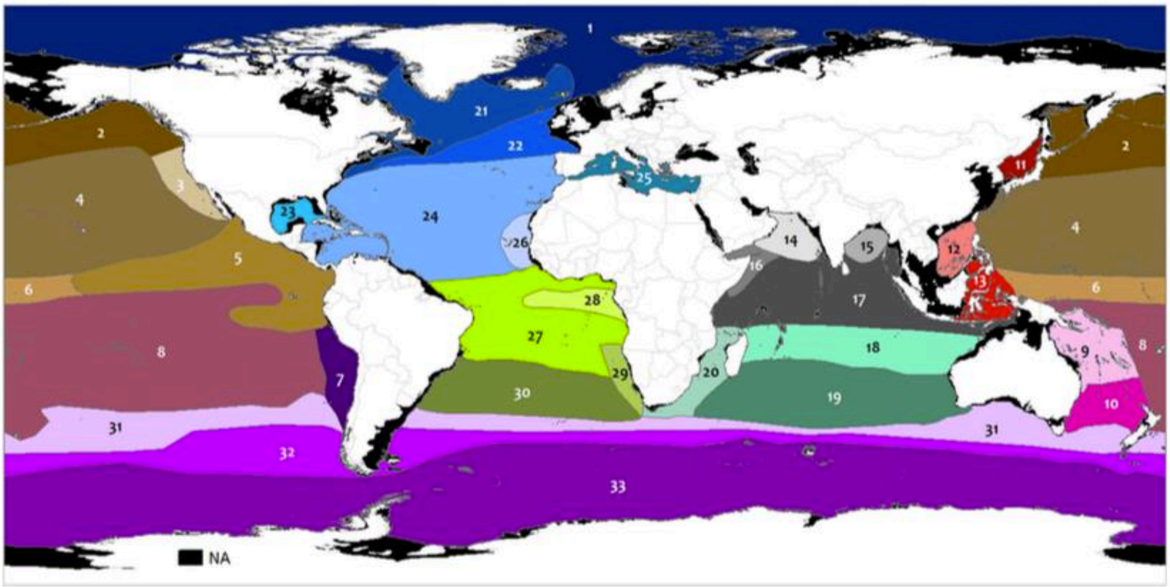

Fig. 2

Proposed mesopelagic ecoregions of the world (from Sutton et al., 2017).

In the tropical North Atlantic Sutton et al. (2017) defined three ecoregions. Ecoregion 26 ‘Mauritania/Cape Verde’ encompasses a small, but very dynamic area around the Cape Verde Islands exhibiting North Atlantic environmental extremes, i.e. highest primary production and lowest oxygen concentrations. Mixing of tropical and subtropical water masses across the Cape Verde Frontal zone (CVFZ) in globally among the most complex transition zones (Pelegrí et al., 2017; Zenk et al., 1991) offers broad opportunities for species dispersal between northern and southern latitudes, resulting in particular mesopelagic faunal communities, including several pseudoceanic and endemic species (Backus, 1986; Badcock, 1981; Hulley, 1981). The annual migration of the Intertropical Convergence zone (ITCZ) drives upwelling along the coast which, at its southernmost location off Senegal, is most intense in boreal winter (Jan–May). South-east of Cape Verde islands is a deep oxygen minimum zone (OMZ) at c. 400 m depth with its core region centred at about 20 °W, 10 °N (Brandt et al., 2015). Minimum dissolved oxygen concentrations (c. 40 µmol/l minimum) are at the threshold of physiologically limiting levels (Ekau et al., 2010). South of the Cape Verde Islands there is a large-scale cyclonic circulation called the Guinea Dome (Siedler et al., 1992). The particular effects of both environmental features on mesopelagic community structure have not yet been explored.

The ecoregion 27 ‘Tropical and West Equatorial Atlantic’ extends meridionally from 5–10 °N to 20–25 °S and latitudinally across the Atlantic (except for a small band in the equatorial east) and is defined by characteristic temperature, salinity and oxygen profiles. In our study we focus on the northern equatorial region which is composed of several narrow zonal current and countercurrent bands (Stramma et al., 2005, 2003). Directly on the equator, the eastward flowing Equatorial Undercurrent (EUC) supplies oxygen-rich water in the thermocline layer, as does at intermediate depths the eastward flowing Northern Intermediate Countercurrent (NICC) at about 2 °N. Between about 3–10 °N, the North Equatorial Countercurrent (NECC) flows generally eastward in a semi-persistent two-core structure (Stramma et al., 2008) and is strongest in summer and fall (Mayer and Weisberg, 1993; Richardson and Reverdin, 1987; Stramma et al., 2008). Related to this migration, the thermocline of the whole tropical Atlantic tilts seasonally about two axes – zonal and meridional, thereby affecting vertical nutrient fields (Garzoli and Katz, 1983). Although this ecoregion is overall characterised by mostly oligotrophic conditions, occasional upwelling in the equatorial band causes periodic higher productivity on limited spatial scales.

As part of the CVFZ, the North Equatorial Current (NEC) flows westward and forms the southern border of the ecoregion 24 ‘Central North Atlantic’. This largest Atlantic ecoregion reaches to c. 40 °N which is the proposed barrier between warm- and coldwater species (Backus et al., 1977). This region exhibits consistent hydrographic conditions and a comparatively uniformly low chlorophyll field. In our study we centre our investigations on the southern Sargasso Sea. The Sargasso Sea is an anticyclonic gyre in ER 24 and traditionally defined by the presence of the free-floating pelagic plant *Sargassum,* which is enclosed by dynamic borders of ocean currents. Mesoscale eddies occur periodically in this region and may influence mesopelagic communities. Between 20–30 °N the Subtropical Convergence Zone (STCZ) is a distinct temporal frontal system between the more productive colder northern subtropical and the less productive southern tropical part of the Sargasso Sea, which acts as weak biogeographic border (Backus et al., 1977; Durand et al., 2001; Hulley and Krefft, 1985).

The biogeographic distribution patterns of communities we see today are the products of the physical environment and competition events of the past. These evolutionary processes are expected to speed up due to climate warming and anthropogenic changes to marine ecosystems, especially in tropical regions where many species show shorter life cycles, and, thus, possibly higher evolutionary rates (Marshall, 1979). The tropical Atlantic is a region with large climate variability on seasonal and multi-decadal scales and an expanding oxygen minimum zone in its eastern part (Stramma et al., 2012, 2008). These environmental changes are accompanied by decade-long anthropogenic fishing pressure on high and mid-trophic level fish species, such as tuna and *Sardinella spp*. which may alter food web structure in this area, as observed elsewhere (Duffy et al., 2017; Olson et al., 2014; Polovina and Woodworth-Jefcoats, 2013; Shannon and Cury, 2004; Smith et al., 2011). To be able to assess and monitor these changes, it is essential to increase our current knowledge on mesopelagic fish species distributions and use the available data to investigate decadal community changes (John et al., 2016). In that regard, observed differences in size-based indicators can be used as indicators of ecosystem changes and environmental status, if detangled from sampling effects (dos Santos et al., 2017; Jennings and Blanchard, 2004; Petchey and Belgrano, 2010; Shin et al., 2005; Trenkel et al., 2004). Body size is a key trait in the study of pelagic ecosystem’s functioning, where many species grow through several orders of magnitude in body mass and two or three trophic levels (Brown, 1995; Dickie et al., 1987; Jennings et al., 2008). Body size defines important aspects of populations and organismal physiology across taxa, regarding metabolism, growth rates, predator-prey relationships, predator-prey size ratios and other factors (Andersen et al., 2016; Brown et al., 2004; Peters, 1983; Romero-Romero et al., 2016; Saint-Germain et al., 2007). Simple and consistent scaling laws describe how biological features change with size (Brown and West, 2005). The size structure of pelagic communities reflects on the one hand trophic structure and community energy flow (Dickie et al., 1987; Jennings et al., 2008; Romero-Romero et al., 2016), which is directly related to ecosystem functioning by affecting the magnitude of flux in the carbon cycle (Brandão et al., 2021; Brun et al., 2019; Hernández-León et al., 2019). In addition a strong relation of body size to the physical environment exists, most notably the temperature-size rule, i.e. smaller body sizes at higher temperatures (Audzijonyte et al., 2019). Although the mechanical causes of this rule are still debated, all likely responses are connected to currently observed environmental changes related to global warming, expansion of oxygen minimum zones and anthropogenic fishing pressure.

Gear selectivity in mesopelagic studies

Sampling methods for mesopelagic fishes have been considerably developed and refined in the course of the past 150 years since the HMS *Challenger* sailed out on the first circum-global attempt to systematically study life in the deep sea (see Priede, 2017 for a review). The method with the longest tradition is net-trawling and our knowledge regarding the influence of net specifics and trawling operations on catch performances has considerably improved during the past decades (Clarke, 1983; Gartner et al., 1989; Harrisson, 1967; Heino et al., 2011; Kaartvedt et al., 2012; Kashkin and Parin, 1983; Pearcy, 1983, 1978; Porteiro, 2005; Priede, 2017; Stein, 1985; Sutton, 2013). Each net shows a particular catchability for a specific size range and taxonomic spectrum, which further varies on spatio-temporal scales (Gartner et al., 1989; Heino et al., 2011). This catchability is governed on the one hand by an interplay of technical aspects, i.e. size, trawl opening area and geometry, trawling speed, towing direction and contamination, while on the other hand behavioural responses in visually attuned mesopelagic fishes are very important, i.e. avoidance, escapement, attraction, entanglement of elongated species, herding, swimming speed and vertical orientation (Gartner et al., 1989; Harrisson, 1967; Heino et al., 2011; Jamieson et al., 2006; Kaartvedt et al., 2012; Kashkin and Parin, 1983; Pearcy, 1983). In addition, spatial patchiness in distribution patterns, especially on vertical scales (Angel, 1993), but further overall densities, which decrease in deeper living and larger species (Angel, 1997; Sutton, 2013) importantly influence the perceived community composition, if not considered by an appropriate sampling scheme. The intuitive solution of combining the data from different types of trawls to capture the full suite of mesopelagic size-spectra is attached with many difficulties (see references in Heino et al., 2011). Nevertheless, net trawled data is indispensable in the study of mesopelagic fishes, by providing valuable biological, physiological and ecological data and precise taxonomic identification.

Unaffected by size-based constraints, optical, biochemical and genetic methods yield additional perspectives that may complement results from net sampling for a more holistic view. Optical methods provide rare behavioural insights e.g. *in situ* observations of predator-prey interactions, posture, flight responses, etc. (Grimaldo et al., 2020; Hunt et al., 2000; Kaartvedt et al., 2019; Robison et al., 2017). These observations allow to interpret the data collected by net trawls more sensibly, despite their lower taxonomic resolution (Barham, 1971; Priede, 2017; Robison et al., 2017). In addition, optical methods allow insights regarding fragile mesopelagic food web components, such as gelatinous fauna, which is often damaged in trawls and unidentifiable in stomach content studies (Hosia et al., 2017; Hoving et al., 2019, 2020; Skjoldal et al., 2013). Since the detection of deep sound scattering layers in 1948 (Eyring et al., 1948), the comparatively cheap and easy collection of hydroacoustic data on a global scale has advanced our views regarding mesopelagic migration patterns (Bianchi et al., 2013b; Bianchi and Mislan, 2016; Klevjer et al., 2016) and the magnitude of the biomass of mesopelagic fishes (Davison et al., 2015; Irigoien et al., 2014; Kaartvedt et al., 2012; Koslow et al., 1997). Our ability to classify sound scattering sources, as well as to relate backscatter values to mesopelagic fish biomass, is constantly improved (Agersted et al., 2021; Ariza et al., 2016; D'Elia et al., 2016; Korneliussen and Ona, 2003; Proud et al., 2019). Therefore, in the future this method has great potential for routine monitoring of the mesopelagic realm (Haris et al., 2021). In trophic studies, fatty acids and stable isotope analysis have become a standard tool to investigate food web structure and connectivity (Choy et al., 2015, 2012; Choy, 2013; Gloeckler et al., 2018; Parzanini et al., 2019; Romero-Romero et al., 2019; Stowasser et al., 2009; Valls et al., 2014). The fact that stable isotopes integrate over a longer period compared to stomach content studies and include also non-identifiable food particles, has proven a major advantage (Layman et al., 2007). Traditionally the ratio of δ^{15}N to δ^{14}N relative to a standard has been used to infer trophic level, however in deep-sea studies this trophic marker has additional importance as indicator of depth occurrence (Choy et al., 2017; Gloeckler et al., 2018; Romero-Romero et al., 2019). Methodological caveats concern the interpretation of data, since e.g. stable isotope data are only indirect indicators that rely on many physiological assumptions, which may not be met in reality, but are overall difficult to assess (Layman et al., 2007). In addition, food web complexity, especially regarding isotopically "invisible" microbial components (Gutiérrez-Rodríguez et al., 2014) is not fully integrated by this method. Genetic metabarcoding allows to investigate aspects of regional substructure in a species (Gordeeva, 2011), while further serving as a potential baseline for confirming species identity from morphological identifications.

Study objectives

By using a comparative approach on spatial (different ecoregions in the tropical Atlantic) and temporal scales (1966–79 *vs*. 2014/2015, spring *vs*. summer), and based on integrative methods (net trawl sampling (pelagic midwater trawl 'Aalnet'), hydroacoustics, stable isotope analysis, genetic analyses) the present study aims

(i) to characterise the biogeographic composition of mesopelagic fish communities constituting sound scattering layers in three ecoregions of the tropical North Atlantic (Chap. I: Articles 1, 2)

(ii) to investigate regional variation in the functional community composition and the hydroacoustic and trophic structure of mesopelagic fishes; focussing on vertical differences between the oxygen minimum zone and the equatorial region in the eastern tropical North Atlantic (Chap. II: Articles 1–3)

(iii) to investigate regional and temporal variability in mesopelagic fish communities of the eastern Atlantic using size-based indicators (Chap. III: Articles 4, 5)

CHAPTER I: Biogeographic composition of mesopelagic fish communities constituting sound scattering layers in three ecoregions of the tropical North Atlantic

Article 1 Community structure of mesopelagic fishes constituting sound scattering layers in the eastern tropical North Atlantic

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Community structure of mesopelagic fishes constituting sound scattering layers in the eastern tropical North Atlantic

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ABSTRACT

Mesopelagic sound scattering layers (SSLs) are predominantly associated with mesopelagic fish taxa with gas-inflated swimbladders that perform active nocturnal diel vertical migration (DVM), like species of the families Myctophidae, Gonostomatidae, Sternoptychidae and Phosichthyidae. Larger-sized species with limited, partial, asynchronous and non-migratory migration pattern (non-DVM) and without gas-bearing swimbladders are presumably invisible by hydroacoustic methods operating at lower frequencies (18–38 kHz). Their vertical migration behaviour and functional role in the mesopelagic community remain largely disregarded. The present study investigated (i) the taxonomic and functional mesopelagic fish composition (migration behaviour and feeding guild as traits) of the main SSLs and (ii) regional variation in the vertical community structure related to the presence of the oxygen minimum zone (OMZ) in the eastern tropical North Atlantic. We analysed hydroacoustic and biological trawl data collected concurrently with a pelagic midwater trawl in distinct SSLs between 45 and 680 m depth by means of ordination, cluster and compositional analyses. Whereas daytime hydroacoustic backscatter profiles demonstrated higher mean S_v (38 kHz) backscatter at shallower depths at low-oxygen (LO) station 309 compared to the equatorial (EQ) station 330, night-time hydroacoustic profiles at LO stations could not be directly related to OMZ conditions. Catch abundances and biomass showed no clear regional pattern between EQ and LO stations. The analysis of trawl samples emphasised the importance of non-DVM species to the composition of tropical SSLs and further indicated regional and vertical variation in the mesopelagic fish community structure. At all stations, non-DVM species made up the largest proportions of total tow community composition (abundance and biomass) in the principal and secondary mesopelagic SSL during night-time (375–680 m) and during most daytime tows (LO: 390–555 m, EQ: 325–500 m). Our analysis suggests a more pronounced gradient structure in the vertical community composition of the LO compared to the EQ. On the one hand, shallower tows at eastern LO stations 306 and 311 were clustered with comparatively deeper tows. The eastern LO stations 306–315 had the highest numbers of non-DVM species in the principal epi- and mesopelagic SSL and the largest proportions of mesopelagic predatory species in the principal mesopelagic SSL. On the other hand, only the dominant DVM-species of the LO (i.e., *Nannobrachium isaacsi*, *Ceratoscopelus warmingii*, *Notoscopelus resplendens, Lepidophanes guentheri* and *Hygophum macrochir*) also showed consistent presence in the principal mesopelagic SSL during night-time. Moreover, our study demonstrates the usefulness of using biomass as additional parameter, when investigating functional aspects of mesopelagic community structure.

1. Introduction

The community structure of meso-and bathypelagic fishes, i.e., fishes inhabiting the pelagic waters below 200 m depth, is determined by their physico-chemical and biotic environment. A global biogeographic classification of the mesopelagic realm defined 33 ecoregions based primarily on the influence of water masses, oxygen minimum conditions, temperature extremes, surface water productivity and biotic partitioning (Sutton et al., 2017). The latter includes predation, competition and patterns of reproduction, which evolved interactively

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and in adaptation to the physical environment and the level of disturbance that is regularly encountered. These factors define species distributions, but also the functional community architecture that determines the role of the mesopelagic community in ecosystem fluxes (Sutton, 2013; Ariza et al., 2015; Klevjer et al., 2016; Klevjer et al., 2020; Melle et al., 2020). Mesopelagic fishes are most importantly characterised by their functional trait 'vertical migration behaviour' which is driven by a complex set of factors predominantly related to food availability, predator avoidance and life history strategy (Pearre, 2003). It varies spatio-temporally by species, their life stages and internal states and distinguishes several modes: (i) active nocturnal diel vertical migration (DVM; up at night, down during the day), (ii) active reverse DVM (up during daytime, down at night), (iii) active limited migration (limited migration amplitude), (iv) active asynchronous/partial migration (part of the population migrates every night or the whole of the population migrates at different daytimes, e.g., bimodal), (v) non-migratory, (vi) inactive ontogenetic descent by larvae, transforming and juvenile parts of the population, (vii) inactive spawning at mesopelagic depths by mature parts of the population (Hopkins et al., 1996;Pearre, 2003; Sutton, 2013;Dove et al., 2021). Migration behaviour is intrinsically linked to the trait 'feeding guild' (Drazen and Sutton, 2017). A large variety in feeding patterns has been observed in mesopelagic fishes, but most occupy mid-trophic levels (Hopkins and Sutton, 1998; Choy et al., 2012; Olivar et al., 2018) and thereby hold key positions by linking bottom-up and top-down processes in global pelagic food webs (Lehodey et al., 2010; Griffiths et al., 2013). Daily migratory zooplanktivorous species predominantly take advantage of vertically moving zooplankton that feeds on epipelagic primary sources at night. Their non-daily migratory and non-migratory counterparts remain at meso- and bathypelagic depths and rely partly on the same food web, but to a greater extent also on organisms that use partially degraded organic material as primary sources (Sutton, 2013; Choy et al., 2015; Drazen and Sutton, 2017; Gloeckler et al., 2018; Richards et al., 2020). The trophic and vertical ecology of meso- and bathypelagic predatory fish species is necessarily linked to that of their vertically mobile prey species (Choy et al., 2017; Richards et al., 2019). Early on, Vinogradov (1962) suggested the concept of vertically overlapping loops of migrations which transfer energy from the sea surface to the deep sea (see also Hernández-León et al., 2020). Despite generally classified as non-migratory, extensive vertical migrations have been reported for a number of species like many families of the order Stomiiformes, the families Chiasmodontidae, Scopelarchidae, Paralepididae and Melamphaidae, anglerfishes (order Lophiiformes) and bathypelagic eels (order Anguilliformes; Marshall, 1960; Fock et al., 2004; Cook et al., 2013). It has further been suggested that fishes without swimbladders for buoyancy regulation have an energetic advantage and potentially larger vertical range compared to gas-bearing species (Alexander, 1972). Acknowledging the vertical magnitude of meso- to bathypelagic ocean realms (1000–~4000 m) and the presumably underestimated biomass of the larger-sized non-DVM species (see references in Sutton, 2013), their reasonable contribution to energy and carbon fluxes can be expected (Eduardo et al., 2020a).

The acoustic-backscattering strength of a fish is influenced by gas in the swimbladder (Davison, 2011). Biomass estimates and carbon export models of mesopelagic fishes that are based on hydroacoustic data, therefore, predominantly target gas-bearing mesopelagic fish taxa of the families Myctophidae, Gonostomatidae, Sternoptychidae and Phosichthyidae that perform active nocturnal DVM (Davison, 2011; Sutton, 2013). Organisms with a density and internal sound speed similar to that of seawater yield a much weaker echo at the given transducer frequencies, but still contribute to the sound scattering layers (SSLs; Ariza et al., 2016). Accordingly, fish species without a gas-filled swimbladder, but with low-density fluids or lipids instead, will only marginally contribute to hydroacoustic backscatter recorded at these frequencies. Regarding this, empirical data demonstrated a six-fold reduction in acoustic-backscattering cross-section of the asynchronously migrating stomiid *Idiacanthus antrostomus* compared to a typical value of an epipelagic fish (Davison, 2011). Through an accordingly reduced ability to hydroacoustically determine, classify and especially quantify these non-gas-bearing, generally larger sized species in the functional and ecological interpretation of acoustic data collected through a hull-mounted echosounder, a significant component of the mesopelagic community is missed (cf. discussion in Koslow et al., 1997; Klevjer et al., 2020).

Migration amplitude and migration behaviour in gas-bearing diel migrators are largely driven by irradiance levels (Røstad et al., 2016; Aksnes et al., 2017; Langbehn et al., 2019; Klevjer et al., 2020), but a pronounced relationship to oxygen concentration has been demonstrated in several studies (Bianchi et al., 2013; Netburn and Anthony Koslow, 2015; Klevjer et al., 2016). In oxygen minimum zones (OMZ), a conspicuously shallower daytime SSL was observed, indicating interacting dynamics between the mesopelagic community and OMZs (Bianchi et al., 2013). In the severe OMZ of the eastern tropical Pacific, biological sampling of macroplankton and small-sized micronekton species and life stages revealed fine-scale vertical ecological gradients in the community structure in response to environmental threshold parameters at the OMZ boundary layers (Maas et al., 2014). It has also been hypothesized that physiologically limiting hypoxic conditions would constrain mesopelagic community components to shallower waters, rendering them more vulnerable to potential predators (Gilly et al., 2013). This mechanism has been linked to a marked decline in mesopelagic fish biomass observed in decadal time series from the California Current region (Koslow et al., 2011). In the eastern tropical North Atlantic stable isotope data demonstrated significant regional variation in the trophic structure of micronekton assemblages between the OMZ and the equatorial region (Czudaj et al., 2020). The relevant processes are poorly understood and there is crucial demand for detailed biological data on mesopelagic fish community structure under OMZ conditions.

The aim of the present study was to investigate the taxonomic and functional mesopelagic fish composition of the main SSLs (migration behaviour and feeding guild as traits) in the eastern tropical North Atlantic (ETNA) based on hydroacoustic data and trawl catches of mesopelagic fishes using a pelagic midwater trawl. We explored the relative contribution of non-DVM species to the composition of the main SSLs and spatial variation in the vertical functional community structure related to the presence of the OMZ in that area. We further considered the relevance of using biomass as a response variable in mesopelagic fish community analyses in addition to abundances. Biomass correlates positively with metabolism and thereby directly relates to energy flow in the community, whereas abundance correlates with energy flow only indirectly through biomass (Brown et al., 2004). Also, regarding interactions, it has been argued earlier that interaction strength is mainly a function of body size (Saint-Germain et al., 2007). Therefore, especially when there is a strong gradient in the underlying size structure, as it is in mesopelagic fishes, body mass may be the more appropriate response variable and may offer a more authentic picture of the functional processes driving differences in community structure (Saint-Germain et al., 2007).

2. Material and methods

2.1. Biological sample collection and processing

Micronekton samples were collected between 23 March and 2 April 2015 during cruise WH383 on the *FRV Walther Herwig III* at ten stations in the eastern tropical North Atlantic (ETNA) between 0 and 12°N and 20–26°W (Fig. 1, Table 1). Biogeographically, stations belonged to three different ecoregions (Sutton et al., 2017): 'Central North Atlantic' (24), 'Mauritania/Cape Verde' (26) and 'Tropical and West Equatorial Atlantic' (27).

A pelagic midwater trawl ('Aalnet', Engel Netze, Bremerhaven,

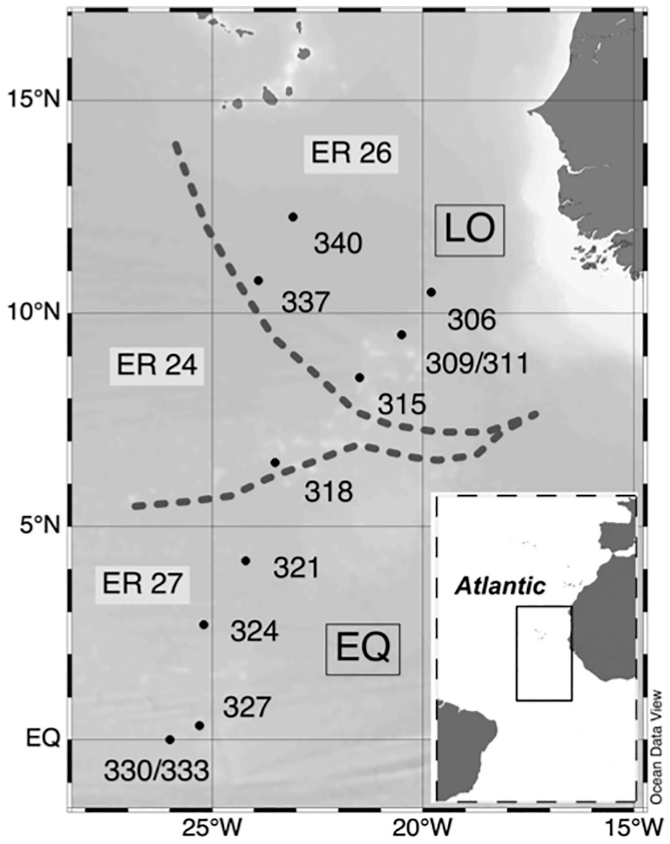


Fig. 1. Stations in the low-oxygen (LO) and equatorial (EQ) region of the eastern tropical North Atlantic sampled in this study. Station 318 showed intermediate characteristics. The dotted line denotes the approximate boundaries between the ecoregions (ER) 24 (Central North Atlantic), 26 (Mauritania/Cape Verde) and 27 (Tropical and West Equatorial Atlantic, Sutton et al. (2017)).

Germany, 16 × 30 m mouth opening, length 150 m including multiple opening-closing device, 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; Harrisson, 1967) was used with a multisampler (Construction Services AS, Bergen, Norway; Engås et al., 1997) allowing depth-stratified sampling. Biomass size spectra for this net showed that catches were fairly representative in the range from the 1 g size class (0.7–1.4 g) to the 128 g size class (maximum 181.0 g; Fock et al., 2019). Regarding the lower limit of 0.7 g, depending on the species and its morphology, this corresponded to fishes having a standard length of ~20 mm and larger. At each station, three depths were selected based on hydroacoustic registrations of micronekton aggregations, resulting in fishing depths from 45 to 680 m (Table 1). The depth strata had a mean thickness of 39 m (range 23–64 m) and were fished in horizontal tows for 30 min each stratum with a mean speed of three knots (2.8–3.3 kn). Lowering the net to the depth of the first trawl at the shallowest depth interval took 40 min, and lowering in-between trawls took 20 min. Night trawls took place at 22:00 local time, and the day-time trawls at 12:00 local time. New moon started 3 days prior to the start of sampling (station 306) and ended with full moon 2 days after sampling the last station (station 340). Individual specimens collected from the fore net that could not be allocated to a specific net were not included in the present analyses. Due to operational requirements, we could not collect all specimens entangled in the fore net, which affected the quantitative catch assessment of foremost elongated species (species of the order Aulopiformes, of the families Nemichthyidae, Serrivomeridae and Stomiidae). 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 in Steedman sorting fluid (Steedman, 1976). Specimens of larger and easily recognisable species that were picked out of the total catch were included when a species was absent from the subsample taken. A minor portion of samples was preserved frozen at −30 °C and measured thawed and blotted. Fish specimens were identified consulting regional identification keys (Bigelow et al., 1964; Nafpaktitis et al., 1977; Whitehead et al., 1986; Carpenter and De

Table 1
Stations sampled for *meso*pelagic fishes during WH383.

Study region	Eco-region	Date	Station	Longitude	Latitude	Start time (local)	Tow 1 (m)	Tow 2 (m)	Tow 3 (m)	SST (°C)	MLD (m)	O_2 min (ml l^{-1})	Prim prod (mg C m^2 day^{-1})
LO	26	23/03/2015	306	−19.8	10.5	22:00	51–76	166–195	397–435	24.4	27	0.9	1220
LO	26	24/03/2015	309	−20.5	9.5	12:00	337–381	390–424	509–556	24.0	27	0.9	4743
LO	26	24/03/2015	311	−20.5	9.5	22:00	47–79	246–288	397–441	24.0	27	0.9	4743
LO	24/26	25/03/2015	315	−21.5	8.5	22:00	52–81	228–282	368–432	23.5	31	0.9	1545
LO/EQ	24/27	26/03/2015	318	−23.5	6.5	22:00	57–85	208–246	388–435	26.1	47	1.5	366
EQ	27	27/03/2015	321	−24.2	4.2	22:00	51–78	134–162	409–445	27.5	38	1.9	294
EQ	27	28/03/2015	324	−25.2	2.7	22:00	46–85	139–176	449–492	27.6	25	2	747
EQ	27	29/03/2015	327	−25.3	0.3	22:00	59–82	380–432	473–502	27.7	52	2	596
EQ	27	30/03/2015	330	−26.0	0.0	12:00	323–424	468–501	617–680	27.9	43	2.1	299
EQ	27	30/03/2015	333	−26.0	0.0	22:00	55–78	373–426	476–523	27.9	43	2.1	299
LO	24/26	02/04/2015	337	−23.9	10.8	22:00	50–83	375–421	587–627	23.9	45	0.9	371
LO	26	03/04/2015	340	−23.1	12.3	22:00	44–84	378–420	555–583	22.7	36	0.9	322

Ecoregion = Ecoregion in reference to Sutton et al. (2017); Start Time (local) = Begin fishing operation (net leaving deck); Tow 1/2/3 = Fished depth interval of tow 1–3; SST = sea surface temperature; MLD = mixed layer depth (based on Kara Isothermal Layer Depth (Kara et al., 2000). O_2min = minimum value of dissolved oxygen concentration sampled in the water column (at ~400 m, uncalibrated value); Prim Prod = net primary production integrated for March 2015 extracted using the ocean net primary production (NPP) *Standard Products* from the website http://www.science.oregonstate.edu/ocean.productivity.

Angelis, 2016a, 2016b) and FishBase (Froese and Pauly, 2019).

2.2. Hydroacoustic data

Hydroacoustic data were recorded with a Simrad EK60 scientific echosounder with hull-mounted, downward looking transducers operated at 18, 38, 120 and 200 kHz. The beam width of all transducers was 7°, except for the 18 kHz transducer that had a beam width of 11°. All transducers were calibrated with the standard-sphere method (Demer et al., 2015) after the survey and calibration settings/results were applied for post-processing of the data. Pulse duration was 1.024 ms with a ping rate of c. 2 s that had been adapted to avoid seabed alias interference. Only data from the 18 and 38 kHz transducers were utilised for further processing and analysis. Signal degradation through different effects of noise and attenuation was mitigated through applying various filters in the post-processing software: Background noise was removed according to De Robertis and Higginbottom (2007), and data with a Signal to Noise Ratio SNR < 15 dB was rejected. After resampling the data, impulse noise, transient noise and attenuated signals were removed according to Ryan et al. (2015), with parameters adapted for best results. All post-processing of hydroacoustic data was conducted using Echoview 11.1.49 (Echoview Software Pty Ltd, 2020). Hydroacoustic data were integrated at a threshold of -70 dB between 15 and 1000 m to allow for layer detection, and the mean volume backscattering coefficient S_v was estimated for bins of 1 nautical mile horizontally and 5 m vertically. Average values were calculated for continuous depth layers characterised by the main sound scattering layers (SSLs) throughout the temporal and spatial expansion of the corresponding station work during trawl sampling (see below).

2.3. Hydrographic data

Hydrographic data (temperature, salinity, dissolved oxygen concentration) were collected using a Seabird © 911plus CTD (Sea-Bird Electronics Inc., Bellevue, WA, USA) from the surface down to 1000 m prior to each fishing operation. Although the oxygen values were not calibrated using in situ sampling, they still can be used to identify low oxygen regions since the last manufacturer calibration with accuracy of 0.02 ml l^{-1} took place 3 months prior to the WH383 cruise. Therefore, the time drift is not expected to be significant for the purpose of this study.

2.4. 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. The station map and hydrographic profiles were visualised using the software Ocean Data View (Schlitzer, 2021). The net primary production (mg C m^{-2} day^{-1}) based on the standard vgpm algorithm (Behrenfeld and Falkowski, 1997), integrated for March 2015, was extracted using the ocean net primary production (NPP) Standard Products from the website http://www.science.oregonstate.edu/ocean.productivity. Mixed layer depth (MLD) was determined based on Kara Isothermal Layer Depth (Kara et al., 2000). To identify groups of stations with similar environmental characteristics, we performed Principal Component Analysis (PCA) using the normalised hydrographic variables temperature, salinity, and dissolved oxygen at depths 0, 50, 100, 200, 300, 400, 500, 600 and 800 m using the package ‘vegan’ (Oksanen et al., 2020). Hydroacoustic data were used to determine and visualise sound scattering layers (SSL): Overall backscatter distribution was estimated through displaying the relative contribution of linearised S_v per depth bin for the whole water column per station. To compare backscatter values across SSLs and stations, mean S_v values per SSL were calculated. Based on the depth and formation of corresponding SSLs observed in concurrently collected hydroacoustic recordings, midwater/multisampler tows were categorised into four main SSL depth strata: principal epipelagic SSL (E), lower epipelagic and transition from epi- to mesopelagic depths (El/EM), principal mesopelagic SSL (M1) and secondary mesopelagic SSL (M2; cf. Fig. 1 in Proud et al. (2017). To differentiate between more than one tow conducted in these main SSLs, we additionally defined substrata (Table 2, Fig. 2).

We estimated catch biomass based on 6820 individual length measurements and 6088 individual weight measurements performed on formaldehyde-preserved specimens. Missing weight information for species with available length data were substituted based on species-specific allometric length-weight relationships. For specimens which lacked length and weight information, species-specific mean lengths were adopted with corresponding weights based on allometric relationships. If no species information was available or not sufficient to generate length-weight relationships, pooled data on the family level was taken. Subsamples were extrapolated to total catch. We used Unweighted Pair Grouping Method with Arithmetic mean (UPGMA) clustering and non-metric multidimensional scaling (nMDS, Kruskal, 1964) to identify the main patterns in the taxonomic and functional community data (Clarke et al., 2014) using the packages ‘vegan’ (Oksanen et al., 2020), ‘gclus’ (Hurley, 2019) and ‘dendextend’ (Galili, 2015). We use the word ‘community’ here and hereafter in the sense of the species present at the sampled SSLs; caught by our respective gear with its inherent sampling limitations. A Similarity Profile Analysis (SIMPROF)

Table 2
Definition of sound scattering layers (SSL).

SSL	Ecological description	Depth interval (m)		Station – Tow sampled	
Night tows		LO	EQ	LO	EQ
E	Principal Epipelagic SSL	45–85	45–85	306–1, 311–1, 315–1, 318–1, 337–1, 340–1	321–1, 324–1, 327–1, 333–1
El	Epipelagic SSL – Lower	135–195	135–175	306–2	321–2, 324–2
EM	Epi-Mesopelagic Transition SSL	210–290	n.s.	311–2, 315–2, 318–2	n.s.
M1c	Principal Mesopelagic SSL – Central	370–440	375–445	306–3, 311–3, 315–3, 318–3, 337–2, 340–2	321–3, 327–2, 333–2
M1l	Principal Mesopelagic SSL – Lower	n.s.	450–525	n.s.	324–3, 327–3, 333–3
M2	Secondary Mesopelagic SSL	555–630	n.s.	337–3, 340–3	n.s.

SSL	Ecological description	Depth interval (m)		Station – Tow sampled	
Day tows		LO	EQ	LO	EQ
M1u	Principal Mesopelagic SSL – Upper	335–380	325–425	309–1	330–1
M1c	Principal Mesopelagic SSL – Central	390–425	n.s.	309–2	n.s.
M1l	Principal Mesopelagic SSL – Lower	510–555	470–500	309–3	330–2
M2	Secondary Mesopelagic SSL	n.s.	615–680	n.s.	330–3

Also presented are the sampled depth intervals (n.s. = not sampled) and respective tows for the low-oxygen region (LO, including station 318) and the equatorial region (EQ).

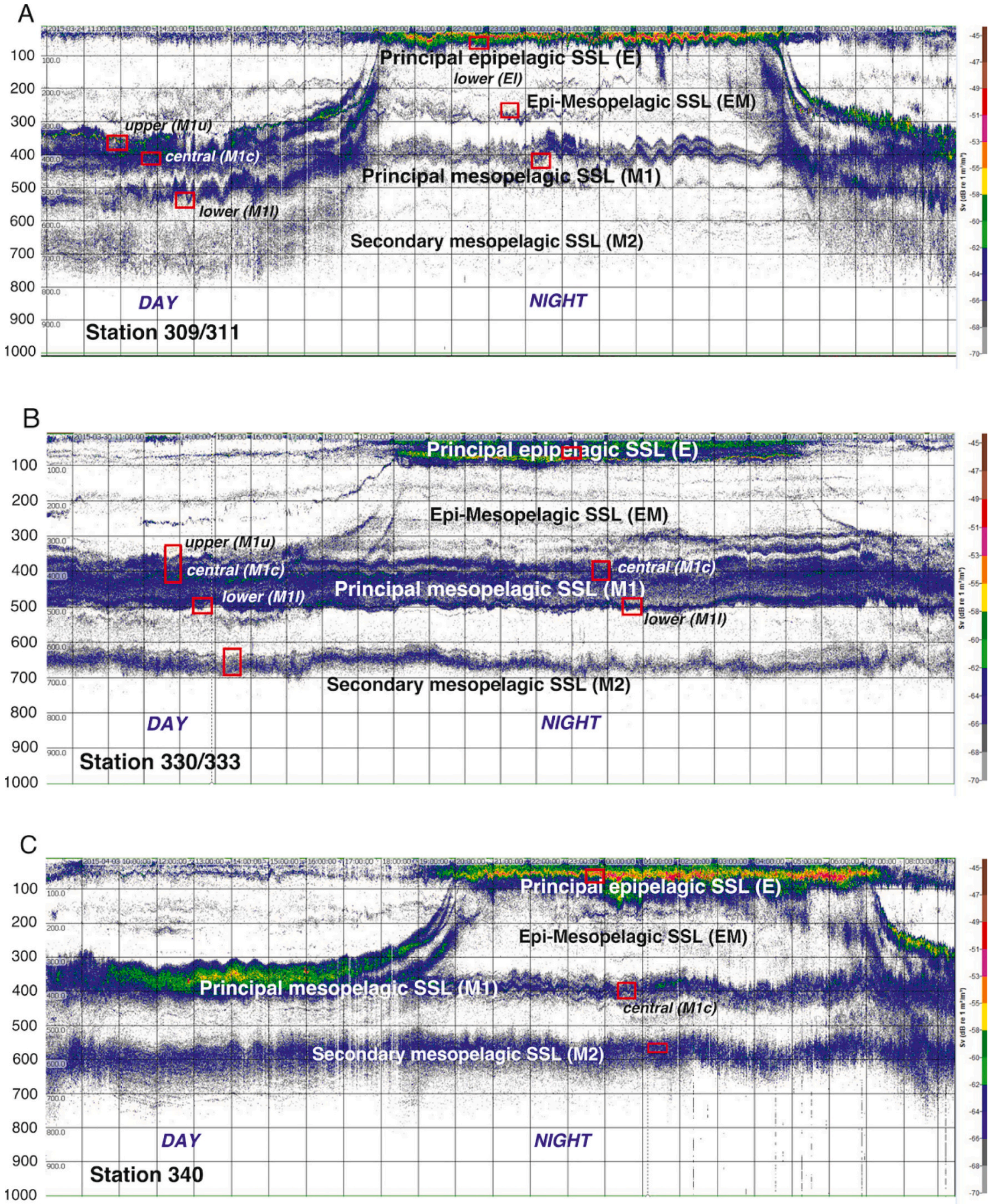


Fig. 2. Examples of 24 h hydroacoustic recordings (38 kHz) showing the main night- and daytime sound scattering layers for each region. a) Station 309/311 (LO), b) Station 330/333 (EQ), c) Station 340 (LO). Red boxes indicate fished depth intervals. (For a colour version of this figure the reader is referred to the web version of this article.) (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

with the assumption of no a priori groups (Clarke et al., 2008) was applied to determine the number of significant clusters (R package 'clustsig'; Whitaker and Christman (2014)). Because the power of SIMPROF to detect structure increases as the number of samples increases, we additionally used the methods silhouette width, matrix comparison and diagnostic species to identify the optimal group number of clusters (Borcard et al., 2018). Total species catch abundances per tow was used as input in the multivariate analyses. For the analysis of species similarities between sites, we compared the results based on the full dataset (244 species, 82% zeros) with a trimmed dataset where species contributing less than 0.1% and those appearing at less than three stations were removed (149 species, 72% zeros). Prior to these analyses, data were fourth root transformed to give more weight to rare species (Clarke et al., 2014). We used Bray-Curtis coefficients (Bray and Curtis, 1957) to calculate the dissimilarity matrix, where joint absences do not contribute to similarity between stations. In the analysis of species associations, we reduced the dataset to include only species accounting for >4% of total abundance in any one tow (Clarke et al., 2014). Because of the large percentage of *Chauliodus* sp. that were only determined to family level (uncertainty due to skin damage) and the overlap in species distributions of *C. schmidti* and *C. sloani,* these species were grouped together with undetermined *Chauliodus* sp. in this analysis. We used a matrix of percentage frequencies per Feeding–Migrator guild as data input for the functional analysis. These revealed the relative contribution of each Feeding–Migrator guild per tow, rather than their absolute quantitative contribution. To calculate the dissimilarity matrix we used the Whittaker index of association (D9; Legendre and Legendre, 2012), where each functional trait is first transformed into a fraction of the total number of individuals at the site before the subtraction to calculate the dissimilarity matrix. Species with undetermined Feeding–Migrator guilds were included in the calculation of percentages, but this group of species was not included in the analyses. Feeding guilds and migration behaviour of the sampled species were based on literature data (Table A.1). We made best effort to use regional and body size-specific data in the categorisation of both traits to account for environmental and ontogenetic variation. Generally, data for maturing and mature adult specimens was presented in the literature and corresponded with our dataset. The functional trait 'migration behaviour' differentiated between 'DVM species', i.e., diel migrators with reported daily vertical migration behaviour over an extended vertical range ($>$ 300 m vertical movement) and 'non-DVM species' that included limited migrators (lm, limited migration amplitude of $<$300 m vertical range), asynchronous/partial migrators (am/pm, part of the population migrates every night or the whole of the population migrates at different daytimes, e.g., bimodal) and non-migrators (nm, no reported migration behaviour). The rationale behind the characterisation of the functional guild 'Feeding–Migrator guild' (FM guild) was described in detail in Czudaj et al. (2020). In the present study this characterisation deviated from the earlier version by including the guild 'pisc–meso' within the guild 'mnkv–meso', because for many species the present knowledge is insufficient to distinguish these guilds (Table A.2).

3. Results

3.1. Oceanographic conditions

Sea surface temperature and salinity were lower at low-oxygen (LO) stations 306–315, 337, 340 and station 318 compared to equatorial (EQ) stations 321–333, with the only exception of low salinity at station 324 closer to the equator (Fig. 3a, b). Mixed layer depth ranged between 25 and 52 m across stations and was with 25–31 m shallowest at stations 306–315 (LO) and 324 (EQ). Because density in the area is largely driven by temperature, thermocline depth matched mixed layer depth. Hypoxic oxygen conditions ($<$0.9 ml l^{-1}), centred at ~400 m depth, were observed at LO stations 306–315, 337 and 340 (Fig. 3c). Based on temperature and salinity values, Tropical Surface Water (TSW) occupied the surface layer of all stations. Imbedded in the TSW was the Subtropical Underwater (STUW) with a salinity maximum at mixed layer depth found at stations 311, 315 and 321–337 (Fig. 3d). Below the STUW the central water mass was found down to ~450–500 m. It was dominated by South Atlantic Central Water (SACW) in the EQ including station 318, whereas in the LO, the T–S diagram indicated the mixing of SACW with Eastern North Atlantic Central Water (ENACW; Fig. 3e). We observed Antarctic Intermediate Water (AAIW) characterised by low salinities below the Central Water mass.

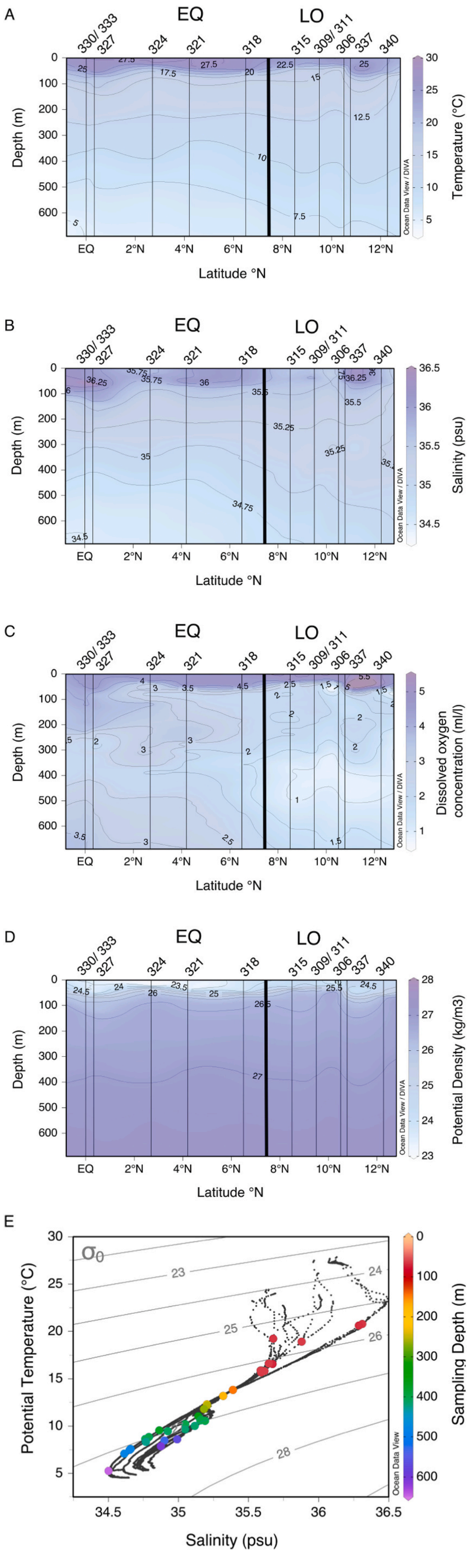
In the Principal Component Analysis (PCA) ordination of the normalised environmental variables temperature, salinity and dissolved oxygen concentration at 0, mixed layer depth, 50, 100, 200, 300, 400, 500, 600 and 800 m the first axis accounted for 74% of the total variation in the data and the second PC for a further 12%, so that the 2-d plot provided an accurate summary of the relationships. The distance biplot shown in Fig. 4 reflects from left to right on the first PC axis mostly the latitudinal location of each station, except for station 324 that is shifted more apart on the second PC axis. The correlation biplot indicates a highly positive correlation between the variables temperature and salinity between 300 and 800 m, which were highly negatively correlated with dissolved oxygen concentrations between 100 and 800 m and temperatures at the sea surface and at mixed layer depths. LO stations 306, 309/311, 315, 337 and 340 with low values for dissolved oxygen concentration and higher values for temperature and salinity at mid-water depths were located nearly directly opposite to station 318 and EQ stations 321, 324, 327 and 330/333 on the PC1 axis. On the second PC, nearly orthogonal to the previous variables, were the variables temperature (50–200 m) and salinity (0, mixed layer depth, 50–200 m), but also dissolved oxygen concentration at mixed layer depth and at 300 m. At stations 337 and 324, the second PC axis explained a comparatively larger part of the variability.

3.2. Acoustic backscatter profiles

Vertical hydroacoustic backscatter profiles (relative mean volume backscattering coefficient S_v at 38 kHz) of the mesopelagic community components showed no clear regional pattern. In the principal epipelagic SSL (E, 0–100 m) during night-time, highest peaks were observed at stations 306–321, and integrated mean backscatter was highest at station 340, followed by stations 318, 321 and 324 (Fig. 5, Table 3). We recorded the lowest integrated mean backscatter in the principal epipelagic SSL (E) at stations 306, 327 and 333. In deeper strata, we observed the highest integrated mean backscatter in the central part of the principal mesopelagic SSL (M1c, 375–425 m) and in the transition zone from epi- to mesopelagic depths, including the lower epipelagic (El/EM, 100–325 m) during night-time. Here, highest values were at stations 327 and 333 in M1c, and at stations 318, 337 and 340 in El/EM. At station 333, also the upper and lower parts of M1 (M1u, 325–375 m and M1l, 425–525 m) showed particularly high backscatter. We measured comparatively low backscatter in El/EM and M1c at stations 306 and 324. In the secondary mesopelagic SSL (M2, 525–775 m), we recorded conspicuously higher mean S_v at stations 337, 333, 340 and 321 compared to the other stations. Daytime acoustic backscatter profiles clearly showed a reduced S_v in the epipelagic SSL. At mesopelagic depths, we recorded the highest backscatter (38 kHz) in the upper and central parts of the principal mesopelagic SSL (M1u and M1c) at LO station 309, which was shallower compared to the highest backscatter in the central and lower parts of the principal mesopelagic SSL (M1c and M1l) at EQ station 330. During daytime, backscatter was higher in the epipelagic SSL compared to the secondary mesopelagic SSL (M2), whereas the lowest S_v was recorded in El/EM in both regions.

3.3. Mesopelagic fish abundances and biomass

Catch abundances and biomass in the principal epipelagic SSL (E) and the principal mesopelagic SSL (M1) showed no clear regional trend (Fig. 6). Vertically, we caught the highest abundances and biomass generally in tows in the principal epipelagic SSL (E), followed by the principal mesopelagic SSL (M1), with lower values in the transition zone from epi- to mesopelagic depths, including the lower epipelagic (El/EM), and in the secondary mesopelagic SSL (M2). On the whole, abundances ranged between 288 and 16,794 individuals per tow (Fig. 6a). We caught overall the highest abundances at LO station 309/311 during night-time in E (16,794 ind.), M1 (3046 ind.) and during daytime in the upper layer of M1 (M1u, 10,706 ind.). In E, highest abundances were at LO stations 311, 318 (8451 ind.) and 306 (5756 ind.), whereas station 315 had among the lowest abundances (2684 ind.), following EQ stations 333 (1653 ind.) and 327 (2554 ind.). Abundances were higher in the transition zone from epi- to mesopelagic depths (EM; 494–717 ind.) compared to the lower epipelagic (El; 399–477 ind.). Compared to station 311, all other night-time tows in different strata of M1 had distinctly lower abundances (M1u/M1c/M1l: 440–910 ind.), with the highest at stations 315 (910 ind.), 333 (M1c, 742 ind.) and 324 (M1l, 658 ind.) and the lowest at stations 327 (M1l, 440 ind.), 340 (495 ind.) and 337 (506 ind.). Abundances in daytime tows in M1 were similar to those in night-time tows (499–687 ind. except tow 309–M1u). In M2, we recorded overall the lowest abundances (288–495); here, the minimum was at station 340.



(caption on next column)

Fig. 3. Vertical sections of a) temperature (°C), b) salinity (psu), c) dissolved oxygen concentration (ml l^{-1}) and d) potential density (kg m^{-3}) from 0 to 700 m across a latitudinal transect from the equator to 12°N. Corresponding station numbers are given on top. e) Temperature–Salinity (T–S) diagram for all stations. Coloured dots in this figure represent mean sampled depths per tow. (For a colour version of this figure the reader is referred to the web version of this article.)

Biomass values ranged from 1006 to 13,798 g per tow (Fig. 6b) and overall matched abundances in station rankings with the notable exception of tow 337–E, which ranked 7th in terms of abundances and third in terms of biomass. In E, the highest biomass was at stations 311 (13,798 g), 318 (11,155 g) and 337 (10,660 g) and the lowest at stations 333 (1817 g), 315 (3919 g) and 327 (4014 g). During night-time, we caught the highest biomass in M1 at stations 311 (8969 g), 315 (M1c, 5064 g) and 324 (M1l, 4905 g) and the lowest at stations 318 (2575 g), 337 (2897 g) and 340 (3176 g). During daytime, except for tow 309–M1u (6545 g), we caught comparatively lower biomass in M1; ranging 1344–3114 g. Biomass was higher in EM (2364–3326 g) compared to El (1006–1971 g). At M2, it was lower during night-time (LO only: 1650–2766 g) than during daytime (EQ only: 3664 g).

Regarding migration pattern, DVM species dominated catch abundances in E, El/EM (stations 318–324) and the LO tow 309–M1u (Fig. 7a) and additionally El/EM tows at stations 306–315 and the daytime tow 330–M2 in terms of catch biomass (Fig. 7b). In all other tows, non-DVM species had 0.3–9.5 times higher abundances and 0.1–10 times higher biomass. We caught the highest percentage abundances of non-DVM species in the central part of M1 (M1c) during night-time at stations 315 (9.5 times), 306 (8 times) and 333 (6 times). In terms of biomass, we caught their highest proportions in M1 during daytime (309–M1c: 10 times, 330–M1u: 8 times) and during night-time at LO stations 306 (7.3 times), 315 (5.8) and 311 (5.1). In E, the highest proportional abundance and biomass of non-DVM species occurred at LO stations 306–318. Contrary, LO stations 337 and 340 had among the lowest quotient of non-DVM-species in both, E and M1. Mesopelagic predatory species (mnkv–*meso*) had considerably higher percentages of total community composition in M1, in terms of both, abundance and biomass, at stations 306–315 (abundance: 8–13%, biomass: 24–27%) and further at station 327 (ab: 9, bm: 21%) compared to the other stations (ab: 3–7%, bm: 0–14%).

3.4. *Mesopelagic fish community composition in the main SSLs*

3.4.1. *Species numbers*

In 36 tows we caught fishes from 12 different taxonomic orders, 46 families and identified a minimum of 192 different species (Table A.1). Species numbers ranged between 14 and 76 per tow during the night-time and between 21 and 53 during daytime (Fig. 8a). In the principal epipelagic SSL, we recorded highest species numbers at stations 311 (39), 318 (35) and 306 (35) and lowest species numbers at stations 324 (14), 337 (18) and 340 (24). Species numbers were considerably higher in the transition zone from epi- to mesopelagic depths (EM, 56–57) compared to the lower epipelagic (El, 39–41). Species numbers peaked in night-time tows in the principal mesopelagic SSL (M1; 50–76). In this SSL they were highest at stations 311 (76), 324 (71) and 327 (M1c, 62) and lowest at stations 306 (50), 327 (M1l, 52) and 333 (M1c, 52). Daytime tows showed considerably lower species numbers in M1 (21–34) compared to night-time tows; apart from tow 309–M1l (51). Species numbers in night- and daytime tows in the secondary mesopelagic SSL (M2) ranged 47–54.

Species numbers of non-DVM fish species were overall higher compared to those of DVM species, except for tows in E and the equatorial tows in the lower epipelagic (Fig. 8b). We caught the highest proportion of non-DVM species in tows in M1 at LO stations 315 (3.9

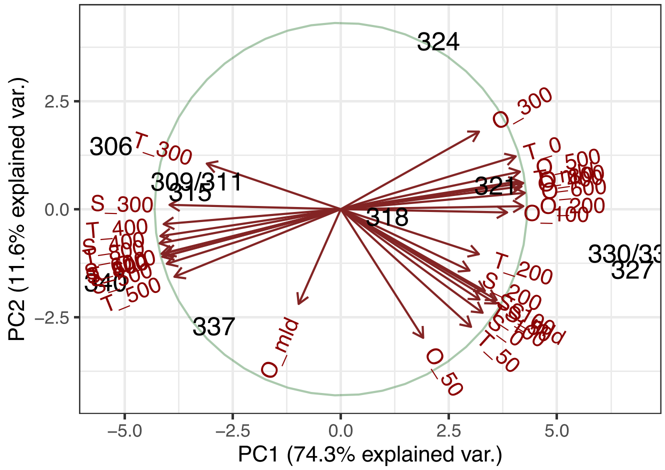


Fig. 4. Distance biplot (scaling 1) showing the first two axes (PC1 and PC2) of a PCA ordination of the normalised environmental variables temperature, salinity and dissolved oxygen concentration at 0, mixed layer depth, 50, 100, 200, 300, 400, 500, 600 and 800 m for the stations of this study (total sum of 86% variance explained).

times as much), 311 (2.8 times) and 306 (2.6 times). In E, non-DVM species had comparatively larger percentages at LO stations 306–318, 337 and 340. At a regional level, the differences between these LO stations and EQ stations 321–333 were significant (*t*-test; $p = .007$). During daytime, non-DVM species contributed relatively more to deeper tows (309–M1c/M1l: 2.0 times, 330–M2: 1.8 times), compared to shallower ones (309/330–M1u: 1.1–1.3 times). At station 315 we noted exceptionally high percentages of mesopelagic predatory fish species numbers (mnkv–meso) in M1 (M1c; 39% vs. 13–24% all other night-time tows in M1c). These were higher than those observed in comparatively deeper tows (M1l/M2; 28–34%).

3.4.2. Taxonomic composition

Based on a site similarity matrix (Bray-Curtis) from fourth root transformed abundance data, results of both, cluster analysis and nMDS ordination, were similar between the full and the trimmed dataset (that retained only species contributing more than 0.1% to total abundances and species that occurred at a minimum of three stations). Only minor differences at lower levels existed between datasets based on abundance vs. biomass data and we only present results based on the full abundance dataset. In the cluster analysis, silhouette width, matrix comparison and diagnostic species methods indicated variable optimum group numbers between two and nine, of which four was the most consistent. At an arbitrary similarity level of 35% these four main clusters differentiated primarily between night-time tows in the principal epipelagic SSL (E), including the two equatorial tows in the lower epipelagic (El), from LO tows in the transition zone from epi- to mesopelagic depths (EM) and mesopelagic SSLs (M1/M2; Fig. 9a). Tows in E were further split regionally, dividing LO stations (306–315, 337, 340) and station 318 (cluster 1) from EQ stations (321–333, cluster 2). In the other group of deeper located tows, a secondary division parted all other night-time tows, including the deepest day-time tows in M1l and M2 (cluster 3), from day-time tows in the principal mesopelagic SSL (M1, cluster 4). Within this main group structure, SIMPROF detected finer gradients of a maximum of 10 (abundance) to 15 (biomass) significant clusters. The 2-dimensional nMDS ordination plot (stress = 0.16) based on the full dataset appeared a usable summary of the sample relationships. The ordination results support the four main groups identified by cluster analysis (Fig. 9b). Compared to the 3-dimensional ordination (stress = 0.11), the 2-dimensional configuration did not as clearly separate the group of daytime tows (cluster 4). The ordination plot visualises the

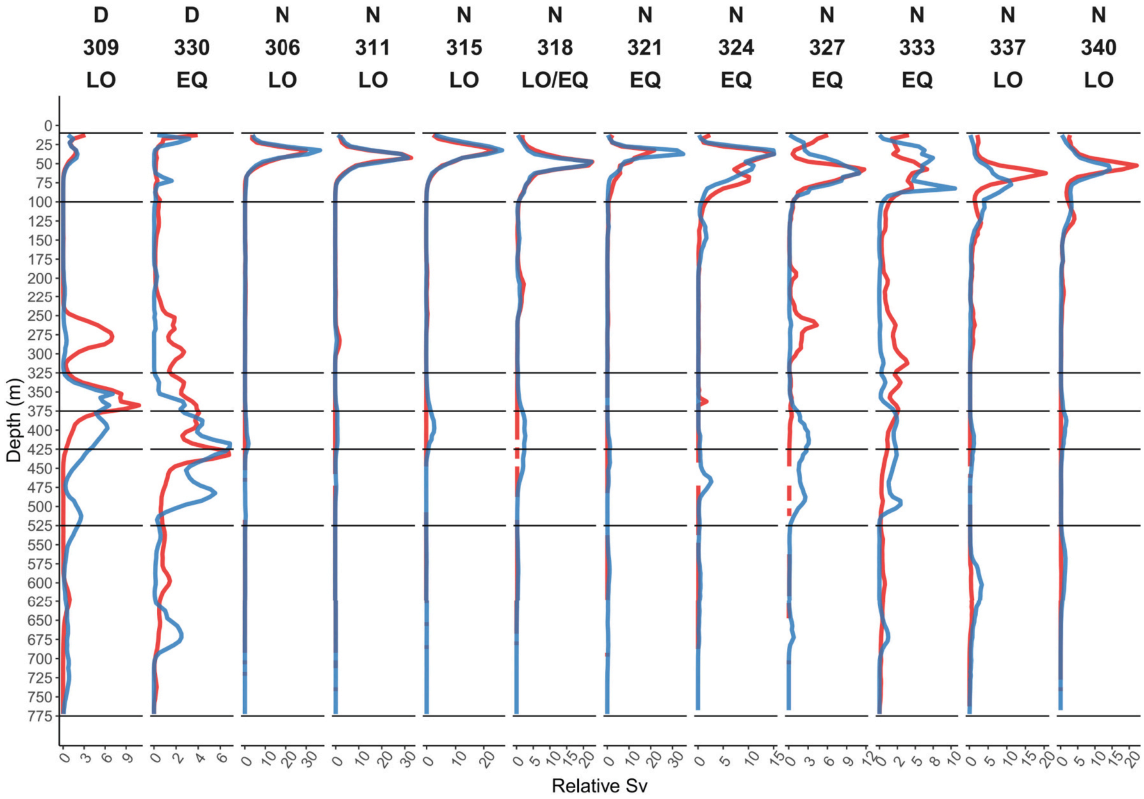


Fig. 5. Relative mean volume backscattering coefficient (S_v) at daytime (D) and night-time (N), binned in cells of 5 m × 1 nautical mile, measured from start of tow 1 until end of tow 3. Blue lines – 38 kHz, Red lines – 18 kHz. Note the difference in scales on the x-axis. (For a colour version of this figure the reader is referred to the web version of this article.) (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 3
Mean volume backscattering coefficient S_v (38 kHz, binned in 5 m × 1 nautical mile cells) per sound scattering layer (SSL: E, El/EM, M1u, M1c, M1l, M2; continuous intervals) during night- (N) and daytime (D) at low-oxygen (LO) and equatorial (EQ) stations (from start of tow 1 until end of tow 3); see Tables 1 and 2 for corresponding fishing depths and times. Grey fields indicate SSLs that were sampled by trawl.

Daytime	Region	Station	E 0–100 m	El/EM 100–325 m	M1u 325–375 m	M1c 375-425 m	M1l 425–525 m	M2 525–775 m
N	LO	306	-70.4	-86.6	-97.2	-88.3	-91.2	-94.7
N	LO	311	-67.7	-83.5	-91.7	-86.6	-92.0	-95.9
N	LO	315	-66.8	-84.4	-82.1	-82.1	-95.2	-94.4
N	LO/EQ	318	-65.1	-77.8	-83.7	-83.8	-90.7	-95.4
N	LO	337	-66.8	-76.5	-96.3	-87.7	-92.4	-81.0
N	LO	340	-63.5	-77.2	-90.3	-81.9	-92.0	-86.7
N	EQ	321	-66.3	-83.8	-93.7	-86.0	-90.8	-87.7
N	EQ	324	-66.4	-87.0	-93.3	-93.6	-87.1	-93.3
N	EQ	327	-69.0	-83.2	-81.0	-76.9	-84.7	-92.2
N	EQ	333	-68.2	-79.1	-72.7	-70.4	-74.8	-84.4
D	LO	309	-81.3	-86.3	-67.6	-68.9	-81.3	-82.7
D	EQ	330	-80.9	-84.5	-72.5	-68.0	-71.4	-82.1

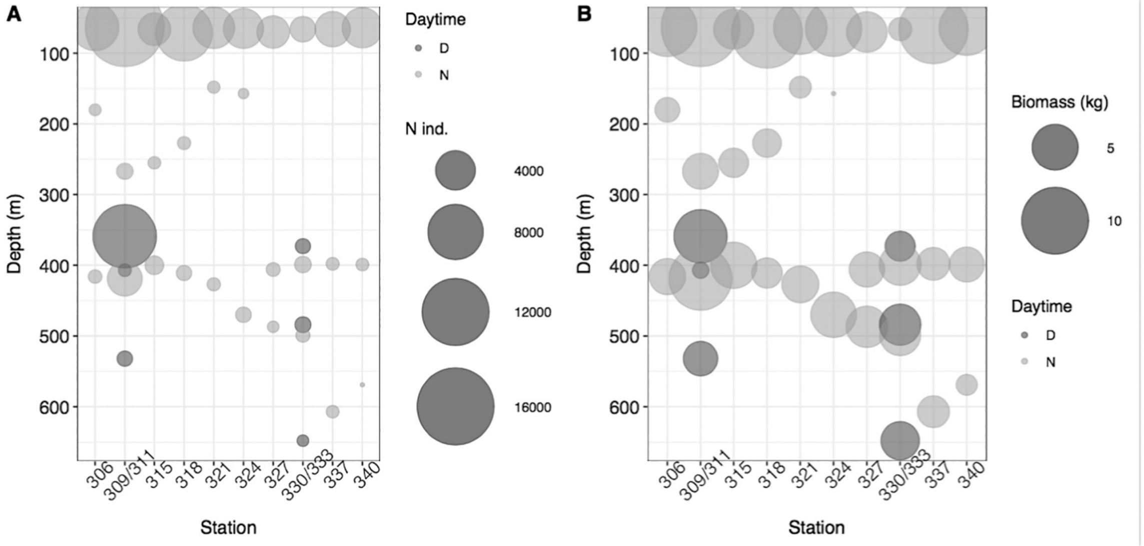


Fig. 6. Vertical sections showing a) Abundance (N ind.) and b) Biomass (kg) of the total fish catch in night- and daytime tows during cruise WH383 at stations 306–340 in the ETNA. (For a colour version of this figure the reader is referred to the web version of this article.)

large spread in the location of tows in cluster 4 compared to night-time tows in similar mesopelagic SSLs; especially compared to night-time equatorial tows. Cluster 1, including night-time tows in E at LO stations and station 318, was dominated by the myctophids *Lepidophanes guentheri*, *Diaphus vanhoeffeni*, *Vinciguerria nimbaria* (Phosichthyidae), *Notoscopelus resplendens*, *Hygophum macrochir* and *Ceratoscopelus warmingii*, in that order (constituting about or > 10% of total abundances; Table 4). In terms of biomass, *N. resplendens* constituted nearly one third of catches in E in the LO, followed by *L. guentheri*. In the equatorial region, catches in E (cluster 2) were numerically and by weight dominated by fewer species, i.e. only the myctophids *Diaphus dumerilii* and *Hygophum taaningii* contributed >10% to total abundances. In terms of biomass, in addition to *D. dumerilii* and *H. macrochir*, the myctophids *Diaphus fragilis*, *Myctophum asperum* and *Diaphus perspicillatus* contributed nearly or > 10% to total biomass in this cluster. Further included in cluster 2 were the equatorial tows in the lower epipelagic. In these, the myctophids *Diaphus brachycephalus* and *Lampanyctus nobilis* were most abundant, while in terms of biomass, in addition the stomiid *Sigmops elongatus* and the myctophid *Diaphus lucidus* contributed most. The largest cluster (cluster 3) included deeper night-time SSL strata in both regions (M1/M2) and the deepest daytime tows (M1l/M2), but also the shallow tow 306–El. Tow 306–El was significantly distinct from the other tows due to the importance of the - generally deeper encountered - melamphaid *Scopelogadus mizolepis* and the myctophid *N. isaacsi* here. Cluster 3 was characterised mainly by large abundances of the myctophid *Nannobrachium isaacsi* in El/EM (LO stations 306–318), as well as of the sternoptychids *Argyropelecus sladeni* and *Argyropelecus affinis* and the myctophid *Electrona risso* in M1. In terms of biomass, other major species in cluster 3 were the stomiid *Chauliodus schmidti*, the myctophid *Nannobrachium atrum* and the diretmid *Diretmus argenteus*. Within this cluster, the deepest night- and daytime tows in M1l and M2 showed the largest difference to the other tows (significant according to SIMPROF). Besides the importance of *N. isaacsi* and *Chauliodus spp.*, these deepest catches showed high biomass of the myctophid *Lampanyctus tenuiformis* and high abundances of the sternoptychid *Sternoptyx diaphana* and the the gonostomatid *Cyclothone* spp. in both regions. Cluster 4 included

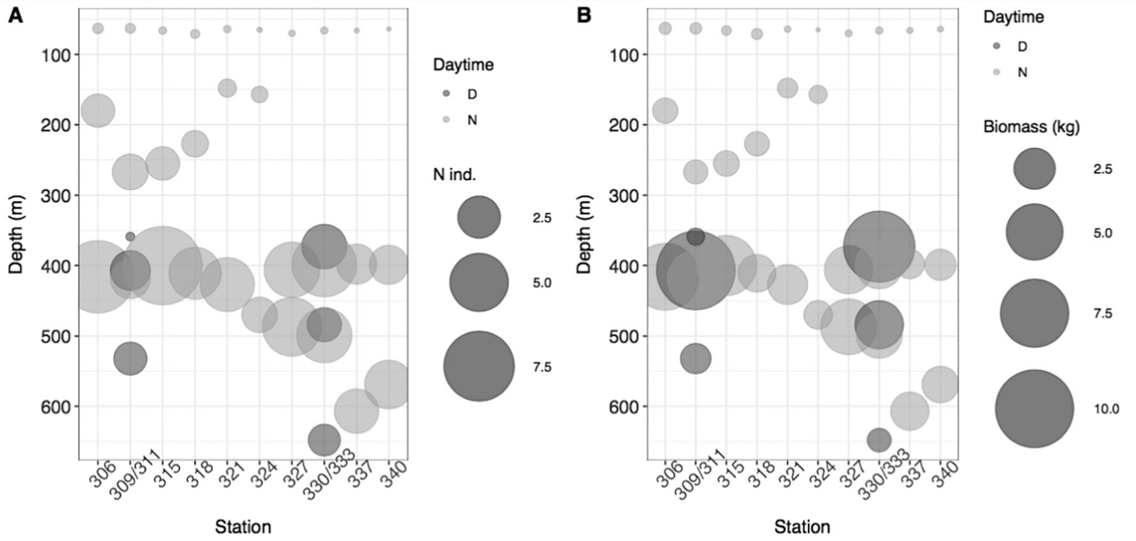


Fig. 7. Vertical sections showing the quotient of a) abundance (N. ind.) and b) biomass of non-DVM species vs. DVM species caught in night- and daytime tows during cruise WH383 at stations 306–340 in the ETNA. (For a colour version of this figure the reader is referred to the web version of this article.)

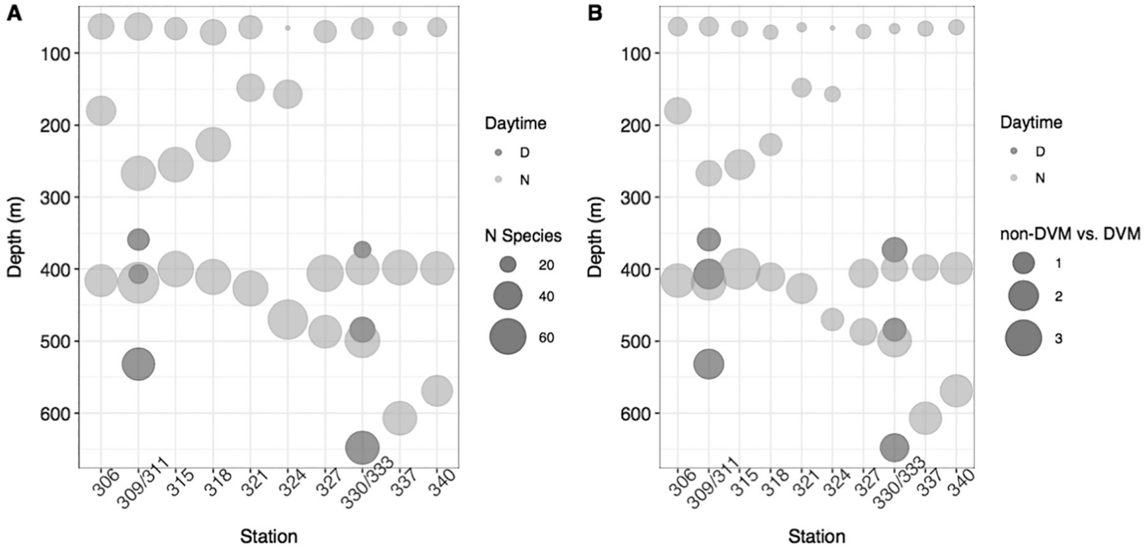


Fig. 8. a) Total species numbers and b) quotient of species numbers of non-DVM fish species vs. DVM fish species caught in night- and daytime tows during cruise WH383 at stations 306–340 in the ETNA.

daytime tows in different layers of the principal mesopelagic SSL (M1u, M1c, and M1l) that were quite heterogeneous in composition. In the equatorial region, *E. risso* dominated the catch in the upper layer of M1 (M1u), while the diretmid *D. argenteus* was most important in the lower layer of M1 (M1l). In the LO, the tow in the upper part of M1 (M1u) was by far dominated by *D. vanhoeffeni*, whereas in the central part of M1 (M1c), *A. affinis, A. sladeni* and *E. risso* chiefly contributed, in addition to *D. vanhoeffeni*.

The analysis of species associations was based on a reduced dataset of 33 species that each accounted for >4% of total abundance in any one tow. Silhouette width, matrix comparison and diagnostic species methods indicated optimum group numbers between two and six. Within this main group structure, SIMPROF detected finer gradients of maximum eleven significant clusters. At an arbitrary similarity level of 35% four groups were distinguished, of which one group was a single species unit. A major division divided between the group of species characteristic of night-time tows in E in the equatorial region, including two more species, and all other species, including those characteristic for tows in E in the LO (Fig. 10, Table 4). If we removed tows in the El and EM in the analysis (because they were mostly sampled at LO stations and might introduce a sampling bias), species that dominated E in the LO were still grouped in the main cluster together with mesopelagic tows. The main dendrogram branch included one single-species unit (*N. atrum*, important in mesopelagic tows at stations 321–327) and a large cluster, which distinguished between two significant clusters. Of these, one cluster included deeper occurring species associated with the secondary mesopelagic SSL (M2) and the lower principal mesopelagic SSL (M1l) in the LO, i.e. L. *tenuiformis, C. schmidti*, the stomiid *Malacosteus niger*, the platytroctid *Searsia koefoedie*, *S. diaphana* and *Cyclothone* spp. The other cluster contained species from different SSLs and regions. Within this cluster, one sub cluster (significant according to SIMPROF) grouped epipelagic species from the LO, that were listed in cluster 2 in the site analysis, together with the myctophid *Lampanyctus nobilis* and the bathylagid *Bathylagoides argyrogaster*. The other sub cluster grouped dominant species that occurred in the principal mesopelagic SSL (M1) and were reported in cluster 3 in the site analysis, and additionally included the stomiid *Bonapartia pedaliota*, the myctophid *Bolinichthys photothorax* and the melamphaid *Melamphaes polylepis*.

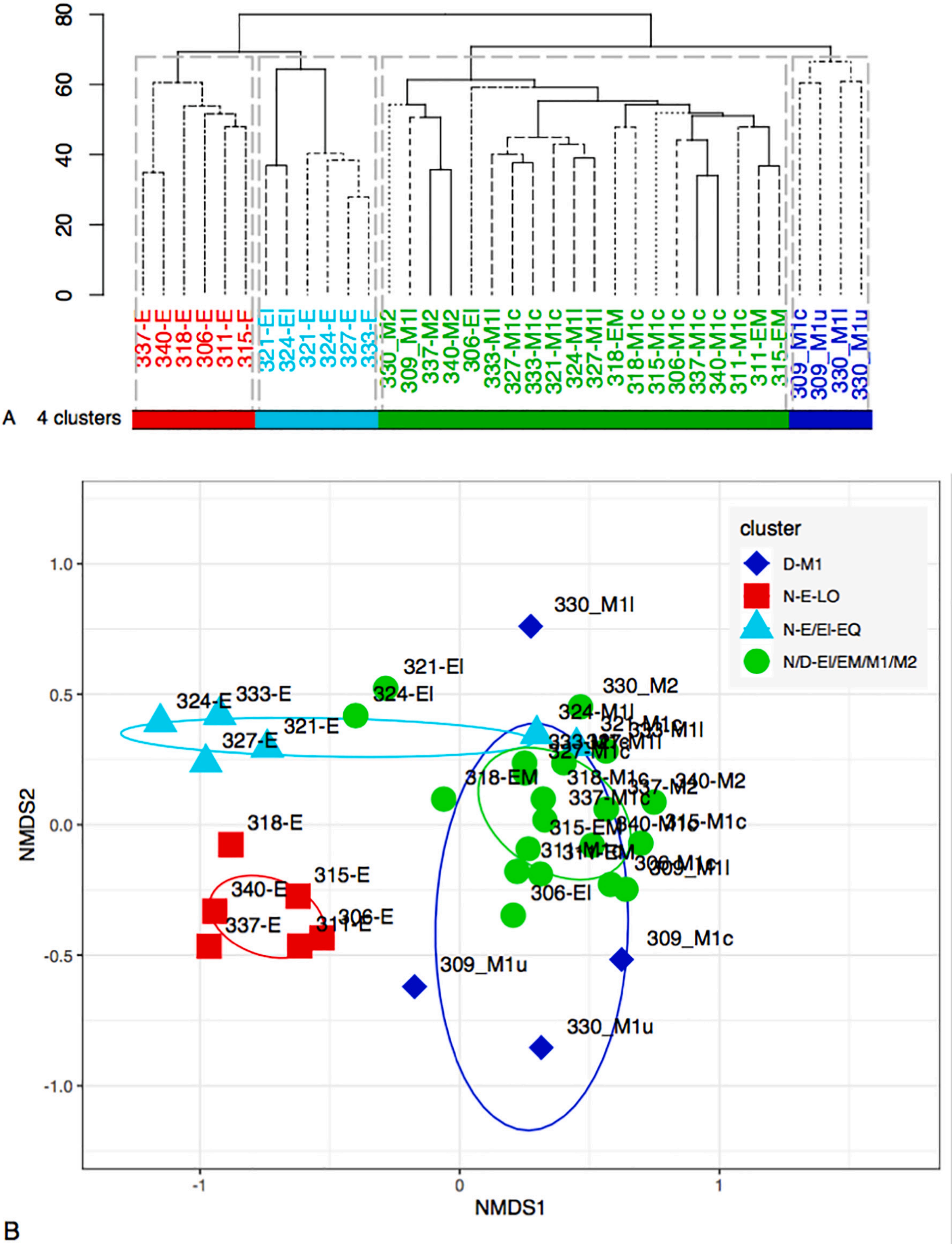


Fig. 9. a) Dendrogram of UPGMA clustering and b) 2-dimensional NMDS ordination (stress = 0.16) on Bray-Curtis tow similarities from fourth root transformed species abundance data based on the full dataset of 244 species. Solid black lines in a) indicate significant clusters identified by Similarity Profile Analysis. Cluster 1 = night-time principal epipelagic, low-oxygen region (N–E–LO), Cluster 2 = night-time principal and lower epipelagic, equatorial tows (N–E/El–EQ), Cluster 3 = day−/night-time lower epipelagic/epi-mesopelagic transition/principal and secondary mesopelagic SSL, all stations (D/N–El/EM/M1/M2–LO/EQ), Cluster 4 = daytime principal mesopelagic D–M1–LO/EQ. (For a colour version of this figure the reader is referred to the web version of this article.)

Lobianchia dofleini formed a single-species unit separated from this large cluster.

3.4.3. *Functional composition*

To investigate the functional community composition, we performed UPGMA clustering and nMDS ordination on tow similarities (Whittaker index of association, D9) from percentage abundances and biomass per functional trait Feeding–Migrator guild per tow. At an arbitrary similarity level of 40%, two main clusters were identified as optimum group number, which clearly distinguished tows in the principal epipelagic SSL

Table 4
Faunal constituents of the main sound scattering layers in the LO (stations 306–315, 337, 340; including station 318), and the EQ (stations 321–333). Only species contributing >3% to each tow in terms of either, abundance or biomass, are listed.

Species	Tax. order	Migr	FM guild	Total BM (g)	% of total BM	Total AB (N ind.)	% of total AB	Species	Tax. order	Migr	FM guild	Total BM (g)	% of total BM	Total AB (N ind.)	% of total AB
Night – E – LO								Night – E – EQ							
Notoscopelus resplendens	MYC	dm	zplv2–epi	17,800	32.6	5122	12.5	*Diaphus dumerilii*	MYC	dm	omni–epi	5499	28.3	3886	30.5
Lepidophanes guentheri	MYC	dm	zplv1–epi	8634	15.8	6451	15.7	***Hygophum taaningi***	MYC	dm	zplv1–epi	4066	20.9	2666	20.9
Hygophum macrochir	MYC	dm	zplv1–epi	4481	8.2	3800	9.2	*Diaphus fragilis*	MYC	dm	zplv1–epi	3131	16.1	1090	8.5
Ceratoscopelus warmingii	MYC	dm	omni–epi	3830	7.0	3752	9.1	*Diaphus perspicillatus*	MYC	dm	zplv2–epi	2124	10.9	477	3.7
Vinciguerria nimbaria	STO	dm	zplv1–epi	3416	6.3	5567	13.5	*Myctophum asperum*	MYC	dm	omni–epi	1537	7.9	1053	8.3
Diaphus vanhoeffeni	MYC	dm	zplv1–epi	2817	5.2	6839	16.6	***Lepidophanes guentheri***	MYC	dm	zplv1–epi	817	4.2	975	7.6
Hygophum macrochir/ taaningi	MYC	dm	zplv1–epi	2792	5.1	1969	4.8	***Notoscopelus resplendens***	MYC	dm	zplv2–epi	704	3.6	242	1.9
Lampanyctus nobilis	MYC	dm	zplv2–epi	1629	3.0	1107	2.7	*Benthosema suborbitale*	MYC	dm	zplv1–epi	239	1.2	889	7.0
								Ceratoscopelus warmingii	MYC	dm	omni–epi	151	0.8	438	3.4
Other fish species				9175	16.8	6503	15.8	Other fish species				1197	6.1	1036	8.1
Total				54,574	100	41,110	100	Total				19,465	100	12,752	100

Species	Tax. order	Migr	FM guild	Total BM (g)	% of total BM	Total AB (N ind.)	% of total AB	Species	Tax. order	Migr	FM guild	Total BM (g)	% of total BM	Total AB (N ind.)	% of total AB
Night – El/EM – LO (stations 306–318)								Night – El – EQ							
Nannobrachium isaacsi	MYC	dm	zplv2–epi	4275	42.0	413	18.9	*Lampanyctus nobilis*	MYC	dm	zplv2–epi	374	13.5	91	9.9
Scopelogadus mizolepis	STE	nm	zplv3–meso	1161	11.4	303	13.9	*Diaphus brachycephalus*	MYC	dm	zplv1–epi	301	10.9	138	15.0
Argyropelecus sladeni	STO	lm	zplv2–meso	598	5.9	255	11.7	*Sigmops elongatus*	STO	dm	zplv2–epi	293	10.6	48	5.2
Notoscopelus resplendens	MYC	dm	zplv2–epi	307	3.0	48	2.2	*Diaphus lucidus*	MYC	dm	zplv2–epi	244	8.8	50	5.5
Electrona risso	MYC	lm	zplv1–meso	298	2.9	146	6.7	*Nannobrachium lineatum*	MYC	dm	zplv2–epi	194	7.0	52	5.7
Bathylagoides argyrogaster	OSM	nm	zplv1–meso	277	2.7	76	3.5	*Diaphus dumerilii*	MYC	dm	omni–epi	146	5.3	89	9.7
Lepidophanes guentheri	MYC	dm	zplv1–epi	118	1.2	65	3.0	***Nannobrachium isaacsi***	MYC	dm	zplv2–epi	109	3.9	27	2.9
Bonapartia pedaliota	STO	nm	zplv2–meso	93	0.9	75	3.4	*Bolinichthys photothorax*	MYC	dm	zplv1–epi	111	4.0	58	6.3
								Ceratoscopelus warmingii	MYC	dm	omni–epi	109	3.9	35	3.8
								Diaphus fragilis	MYC	dm	zplv1–epi	94	3.4	17	1.9
								Undetermined juvenile	NA	NA	NA	44	1.6	41	4.5
								Bregmaceros spp.	GAD	dm	zplv2–epi	36	1.3	29	3.2
Other fish species				3041	29.9	801	36.7	Other fish species				711	25.7	242	26.4
Total				10,168	100	2182	100	Total				2766	100	917	100

Species	Tax. order	Migr	FM guild	Total BM (g)	% of total BM	Total AB (N ind.)	% of total AB	Species	Tax. order	Migr	FM guild	Total BM (g)	% of total BM	Total AB (N ind.)	% of total AB
Night – M1c – LO								Night – M1c – EQ							
Argyropelecus affinis	STO	lm	zplv2–meso	3488	13.4	1330	21.7	***Electrona risso***	MYC	lm	zplv1–meso	1599	14.7	323	17.7
Nannobrachium isaacsi	MYC	dm	zplv2–epi	2386	9.2	344	5.6	*Nannobrachium atrum*	MYC	dm	zplv2–epi	903	8.3	31	1.7
Electrona risso	MYC	lm	zplv1–meso	2013	7.7	328	5.3	***Argyropelecus affinis***	STO	lm	zplv2–meso	820	7.5	270	14.8
Chauliodus schmidti	STO	am	mnkv–meso	1884	7.2	213	3.5	*Diretmus argenteus*	BER	nm	zplv1–meso	722	6.6	112	6.2
Argyropelecus sladeni	STO	lm	zplv2–meso	1848	7.1	742	12.1	***Nannobrachium isaacsi***	MYC	dm	zplv2–epi	624	5.7	46	2.5
Searsia koefoedi	OSM	nm	zplv1–meso	1202	4.6	82	1.3	***Argyropelecus sladeni***	STO	lm	zplv2–meso	533	4.9	83	4.6
	STE	nm	zplv3–meso	1046	4.0	312	5.1		STO	nm	zplv2–meso	468	4.3	276	15.2

(*continued on next page*)

Table 4 (*continued*)

Species	Tax. order	Migr	FM guild	Total BM (g)	% of total BM	Total AB (N ind.)	% of total AB
Night – M1c – LO							
Scopelogadus mizolepis							
Hygophum macrochir	MYC	dm	zplv1–epi	370	1.4	310	5.1
Other fish species				11,802	45.3	2477	40.4
Total				26,039	100	6138	100

Species	Tax. order	Migr	FM guild	Total BM (g)	% of total BM	Total AB (N ind.)	% of total AB
Night – M1c – EQ							
Bonapartia pedaliota							
Diretmoides pauciradiatus	BER	nm	zplv1–meso	463	4.2	24	1.3
***Chauliodus* sp.**	STO	am	mnkv–meso	394	3.6	26	1.4
Melamphaes polylepis	STE	nm	zplv3–meso	215	2.0	93	5.1
Other fish species				4156	38.1	536	29.5
Total				10,897	100	1820	100

Species	Tax. order	Migr	FM guild	Total BM (g)	% of total BM	Total AB (N ind.)	% of total AB
Night – M2 – LO (stations 337, 340)							
Lampanyctus tenuiformis	MYC	dm	zplv1–epi	788	17.8	59	7.5
Malacosteus niger	STO	am	zplv2–meso	662	15.0	60	7.6
Chauliodus schmidti	STO	am	mnkv–meso	639	14.5	49	6.2
Searsia koefoedi	OSM	nm	zplv1–meso	531	12.0	48	6.1
Nannobrachium isaacsi	MYC	dm	zplv2–epi	369	8.3	44	5.6
Argyropelecus gigas	STO	lm	zplv2–meso	241	5.5	30	3.8
Sternoptyx diaphana	STO	nm	omni–meso	187	4.2	172	21.9
Cyclothone spp.	STO	nm	zplv2–meso	9	0.2	92	11.7
Other fish species				996	22.5	232	29.5
Total				4422	100	786	100

Species	Tax. order	Migr	FM guild	Total BM (g)	% of total BM	Total AB (N ind.)	% of total AB
Night – M1l – EQ							
Diretmus argenteus	BER	nm	zplv1–meso	1694	12.9	200	12.0
Nannobrachium atrum	MYC	dm	zplv2–epi	1808	13.8	75	4.5
Chauliodus sloani	STO	am	mnkv–meso	1453	11.1	85	5.1
Electrona risso	MYC	lm	zplv1–meso	978	7.4	119	7.1
Nannobrachium isaacsi	MYC	dm	zplv2–epi	909	6.9	79	4.7
Chauliodus schmidti	STO	am	mnkv–meso	675	5.1	56	3.4
Argyropelecus affinis	STO	lm	zplv2–meso	628	4.8	250	15.0
Poromitra crassiceps	STE	nm	zplv3–meso	537	4.1	21	1.3
Chauliodus sp.	STO	am	mnkv–meso	463	3.5	26	1.6
Melamphaes polylepis	STE	nm	zplv3–meso	410	3.1	110	6.6
Bonapartia pedaliota	STO	nm	zplv2–meso	113	0.9	61	3.7
Other fish species				3473	26.4	585	35.1
Total				13,141	100	1667	100

Species	Tax. order	Migr	FM guild	Total BM (g)	% of total BM	Total AB (N ind.)	% of total AB
Day – M1u – LO							
Diaphus vanhoeffeni	MYC	dm	zplv1–epi	4057	61.7	8989	83.7
Electrona risso	MYC	lm	zplv1–meso	894	13.6	176	1.6
Vinciguerria nimbaria	STO	dm	zplv1–epi	331	5.0	435	4.1
Argyropelecus sladeni	STO	lm	zplv2–meso	255	3.9	84	0.8
Myctophidae gen. sp.	MYC	dm	zplv1/ 2–epi	113	1.7	578	5.4
Other fish species				930	14.1	477	4.4
Total				6580	100	10,739	100

Species	Tax. order	Migr	FM guild	Total BM (g)	% of total BM	Total AB (N ind.)	% of total AB
Day – M1u – EQ							
Electrona risso	MYC	lm	zplv1–meso	1895	74.9	311	49.3
Bonapartia pedaliota	STO	nm	zplv2–meso	141	5.6	91	14.4
Diaphus perspicillatus	MYC	dm	zplv2–epi	85	3.4	53	8.4
Argyropelecus affinis	STO	lm	zplv2–meso	77	3.0	19	3.0
Lobianchia dofleini	MYC	dm	zplv2–epi	62	2.4	48	7.6
Diaphus mollis	MYC	dm	zplv1–epi	25	1.0	21	3.3
Ichthyococcus ovatus	STO	nm	zplv2–epi	30	1.2	19	3.0
Other fish species				216	8.5	69	10.9
Total				2531	100	631	100

Species	Tax. order	Migr	FM guild	Total BM (g)	% of total BM	Total AB (N ind.)	% of total AB
Day – M1c – LO							
Electrona risso	MYC	lm	zplv1–meso	555	41.3	62	12.4
Argyropelecus affinis	STO	lm	zplv2–meso	298	22.2	113	22.6
Argyropelecus sladeni	STO	lm	zplv2–meso	142	10.6	55	11.0

Species	Tax. order	Migr	FM guild	Total BM (g)	% of total BM	Total AB (N ind.)	% of total AB
Day – M1l – EQ							
Diretmus argenteus	BER	nm	zplv1–meso	2290	55.4	236	34.4
Myctophum asperum	MYC	dm	omni–epi	444	10.7	126	18.3
Chauliodus schmidti	STO	am	mnkv–meso	315	7.6	33	4.8

(*continued on next page*)

Table 4 (*continued*)

Species	Tax. order	Migr	FM guild	Total BM (g)	% of total BM	Total AB (N ind.)	% of total AB
Day – M1c – LO							
Chauliodus schmidti	STO	am	mnkv–meso	109	8.1	25	5.0
Diaphus vanhoeffeni	MYC	dm	zplv1–epi	24	1.8	118	23.6
Polyipnus polli	STO	nm	zplv1–meso	22	1.6	17	3.4
Cyclothone spp.	STO	nm	zplv2–meso	4	0.3	43	8.6
Other fish species				190	14.1	66	13.2
Total				1344	100	499	100

Species	Tax. order	Migr	FM guild	Total BM (g)	% of total BM	Total AB (N ind.)	% of total AB
Day – M1l – EQ							
Electrona risso	MYC	lm	zplv1–meso	313	7.6	31	4.5
Gonostoma denudatum	STO	dm	zplv2–epi	144	3.5	12	1.7
Argyropelecus sladeni	STO	lm	zplv2–meso	130	3.1	64	9.3
Diaphus dumerilii	MYC	dm	omni–epi	94	2.3	44	6.4
Other fish species				403	9.8	141	20.5
Total				4133	100	687	100

Species	Tax. order	Migr	FM guild	Total BM (g)	% of total BM	Total AB (N ind.)	% of total AB
Day – M1l – LO							
Chauliodus schmidti	STO	am	mnkv–meso	513	16.5	57	8.8
Lampanyctus tenuiformis	MYC	dm	zplv1–epi	495	15.9	59	9.1
Malacosteus niger	STO	am	zplv2–meso	400	12.8	55	8.5
Gonostoma denudatum	STO	dm	zplv2–epi	357	11.5	39	6.0
Nannobrachium isaacsi	MYC	dm	zplv2–epi	243	7.8	25	3.8
Argyropelecus gigas	STO	lm	zplv2–meso	237	7.6	15	2.3
Argyropelecus sladeni	STO	lm	zplv2–meso	164	5.3	39	6.0
Hygophum macrochir	MYC	dm	zplv1–epi	104	3.3	77	11.8
Sternoptyx diaphana	STO	nm	omni–meso	42	1.3	41	6.3
Bolinichthys indicus	MYC	dm	zplv1–epi	22	0.7	22	3.4
Cyclothone spp.	STO	nm	zplv2–meso	16	0.5	108	16.6
Other fish species				521	16.7	113	17.4
Total				3114	100	650	100

Species	Tax. order	Migr	FM guild	Total BM (g)	% of total BM	Total AB (N ind.)	% of total AB
Day – M2 – EQ							
Bolinichthys supralateralis	MYC	dm	zplv1–epi	739	20.2	43	9.6
Lampanyctus tenuiformis	MYC	dm	zplv1–epi	694	18.9	33	7.4
Nannobrachium isaacsi	MYC	dm	zplv2–epi	503	13.7	46	10.3
Chauliodus sloani	STO	am	mnkv–meso	397	10.8	28	6.3
Chauliodus schmidti	STO	am	mnkv–meso	349	9.5	26	5.8
Lampanyctus nobilis	MYC	dm	zplv2–epi	169	4.6	33	7.4
Melamphaes polylepis	STE	nm	zplv2–epi	78	2.1	15	3.3
Sternoptyx diaphana	STO	nm	omni–meso	56	1.5	59	13.2
Lepidophanes guentheri	MYC	dm	zplv1–epi	39	1.1	23	5.1
Cyclothone spp.	STO	nm	zplv2–meso	3	0.1	25	5.6
Other fish species				637	17.4	117	26.1
Total				3664	100	448	100

Tax. order = taxonomic order (BER = Beryciformes, MYC = Myctophiformes, STE = Stephanoberyciformes, STO = Stomiiformes), Migr = Migration behaviour (am = asynchronous/partial migrator, dm = diel migrator, lm = limited migrator, nm = non-migrator, see Section 2.4), FM guild = Feeding–Migrator guild (for definitions see Table A.2), AB = Abundance, BM = Biomass. Species in bold were present in both regions at comparable depths.

(E) from deeper located tows based on abundance data (Fig. 11a). Based on abundances, tows in E were dominated by epipelagic copepod feeders (zplv1–epi; 24–73%), epipelagic mixed crustacean feeders (zplv2–epi; 12–59%) and/or epipelagic omnivores (omni–epi; 0–55%). The latter guild was comparatively more abundant at equatorial stations, especially at station 321 (55%). The shallowest LO daytime tow (309–M1u) was included in this epipelagic group due to its large contribution of the myctophid *Diaphus vanhoeffeni* (zplv1–epi). In the cluster of deeper located tows, SIMPROF identified significant vertical variation between tows in the lower epipelagic (El) and transition from epi- to mesopelagic depths (EM) and mesopelagic tows (M1/M2). Also within mesopelagic tows, significant vertical variation existed according to SIMPROF, while further significant regional differences between the EQ and the LO were indicated in the El/EM. The equatorial tows in the lower epipelagic (El) were characterised by a higher contribution of epipelagic copepod feeders (zplv1–epi) and epipelagic mixed crustacean feeders (zplv2–epi). Contrary, the LO tow from the same depth resembled more closely LO tows in the transition from epi- to mesopelagic depths (EM). Except for tow 311–EM, these showed a greater percentage of mesopelagic non-crustacean/gelatinous feeders (zplv3–meso, 24–35%). Tows in M1 and M2 were generally characterised by a strongest component of mesopelagic copepod feeders (zplv1–meso; M1: 23–58%, M2: 21–46%). Tows in M2, including tows 309–M1l and 311–M1c, showed additional importance of mesopelagic mixed crustacean feeders (zplv2–meso; 24%) and mesopelagic micronektonivores (mnkv–meso; 19–21%). The 2-dimensional nMDS ordination plot (stress = 0.11) of tow similarities visualised these sample relationships well (Fig. 12a). Clustering and ordination results based on species biomass per tow revealed a group structure that differed in some aspects (Figs. 11b, 12b). Firstly, the equatorial tows in the lower epipelagic (El) and secondly, tows in the secondary mesopelagic SSL (M2), including tow 309–M1l, were grouped together with tows in E. In the latter case, this was due to epi-migrating copepod feeders (zplv1–epi) caught in these tows, which were less abundant, but had comparatively large biomass. Thirdly, based on biomass data, all LO tows in the El/EM were associated with tows in M1 from stations 337, 340, 318 and 333, because of the larger importance of epipelagic mixed crustacean feeders (zplv2–epi) over mesopelagic non-crustacean/gelatinous feeders (zplv3–meso) in terms of weight. This group of tows was significantly different from the other tows in M1, that were characterised by a stronger contribution of the predatory feeding guild (mnkv–meso) based on biomass data. In addition, daytime tows in M1 (EQ–M1u/M1l, LO–M1c) were grouped distinctly separate from the other mesopelagic tows.

4. Discussion

4.1. Hydroacoustic SSL structure

Subsurface oxygen was shown to correlate with migration amplitude on larger scales, especially in oxygen minimum regions (OMZ; Bianchi

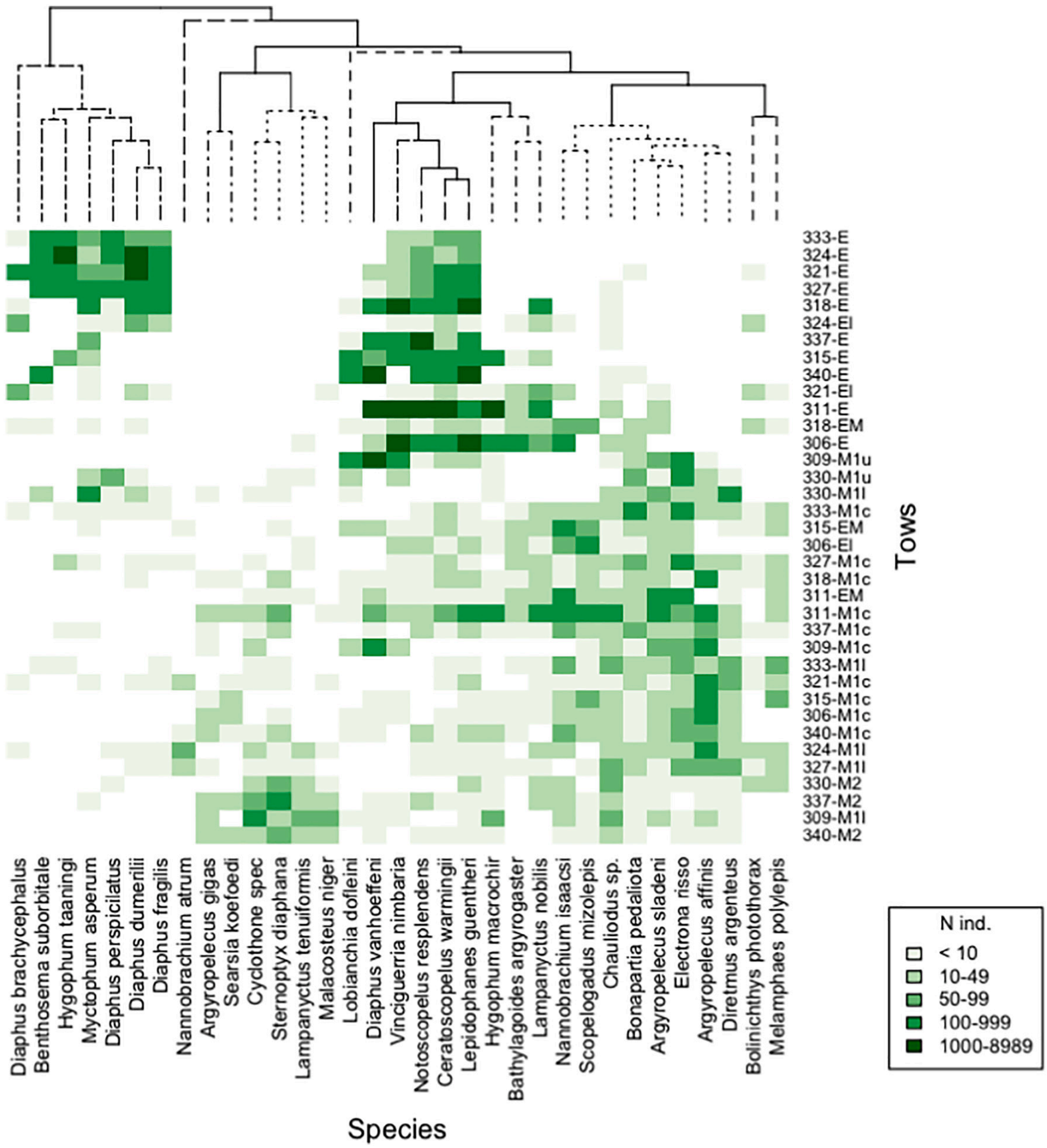


Fig. 10. Heat map of the doubly ordered community table, with dendrogram of UPGMA clustering on species similarities (Bray-Curtis) from fourth root transformed abundance data. Solid black lines in the dendrogram denote significant clusters identified by Similarity Profile Analysis. Only the 33 most important species accounting for > 4% of total abundance in any one tow were retained from an original list of 244 species. Their raw abundances were recoded to a 0–5 scale based on absolute abundances in catches.

and Mislan, 2016) and also during our study in the eastern tropical North Atlantic (ETNA) daytime hydroacoustic backscatter profiles demonstrated higher mean S_v (38 kHz) backscatter at shallower depths at low-oxygen (LO) station 309 compared to equatorial (EQ) station 330. However, night-time hydroacoustic profiles in the LO could not be directly related to OMZ conditions. Mean S_v values in SSLs corresponding to the core depth (~400 m, M1c) and the upper and lower oxycline of the OMZ (M1u and M1l), covered the same range at LO stations (306–315, 337, 340) as at stations 318 and 321 which had high midwater oxygen levels. The variability in night-time hydroacoustic profiles observed in our study region may be due to various factors. At local scales, variable hydrographic conditions in this region (Stramma et al., 2005) and associated nutrient concentrations influence light penetration, which likely affected vertical community structure (Røstad et al., 2016; Aksnes et al., 2017; Langbehn et al., 2019; Klevjer et al., 2020). Connected to the most southern location of the Intertropical Convergence Zone in early boreal spring (Stramma et al., 2005), satellite data of integrated surface primary productivity for March 2015 suggest increased productivity at the LO stations as a result of their closer proximity to coastal upwelling at the African continent. Seasonal upwelling in this region is associated with the presence of larger-sized phytoplankton, which increases turbidity (Marañón et al., 2001) and thereby may affect migration depth (Klevjer et al., 2020). In addition, methodological aspects need to be considered when relating measurements of hydroacoustic backscatter to abundances and species composition of mesopelagic fishes. When ensonified at the 38 kHz frequency

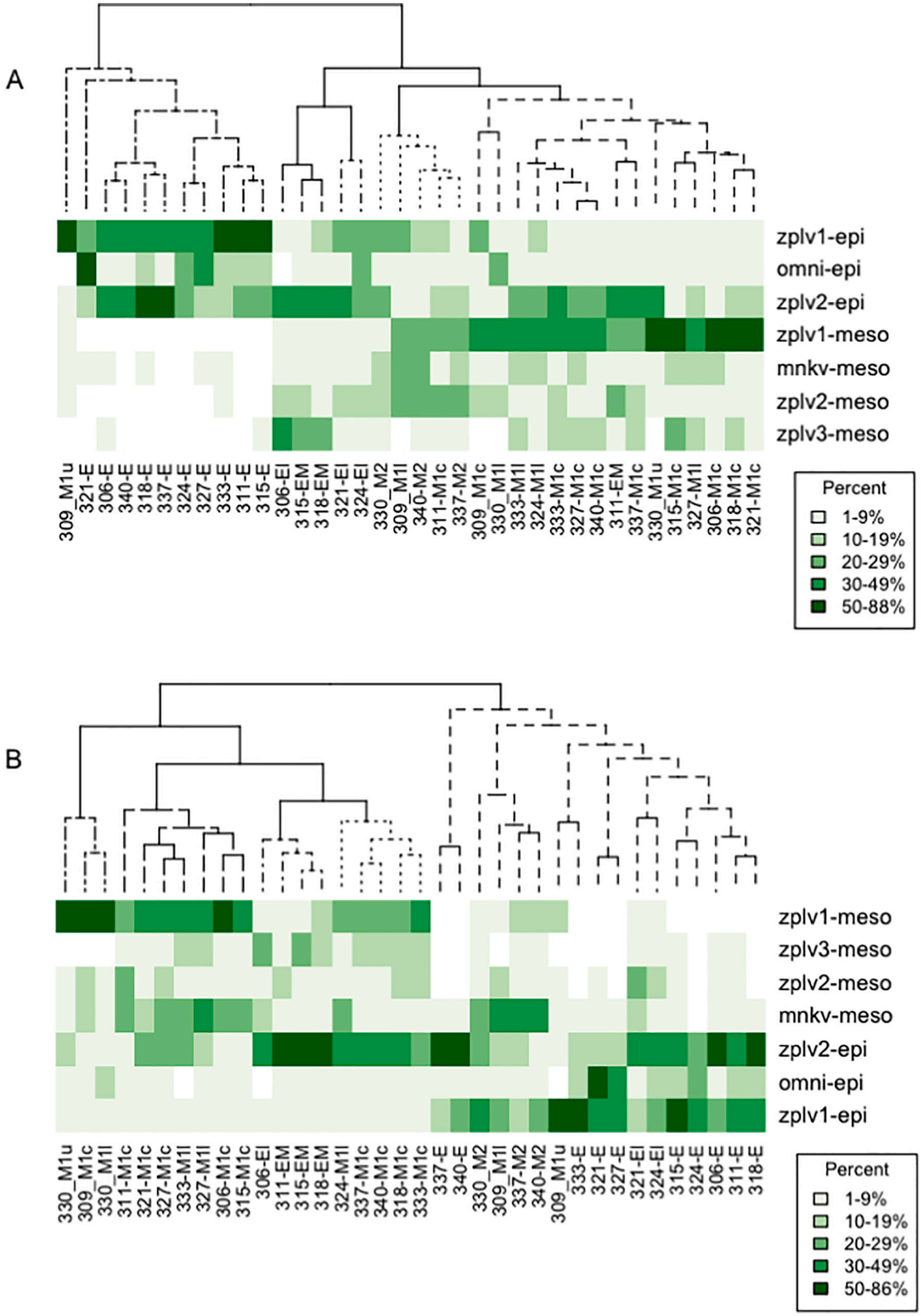


Fig. 11. Heat map of the doubly ordered table of the functional trait Feeding–Migrator guild, with dendrogram using UPGMA clustering on tow similarities (Whittaker index of association) from percentage a) abundances (number of individuals) and b) biomass values (g) per functional trait Feeding–Migrator guild (Table A.2). Solid black lines indicate significant clusters identified by Similarity Profile Analysis.

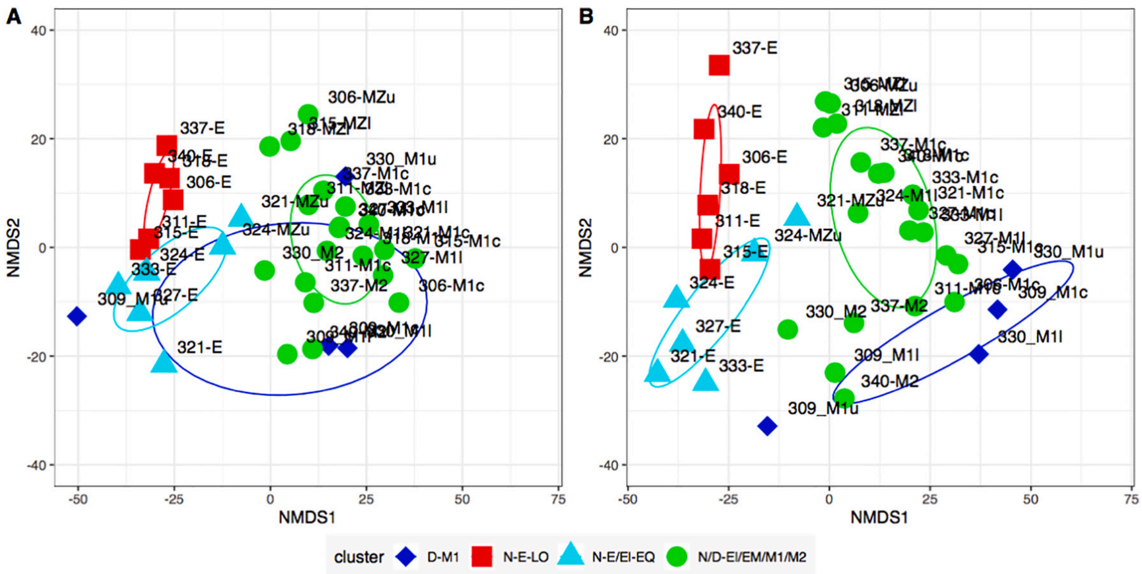


Fig. 12. NMDS ordination of tow similarities (Whittaker index of association) based on the proportional a) abundances (number of individuals) and b) biomass values (g) per functional trait Feeding–Migrator guild (Table A.2). The stress was 0.11 (abundance) and 0.10 (biomass) for the 2-dimensional configuration. Clusters based on UPGMA clustering on Bray-Curtis tow similarities from fourth root transformed species abundance data based on the full dataset of 244 species (Fig. 9). Cluster 1 = night-time principal epipelagic, low-oxygen region (N–E–LO), Cluster 2 = night-time principal and lower epipelagic, equatorial tows (N–E/El–EQ), Cluster 3 = day–/night-time lower epipelagic/epi-mesopelagic transition/principal and secondary mesopelagic SSL all stations (D/N–El/EM/M1/M2–LO/EQ), Cluster 4 = daytime principal mesopelagic D–M1–LO/EQ. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

used in this study, gas-filled structures of organisms produce close to 100% of the backscatter measured (see Proud et al. (2019) and references therein). This implies that by using this method, the contribution of e.g. fishes without a gas-filled swimbladder to the total echo measured in these layers remains unknown. Further, a part of the hydroacoustic backscatter measured may also originate from other mesopelagic taxa like siphonophores with gas-filled pneumatophores, as well as crustaceans, gelatinous zooplankton and cephalopods (Proud et al., 2019). Due to the lack of biological samples of all these taxa, and lower catch representation of mesopelagic fish species and size fractions <0.7 g by the Aalnet trawl used in this study, we did not directly relate hydroacoustic and fish catch data, that often did not match up. This was very obvious at station 311 where clearly the highest catch abundances in the epipelagic and principal mesopelagic SSL were not reflected in equally the highest mean S_v values. Further, the attempt of allocating the species responsible for the strongest backscatter was not straightforward. As an example, stations 327 and 333 had the highest mean S_v in all parts of the principal mesopelagic SSL (M1u, M1c, M1l). There, a comparable group of gas-bladdered species consisting of the myctophid *Electrona risso,* the stomiid *Bonapartia pedaliota*, the sternoptychids *Argyropelecus affinis* and *A. sladeni,* the melamphaid *Melamphaes polylepis* and the diretmid *Diretmus argenteus* dominated the trawl catch in tows in M1c and M1l. Although abundances of these species did not vary much in M1l between stations 327 and 333, mean S_v values largely differed. Furthermore, most of these species were caught in higher abundances at other stations with considerably lower backscatter.

4.2. Abundance and biomass of mesopelagic fishes

We did not observe a clear regional pattern in the catch abundances/biomass of tows in either, the principal epipelagic or the principal mesopelagic SSL in our study, which could be related to a variety of aspects. Known limitations of net sampling are avoidance, escapement, swimming behaviour, vertical orientation and sensory capabilities of the fish (Gjøsæter and Kawaguchi, 1980; Heino et al., 2011; Sutton, 2013). Foremost, the efficiency and species and size selectivity of the net employed is an important factor that, in every study using just one gear, introduces an inherent bias in the reported species quantities and community composition. In a previous study we showed that in biomass size spectra of the pelagic midwater trawl 'Aalnet' employed in our study, the catch representation was sufficient for fishes within the body size class of 1 g, representative of a range from 0.7 g to 1.4 g (Fock et al., 2019). Further, there is the potential for contamination between multisampler nets, or reduction in catch efficiencies when using a cod-end sampler (e.g. Gauthier et al., 2014), which was, however, not observed in our study. In addition, patchiness of mesopelagic organisms in the vertical space in response to biotic (e.g. prey aggregations) or environmental conditions, has been observed earlier (Greenlaw and Pearcy, 1985; Angel, 1993; Grados et al., 2012; Maas et al., 2014). Because we did not sample consecutively the whole water column, but instead discrete disconnected depth intervals related to peak hydroacoustic backscatter, species populations were sampled with an arbitrary upper and lower vertical cut-off in their respective density gradients. Moreover, regional differences in local thermocline depth, lunar conditions and/or a species' local ontogenetic population structure could have introduced additional variation by influencing the upper migration limit of individual DVM- or non-DVM species or parts of a species' population. Regarding the exceptional high catches of the myctophid *Diaphus vanhoeffeni* at station 309/311, these were consistently recorded in the principal epi- and principal mesopelagic SSL during night-time, as well as in the shallowest mesopelagic depth layer sampled during daytime (M1u). This strengthens the notion that these comparatively large catches were not by chance alone, but due to actual increased occurrences of this species.

In our study, non-DVM species dominated the mesopelagic fish community of the ETNA in the principal and secondary mesopelagic SSL during night-time, as well as in the central and lower part of the principal mesopelagic SSL during daytime in terms of abundance, biomass and species numbers. This included species of the families Stomiidae (especially *Chauliodus spp.*), Bathylagidae and Platytroctidae without a gas filled swimbladder (Marshall, 1960). Many species of these families show a large vertical range and likely contribute importantly to vertical energy fluxes. The viperfish *Chauliodus* spp., e.g., was reported as regionally dominant prey component of Atlantic Bluefin Tuna in the central Mediterranean Sea (Battaglia et al., 2013). Species of this genus made up 20% of catch abundances in the lower part of the principal mesopelagic SSL (M1l) and in the secondary principal mesopelagic SSL (M2) in the EQ in the present study (Table 4). This corresponds with data from the western part of the tropical Atlantic that also highlighted its ecological importance (Eduardo et al., 2020a). During fishing operations undetermined quantities of elongated fish species (e.g., species of the families Stomiidae, Serrivomeridae, Nemichthyidae) got entangled in the net during our study, but due to operational constrains could not be collected and included in the catch. Regarding the interpretation of our results, this means, that our estimates of non-DVM species and predatory species, are, in fact, rather conservative, since these quantities were not included. Our estimates of the proportional contribution of non-DVM mesopelagic fishes are larger than earlier reports using a comparatively large-mouthed modified international Young Gadoid Pelagic Trawl (Koslow et al., 1997).

4.3. *Community structure of mesopelagic fishes constituting the main sound scattering layers in the ETNA*

In the present study we used clustering analysis and nMDS ordination to identify regional and vertical patterns in the mesopelagic fish taxonomic and functional community structure based on tows sampling the main SSLs in the ETNA. Our results indicate significant regional variation in the taxonomic species composition of the principal epipelagic SSL between the low-oxygen (LO) and the equatorial region (EQ). This corresponds with separation of stations based on oceanographic parameters and with the known mesopelagic biogeography (Sutton et al., 2017). Although all deeper located night-time tows, including the deepest daytime tows, showed general similarity in their taxonomic community composition, at finer scales, SIMPROF analysis supported the presence of significant vertical and regional gradients between SSLs and between the LO and the EQ. It further suggested greater variability between LO stations compared to equatorial stations, which was supported by the nMDS ordination. Daytime tows in the principal mesopelagic SSL (M1) were significantly distinct in their species composition from night-time tows in the same SSL, despite the fact that the dominant species in M1 were limited or non-migrators (Table 4, Fig. 10). This suggests a large extent of daily vertical movements of species less commonly caught in our study, which importantly affected community composition in this SSL. This change in the dominance of individual species seemed to be less pronounced in the secondary mesopelagic SSL (M2).

Our results indicate the presence of increased association between epi- and mesopelagic fish species in the LO, thereby suggesting a more pronounced gradient structure in the vertical community composition of the LO compared to the EQ. Unlike dominant epipelagic myctophids from the EQ, the dominant epipelagic species from the LO, i.e. the myctophids *D. vanhoeffeni*, *Notoscopelus resplendens*, *Ceratoscopelus warmingii*, *Lepidophanes guentheri* and *Hygophum macrochir* and the phosichthyid *Vinciguerria nimbaria* showed consistent presence also in the principal mesopelagic SSL (M1). These epi-migrating species are not generally known for ontogenetic changes in vertical distribution patterns after becoming adult. In addition, our results hint at shallower presence of generally deeper occurring species and functional groups in the LO. At stations 306 and 311, tows 306–El, 311–EM and 311–M1c were clustered with comparatively deeper located tows based on their functional composition, and tow 306-El additionally based on its taxonomic composition. We further observed comparatively high proportional importance of non-DVM species and mesopelagic predatory species (mnkv–meso) in E and M1c at LO stations 306, 311 and 315. Mesopelagic micronektonivores (mnkv–meso) generally have their main depth distributions in the lower meso- and bathypelagic realms below 500 m (see Table A.1). The observed enhanced shallower occurrences of predatory species in the LO could be related to increased foraging opportunities at comparatively shallow depths, due to a biological structuring effect of the OMZ. The agglomeration of zooplankton at biogeochemical boundary layers has been reported from other OMZs (Wishner et al., 2013; Maas et al., 2014), which my act as prey resource for zooplanktivores, as well as for predatory species. Only at LO stations 309, 311, 337 and 340, we observed increased occurrences of the stomiid *Malacosteus niger* (world-wide distribution) in the deepest night- and daytime tows at depths corresponding to the lower oxycline and the depth of the secondary zooplankton maximum (see references in Williams et al., 2014). Besides occasional fish meals, *M. niger* was shown to feed on large proportions of copepods (Sutton, 2005). Comparatively low nitrogen isotope values were observed in mesopelagic predatory species at LO stations 306–315, contrary to results from the EQ and previously published data (Czudaj et al., 2020), which would be in line with this hypothesis of comparatively shallow feeding. It has further been argued that the OMZ itself may act as refuge for daytime dwellers, which would seem advantageous with respect to larger epipelagic predators with high metabolic demands, such as e.g. tuna or dolphins (Prince and Goodyear, 2006; Olivar et al., 2017). Meso- and bathypelagic predatory species with reduced oxygen demands, on the other hand, are expected not to be restricted by the comparatively light hypoxic conditions in this region (Torres et al., 1979). In addition, community changes involving increases of gelatinous organisms have been observed in many OMZ regions (see references given in Thuesen et al., 2005). Gelatinous and non-crustacean feeders (zplv3–*meso*) were numerically quite important in the lower epipelagic (El) and epi- to mesopelagic transition (EM) at stations 306, 315 and 318. Because we did not sample EM in the EQ, these data cannot be directly regionally compared. More recent evidence based on stable isotope data suggest the general importance of gelatinous prey for several mesopelagic fishes in tropical regions (McClain-Counts et al., 2017; Czudaj et al., 2020; Eduardo et al., 2020b). The pronounced differences in community composition which we observed between LO stations 337 and 340 and LO stations 306–315 suggest that OMZ conditions were not the primary driver of mesopelagic community composition in the ETNA during the time of our study. Local differences in hydrographic and nutrient conditions and their seasonal variation seem to be equally important. The geographical vicinity of stations 337 and 340 to the Guinea Dome, a large-scale cyclonic circulation at about 10°N, 22°W that generates upwelling during boreal summer, possibly offers distinct conditions at smaller scales (Siedler et al., 1992).

Whereas results of the taxonomic analysis were overall comparable based on either, abundance or biomass data, the analysis of functional community composition revealed different structures based on biomass. Due to the comparatively large-sized daily migratory myctophids *Lampanyctus tenuiformis* and *Nannobrachium isaacsi*, equatorial tows in the lower epipelagic (El) and night-time tows in the secondary mesopelagic SSL (M2) were included in the functional group dominated by epi-migrating Feeding-Migrator guilds based on biomass data. Although not caught in large abundances (but consider avoidance behaviour), the relative importance, also in M1, of the large-sized myctophids *Nannobrachium atrum*, *N. isaacsi*, *Lampanyctus lineatum* and L. *tenuiformis* in terms of biomass suggests their functional importance in the ecosystem. The swimbladders of these myctophids are known to ontogenetically regress and become fat-invested as an adaptation to a – presumably energetically more advantageous – mesopelagic lifestyle. These findings demonstrate the usefulness of biomass as an additional parameter when investigating functional aspects of mesopelagic communities.

4.4. Conclusions

Mesopelagic studies using large-mouthed pelagic trawls are imperative for a holistic understanding of mesopelagic fish ecosystem functioning. Our results give further evidence for the importance of limited, asynchronous, partial and non-migratory fishes to the composition of SSLs and vertical energy flow. Overall, this study provides essential data on spatial and vertical dynamics in mesopelagic fish communities in tropical OMZ regions. The functional-structural data of mesopelagic communities provided by this study are valuable as input to refine biogeochemical and food web models, which currently work with large uncertainties regarding important community parameters.

Author contribution

HF conceived the study; HF and SC planned the study; SC conducted the lab work; SC, HF, MS contributed data; SC, HF, MS analysed the data; SC wrote the manuscript; HF, SC, MS, RK and CM critically reviewed the manuscript.

Declaration of Competing Interest

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Table A.1
Literature references for the characterisation of the functional trait Feeding–Migrator guild (for definitions see Section 2.4 and Table A.2).

Species	Family	Migration behaviour	Feeding–Migrator guild	Night-time (Core) depth range (m) – literature	Daytime (Core) depth range (m) – literature	Night-time (Daytime) WH383 range (m)	Vertical occurrence/ migration pattern reference	Feeding guild reference
Anguilliformes								
Derichthys serpentinus	Derichthyidae	am	mnkv–meso	200–700	200–700	245–445	Mundy (2005)	Bauchot and Saldanha (1984)
Nessorhamphus ingolfianus	Derichthyidae	am	mnkv–meso	0–1800	0–1800	475–625	Bauchot and Saldanha (1984)	Bauchot and Saldanha (1984)
Anguilliformes fam. gen. sp.	–	am	mnkv–meso	0–6000	0–6000	230–625 (615–680)	mean value of species of the order Anguilliformes	–
Nemichthyidae gen. sp.	Nemichthyidae	am	mnkv–*meso*	0–2000	0–2000	55–80 (470–500)	Nielsen (1984)	Nielsen (1984)
Nemichthys scolopaceus	Nemichthyidae	am	mnkv–meso	100–1000	100–1000	50–525	Mundy (2005)	Nielsen (1984)
Serrivomer sp.	Serrivomeridae	am	mnkv–meso	200–6000	200–6000	370–430	Bauchot (1986)	Bauchot (1986)
Serrivomer beanii	Serrivomeridae	am	mnkv–meso	150–3000	150–3000	370–625 (520–565)	Bauchot (1986)	Bauchot (1986)
Serrivomer lanceolatoides	Serrivomeridae	am	mnkv–meso	800–1000	800–1000	210–435 (400–680)	Tighe (1989)	Bauchot (1986)
Aulopiformes								
Alepisaurus ferox	Alepisauridae	am	mnkv–meso	0–>1000	0–>1000	370–430	Fedorov et al. (2003)	Post (1984a)
Evermannella sp.	Evermannellidae	nm	mnkv–meso	200–1000	200–1000	450–490	Johnson (1984a)	Johnson (1984a)
Evermannella balbo	Evermannellidae	nm	mnkv–meso	400–1000	400–1000	370–625	Reiner (1996)	Johnson (1984a)
Odontostomops normalops	Evermannellidae	nm	mnkv–meso	100–1000	400–1000	210–625	Johnson (1984a)	Johnson (1984a); Hopkins et al. (1996)
Gigantura chuni	Giganturidae	nm	mnkv–meso	500–1300	500–1300	390–625 (510–565)	Johnson and Bertelsen (1991)	Johnson and Bertelsen (1991); Hopkins et al. (1996)
Ahliesaurus berryi	Notosudidae	nm	zplv1–meso	deep meso–to bathypelagic	deep meso–to bathypelagic	365–625	Krefft (1984)	Krefft (1984)
Notosudidae gen. sp.	Notosudidae	nm	omni–meso	0–1000	0–1000	45–280	Krefft (1984)	Krefft (1984); Hopkins et al. (1996)
Omosudis lowei	Omosudidae	nm	mnkv–meso	700–1830	700–1830	Deck catch	Post (1984d);Maul (1986)	Appelbaum (1982); Post (1984d); Hopkins et al. (1996)
Lestidiops sp.	Paralepididae	nm	mnkv–meso	0–2000	200–2000	50–75	Post (1984e)	Hopkins et al. (1996);Post (1984e)
Lestidiops affinis	Paralepididae	nm	mnkv–meso	0–2000	200–2000	45–175	Post (1984e)	Hopkins et al. (1996);Post (1984e)
Lestidium atlanticum	Paralepididae	nm	mnkv–meso	50–1270	50–1270	475–525	Post (1984e)	Hopkins et al. (1996);Post (1984e)
Lestidiops jayakari	Paralepididae	nm	mnkv–meso	300–600	300–600	45–585 (510–680)	Post (1984e)	Post (1984e); Hopkins et al. (1996)
Lestrolepis intermedia	Paralepididae	nm	mnkv–meso	400–800	400–800	45–245 (470–500)	Post (1990)	Hopkins et al. (1996);Post (1990)

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Table A.1 (*continued*)

Species	Family	Migration behaviour	Feeding–Migrator guild	Night-time (Core) depth range (m) – literature	Daytime (Core) depth range (m) – literature	Night-time (Daytime) WH383 range (m)	Vertical occurrence/ migration pattern reference	Feeding guild reference
Magnisudis atlantica	Paralepididae	nm	mnkv–meso	500–1000	500–1000	400–625	Post (1984e)	Post (1984e); Hopkins et al. (1996)
Arctozenus risso	Paralepididae	nm	mnkv–meso	200–1000	200–1000	60–500 (470–680)	Mundy (2005)	Hopkins et al. (1996);Post (1984e)
Paralepididae gen. sp.	Paralepididae	nm	mnkv–meso	200–1000	200–1000	55–585 (335–380)	Post (1984e)	Hopkins et al. (1996);Post (1984e)
Paralepis brevirostris	Paralepididae	nm	mnkv–meso	100–600	100–600	370–430	Post (1990)	Hopkins et al. (1996), Post (1984e)
Scopelarchidae gen. sp.	Scopelarchidae	nm	mnkv–meso	500–1000	500–1000	50–85 (325–425)	Johnson (1984b)	Hopkins et al. (1996)
Scopelarchus analis	Scopelarchidae	nm	mnkv–meso	500–820	500–820	165–625 (335–555)	Johnson (1984b)	Johnson (1984b); Hopkins et al. (1996)
Scopelarchus michaelsarsi	Scopelarchidae	nm	mnkv–meso	250–> 500	250–>500	135–245	Johnson (1984b)	Johnson (1984b); Hopkins et al. (1996)
Beryciformes								
Anoplogaster cornuta	Anoplogastridae	nm	mnkv–meso	0–5000	0–5000	370–445	Post (1984b)	Hopkins et al. (1996);Post (1984b); Clarke and Wagner (1976)
Diretmus argenteus	Diretmidae	nm	zplv1–meso	500–700	500–700	230–625 (325–680)	Post (1984c)	Post (1984c)
Diretmichthys parini	Diretmidae	nm	zplv1–meso	300–800	300–800	400–435	Post (1984c)	Post (1984c)
Diretmoides pauciradiatus	Diretmidae	nm	zplv1–*meso*	300–800	300–800	45–585 (335–680)	Post (1984c)	Post (1984c)
Gadiformes								
Bregmaceros sp.	Bregmacerotidae	dm	zplv2–epi	NA	NA	45–175 (615–680)	Cohen (1986a)	Cohen (1986)
Bregmaceros atlanticus	Bregmacerotidae	dm	zplv2–epi	NA	NA	50–75	Cohen (1986)	Cohen (1986); Hopkins et al. (1996)
Macrouridae gen. sp.	Macrouridae	nm	omni–*meso*	200–2000	200–2000	400–440	Nelson (1994)	Geistdoerfer (1986)
Odontomacrurus murrayi	Macrouridae	nm	mnkv–meso	0–2500	0–2500	165–500	Geistdoerfer (1986)	Geistdoerfer (1986)
Melanonus zugmayeri	Melanonidae	nm	zplv1–meso	350–5100	350–5100	165–625 (390–425)	Henriques et al. (2001)	Koefoed (1953)
Moridae gen. sp. *I – III*	Moridae	nm	omni–meso	0–>2500	0–> 2500	230–625 (510–555)	Cohen (1990)	Cohen (1986b)
Lampriformes								
Stylephorus chordatus	Stylephoridae	lm	zplv1–meso	300–600	625–800	375–500	Mundy (2005); Johnson and Berman (1986)	Johnson and Berman (1986)
Lophiiformes								
Ceratias holboelli	Ceratiidae	nm	mnkv–meso	400–2000	400–2000	50–490	Fernández-Ovies and González (1996)	Bertelsen (1986)
Cryptopsaras couesii	Ceratiidae	nm	mnkv–meso	500–1250	500–1250	50–625 (335–380)	Watson (1996)	Bertelsen (1986)
Ceratioidei fam. Gen. sp.I – III	Ceratiidae	nm	mnkv–meso	400–2000	400–2000	555–585	cf. *C. hoelboelli*	Bertelsen (1986)
Himantolophus sp.	Himantolophidae	nm	mnkv–meso	400–2000	400–2000	50–585	cf. *C. hoelboelli*	Bertelsen (1986)
Melanocetus johnsonii	Melanocetidae	nm	mnkv–meso	100–1500	100–1500	230–625 (615–680)	Pietsch (1986)	Bertelsen (1986)
Oneirodidae gen. sp. I – IV	Oneirodidae	nm	mnkv–meso	400–2000	400–2000	50–625 (510–555)	cf. *C. hoelboelli*	Bertelsen (1986)
Myctophiformes								
Benthosema glaciale	Myctophidae	dm	zplv1–*epi*	12–200	275–850	450–490	Nafpaktitis et al. (1977)	Kinzer (1977); Appelbaum (1982); Kinzer (1982)
Benthosema suborbitale	Myctophidae	dm	zplv1–epi	0–125	375–750	45–525 (400–500)	Nafpaktitis et al. (1977)	Hopkins and Gartner (1992)
Bolinichthys sp.	Myctophidae	dm	zplv1–epi	NA	NA	45–430	cf. *Bolinichthys indicus*	cf. *Bolinichthys photothorax*
Bolinichthys supralateralis	Myctophidae	dm	zplv1–epi	40–325	425–800	45–440 (510–565)	Nafpaktitis et al. (1977)	Appelbaum (1982)
Bolinichthys photothorax	Myctophidae	dm	zplv1–epi	40–500	425–800	50–525 (615–680)	Nafpaktitis et al. (1977)	Hopkins and Gartner (1992)
Bolinichthys supralateralis	Myctophidae	dm	zplv1–*epi*	40–650	375–750	140–625 (510–680)	Nafpaktitis et al. (1977)	Hopkins et al. (1996)
Ceratoscopelus maderensis	Myctophidae	dm	omni–*epi*	0–175	225–1000	450–490 (400–445)	Nafpaktitis et al. (1977)	Kinzer (1982);Bernal et al. (2015);S. Czudaj, unpublished data

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Table A.1 (*continued*)

Species	Family	Migration behaviour	Feeding–Migrator guild	Night-time (Core) depth range (m) – literature	Daytime (Core) depth range (m) – literature	Night-time (Daytime) WH383 range (m)	Vertical occurrence/ migration pattern reference	Feeding guild reference
Ceratoscopelus warmingii	Myctophidae	dm	omni–epi	75–100	550–750	45–625 (335–565)	Nafpaktitis et al. (1977);Hulley (1984)	Appelbaum (1982); Robison (1984); Kinzer and Schulz (1985);Duka (1987); Hopkins et al. (1996);Takagi et al. (2009)
Diaphus/Lobianchia sp.	Myctophidae	dm	zplv1–epi	NA	NA	60–490	cf. other *Diaphus* species	cf. other *Diaphus* species
Diaphus sp.	Myctophidae	dm	zplv1–epi	NA	NA	165–490 (335–500)	cf. other *Diaphus* species	cf. other *Diaphus* species
Diaphus bertelseni	Myctophidae	dm	zplv1–epi	60–175	200–300	245–435	Nafpaktitis et al. (1977)	cf. other *Diaphus* species
Diaphus brachycephalus	Myctophidae	dm	zplv1–epi	0–225	175–550	50–490	Nafpaktitis et al. (1977)	Kinzer and Schulz (1985); Hopkins et al. (1996)
Diaphus dumerilii	Myctophidae	dm	omni–*epi*	0–125	450–500	45–500 (325–565)	Nafpaktitis et al. (1977)	Kinzer and Schulz (1985);De Alwis and Gjøsaeter (1988); Hopkins et al. (1996); S. Czudaj, unpublished data
Diaphus fragilis	Myctophidae	dm	zplv1–*epi*	15–125	375–750	45–525 (470–500)	Nafpaktitis et al. (1977)	Hopkins et al. (1996)
Diaphus garmani	Myctophidae	dm	zplv1–epi	40–125	325–750	55–80	Nafpaktitis et al. (1977)	cf. other *Diaphus* species
Diaphus holti	Myctophidae	dm	zplv1–epi	40–275	225–650	55–525 (330–425)	Nafpaktitis et al. (1977)	Kinzer (1982);Kinzer and Schulz (1985)
Diaphus lucidus	Myctophidae	dm	zplv2–*meso*	40–550	425–750	0–525 (615–680)	Nafpaktitis et al. (1977)	Hopkins et al. (1996)
Diaphus mollis	Myctophidae	dm	zplv1–epi	50–300	300–600	45–490 (325–680)	Nafpaktitis et al. (1977)	Hopkins et al. (1996)
Diaphus perspicilatus	Myctophidae	dm	zplv2–*epi*	0–125	375–750	45–490 (325–680)	Nafpaktitis et al. (1977)	Hopkins et al. (1996); S. Czudaj (unpublished data)
Diaphus problematicus	Myctophidae	dm	zplv2–epi	40–225	375–750	50–525 (470–500)	Nafpaktitis et al. (1977)	Hopkins et al. (1996)
Diaphus splendidus	Myctophidae	dm	zplv2–*meso*	40–225	375–750	50–490 (615–680)	Nafpaktitis et al. (1977)	Hopkins et al. (1996)
Diaphus subtilis	Myctophidae	dm	zplv1–epi	40–550	375–750	380–500 (400–565)	Nafpaktitis et al. (1977)	Hopkins et al. (1996)
Diaphus taaningi	Myctophidae	dm	omni–epi	40–250	325–475	450–490	Nafpaktitis et al. (1977)	De Alwis and Gjøsaeter (1988)
Diaphus vanhoeffeni	Myctophidae	dm	zplv1–epi	40–125	275–750	45–440 (330–555)	Nafpaktitis et al. (1977)	Tkach (1987a;1987b)
Diogenichthys atlanticus	Myctophidae	dm	zplv1–epi	50–100	500–700	45–420 (510–565)	Hulley (1990)	Hopkins et al. (1996)
Electrona risso	Myctophidae	lm	zplv1–*meso*	90–550	225–750	165–585 (325–680)	Nafpaktitis et al. (1977)	Podrazhanskaya (1993)
Gonichthys cocco	Myctophidae	dm	zplv2–*meso*	0–175	425–650	210–245 (400–445)	Hulley (1990)	Hopkins et al. (1996)
Hygophum macrochir	Myctophidae	dm	zplv1–epi	0–125	275–750	45–625 (325–680)	Nafpaktitis et al. (1977)	Hopkins et al. (1996); S. Czudaj, unpublished data
Hygophum macrochir/ taaningi	Myctophidae	dm	zplv1–epi	0–250	275–1000	45–85	cf. *H. macrochir/ taaningi*	cf. *H. macrochir/ taaningi*
Hygophum reinhardtii	Myctophidae	dm	zplv2–epi	0–175	475–850	45–175 (330–370)	Nafpaktitis et al. (1977)	Hopkins et al. (1996)
Hygophum taaningi	Myctophidae	dm	zplv1–epi	0–250	450–1000	45–525 (330–565)	Nafpaktitis et al. (1977)	Appelbaum (1982)
Lampadena sp.	Myctophidae	dm	NA	NA	NA	45–625	NA	NA
Lampadena anomala	Myctophidae	nm	zplv2–*meso*	> 1000	800–2000	475–525	Hulley (1990); Mundy (2005)	cf. *L. atlantica*
Lampadena atlantica	Myctophidae	dm	zplv2–epi	60–225	550–1000	400–440	Hulley (1990)	Appelbaum (1982)
Lampadena luminosa	Myctophidae	dm	zplv2–epi	40–225	425–800	140–565	Nafpaktitis et al. (1977)	cf. L. *atlantica*
Lampadena pontifex	Myctophidae	dm	zplv2–epi	90–275	275–750	375–490	Nafpaktitis et al. (1977)	cf. *L. atlantica*
Lampadena speculigera	Myctophidae	dm	zplv2–epi	60–750	475–950	245–290	Nafpaktitis et al. (1977)	cf. *L. atlantica*

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Table A.1 (*continued*)

Species	Family	Migration behaviour	Feeding–Migrator guild	Night-time (Core) depth range (m) – literature	Daytime (Core) depth range (m) – literature	Night-time (Daytime) WH383 range (m)	Vertical occurrence/ migration pattern reference	Feeding guild reference
Lampanyctus/ Nannobrachium sp. I – III	Myctophidae	dm	zplv2–*epi*	NA	NA	45–625 (390–565)	cf. other *Lampanyctus/ Nannobrachium* species	cf. other *Lampanyctus/ Nannobrachium* species
Lampanyctus alatus	Myctophidae	dm	omni–epi	40–275	275–1000	45–625 (520–565)	Nafpaktitis et al. (1977)	Kinzer and Schulz (1985); Hopkins et al. (1996)
Lampanyctus festivus	Myctophidae	dm	zplv2–*epi*	40–325	475–1000	410–445 (520–565)	Nafpaktitis et al. (1977)	cf. other *Lampanyctus/ Nannobrachium* species
Lampanyctus nobilis	Myctophidae	am	zplv2–epi	40–500	475–>900	45–625 (330–680)	Nafpaktitis et al. (1977)	Hopkins et al. (1996)
Lampanyctus photonotus	Myctophidae	dm	zplv2–epi	40–175	550–1550	50–490	Nafpaktitis et al. (1977)	Appelbaum (1982)
Lampanyctus tenuiformis	Myctophidae	dm	zplv1–epi	40–325	300–750	50–625 (510–680)	Nafpaktitis et al. (1977)	Hopkins et al. (1996)
Lepidophanes guentheri	Myctophidae	dm	zplv2–epi	50–125	425–750	45–625 (335–680)	Nafpaktitis et al. (1977)	Hopkins et al. (1996); Kinzer and Schulz (1985)
Lobianchia dofleini	Myctophidae	dm	zplv2–epi	20–200	300–700	45–400 (325–555)	Nafpaktitis et al. (1977)	De Alwis and Gjøsaeter (1988); Bernal et al. (2015)
Lobianchia gemellari	Myctophidae	dm	zplv2–epi	25–175	325–800	50–585	Nafpaktitis et al. (1977)	Hopkins et al. (1996)
Myctophidae gen. sp.	Myctophidae	dm	NA	NA	NA	45–440 (330–680)	mdo: mean of family *Myctophidae*	NA
Myctophum affine	Myctophidae	dm	zplv1–epi	0–275	300–750	45–245 (330–555)	Nafpaktitis et al. (1977)	De Alwis and Gjøsaeter (1988)
Myctophum asperum	Myctophidae	dm	omni–epi	0–125	425–750	45–625 (325–565)	Nafpaktitis et al. (1977)	Watanabe et al. (2002);Takagi et al. (2009)
Myctophum nitidulum	Myctophidae	dm	omni–epi	0–200	475–850	50–500 (520–680)	Nafpaktitis et al. (1977)	De Alwis and Gjøsaeter (1988); Watanabe et al. (2002)
Myctophum obtusirostre	Myctophidae	dm	zplv1–epi	0–125	325–700	60–500 (470–500)	Nafpaktitis et al. (1977)	cf. other *Myctophum* species
Myctophum punctatum	Myctophidae	dm	zplv1–epi	0–200	225–750	55–440 (470–680)	Nafpaktitis et al. (1977)	Kinzer (1982)
Myctophum sp.	Myctophidae	dm	zplv1–epi	NA	NA	45–85	cf. other *Myctophum* species	cf. other *Myctophum* species
Nannobrachium atrum	Myctophidae	dm	zplv2–epi	100–150	550–850	230–500	Nafpaktitis et al. (1977)	cf. *N. lineatum* in Hopkins et al. (1996)
Nannobrachium isaacsi	Myctophidae	dm	zplv2–epi	100	550–750	50–625 (510–680)	Nafpaktitis et al. (1977)	cf. *N. lineatum* in Hopkins et al. (1996); S. Czudaj unpublished data
Nannobrachium lineatum	Myctophidae	dm	zplv2–epi	100	650–1150	135–525 (615–680)	Nafpaktitis et al. (1977)	Hopkins et al. (1996)
Neoscopelus macrolepidotus	Myctophidae	nm	NA	300–800	300–800	585–625	Shcherbachev (1987)	NA
Notoscopelus caudispinosus	Myctophidae	dm	zplv1–epi	0–175	600–1150	375–585	Nafpaktitis et al. (1977)	Appelbaum (1982); Hopkins et al. (1996)
Notoscopelus resplendens	Myctophidae	dm	zplv2–epi	0–125	600–800	45–625 (330–380)	Nafpaktitis et al. (1977)	Hopkins et al. (1996); S. Czudaj unpublished data
Symbolophorus rufinus	Myctophidae	dm	zplv1–epi	0–125	425–850	55–85 (520–680)	Nafpaktitis et al. (1977)	cf. *S. veranyi*
Symbolophorus veranyi	Myctophidae	dm	zplv1–epi	0–90	550–750	45–525 (510–555)	Nafpaktitis et al. (1977)	Appelbaum (1982)
Taaningichthys bathyphilus	Myctophidae	nm	NA	625–1000	800–1550	585–625	Mundy (2005)	NA
Osmeriformes								
Alepocephalidae gen. sp.	Alepocephalidae	nm	zplv3–*meso*	> 1000	> 1000	380–430	Markle and Quéro (1984)	Markle and Quéro (1984)
Bathylagidae gen. sp.	Bathylagidae	nm	zplv3–meso	NA	NA	50–420 (335–380)	mean of shallow occurring species of the familiy Bathylagidae	Priede (2017)

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Table A.1 (*continued*)

Species	Family	Migration behaviour	Feeding–Migrator guild	Night-time (Core) depth range (m) – literature	Daytime (Core) depth range (m) – literature	Night-time (Daytime) WH383 range (m)	Vertical occurrence/ migration pattern reference	Feeding guild reference
Bathylagoides argyrogaster	Bathylagidae	nm	zplv3–meso	200–300	200–300	45–525	Kobylyanskiy (1985)	Cohen (1984b); Priede (2017)
Bathylagichthys greyae	Bathylagidae	nm	zplv3–meso	25–500	600–900	245–625	Cohen (1984b); Kobylyanskiy (1985)	Cohen (1984b); Priede (2017)
Melanolagus bericoides	Bathylagidae	nm	zplv3–meso	100–1700	100–1700	375–625	Mundy (2005)	Cohen (1984b); Priede (2017)
Microstoma microstoma	Microstomatidae	nm	zplv2–meso	200–1000	<1000	230–290	Cohen (1984a)	Cohen (1984a); cf. family information in Hopkins et al. (1996)
Monacoa grimaldii	Opisthoproctidae	nm	zplv1–*meso*	300–400	300–2000	210–500	Bigelow et al. (1964)	Hartel and Orrell (2016)
Nansenia sp.	Microstomatidae	nm	omni–meso	NA	NA	210–245	mean of *Nansenia* spp. presented here as mdo	Cohen (1984a)
cf. *Nansenia atlantica*	Microstomatidae	nm	omni–meso	0–580	0–580	230–420	Kawaguchi and Butler (1984)	Cohen (1984a)
cf. *Nansenia longicauda*	Microstomatidae	nm	omni–meso	400–1100	400–1100	380–500	Mundy (2005)	Cohen (1984a)
cf. *Nansenia megalopa*	Microstomatidae	nm	omni–meso	0–1300	500–1300	375–500	Bigelow et al. (1964);Kawaguchi and Butler (1984)	Cohen (1984a)
cf. *Nansenia pelagica*	Microstomatidae	nm	omni–meso	0–2000	0–2000	370–445 (615–680)	Kawaguchi and Butler (1984); Mundy (2005)	Cohen (1984a)
Xenophthalmichthys danae	Microstomatidae	nm	omni–meso	0–1250	0–1250	410–445	Bigelow et al. (1964)	Cohen (1984a)
Bathylychnops brachyrhynchus	Opisthoproctidae	nm	zplv1–meso	300–2000	300–2000	375–430	Hartel and Orrell (2016)	Hartel and Orrell (2016)
Opisthoproctus sp.	Opisthoproctidae	nm	zplv1–meso	NA	NA	– (470–500)	mean of family *Opisthoproctidae* spp. presented here as mdo	Hartel and Orrell (2016)
Opisthoproctus soleatus	Opisthoproctidae	nm	zplv1–meso	500–700	500–700	245–525 (390–555)	Cohen (1984c)	Hartel and Orrell (2016)
Rhynchohyalus natalensis	Opisthoproctidae	nm	zplv1–meso	?–775	?–775	375–420	Bigelow et al. (1964); Cohen (1984c)	Hartel and Orrell (2016)
Winteria telescopa	Opisthoproctidae	nm	zplv1–meso	500–700	500–700	370–625 (510–680)	Quéro (1990)	Hartel and Orrell (2016)
Maulisia mauli	Platytroctidae	nm	zplv1–meso	271–1524	271–1524	400–435	Bigelow et al. (1964)	cf. *Searsia koefoedi*
Sagamichthys schnakenbecki	Platytroctidae	nm	zplv1–meso	365–1200	365–1200	165–525	Bigelow et al. (1964);Quéro et al. (1984)	cf. *Searsia koefoedi*
Searsia koefoedi	Platytroctidae	nm	zplv1–meso	500–600	450–1500	370–625	Quéro et al. (1984)	Quéro et al. (1984); Hopkins et al. (1996)
Perciformes								
Bramidae gen sp.	Bramidae	nm	NA	200–1000	200–1000	45–85 (520–565)	Haedrich (1986a)	NA
Antigonia capros	Caproidae	nm	omni–*epi*	100–300	100–300	50–430	Quéro (1986)	Quéro (1986)
Selene dorsalis	Carangidae	nm	zplv2–epi	20–100	20–100	45–440	Smith-Vaniz (1986)	Smith–Vaniz (1986), but juveniles caught
Paracaristius maderensis	Caristiidae	nm	NA	300–2000	300–2000	245–290	Post (1986)	NA
Platyberyx opalescens	Caristiidae	nm	NA	200–900	200–900	45–625	Post (1986)	NA
Chiasmodontidae gen. sp.	Chiasmodontidae	am	mnkv–meso	>750	>750	140–195	Johnson and Keene (1984)	Hopkins et al. (1996); cf. family information in Johnson and Keene (1984)
Chiasmodon niger	Chiasmodontidae	am	mnkv–*meso*	700–2745	700–2745	210–625 (615–680)	Johnson and Keene (1984)	Hopkins et al. (1996)
Kali macrura	Chiasmodontidae	am	mnkv–meso	>1000	>1000	400–435	Johnson and Keene (1984)	Hopkins et al. (1996); cf. family information in Johnson and Keene (1984)

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Table A.1 (*continued*)

Species	Family	Migration behaviour	Feeding–Migrator guild	Night-time (Core) depth range (m) – literature	Daytime (Core) depth range (m) – literature	Night-time (Daytime) WH383 range (m)	Vertical occurrence/ migration pattern reference	Feeding guild reference
Kali macrodon	Chiasmodontidae	am	mnkv–meso	>1500	>1500	370–440 (510–555)	Johnson and Keene (1984)	Hopkins et al. (1996); cf. family information in Johnson and Keene (1984)
Pseudoscopelus sp.	Chiasmodontidae	am	mnkv–meso	280–?	540–?	210–425 (520–565)	Johnson and Keene (1984)	Hopkins et al. (1996)
Pseudoscopelus altipinnis	Chiasmodontidae	am	mnkv–meso	50–1870	50–1870	135–585 (615–680)	Hulley (1981); Johnson and Keene (1984)	Hopkins et al. (1996)
Gempylidae gen. sp.	Gempylidae	dm	mnkv–meso	150–1200	150–1200	50–80	Parin (1986a)	cf. family level in Hopkins et al. (1996); Parin (1986a)
Nealotus tripes	Gempylidae	dm	mnkv–meso	0–550	0–550	45–195 (335–565)	Parin (1986a)	Parin (1986a)
Bathysphyraenops simplex	Howellidae	dm	zplv2–meso	100–500	100–500	75–490	Mundy (2005)	Heemstra (2016)
Howella atlantica	Howellidae	dm	zplv2–meso	100–1100	100–1100	45–525 (470–680)	Post and Quéro (1991)	Heemstra (2016)
Howella sherborni	Howellidae	dm	zplv2–meso	26–950	26–950	140–175	Heemstra (1986)	Heemstra (2016)
Howellidae gen. sp.	Howellidae	dm	zplv2–meso	–	–	380–430	mean of family Howellidae present in this study	Gorelova et al. (1994)
Cubiceps gracilis	Nomeidae	nm	zplv3–meso	0–1000	0–1000	45–500	Haedrich (1986b)	Gorelova et al. (1994)
Cubiceps pauciradiatus	Nomeidae	nm	zplv3–meso	0–1000	0–1000	50–625	Haedrich (1986b)	Gorelova et al. (1994)
Nomeidae gen sp.	Nomeidae	nm	zplv3–meso	0–1000	0–1000	45–85	Haedrich (1986b)	Gorelova et al. (1994)
Scombrolabrax heterolepis	Scombrolabracidae	nm	mnkv–meso	100–600	100–600	45–175	Parin (1986b)	Parin (1986b)
Tetragonurus cuvieri	Tetragonuridae	nm	zplv3–meso	200–1000	200–1000	230–440	Haedrich (1986b)	Haedrich (1986b)
Stephanoberyciformes								
Melamphaes sp.	Melamphaidae	nm	zplv3–meso	NA	NA	400–440	mean of *Melamphaes spp.*	cf. *Scopelogadus mizolepis* in Hopkins et al. (1996)
Melamphaes eulepis	Melamphaidae	nm	zplv3–meso	150–?	150–?	135–490 (520–565)	Ebeling (1962)	cf. *Scopelogadus mizolepis* in Hopkins et al. (1996)
Melamphaes leprus	Melamphaidae	nm	zplv3–meso	150–350	150–1550	165–625	Kotlyar (2011)	cf. *Scopelogadus mizolepis* in Hopkins et al. (1996)
Melamphaes longivelis	Melamphaidae	nm	zplv3–meso	500–1500	500–1500	210–525	Ebeling (1962); Masuda et al. (1984)	cf. *Scopelogadus mizolepis* in Hopkins et al. (1996)
Melamphaes polylepis	Melamphaidae	nm	zplv3–meso	300–2250	300–2250	135–525 (610–680)	Ebeling (1962)	cf. *Scopelogadus mizolepis* in Hopkins et al. (1996)
Melamphaes simus	Melamphaidae	nm	zplv1–meso	150–>1000	150–>1000	50–430	Ebeling (1962); Kotlyar (2016)	Hopkins et al. (1996)
Melamphaes typhlops	Melamphaidae	nm	zplv3–meso	500–>1000	500–>1000	165–625	Ebeling (1962)	cf. *Scopelogadus mizolepis* in Hopkins et al. (1996)
Poromitra crassiceps	Melamphaidae	nm	zplv3–meso	600–800	600–800	375–525	Bailey and Robison (1986);Kotlyar (2008)	cf. *P. gibbsi* in Hopkins et al. (1996)
Poromitra megalops	Melamphaidae	nm	zplv1–meso	400–1000	400–1000	370–625 (510–555)	Sandknop and Watson (1996)	cf. *M. simus*
Scopelogadus beanii	Melamphaidae	nm	zplv3–meso	800–1000	800–1000	375–585	Ebeling and Weed (1963)	Gartner and Musick (1989)
Scopelogadus mizolepis	Melamphaidae	nm	zplv3–meso	>500	>500	165–625 (390–555)	Ebeling and Weed (1963)	Ebeling and Weed (1963); Hopkins et al. (1996)
Stomiiformes								
Bonapartia pedaliota	Gonostomatidae	nm	zplv2–epi	100–700	100–700	45–625 (325–680)	Badcock (1984a)	Hopkins et al. (1996)
Cyclothone sp.	Gonostomatidae	nm	zplv1–meso	300–3000	300–3000	245–625 (390–680)	Badcock (1984a)	Hopkins et al. (1996)

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Table A.1 (*continued*)

Species	Family	Migration behaviour	Feeding–Migrator guild	Night-time (Core) depth range (m) – literature	Daytime (Core) depth range (m) – literature	Night-time (Daytime) WH383 range (m)	Vertical occurrence/ migration pattern reference	Feeding guild reference
Diplophos taenia	Gonostomatidae	dm	zplv2–epi	0–200	300–800	45–625 (335–500)	Badcock (1984a)	Hopkins et al. (1996)
Gonostomatidae gen. sp.	Gonostomatidae	dm	zplv2–epi	200–3000	200–3000	165–195	mean of *Gonostoma* spp. presented	Badcock (1984a)
Gonostoma atlanticum	Gonostomatidae	dm	zplv2–epi	50–200	300–500	400–490	Badcock (1984a)	Badcock (1984a)
Gonostoma denudatum	Gonostomatidae	dm	zplv2–meso	100–200	400–700	45–585 (390–680)	Badcock (1984a)	cf. *G. atlanticum*, Badcock (1984a)
Sigmops elongatus	Gonostomatidae	dm	zplv2–meso	50–400	500–1200	45–625 (510–680)	Badcock (1984a)	Appelbaum (1982); Badcock (1984a); Lancraft et al. (1988); Hopkins et al. (1996)
Manducus maderensis	Gonostomatidae	dm	zplv2–epi	0–200	400–800	– (510–555)	Schaefer et al. (1986)	cf. *G. atlanticum*, Badcock (1984a)
Margrethia obtusirostra	Gonostomatidae	nm	mnkv–meso	100–600	100–600	210–245	Badcock (1984a)	Badcock (1984a); Hopkins et al. (1996)
Ichthyococcus ovatus	Phosichthyidae	nm	zplv2–epi	200–500	200–500	45–445 (325–680)	Badcock (1984b)	Badcock (1984b)
Polymetme corythaeola	Phosichthyidae	nm	zplv2–epi	300–500	300–500	475–525	Badcock (1984b)	cf. other Phosichthyidae gen. Spp.
Vinciguerria nimbaria	Phosichthyidae	dm	zplv1–epi	0–100	200–400	45–625 (325–555)	Badcock (1984b)	Shevchenko (1987); Tkach and Shevchenko (1988); Shevchenko (1995); Hopkins et al. (1996);N'goran and Pagano (1999);S. Czudaj unpublished data
Maurolicus muelleri	Sternoptychidae	dm	zplv2–epi	0–100	200–400	50–80	Badcock (1984c)	Hopkins et al. (1996); Badcock (1984c)
Valenciennellus tripunctulatus	Sternoptychidae	lm	zplv1–epi	100–550	100–550	245–290 (325–370)	Badcock (1984c)	Merret and Roe (1974);Badcock (1984c)
Argyropelecus sp.	Sternoptychidae	lm	omni–epi	100–600	200–800	45–445 (325–425)	Badcock (1984c)	Badcock (1984c)
Argyropelecus aculeatus	Sternoptychidae	dm	zplv2–epi	100–300	300–600	– (330–425)	Badcock (1984c)	Badcock (1984c)
Argyropelecus affinis	Sternoptychidae	lm	zplv1–meso	300–600	500–600	370–625 (325–680)	Badcock (1984c); Bailey and Robison (1986);Kinzer and Schulz (1988); Olivar et al. (2017)	Kinzer and Schulz (1988); cf. *Argyropelecus aculeatus* in Hopkins et al. (1996)
Argyropelecus gigas	Sternoptychidae	nm	omni–epi	300–650	300–650	370–625 (390–555)	Badcock (1984c)	cf. *Argyropelecus aculeatus* in Hopkins et al. (1996)
Argyropelecus hemigymnus	Sternoptychidae	dm	zplv2–meso	100–600	200–800	330–370 (375–425)	Badcock (1984c)	Hopkins et al. (1996)
Argyropelecus sladeni	Sternoptychidae	lm	zplv2–meso	200–300	300–400	45–625 (325–680)	Kinzer and Schulz (1988);Bailey and Robison (1986); Olivar et al. (2017)	Kinzer and Schulz (1988); cf. *Argyropelecus aculeatus* in Hopkins et al. (1996)
Polyipnus polli	Sternoptychidae	nm	zplv1–*meso*	100–400	100–400	230–440 (325–680)	Badcock (1984c)	cf. *P. asteroides*; Hopkins et al. (1996)
Sternoptyx sp.	Sternoptychidae	nm	zplv2–meso	500–2000	500–2000	375–435 (510–555)	Badcock (1984c)	Hopkins et al. (1996); Badcock (1984c)
Sternoptyx diaphana	Sternoptychidae	nm	zplv2–meso	300–1100	300–1100	230–625 (325–680)	Baird (1971); Badcock (1984c)	Hopkins et al. (1996)
Sternoptyx pseudobscura	Sternoptychidae	nm	zplv2–meso	800–1500	800–1500	– (335–680)	Badcock (1984c)	Hopkins et al. (1996)
Astronesthes sp.	Stomiidae	am	zplv2–meso	0–>500	>500	60–625	cf. subfamily information in Gibbs (1984a)	Hopkins et al. (1996);Sutton and Hopkins (1996)
Astronesthes caulophorus	Stomiidae	am	zplv2–meso	0–>500	>500	400–440	cf. subfamily information in Gibbs (1984a)	Hopkins et al. (1996); Sutton and Hopkins (1996)

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Table A.1 (*continued*)

Species	Family	Migration behaviour	Feeding–Migrator guild	Night-time (Core) depth range (m) – literature	Daytime (Core) depth range (m) – literature	Night-time (Daytime) WH383 range (m)	Vertical occurrence/ migration pattern reference	Feeding guild reference
Astronesthes cyaneus	Stomiidae	am	zplv2–meso	0–>500	>500	50–490	cf. subfamily information in Gibbs (1984a)	Hopkins et al. (1996); Sutton and Hopkins (1996)
Astronesthes indicus	Stomiidae	am	zplv2–meso	0–>500	>500	210–625	cf. subfamily information in Gibbs (1984a)	Hopkins et al. (1996); Sutton and Hopkins (1996)
Astronesthes neopogon	Stomiidae	am	zplv2–meso	0–>500	>500	135–430	cf. subfamily information in Gibbs (1984a)	Hopkins et al. (1996); Sutton and Hopkins (1996)
Astronesthes niger	Stomiidae	am	zplv2–meso	0–>500	>500	165–625 (510–680)	cf. subfamily information in Gibbs (1984a)	Hopkins et al. (1996); Sutton and Hopkins (1996)
Astronesthes richardsoni	Stomiidae	am	zplv2–meso	0–>500	>500	45–625 (510–680)	Coad and Reist (2004); cf. subfamily information in Gibbs (1984a)	Hopkins et al. (1996); Sutton and Hopkins (1996)
Borostomias elucens	Stomiidae	am	mnkv–meso	0–>500	>500	475–625 (615–680)	cf. subfamily information in Gibbs (1984a)	Sutton and Hopkins (1996)
Borostomias mononema	Stomiidae	am	mnkv–meso	0–>500	>500	– (510–555)	cf. subfamily information in Gibbs (1984a)	Sutton and Hopkins (1996)
Heterophotus ophistoma	Stomiidae	am	mnkv–meso	0–>500	>500	380–525 (470–680)	Gibbs (1990)	cf. subfamily information in Gibbs (1984)
Chauliodus sp.	Stomiidae	am	mnkv–meso	0–>1000	>1000	45–525 (510–680)	Gibbs (1984b)	Gibbs (1984b)
Chauliodus danae	Stomiidae	am	mnkv–meso	0–>1000	>1000	450–490	Gibbs (1984b)	Gibbs (1984b)
Chauliodus schmidti	Stomiidae	am	mnkv–meso	0–>1000	>1000	45–625 (335–680)	cf. *Chauliodus sloani*	cf. *Chauliodus sloani*
Chauliodus sloani	Stomiidae	am	mnkv–meso	0–>1000	>1000	50–525 (390–680)	Gibbs (1984b)	Borodulina (1971); Appelbaum (1982); Roe and Badcock (1984);Sutton and Hopkins (1996)
Aristostomias sp.	Stomiidae	am	mnkv–meso	NA	NA	55–490	mean of *Aristostomias* spp. presented	Hopkins et al. (1996); Sutton and Hopkins (1996)
Aristostomias grimaldii	Stomiidae	am	mnkv–meso	25–800	500–800	230–585 (510–680)	Gibbs (1984c); Mundy (2005)	Hopkins et al. (1996); Sutton and Hopkins (1996)
Aristostomias tittmanni	Stomiidae	am	mnkv–meso	15–2000	15–2000	210–425	Gibbs (1984c); Mundy (2005)	Hopkins et al. (1996); Sutton and Hopkins (1996)
Malacosteus niger	Stomiidae	am	mnkv–meso	>500	>500	135–625 (510–555)	Marshall (1960); Gibbs (1984c); Kenaley (2007)	Hopkins et al. (1996), Sutton (2005)
Photostomias sp.	Stomiidae	am	mnkv–meso	0–>500	>500	165–430	cf. *P. guernei*	Hopkins et al. (1996)
Photostomias guernei	Stomiidae	am	mnkv–meso	0–>500	>500	450–490	Marshall (1960); Gibbs (1984c)	Hopkins et al. (1996)
Bathophilus sp. I – III	Stomiidae	am	mnkv–meso	0–>500	>500	475–525 (400–425)	Mundy (2005); cf. subfamily information in Gibbs (1984d); cf. *B. pawneei*	Hopkins et al. (1996); Sutton and Hopkins (1996)
Bathophilus brevis	Stomiidae	am	mnkv–meso	75–1650	75–1650	230–430 (325–500)	Mundy (2005); cf. subfamily information in Gibbs (1984d); cf. *B. pawneei*	Hopkins et al. (1996);Sutton and Hopkins (1996)
Bathophilus nigerrimus	Stomiidae	am	mnkv–meso	0–>500	>500	– (325–370)	cf. subfamily information in Gibbs (1984d); cf. *B. pawneei*	Hopkins et al. (1996); Sutton and Hopkins (1996)
Bathophilus pawneei	Stomiidae	am	mnkv–meso	0–>500	>500	55–85	Marshall (1960); cf. subfamily information in Gibbs (1984d)	Hopkins et al. (1996); Sutton and Hopkins (1996)
Echiostoma barbatum	Stomiidae	am	mnkv–meso	0–>500	>500	370–435	cf. subfamily information in Gibbs (1984d); cf. *E. tanneri*	Hopkins et al. (1996)

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Table A.1 (*continued*)

Species	Family	Migration behaviour	Feeding–Migrator guild	Night-time (Core) depth range (m) – literature	Daytime (Core) depth range (m) – literature	Night-time (Daytime) WH383 range (m)	Vertical occurrence/ migration pattern reference	Feeding guild reference
Eustomias sp.	Stomiidae	am	mnkv–meso	0–>500	>500	– (390–425)	cf. subfamily information in Gibbs (1984d); cf. *E. tanneri*	Hopkins et al. (1996); Sutton and Hopkins (1996)
Eustomias bigelowi	Stomiidae	am	mnkv–meso	0–>500	>500	– (615–680)	cf. subfamily information in Gibbs (1984d); cf. *E. tanneri*	Hopkins et al. (1996); Sutton and Hopkins (1996)
Eustomias filifer	Stomiidae	am	mnkv–meso	0–>500	>500	Deck catch	cf. subfamily information in Gibbs (1984d); cf. *E. tanneri*	Hopkins et al. (1996); Sutton and Hopkins (1996)
Flagellostomias boureei	Stomiidae	am	mnkv–meso	0–>500	>500	165–625	cf. subfamily information in Gibbs (1984d)	cf. subfamily information in Gibbs (1984)
Leptostomias sp.	Stomiidae	am	mnkv–meso	0–>500	>500	135–625 (615–680)	cf. subfamily information in Gibbs (1984d)	Hopkins et al. (1996); Sutton and Hopkins (1996)
Melanostomias melanopogon	Stomiidae	am	mnkv–meso	0–>500	>500	245–430	cf. subfamily information in Gibbs (1984d)	Hopkins et al. (1996); Sutton and Hopkins (1996)
Melanostomiinae gen sp.	Stomiidae	am	mnkv–meso	0–>500	>500	55–435 (615–680)	cf. subfamily information in Gibbs (1984d)	Hopkins et al. (1996); Sutton and Hopkins (1996)
Melanostomias valdiviae	Stomiidae	am	mnkv–meso	0–>500	>500	230–280 (510–555)	cf. subfamily information in Gibbs (1984d)	Hopkins et al. (1996); Sutton and Hopkins (1996)
Pachystomias microdon	Stomiidae	am	mnkv–meso	0–>500	>500	450–625 (510–555)	cf. subfamily information in Gibbs (1984d)	Hopkins et al. (1996)
Photonectes sp.	Stomiidae	am	mnkv–meso	0–>500	>500	245–490	cf. subfamily information in Gibbs (1984d)	Hopkins et al. (1996)
Photonectes mirabilis	Stomiidae	am	mnkv–meso	0–>500	>500	165–195	cf. subfamily information in Gibbs (1984d)	Hopkins et al. (1996)
Thysanactis dentex	Stomiidae	am	mnkv–meso	100–1000	100–1000	370–525 (615–680)	cf. subfamily information in Gibbs (1984d); Mundy (2005)	Hopkins et al. (1996)
Stomiidae gen. sp.	Stomiidae	am	mnkv–meso	0–>500	>500	390–435	cf. subfamily information in Gibbs (1984e)	Hopkins et al. (1996)
Stomias sp.	Stomiidae	am	mnkv–meso	0–>1000	500 > 1000	45–440 (335–380)	cf. subfamily information in Gibbs (1984e)	Borodulina (1971); Appelbaum (1982); Sutton and Hopkins (1996)
Stomias affinis	Stomiidae	am	mnkv–meso	0–>1000	0–3182	45–625 (335–565)	cf. subfamily information in Gibbs (1984e)	Hopkins et al. (1996);Sutton and Hopkins et al. (1996); Sutton (2005)
Stomias boa boa	Stomiidae	am	mnkv–meso	0–>1000	500 > 1000	50–625	cf. subfamily information in Gibbs (1984e)	Borodulina (1971); Appelbaum (1982); Roe and Badcock (1984);Sutton and Hopkins (1996)
Stomias colubrinus	Stomiidae	am	mnkv–meso	0–>1000	22–1314	45–80	Marshall (1960); Nakamura et al. (1986); cf. subfamily information in Gibbs (1984e)	Borodulina (1971); Sutton and Hopkins (1996)

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Table A.2

Characterisation of the traits migration pattern and Feeding–Migrator guild based on literature data (Table A.1), referring to the feeding guilds established by Hopkins et al. (1996).

Feeding–Migrator guild	Characteristics
zplv1–epi	*Copepod feeders*: copepods are major diet component in terms of biomass *DVM species* that ascend to within the upper 200 m
zplv1–meso	*Copepod feeders*: copepods are major diet component in terms of biomass *Non-DVM species* generally not reaching the epipelagic
zplv2–epi	*Mixed crustacean feeders*: proportionally greater fraction of euphausiids and decapods, mixed crustacean diet *DVM species* that ascend to within the upper 200 m
zplv2–meso	*Mixed crustacean feeders*: proportionally greater fraction of euphausiids and decapods, mixed crustacean diet *Non-DVM species* generally not reaching the epipelagic
zplv3–meso	*Non-crustacean feeders*: non-crustacean invertebrates (pelagic gastropods) and gelatinous food (tunicates, siphonophores) predominant *Non-DVM species* generally not reaching the epipelagic
mnkv–meso	*Micronektonivores*: mostly fish, but also larger crustaceans and decapods *Non-DVM speciess* generally not reaching the epipelagic

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Article 2 Distribution and diel vertical migration of mesopelagic fishes in the Southern Sargasso Sea – Observations through hydroacoustics and stratified catches

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SENCKENBERG

ORIGINAL PAPER

Distribution and diel vertical migration of mesopelagic fishes in the Southern Sargasso Sea — observations through hydroacoustics and stratified catches

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Abstract

Vertical distribution patterns and relative abundance of mesopelagic fish species and other major taxonomic groups were investigated through vertically stratified trawl sampling and hydroacoustic analyses along the subtropical convergence zone from 52° W to 70° W in the oligotrophic Sargasso Sea. Persistent stationary layers and several migrating components of different scattering characteristics were detected. The results reveal varying vertical migration patterns, including different times of onset of diel vertical migration in different depths and a migrant pathway emerging daily from the lower deep scattering layer (DSL) at dusk and migrating through the upper DSL without affecting its composition. Fish species identification was made based on morphological characteristics and confirmed by genetic barcoding analyses of subsamples. In total, 5022 fish specimens from 27 families, 62 genera and 70 species were caught. In terms of relative abundance (A) and biomass (M), catches were dominated by species of the families Myctophidae (A=59.1%, M=47.4% of total fish catch) and Melamphaidae (A=22.5%, M=17.1%). Myctophidae and Stomiidae were the most species-rich families with 31 and 12 species, respectively. Catches at the two easternmost stations were dominated by *Scopelogadus mizolepis* and *Nannobrachium cuprarium,* while *Bolinichthys photothorax* and *Ceratoscopelus warmingii* were the most abundant species in catches from the two westernmost stations. This study provides insights into distribution and vertical migration behaviour of mesopelagic fish in the Sargasso Sea and adds to our understanding of the mesopelagic community in this large oceanic area.

Keywords Pelagic ecology · Micronekton · Deep scattering layers · Western Atlantic

Introduction

Mesopelagic fish, living in depths of 200 to 1000 m, are dominating the fish biomass in large parts of the world's oceans. A recent estimate of their global biomass was even a magnitude higher than the former estimate of approximately 1,000 million tons (Lam and Pauly 2005; Irigoien et al. 2014). Through extended diel vertical migrations (DVM) into shallower layers predominantly for feeding, the sheer biomass of mesopelagic fish has large influences on trophic connectivity and the carbon flux in the oceans (Saba et al. 2021). While the importance of pelagic fish communities for the nutrient flow in the oceans is widely acknowledged (e.g. Davison et al. 2013; Anderson et al. 2019; Saba et al. 2021), our understanding and knowledge of the vertical ecology of mesopelagic organisms in relation to their physico-chemical environment is still limited (St. John et al. 2016; Olivar et al. 2017; Proud et al. 2019; Romero-Romero et al. 2019) and studies on globally available data sets have demonstrated profound differences in the depth of day-time sound scattering layers between productive and oligotrophic regions (Bianchi and Mislan 2016; Klevjer et al. 2016).

From an oceanographic perspective, the Sargasso Sea is a particularly relevant transitional area in the western part of the North Atlantic. It is situated within the North Atlantic

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Subtropical Gyre and surrounded by ocean currents, which can trap the water in the core of the Sargasso Sea for decades (Maximenko et al. 2012). This large marine ecoregion is influenced by various hydrographical features, including complex patterns of thermal fronts, mesoscale eddies, advective transport of water masses and seasonal convective overturn, which all have an influence on the biota and lead to a pronounced spatio-temporal variability in planktonic productivity (McGillicuddy et al. 1998; Hansell and Carlson 2001; Palter et al. 2005; Eden et al. 2009; Hellenbrecht et al. 2019). Based on the prevailing low nutrient levels, the Sargasso Sea is generally classified as oligotrophic. However, in spite of this fact, it has a high net primary production rate per unit area (Steinberg et al. 2001; Laffoley et al. 2011).

Besides environmental factors like primary production, oxygen concentration and light intensity (Irigoien et al. 2014; Klevjer et al. 2016; Aksnes et al. 2017), the distribution of pelagic fish in the Sargasso Sea may also be influenced by distinct temperature fronts in the upper 150 m of the ocean. These fronts may form zoogeographic boundaries for certain mesopelagic fish (Backus et al. 1969) and cephalopod species (Lischka et al. 2017) caused by temperature-related changes in e.g. productivity or stratification. Changes in mesopelagic fish species composition across fronts have been reported, for example at frontal systems in the southern California Current region, demonstrating incongruent patterns in the spatial distribution of migrators and non-migrators (Netburn and Koslow 2018). In the Sargasso Sea, these fronts are caused by the confluence of warm and cold-water masses in the subtropical convergence zone (STCZ) (Katz 1969). It has also been demonstrated that distribution and transport of midwater fish species can be driven by eddies (Olson and Backus 1985; Godø et al. 2012) including also the transport into or out of the Sargasso Sea (Craddock et al. 1992).

A large number of studies describe vertical distribution patterns of mesopelagic fish (e.g. Sutton 2013; Klevjer et al. 2016; Olivar et al. 2016; Proud et al. 2017; Sutton et al. 2017). The distribution of mesopelagic fish species in deep scattering layers (DSL) and the species composition of those layers have been identified on a regional scale in the temperate north-eastern Atlantic and in the subtropical and tropical western Atlantic and adjacent waters (Roe and Badcock 1984; Wienerroither et al. 2009; Peña et al. 2014; Ariza et al. 2016; D'Elia et al. 2016). Abundance and distribution of mesopelagic fish have also been investigated in the Sargasso Sea (Backus et al. 1969; Backus et al. 1970; Jahn and Backus 1976; Backus and Craddock 1977; Gartner Jr et al. 1989; Sutton et al. 2010; Ayala et al. 2016). However, as for most ocean areas, current data on mesopelagics from this remote region are scarce.

To further increase our knowledge about the distribution and abundance of mesopelagic fish species in the Sargasso Sea, a hydroacoustic analysis of scattering layers and a series of depth stratified mesopelagic trawl samplings were conducted during an extensive multipurpose pelagic fishery survey along the subtropical convergence zone from 52° W to 70° W. Stratified catches were compared with hydroacoustic data, in order to assess the vertical migration behaviour of mesopelagic fish and to characterize the composition of deep scattering layer, providing insights into the horizontal and vertical distribution of fish species over this large oceanic area.

Material and methods

Fishing gear and sampling methodology

Sampling took place from March 20 to April 6, 2014, during an extensive multipurpose fishery survey (WH373) on the German R/V Walther Herwig III in the Sargasso Sea with a pelagic trawl (Engel Netze, Bremerhaven, Germany). The net had an opening width of 30 m, a height of 20 m, a length of 145 m, and mesh sizes (knot to knot) from 90 cm decreasing stepwise to 40, 20, 10, 5, 4, 3, 2 cm, with a 1.5 cm mesh in the 27 m long codend. It was equipped with a multi-closing system that enabled fishing in three defined depth strata by a time-controlled closing mechanism (multisampler).

Seven stations between 25°30′ and 29°30′ N and 52°00′ and 70°00′ W were sampled (Table 1, Fig. 1). Five stations (228, 240, 259, 284, 300, hereafter *regular stations*) were fished at night (starting time between 22:44 and 00:57 local time) at depths between ca. 150 and 370 m (Table 1). In addition, two deep hauls sampled the main scattering layers as observed by hydroacoustics (stations 233 and 316, hereafter *deep stations*): one during day-time (station 233: depth 108–698 m, 06:47–11:47 local time), and one during night-time (station 316: depth 31–965 m, 23:25–03:50) (Table 1).

Trawl duration at all stations was 225 min, with each of the 3 nets open for 75 min, apart from station 233, where net 1 was opened for 90 min and nets 2 and 3 for 105 min each (Table 1). All hauls were towed obliquely from shallower to deeper layers. Towing speed through water was 3 knots at all stations. The multisampler codends were cleaned from remaining fish after each haul.

Hydroacoustic data

Hydroacoustic data were collected continuously with a Simrad EK60 scientific echosounder operated at 18, 38, 120 and 200 kHz with hull-mounted transducers at a ship speed of approximately 12 knots during transit and 3 knots during fishing operations. Only data from the 18 kHz and 38 kHz transducer were used for further analyses. Beam widths of the transducers were 11° (18 kHz) and 7° (38 kHz), respectively, and both were operated at 2000 W. The pulse length was 1.024 ms with the ping rate set to maximum. To account for

Table 1 Sampling stations

Station	Date	Start position		Depth	Time		Time (local)		Duration
Net		lat (°N)	lon (°W)	(m)	Start (hrs:min) after sunset	End (hrs:min) before sunrise	Start	End	(min)
228	20.03.2014	27°30′	69°59′	152–346	05:03	02:44	22:54	02:59	225
net 1				152–208	05:03	05:34	22:54	00:09	75
net 2				225–275	06:28	04:09	00:19	01:34	75
net 3				293–346	07:53	02:44	01:44	02:59	75
240	23.03.2014	27°30′	66°59′	146–350	05:13	02:28	23:54	03:59	225
net 1				146–205	05:13	05:18	23:54	01:09	75
net 2				225–271	06:38	03:53	01:19	02:34	75
net 3				298–350	08:03	02:28	02:44	03:59	75
259	26.03.2014	25°33′	63°55′	157–356	06:27	01:10	00:57	05:02	225
net 1				157–208	06:27	04:00	00:57	02:12	75
net 2				220–277	07:52	02:35	02:22	03:37	75
net 3				265–356	09:17	01:10	03:47	05:02	75
284	30.03.2014	29°29′	60°59′	145–368	05:20	02:09	23:41	03:46	225
net 1				145–196	05:20	04:59	23:41	00:56	75
net 2				220–278	06:45	03:34	01:06	02:21	75
net 3				288–368	08:10	02:09	02:31	03:46	75
300	02.04.2014	26°29′	57°59′	150–342	04:35	02:52	22:44	02:49	225
net 1				150–230	04:35	05:42	22:44	23:59	75
net 2				225–265	06:00	04:17	00:09	01:24	75
net 3				295–342	07:25	02:52	01:34	02:49	75
233	21.03.2014	26°34′	69°59′	108–698	na	na	06:47	11:47	300
net 1				108–362	na	na	06:47	08:17	90
net 2				362–450	na	na	08:17	10:02	105
net 3				450–698	na	na	10:02	11:47	105
316	06.04.2014	27°02′	51°58′	32–965	04:37	02:22	23:25	03:50	225
net 1				32–152	04:37	05:32	23:25	00:40	75
net 2				482–606	06:17	03:52	01:05	02:20	75
net 3				774–965	07:47	02:22	02:35	03:50	75

surface turbulence and the transducer near-field, acoustic data were collected from 15 m below the surface down to 1000 m. The echosounder could not be calibrated prior, during or after survey operations, but had been calibrated on a dedicated hydroacoustic survey a few months prior with the standard sphere method (Foote et al. 1987; Demer et al. 2015). These

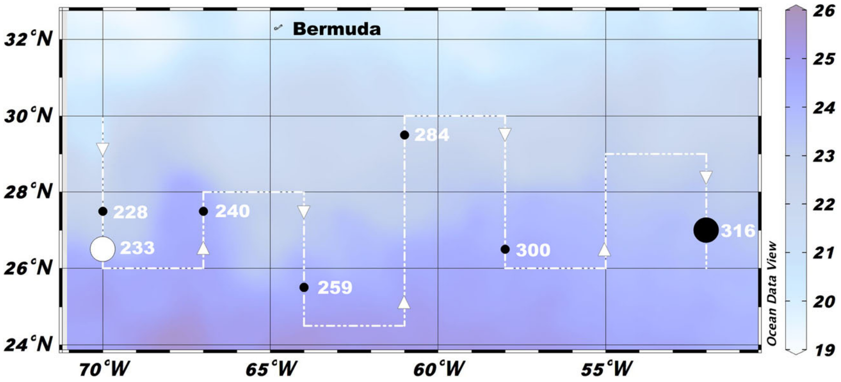

Fig. 1 Map of sampling stations. Colours represent sea surface temperature in °C on March 28 2014 (the mid-point of the sampling period). Small black circles represent *regular stations* and *deep stations* are presented by big circles (white=day-time, black=night-time). Cruise track and direction are represented by a dashed line and arrows

calibration results and parameters were used during data recording and post-processing, with ambient hydrographic parameters measured and implemented during recording based on CTD casts. Hydroacoustic data were post-processed using Echoview 12 software (Echoview Software Pty Ltd, Hobart, Australia). To mitigate signal degradation effects of noise and attenuation, different filters were applied to remove impulsive noise, transient noise and background noise (De Robertis and Higginbotto 2007; Ryan et al. 2015).

High backscattering values originate from targets with a density that differs strongly from the surrounding seawater that resonate when their dimensions are near the wavelength of a given frequency. Organisms with a density that is very similar to the surrounding medium produce a much weaker echo (Simmonds and MacLennan 2006). The former echoes mostly originate from organisms that bear a gas-filled structure, i.e. swimbladdered fishes, but also physonect siphonophores (Stanton et al. 1998; Korneliussen and Ona 2003; Proud et al. 2019), the latter from so-called fluid-like scatterers like cephalopods and crustaceans (Korneliussen and Ona 2003). Based on these backscattering characteristics, organisms that produce resonance at different incident frequencies can be classified.

A corresponding classification based on 18 and 38 kHz acoustic data was conducted. Acoustic backscatter was translated into volume backscattering ($S_{v,}$ dB re 1 m^{-1}) and binned into cells of 2 min x 1 m depth for the duration of trawl sampling on each station and for 10 min x 10 m depth for a representative 72-h time-series of hydroacoustic data recorded on a transect section at 70° W illustrating several cycles of diel vertical migration. For each resulting cell, mean S_v was calculated at an integration threshold of −80 dB, and synthetic variable Δ_{Sv} was created by calculating S_v18-S_v38. This variable was used to identify functional groups of mesopelagic scatterers following a classification tree described by D'Elia et al. (2016). This classification is based on the size and scattering properties of different organism groups and allocates four categories to bins according to the following properties: small swimbladdered fishes (including small non-swimbladdered fishes and crustaceans; sm.(N)SB/Crust.) are -14 dB < $\Delta_{Sv18kHz-38kHz}$ < -3 dB; large non-swimbladdered fishes (Lrg.NSB) are -3 dB < $\Delta_{Sv18kHz-38kHz}$ < 0 dB; gelatinous zooplankton, cephalopods and pteropods, i.e. fluid-like scatterers (FL), are 0 dB < $\Delta_{Sv18kHz-38kHz}$ < 3 dB, and large swimbladdered fishes (Lrg.SB) are 3 dB < $\Delta_{Sv18kHz-38kHz}$ < 12 dB. Cells in which S_v was below the threshold (−80 dB, D'Elia et al. 2016) in either the 38 kHz or the 18 kHz data were classified as dominant Dom18 and Dom38, respectively. The corresponding acoustic scattering measured in both such cells can most likely be attributed to swimbladder-bearing fishes (Love 1978).

To evaluate the contribution of different taxonomic (fish) groups to the post-processed echograms, a classification of fishes according to the presence of a gas-filled (i.e. resonant) swimbladder was conducted and the corresponding families were categorized accordingly. A corresponding categorization was achieved using (identification) literature and swimbladder catalogues (Marshall 1960; Whitehead et al. 1986; Saenger 1989). Accordingly, the families Anoplogastridae, Bregmacerotidae, Chiasmodontidae, Gonostomatidae, Howellidae, Melamphaidae, Myctophidae, Phosichthyidae, Scombrolabracidae and Sternoptychidae were classified as fishes with swimbladder, whereas Evermannelidae, Notosudidae, Paralepididae and Stomiidae were classified as fishes without swimbladder. Species for which no information could be gathered were categorized into “other fish”. Ontogenetic changes in swimbladder-structure (i.e. gas-filled in juveniles and lipid-filled in adults) as occurring in some families/genera were not taken into account.

CTD and sea surface temperature satellite data

In situ hydrographic measurements were conducted with a SBE 9/11 conductivity-temperature-depth probe (CTD) (Sea-Bird Electronic, Bellevue, WA, USA). CTD casts were made at all stations (depth 300–1000 m), recording conductivity, temperature, salinity and pressure (depth).

Prominent temperature fronts along the STCZ in the study area were observed via sea surface temperature (SST) data. SST data were derived from the Operational Sea Surface Temperature and Sea Ice Analysis (OSTIA) system (https://opendap.jpl.nasa.gov/opendap/OceanTemperature/ghrsst/data/L4/GLOB/UKMO/OSTIA/2014/028/contents.html). Figure 1 depicts SST on March 28, 2014, as this date represents the mid-point of the sampling period.

Catch analysis and species identification

Total catches were sorted and divided into major taxonomic groups immediately after each haul and frozen at −20°C for transport and further utilization. After thawing, all fish specimens were identified to the lowest possible taxonomic level by the use of region-specific identification keys (Whitehead et al. 1986; FWNA 1989; Carpenter 2002; Richards 2005) and standard length and weight were assessed individually to the lowest 1.0 mm and rounded to the nearest 0.1 g, respectively. Regarding invertebrates, the analysis was limited to the assessment of total weight per group (mollusca, crustacea, gelatinous plankton) and haul.

Genetic analyses of subsamples of fish species were used to verify the morphological identification (for analytical methods see below). In case the results did not match with morphological species identification, morphological examination and identification were repeated and species names were revised or assigned to higher taxonomic ranks.

The influence of sea surface temperature on the abundance of the most dominant species was tested by a linear regression model (R Core Team 2019).

Genetic analysis

Tissue samples of representative individuals from each species or group were preserved in ethanol (96% abs.) for subsequent genetic analysis. DNA was extracted using Chelex100 (Walsh et al. 1991) and stored at +4°C or at −80°C for long-term storage. For DNA barcoding, the mitochondrial markers Cytochrome c oxidase I (COI) and Cytochrome b (Cytb) and the nuclear marker Myosin heavy chain 6 (myh6) were amplified by polymerase chain reactions (PCR). All PCRs were carried out using High-Fidelity PCR Master Mix with HF Buffer (Phusion, New England Biolabs), 0.25 μM of each primer (Table 2), 3 μl template (using the supernatant of the Chelex extracted samples). Finally, nuclease-free water was added until a final volume of 20 μl was reached. Amplification was accomplished with a T3 Thermocycler (Biometra/Analytik Jena, Germany) with the following cycling conditions: initial denaturation at 98°C for 30 s, followed by 32 cycles for COI and 35 cycles for Cytb, consisting of 98°C for 10 s, primer annealing for 30 s (COI at 53°C, Cytb at 51°C), extension at 72°C (COI for 20 s, Cytb for 40 s) and a final extension step at 72°C for 8 min. For myh6 amplification, a special cycling protocol was used with the following conditions: initial denaturation at 98°C for 30 s, followed by a primer annealing touchdown step with 8 cycles, consisting of 98°C for 10 s, primer annealing decreasing with 1°C from 62°C to 54°C in each cycle for 30 s, extension at 72°C for 30 s, followed by 30 cycles with 98°C for 10 s, 54°C for 30 s, 72°C for 30 s and final extension at 72°C for 7 min. As a quality check, 5 μl of each PCR product was analysed with standard agarose gel electrophoresis (1% agarose, stained with ethidium bromide). PCR products showing strong sharp and clear bands with the right amplicon size were diluted with ultra-pure water. Products showing weak bands were purified and concentrated using PCR and DNA Cleanup Kits (Monarch, New England Biolabs, T1030) prior to sequencing. Sequence raw data were checked and edited with CodonCode Aligner Software (Centerville MA, USA) by cutting off primer sites and generating consensus sequences. To verify the results of the morphological identification, all obtained sequences were compared with NCBIs Nucleotide Sequence Database by BLAST (Altschul et al. 1990).

Results

Hydrography

Depth profiles of temperature and salinity varied among sampling stations (Fig. 2). A well-defined thermocline was present at all stations between 100 and 200 m depth. Sea surface temperatures varied between 22.5 and 24.9°C, with the lowest temperatures being measured at northern-, western- and easternmost stations (stations 284, 228 and 316) (Fig. 1). Within the upper 200 m, temperatures dropped at about 4–5°C to 18.5–20.7°C and at 500 m depth temperatures between 15.5 and 17.2°C were measured. Trawls at *regular stations* took place in depths with temperatures between 18 and 22°C, while *deep stations* reached temperatures below 7°C at greater depths. Sea surface temperature data showed a distinct temperature front between 24° N and 30° N in the western part of the study area, with temperatures decreasing northwards from above 25°C to below 22°C (Fig. 1). In the eastern part of the study area, the front was less pronounced.

Water salinity decreased vertically from around 36.5 near the surface to 35 at 1000 m depth. Within the upper 500 m, salinity values ranged from 36.1 to 37.2.

Table 2 List of primers for genetic analyses

Barcoding marker	Primer name	Primer sequence (5′-3′)
COI	VF2_t1_M13	TGTAAAACGACGGCCAGTCAACCAACCACAAAGACATTGGCAC
	FishF2_t1_M13	TGTAAAACGACGGCCAGTCGACTAATCATAAAGATATCGGCAC
	FishR2_t1_M13	CAGGAAACAGCTATGACACTTCAGGGTGACCGAAGAATCAGAA
	FR1d_t1_M13	CAGGAAACAGCTATGACACCTCAGGGTGTCCGAARAAYCARAA
	Ivanova et al. 2007 (modified with M13 sequencing sites)	
Cytb	FishcytB-F_M13F	TGTAAAACGACGGCCAGTACCACCGTTGTTATTCAACTACAAGAAC
	TruccytB-R _M13R	CAGGAAACAGCTATGACCCGACTTCCGGATTACAAGACCG
	Sevilla et al. 2007 (modified with M13 sequencing sites)	
Myh6	myh6_F507_M13	TGTAAAACGACGGCCAGTGGAGAATCARTCKGTGCTCATCA
	myh6_R1322_M13	CAGGAAACAGCTATGACCCTCACCACCATCCAGTTGAACAT
	Li et al. 2007 (modified with M13 sequencing sites)	

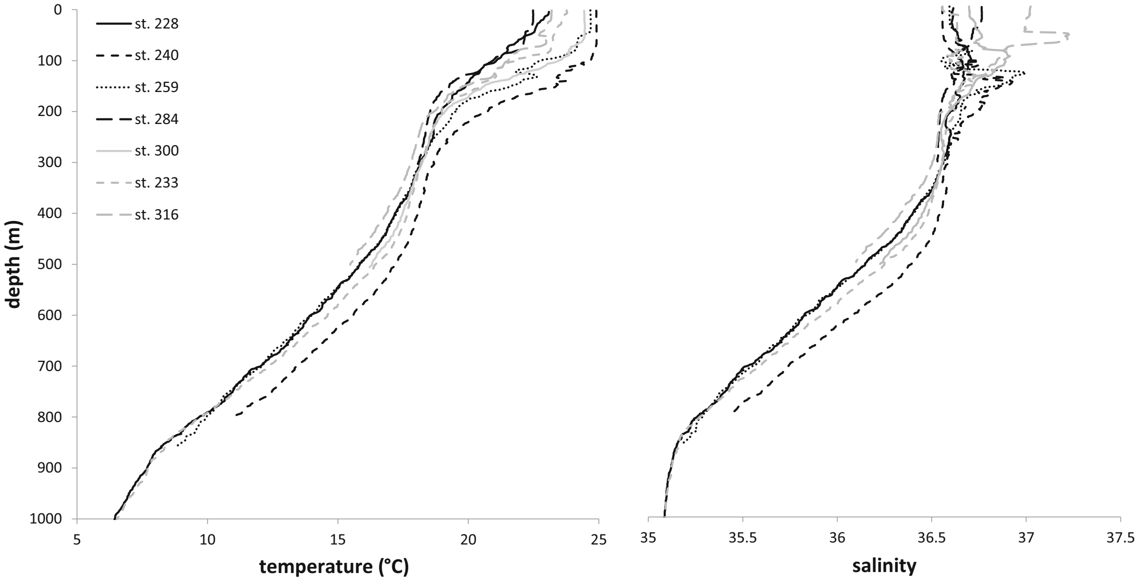

Fig. 2 Temperature and salinity depth profiles at sampling stations

Hydroacoustics: general mesopelagic habitat structure

From hydroacoustic data, a common pattern of scattering layers was evident throughout the survey area and along the sampled transects, with persistent stationary and several migrating components of different scattering characteristics (Figs. 3, 4 and 5). In the epipelagic zone, dense stationary echoes were visible especially in the upper 150 m of the water column (epipelagic layer, hereafter referred to as layer 1). In the mesopelagic zone, two separate deep scattering layers (DSLs) were evident: one dense layer was most prominent in the 18 kHz echodata between 450 and 600 m (Figs. 3, 4 and 5b) and between 400 and 700 m in the 38 kHz data (upper mesopelagic scattering layer, hereafter referred to as principal DSL and layer 2). A weaker scattering layer around 800–900 m depth was most prominent in the 18 kHz data (Figs. 3, 4 and 5a) (lower mesopelagic scattering layer, hereafter referred to as secondary DSL and layer 3). Based on the classification of acoustic data through Δ_{Sv}, layer 1 contained echoes originating from a variety of organisms, namely swimbladdered as well as non-swimbladdered fishes, fluid-like scatterers and crustaceans — with varying contributions during day- and night-time. The upper part of the principal DSL (layer 2) (400–500 m) consisted mostly of (large) swimbladdered and non-swimbladdered fishes with clear contributions of fluid-like scatterers, while the deeper parts of the principal DSL (layer 2) (500–700 m) were dominated by small swimbladdered and non-swimbladdered fishes and crustaceans (Figs. 3, 4 and 5c).

From the echograms recorded at either frequency, a clear and regular diel pattern was evident with different components emerging from both DSLs at different times and undertaking diel vertical migration (Fig. 3).

Beginning from ca. 16:00 h local time (ca. 2 h before sunset), an upward migrating layer emerged from the principal DSL (layer 2) and by 19:00 h merged with layer 1. A second cohort of organisms undertaking DVM emerged from the deeper secondary DSL (layer 3) around 17:00 h. This group ascended through the principal DSL (layer 2) and merged during its ascent with the previous cohort from this layer shortly before merging with layer 1. The migrating components appeared to mostly consist of swimbladdered and non-swimbladdered fishes as well as fluid-like scatterers. For the next ca. 9 h, layer 1 appeared both denser (in terms of acoustic backscatter) and of different composition (through the contribution of the migrating components). While during day-time the epipelagic layers seemed to be mostly dominated by small swimbladdered and non-swimbladdered fishes and crustaceans, distinct additional contributions of fluid-like scatterers as well as large swimbladdered and non-swimbladdered fishes were evident during night (Fig. 3c). Starting from ca. 04:00 h, several descending layers became evident leaving layer 1 and the epipelagic zone, with the components from the secondary DSL (layer 3) showing a faster descent into that depth than the components of the principal DSL (layer 2). By ca. 07:00 h, the faster descending migrating component of layer 3 merged into that layer again, while the migrating organisms from layer 2 merged into the stationary component ca. 1 h later.

Depth distribution of mesopelagic fish and taxonomic composition of scattering layers

Regular stations

Night-time multisampler hauls in depths between ca. 150 and ca. 360 m at stations 228, 240, 259, 284 and 300 were

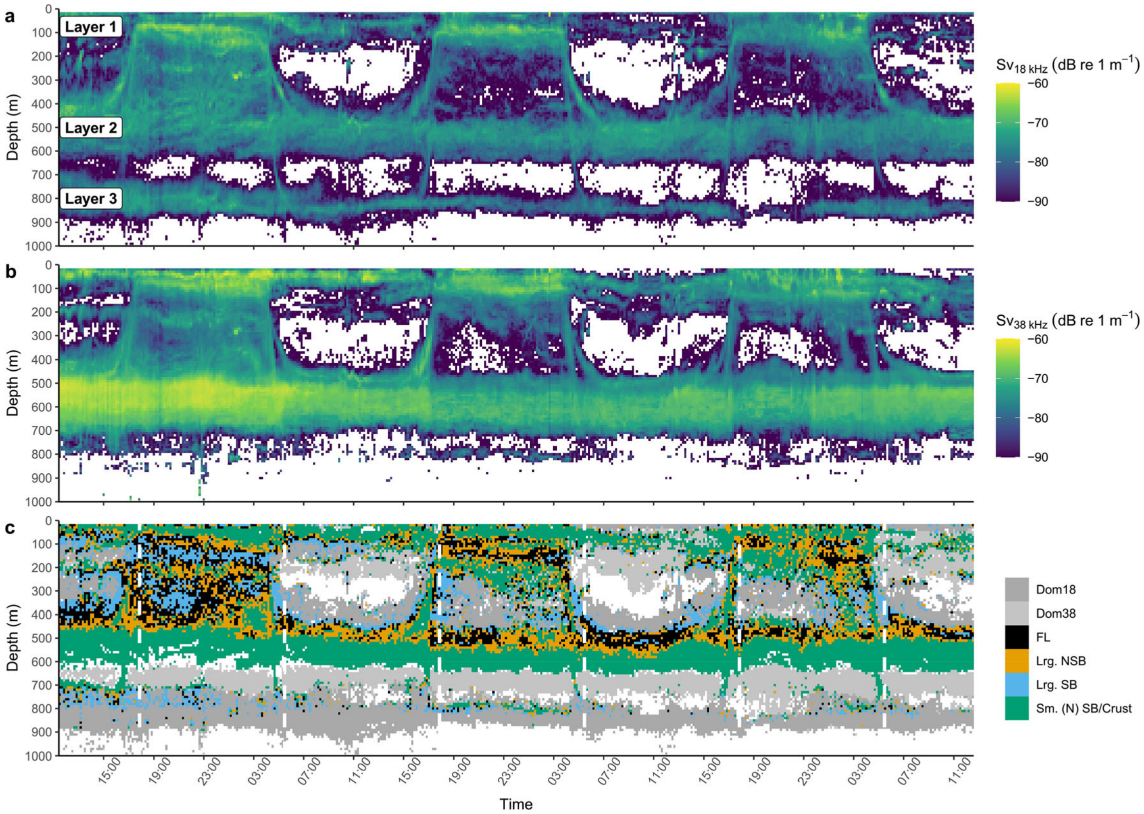

Fig. 3 Example of hydroacoustic data recorded along a 72-h period on the latitudinal transect following 70° W showing three cycles of diel vertical migration. Scattering layers as investigated and referred to in the main text are indicated in panel **a** (layer 1 — epipelagic layer; layer 2 — principal DSL; layer 3 — secondary DSL). **a** Volume backscattering Sv recorded at 18 kHz; **b** Sv recorded at 38 kHz; **c** classification of hydroacoustic data based on Δ_{Sv} (S_v18-S_v38) (D´Elia et al. 2016): FL, fluid-like scatterers (gelatinous zooplankton, cephalopods and pteropods); Lrg. NSB, large non-swimbladdered fishes; Lrg. SB, large swimbladdered fishes; sm. (N)SB/Crust., small swimbladdered fishes (including small non-swimbladdered fishes and crustaceans). Cells in which S_v was below the threshold in either the 38 kHz or the 18 kHz data were classified as dominant Dom18 and Dom38, respectively. The corresponding acoustic scattering measured in both such cells can most likely be attributed to swimbladder-bearing fishes (Love 1978). White, dashed vertical lines indicate sunset and sunrise, respectively

conducted with uniform trawl paths and depth profiles. There, the upper net 1 (ca. 150–220 m) partly covered the dense epipelagic layer (layer 1) that appeared during night-time after migrating organisms had completed their DVM. Layer 1 was classified as most likely consisting of a mixture of components, with contributions of swimbladdered, non-swimbladdered and fluid-like scatterers. Nets 2 (ca. 220–280 m) and 3 (ca. 280–360 m) covered depths below layer 1, in which echoes were less dense and most likely originated from resonant, swimbladdered fish and, to a lesser extent, of fluid-like scatterers (Fig. 4c). In all depth layers covered by the multisampler tows, swimbladdered fish species dominated the catches by total catch weight, and fishes without a swimbladder only marginally contributed to the bulk catch across all depth layers (Fig. 6). In these night-time catches, Myctophidae dominated especially the shallowest samples taken from layer 1 (net 1), while their number decreased in deeper samples (nets 2 and 3) (Table 3). The second most dominant family was Melamphaidae, with highest numbers in net 2 and lowest numbers in the deepest samples. Other important families that contributed to the catch in all sampled layers, albeit in distinctly lower numbers, were Gonostomatidae (all *Sigmops elongatus*), Stomiidae, Scombrolabracidae (all *Scombrolabrax heterolepis*) and Evermannellidae (mostly *Coccorella atlantica*). In all but the Gonostomatidae (i.e. *S. elongatus)*, numbers were highest in shallower samples (nets 1 and 2). The latter occurred in higher numbers in the deeper tows (nets 2 and 3). Sternoptychidae were only sampled in the deeper layers (nets 2 and 3) with highest numbers in the deepest tows. Other fish families were caught in distinctly lower numbers.

No clear trend was evident in the fractions of other organisms across hauls. The second most important organism group were molluscs (mostly cephalopods). In general, molluscs contributed stronger to the total catch weight of the shallowest net than of the deeper nets and they are assumed to contribute to the fluid-like backscatter measured in these depths. Crustaceans were also present in all hauls with similar fractions across all sampled depth layers (Fig. 6). Gelatinous zooplankton only marginally contributed to the catches.

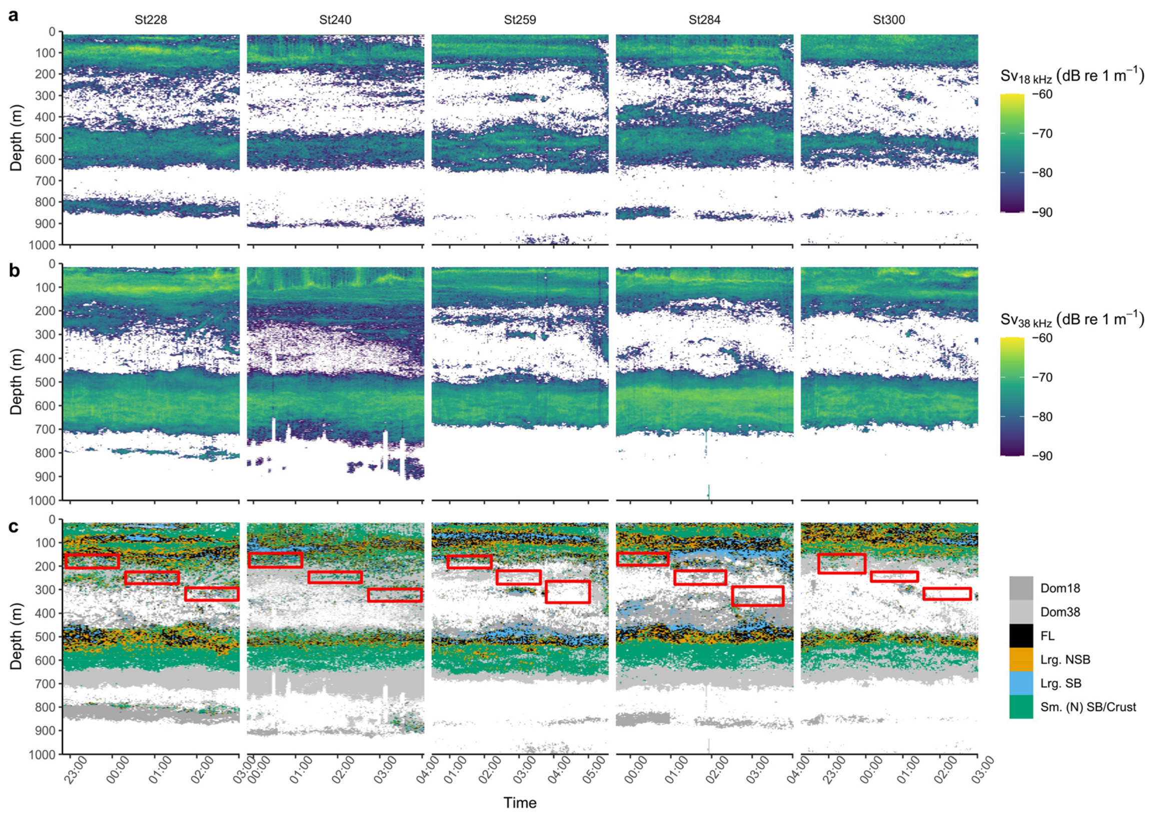

Fig. 4 Hydroacoustic data recorded at *regular stations*. **a** Volume backscattering Sv recorded at 18 kHz; **b** Sv recorded at 38 kHz; **c** classification of hydroacoustic data based on Δ_{Sv} (S_v18-S_v38) (D´Elia et al. 2016): FL, fluid-like scatterers (gelatinous zooplankton, cephalopods and pteropods); Lrg. NSB, large non-swimbladdered fishes; Lrg. SB, large swimbladdered fishes; sm. (N)SB/Crust., small swimbladdered fishes (including small non-swimbladdered fishes and crustaceans). Cells in which S_v was below the threshold in either the 38 kHz or the 18 kHz data were classified as dominant Dom18 and Dom38, respectively. The corresponding acoustic scattering measured in both such cells can most likely be attributed to swimbladder-bearing fishes (Love 1978). For each station, trawl paths, i.e. regions and layers covered by the three nets of the multisampler, are indicated by red rectangles in panel **c**

Deep stations

On the deep day-time station (233), located at the western part of the study area, an increase in total catch (abundance and biomass) was evident with increasing depth and a dominance of different organism groups in terms of catch weight became evident (Table 4). Samples collected at that station were taken in depths covering the layers 1 (net 1, 108–362 m) and 2 (net 2, 362–450 m and net 3, 450–698 m). Net 1 was dominated by molluscs (ca. 60% of catch weight), followed by crustaceans and swimbladdered fishes (both ca. 20% of catch weight) (Fig. 6). According to the scattering properties described above, this depth contained swimbladdered fishes as well as fluid-like scatterers and contributions of small swimbladdered and non-swimbladdered fishes and crustanceans (Fig. 5c). Net 2, i.e. samples from the upper part of layer 2, was dominated by gelatinous zooplankton (ca. 50% of catch weight), followed by swimbladdered fishes (ca. 30% of catch weight) and crustaceans (ca. 20% of catch weight). Corresponding echo signals were classified as consisting mainly of swimbladdered fishes and fluid-like scatterers (Fig. 5c). Net 3, the main part of layer 2, showed a similar catch composition, with gelatinous zooplankton contributing ca. 75% to the catch weight, swimbladdered fishes accounting for ca. 20% and crustaceans for ca. 5%. The depth range covered by net 3 was dominated by the acoustic classes of small swimbladdered and non-swimbladdered fishes and crustaceans (Fig. 5c).

Myctophidae, followed by Gonostomatidae, was the most important fish family caught at that station. The bulk of specimens was caught in the deepest net 3 sampling layer 2 (ca. 450–700 m), with distinctly lower numbers in net 2 and lowest numbers in net 1. Gonostomatidae were absent from the shallower nets 1 and 2.

The deep night-time station (316) was located approximately 1,790 km further east from the deep day-time station (233) and covered the water column down to 965 m. At this station, layer 1 (net 1, 32–152 m) and the upper part of layer 2 (net 2, 482–606 m) as well as layer 3 (net 3, 775–965 m) were sampled (Fig. 5c) and a decrease in the number of individuals became evident with increasing depth. Catches in terms of weight were dominated by swimbladdered fishes in the shallowest net (net 1, ca. 85%) with small contributions of gelatinous zooplankton and molluscs (ca. 6% each) and

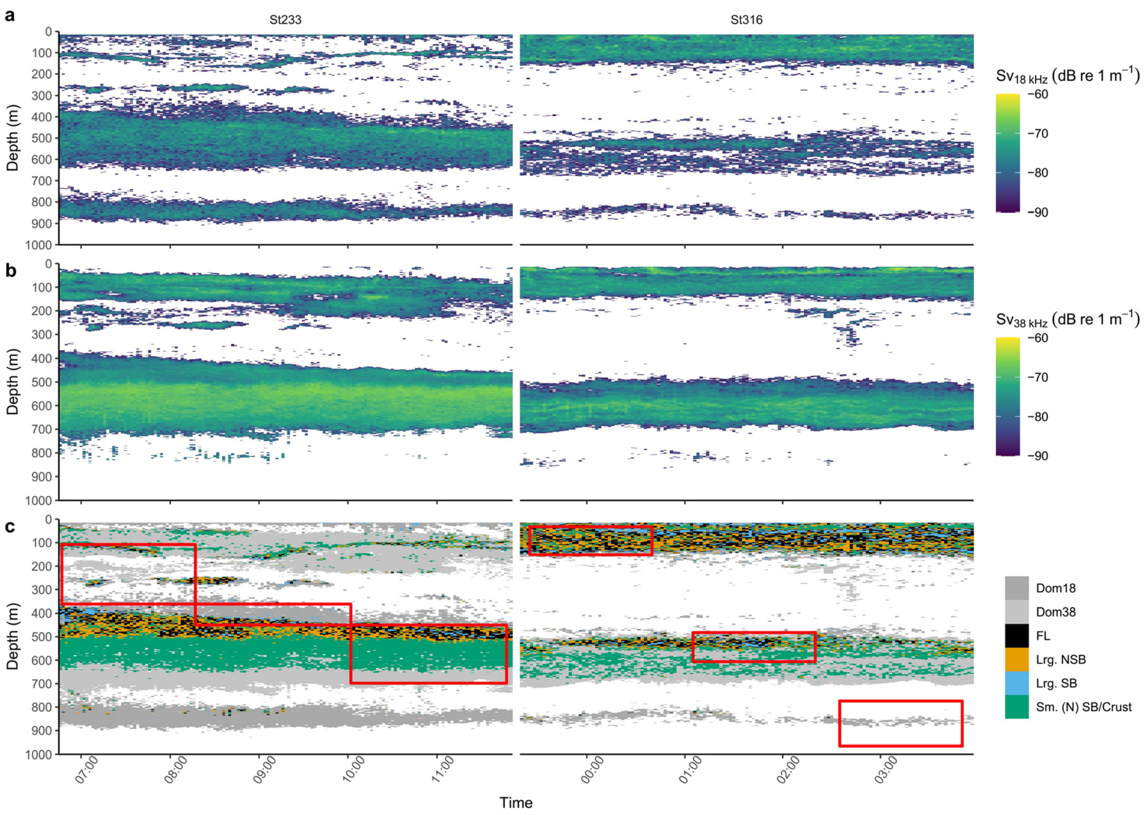

Fig. 5 Hydroacoustic data recorded at *deep stations*. St. 233 (left panels) was sampled during day-time, St. 316 (right panels) was sampled at night. **a** Volume backscattering Sv recorded at 18 kHz; **b** Sv recorded at 38 kHz; **c** classification of hydroacoustic data based on Δ_{S_v} (S_v18-S_v38) (D´Elia et al. 2016): FL, fluid-like scatterers (gelatinous zooplankton, cephalopods and pteropods); Lrg. NSB, large non-swimbladdered fishes; Lrg. SB, large swimbladdered fishes; sm. (N)SB/Crust., small swimbladdered fishes (including small non-swimbladdered fishes and crustaceans). Cells in which S_v was below the threshold in either the 38 kHz or the 18 kHz data were classified as dominant Dom18 and Dom38, respectively. The corresponding acoustic scattering measured in both such cells can most likely be attributed to swimbladder-bearing fishes (Love 1978). For each station, trawl paths, i.e. regions and layers covered by the three nets of the multisampler, are indicated by red rectangles in panel **c**

negligible fractions of crustaceans. A mixture of the corresponding categories had also been allocated to the hydroacoustic data collected from this layer. Fishes collected with that net were almost exclusively Myctophidae, with Phosichthyidae and Melamphaidae only marginally contributing to the catch (Table 4). Catches from net 2, sampling layer 2, were also dominated by fishes, with fishes without a swimmbladder constituting the bulk (50%) and fishes with a swimbladder and uncategorized fishes contributing smaller fractions (17 and 11%, respectively) (Fig. 6). Crustaceans contributed with 15%, while gelatinous zooplankton and molluscs each contributed with less than 5% to the total catch weight. Among fishes, Melamphaidae, Myctophidae and Gonostomatidae were dominant, albeit in far lower numbers than in the upper 150 m (Table 4). Other families, such as Evermannellidae, Stomiidae, Chiasmodontidae and Sternoptychidae, also contributed to the catch with several individuals of each family. In the deepest net (net 3), gelatinous zooplankton was the dominant fraction (40%), followed by crustaceans (20%) and fish (swimbladdered, no swimbladder and others with 19, 14 and 4%, respectively). Fish families sampled at that depth were mostly Stomiidae, Myctophidae, Gonostomatidae and Sternoptychidae (Table 4). Species that were caught exclusively at depth below 360 m were *Bonapartia pedaliota* (*N*=67), *Cyclothone* spec. (*N*=9), *Serrivomer beanii* (*N*=4) and *Poromitra crassiceps* (*N*=1).

Taxonomic and quantitative fish catch composition

The total catch consisted of 5022 fish specimens from 27 families, 62 genera and 70 species of which 4050 individuals (80.7%) were identified to species level, 813 (16.2%) to genus level, and 137 (2.7%) to family level. Twenty-two specimens (0.4%) remained entirely unidentified due to mechanical damages in the net during trawling. An overview of the total catch at stations and depths is presented in Table 5, detailed information about catch composition is given in Table 6, and length and weight data as well as results from genetic analyses are presented in Table 7.

In terms of abundance (N), relative abundance (A) and biomass (M), the total fish catch was dominated by Myctophidae (N=2970, A=59.1%, M=47.4% of total catch),

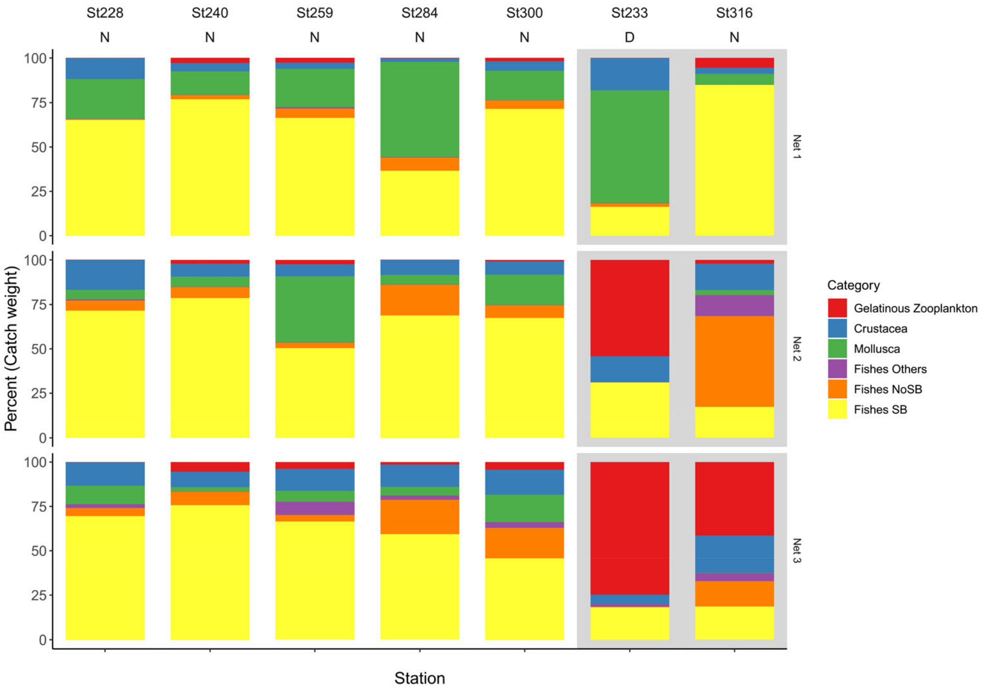

Fig. 6 Catch composition (percentage of total catch weight per net) of major taxonomic categories in different depth strata covered during *regular* and *deep* night- (N) and day-time (D) stations. *Regular stations*: net 1 (upper panel): 150–220 m; net 2 (middle panel): 220–280 m; net 3 (lower panel): 280–350 m. *Deep stations* (panels with grey background). Station 233: net 1: 100–350 m; net 2: 350–450 m; net 3: 450–700 m. Station 316: net 1: 30–150 m; net 2: 480–600 m; net 3: 775–965 m. NOSB, without swimbladder; SB, with swimbladder

Melamphaidae (N=1192, A=22.5%, M=17.1%), Gonostomatidae (N=225, A=4.5%, M=11.3%), Stomiidae (N=106, A=2.1%, M=8.5%) and Sternoptychidae (N=81, A=1.6%, M=2.9%). Four species accounted for 50.3% of the total number of fishes: the melamphaid *Scopelogadus mizolepis* was the most abundant species (N=962,

Table 3 Total number of caught specimen (N), relative abundance (A), total catch weight and relative biomass (M) of fish families at depth (*regular stations* 228, 240, 259, 284 and 300). The table includes all families that contain more than 5 specimens

Family	Net 1 (ca. 150-220 m)				Net 2 (ca. 220–280 m)				Net 3 (280–360 m)			
	Number (N)	A (%)	Weight (kg)	M (%)	Number (N)	A (%)	Weight (kg)	M (%)	Number (N)	A (%)	Weight (kg)	M (%)
Myctophidae	1511	69.2	2.972	74.4	348	32.9	0.737	27.8	304	39.3	0.740	27.5
Melamphaidae	407	18.6	0.431	10.8	494	46.6	0.871	32.9	268	34.7	0.542	20.1
Gonostomatidae	32	1.5	0.083	2.1	63	5.9	0.419	15.8	53	6.9	0.650	24.1
Stomiidae	43	2.0	0.186	4.7	23	2.2	0.164	6.2	17	2.2	0.239	8.9
Scombrolabracidae	35	1.6	0.070	1.8	31	2.9	0.116	4.4	3	0.4	0.007	0.2
Sternoptychidae	0	n.a.	n.a.	n.a.	15	1.4	0.053	2.0	48	6.2	0.226	8.4
Evermannellidae	21	1.0	0.053	1.3	24	2.3	0.092	3.5	16	2.1	0.068	2.5
Anoplogastridae	5	0.2	0.003	0.1	13	1.2	0.013	0.5	19	2.5	0.019	0.7
Bregmacerotidae	30	1.4	0.060	1.5	3	0.3	0.011	0.4	2	0.3	0.007	0.3
Howellidae	15	0.7	0.032	0.8	11	1.0	0.055	2.1	3	0.4	0.020	0.7
Notosudidae	19	0.9	0.058	1.5	6	0.6	0.032	1.2	2	0.3	0.014	0.5
Chiasmodontidae	4	0.2	0.003	0.1	12	1.1	0.072	2.7	10	1.3	0.049	1.8
Paralepididae	16	0.7	0.023	0.6	6	0.6	0.010	0.4	1	0.1	0.005	0.2
Phosichthyidae	11	0.5	0.002	0.0	1	0.1	0.001	0.0	8	1.0	0.001	0.0
Tetraodontidae	13	0.6	0.001	0.0	0	n.a.	n.a.	n.a.	0	0.0	n.a.	n.a.
Scopelarchidae	0	n.a.	n.a.	n.a.	2	0.2	0.0002	0.0	9	1.2	0.0214	0.8
Bramidae	9	0.4	0.008	0.2	0	n.a.	n.a.	n.a.	0	n.a.	n.a.	n.a.
Trichiuridae	5	0.2	0.002	0.1	1	0.1	0.003	0.1	1	0.1	0.045	1.7
Molidae	5	0.2	0.0004	0.0	0	n.a.	0.737	n.a.	1	0.1	0.0001	0.0

Table 4 Total number of caught specimens and total weight of fish per family at *deep stations* (233 and 316)

Family	Station 233					
	Net 1 (108–362 m)		Net 2 (362–450 m)		Net 3 (450–698 m)	
	Number (N)	Weight (kg)	Number (N)	Weight (kg)	Number (N)	Weight (kg)
Myctophidae	4	0.008	5	0.005	77	0.077
Gonostomatidae	n.a.	n.a.	n.a.	n.a.	57	0.057
Phosichthyidae	n.a.	n.a.	10	0.01	n.a.	n.a.
Sternoptychidae	1	0.0002	7	0.007	3	0.003
Stomiidae	n.a.	n.a.	n.a.	n.a.	6	0.006
Melamphaidae	n.a.	n.a.	2	0.002	1	n.a.
Howellidae	n.a.	n.a.	2	0.002	2	0.002
Diretmidae	n.a.	n.a.	n.a.	n.a.	2	0.002
Molidae	n.a.	n.a.	n.a.	n.a.	2	n.a.
Paralepididae	1	0.001	n.a.	n.a.	n.a.	n.a.
Tetraodontidae	1	n.a.	n.a.	n.a.	n.a.	n.a.
Anoplogastridae	1	0.0004	n.a.	n.a.	n.a.	n.a.
Scopelarchidae	n.a.	n.a.	n.a.	n.a.	1	0.001
	Station 316					
	Net 1 (32–152 m)		Net 2 (482–606 m)		Net 3 (775–965 m)	
Myctophidae	698	0.617	12	0.021	11	0.02
Gonostomatidae	n.a.	n.a.	11	0.017	9	0.003
Phosichthyidae	4	0.001	19	0.034	1	0.018
Sternoptychidae	n.a.	n.a.	3	0.006	9	0.006
Stomiidae	n.a.	n.a.	3	0.201	13	0.149
Evermannellidae	n.a.	n.a.	6	0.069	n.a.	n.a.
Melamphaidae	2	n.a.	n.a.	n.a.	n.a.	n.a.
Chiasmodontidae	n.a.	n.a.	3	0.015	1	0.152
Serrivomidae	n.a.	n.a.	n.a.	n.a.	4	0.043
Diretmidae	n.a.	n.a.	n.a.	n.a.	1	0.002
Melanocetidae	n.a.	n.a.	1	0.062	n.a.	n.a.
Notosudidae	n.a.	n.a.	1	0.003	n.a.	n.a.

A=19.2%) followed by three myctophids (*Ceratoscopelus warmingii* (N=637, A=12.7%), *Nannobrachium* (*cf.*) *cuprarium* (N=612, A=12.2%) and *Bolinichthys photothorax* (N=309, A=6.2%)). Considerable numbers of *S. elongatus* (N=148, A=2.9%), *Lepidophanes guentheri* (N=148, A=2.9%), *Lampanyctus photonotus* (N=143, A=2.8%), *Lobianchia gemellari* (N=118, A=2.3%), *Lampadena atlantica* (N=104, A=2.1%) and *Diaphus mollis* (N=95, A=1.9%) were also recorded.

Table 5 Total number of caught specimens (N) and total catch weight per group at stations

Station	Depth (m)	Fish (N)	Fish (kg)	Mollusca (kg)	Crustacea (kg)	Gelat. zoopl. (kg)
228	152–346	602	1.37	0.22	0.26	0.00
240	146–350	786	1.78	0.18	0.15	0.08
259	157–356	1083	2.24	0.78	0.23	0.09
284	145–368	839	2.36	1.28	0.21	0.02
300	150–342	706	1.58	0.35	0.16	0.04
233	108–698	194	0.31	0.04	0.09	1.00
316	32–965	812	1.44	0.06	0.33	0.49

The most species-rich families were Myctophidae (14 genera, 31 species) and Stomiidae (12 genera, 12 species) followed by Sternoptychidae and Phosichthyidae (3 genera, 4 species), and Melamphaidae, Evermannellidae, Gonostomatidae and Paralepididae (3 genera, 3 species). Genera with more than two species were *Diaphus* (10 species) and *Hygophum* (4) (both myctophids).

Genetic analysis of samples from 77 different species and groups of higher taxa were performed. In 58 cases, the morphologic identification was confirmed by genetic results. In 11 of these cases, specimens were assigned to higher taxonomic ranks, because morphologic and genetic identification did not match at species level (i.e. results did not match with sufficient

Table 6 Fish species per station and depth

Order Family Species		Regular stations															Deep stations					
		Station 228			Station 240			Station 259			Station 284			Station 300			Station 233			Station 316		
		Net 1	Net 2	Net 3	Net 1	Net 2	Net 3	Net 1	Net 2	Net 3	Net 1	Net 2	Net 3	Net 1	Net 2	Net 3	Net 1	Net 2	Net 3	Net 1	Net 2	Net 3
	Depth (m)	152–208	225–275	293–346	146–205	225–271	298–350	157–208	220–277	265–356	145–196	220–278	288–368	150–230	225–265	295–342	108–362	362–450	450–698	32–152	482–505	774–965
	Time (local)	22:54–00:09	00:19–01:34	01:44–02:59	23:54–01:09	01:19–02:34	02:44–03:59	00:57–02:12	02:22–03:37	03:47–05:02	23:41–00:56	01:06–02:21	02:31–03:46	22:44–23:59	00:09–01:24	01:34–02:49	06:47–08:17	08:17–10:02	10:02–11:47	23:25–00:40	01:05–02:20	02:35–03:50
	Total catch	Catch per net			Catch per net			Catch per net			Catch per net			Catch per net			Catch per net			Catch per net		
	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N
Anguilliformes																						
Derichthyidae																						
Derichthys serpentinus	1						1															
Nemichthyidae																						
Nemichthys scolopaceus	1												1									
Serrivomeridae																						
Serrivomer beanii	4																					4
Serrivomeridae spec.	2						1									1						
Aulopiformes																						
Evermannellidae																						
Coccorella atlantica	63		8	4	1					1	18	14	1	1	2	7					6	
Evermannella indica	1												1									
Odontostomops normalops	1												1									
Evermannellidae spec.	2				1											1						
Notosudidae																						
Scopelosaurus smithii	26				2	1		10	2	1	1		1	5	2						1	
Scopelosaurus spec.	2	1	1																			
Paralepididae																						
Lestidiops spec.	17				3	3					5			5	1							
Macroparalepis brevis	1											1										
Sudis spec.	4			1	1				1								1					
Paralepididae spec.	2	2																				
Scopelarchidae																						
Scopelarchus analis	2									1									1			
Scopelarchus spec.	10		1	5		1										3						
Beryciformes																						
Anoplogastridae																						
Anoplogaster spec.	38		2	2	2	2	4	2	5	5	1	1	6		3	2	1					
Diretmidae																						
Diretmoides spec.	5		2																2			1
Gadiformes																						
Bregmacerotidae																						
Bregmaceros spec.	35	6	2	2	1			5			4	1		14								
Melanonidae																						
Melanonus zugmayeri	3			1						1	1											
Lophiiformes																						
Melanocetidae																						
Melanocetus johnsonii	1																				1	
Myctophiformes																						
Myctophidae																						
Bolinichthys indicus	22		2	1							1								4	14		
Bolinichthys photothorax	309	87	12	9	24	3	6	81	28	17	7	1	1	26	3	3				1		
Bolinichthys spec.	3				1							1										1
Ceratoscopelus warmingii	638	22	2	2	90	14	51	78	24	29	21	2	2	48	3	2				242	3	3
Diaphus brachycephalus	63	9	9	1	1	3		1	3		14	7	1	5	5		3				1	
Diaphus dumerilii	6				2														4			

Table 6 (continued)

Diaphus fragilis	2							2														
Diaphus lucidus	9	1						4	1		1			1	1							
Diaphus mollis	95	1		1	21		1	17	2	2	3		1	6		2			31	6	1	
Diaphus perspicillatus	5																		1	4		
Diaphus problematicus	39	8	7		2			13		1	4			2	1				1			
Diaphus raffinesquii	3																		3			
Diaphus splendidus	43	12	2		5			4		1	2			13	1	1			2			
Diaphus spec.	1															1						
Hygophum hygomii	11																			11		
Hygophum macrochir	1	1																				
Hygophum reinhardtii	62	7	2					11			8	3		2	4	1				24		
Hygophum taaningi	11	3	1			4	3															
Hygophum cf. taaningi	20				20																	
H. cf. taaningi/macrochir	205		1		1															203		
Hygophum spec.	2				1			1														
Lampadena atlantica	104	4	5	5	29	1	2	12	1	2	30	3	1	7	1						1	
Lampanyctus nobilis	25	1	4		8	1		1	1	1	4			3	1							
Lampanyctus photonotus	144		5	2	32	1	1	32	3	1	6			2						54	3	2
Lampanyctus spec.	5				1					4												
Lepidophanes guentheri	148	1			1			1	1		7	1		5						131		
Lobianchia gemellari	118	15	9	6	5	6	3	5		6	20	3	5	20	4				10		1	
Lobianchia cf. gemellari	16				3			2	11													
Lobianchia spec.	1							1														
Loweina rara	2										1			1								
Loweina spec.	1										1											
Myctophum nitidulum	8				2			1	1		1	1								2		
Myctophum selenops	21			1	1		1	2			2		6	2	2		1	2	1			
Nannobrachium cuprarium	461	16	27	24			24			32	133	14	5	157	17	7					1	4
Nannobrachium cf. cuprarium	151				108	27			16													
Nannobrachium lineatum	7				1		2					1		1	2							
Nannobrachium/Lampanyctus	78	7						70	1													
Notoscopelus caudispinosus	29			1	13			6						8	1							
Notoscopelus resplendens	5										1									4		
Symbolophorus rufinus	3							1		1				1								
Taaningichthys minimus	50			4		2			2	3	9	13	8		3	5					1	
Taaningichthys minimus	50			4		2			2	3	9	13	8		3	5					1	
Myctophidae spec.	26	1	2			2		1			3							3	11	2		1
Osmeriformes																						
Bathylagidae																						
Dolicholagus longirostris	1													1								
Perciformes																						
Bramidae																						
Pteraclis carolinus	9	5						4														

Table 6 (continued)

Chiasmodontidae																						
Pseudoscopelus altipinnis	6										1				2	2					1	
Pseudoscopelus cf. altipinnis	5									2		3										
Pseudoscopelus spec.	17		1	1	1		3	1	6		1		1								2	
Howellidae																						
Howella brodiei	33	13						7			2			7				2	2			
Nomeidae																						
Cubiceps gracilis	1	1																				
Scombrolabracidae																						
Scombrolabrax heterolepis	62	3	4	1	10	7		9	18	1	5	2		2								
Scombrolabrax cf. heterolepis	7						1	6														
Trichiuridae																						
Trichiuridae spec.	7	3	1							1	2											
Stephanoberyciformes																						
Melamphaidae																						
Melamphaes cf. typhlops	139	1	22	9		5		5	10	16	4	20	11	2	3	16					15	
Melamphaes pumilus	9			2							4				3							
Melamphaes spec.	64	2	5	1	4	1	8	3	1	1	10	15		9	1					2	1	
Poromitra crassiceps	1																					1
Scopelogadus mizolepis	962		19	42	17	32	72	117	170	74	132	95	7	90	86	9						
Scopelogadus spec.	3																				3	
Melamphaidae spec.	14		2		7	4													1			
Stomiiformes																						
Gonostomatidae																						
Bonapartia pedaliota	67																		57		10	
Cyclothone spec.	9																					9
Sigmops elongatus	149	7	10	9	1	5	12	4	7	9	11	28	18	9	13	5					1	
Phosichthyidae																						
Ichthyococcus ovatus	1																	1				
Pollichthys mauli	13	2									2							5		4		
Vinciguerria attenuata	7			2			4				1											
Vinciguerria poweriae	4																	4				
Vinciguerria spec.	6	2											1	1	1	1						
Yarella spec.	1				1																	
Phosichthyidae spec.	2	1									1											
Sternoptychidae																						
Argyropelecus aculeatus	64		8	21			10			4		4	11		1	1		1	2		1	
Argyropelecus hemigymnus	2																				2	
Maurolicus weitzmani	2					2																
Sternoptyx pseudobscura	13																1	2	1			9
Stomiidae																						
Astronesthes spec.	5							1		1			2	1								
Borostomias cf. mononema	1			1																		
Chauliodus danae	43	2			5			6	2		7	5	1	3							2	10
Chauliodus cf. danae	6																		6			
Chauliodus sloani	18	2	3	1	1		2		1			3		1							1	3
Chauliodus spec.	2									2												

Table 6 (continued)

Echiostoma barbatum	6				1						3			1	1				
Echiostoma spec.	1										1								
Eustomias spec.	1	1																	
Leptostomias haplocaulus	1					1													
Leptostomias spec.	6						2	1	1		1				1				
Melanostomias tentaculatus	1											1							
Melanostomias spec.	3						1	2											
Neonesthes capensis	1														1				
Photonectes spec.	2											1	1						
Photostomias guernei	1					1													
Stomias brevibarbatus	4					1				1	1					1			
Idiacanthus fasciola	1									1									
Stomias spec.	1							1											
Stomiidae spec.	2	1														1			
Tetraodontiformes																			
Molidae																			
Masturus lanceolatus	9				2			2	1					1		1			2
Tetraodontidae																			
Canthigaster spec.	14				6			7									1		

quality to any species in identification keys and NCBI Nucleotide Sequence Database). In 19 cases, a genetic confirmation was not possible because the identified taxa were not included in the Database, and in 40 cases, genetic analyses were not performed.

The relative abundance of Myctophidae was high (42.9–67.7% of total catch) in catches from all *regular stations* (stations 228, 240, 259, 284, 300), whereas Melamphaidae showed lower abundances at western stations (stations 228 and 240; 17.4–19.1%) compared to the central and eastern sampling area (stations 259, 284, 300; 31.0–36.7%) (Fig. 7). The dominance of single species in catches was more pronounced in the eastern part of the survey area compared to the west. At the easternmost station (300), the two most abundant species accounted for 51.8% of total catch, while at intermediate stations three species and at the westernmost station (228) six species summed up to 50% of total catch. The share of the two most abundant species increased in catches from west to east (228: 29.1%; 240: 36.8%; 259: 45.4%; 284: 46.0%; 300: 51.8%). Catches at eastern *regular stations* (st. 284 and 300) were dominated by *S. mizolepis* (A=26.2–27.9%), followed by *N. cuprarium* (18.1–25.6%). While *S. mizolepis* also dominated the catch at station 259 (33.3%), *B. photothorax* (17.9%) and *C. warmingii* (19.6%) were the most abundant species in catches from the western stations 228 and 240, respectively. No significant correlations of sea surface temperature and abundance of the four most important species were detected (*S. mizolepis*: t=0.390, p=0.72, R^2=0.05; *N. (cf.) cuprarium*: t=0.31, p=0.77, R^2=0.03; *C. warmingii*: t=2.95, p=0.06, R^2=0.74; *B. photothorax*: t= 0.36, p=0.74, R^2=0.04).

Among *regular stations*, species richness was highest in catches at the northernmost station (station 284), where 50 different species have been caught. *Evermannella indica*, *Macroparalepis brevis*, *Melanostomias tentaculatus*, *Nemichthys scolopaceus* and *Odontostomops normalops* were exclusively caught at that station. Catches at *regular stations* further south contained 44 to 46 different species.

Discussion

The catch composition of mesopelagic fish species during this survey is similar to catches reported from previous investigations in the Sargasso Sea and other North-Atlantic areas (Backus et al. 1969; Ross et al. 2010; Olivar et al. 2017). Stratified night-time catches in layers 1 (epipelagic layer) and 2 (principal DSL) at *regular stations* generally reflected the taxonomic and quantitative composition that was encountered in previous surveys in the eastern part of the Atlantic in the same ecoregion “Central North Atlantic” (Ariza et al. 2016;

Table 7 Length and weight per species and results of genetic analyses. DB database

Species	Standard length (cm)			Weight (g)			Genetic analysis
	N	Mean	SD	N	Mean	SD	
Anoplogaster spec.	34	2.3	0.6	34	1	0.6	Confirmed
Argyropelecus aculeatus	61	5	1.0	63	4.9	3.1	Confirmed
Argyropelecus hemigymnus	1	2.2	0.0	1	0.2		Not tested
Astronesthes spec.	5	10.6		5	9.8	8.0	Confirmed
Bolinichthys indicus	22	3.4	0.3	20	0.5	0.2	Confirmed
Bolinichthys photothorax	307	5.5	0.8	303	2.2	0.8	Confirmed
Bolinichthys spec.	3	4.6	3.4	3	2.5	3.9	Confirmed
Bonapartia pedaliota	66	5.6	0.5	66	1.3	0.3	Confirmed
Borostomias cf. mononema	1	8.3		1	3.1		Not tested
Bregmaceros spec.	26	6.9	1.3	26	2.5	1.4	Not in DB
Canthigaster spec.	14	0.9	0.2	9	0.1	0.1	Not in DB
Ceratoscopelus warmingii	633	5.5	1.0	633	2.2	1.0	Confirmed
Chauliodus cf. danae	5	6.7	1.8	5	0.8	0.2	Not tested
Chauliodus danae	37	10.3	2.2	39	2.1	1.7	Confirmed
Chauliodus sloani	16	17.2	5.6	15	28	49.0	Confirmed
Chauliodus spec.	1	10.7		1	2.3		Not tested
Coccorella atlantica	62	7.3	2.3	62	4.4	6.2	Confirmed
Cubiceps gracilis	0			0			Not tested
Cyclothone spec.	9	4.6	0.5	9	0.3	0.1	Confirmed
Derichthys serpentinus	1	7		1	0.1		Confirmed
Diaphus brachycephalus	60	3.9	0.4	59	1.2	0.3	Confirmed
Diaphus dumerilii	6	5.3	0.4	6	1.7	0.5	Not in DB
Diaphus effulgens	6	4.2	1.3	6	1.8	3.1	Confirmed
Diaphus fragilis	2			2			Confirmed
Diaphus lucidus	9	6	1.1	8	3.6	1.9	Confirmed
Diaphus mollis	95	4	0.5	94	0.9	0.3	Confirmed
Diaphus perspicillatus	5	5.5	0.8	5	3.2	1.1	Confirmed
Diaphus problematicus	39	6.7	0.8	31	4.9	1.3	Not in DB
Diaphus raffinesquii	3	8.4	0.4	3	9	0.8	Confirmed
Diaphus spec.	1	4.8		1	2.1		Not tested
Diaphus splendidus	43	6	0.7	31	2.8	1.0	Confirmed
Diretmoides spec.	3	5.2	1.4	3	6.6	3.9	Confirmed
Dolicholagus longirostris	1	8		1	1.5		Confirmed
Echiostoma barbatum	6	17.5	2.1	6	19	6.0	Confirmed
Echiostoma spec.	0			0			Not tested
Eustomias spec.	0			0			Confirmed
Evermannella indica	1	7.1		1	2.3		Not tested
Evermannellidae spec.	2			2			Not tested
Howella brodiei	11	5	0.9	11	2.8	2.0	Confirmed
Hygophum cf. taaningi	18	3.5	0.5	19	0.5	0.3	Not tested
H. cf. taaningi/macrochir	192	3.3	0.5	199	0.5	0.3	Not tested
Hygophum hygomii	11	4.7	0.3	11	1.6	0.5	Not tested
Hygophum macrochir	1	3.6		0			Not tested
Hygophum reinhardtii	58	3.4	0.4	49	0.4	0.2	Confirmed
Hygophum spec.	1	4.3	1.1	1	1		Confirmed
Hygophum taaningi	11	3.5	0.5	8	0.8	0.3	Confirmed
Ichthyococcus ovatus	1	1.7		0			Not tested
Idiacanthus fasciola	1	23		1	1.4		Confirmed
Lampadena atlantica	103	5.8	1.6	102	3.1	2.7	Confirmed
Lampanyctus nobilis	25	9.8	1.1	24	8	2.8	Confirmed
Lampanyctus photonotus	142	5.5	0.5	143	1.5	0.5	Confirmed
Lampanyctus spec.	4	5.9	3.5	5	2.1	2.4	Not tested
Lepidophanes guentheri	142	3.6	1.1	93	0.5	0.7	Confirmed
Leptostomias haplocaulus	1	16.3		1	6.9		Not tested
Leptostomias spec.	4	18.8	5.9	4	11.4	7.0	Not in DB
Lestidiops spec.	15	9.4	1.8	15	2	1.1	Not in DB
Lobianchia cf. gemellari	16	4.5	0.6	16	1.4	0.5	Not tested
Lobianchia gemellari	113	4.7	0.6	102	1.6	0.6	Confirmed
Lobianchia spec.	1	4.3		1	0.9		Not tested
Loweina rara	2			2			Not tested
Loweina spec.	1	3.5		1	0.4		Not in DB
Macroparalepis brevis	1	11		1	2.4		Not tested
Masturus lanceolatus	8	0.7	0.3	5	0.1	0.0	Confirmed

Table 7 (continued)

Species	Standard length (cm)			Weight (g)			Genetic analysis
	N	Mean	SD	N	Mean	SD	
Maurolicus weitzmani	2			2			Not tested
Melamphaes cf. typhlops	124	4.1	0.6	134	1.5	0.7	Not in DB
Melamphaes pumilus	5	2	0.1	3	0.1	0.0	Not tested
Melamphaes spec.	61	2.2	0.8	59	0.3	0.6	Not in DB
Melamphaidae spec.	6	1.8	0.2	0			Not in DB
Melanocetus johnsonii	1	8.6		1	62		Confirmed
Melanonus zugmayeri	3	10.7	2.0	3	7.3	3.8	Confirmed
Melanostomias spec.	3	10.4	3.4	3	3.6	4.2	Not in DB
Melanostomias tentaculatus	1	16.1		1	8.1		Not in DB
Myctophidae spec.	21	4.1	1.7	21	1.4	2.1	Not tested
Myctophum nitidulum	8	6.1	0.9	8	3.6	1.6	Confirmed
Myctophum selenops	21	6	1.1	21	4.8	2.0	Confirmed
Nannobrachium cf. cuprarium	146	6.2	0.9	146	1.3	0.5	Not tested
Nannobrachium cuprarium	448	6.4	0.8	444	1.5	0.5	Confirmed
Nannobrachium lineatum	4	10.3	1.6	4	4.4	1.8	Confirmed
Nannobrachium/Lampanyctus	74	6.2	1.2	74	1.3	0.7	Not tested
Nemichthys scolopaceus	0			1	16.2		Not tested
Neonesthes capensis	1	10.6		1	6.8		Confirmed
Notoscopelus caudispinosus	29	8.6	0.5	29	8.8	1.8	Confirmed
Notoscopelus resplendens	5	8.1	1.1	5	7.2	2.9	Confirmed
Odontostomops normalops	1	8.2		1	4.8		Confirmed
Paralepididae spec.	0			0			Not tested
Phosichthyidae spec.	1	3		1	0.2		Not tested
Photonectes spec.	2			2			Not in DB
Photostomias guernei	1	7.4		1	1.2		Confirmed
Pollichthys mauli	12	4	0.4	12	0.2	0.1	Confirmed
Poromitra crassiceps	1	10.5		1	17.5		Confirmed
Pseudoscopelus altipinnis	5	8.6	0.6	5	5.9	2.2	Not in DB
Pseudoscopelus cf. altipinnis	5	8	1.1	5	5.6	2.4	Not in DB
Pseudoscopelus spec.	16	7.7	2.0	16	5	3.8	Not tested
Pteraclis carolinus	4	4.6	1.3	4	2	1.6	Not in DB
Scombrolabrax cf. heterolepis	7	4.7	0.7	7	1.5	0.5	Not tested
Scombrolabrax heterolepis	55	5.2	2.2	55	3.3	9.9	Confirmed
Scopelarchus analis	2			2			Not tested
Scopelarchus spec.	9	5.1	1.3	9	2	1.4	Confirmed
Scopelogadus mizolepis	884	4.9	0.9	924	1.8	1.1	Confirmed
Scopelogadus spec.	0			2			Not tested
Scopelosaurus smithii	26	9.6	2.6	26	4	3.2	Not in DB
Scopelosaurus spec.	1	10.3		1	4		Not tested
Serrivomer beanii	0			4	10.8	8.4	Confirmed
Serrivomeridae spec.	1	15.3		1	0.6		Not tested
Sigmops elongatus	144	13.2	3.0	144	8	6.5	Confirmed
Sternoptyx pseudobscura	13	2.4	0.3	13	0.6	0.2	Confirmed
Stomias brevibarbatus	4	14.2	2.2	4	7.6	3.3	Not in DB
Stomias spec.	1	9.4		1	1.7		Not tested
Stomiidae spec.	1	9.7		1	4.3		Not tested
Sudis spec.	3	8	1.8	3	2.4	1.8	Confirmed
Symbolophorus rufinus	3	7.9	0.5	3	7.6	1.7	Confirmed
Taaningichthys minimus	50	4.1	0.7	50	0.8	1.2	Confirmed
Trichiuridae spec.	3	22.6	10.7	3	16.9	24.6	Not in DB
Vinciguerria attenuata	3	2.8	0.5	2			Not tested
Vinciguerria poweriae	3	2.6	0.1	4	0.1	0.1	Not tested
Vinciguerria spec.	4	3.6	0.3	4	0.3	0.1	Not tested
Yarella spec.	1	5.7		1	0.6		Not tested

Olivar et al. 2017; Sutton et al. 2017). It is known that organisms from epi- and upper mesopelagic layers exhibit strong DVM and generally show the strongest differences in day- and night-time distribution with aggregations in the epipelagic zone during night (Roe and Badcock 1984; Olivar et al. 2017). This diel vertical migrating functional group also comprises — among others — Gonostomatidae, Sternoptychidae, Phosichthyidae and Stomiidae, together with invertebrate micronekton (crustaceans and molluscs) (Sutton 2013). In this study, different components of the migrating group constituting the bulk of catches originate from different zones of the mesopelagial: while many of the sampled myctophids can be considered to originate from the principal DSL (layer 2), other taxonomic groups like melamphaids and some gonostomatids and sternoptychids are expected to have migrated from the deeper secondary DSL (layer 3). As found in previous studies, species of the family Melamphaidae are characteristic of the deeper mesopelagic fish community and usually show maximum concentrations between 400 and 800 m during the day and a more widespread distribution during night-time (Barlow and Sutton 2008; Sutton et al. 2008; Sutton 2013; Olivar et al. 2017). Some gonostomatid species are not known to display extensive DVM and usually are found in layers below the epipelagial both during day- and night-time (McClain et al. 2001; Olivar et al. 2017). While in this study similar observations were also made from the deep hauls, where Gonostomatidae were sampled in the corresponding layers, the species sampled in epipelagic night-time catches are characteristic of the upper mesopelagic zone and are known to undertake DVM (Sutton 2013). The here presented catches of stomiids reflected their known distribution and migration pattern as previously reported by Kenaley (2008) and Olivar et al. (2017), with night catches of individual specimens in layer 1, while during day-time this family was only sampled below 400 m depth. The comparatively large number of species of the subfamily Melanostomiinae caught in this study during night-time in layers 1 and 2 is a further indication of vertical migration behaviour in these

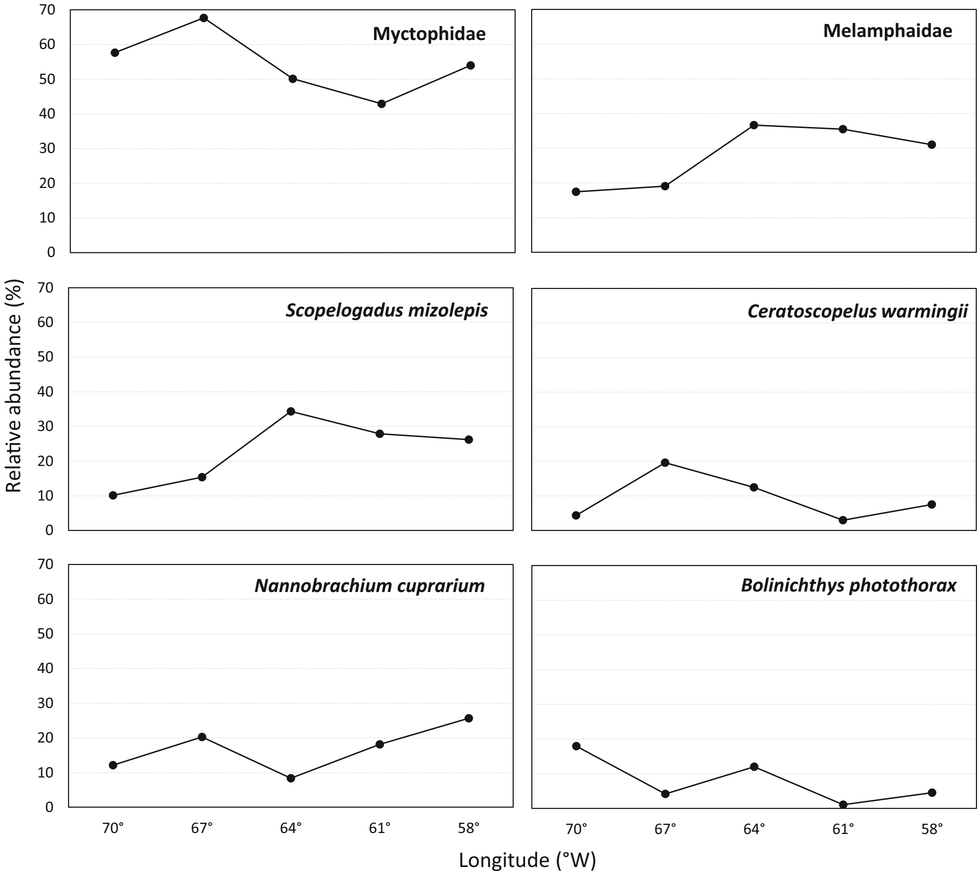

Fig. 7 Relative abundance of Myctophidae and Melamphaidae and the four most abundant species (*Scopelogadus mizolepis, Ceratoscopelus warmingii, Nannobrachium cuprarium, Bolinichthys photothorax*) in catches at geographical longitude

species. This corroborates accumulating evidence from oligotrophic, but also productive regions, that these species, despite remaining likely invisible in hydroacoustic recordings, contribute considerably to vertical energy fluxes (Cook et al. 2013; Eduardo et al. 2020a; Czudaj et al. submitted). Sternoptychidae in general are considered limited or only partial migrants (Kinzer and Schulz 1988) and usually occur preferentially in deeper layers, although some shallower occurrences can be observed during night hauls, especially in oligotrophic regions as shown for the south western Atlantic (Olivar et al. 2017; Eduardo et al. 2020b). This is well in line with the observations in this study, as night-time catches of sternoptychids, mainly dominated by *Argyopelecus aculeatus*, were present in the deeper nets of the epipelagic zone (below layer 1) and also occurred in layers 2 and 3 both during day and night (Table 6). The general observation of characteristic scattering layers in different depths in this study that show rather unique backscattering characteristics and regular DVM of organisms originating from different depth zones, was consistent with observations from adjacent areas and also from across the pelagic zones of the global ocean (Sutton 2013; Peña et al. 2014; Ariza et al. 2016; D'Elia et al. 2016; Klevjer et al. 2016). The observed presence of an epipelagic layer (layer1), a strong upper mesopelagic deep scattering layer (layer 2, principal DSL) as well as a weaker lower deep scattering layer (layer 3, secondary DSL) was in line with general descriptions of the ocean's deep mesopelagic zone (Proud et al. 2017). The detected layers with different scattering properties highly resembled layers characterized at the Canary Islands in the eastern Atlantic and the Northeastern Atlantic in general: an epipelagic layer with strong diel differences in scattering characteristics; a stationary upper layer of the upper principal DSL (upper layer 2) dominated by 18 kHz (450–550 m); a stationary lower layer of the principal DSL (layer 2) with a dominance of 38 kHz (ca. 600–700 m) and a mixed layer between; weak or no signals between 700 and 800 m; a permanent weak layer dominant at 18 kHz (secondary DSL, layer 3) between ca. 800 and 1000 m (Ariza et al. 2016; Klevjer et al. 2016). Additionally, similar patterns of a different but recurrent temporal onset of DVM of groups with differing backscattering characteristics at nightfall and the later descent into deeper layers with sunrise, as shown in this study, have been observed in nearby regions to the southwest (D'Elia et al. 2016) and east (Ariza et al. 2016) of the survey area. However, in this study, the sampling regime did not allow targeting and resolving the different upward and downward migrating fractions from different layers or the composition of the different layers itself. Nonetheless, based on the backscattering characteristics, and in comparison with previous studies, it seems likely that the upper part of the principal DSL (layer 2) mostly consisted of small, swimbladdered fishes resonant at 18 kHz like myctophids that also contributed the bulk of migrating fish emerging from that layer at nightfall (Peña et al. 2014, 2020; Ariza et al. 2016). While the lower part of the principal DSL (layer 2) remained rather stationary, migrant fauna also contributed to this layer, albeit to a lower extent. Although it was only caught in low numbers in this study, the gonostomatid *Cyclothone* spp. seem to be the dominant fish in the principal DSL (layer 2) (compare Ariza et al. (2016)). In contrast to Ariza et al. (2016) and Sutton (2013), who described the lower mesopelagic zone/secondary DSL (800–1000 m) as permanent and stationary, but identified a weak migrant signal between 700 and 800 m that disappeared at night, in this study a migrant pathway clearly became visible emerging from the secondary DSL (layer 3) and migrating upward through the principal DSL (layer 2), with no clear changes in the signal of the stationary fraction of that zone. Based on the dominance of the 18 kHz echoes, it can be assumed that the migrating and the stationary signal also originate from swimbladdered fishes and gas-bearing organisms. From that layer not only a peak in non-migrant fishes like *Cyclothone* spp. was reported earlier, but also of migrating fishes like the myctophid *Notoscopelus* spp. (Badcock and Merrett 1976; Roe and Badcock 1984; Sutton 2013; Ariza et al. 2016). The latter have — among others — contributed to epipelagic night-time catches made during this study. It has to be mentioned that a certain amount of backscattering in the lower frequency range also is highly likely to originate from physonect siphonophores carrying a gas-filled pneumatophore for buoyancy (Kloser et al. 2016; Proud et al. 2019). While comparatively little is known on actual vertical distribution or migration of these organisms (Pugh 1975; Pugh 1984; Lüskow et al. 2019), siphonophores are known to inhabit a broad depth range in the epi- as well as the upper mesopelagial, and some species also undertake DVM. Despite gelatinous zooplankton not being identified to lower taxonomic levels due to the fragility of the organisms and their condition in the codend of the multisampler nets, the contribution of gelatinous zooplankton to the total catch weight especially in the deep tows (net 3 of stations 233

(450–698 m) and 316 (774–965 m)) indicates that a certain fraction of the scattering layers with a dominance at 18 and 38 kHz may be assigned to a contribution from siphonophores.

The presence and condition of swimbladders changes among and within taxonomic groups of mesopelagic fish — and even may vary within genera and species based on developmental stage and length (Marshall 1960). It has been shown that e.g. biomass estimates of mesopelagic fish based on acoustic data collected at 38 kHz can be complicated because of the small physical size of mesopelagic fauna, ontogenetic changes in swimbladder morphology, inflation and regression (Davison et al. 2015). Additionally, the backscatter is depth-sensitive and non-linear with respect to size; at the same time, the size structure of mesopelagic fish is skewed with abundance driven by the smallest and biomass driven by the largest fishes. Echograms accordingly rather reflect the distribution of the strongest scatterers — e.g. (small) fishes with swimbladders — than the actual distribution of biomass (Davison et al. 2015). While some of the individual species identified in the multinet hauls may have different swimbladder characteristics than other genera/species from the same family, it is assumed that the main drivers of backscatter characteristics of scattering layers are still correctly identified through the classification used in this study.

A classification of hydroacoustic data into categories based on their scattering properties (e.g. D´Elia et al. 2016) and in combination with trawl net hauls is feasible, but a comprehensive interpretation of the aggregated results is challenging and corresponding sampling biases have been reported (Kaartvedt et al. 2012). This also affects contributions of gelatinous zooplankton and other invertebrates that may significantly contribute to backscatter through resonance at low frequencies but will be virtually absent from trawl haul catches due to the small and/or fragile nature of these organisms. It can safely be assumed that the corresponding layers identified using the method described by D'Elia et al. (2016) are not exclusively inhabited by the dominant taxonomic groups triggering the classification, but also by a magnitude of other species whose acoustic signal is masked by the dominant scatterers as well as the range limitation inherent in hydroacoustic data from higher frequencies. An indication for such a masking and/or a "missed classification" is evident from the catch composition of some tows that were conducted within layers with typical characteristics and dominance of gas-bearing organisms (i.e. resonant at 18 and 38 kHz), but also contained fluid-like zooplankton organisms like crustaceans and molluscs. As the scientific echosounder could not be calibrated directly prior to, during or after the survey, but had been calibrated with good results on a previous survey and was again calibrated a few weeks after the survey, the utilization of transducer parameters from a preceding calibration updated with ambient physical measurements from the current survey is considered sufficiently precise for the classification attempted here. The classification approach followed in this study is based on Sv intervals that are used to differentiate biological groups. D'Elia et al. (2016) derived the corresponding parameters from length measurements of representative organisms from concurrent net samples and on theoretical models relating these lengths to target strengths and subsequently to the Δ_{Sv} intervals. Since this study was conducted in a different, albeit adjacent, ecoregion with potentially different species and length compositions (e.g. Sutton et al. 2017), a certain degree of misclassification cannot be ruled out. Cells that did not match Δ_{Sv} intervals specified in D'Elia et al. (2016) could nevertheless be allocated to e.g. swimbladder-bearing fishes based on their scattering properties (Love 1978). Accordingly, the overall classification is considered robust enough for the analyses conducted.

According to Backus et al. (1970), who defined oceanic areas in the Atlantic on the basis of characteristic water masses, and supported by the hydrographic data obtained during this survey, the here investigated area is part of the Southern Sargasso Sea. This zone is characterized by distinct temperature fronts (Fig. 1), which are present from fall to spring (Halliwell et al. 1991). In this study, species richness was slightly higher at the northernmost station (lowest SST) compared to warmer stations further south with five species exclusively caught at the northernmost station. However, since only single individuals of these species were caught, the observed higher species richness north of the front might also be an artefact of low sampling effort. Nonetheless, similar results were reported by Backus et al. (1969), who caught a number of species north of the temperature front that were absent further south. In this study, northern and southern fish communities could not be compared in detail, since the sampling grid was not designed accordingly, but the total survey area comprised the Central Atlantic Mesopelagic Ecoregion that in general has a distinct faunal composition, albeit with spatial differences that are based primarily on abundance and rank order rather than presence or absence of species (Sutton et al. 2017).

Variations were observed between eastern and western stations with regard to the predominant species in catches (i.e.

S. mizolepis and *N. cuprarium* vs. *B. photothorax* and *C. warmingii*). These differences were apparently not driven by water temperature, since no significant correlation was evident between SST and the abundance of the four most abundant fish species. However, in case of *C. warmingii* (p=0.06, R^2=0.74), the absence of a significant correlation might be the result of the limited number of sampling stations. The relevance of temperature as a major driver for fish distribution might be lower in species that experience strong temperature gradients on a daily basis caused by DVM. Other environmental conditions like primary production, oxygen concentration and light attenuation where also shown to affect the distribution of mesopelagic fish species (Irigoien et al. 2014; Klevjer et al. 2016; Aksnes et al. 2017), but were not analysed in this study. Hence, the SST data collected in this study do not provide a full picture of environmental influences on the mesopelagic fish community, but contain information about the potential effect of horizontal temperature structures like temperature fronts on the distribution of mesopelagic fish. Nonetheless, the absence of a temperature effect on changes in the distribution of the dominant species suggests that the here observed changes in catch composition reflect differing regional influences from adjacent water masses.

Due to methodological constraints in sampling (large mesh size, relatively small number of stations, sampling not only in peak scattering layers), the data obtained and presented here do not provide a fully comprehensive and representative picture of the mesopelagic species composition of the investigated area. Stations, catch depths and trawl paths of this study were defined by the needs of the original purpose of the survey and not for the investigation of the mesopelagic fish community, which was only an additional benefit of the survey. As a consequence, no day-time samples were collected from the epipelagic scattering layer (layer 1) and the deep scattering layers (layers 2 and 3) could only be sampled at two stations at the far ends of the survey area. This study design hampers the discernibility of permanent residents and migrators in the different layers and complicates a more detailed interpretation of catches with regard to DVM. Another limitation of this study is the relatively large mesh size of the mesopelagic trawl. This might have led to the under-representation of certain small and thin species in catches, despite a general capture efficiency of the gear also for small-sized species < 30 mm (Fock and Czudaj 2018). For example, bristlemouths of the genus *Cyclothone* are usually found in high abundance in the investigated area and have been reported as resonant scatterers at depth (Peña et al. 2014). In this study, *Cyclothone* represents only a minor fraction of the trawl samples, which most likely is due to the large mesh sizes in the codend of the trawl net employed (1.5 cm), as it already was the case in the eastern tropical North Atlantic (Fock and Czudaj 2018; Czudaj et al. submitted). Large mesh sizes may also be the reason why *Ranzania laevis*, a small species of the sunfish family Molidae, was not present in any of the hauls, even though spawning activity and increased larval and post-larval abundance during the March and April in the area were recently described by Hellenbrecht et al. (2019). It is noteworthy though that nine post-larval (Molacanthus stage) specimens of *Masturus lanceolatus*, another fairly unexplored species of Molidae, were caught in this study.

Despite aforementioned limitations, the current study provides valuable insights into the distribution and vertical migration behaviour of mesopelagic fishes in the Sargasso Sea and adds to our understanding of the mesopelagic community in this large oceanic area. To assess how and to what extent the fish community in this ecoregion is affected by the influence of adjacent areas and by (changing) hydrographic conditions requires additional effort and extensive further investigations.

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Declarations

Conflict of interest The authors declare no competing interests.

Ethical approval All necessary permits for sampling and observational field studies have been obtained by the authors from the competent authorities and are mentioned in the acknowledgements, if applicable.

Sampling and field studies All necessary permits for sampling and observational field studies have been obtained by the authors from the competent authorities and are mentioned in the acknowledgements, if applicable. The study is compliant with CBD and Nagoya protocols.

Data availability The datasets generated during and/or analysed during the current study are available from the corresponding author on request

Author contributions LM and MS conceived and designed research and analysed the data. LM, MF, JP, KW, SC and RH conducted morphological species identification. MF and JP analysed CTD and SST data. TB made genetic analyses. All authors contributed to manuscript writing and read and approved the manuscript.

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CHAPTER II: Regional variation in the vertical and functional community composition and trophic structure of mesopelagic fishes in the tropical Atlantic

Articles 1–2

Article 3 Spatial variation in the trophic structure of micronekton assemblages from the eastern tropical North Atlantic in two regions of differing productivity and oxygen environments

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Spatial variation in the trophic structure of micronekton assemblages from the eastern tropical North Atlantic in two regions of differing productivity and oxygen environments

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ABSTRACT

The ecology of vertically migrating mesopelagic micronekton is affected by physical properties of their environment. Increased light attenuation in particle-rich productive waters, as well as low oxygen conditions decrease the migration amplitude. This likely has implications on the trophic organisation of micronekton communities, which are predominantly governed by niche partitioning in the vertical dimension. We investigated trophic structures of pelagic communities in the eastern tropical North Atlantic by comparing micronekton species assemblages from the low-oxygen region influenced by Mauritanian upwelling between 8° and 11° N (LO) and the less productive and more oxygenated equatorial area between 0 and 4°N (EQ). We analysed stable isotopes of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) in body tissues of 35 species of mesopelagic fishes, four species of cephalopods, two species of cnidarians, and two species of decapods and used these values as a proxy for their trophic niche and correlated them with the traits feeding guild, migration pattern, mean depth of occurrence and body size. Our results demonstrate significant regional differences in the food web structure and vertical trophic interactions of the investigated micronekton assemblages. Diurnally migrating fishes that predominantly feed on copepods exhibited higher $\delta^{15}N$ values in the LO (9.6‰) than in the EQ (8.9‰), reflecting changes in baseline values of pelagic tunicates. Contrary, all other Feeding – Migrator guilds show lower or similar $\delta^{15}N$ values in the LO compared to the EQ, indicating reduced isotopic enrichment between trophic levels (TL) in the LO compared to the EQ. Further, a generally lower $\delta^{15}N$ enrichment between TL3 – TL4 compared to TL2 – TL3 was observed (LO: TL2 – TL3: ~2.2‰, TL3 – TL4: ~1.2‰; EQ: TL2 – TL3: ~3.5‰, TL3 – TL4: ~2.2‰). Quantitative isotopic niche metrics suggest enhanced competition in trophic niche space, whereas relative isotopic niche positions indicate an increased importance of food from lower trophic levels (non-crustacean and/or gelatinous prey resources) for fishes from the LO compared to the EQ. The absence of a depth-related increase in $\delta^{15}N$ values of partial- and nonmigrators of the LO is contrary to results from the EQ and previously published data. Low $\delta^{15}N$ values in partially and nonmigrating micronektonivores of the LO in comparison with those of the EQ could be due to feeding on lower trophic prey components in the LO, as is indicated by an overlap in isotopic niche with that of partially and nonmigrating mixed crustacean feeders in the LO. Alternatively, driving mechanisms could be the consumption of prey from shallower waters, regional differences in $\delta^{15}N$ enrichment, species-specific ecological differences or a combination of these processes. Each of these explanations is likely tightly correlated to a vertical biogeochemical structuring effect of low oxygen midwater layers fuelled by high nitrate inputs from the Mauritanian upwelling region. Our study provides crucial ecological insights for a better understanding of large-scale gradients in micronekton migration patterns.

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1. Introduction

Micronekton organisms are important trophic components for the functioning of offshore pelagic ecosystems (e.g. Irigoien et al., 2014). The term micronekton generally encompasses different taxonomic organisms that include small species and juvenile stages of pelagic and deep-sea fishes and cephalopods, as well as larger crustacean species and gelatinous organisms in the size range between 2 and 20 cm (Brodeur and Yamamura, 2005). Due to ubiquitous vertical migrations of a large proportion of micronekton species and as intermediate trophic channels, they effectively link the surface production to higher consumers that inhabit epipelagic and deep-sea ecosystems (Drazen and Sutton, 2017). Not all migrators ascend to surface layers; some perform migrations in limited depth extension and some species migrate asynchronously, whereby only part of the population vertically moves each night, while the other part remains at depth (Kinzer and Schulz, 1988; Sutton and Hopkins, 1996a,b). This niche partitioning in the vertical space occurs via ontogenetic and species-specific depth preferences and migration patterns and reduces competition, but also governs the trophic structure of the community (Hopkins and Sutton, 1998; Bernal et al., 2015). By the consumption of both, surface production and organic matter that has already been (partially) degraded by microbial life as it sinks down through the water column, micronekton organisms occupy and link different positions in parallel existing food webs (Hannides et al., 2013; Choy et al., 2015; Wang et al., 2019). The migration amplitude of migrating species is driven by avoidance behaviour of visually attuned predators and, therefore, globally governed by common optical depth layers, resulting from physico-chemical properties of the water colum (Sutton, 2013). It has been shown that elevated light attenuation in productive upwelling regions and oxygen-depleted mesopelagic waters (OMZ) reduces the overall migration amplitude and affects the day-time vertical occurrence of migrating micronekton species (Bianchi et al., 2013; Klevjer et al., 2016; Aksnes et al., 2017). Since species distributions are connected, this likely implicates differences in vertical trophic dynamics. In OMZs, established species distributions may become additionally disrupted as a consequence of differential physiological oxygen tolerances, which forces some species to stay above the hypoxic boundary layer; thereby becoming more vulnerable to visually cued predation (Ekau et al., 2010; Koslow et al., 2011; Maas et al., 2014). The vertical occurrence of zooplankton and micronekton species and their trophic interactions in the OMZ of the eastern tropical North Pacific is structured as a result of biogeochemical processes that affect nutrient, and, therefore, prey availability (Wishner et al., 2013; Maas et al., 2014; Williams et al., 2014).

In the present study samples were collected in the eastern tropical North Atlantic (ETNA) between the equator and 11°N. The ETNA is characterised by regional and seasonal shifts in nutrient supply and productivity, as well as intensifying hypoxic conditions (minimum value $\sim$0.9 ml l^{-1}), southeast of Cape Verde (Stramma and Schott, 1999; Stramma et al., 2008; Ekau et al., 2010). The productive region between 5 and 20°N (LO) is under the influence of the OMZ and coastal upwelling, resulting in a distinct phytoplankton community structure, biomass and productivity patterns during boreal spring. These patterns separate the LO region from the less productive equatorial belt and stratified oligotrophic regions between 5°N and 5°S (EQ; Herbland et al., 1985; Marañón et al., 2001). Generally, a similar species assemblage of tropical to subtropical mesopelagic fish species with few dominant species occurs in the ETNA, but some endemic species make the LO distinct (Backus et al., 1977; Hulley, 1981). Reported differences in the size structure of mesopelagic fishes from the ETNA between data collected in the 1960/70ies and during the present cruise, as well as between the LO and the EQ, were likely partly related to low-oxygen conditions and differences in productivity (Fock and Czudaj, 2018).

Analysis of stable isotopes (SIA) has been successfully applied in trophic studies of various contexts and habitats (reviewed by Boecklen et al., 2011; Layman et al., 2012). This technique utilizes the medium term integration of stable isotopes in body tissues via food sources, as opposed to traditional stomach content analysis which only gives a snapshot of recent feeding history. Due to selective excretion of the kinetically more reactive lighter compounds within an organism, the ratio of heavy to light isotopes (expressed as δ notations relative to a standard in parts per thousand, ‰) increases from prey to predator. Whereas the ratio of the carbon isotope ^{13}C–^{12}C ($\delta^{13}C$) is used to trace the source of energy, the ratio of ^{15}N–^{14}N ($\delta^{15}N$) relative to a standard provides an estimate of the trophic level (DeNiro and Epstein, 1978; DeNiro and Epstein, 1981; Vanderklift and Ponsard, 2003). In the open ocean, the carbon isotopic values of particulate organic matter vary primarily related to sea surface temperature and phytoplankton community composition (Trueman et al., 2012). Nitrogen isotope ratios in surface particulate organic matter depend on the abundance and forms of inorganic nitrogenous nutrient inputs (Michener and Kaufman, 2007). Additionally, nitrogen isotope enrichment occurs with depth via bacterial degradation of sinking suspended particulate organic matter, which is grazed upon by zooplankton (Koppelmann et al., 2009; Hannides et al., 2013). As a result, $\delta^{15}N$ is an indirect indicator of feeding depth of micronekton organisms in deep-sea habitats (Choy et al., 2015; Romero-Romero et al., 2019). The combined variability of nitrogen and carbon stable isotope ratios in tissues provides the isotopic niche, which may serve as a proxy for the trophic niche (Bearhop et al., 2004; Newsome et al., 2007). Dedicated isotopic studies on mesopelagic fishes are most numerous for myctophid species (summarised by Olivar et al., 2018). Only scattered isotopic information exists for other mesopelagic fish taxa (Chouvelon et al., 2012; Choy et al., 2012, 2015; Ménard et al., 2014; Valls et al., 2014; McClain-Counts et al., 2017; Annasawmy et al., 2018; Romero-Romero et al., 2019; Wang et al., 2019), as well as deep-sea cephalopods (summarised by Navarro et al., 2013; Merten et al., 2017; Golikov et al., 2019), deep-sea macrocrustaceans (Chouvelon et al., 2012; Ménard et al., 2014; Annasawmy et al., 2018; Iitembu and Dalu, 2018) and cnidarians (see references in Fleming et al., 2015). Previous studies that looked at the isotopic niche in micronekton assemblages identified niche segregation and differences in trophic structure in response to regional hydrographic conditions (Sugisaki and Tsuda, 1995; Cherel et al., 2010; Annasawmy et al., 2018).

The aim of this study is to identify whether differences exist in the trophic structure of micronekton assemblages related to differences in the extent of migration depth of diel migrators between (i) the more productive low-oxygen region (LO) exhibiting increased light attenuation and (ii) the less productive oxygenated equatorial region (EQ) with clearer waters. During our net sampling, congruent day-time hydroacoustic data (38 kHz) were collected, which revealed that the strongest backscattering was observed at shallower depths in the LO compared to the EQ (unpublished data). In here, we hypothesise that the shallower day-time occurrence of scattering migratory species in the LO compared to the EQ results in an increased trophic competition in shallower waters and altered feeding preferences in migratory species of the LO. Additionally, we hypothesise that differences in species interactions and trophic relationships occur as a result of changes in the vertical occurrence of partial- and nonmigratory species in response to their migratory prey species. We investigated these hypotheses by an analysis of the stable carbon and nitrogen isotopic composition of bulk C and N in 43 migratory and partial/nonmigratory micronekton species. In an effort to separate the trophic and depth-related effects on isotopic signatures, we grouped species according to their feeding guild and migration pattern and further estimated their mean depth of occurrence based on literature data. We specifically addressed the following questions: (i) What is the mean isotopic difference per trophic level from primary to tertiary consumer and does it differ between the two regions investigated? (ii) Are there differences in the isotopic niche structure and trophic interactions of the fish and cephalopod assemblage between the two regions? (iii) Are there regional differences in the relationship of $\delta^{13}C$ and $\delta^{15}N$ isotope values of migratory and partial/nonmigratory fishes with increasing mean depth of occurrence and body size?

2. Material and methods

2.1. Sample collection

Micronekton samples were collected between 23 and 31 March 2015 during the cruise WH383 on the *FRV Walter Herwig III* at seven stations (Fig. 1). A pelagic midwater trawl (Engel Netze, Bremerhaven, Germany, length 18 m, 16 × 30 m mouth opening, cod end 20 mm stretched mesh-opening, 1.8 mm inlet sewn into last 1 m of cod end) was used with a multisampler allowing depth-stratified sampling. At each station, three depths were selected based on acoustic information on micronekton aggregations, resulting in fishing depths from 45 to 680 m. The depth strata had a mean thickness of 39 m (range 23–64 m) and were fished in horizontal tows for 30 min each stratum with a mean speed of three knots. Veering took 40 min to the depth of the first trawl, and 20 min in-between trawls. Night trawls took place at 22:00 local time, and the day-time trawls at 12:00 local time (Table 1).

Pelagic tunicate samples (appendicularians, pyrosomes, salps) provided the baseline values for stable isotope analyses and were collected using a Hydrobios © MultiNet Maxi (300 μm, 0.5 m^2 opening, 9 net bags, CT set). These organisms were collected via sampling in a 0–50 m stratum in surface waters about 2 h prior to micronekton fishing operations. Hydrographic data (temperature, salinity, dissolved oxygen concentration) were collected using a Seabird © 911 plus profiler (Sea-Bird Electronics Inc., Bellevue, WA, USA). Although the oxygen values were not calibrated using *in situ* sampling, they still can be used to identify low oxygen regions since the last manufacturer calibration with accuracy of 0.02 ml l^{-1} took place three months prior to the WH383 cruise. Therefore the time drift is not expected to be significant for the purpose of this study.

2.2. Sample processing and bulk stable isotope analysis (SIA)

Dorsal white muscle tissue samples of similarly-sized mesopelagic fish specimens, mantle material of cephalopod specimens, umbrella material of cnidarian specimens or abdominal tissues of decapod crustaceans were stored in liquid nitrogen until return to the laboratory onshore, where they were transferred to −30 °C and subsequently freeze-dried and ground. Due to their small size, complete, decapitated and degutted specimens of the myctophid *Diaphus vanhoeffeni* and the phosichthyid *Vinciguerria nimbaria* were sampled. Freezing does not affect isotopic condition significantly (e.g. Sweeting et al., 2004). For the SI baseline, pelagic tunicate samples were stored in 4% formaldehyde-seawater solution (buffered with sodium-tetraborate) and sorted in Steedman sorting fluid during processing (Steedman, 1976). A comparison of formaldehyde-preserved samples (FSL; 2 months) and frozen appendicularian samples (FRZ) collected north of Cape Verde indicated negligible differences in δ^{15}N values for this species group (*t*-test, mean ± SD: 7.8 ± 0.2 (FSL, $n = 6$) *versus* 7.6 ± 0.3 (FRZ, $n = 6$), $p = 0.11$). Earlier studies support the use of formaldehyde-preserved zooplankton samples for nitrogen isotope analysis, but suggest that δ^{13}C values are significantly affected. Therefore, we did not consider δ^{13}C values of formaldehyde-preserved samples in our analysis (Rau et al., 2003; Koppelmann et al., 2009; Bicknell et al., 2011). Samples for δ^{13}C analysis were lipid-extracted using a simplified version of the Smedes method by washing powdered sample material in cyclohexane (C_6H_{12}) three times using a vortex and ultrasonic bath (Smedes, 1999). Bulk SIA was performed at Thünen Institute of Climate-Smart Agriculture using an isotope ratio mass spectrometer (Delta plus, Thermo Fisher Scientific) coupled to an elemental analyser (FLASH EA 1112, CE Instruments) via Conflo II. Isotopic values are reported in standard δ-notation relative to atmospheric N$_2$ and V-PBD for N and C, respectively. The measured values were corrected using the international reference material USGS 40 and USGS 41 (L-glutamic acid), as well as the secondary laboratory standard acetanilide, which were analysed every 12 samples. Replicate measurements using these laboratory standards indicate an accuracy and precision of ≤0.2‰ (SD).

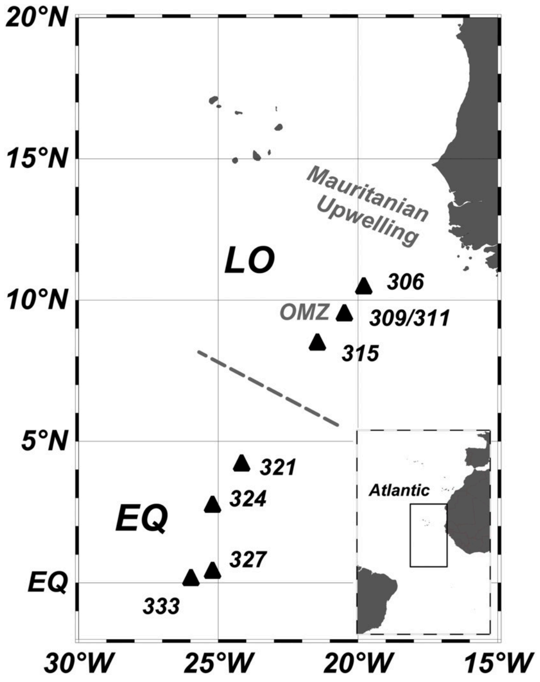

Fig. 1. Sampling locations of tunicates and micronekton in the low-oxygen region (LO) and the equatorial region (EQ) of the eastern tropical North Atlantic in March 2015.

2.3. Characterisation of Feeding – Migrator guilds

In the regional comparison of trophic structure we a-priori characterised fish species into Feeding – Migrator guilds based on available literature data from trawl studies (Table 2–4). Because both, trophic and depth-related effects, influence δ^{15}N values in tissues of deep-sea species, we combined a species' feeding guild and its assumed main feeding depth (according to its vertical migration pattern: 'epi' or 'meso') into a Feeding – Migrator guild in an effort to separate both effects. Epipelagic species ('epi') predominantly access a food web based on surface material with lower source δ^{15}N values while mesopelagic fish species ('meso') proportionally increase reliance on a food web based on microbially reworked organic matter with higher source δ^{15}N values (Choy et al., 2015; Romero-Romero et al., 2019). We use the nomenclature of feeding guilds as established by Hopkins et al. (1996), who did a comprehensive stomach content study on a wide variety of tropical Atlantic mesopelagic fish taxa, also separating them in different size classes. The myctophids *Ceratoscopelus warmingii* and *Diaphus dumerilii* are characterised in the literature as opportunistic feeders that access a variety of prey species. But because copepods generally constitute a large fraction of their diet, we included them in the zplv1 – epi guild to minimise overall guild numbers. The myctophid *Lepidophanes guentheri*, characterised by Hopkins et al. (1996) as a mixed crustacean feeder (zplv2, see Table 2), was assigned to the zplv1 – epi group, since in both regions its isotopic niche matched this group better than the other zplv2 – epi species that exhibited comparatively higher δ^{15}N values. Literature data for depth distributions were used since the sampling during our cruise did not cover the whole depth range of all the species we included in our analysis and sampling was not performed over the whole water column. The vertical migration pattern was either directly reported in the literature or inferred from night- and day-time core depth ranges, thereby taking into account the ontogenetic stage of the sampled specimens based on body size whenever possible (Table 4). Due to the limited number of samples available for partial migrators and non-migrators, these two migratory groups were pooled in the analyses,

Table 1

Stations sampled during the cruise WH383 for micronekton and pelagic tunicates.

Region	Date	Station	Longitude °W	Latitude °N	Start Time (local)	Tow 1 (m)	Tow 2 (m)	Tow 3 (m)	SST (°C)	MLD (m)	O_2 min (ml l^{-1})	Prim Prod (mg C m^2 day^{-1})
LO	23/03/2015	306	−19.8	10.5	22:00	51–76	166–195	397–435	24.4	27	0.9	1220
LO	24/03/2015	309	−20.5	9.5	12:00	337–381	390–424	509–556	24.0	27	0.9	4743
LO	24/03/2015	311	−20.5	9.5	22:00	47–79	246–288	397–441	24.0	27	0.9	4743
LO	25/03/2015	315	−21.5	8.5	22:00	52–81	228–282	368–432	23.5	31	0.9	1545
EQ	27/03/2015	321	−24.2	4.2	22:00	51–78	134–162	409–445	27.5	38	1.9	294
EQ	28/03/2015	324	−25.2	2.7	22:00	46–85	139–176	449–492	27.6	25	2.0	747
EQ	29/03/2015	327	−25.3	0.3	22:00	59–82	380–432	473–502	27.7	52	2.0	596
EQ	30/03/2015	333	−26.0	0.0	22:00	55–78	373–426	476–523	27.9	43	2.1	299

Start Time (local) = Fishing operation (net leaving deck) start time; Tow 1/2/3 = interval of fished depth of tow 1–3; SST = sea surface temperature; MLD = mixed layer depth (based on Kara Isothermal Layer Depth (Kara et al., 2000)). O_2min = minimum value of dissolved oxygen concentration sampled in the water column (at ~400 m, uncalibrated value); Prim Prod = net primary production extracted using the ocean net primary production (NPP) *Standard Products* from the website http://www.science.oregonstate.edu/ocean.productivity. Pelagic tunicates were sampled by Multinet in depths between 0 and 50 m each station ~2 h prior to the start of fishing operations.

acknowledging their ecological and trophic differences. Partial migrators include limited (limited migration amplitude of few hundreds of meters (c. 100–300 m) within 200–1500 m) and asynchronous migrators (only part of the population migrates every night (Hopkins and Sutton, 1996)).

2.4. Data analysis

All analyses were conducted in the statistical computing package R (R Core Team, 2019; https://www.R-project.org/). The station map and hydrographic profiles were visualised using the software Ocean Data View (Schlitzer, 2016). The net primary production (C m^{-3} day^{-1}) based on the standard vgpm algorithm (Behrenfeld and Falkowski, 1997), integrated for March 2015, was extracted using the ocean net primary production (NPP) *Standard Products* from the website http://www.science.oregonstate.edu/ocean.productivity. Mixed layer depth (MLD) was determined based on Kara Isothermal Layer Depth (Kara et al., 2000). To identify groups of stations with similar environmental characteristics, principal coordinate analysis (PCoA) was performed using the normalised environmental variables temperature, salinity, and dissolved oxygen at depths 0, MLD, 50, 100, 200, 300, 400, 500, 600, and 800 m. The distance matrix was based on Euclidean distances. Stations were clustered using the *k*-means method. Biomass data were calculated from length-weight distributions obtained from samples collected during the WH383 cruise in the ETNA region (for details see Fock and Czudaj, 2018).

Significant differences in mean isotope values between groups were explored applying Welch's unequal variances *t*-tests. All analyses of the isotopic niche structure in the two investigated regions were performed using the R package *Stable Isotope Bayesian Ellipses in R* (SIBER). SIBER allows robust statistical comparisons of communities or community members via Bayesian inference techniques that result in probability distributions (Jackson et al., 2011). To quantify regional structural differences at the assemblage level, we compared six niche/community metrics (Layman metrics) proposed by Layman et al. (2007). These metrics include: the range in $\delta^{15}N$ (NR) as an indicator of vertical trophic diversity, the range in $\delta^{13}C$ (CR) as a proxy for the variety of available basal resources, the total area of the convex hull (TA) as indicator of total niche width occupied by a species/community, the mean Euclidean distance of each isotopic sample to the biplot centroid (CD) providing a measure of niche dispersion, mean nearest neighbour distance (NND) as a proxy for the density and packing of species in the community, and the standard deviation of mean nearest neighbour distance (SDNND) giving information on the evenness of spatial clustering. In this analysis of isotopic niche metrics, we excluded the species *Searsia koefoedi* (family Platytroctidae) that did not have an ecological equivalent in the EQ, as well as four outlier data points from three species that exhibited comparatively low $\delta^{15}N$ values for micronektonivorous species living in deeper waters (cf. Table 3). We further fitted sample size-corrected maximum likelihood standard ellipses (SEAc) containing approximately 40% of the data for each Feeding – Migrator guild to explore regional differences in each guild's isotopic niche size, relative position and overlap as indicators of trophic interactions.

In addition, analysis of covariance (ANCOVA) was used to test for statistically significant differences in $\delta^{13}C$ and $\delta^{15}N$ values between the EQ and LO and diurnally migrating and partial/nonmigrating fishes, controlling for mean depth of occurrence at night (mdo) and standard length body size (SL). The mdo at night was either reported as mean night-time depth from the literature or as the measured night-time core depth for each species considering the ontogenetic stage based on body size. For asynchronous migrators with only vague literature estimates of night-time core depth ranges of 0 – >500 m (the stomiids *Astronesthes richardsoni*, *Flagellostomias boureei* and *Heterophotus ophistoma*) and 0 – >1000 m (the stomiid *Chauliodus* spec.) the mdos were assigned to 400 m and 500 m, respectively. For better comparability, the mdo of *Kali macrodon* (family Chiasmodontidae) was adjusted from >1500 m (Johnson and Keene, 1984) to a mean of 1000 m in the analysis, in accordance with catches of this species at 400–500 m during the WH383 cruise. We evaluated the contribution of each factor after considering the contributions of all the other factors in the model by evaluating Type III sum of squares. Model selection was based on Akaike Information Criteria (AIC). Inspection of the model residuals indicated no serious violations of the underlying assumptions of normality and homogeneity. In the analysis of $\delta^{15}N$ values, we excluded the species *Searsia koefoedi* and one specimen each of the myctophid *Diaphus dumerilii* and the melamphaid *Poromitra crassiceps* as identified being influential by Cook statistic. Similarly, in the analysis of $\delta^{13}C$ values, one specimen each of the myctophid *Lepidophanes guentheri* and *P. crassiceps* were excluded. We further fitted individual models for each regional dataset with $\delta^{15}N/\delta^{13}C$ as response variable, two continuous covariates (mdo and SL), and one categorical covariate (migratory type) to point out regional differences in the model results.

Table 2
Characterisation of Feeding – Migrator guilds based on literature data (cf. Tables 3 and 4), referring to the feeding guilds established by Hopkins et al. (1996).

Feeding – Migrator guild	Characteristics	Species families
zplv1 – epi	***copepod feeders***: copepods are major diet component in terms of biomass; ***diel migrators*** that ascend to within the upper 200 m	Myctophidae
zplv1 – meso	***copepod feeders***: copepods are major diet component in terms of biomass; ***partial and nonmigrators*** generally not reaching the epipelagic	Myctophidae, Sternoptychidae, Platytroctidae, Diretmidae
zplv2 – epi	***mixed crustacean feeders***: proportionally greater fraction of euphausiids and decapods, mixed crustacean diet; ***diel migrators*** that ascend to within the upper 200 m	Myctophidae
zplv2 – meso	***mixed crustacean feeders***: proportionally greater fraction of euphausiids and decapods, mixed crustacean diet; ***partial and nonmigrators*** generally not reaching the epipelagic	Gonostomatidae, Microstomatidae, Stomiidae, Sternoptychidae
zplv3 – meso	***non-crustacean feeders***: non-crustacean invertebrates (pelagic gastropods) and gelatinous food (tunicates, siphonophores) predominant; ***partial and nonmigrators*** generally not reaching the epipelagic	Melamphaidae, Bathylagidae
mnkv – meso	***micronektonivores***: mostly fish, but also larger crustaceans and decapods; ***partial and nonmigrators*** generally not reaching the epipelagic	Stomiidae, Paralepididae, Giganturidae, Chiasmodontidae, Scopelarchidae, Alepisauridae
pisc – meso	***piscivores***: *Chauliodus sp.* specimens >120 mm pure piscivores; ***partial and nonmigrators*** generally not reaching the epipelagic	Stomiidae

Partial migrators include limited (limited migration amplitude within 200–1500 m) and asynchronous migrators (only part of the population migrates every night). For each guild the species families that were analysed in this study are presented.

3. Results

3.1. Oceanographic setting

Two regions were separated based on principal coordinate analysis of hydrographic parameters (Fig. 2): Stations 306, 309/311, and 315 (LO) constitute a hydrographically fairly homogenous area under the influence of the Mauritanian upwelling and exhibiting low oxygen at midwater depths (>0.9 ml l^{-1}). The oxygenated less productive equatorial region (EQ) encompasses stations at the equator (stations 327, 333), and at 2.7° and 4.2°N (stations 321, 324), which were primarily characterised by higher sea surface and lower mid-depth values for temperature and salinity and higher mid-depth oxygen values (Fig. 3a – c).

3.2. Bulk nitrogen and carbon isotope analysis of micronekton species from the EQ and LO

A total of 265 micronekton specimens from the EQ ($n = 137$) and the LO ($n = 128$) were analysed for nitrogen and carbon isotopes. We analysed specimens of 35 mesopelagic fish species of 14 families (all adults; EQ $n = 113$; LO $n = 103$), four cephalopod species (EQ $n = 17$; LO $n = 17$), two species of jellyfish, and two decapod species (Table 3). Migratory (dm) and partial/nonmigratory (pm/nm) mesopelagic fish species selected for SIA included the most important species sampled in terms of relative abundance and biomass (Table 3). The range in mdo estimates differed between the two regions in our study (EQ: 0–750 m; LO: 0–1000 m).

3.2.1. Regional differences in the mean δ^{15}N and δ^{13}C isotope values between different Feeding – Migrator guilds

3.2.1.1. δ^{15}N values. Pelagic tunicate baseline δ^{15}N values were significantly lower in the EQ compared to the LO (Welch's *t*-test, EQ: 5.4 ± 1.1‰; LO: 7.4 ± 0.7‰ (mean ± SD), $p < .001$; Fig. 4a and b). Only δ^{15}N values of epipelagic copepod feeders (zplv1 – epi) corresponded with these baseline values by exhibiting significantly higher δ^{15}N values in the LO compared to the EQ (Welch's *t*-test, EQ: 8.9 ± 1.1‰; LO: 9.6 ± 0.9‰ (mean ± SD), $p = .009$). Contrary, significantly lower δ^{15}N values were measured in the non-crustacean feeders (zplv3 – meso; Welch's *t*-test, EQ: 12.5 ± 0.8‰; LO: 9.9 ± 0.8‰ (mean ± SD), $p < .001$) and the piscivore (pisc – meso) stomiid *Chauliodus* sp. (Welch's *t*-test, EQ: 10.3 ± 0.5‰; LO: 9.6 ± 0.3‰ (mean ± SD), $p = .003$) in the LO compared to the EQ. All other Feeding – Migrator guilds and the cephalopods showed comparable δ^{15}N values between the two regions (Table 5). The difference in δ^{15}N values between pelagic tunicates (assumed TL 2) and epipelagic copepod feeders (zplv1 – epi, assumed TL 3) was ~3.5‰ in the EQ, and ~2.2‰ in the LO, respectively. A lower difference in δ^{15}N values of ~2.2‰ and ~1.2‰, in the EQ and LO, respectively, existed between epipelagic copepod feeders (zplv1 – epi, assumed TL 3) and micronektonivores (mnkv – meso, assumed TL 4). In the EQ, the difference in δ^{15}N values between epipelagic copepod feeders (zplv1 – epi) and the piscivore (pisc – meso) *Chauliodus* sp. (1.4‰) was lower compared to micronektonivores (mnkv – meso), whereas in the LO, the piscivore (pisc – meso) *Chauliodus schmidti* measured δ^{15}N values equal to those of epipelagic copepod feeders (zplv1 – epi).

Considering just migratory type, in the EQ, the mean δ^{15}N of migratory fishes was significantly lower (9.7 ± 1.5‰, mean ± SD) compared to partial/nonmigrators (11.1 ± 1.1‰ (mean ± SD), Welch's *t*-test, $p < .001$). Contrary, in the LO, diurnally migratory fishes (10.1 ± 0.9‰, mean ± SD) did not have significantly lower δ^{15}N values than partial/nonmigratory fishes (10.4 ± 1.1‰ (mean ± SD), Welch's *t*-test, $p = .07$). Whereas diurnal migrators had similar mean δ^{15}N values in both regions (Welch's *t*-test, $p = .11$), the mean δ^{15}N value of partial/nonmigratory fishes (Welch's *t*-test, $p = .003$) was significantly higher in the EQ compared to the LO.

3.2.1.2. δ^{13}C values. Since we only measured one frozen salp sample in the LO, no regional statistical comparison was possible regarding δ^{13}C values of the baseline (EQ: 21.9 ± 0.5‰; LO: −20.8‰, mean ± SD). Epipelagic copepod feeders (zplv1 – epi; Welch's *t*-test, EQ: −19.1 ± 0.6‰; LO: −19.6 ± 0.3‰ (mean ± SD), $p < .001$) and non-crustacean feeders (zplv3 – meso; Welch's *t*-test, EQ: −19.3 ± 0.5‰; LO: −19.9 ± 0.5‰ (mean ± SD), $p = .001$) had significantly more negative δ^{13}C values in the LO compared to the EQ (Fig. 4a and b). Contrary, the micronektonivores (mnkv – meso) had significantly more positive δ^{13}C values in the LO than in the EQ (Welch's *t*-test, EQ: −19.2 ± 0.6‰; LO: −18.3 ± 0.4‰ (mean ± SD), $p = .001$). All other Feeding – Migrator guilds, as well as the cephalopods showed comparable δ^{13}C values among the two regions (Table 5). The difference in δ^{13}C values between pelagic tunicates and epipelagic copepod feeders (zplv1 – epi) was ~2.8‰ in the EQ, and ~1.3‰ in the LO, respectively. In the EQ, micronektonivores (mnkv – meso) had more negative δ^{13}C values than epipelagic copepod feeders (zplv1 – epi), whereas in the LO the difference was 1.2‰. The piscivore stomiid *Chauliodus* sp. (pisc – meso) had comparable δ^{13}C values to epipelagic copepod feeders (zplv1 – epi) in both regions.

In both regions, diurnal migratory (dm) and partial/nonmigratory

Table 3
Micronekton species sampled for bulk $\delta^{15}N$ and $\delta^{13}C$ at stations in the eastern tropical North Atlantic.

Species	Family	*n*	Station - Tow	Feeding – Migrator guild	Migrator guild	Mdo night	$\delta^{15}N$	$\delta^{13}C$	SL	% Abund (Rank)	% BM (Rank)
Fishes			LO								
Ceratoscopelus warmingii	Myctophidae	5	315–1	zplv1 – epi**	dm	87.5	8.6 ± 0.5	−20.0 ± 0.3	57 ± 4	7.2 (5.)	3.2 (10.)
Diaphus vanhoeffeni	Myctophidae	6	309–1	zplv1 – epi	dm	50	10.6 ± 0.2	−18.9 ± 0.7	32 ± 2	11.1 (1.)	2.3 (16.)
		5	315–1				10.4 ± 1.1	−19.9 ± 0.3	33 ± 2		
Electrona risso	Myctophidae	6	309–2	zplv1 – meso	lm	500	10.8 ± 0.3	−19.1 ± 0.3	71 ± 2	1.7 (16.)	4.4 (6.)
Hygophum macrochir	Myctophidae	6	315–1	zplv1 – epi	dm	50	9.3 ± 0.4	−19.4 ± 0.1	52 ± 3	8.5 (3.)	5.0 (4.)
Lepidophanes guentheri	Myctophidae	6	315–1	zplv1 – epi*	dm	87.5	9.6 ± 0.8	−19.3 ± 0.2	64 ± 5	6.7 (6.)	4.9 (5.)
cf. Nannobrachium atrum	Myctophidae	1	315–2	zplv2 – epi	dm	150	9.1	−19.2	133	0.2 (40.)	2.9 (13.)
Nannobrachium isaacsi	Myctophidae	4	315–2	zplv2 – epi	dm	100	10.8 ± 1.0	−19.1 ± 0.4	135 ± 22	2.2 (13.)	7.2 (1.)
cf. Nannobrachium lineatum	Myctophidae	1	315–2	zplv2 – epi	dm	100	9.4	−19.6	133	0.2 (49.)	0.5 (37.)
Notoscopelus resplendens	Myctophidae	5	311–1	zplv2 – epi	dm	90	10.7 ± 0.4	−19.1 ± 0.3	83 ± 7	5.8 (7.)	5.9 (2.)
Vinciguerria nimbaria	Phosichthyidae	6	315–1	zplv1 – epi	dm	50	10.0 ± 0.6	−19.5 ± 0.1	45 ± 2	8.9 (2.)	2.5 (15.)
Chauliodus schmidti	Stomiidae	6	315–3	pisc – meso	am	500	9.6 ± 0.3	−19.3 ± 0.4	176 ± 14	0.6 (29.)	2.8 (14.)
Flagellostomias boureei	Stomiidae	3	315–3	mnkv – meso	am	400	11.1 ± 0.4	−18.3 ± 0.2	211 ± 8	0.0 (99.)	0.2 (53.)
Gonostoma denudatum	Gonostomatidae	4	311–3	zplv2 – meso	dm	150	11.3 ± 0.3	−18.1 ± 0.6	111 ± 12	0.2 (39.)	0.7 (33.)
Sigmops elongatus	Gonostomatidae	5	311–3	zplv2 – meso	dm	225	10.4 ± 0.7	−18.5 ± 0.4	184 ± 16	0.2 (48.)	0.7 (34.)
Argyropelecus affinis	Sternoptychidae	5	311–3	zplv1 – meso	lm	450	10.8 ± 0.5	−19.2 ± 0.1	61 ± 4	2.9 (9.)	4.1 (8.)
Melamphaes polylepis	Melamphaidae	5	311–2	zplv3 – meso	nm	700	10.4 ± 0.4	−20.0 ± 0.8	43 ± 2	0.7 (28.)	1.0 (24.)
Scopelogadus mizolepis	Melamphaidae	5	311–2	zplv3 – meso	nm	800	9.8 ± 0.3	−20.2 ± 0.3	72 ± 5	1.0 (19.)	1.7 (21.)
		6	311–3				10.3 ± 0.6	−19.5 ± 0.2	80 ± 4		
Lestidiops jayakari	Paralepididae	1	315–3	mnkv – meso	nm	450	10.0	−18.9	155	0.1 (56.)	0.0 (88.)
Magnisudis atlantica	Paralepididae	1[‡]	315–3	mnkv – meso	nm	750	8.2	−19.4	184	0.0 (131.)	0.0 (84.)
Gigantura chuni	Giganturidae	1	309–3	mnkv – meso	nm	900	10.1	−18.9	c. 125	0.0 (191.)	0.0 (173.)
Microstoma microstoma	Microstomatidae	1	311–2	zplv2 – meso	nm	600	9.6	−18.5	105	0.0 (132.)	0.0 (130.)
Bathylagoides argyrogaster	Bathylagidae	3	311–2	zplv3 – meso	nm	250	8.6 ± 0.4	−20.0 ± 0.2	104 ± 7	0.7 (27.)	0.8 (25.)
Searsia koefoedi	Platytroctidae	3	315–3	zplv1 – meso	nm	550	13.4 ± 0.3	−19.6 ± 0.1	134 ± 4	0.2 (45.)	1.3 (22.)
Kali macrodon	Chiasmodontidae	3	315–3	mnkv – meso	am	1000[†]	10.7 ± 0.3	−18.2 ± 0.5	154 ± 4	0.0 (73.)	0.5 (35.)
Pseudoscopelus altipinnis	Chiasmodontidae	2[‡]	311–2	mnkv – meso	am	900	7.4 ± 1.7	−20.3 ± 1.2	86 ± 17	0.0 (76.)	0.4 (40.)
		1	315–3				11.1	−18.1	c. 125		
Fishes			**EQ**								
Ceratoscopelus warmingii	Myctophidae	6	321–2	zplv1 – epi**	dm	87.5	8.8 ± 0.8	−19.3 ± 0.1	67 ± 5	7.2 (5.)	3.2 (10.)
Diaphus dumerilii	Myctophidae	6	321–1	zplv1 – epi**	dm	50	9.5 ± 1.6	−19.4 ± 0.4	50 ± 4	8.2 (4.)	5.8 (3.)
Electrona risso	Myctophidae	5	327–2	zplv1 – meso	lm	500	10.7 ± 0.4	−19.7 ± 0.3	61 ± 6	1.7 (16.)	4.4 (6.)
Hygophum taaningi	Myctophidae	6	321–1	zplv1 – epi	dm	100	8.2 ± 0.6	−18.8 ± 0.6	52 ± 2	5.7 (8.)	4.4 (7.)
		6	327–1				9.9 ± 0.4	−19.5 ± 0.1	48 ± 2		
Lepidophanes guentheri	Myctophidae	4	321–1	zplv1 – epi*	dm	87.5	7.8 ± 0.4	−19.0 ± 0.1	54 ± 5	6.7 (6.)	4.9 (5.)
		5	327–1				8.9 ± 0.3	−18.7 ± 1.1	54 ± 2		
Nannobrachium atrum	Myctophidae	3	327–2	zplv2 – epi	dm	150	11.5 ± 0.9	−18.9 ± 0.5	170 ± 11	0.2 (40.)	2.9 (13.)
Nannobrachium lineatum	Myctophidae	3	327–2	zplv2 – epi	dm	100	12.7 ± 0.3	−19.1 ± 0.3	163 ± 14	0.2 (49.)	0.5 (37.)
Notoscopelus resplendens	Myctophidae	6	324–1	zplv2 – epi	dm	90	10.1 ± 1.0	−19.2 ± 0.1	68 ± 8	5.8 (7.)	5.9 (2.)
Astronesthes richardsoni	Stomiidae	5	324–2	zplv2 – meso	am	400	10.1 ± 0.6	−17.8 ± 0.5	100 ± 15	0.3 (37.)	0.5 (36.)
Chauliodus schmidti	Stomiidae	6	327–2	pisc – meso	am	500	10.2 ± 0.3	−19.2 ± 0.2	164 ± 10	0.6 (29.)	2.8 (14.)
		2	327–3				10.3 ± 1.0	−18.9 ± 0.1	214 ± 2		
Chauliodus sloani	Stomiidae	3	327–3	pisc – meso	am	500	10.4 ± 0.6	−19.1 ± 0.3	214 ± 11	0.2 (38.)	1.8 (19.)
Heterophotus ophistoma	Stomiidae	1	333–dc	mnkv – meso	am	400	10.9	−17.6	c. 250	0.0 (165.)	0.1 (82.)
Sigmops elongatus	Gonostomatidae	5	321–2	zplv2 – meso	dm	225	11.2 ± 0.6	−19.1 ± 0.5	123 ± 7	0.2 (48.)	0.7 (34.)
Argyropelecus affinis	Sternoptychidae	6	324–3	zplv1 – meso	lm	450	10.5 ± 0.3	−18.9 ± 0.2	62 ± 5	2.9 (9.)	4.1 (8.)

(*continued on next page*)

Table 3 (*continued*)

Species	Family	*n*	Station - Tow	Feeding – Migrator guild	Migrator guild	Mdo night	δ^{15}N	δ^{13}C	SL	% Abund (Rank)	% BM (Rank)
Argyropelecus sladeni	Sternoptychidae	6	324–3	zplv2 – meso	lm	250	10.4 ± 0.8	−18.4 ± 0.6	63 ± 11	2.2 (12.)	3.0 (11.)
Melamphaes polylepis	Melamphaidae	6	327–3	zplv3 – meso	nm	700	11.9 ± 0.4	−19.3 ± 0.1	60 ± 4	0.7 (28.)	1.0 (24.)
Poromitra crassiceps	Melamphaidae	5	321–3	zplv3 – meso	nm	700	12.7 ± 0.5	−19.1 ± 0.8	113 ± 6	0.0 (77.)	0.8 (29.)
		6	327–3				12.9 ± 1.0	−19.6 ± 0.3	113 ± 5		
Alepisaurus ferox	Alepisauridae	1[‡]	321–dc	mnkv – meso	pm	500	8.3	−17.0	720	0.0 (177.)	0.0 (120.)
Scopelarchus analis	Scopelarchidae	6	321–3	mnkv – meso	nm	650	10.6 ± 0.5	−19.5 ± 0.3	92 ± 2	0.0 (70.)	0.3 (47.)
		3	327–3				12.3 ± 0.3	−19.3 ± 0.1	105 ± 7		
Diretmus argenteus	Diretmidae	3	327–3	zplv1 – meso	nm	600	10.7 ± 0.6	−19.6 ± 0.1	57 ± 4	0.8 (24.)	3.0 (12.)
Cnidarians			**LO**								
Atolla wyvillei	Atollidae	1	306–2	cnid			11.1	−17.7			
Atolla wyvillei	Atollidae	1	306–3	cnid			11.7	−19.6			
Periphylla periphylla	Periphyllidae	1	306–3	cnid			12.2	−17.6			
Cnidarians			**EQ**								
Atolla wyvillei	Atollidae	3	324–3	cnid			9.2 ± 1.7	−18.2 ± 0.1			
Cephalopods			**LO**								
Bathyteuthis abyssicola	Bathyteuthidae	6	311–3	ceph	pm	800	9.8 ± 0.5	−20.5 ± 0.2	38 ± 6		
Helicocranchia pfefferi	Cranchiidae	6	315–1	ceph	nm	150	9.4 ± 1.0	−20.3 ± 0.4	31 ± 3		
Liocranchia reinhardti	Cranchiidae	3	315–1	ceph	nm	100	9.2 ± 1.1	−19.2 ± 0.2	60 ± 10		
Octopoteuthis sicula	Octopoteuthidae	2	306–3	ceph	nm	1000	14.1 ± 1.0	−19.9 ± 0.7	107 ± 47		
Cephalopods			**EQ**								
Bathyteuthis abyssicola	Bathyteuthidae	6	327–2 333–2	ceph	pm	800	10.8 ± 0.2	−20.3 ± 0.2	40 ± 7		
Helicocranchia pfefferi	Cranchiidae	6	333–2	ceph	nm	150	10.3 ± 0.9	−20.1 ± 0.2	39 ± 4		
Liocranchia reinhardti	Cranchiidae	3	327–1	ceph	nm	100	7.8 ± 0.3	−19.8 ± 0.1	42 ± 2		
Octopoteuthis sicula	Octopoteuthidae	2	327–2	ceph	nm	1000	13.5	−20.5	184		
			333–2				14.5	−19.4	116		
Crustaceans			**LO**								
Decapoda sp.1		4	315–2	crus			8.3 ± 0.2	−18.5 ± 0.2			
Decapoda sp.2		1	309–1	crus			10.9	−18.6			
Crustaceans			**EQ**								
Decapoda		4	324–3	crus			11.5 ± 0.10	−18.4 ± 0.4			
Primary consumers			**LO**								
Appendicularia		7	306–0 309–0 311–0 315–0	herb			7.4 ± 0.6				
Salpidae gen. sp.1	Salpidae	1	306–1	herb			8.2	−20.8			
Salpidae gen. sp.2	Salpidae	1[‡]	306–1	herb			8.2	−17.2			

(*continued on next page*)

Table 3 (*continued*)

Species	Family	*n*	Station - Tow	Feeding – Migrator guild	Migrator guild	Mdo night	$\delta^{15}N$	$\delta^{13}C$	SL	% Abund (Rank)	% BM (Rank)
Primary consumers			**EQ**								
Appendicularia		4	321–0 324–0	herb			3.9 ± 0.6				
Appendicularia		5	327–0 333–0				5.1 ± 0.5				
Pyrosoma atlanticum	Pyrosomatidae	7	333–0	herb			6.3 ± 0.2	−22.1 ± 0.1 (4)			
Salpidae gen. sp.	Salpidae	3	327–0 333–0	herb			6.2 ± 0.8	−21.3 (1)			

Taxonomic species name and family, *n* = number of specimens analysed for SIA, Station - Tow = Station and tow (cf. Table 1; 0 = 0–50 m (Multinet), dc = deck catch), Feeding – Migrator guild = Feeding guild and migration pattern based on literature references (cf. Table 2), Migrator guild = migration pattern based on literature references (am = asynchronous migrator, dm = diurnal migrator, lm = limited migrator, nm = nonmigrator; cf. Table 4), Mdo night = mean depth of occurrence at night based on literature references (cf. Table 4), $\delta^{15}N/\delta^{13}C$ = Mean delta isotopic value ± standard deviation, SL = Standard length body size, % Abund/BM (Rank) = Relative abundance/biomass (ranked) – all stations from both regions combined. ** characterized as omnivorous in the literature, cf. subsection 2.3; *characterised as zplv2 – epi by Hopkins et al. (1996), cf. subsection 2.3; † literature value > 1500 m, cf. subsection 2.3; ‡ was excluded in the analysis cf. subsection 2.4. Primary consumer $\delta^{13}C$ values measured solely in frozen specimens, numbers given in parentheses.

(pm/nm) fishes exhibited comparable $\delta^{13}C$ values (EQ-dm: −19.1 ± 0.5‰, EQ-pm/nm: −19.1 ± 0.6‰ (mean ± SD), $p = .68$; LO-dm: −19.2 ± 0.6‰, LO-pm/nm: −19.3 ± 0.7‰ (mean ± SD), $p = .30$). Between the two regions, $\delta^{13}C$ values differed significantly in partial/nonmigrators (Welch's *t*-test, $p = .04$), but not in migrators (Welch's *t*-test, $p = .45$).

3.2.2. Isotopic niche structure

An analysis of quantitative Layman metrics (excluding *Searsia koefoedi* (family Platytroctidae), cf. subsection 2.4) demonstrated significant regional differences in the isotopic niche structure of the whole fish assemblage (Fig. 4a and b). The range in $\delta^{15}N$ values was significantly larger (Bayesian probability (Bay.pr.) = .99), whereas the range in $\delta^{13}C$ values was smaller in the EQ compared to the LO (Bay.pr. = .89). The other Layman metrics were smaller in the LO compared to the EQ, significantly in the case of nearest neighbour difference (NND, Bay. pr. = .95; SDNND, Bay.pr. = .92; TA, Bay.pr. = .84; CD, Bay.pr. = .87). Further significant regional differences existed in the size of the maximum likelihood standard ellipse of four Feeding – Migrator guilds (Table 6). Comparatively larger sizes, significant for three Feeding – Migrator guilds, existed in the EQ for epi- and mesopelagic copepod feeders (zplv1 – epi: Bay.pr. = .90; zplv1 – meso: Bay.pr. = .97), epi- and mesopelagic mixed crustacean feeders (zplv2 – epi: Bay.pr. = .95; zplv2 – meso: Bay.pr. = .89) and mesopelagic micronektonivores (mnkv – meso: Bay.pr. = .99). Contrary, the standard ellipse of cephalopods was significantly smaller in the EQ (Bay.pr. = .95). The ellipse sizes of mesopelagic non-crustacean feeders (zplv3 – meso) and the piscivore stomiid *Chauliodus* sp. (pisc – meso) were comparable between the two regions.

3.2.2.1. Equatorial region (EQ).

In the EQ, epipelagic copepod feeders (zplv1 – epi) and the cephalopod *Liocranchia reinhardti* (family Cranchiidae) measured the lowest $\delta^{15}N$ values, while the non-crustacean feeding melamphaids (zplv3 – meso, *Poromitra crassiceps* and *Melamphaes polylepis*) and the cephalopod *Octopoteuthis sicula* (family Octopoteuthidae) had the highest $\delta^{15}N$ values (Fig. 4a, Table 3). Epipelagic copepod feeders were clearly separated in niche space from mesopelagic copepod feeders (zplv1 – meso), as well as from all other Feeding – Migrator guilds (Table 6). In both regions, epipelagic (zplv2 – epi) and mesopelagic mixed crustacean feeders (zplv2 – meso) were separated not in $\delta^{15}N$, but in $\delta^{13}C$ niche space; the latter guild occupying more positive $\delta^{13}C$ values. Epipelagic mixed crustacean feeders (zplv2 – epi) further largely overlapped with mesopelagic copepod feeders (zplv1 – meso), mesopelagic micronektonivores (mnkv – meso) and the piscivore stomiid (pisc – meso) *Chauliodus* sp. Compared to the mesopelagic micronektonivore (mnkv – meso) *Scopelarchus analis* (family Scopelarchidae), which constituted the bulk of samples of the mnkv – meso guild in the EQ, $\delta^{15}N$ values of the piscivore (pisc – meso) *Chauliodus schmidti/sloani* were lower. The four cephalopod species occupied the whole range of $\delta^{15}N$ values of the fish assemblage and displayed the most negative $\delta^{13}C$ values, with little niche overlap.

3.2.2.2. Low-oxygen region (LO).

In the LO, the omnivore myctophid *Ceratoscopelus warmingii* (zplv1 – epi) and the non-crustacean feeder (zplv3 – meso) *Bathylagoides argyrogaster* (family Bathylagidae) had the lowest values for $\delta^{15}N$, while the highest $\delta^{15}N$ values were exhibited by the mesopelagic copepod feeder (zplv1 – meso) *Searsia koefoedi* (family Platytroctidae) and the cephalopod *Octopoteuthis sicula* (family Octopoteuthidae; Table 3). Several Feeding – Migrator guilds occupied different isotopic niches in the LO compared to the EQ (Fig. 4, between the EQ and LO). Epipelagic copepod feeders (zplv1 – epi) were less well separated in $\delta^{15}N$ niche space from mesopelagic copepod feeders (zplv1 – meso). Contrary to the EQ, epipelagic copepod feeders (zplv1 – epi) overlapped in niche with several other Feeding – Migrator guilds, namely mesopelagic copepod feeders (zplv1 – meso), epipelagic mixed crustacean feeders (zplv2 – epi), mesopelagic non-crustacean feeders

Table 4
Literature references for feeding guild, migratory type and depth range for each species listed in Table 3 and core depth ranges for night- and day-time occurrence.

Species	Feeding guild Reference	Depth range/Migratory type Reference	Night-time (Core) Depth Range (m)	Day-time (Core) Depth Range (m)
Fishes				
Alepisaurus ferox	Post (1984a)	Fedorov et al. (2003)	0 - >1000	0 - >1000
Argyropelecus affinis	Kinzer and Schulz (1988); cf. *A. aculeatus* in Hopkins et al. (1996)	Badcock (1984c); Bailey and Robison (1986); Kinzer and Schulz (1988); Olivar et al. (2017)	300–600	500–600
Argyropelecus sladeni	Kinzer and Schulz (1988); cf. *A. aculeatus* in Hopkins et al. (1996)	Kinzer and Schulz (1988); Bailey and Robison (1986); Olivar et al. (2017)	200–300	300–400
Astronesthes richardsoni	Hopkins et al. (1996); Sutton and Hopkins (1996a,b)	Coad and Reist (2004); cf. subfamily information in Gibbs (1984a)	0 - >500	>500
Bathylagoides argyrogaster	Cohen (1984b)	Kobylyanskiy (1985)	200–300	200–300
Ceratoscopelus warmingii	Appelbaum (1982); Robison (1984); Kinzer and Schulz (1985); Duka (1987); Hopkins et al. (1996); Takagi et al. (2009)	Nafpaktitis et al. (1977); Hulley (1984)	75–100	550–750
Chauliodus schmidti	cf. *Chauliodus sloani*	cf. *Chauliodus sloani*	0 - >1000	>1000
Chauliodus sloani	Borodulina (1971); Appelbaum (1982); Roe and Badcock (1984); Sutton and Hopkins (1996a,b)	Gibbs (1984b)	0 - >1000	>1000
Diaphus dumerilii	Kinzer and Schulz (1985); De Alwis and Gjøsaeter, 1988; Hopkins et al. (1996); S. Czudaj, unpublished data	Nafpaktitis et al. (1977)	0–125	450–500
Diaphus vanhoeffeni	Tkach (1987a,b)	Nafpaktitis et al. (1977)	40–125	275–750
Diretmus argenteus	Post (1984b)	Post (1984b)	500–700	500–700
Electrona risso	Podrazhanskaya (1993)	Nafpaktitis et al. (1977)	90–550	225–750
Flagellostomias boureei	cf. subfamily information in Gibbs (1984c)	cf. subfamily information in Gibbs (1984c)	0 - >500	>500
Gigantura chuni	Johnson and Bertelsen (1991); Hopkins et al. (1996)	Johnson and Bertelsen (1991)	500–1300	500–1300
Gonostoma denudatum	cf. *G. atlanticum*, Badcock (1984a)	Badcock (1984a)	100–200	400–700
Heterophotus ophistoma	cf. subfamily information in Gibbs (1984a)	Gibbs (1990)	0 - >500	>500
Hygophum macrochir	Hopkins et al. (1996); unpublished data	Nafpaktitis et al. (1977)	0–125	275–750
Hygophum taaningi	Appelbaum (1982)	Nafpaktitis et al. (1977)	0–250	450–1000
Kali macrodon	cf. family information in Johnson and Keene (1984)	Johnson and Keene (1984)	>1500	>1500
Lepidophanes guentheri	Kinzer and Schulz (1985); Hopkins et al. (1996)	Nafpaktitis et al. (1977)	50–125	425–750
Lestidiops jayakari	Post (1984c); Hopkins et al. (1996)	Post (1984c)	300–600	300–600
Magnisudis atlantica	Post (1984c); Hopkins et al. (1996)	Post (1984c)	500–1000	500–1000
Melamphaes polylepis	cf. family information in Hopkins et al. (1996)	Ebeling (1962)	300–2250	300–2250
Microstoma microstoma	Cohen (1984a); cf. family information in Hopkins et al. (1996)	Cohen (1984a)	200 - 1000	<1000
Nannobrachium atrum	cf. *N. lineatum* in Hopkins et al. (1996)	Nafpaktitis et al. (1977)	100–150	550–850
Nannobrachium isaacsi	cf. *N. lineatum* in Hopkins et al. (1996); S. Czudaj unpublished data	Nafpaktitis et al. (1977)	100	550–750
Nannobrachium lineatum	Hopkins et al. (1996)	Nafpaktitis et al. (1977)	100	650–1150
Notoscopelus resplendens	Hopkins et al. (1996); S. Czudaj unpublished data	Nafpaktitis et al. (1977)	0–125	600–800
Poromitra crassiceps	cf. *P. gibbsi* in Hopkins et al. (1996)	Bailey and Robison (1986); Kotlyar (2008)	600–800	600–800
Pseudoscopelus altipinnis	Hopkins et al. (1996)	Hulley (1981); Johnson and Keene (1984)	50–1870	50–1870
Scopelarchus analis	Johnson (1984); Hopkins et al. (1996)	Johnson (1984)	500–820	500–820
Scopelogadus mizolepis	Ebeling and Weed (1963); Hopkins et al. (1996)	Ebeling and Weed (1963)	>500	>500
Searsia koefoedi	Quéro et al. (1984); Hopkins et al. (1996)	Quéro et al. (1984)	500–600	450–1500
Sigmops elongatus	Appelbaum (1982); Badcock (1984a); Lancraft et al. (1988); Hopkins et al. (1996);	Quéro et al. (1990)	50–400	500–1200
Vinciguerria nimbaria	Tkach and Shevchenko (1988); Shevchenko (1987); Shevchenko (1995); Hopkins et al. (1996); N'goran and Pagano (1999); S. Czudaj unpublished data	Badcock (1984b)	0–100	200–400
Cephalopods				
Bathyteuthis abyssicola		Clarke and Lu (1975); Lu and Clarke (1975); Roper and Jereb (2010c)	700–2000	700–2000
Helicocranchia pfefferi		Roper and Jereb (2010a)	0–1000	0–1000
Liocranchia reinhardti		Reid et al. (1991); Arkhipkin (1996); Roper and Jereb (2010a)	0–1200	0–1200
Octopoteuthis sicula		Roper and Jereb (2010b)	200–2000	200–2000

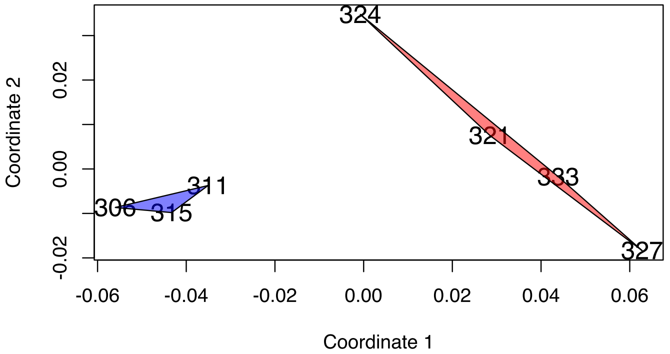

Fig. 2. Station grouping obtained by Principal Coordinate Analysis (PCoA). The distance matrix was based on Euclidean distances. Station grouping was performed using k-means clustering. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

(zplv3 – meso) and the piscivore stomiid *Chauliodus schmidti* (pisc – meso; Table 6). Only in the LO, the omnivore myctophid *C. warmingii* (zplv1 – epi), the myctophid *Diaphus vanhoeffeni* (zplv1 – epi; not sampled in the EQ) and the melamphaids *Melamphaes polylepis* and *Scopelogadus mizolepis* (zplv3 – meso) showed overlap in niche with the cephalopods *Helicocranchia pfefferi* (family Cranchiidae) and *Bathyteuthis abyssicola (family Bathyteuthidae)*. The cephalopod *Liocranchia reinhardti* (family Cranchiidae) exhibited comparatively higher δ^{15}N and more positive δ^{13}C values in the LO. Here, complete overlap existed between mesopelagic mixed crustacean feeders (zplv2 – meso) and mesopelagic micronektonivores (mnkv – meso). Mesopelagic micronektonivores (mnkv – meso) exhibited lower δ^{15}N and more positive δ^{13}C values compared to the EQ, thereby being clearly separated in niche space from the piscivore (pisc – meso) *C. schmidti*. The two coronate scyphozoans analysed, *Periphylla periphylla* and *Atolla wyvillei,* measured comparatively higher δ^{15}N values in the LO compared to the EQ, as well as compared to other Feeding - Migrator guilds. These values were supported by data from the eastern part of the LO (*A. wyvillei*: $n = 3$; lat. 10.8°N, long. −23.9°W, δ^{15}N: 10.3 ± 0.2‰, δ^{13}C: −18.6 ± 0.2‰; *P. periphylla*: $n = 1$; δ^{15}N: 10.5‰, δ^{13}C: −16.7‰). In both regions, decapod crustaceans had relatively positive δ^{13}C values and exhibited comparatively low and high δ^{15}N values.

3.2.3. Relationship of δ^{15}N and δ^{13}C isotope values of migratory and partial/nonmigratory fishes with increasing mean depth of occurrence at night (mdo) and standard length body size (SL)

3.2.3.1. δ^{15}N values. Model results from the ANCOVA with δ^{15}N as response variable, two continuous covariates (mdo and SL), and two categorical covariates (region and migratory type) were highly significant and showed a reasonable fit (Fig. 5a and b; Table 7). Because the four-way interaction term was nearly significant in the maximum model ($p = .05$), we retained it in the optimised model. The 95% confidence intervals showed higher predictive capabilities for the EQ than for the LO. This was further expressed in the regional model, which was highly significant in the EQ and showed a good fit (not shown; Adj. $R^2 = .67$, $F_{(5,\ 105)} = 45.3$, $p < .001$). Contrary, the regional model of the LO was insignificant and poorly fitted (not shown; Adj. $R^2 = .02$, $F_{(3,\ 100)} = 1.9$, $p = .14$). The models predicted that in diurnal migrators of both regions, neither the relationship of δ^{15}N values with increasing mdo, nor with the interaction of body size and mdo were significant. In diurnal migrators of the EQ, δ^{15}N values increased with increasing body sizes; being significantly different from diurnal migrators of the LO, which did not exhibit a significant relationship of δ^{15}N values with increasing body sizes. Partial/nonmigrators of the EQ showed a significantly positive relationship of δ^{15}N values with the interaction of increasing mdo and increasing body sizes. The regional model of the EQ pointed out that this response became effective in species with an mdo larger than ~550 m. Contrary, partial/nonmigrators of the LO did not exhibit a significant relationship of δ^{15}N values with neither increasing mdo, increasing body size nor their interaction.

3.2.3.2. δ^{13}C values. The ANCOVA model with δ^{13}C as response variable, two continuous covariates (mdo and SL) and two categorical covariates (region and migratory type) was highly significant, but comparatively less well fitted (Fig. 6a and b; Table 8). The 95% confidence bands indicated similar performance in the EQ and the LO, which was confirmed by the regional models (not shown; EQ: Adj. $R^2 = .30$, $F_{(3,\ 107)} = 16.8$, $p < .001$; LO: Adj. $R^2 = .36$, $F_{(4,\ 102)} = 15.8$, $p < .001$). In diurnal migrators of the EQ, δ^{13}C values were not significantly related to neither increasing mdo, increasing body size nor the interaction of both. The models showed that in partial/nonmigratory fishes of the EQ, δ^{13}C values were significantly declining with increasing mdo. However, it has to be noted, that in the LO, the three species occurring deeper than 750 m were highly influential in levelling the slope of δ^{13}C values with increasing mdo in partial/nonmigratory fishes. In the EQ, δ^{13}C values of partial/nonmigrators were not significantly related to body size. Contrary, in both migratory groups of the LO there was a significant relationship of δ^{13}C values with the interaction of increasing mdo and increasing body sizes.

4. Discussion

4.1. Regional differences in micronekton food web structure between the EQ and the LO

Based on the concept of the ‘classical’ food web (phytoplankton – mesozooplankton – fish; e.g. Landry and Décima, 2017), the isotopic δ^{15}N difference of 3.5‰ between pelagic tunicates or herbivorous copepods (Olivar et al., 2018; assumed trophic level (TL) 2) and epipelagic copepod feeders (zplv1-epi; assumed TL3) as observed here for the equatorial region (EQ), matches the commonly used mean value of 3.4‰ increase per TL (Post, 2002; Hussey et al., 2014; Pakhomov et al., 2019). However, the food web base of the EQ is the ‘alternate’ microbial food web (heterotrophic nanoflagellates – ciliated protozoa – mesozooplankton – fish; Marañón et al., 2001; Landry and Décima, 2017), which is likely interconnected to the ‘classical’ food web prevalent in the productive low-oxygen region (LO; Stoecker and Capuzzo, 1990; López-Urrutia et al., 2004; Landry and Décima, 2017). For example, pelagic tunicates are qualitatively, as well as quantitatively, important prey for a wide range of zooplankton species (copepods, heteropod molluscs, medusae, siphonophores, ctenophores, chaetognaths, fish larvae; Alldredge and Madin, 1982; López-Urrutia et al., 2004; Purcell et al., 2004; Hays et al., 2018), but also for mesopelagic fishes (Kinzer and Schulz, 1985; Tkach, 1987a,b; Bernal et al., 2015; McClain-Counts et al., 2017; Olivar et al., 2018). Therefore, longer food chains with intermediate trophic links can be expected in the EQ that would result in TLs of 3–5 in zooplanktivorous fishes and 4–6 in micronektonivores (Sommer et al., 2002). Yet, since the enrichment in microzooplankton is unknown (Sommer et al., 2002; Landry and Décima, 2017), this longer food web is generally not reflected in TL estimates based on stable isotope analysis that report TLs of ~2–4 in mesopelagic fishes of the families Myctophidae and Stomiidae (Choy et al., 2012; Olivar et al.,

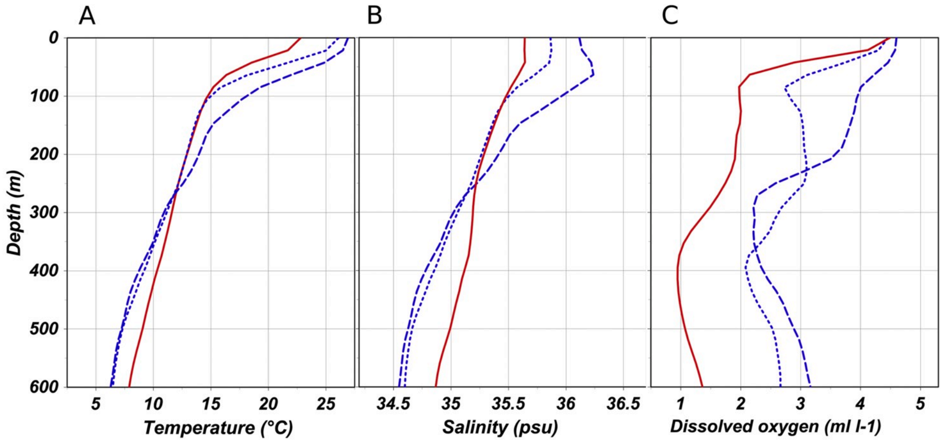

Fig. 3. Moving average of a) temperature, b) salinity and c) dissolved oxygen concentration for the LO (stations 306, 311, 315; red solid line) and the EQ (stations 321/324 (blue dotted line) and 327/333 (blue dashed line)). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

2018). In fishes of TL3 and TL4 that consume protein-rich prey with amino acid profiles that match their own, isotopic δ^{15}N enrichment is reduced compared to fishes at trophic levels between TL2 and TL3 (Hussey et al., 2014; McMahon et al., 2015). This could be one explanation of the smaller isotopic δ^{15}N difference between mesopelagic micronektonivores (mnkv – meso; TL 4) and their presumed prey species of the zplv1 – epi guild (TL3) that was observed in this study and elsewhere (e.g. Choy et al., 2012; Wang et al., 2019). Low metabolic rates and slower protein turnover could be additional factors contributing to this low isotopic δ^{15}N enrichment as discussed by Choy et al. (2012). Non-daily feeding that is expressed by adult specimens (>120 mm) of the asynchronously migrating stomiid *Chauliodus* sp. (Borodulina, 1971; Sutton and Hopkins, 1996b) might be responsible for the even lower (EQ) or non-existent (LO) isotopic δ^{15}N enrichment observed in this species in our study.

We expected comparatively increased trophic competition and altered feeding preferences in migratory species of the LO due to migratory species residing in shallower waters during the day-time in the LO compared to the EQ. Our results provide evidence to support this hypothesis. Enhanced competition in niche space in the LO was suggested by smaller values for the Layman metrics CD and NND, that are proxies for the density and packing of species in the community. A comparatively narrower food spectrum exploited in this region by the Feeding – Migrator guilds epi- and mesopelagic copepod feeders (zplv1 – epi/meso), epi- and mesopelagic mixed crustacean feeders (zplv2 – epi/meso) and mesopelagic micronektonivores (mnkv – meso) was indicated

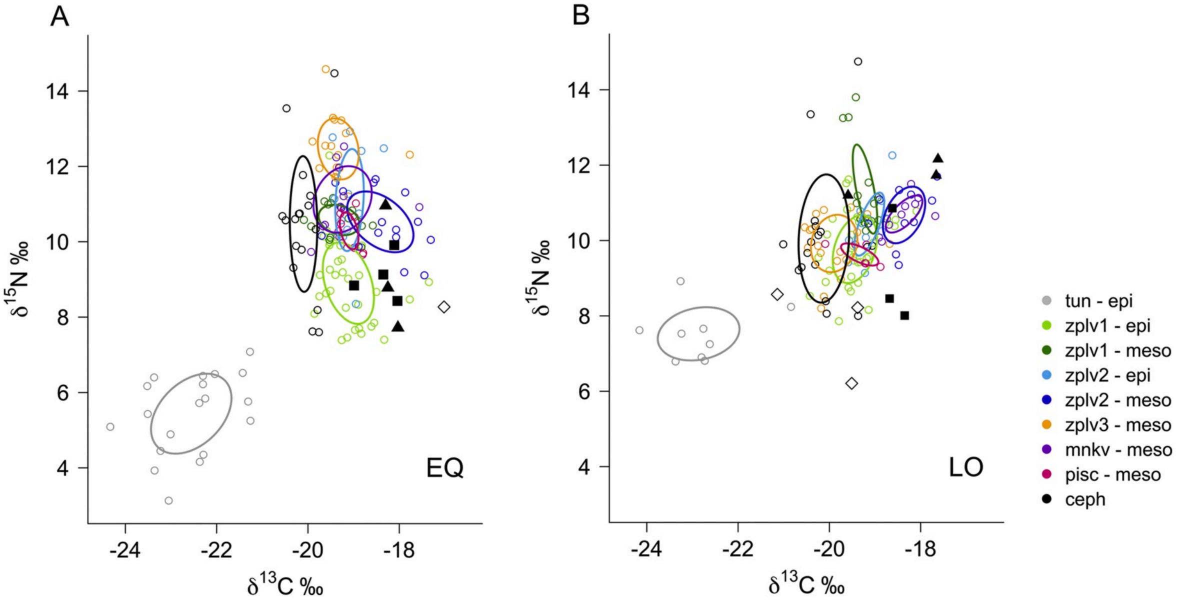

Fig. 4. Variation in isotope data for pelagic tunicates (tun – epi), the different Feeding – Migrator guilds (for a characterisation cf. Table 2) and cephalopods (ceph) with their respective small sample-size corrected maximum likelihood standard ellipses containing approximately 40% of the data (SEAc). a) EQ (n = 137), b) LO (n = 128). Solid triangles denote cnidarians (EQ: n = 3; LO: n = 3), solid squares denote decapod crustaceans (EQ: n = 4; LO: n = 5). Open diamonds denote excluded values. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

Table 5

δ^{15}N and δ^{13}C values (mean ± SD, significance (*p*-value); Welch's *t*-test) for each Feeding – Migrator guild (cf. Table 2) by region (EQ/LO).

Feeding – Migrator guild	δ^{15}N [‰] (mean ± SD)		*p*-value	δ^{13}C [‰] (mean ± SD)		*p*-value
	EQ	LO		EQ	LO	
pelagic tunicates (tun – epi)	5.4 ± 1.1	7.4 ± 0.7	**< .001**	−21.9 ± 0.5	−20.8	**n.a.**
zplv1 – epi	8.9 ± 1.1	9.6 ± 0.9	**.009**	−19.1 ± 0.6	−19.6 ± 0.3	**< .001**
zplv1 – meso	10.6 ± 0.4	10.8 ± 0.5	**.43**	−19.3 ± 0.5	−19.2 ± 0.1	**.27**
zplv2 – epi	11.1 ± 1.4	10.4 ± 0.8	**.17**	−19.1 ± 0.3	−19.1 ± 0.3	**.79**
zplv2 – meso	10.5 ± 0.8	10.7 ± 0.8	**.64**	−18.4 ± 0.7	−18.4 ± 0.5	**.83**
zplv3 – meso	12.5 ± 0.8	9.9 ± 0.8	**< .001**	−19.3 ± 0.5	−19.9 ± 0.5	**.001**
mnkv – meso	11.1 ± 0.9	10.8 ± 0.5	**.31**	−19.2 ± 0.6	−18.3 ± 0.4	**.001**
pisc – meso	10.3 ± 0.5	9.6 ± 0.3	**.003**	−19.1 ± 0.2	−19.3 ± 0.4	**.23**
cephalopods	10.5 ± 1.8	10.1 ± 1.7	**.49**	−20.1 ± 0.3	−20.1 ± 0.6	**.88**

by comparatively smaller standard ellipses and values for SDNND (measure of evenness of the distribution) in the LO. In addition, increased importance of low-trophic level non-crustacean invertebrate and/or gelatinous resources in the LO compared to the EQ was suggested by organisms occupying a niche space with negative carbon values. These organisms were mesopelagic non-crustacean consumers (zplv3 – meso; family Melamphaidae and Bathylagidae), the omnivore myctophid *C. warmingii* (zplv1 – epi) and the epipelagic copepod feeder *Diaphus vanhoeffeni* (reportedly appendicularians may constitute a dominant part of the diet of these two myctophids, Table 4) and the cephalopods *Bathyteuthis abyssicola* (family Bathyteuthidae) and *Helicocranchia pfefferi* (family Cranchidae) for which no diet data are available (Fig. 4, between the EQ and LO). With respect to melamphaids, it has to be noted that the change in isotopic niche between the two regions could also be due to species-specific differences in feeding ecology between *Poromitra crassiceps* sampled in the EQ *versus Scopelogadus mizolepis* sampled in the LO. However, the melamphaid *Melamphaes polylepis* that was sampled in both regions also displayed regional differences in its niche. In the EQ, diurnally migrating copepod feeders (zlpv1 – epi) could be clearly distinguished from partially or nonmigrating copepod feeders (zplv1 – meso) in δ^{15}N space, thereby showing indirect evidence for the differences in food web baseline δ^{15}N values between epipelagic and deeper waters (Choy et al., 2015; Romero-Romero et al., 2019). In the LO, more overlap in scatter points

Table 6

Comparison of sample-size corrected standard ellipse area (SEAc) size between the EQ and LO and the overlap between each pair of Feeding – Migrator guild (cf. Table 2) for each region.

EQ \ LO	zplv1 – epi (1.3)	zplv1 – meso (0.8)	zplv2 – epi (0.7)	zplv2 – meso (1.1)	zplv3 – meso (1.3)	mnkv – meso (0.5)	pisc – meso (0.4)	cephalopods (3.1)
zplv1 – epi (1.8)	0.90	0.2	0	0	0.3	0	0.2	0.1
zplv1 – meso (0.6)	0	0.97	0.3	0	0	0	0	0
zplv2 – epi (1.4)	0	0.4	0.94	0	0	0	0.1	0
zplv2 – meso (1.8)	0	0.1	0.3	0.89	0	0.5	0	0
zplv3 – meso (1.2)	0	0	0.3	0	0.43	0	0.1	1.1
mnkv – meso (2.0)	0	0.6	1.0	0.4	0.2	0.99	0	0
pisc – meso (0.3)	0	0.2	0.3	0.1	0	0.2	0.44	0.1
cephalopods (1.8)	0	0	0	0	0	0.1	0	0.05

The regional SEAc size (maximum likelihood fitted standard ellipses) of each Feeding - Migrator guild is given in parentheses. The dark shaded diagonal row states the Bayesian probability that the size of the SEAc of the Feeding - Migrator guild in the EQ (left column) is larger than that of the respective Feeding Migrator guild in the LO (top line). The overlap of the SEAc is the proportion of the non-overlapping area of the two ellipses to be compared in one region (EQ: left lower corner, shaded; LO: right upper corner, unshaded). The platytroctid *Searsia koefoedi* (zplv1 – meso) was excluded from this comparison (cf. subsection 2.4).

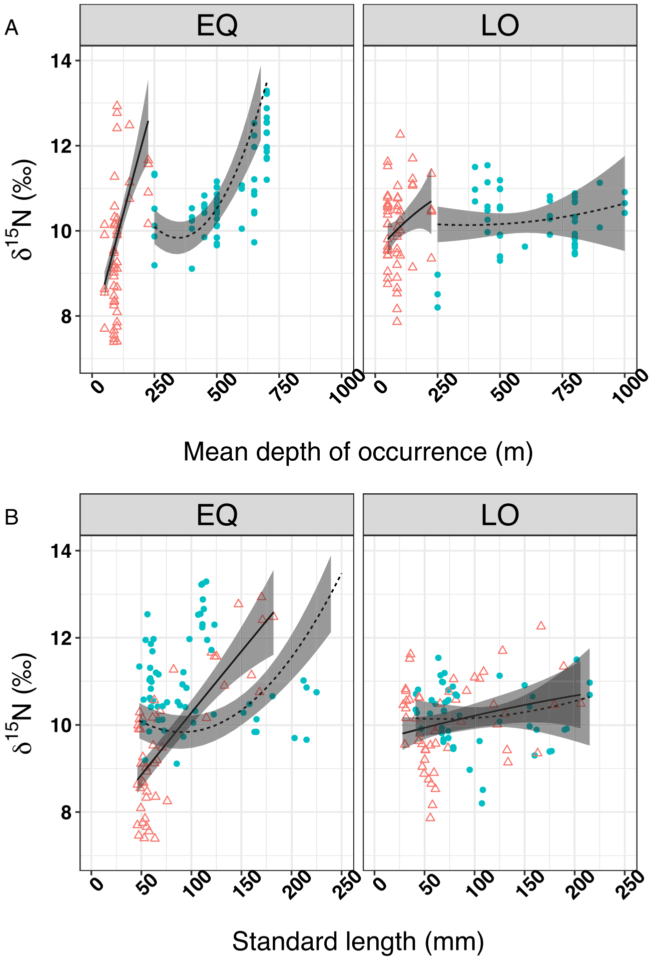

Fig. 5. Relationship between δ^{15}N values of migrating (dm, open triangles) and partially/nonmigrating (nm, solid circles) fishes and a) mean depth of occurrence at night (m) or b) standard length body size (mm) in the EQ and LO. Superimposed are the linear regression fits for migrators (solid) and partial/ nonmigrators (dashed) and the corresponding 95% confidence intervals. (For a colour version of this figure, the reader is referred to the Web version of this article.)

Table 7
Results of ANCOVA with region (reg, EQ/LO) and migration type (migr, dm/nm) as covariate comparing δ^{15}N composition of fishes correcting for mdo and SL.

coefficients	Estimate	Std. Error	Type III Sum Sq.	Df	*t*-value	*p*-value
(Intercept)	7.411	0.292	442.3	1	25.4	< .001
regLO	2.212	0.436	17.7	1	5.1	< .001
migrnm	3.608	0.384	60.7	1	9.4	< .001
SL	0.029	0.006	15.2	1	4.7	< .001
regLO:migrnm	−2.988	0.570	18.9	1	−5.2	< .001
migrnm:SL	−0.064	0.008	44.1	1	−8.0	< .001
regLO:migrdm:SL	−0.023	0.009	22.6	2	−2.4	.017
regLO:migrnm:SL	0.032	0.006			5.2	< .001
regEQ: migrdm:SL:mdo	−0.000	0.000	37.7	4	−0.1	.93
regLO: migrdm:SL:mdo	−0.000	0.000			−0.2	.82
regEQ: migrnm:SL:mdo	0.044	0.006			7.3	< .001
regLO: migrnm:SL:mdo	0.000	0.000			1.1	.26
Residuals			139.4	203		

Residual standard error: 0.83 on 203 degrees of freedom. Multiple $R^2 = .54$, Adj. $R^2 = .51$, $F_{(11,\ 203)} = 21.5$, $p < .001$. Excluded influential specimens of the platytroctid *Searsia koefoedi* ($n = 3$), the myctophid *Diaphus dumerilii* ($n = 1$) and the melamphaid *Poromitra crassiceps* ($n = 1$).

between epipelagic (zplv1 – epi) and mesopelagic copepod feeders (zplv1 – meso) suggested increased mixing of shallow and deeper originating food sources between these two guilds, which is in line with observations from the OMZ of the eastern tropical North Pacific (ETNP). Here, a strong increasing depth gradient in zooplankton δ^{15}N values in the lower oxycline below the OMZ core was observed, indicating increased trophic cycling and a change in base food web sources from shallow to deep water particulate organic matter (Williams et al., 2014). The absence of a size-related δ^{15}N increase in migrators of the LO, that was present in the EQ, further hints at differences in resource use in migrators between the LO and EQ. The occurrence of daytime feeding in epipelagic copepod feeders (e.g. Romero-Romero et al., 2019 and references therein) seems to be a more prominent feature in productive upwelling areas, as observed in NW Africa (Kinzer and Schulz, 1985), and might be the driving mechanism of regional depth-related differences in feeding patterns of migrators. Additionally, increased competition, but also predator avoidance reactions due to the more frequent occurrence of small pelagic fish species in continental shelf waters (Modica et al., 2015), as well as in response to gelatinous predators that thrive under low-oxygen conditions could be partially responsible (Choy et al., 2017).

The depth-related increase in δ^{15}N values observed in partial/nonmigratory fishes of the EQ in our study matched previous results from Hawaiian waters that, like our study area in the EQ, is a low-productive oxygenated region (Romero-Romero et al., 2019). The poor and insignificant fit of the same regression model in the LO, resulting from comparable δ^{15}N values downwards from ~400 m, suggests that processes related to productivity and/or low oxygen conditions affected δ^{15}N values of partial/nonmigratory fishes in this region (Fig. 5a). We found comparatively low δ^{15}N values in mesopelagic micronektonivores (mnkv – meso) from the LO which constituted the bulk of the partial/nonmigratory fish group (Table 3). This pattern could be indicative for either, (i) feeding on lower trophic prey components, (ii) feeding on a food web based on shallower origin, (iii) reduced isotopic δ^{15}N enrichment and/or (iv) species-specific differences. The overlap in isotopic niche of mesopelagic micronektonivores (mnkv – meso) with mesopelagic mixed crustacean feeders (zplv2 – meso) in the LO, – the latter occupying a similar niche in both regions, – suggests similar prey consumption of these two guilds in the LO and, thus, supports the first explanation. δ^{15}N values of the few analysed decapod crustaceans match as suitable prey species for mesopelagic mixed crustacean feeders (zplv2 – meso) and mesopelagic micronektonivores (mnkv – meso) in the LO, considering an enrichment of ~3.4‰ in δ^{15}N and ~1.0‰ in δ^{13}C. Further, a secondary zooplankton biomass peak at mesopelagic depths just below the OMZ core was noted in a number of studies of the ETNP and was also observed in zooplankton samples collected during our study (unpublished data; see references in Williams et al., 2014). Deeper

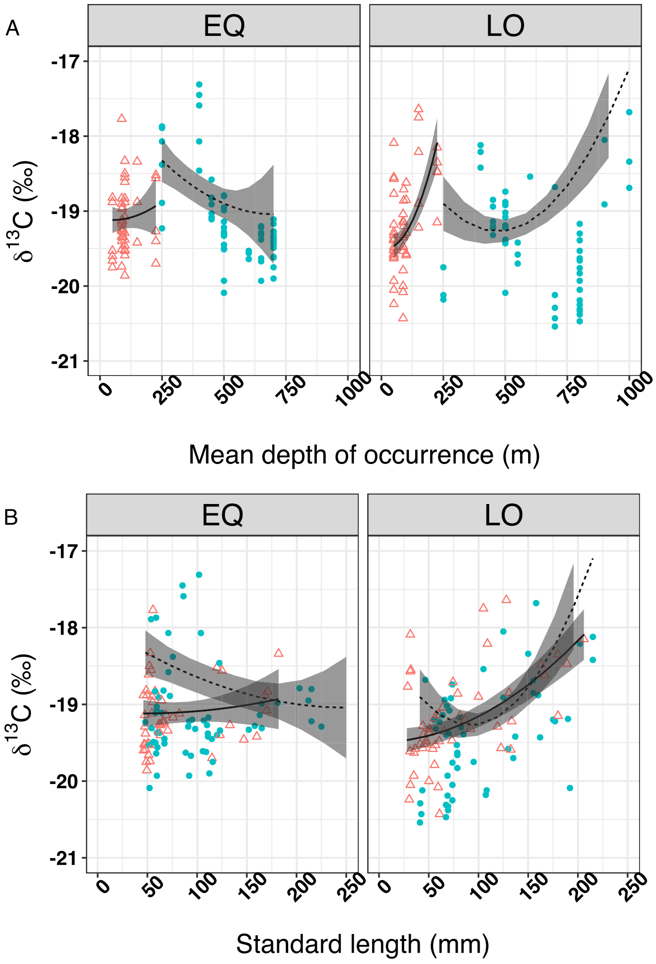

Fig. 6. Relationship between δ^{13}C values of migrating (dm, open triangles) and partially/nonmigrating (nm, solid circles) fishes and a) mean depth of occurrence at night (m) or b) standard length body size (mm) in the EQ and LO. Superimposed are the linear regression fits for migrators (solid) and partial/nonmigrators (dashed) and the corresponding 95% confidence intervals. (For a colour version of this figure, the reader is referred to the Web version of this article.)

Table 8

Results of ANCOVA with region (reg, EQ/LO) and migration type (migr, dm/nm) as covariate comparing δ^{13}C composition of fishes correcting for mdo and SL.

coefficients	Estimate	Std. Error	Type III Sum Sq.	Df	*t*-value	*p*-value
(Intercept)	−19.100	0.136	4738.6	1	−140.0	< .001
regLO	−0.376	0.101	3.4	1	−3.7	< .001
migrnm	1.680	0.364	5.1	1	4.6	< .001
migrdm:mdo	−0.000	0.002	12.4	2	−0.4	.68
migrnm:mdo	−0.004	0.000			−5.2	< .001
regEQ:mdo:SL	0.000	0.000	14.1	2	0.9	.37
regLO:mdo:SL	0.000	0.000			5.5	< .001
regEQ:migrnm: SL	−0.002	0.005	8.2	2	−0.4	.71
regLO: migrnm: SL	−0.013	0.003			−3.9	< .001
Residuals			50.5	209		

Residual standard error: 0.49 on 209 degrees of freedom. Multiple $R^2 = .36$, Adj. $R^2 = .33$. $F_{(8,\ 209)} = 14.5$, $p < .001$. Excluded influential specimens of the myctophid *Lepidophanes guentheri* ($n = 1$) and the melamphaid *P. crassiceps* ($n = 1$).

occurring micronektonivorous fishes (mnkv – meso) of the LO likely take advantage of the increased foraging opportunities on zooplanktivorous prey species that this vertical structuring effect provides. They would thereby access prey with lower δ^{15}N source values than those they would encounter if they fed at greater depths. Moreover, the mesopelagic micronektonivore guild (mnkv – meso) was composed of different species in both regions (Table 3). Although - with the exception of *Heterophotus ophistoma* (family Stomiidae, subfamily Astronesthinae) - all of the here examined families have been characterised as piscivorous in a study conducted in the Gulf of Mexico (Hopkins et al., 1996), they employ different feeding strategies. Compared to the stomiid *Chauliodus* sp., which is a sit-and-wait ambush predator, species of the families Paralepididae, Chiasmodontidae and Scopelarchidae are active hunters (Gartner et al., 1997). The family Giganturidae has been characterized as generalist (Drazen and Sutton, 2017) and *H. ophistoma* was noted to be the only stomiid species feeding on cephalopods (Sutton and Hopkins, 1996a,b). These ecological differences might affect their biochemical body composition and metabolic rates (and thereby isotopic δ^{15}N enrichment as discussed earlier), but also their vertical ecology and prey selection behaviour in response to different physico-chemical conditions.

We could not observe a significant depth effect in δ^{13}C values of migratory or partial/nonmigratory species in both regions. Because species below 750 m significantly influenced the slope of the relationship of δ^{13}C values with increasing mdo in the LO, we did not consider the significantly negative relationship of δ^{13}C values with increasing mdo observed in the EQ as ecologically robust. This result is supported by data from the ETNP (Choy et al., 2015).

A worldwide meta-analysis of SI values in cephalopods summarised the same mean δ^{13}C value of −17.8 ± 1.0‰ for the Atlantic and tropical regions (Navarro et al., 2013). The comparatively negative δ^{13}C values of −20.1 ± 0.4‰ measured in cephalopods in our study suggest feeding on low trophic food web components. Such feeding may be related to the relatively inactive lifestyle, low metabolic rates and reduced locomotory abilities of these species compared to other cephalopods (Seibel et al., 1997). The coronate scyphozoan *Atolla wyvillei* is an active swimmer that avoids minimum oxygen regions, but has been associated with water masses above the OMZ core in Monterey Bay, CA, USA (Osborn et al., 2007). This distribution might be reflected in its high δ^{15}N values in the LO. In Norwegian fjords, *Periphylla periphylla*, another coronate scyphozoan, feeds primarily on calanoid copepods, ostracods and large euphausiids (Fosså, 1992; Sørnes et al., 2008). The single specimen from the LO measured some of the highest δ^{15}N values and the most positive δ^{13}C values in our study. These results indicate that *P. periphylla* feeds at greater depth than the Norwegian population and/or that eastern tropical North Atlantic specimens have a more carnivorous diet (Choy et al., 2017).

4.2. *Methodological constraints*

In this study, stable isotope analysis of surface-sampled (0–50 m) appendicularians, salps and pyrosomes provided the regional baseline δ^{15}N values. These pelagic tunicates are filter-feeders and as primary consumers represent the lowest position in the food web (Alldredge and Madin, 1982). However, because pelagic tunicates selectively consume the smaller heterotrophic size fraction (bacteria, pico- and nanoplankton) from the available particulate organic matter pool, it has been argued that in productive areas, pelagic tunicate isotope values do not reflect the isotope values of larger nano- and microzooplankton that are predominantly exploited by mesozooplankton and fishes (Pakhomov et al., 2019). In the choice of a primary consumer baseline in trophic studies using SIA, it is therefore imperative to consider the underlying phytoplankton community of the ecosystem (Pakhomov et al., 2019). We did not sample the phytoplankton community during the time of our study. However, dedicated studies in the ETNA found the pico- and nanoplankton size class to be generally dominant in biomass in the equatorial, as well as the upwelling influenced region (Marañón et al., 2001). Consequently, an important role of pelagic tunicates in the sampled food webs can be expected (Pakhomov et al., 2019). The validity of using pelagic tunicates as representative primary consumer surrogates in our study is corroborated by data from a study conducted during the same period in the same region as the present study (Olivar et al., 2018). This study reported mean δ^{15}N values of 5.5 and 7.4‰ in herbivorous copepods in regions similar in hydrography as the EQ and LO, respectively (Olivar et al., 2017). These results are very close to our mean estimates of 5.4 and 7.4‰ for pelagic tunicates. Also Martin et al. (2017) stated that thaliaceans are on a similar trophic level as particulate organic matter, although with temporal fluctuations. Based on this, we considered the δ^{15}N values obtained from pelagic tunicates to be appropriate as a baseline reference to enable relative comparison among regions. Our δ^{13}C values of four frozen pyrosomes were similar to δ^{13}C values of −21.8 ± 0.9‰ and −21.9 ± 0.8‰ measured in herbivorous copepods by Olivar et al. (2018) in regions corresponding to the EQ and the LO, respectively, and during the same time.

Due to the large and diverse catches (>190 species) collected under tropical conditions, species identity was largely determined in the lab onshore, therefore samples available were not always ideal comparisons. Consequently, regional differences in the species composition of some of the Feeding – Migrator guilds may have affected the mean position and size of the isotopic niche and influenced our conclusions. Furthermore, the EQ pooled stations from 0°, 2.7° and 4.2°N which were oceanographically more heterogeneous than the LO region (Fig. 2). The comparatively large isotopic niche of the zplv1 – epi guild in the EQ was in part due to inter-station variability between samples from stations at the equator and at 4°N. But also at the same station, relatively large intra-specific variability in δ^{15}N and δ^{13}C values of similarly sized specimens was apparent in some species; signalling due care in the interpretation of the limited sample sizes analysed in this study. Further, the choice of standard ellipse size is a crucial factor influencing the interpretation of the amount of overlap between different guilds. In order to understand the relationship between isotopes and depth of occurrence, reliable data on depth distribution is critical, but this is incomplete for many species, based on few samples and broadly characterised in the literature. Therefore our estimate of mdo at night might not be realistic for some species in our sampling area. Although body size is a rough indicator of ontogenetic stage, additional data on sex and maturity would provide more detailed insights on depth-dependent community-cohort structure and niche occupation (Fanelli et al., 2014; Wang et al., 2019).

5. Conclusions

This study established significant regional differences in the trophic structure of the sampled micronekton assemblages. Our results indicate a more complex potentially microbial food web acting between TL2 and TL4 in the oligotrophic oxygenated equatorial region as compared to a more ‘classic’ food chain in the productive, but low oxygen region. In addition, in micronektonivorous and piscivorous fishes, we found support for lower isotopic enrichment than the generally applied literature value of 3.4‰. We also found evidence for a comparatively increased trophic competition and altered feeding preferences towards lower-trophic components in migratory fishes of the low oxygen region. The absence of a depth-related increase in δ^{15}N values with increasing mean depth of occurrence in partial/nonmigratory fishes of the productive low-oxygen region and comparatively low δ^{15}N values observed in micronektonivores of the low-oxygen region could be due to either, (i) lower-trophic level prey resources, (ii) feeding on base food web sources of shallower origin, (iii) regional differences in isotopic δ^{15}N enrichment and/or (iv) species-specific differences or a combination of the above. Whereas the direct causes of the observed regional differences in trophic structure remain unresolved, the available data are well related to a vertical biogeochemical structuring effect of low oxygen midwater layers fuelled by high nitrate inputs from the Mauritanian upwelling region. Our results support the hypothesis that important spatial variations in the vertical extent and relative quantities of biologically driven biogeochemical fluxes are partially controlled by regional behavioural adaptations of micronekton organisms to their physical-chemical environment that affect their migration depth and thereby trophic interactions (Klevjer et al., 2016).

Author contributions

S. Czudaj, H. Fock, A. Giesemann, H.-J. Hoving and F. Lüskow participated in the research and wrote the paper; R. Koppelmann and C. Möllmann wrote the paper.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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CHAPTER III: Size-based indicators of regional and long-term variability in mesopelagic fish communities of the eastern Atlantic

Article 4 Length-weight relationships of mesopelagic fishes from the eastern tropical North Atlantic: across- and within-species variation (body shape, ontogenetic growth stanza, condition factors)

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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 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; Prellezo & 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; Harrisson, 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; Harrisson, 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

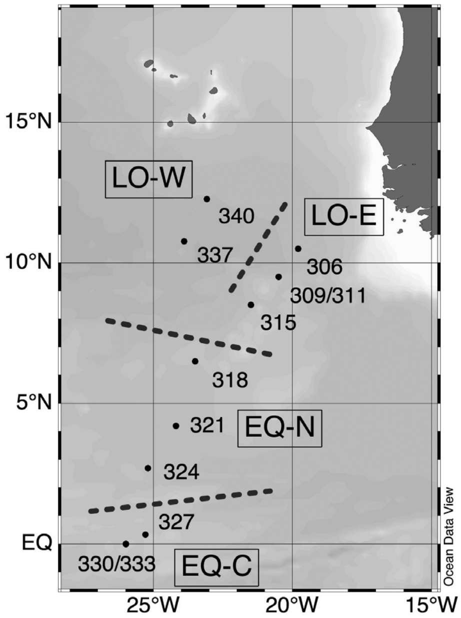

FIGURE 1 Stations in the eastern low-oxygen (LO–E), western low-oxygen (LO–W), northern equatorial (EQ–N) and central equatorial (EQ–C) regions of the eastern tropical North Atlantic sampled in this study

(Steedman, 1976). A minor portion of samples was preserved frozen at −30°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 ≥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_{rel} *vs*. standard length (cm) and an ANCOVA with 'region' as covariate comparing K_{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. $K_{rel} = W/a \times SL^b$ (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_{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	Migr	Body shape	Max SL lit. (cm)	*N*	SL (cm)	TW (g)	log *a* and 95% CI log *a*	*b* and 95% CI *b*	*b* Std. error	*R*^{2}	*P* value allom. growth
Bathylagidae	*Bathylagoides argyrogaster* (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	*Platyberyx opalescens* 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	*Diretmus argenteus* 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	*Diretmoides pauciradiatus* (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	*Diplophos taenia* 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	*Gonostoma denudatum* 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	*Sigmops elongatus* (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	*Zaphotias pedaliotus* (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
Melamphaidae	*Melamphaes polylepis* 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
Melamphaidae	*Melamphaes typhlops* (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
Melamphaidae	*Scopelogadus mizolepis* (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	*Benthosema suborbitale* (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	*Bolinichthys indicus* (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	*Bolinichthys photothorax* (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	*Bolinichthys supralateralis* (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	*Ceratoscopelus warmingii* (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	*Dasyscopelus asper* (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	*Diaphus brachycephalus* Tåning 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	*Diaphus dumerilii* (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	*Diaphus fragilis* Tåning 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	*Diaphus holti* Tåning 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	*Diaphus lucidus* (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	*Diaphus mollis* Tåning 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	*Diaphus perspicillatus* (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	*Diaphus vanhoeffeni* (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	*Electrona risso* (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	*Hygophum macrochir* (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	*Hygophum taaningi* 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	*Lampanyctus ater* Tåning 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	*Lampanyctus isaacsi* 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	*Lampanyctus lineatus* Tåning 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

TABLE 1 (Continued)

Family	Species	Migr	Body shape	Max SL lit. (cm)	*N*	SL (cm)	TW (g)	log *a* and 95% CI log *a*	*b* and 95% CI *b*	*b* Std. error	R^2	*P* value allom. growth
Myctophidae	*Lampanyctus nobilis* Tåning 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	*Lampanyctus tenuiformis* (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	*Lepidophanes guentheri* (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	*Lobianchia dofleini* (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	*Myctophum nitidulum* 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	*Notoscopelus resplendens* (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	*Symbolophorus veranyi* (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	*Cubiceps gracilis* (Lowe 1843)	NA	(fusi)	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
Opisthotroctidae	*Opisthoproctus soleatus* 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	*Lestidiops affinis* (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	*Lestidiops jayakari* (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	*Lestrolepis intermedia* (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	*Ichthyococcus ovatus* (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	*Vinciguerria nimbaria* (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
Platytroctidae	*Searsia koefoedi* 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	*Argyropelecus affinis* 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	*Argyropelecus gigas* 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	*Argyropelecus sladeni* 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	*Polyipnus polli* 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	*Sternoptyx diaphana* 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	*Astronesthes richardsoni* (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	*Chauliodus schmidti* 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	*Chauliodus sloani* 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	*Chauliodus* 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	*Stomias affinis* 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 *a* and 95% CI log *a*, 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^2, coefficient of determination; *P* value allometric growth <0.05 indicates significant departure from isometric growth. Bold font indicates new maximum sizes for a species.

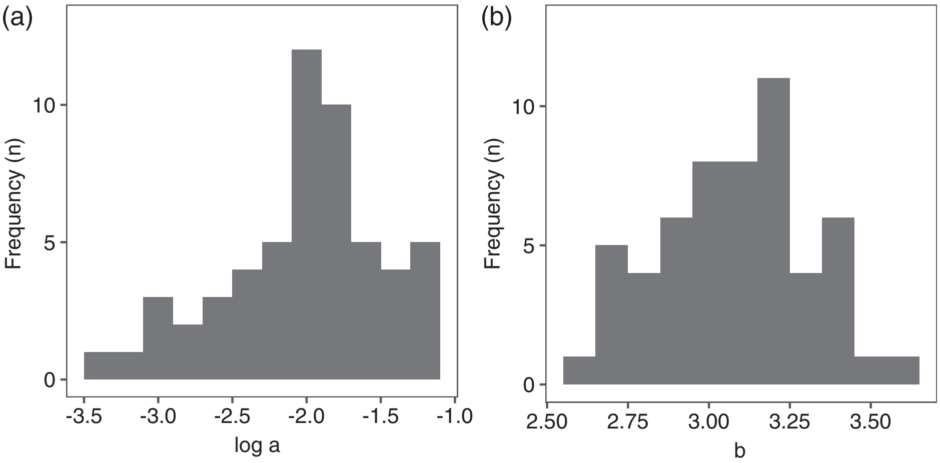

FIGURE 2 Frequency distribution of (a) mean log *a* (binwidth 0.2) and (b) mean exponent *b* (binwidth 0.1) based on 55 records (measured in centimetres and grams) of mesopelagic species of the eastern tropical North Atlantic during cruise WH383

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_{rm}) 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: *Argyropelecus 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* Tåning 1928, *Lampanyctus isaacsi* 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 melamphaids *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.

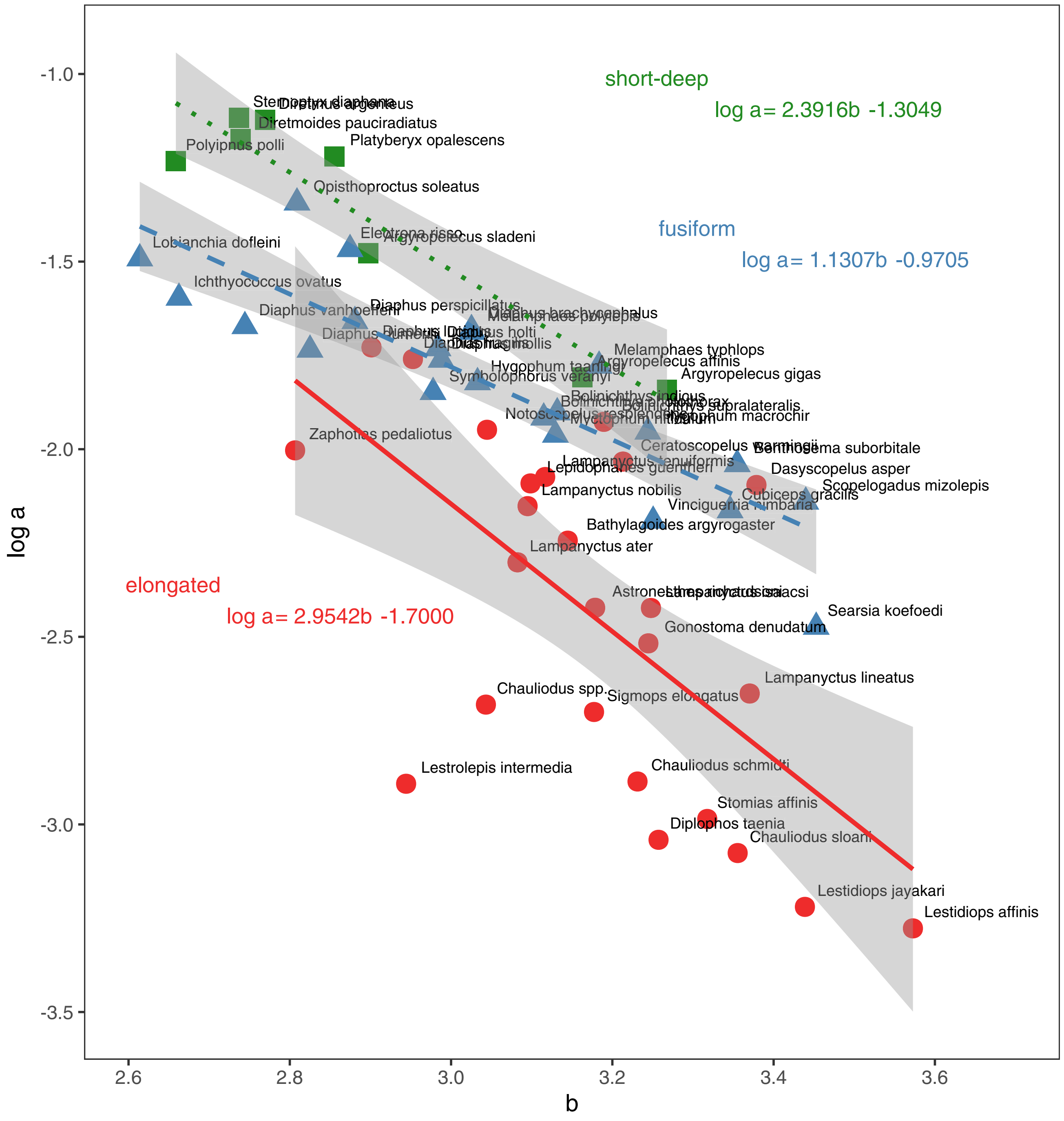

FIGURE 3 Scatter plot of mean log *a* (SL) over mean *b* for 55 mesopelagic species with information on body shape. Body shape: ●, elongated; ▲, fusiform; ■, short-deep

$R^2 = 0.84$, $F_{(5,50)} = 58.5$, $P < 0.001$, 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 (≤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

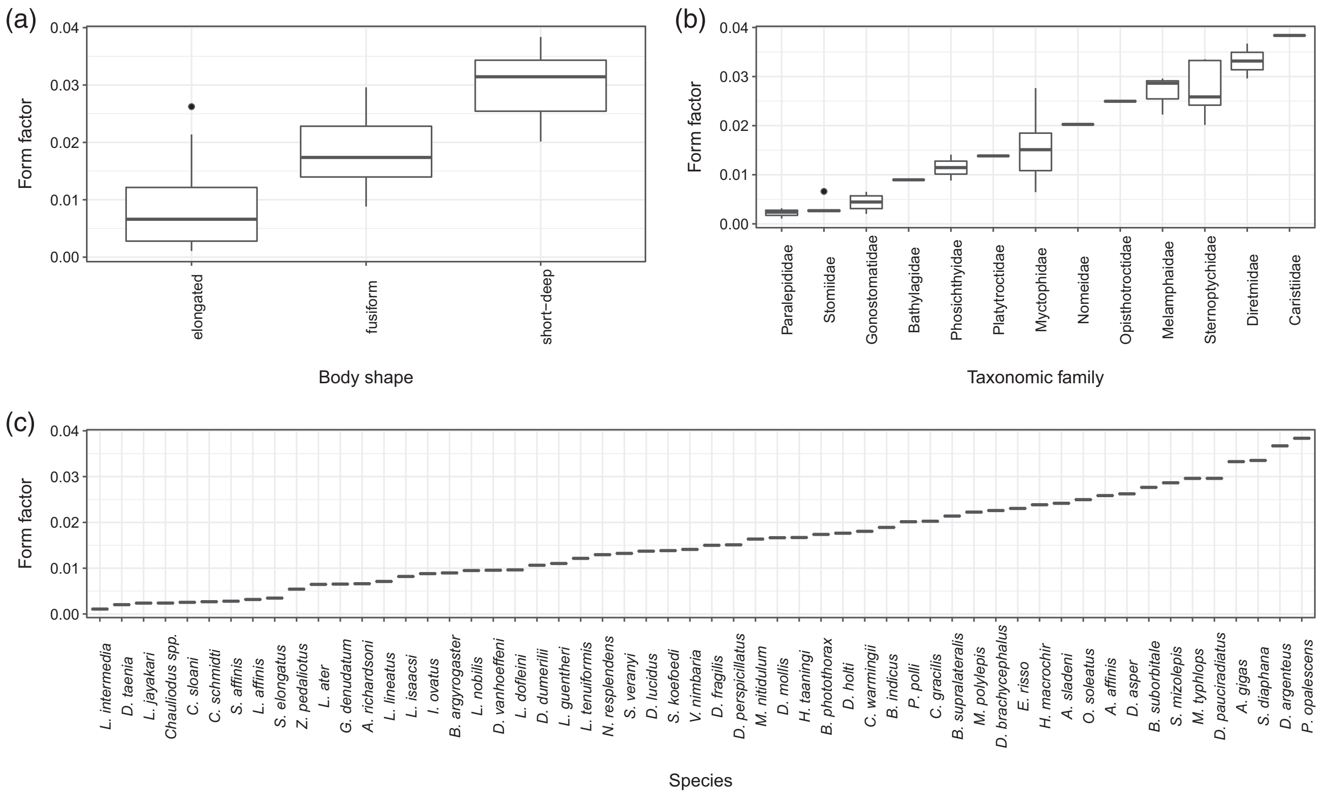

FIGURE 4 Distribution of form factor $a_{3.0}$ for 55 mesopelagic species related to (a) body shape, (b) taxonomic family and (c) species. Form factor calculated from Equation 2 using across-species slope of $S = -1.358$ based on 1223 fish species presented in equation 17 in Froese (2006)

(Diretmidae), *Diretmoides pauciradiatus* (Woods 1973) (Diretmidae), *O. soleatus* (Opisthotroctidae) and *Z. pedaliotus* (Gonostomatidae), but also the migratory myctophids *Lobianchia dofleini* (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 jayakari* (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 (Platytroctidae), *S. mizolepis* (Melamphaidae), *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* Tåning 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%) _l	CI (95%) _u	Slope 2	Std. err.	CI (95%) _l	CI (95%) _u	Diff.
BAT	*Bathylagoides argyrogaster*	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	*Diretmus argenteus*	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	*Zaphotias pedaliotus*	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	*Diplophos taenia*	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	*Melamphaes polylepis*	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	*Scopelogadus mizolepis*	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	*Bolinichthys supralateralis*	11.7	9.0	63	4.1–10.5	n.e.										0.00
MYC	*Ceratoscopelus warmingii*	8.1	4.4	428	1.7–7.4	n.e.	0.018									0.00
MYC	*Dasyscopelus asper*	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	*Diaphus brachycephalus*	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	*Diaphus dumerilii*	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	*Diaphus fragilis*	9.9	5.8	112		n.e.										0.00
MYC	*Diaphus mollis*	6.6	3.0	101		n.e.										0.00
MYC	*Diaphus perspicillatus*	7.1	5.4	107		n.e.										0.00
MYC	*Electrona risso*	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	*Lampanyctus isaacsi*	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	*Lampanyctus lineatus*	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	*Lampanyctus nobilis*	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	*Lampanyctus tenuiformis*	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	*Lepidophanes guentheri*	7.8	4.7	787	2.4–7.7	n.e.										0.00
MYC	*Lobianchia dofleini*	5.0	3.1	110		n.e.										0.00
MYC	*Notoscopelus resplendens*	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	*Vinciguerria nimbaria*	5.3	3.4	444	1.9–5.0	n.e.										0.00
PHO	*Ichthyococcus ovatus*	6.0	NA	43		n.e.										0.00
SEA	*Searsia koefoedi*	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	*Argyropelecus affinis - LO-E*	8.4	NA	406		n.e.										0.00
STE	*Argyropelecus affinis - LO-W, EQ-N, EQ-C*	8.4	NA	670	2.5–7.8	4.2	0.020	2.857				3.188				0.33
STE	*Argyropelecus gigas*	12.0	NA	93	3.2–9.4	n.e.										0.00

(Continues)

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%) _l	CI (95%) _u	Slope 2	Std. err.	CI (95%) _l	CI (95%) _u	Diff.
STE	*Argyropelecus sladeni*	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	*Astronesthes richardsoni*	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	*Chauliodus schmidti*	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	*Chauliodus schmidti/sloani/* 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 ½, parameter *b* of slope 1/2; CI (95%)_l/CI (95%)_u, 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. dumerilii* 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

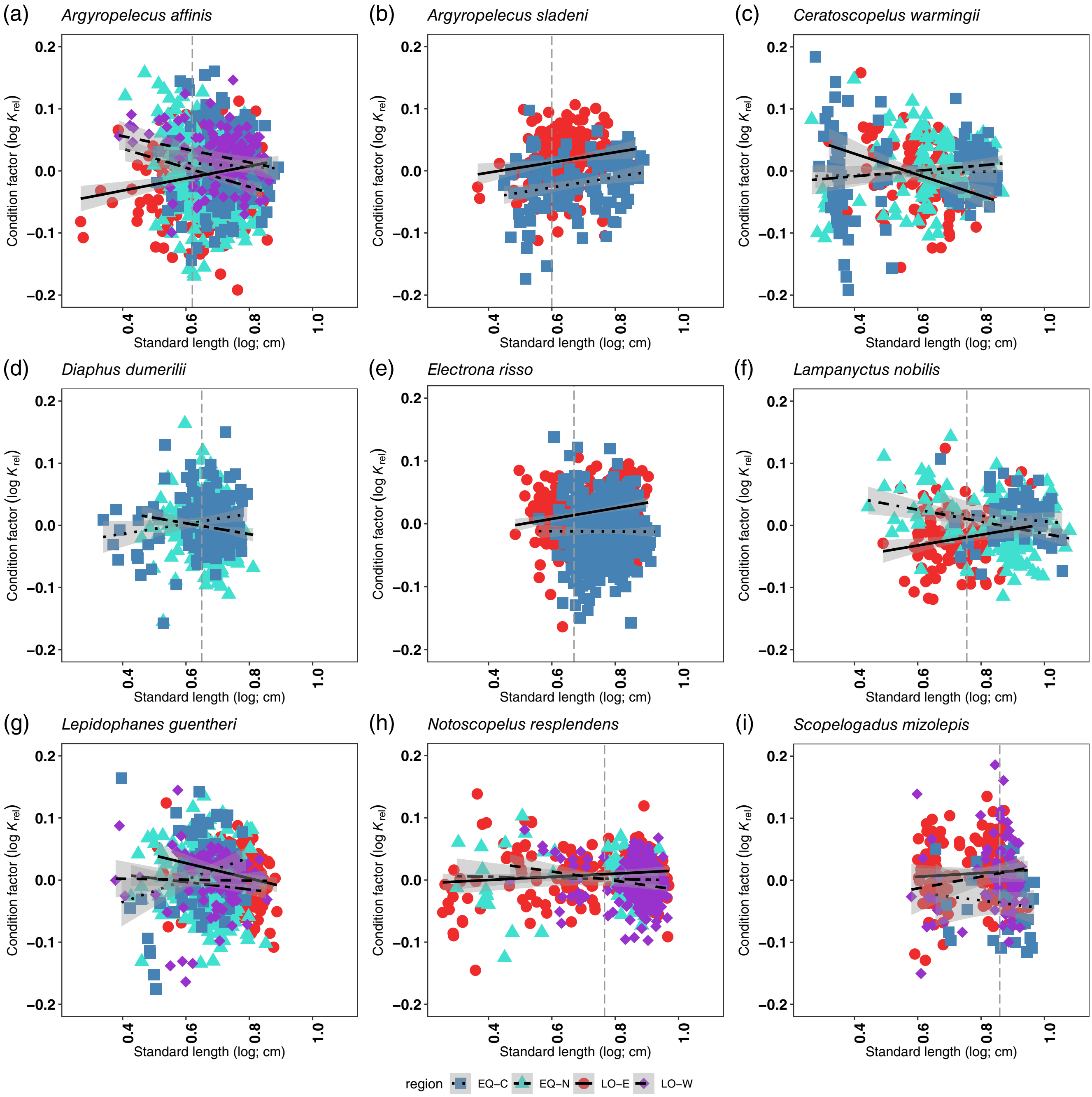

FIGURE 5 Log–log plot of the relative condition factor (K_{rel}) *vs.* standard length (cm) calculated from length–weight relationships (LWRs) of the species (a) *Argyropelecus affinis*, (b) *Argyropelecus sladeni*, (c) *Ceratoscopelus warmingii*, (d) *Diaphus dumerilii*, (e) *Electrona risso*, (f) *Lampanyctus 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 NorthAtlantic

							ANCOVA *P* value		
Species	**Region**	***N***	**SL range**	**log *a* (cm, g)**	***b***	**Adj. R^2**	**EQ–N**	**LO–E**	**LO–W**
Argyropelecus affinis	EQ–C	165	3.2–7.8	0.0166	3.1324	0.9482	**0.04**	**0.001**	**0.02**
Argyropelecus affinis	EQ–N	369	2.6–6.9	0.0199	2.9939	0.9474		**<0.0001**	0.17
Argyropelecus affinis	LO–E	406	1.5–7.2	0.0130	3.2697	0.9803			**<0.0001**
Argyropelecus affinis	LO–W	137	2.5–7.3	0.0194	3.0568	0.9818			
Argyropelecus sladeni	EQ–C	142	2.8–7.8	0.0279	2.9800	0.9875		0.06	
Argyropelecus sladeni	LO–E	283	2.3–7.3	0.0307	2.9793	0.9681			
Ceratoscopelus warmingii	EQ–C	122	1.7–7.1	0.0092	3.2188	0.9897	0.43	**0.04**	
Ceratoscopelus warmingii	EQ–N	155	1.8–7.4	0.0088	3.2570	0.9884		**0.0004**	
Ceratoscopelus warmingii	LO–E	128	2.1–6.9	0.0121	3.0107	0.9693			
Diaphus dumerilii	EQ–C	152	2.2–6.2	0.0165	2.9061	0.9579	**0.0007**		
Diaphus dumerilii	EQ–N	360	2.9.6.5	0.0209	2.7376	0.9348			
Electrona risso	EQ–C	525	3.6–8.4	0.0333	2.8716	0.9756		**<0.0001**	
Electrona risso	LO–E	323	3.1–8.0	0.0308	2.9601	0.9854			
Lampanyctus nobilis	EQ–C	55	4.7–11.4	0.0080	3.0545	0.9798	0.22	0.07	
Lampanyctus nobilis	EQ–N	143	2.8–12.0	0.0087	2.9975	0.9874		**<0.0001**	
Lampanyctus nobilis	LO–E	135	3.1–9.2	0.0059	3.1857	0.9834			
Lepidophanes guentheri	EQ–C	98	2.5–6.2	0.0063	3.2782	0.9598	**0.0001**	**<0.0001**	0.09
Lepidophanes guentheri	EQ–N	426	2.7–7.1	0.0089	3.0283	0.9478		**0.02**	0.51
Lepidophanes guentheri	LO–E	151	3.2–7.7	0.0102	2.9760	0.9735			0.07
Lepidophanes guentheri	LO–W	112	2.4–7.2	0.0082	3.0917	0.9757			
Notoscopelus resplendens	EQ–N	63	2.0–8.7	0.0115	3.0356	0.9937		0.30	0.42
Notoscopelus resplendens	LO–E	208	1.8–9.3	0.0112	3.0636	0.9963			**0.007**
Notoscopelus resplendens	LO–W	331	2.9–9.2	0.0129	2.9712	0.9816			
Scopelogadus mizolepis	EQ–C	31	4.5–9.3	0.0075	3.3758	0.9718		0.39	0.27
Scopelogadus mizolepis	LO–E	154	3.9–8.9	0.0070	3.4708	0.9815			0.72
Scopelogadus mizolepis	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* (Platytroctidae), *S. mizolepis* (Melamphaidae), *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* (Opisthoproctidae) 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 supported by European H2020 grant agreement 817,578, TRIATLAS project.

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Article 5 Size structure changes of mesopelagic fishes and community biomass size spectra along a transect from the equator to the Bay of Biscay collected in 1966–1979 and 2014–2015

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Size structure changes of mesopelagic fishes and community biomass size spectra along a transect from the equator to the Bay of Biscay collected in 1966–1979 and 2014–2015

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Size-based criteria [length frequency distributions (LFDs), size ranges, size class structure and biomass size spectra] were applied to investigate changes between mesopelagic historical (HA, 1966–1979) and present fish assemblages (PA, 2014–2015) on the basis of a total of 35 566 length measurements. Under-sampling, collection bias, time-averaging, and environmental change were considered as sources of uncertainty. In PA comparisons, size-based criteria allowed for a distinction between seasonal (spring vs. summer) and environmental (oxygen minimum zone vs. tropics) factors. In HA–PA comparisons, significant differences in LFDs were indicated in 20 out the 28 species–region combinations, however, without association to changes in size ranges. In 8 species, younger size classes increased in dominance, whereas in 10 cases older size classes increased. In two species, a shift in modal length was observed. At community level, smaller specimens increased in relative abundance in the subtropical and tropical regions in PA samples. Slopes of normalized biomass size spectra steepened in 2015 for the tropical (−0.59 to −1.03) and subtropical region (−1.03 to −1.28) and are in line with published modelling results for unfished assemblages. The slope for the temperate region was −0.50 in 1966 − 1979. It is concluded that observed differences in length structure are owing to environmental changes.

Keywords: climate change, length frequency distributions, Myctophidae, North Atlantic, oxygen minimum zone, permutation test, time-averaging

Introduction

> ... one may readily appreciate how much fraught with difficulty is the task of sampling the yet larger and still more active fishes.
>
> C.M.H. Harrison (1967) *On methods for sampling mesopelagic fishes*

Integrating observations at decadal or centennial scales is necessary to obtain an understanding of the present day status of marine systems (Jackson *et al.*, 2001; Worm *et al.*, 2006; Kidwell, 2015). Integrating depends on the knowledge of sampling conditions indicating how good the sampling was, and environmental conditions when the samples were taken including site history prior to the time of sampling in terms of an "unsuspected past" (Pickett, 1989; Kidwell, 2013). For deep sea fishes, observations exist mostly in terms of net samples of spatially and temporally confined collections in relation to topographic features and frontal systems (e.g. Angel, 1989; Sutton *et al.*, 2008) or large-scale sampling (e.g. Krefft, 1976). Several factors need to be considered when comparing fish catches from different trawling campaigns (Fock *et al.*, 2002; Heino *et al.*, 2011): net geometry and opening, ease of avoidance of net, retention through mesh selection, escapement from net, trawling operation, and herding effect. For midwater trawling, the possession of light organs in many deep-sea fishes may have further implications for sampling, i.e. induced bioluminescence may lead to either a further herding effect, an attraction effect in terms of "baited-can-effect" for predators or enhanced avoidance (Harrison, 1967; Jamieson *et al.*, 2006). Pearcy (1983) showed that catchability changes significantly with time of day with lower catches during daytime (after taking account of vertical migration effects), so that reaction distance of fish towards the trawl also depends on visibility conditions. Significant trawl avoidance was shown for myctophids (Kaartvedt *et al.*, 2012), whereas in other cases large predators were apparently attracted and "accidentally" caught even from the outside of plankton nets (Harrison, 1967). Accordingly, biomass estimations of deep sea fishes depend on the methodologies chosen (Fock and Ehrich, 2010; Irigoien *et al.*, 2014).

We aim at integrating observations from 1966 to 1979 (Krefft, 1974, 1976; Post, 1987) and 2014–2015 to analyse long-term changes. The historic assemblages (HAs) have been investigated so far with regard to biogeographic distribution (Hulley and Krefft, 1985), regional assemblage structure (Fock *et al.*, 2004), and large-scale diversity gradients (Fock, 2009). We employ size-based criteria, length frequency distributions (LFDs) and biomass size spectra to distinguish between different sources of uncertainty at species and assemblage level. Size-based criteria and behaviour are important traits to understand the catchability of deep sea fishes (Harrison, 1967; Fock *et al.*, 2002). We assume that a systematic sampling bias owing to differences in gear selectivity would be evident in terms of correlated changes between gear- and size-based criteria. In turn, environmental effects on size structure and biomass size spectra would be indicated, if changes in size parameters and selectivity pattern were correlated with habitat, season, or a gradient other than gear. In particular biomass size spectra are considered indicative of environmental change by means of altering predator–prey relationships through exploitation and species removals (Petchey and Belgrano, 2010; Menezes dos Santos *et al.*, 2017), so that the so-called "mesopredators" increase in abundance after removal of top predators (Baum and Worm, 2009).

The study design will not allow to distinguish between different environmental impacts, because in three major sectors impacts occurred simultaneously in the tropical and subtropical Eastern Atlantic, i.e. fisheries with a change in stock structure of large predatory species such as tuna, multi-decadal variability (MDV) in ocean climate with an increase in sea surface temperature (Figure 1), and a vertical expansion of the oxygen minimum zone (OMZ) in proximity to the coastal upwelling in the eastern Tropical Atlantic (Stramma *et al.*, 2008; Hahn *et al.*, 2017). Theory predicts that warming will negatively affect growth by constrained uptake of oxygen (see Pörtner and Peck, 2010; Cheung *et al.*, 2012), so that OMZ conditions and climate change should yield similar effects. Temperature variability in the North Atlantic is linked to MDV in the Atlantic with a period length of 50–80 years (Keenlyside and Latif, 2008; Polyakov *et al.*, 2010). During the present positive MDV phase trade winds were enhanced (Polyakov *et al.*, 2010) with corresponding positive effects on the coastal wind-driven upwelling systems. To investigate changes along an environmental gradient, a regional comparison is undertaken for the tropical region and the East Atlantic OMZ, which was also sampled in 2015 during the same cruise. In our study, minimum oxygen concentrations of ca. 40 µmol l^{-1} were measured (0.9 ml l^{-1}, Supplementary Material S1), which according to Ekau *et al.* (2010) meet criteria for hypoxic conditions of <60 µmol.

Material and methods

Rationale

Studies on gear selectivity and comparison are generally done on paired samples from the same assemblage in terms of size based metrics such as size distributions (Gartner *et al.*, 1989; Hilborn and Walters, 1992), length, or biomass spectra (Gartner *et al.*, 1989; Trenkel *et al.*, 2004) or assemblage structure (Trenkel *et al.*, 2004; Porteiro, 2005; Antacli *et al.*, 2010; Heino *et al.*, 2011; Lauretta *et al.*, 2013). This is not applicable in this study with an HA from 1966 to 1979 and a present assemblage (PA) from 2014 to 2015. In turn, we encounter the sources of uncertainty as in many paleobiological studies summarized by Kidwell (2013), of which four apply to this study, i.e. under-sampling, collection bias, time-averaging, and ecological change (Table 1).

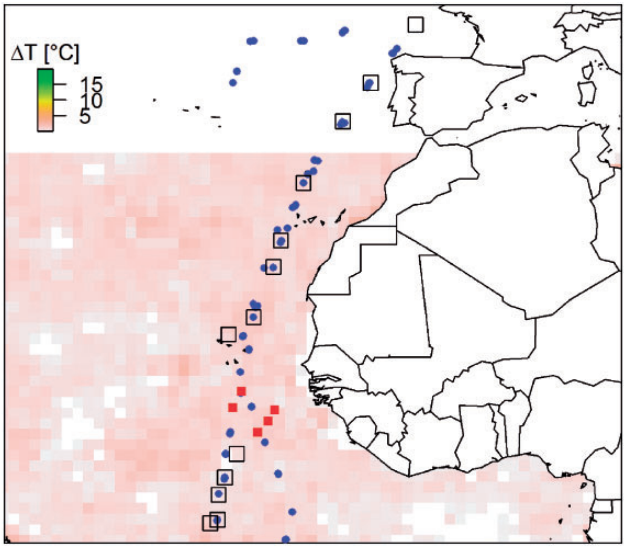

Figure 1. Changes in water temperature 1965/1974 to 2005/2012 and sampling stations 1966–1971, 1979, and 2015. Blue—sampling 1966–1971 and 1979 (stations west of Bay of Biscay), black—sampling stations in 2015, red—OMZ stations 2015. Changes in water temperature calculated from World Ocean Atlas data for the upper 100 m (https://www.nodc.noaa.gov/OC5/woa13/).

In the first part of the analysis, we address issues of under-sampling, collection bias and time-averaging, whereas the second part focuses on the analysis of change in size structure between the two periods. The sampling units in space and time and their associated uncertainties are tested within 4 analysis blocks (Figure 2). Under-sampling is related to sample size and survey design, for the latter, PA fishing locations and depths were aligned to HA sampling locations (Figure 1). To account for different sample sizes in PA and HA, an inclusion index is applied to indicate the likelihood of an observation in the larger sample to also be present in the smaller sample.

Collection bias refers to methodological issues such as gear and time of survey, e.g. seasonal effect. HA and PA samples differed in terms of gear although gears were similar (Supplementary Material S2), month of sampling, and trawling operations. Size-based criteria at species level are size class structure, maximum and minimum sizes, and LFD. Larger specimens are relatively faster and thus are less likely to be caught with smaller nets (Harrison, 1967; Pearcy, 1983). This feature fuelled the discussion on the value of larger and often non-closing nets in the study of deep sea fishes (Krefft, 1976; Gjoesaeter and Kawaguchi, 1980) while certain disadvantages pertain to this net type, i.e. contamination with specimens from shallower depths and unclear volumes of filtered seawater (Pearcy, 1983; Hulley and Krefft, 1985; Fock *et al.*, 2004). Sizes depend on growth and thus could depend on the time of sampling indicating a seasonal effect, whereas size class structure is assumed

Table 1. Sources of uncertainty in long-term comparisons of historical (HA) and present assemblage data (PA) and respective solutions with reference to text or analysis block.

Source of uncertainty	Observation, e.g.	Effective when . . .	Solution	Analysis block (I–IV) or reference to table or figure
Under-sampling	Species is rare in HA	Sample size HA is small and HA<<PA	Inclusion index reveals susceptibility to type II errors	Ia, IV
–	Species is abundant in HA but not in PA	PA study not well designed	Congruency in HA and PA study designs	Suppl. Material S3, Table S2
Collection bias	Abundant species in HA is rare in PA	Gear bias due to effect of catchability from different gears	Analysis of changes in size metrics correlated with gear	Ia, b, III, IV
–	Abundant traits in HA underrepresented in PA	Gear bias due to differently operated gears	Analysis with different combinations of traits involved	IV, Suppl. Material S8
–	Species undergoes seasonal fluctuations	Seasonal pattern in HA cannot be resolved by PA	Inter-comparisons to evaluate how seasonal effects and aggregation would affect assemblage structure and size metrics	Ia, II
Time-averaging in HA	Species traits in HA with a wider range than in PA	Averaging over longer period in HA	Analysis of joint minima and maxima in metrics indicative of higher variability in HA (Hunt, 2004)	Table 4
–	Species is abundant in HA in all subsections	Averaging over longer period in HA	Repeated of analysis of HA subunits (Terry, 2010)	III, IV
Ecological change	Species abundance changes correlated with changes in traits	Changes in important environmental drivers	Analysis of correlated changes in in LFD and size metrics in relation to region or other environmental factors—does not reveal causal relationship	Table 4, Figure 8

Modified after Kidwell (2013).

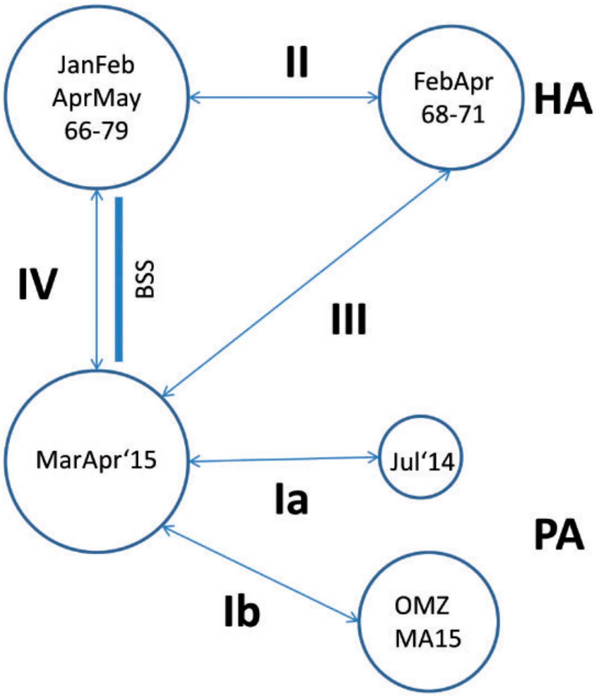

Figure 2. Defining four analysis blocks I–IV with regard to HA and PA data. Circle sizes represent availability of data. Subsets in terms of time or region are indicated. BSS, biomass size spectra analysis; OMZ, oxygen minimum zone.

to represent a qualitative measure of population structure less sensitive to time of sampling. Otolith age readings in myctophids allow us to understand size classes as age groups (Linkowski, 1987). To evaluate seasonal effects, PA summer samples from July 2014 are compared with 2015 PA spring samples.

At community level, relative community LFDs are evaluated, and biomass size distributions are investigated to evaluate the selectivity pattern in analogy to catch curve analysis. Two processes contribute to the generation of biomass size distributions (see Hilborn and Walters, 1992), i.e. first, the probability of capture increases for smaller specimens with increasing size; and second, after full catchability is attained a decline in abundance with size for larger size classes occurs owing to natural mortality or net avoidance. The negative slope of the downward branch of the curve describes the negative relationship between body size and community biomass in biomass size spectra (Kerr and Dickie, 2001). The point of inflection between positive and negative branch can be used to evaluate the gear selectivity pattern.

In terms of behavioural traits that would affect catch in differently operated trawls, optical investigations indicate that many mesopelagic species, in particular elongated species, have a 45° to vertical orientation in the water column, which depends on their predatory behaviour. For horizontally towed nets, the presumed escape angle would easily lead the animals out of the path of a horizontally towed net (Harrison, 1967). The potential bias in terms of behavioural traits is investigated in that patterns are analysed by partially excluding groups for which Harrison (1967) predicted that vertically oriented species would be proportionally caught in higher numbers in the upward cast of double oblique hauls when compared with horizontal tows, i.e. stomiids, paralepidids, and anguilliform species. Stomiidae and Anguilliformes entangle easily in the forenet and could not be assigned to catching depths in the 2015 survey, while were collected and assigned to the catch in 1966–1979. Gartner *et al.* (1989) showed that morphological traits such as body shape in myctophids also affect selectivity, but this is not analysed in this study.

In paleobiological studies, time-averaging describes the process of accumulation and mixing of material into one time horizon of sedimentary records. We conduct time-averaging by combining different historical surveys (census assemblages sensu, Kidwell, 1997) in order to obtain sufficient HA sample sizes (see Supplementary Material S3), otherwise, 20 040 observations from March and April 2015 would have been directly comparable to only 4078 observations from April 1971, however, not evenly distributed across the survey area. Time-averaging is efficient in revealing large-scale patterns, but not effective on smaller scale (Tomašových and Kidwell, 2010). As a corollary, PA should be pooled, which is common practice in mesopelagic studies to overcome effects from small scale patchiness (Krefft, 1976; Olivar *et al.*, 2017). This is comparable to the space-for-time substitution approach, when along an environmental gradient different successional stages are sampled to replace a time series. In both time-averaged (Hunt, 2004) and space-for-time substituted assemblages trait variance, e.g. body size, increases, so that a potential time-averaging bias would be indicated by presence of simultaneously smaller and larger specimens in HA.

Sampling with large pelagic trawls

The major HA and PA components are 15 577 length records from January to May 1966–1979 and 20 040 records from March and April 2015 for an area from the equator to the Bay of Biscay and delimited by 25.96°W longitude (Figure 1; Supplementary Material S3), of which 5380 length measurements from 2015 were read in OMZ locations (Figure 1). Additionally, 1800 records from July 2014 were read to analyse seasonal effects. Owing to the low sample coverage in 2014, sample size in 2015 was adjusted to a "reduced 2015 data set" for analysis block Ia (Figure 2).

Historical survey design and the application of large commercial trawls were mimicked in 2015 (Figure1; station data in Supplementary Material S4). In 1966–1979, a commercial Engel MT 1600 trawl was deployed (Supplementary Material S2). Gjoesaeter and Kawaguchi (1980) assume that this net has an effective mouth opening of 300 m^2, given that fishes are able to escape through the large meshes in the forenet. To avoid contamination, nets were retrieved very speedily (Krefft, 1976), while vessel speed was reduced to 1.5 kn during retrieval (Krefft, 1967). Sampling was carried out as double oblique haul with a nominal duration at designated depth of 30 min. For a mesopelagic haul (500 m nominal depth), further handling time during lowering and retrieval time accounted for 20 and 40 min, respectively. After retrieval, the forenet area was carefully sampled by hand.

For PA, a so-called "Aal"-trawl was deployed, equipped with a multiple closing device with three net bags. At designated depths, net bags were opened for 30 min. Tows were done horizontally. Specimens from the forenet were collected on deck, but not assigned to one of the three net samples.

Samples were assigned to three broader biogeographical regions, i.e. tropics [equator to 12°N to avoid mixture with OMZ region for HA, PA selected according to oxygen profiles (Supplementary Material S1)], subtropics (19–40°N) and temperate [>40°N, which is in accordance with an analysis of fish larvae from the same cruise (Dove, 2017)] and cluster analysis of the 2015 data (Supplementary Material S5). All samples within a geographical region were pooled [see Olivar *et al.* (2017)]. For historical sampling, only samples shallower than 800 m were included in the analysis. Historical data from 1966 to 1971 were available for all three regions, whereas further data from 1979 were used only from the temperate zone.

Processing of length data

Length measurements were conducted on preserved material. Length data were binned to 5 mm length classes. Five types of length measurements in historical and 2015 datasets were applied, all adjusted to standard length (SL, in mm): "fd" (frequency distribution), "min-max" (minimum and maximum sizes indicated), "rge" (unmeasured subsample of specimens that are raised to their respective "fd" or "min–max" distributions), "unm" (unmeasured), and "fix" (single measurements). To analyse length distributions at species level, raised "fd"- were combined with "fix"-measurements, comprising 15 577 and 12 933 records for these 2 categories in 1966–1979 and 2015, respectively. Only 4078 length measurements were available for direct comparisons from April 1971 to compare with the March–April data from 2015 (Supplementary Material S3), and thus historical length measurements were aggregated into two reference periods and applied separately, i.e. February–April with 5528 measurements and January–May with all available historical data.

To analyse LFDs and biomass size spectra at community level, raised fd, fix, and raised min–max and unm-records were applied. For min–max measurements, the range between minimum and maximum was evenly split into 10 length values. This uniform distribution was raised by a factor corresponding to the number of "rge" specimens for this species. For "unm" specimens, average abundance weighted mean length by species was applied, in the first place from the respective period and regional outline. With no match, both periods were pooled and further historical dataset records from the entire North Atlantic were acquired to obtain mean lengths. In the data records, "unm" applied in particular to species groups that were originally measured and determined but subsequently redetermined without remeasuring lengths or indicating, which individuals were taken out of the sample, for instance in some cases of melamphaids or the myctophid congeners *Hygophum macrochir/H. taaningii* and *Ceratoscopelus warmingii/C. maderensis.*

Testing for differences in species LFDs

The Cramer-von Mises two-sample test (CvM) is one of the best-known distribution-free two-sample tests and more accurate than the Kolmogorov–Smirnov test (Anderson, 1962). The test is on the basis of the difference between two empirical distributions function (EDF) of cumulative proportions x in size classes $\leq i$ of two samples N, M:

$$\omega^2 = \sum_i \left(F_N\left(x_{N,i}\right) - G_M\left(x_{M,i}\right) \right)^2 \quad (1)$$

CvM is as EDF test insensitive to changes in abundance in N, M but not to change in distribution parameters. The frequency distributions of the test static is obtained by means of a permutation test (Syrjala, 1996), in this study on the basis of 500 permutations on bootstrap samples, each consisting of 200 draws, i.e. 100 for either category *N*, *M*, and sampled with replacement. A minimum of 20 records for either *N*, *M* was applied to run the test.

Inclusion index

An inclusion index I was calculated to evaluate type II error in assessment blocks I, II, and IV, i.e. the probability of a binomial distributed extreme event *z* such as minimum or maximum size to be present also in the smaller one of samples *N* and *M* (see Equation (6) in Fock *et al.*, 2014). The value was rescaled by 0.63 so that the index is distributed in the interval [0, 1], where 1 applies to the case that both *N* and *M*are of same size in terms of numbers of records, i.e.

$$I = \frac{P(z_{\min(N,M)} \neq 0)}{0.63} = \frac{1 - P(z_{\min(N,M)} = 0)}{0.63} \qquad (2)$$

A value of 0.75 was taken as reference value indicative of a probability of ca. 50% of *z* to be present in the smaller sample.

Association tests

Size metrics and LFD distributions were analysed in four analysis blocks to indicate whether changes were associated with season, aggregation of HA samples, region or long-term changes (Figure 2). Assessment block I analyses PA changes with regard to season and region in 2014–2015, block II investigates the aggregation in HA with regard to two reference periods (February–April vs. January–May), blocks III and IV investigate long-term changes between HA and PA for the two HA reference periods. Association was tested with the χ^2 measure of association with one factor or Fisher's exact test for contingency tables. Fisher's exact test accepts zero cell frequencies (Zar, 1996). The null hypothesis H_0 was uniform probability. Where indicated, association tests in assessment blocks I and IV were repeated for species–region combinations with an inclusion index >0.75.

Community LFDs

A log difference *d* for abundance proportions *x* at size class *i* between two samples *N*, *M* was applied, assuming log-normal errors and applying the log-ratio transformation (Aitchison *et al.*, 2000):

$$d_i = \log\frac{x_{N,i}}{g(x_N)} - \log\frac{x_{M,i}}{g(x_M)}, \qquad (3)$$

where $g(x)$ is the geometric mean for the distribution of proportions. The log-ratio transformation is preferable over the Euclidean distance in that it is invariant in terms of scale (proportions, percentage), selection of subsets and permutation. Opposite to the Aitchison distance, the log difference indicates the direction of change by means of its sign.

Biomass size spectra

Biomass data were calculated from length distributions with allometric length-weight relationships on the basis of 177 species-specific length–weight relationships obtained from the 2015 cruise. Missing relationships were substituted by 0.01 as factor and 3 as power for sizes in cm standard length and weights in g (see method 4 in Fock and Ehrich, 2010). Biomass data were binned into size classes *w* from 2^{-7} to 2^7 g (octaves). Bin width was calculated according to Rossberg (2013) as $w *2^{-0.5}$ to $w *2^{0.5}$. Biomass within an interval was divided by bin width to obtain normalized estimates, standardized to 30 min haul duration, and plotted on log10 axes referring to the LBNbiom method in Edwards *et al.* (2017, Figure 2f). The maximum value of the biomass size distribution was taken as inflection point. The normalized slope $-a$ of the biomass size spectrum is related to the un-normalized slope as $-a+1$ (Kerr and Dickie, 2001; Edwards *et al.*, 2017, their Figure 2e).

Results

Sixty-four trawl samples station× depth were available for the historical period, whereas 45 samples were collected in 2015 for the 3 regions and 7 in 2014 (Supplementary Material S3). In particular, low coverage was obtained for the temperate region in 2015 with two stations totalling six trawl samples. The list of 27 species analysed accounted for 56 and 28% of total abundance in 2015 and 1966–1979, respectively (LFDs in Supplementary Material S7).

Species level LFDs and analysis blocks I–IV

Eight species× region combinations could be performed to analyse differences between samples from July 2014 and March/April 2015 within analysis block Ia (Table 2), whereas more comparisons were possible with regard to analysis block Ib (14, Supplementary Material S6), blocks II and III (21, Table 3) and analysis block IV (28, Table 3).

For analysis block Ia, in six out of the eight cases significant differences in LFDs were indicated equivalent to a 3:1 ratio considering combinations with an inclusion index >0.75, which was not significant in relation to season (Table 4, hypothesis I.1). In turn, a difference in maximum size was indicated (Table 4, I.2), i.e. summer LFDs from 2014 had a tendency to smaller maximum sizes and increases in younger size classes (*Ceratoscopelus warmingii*, Figure 3).

When considering the OMZ—tropics differences in 2015 (analysis block Ib), significant changes along this gradient were evident for LFDs and maximum sizes (Table 4, hypotheses I.4 and I.5). In 11 out of 14 cases a significant change in LFD was indicated (Supplementary Material S6). All species available for the comparison between tropics and OMZ had a smaller maximum size inside the OMZ. *Ceratoscopelus warmingii* had a maximum size of 69.2 mm in the OMZ when compared with 73 mm in the subtropics and 75.9 mm in the tropics, with a small shift in modal size from 42.5 mm to 37.5 in the OMZ (Figure 4). Although minute differences appeared for some species (i.e. *Lepidophanes guentheri*, 78 mm compared with 77.2 mm), it is noteworthy, that with the exception of *Myctophum affine*, no other species showed an increase in maximum size (LFDs in Supplementary Material S9).

On the basis of analysis blocks II–IV, species–region combinations were categorized into five groups A–E. Category A combinations were data deficient in the HA reference period February–April to compare with HA reference period January–May, which applied to seven species–region combinations (Table 3, category A). Accordingly, overall inclusion index was low in analysis block III (mean 0.37) when compared with analysis block IV (mean 0.55). In analysis block III, only 1 species–region combination reached

Table 2. Seasonal comparison of length frequency distributions by species in the tropics and subtropics in 2014 (July) and 2015 (March/April), corresponding size ranges and changes in population structure sampled with "Aal"-net.

Family	Species	Region	Seasons compared	Analysis block Ia: LFD differences [CvM]	Analysis block Ia: inclusion index	Size range Jul 2014	Size range Mar/April 2015	Changes in LFD characteristics in 2014
Myctophidae	*Ceratoscopelus warmingii*	TROPICS	July–Mar/April	$p > 0.95$	0.62	21.14–56.29	31.1–73.5	–
Myctophidae	*Ceratoscopelus warmingii*	SUBTROPICS	July–Mar/April	n.s	0.79	22.98–67	21–71.9	Increase in younger size class
Myctophidae	*Diaphus rafinesquii*	SUBTROPICS	July–Mar/April	$p > 0.95$	0.65	54.26–79.57	57–84	–
Gonostomatidae	*Diplophos taenia*	TROPICS	July–Mar/April	n.s	0.54	64.6–126.56	55.5–131.8	–
Myctophidae	*Lepidophanes guentheri*	TROPICS	July–Mar/April	$p > 0.95$	0.2	29.21–70.7	34.3–77	–
Myctophidae	*Notoscopelus resplendens*	SUBTROPICS	July–Mar/April	$p > 0.95$	0.96	23–55	22–84	–
Myctophidae	*Notoscopelus resplendens*	TROPICS	July–Mar/April	$p > 0.95$	0.84	21.08–89.53	19.9–95.5	Increase in younger size class
Phosichthyidae	*Vinciguerria nimbaria*	TROPICS	July–Mar/April	$p > 0.95$	0.99	17.25–45.34	22.3–50.4	Increase in younger size class

CvM - Cramer von Mises test. Due to the low sample coverage in 2014, the number of stations and sampling depths in 2015 was adjusted to a 'reduced 2015 data set'.

the 0.75-criterion for the inclusion index, i.e. *Argyropelecus hemigymnus* in the subtropics. The analysis block II indicated, that for the remaining species–region combinations, results from both historical reference periods were strongly correlated, i.e. with 15 species–region combinations in categories B and C when compared with 6 (categories D and E), there was a significant similarity between LFDs in the historical reference periods February–April and January–May (Table 4, II.8).

Only four species–region combinations showed no significant changes between 1966–1971 and 2015 (Table 3, category B; 1979 only refers to temperate region for which no CvM tests were run owing to low coverage of data). The other categories are interpreted as no change in the historical reference periods but change in relation to 2015 (category C), a change in reference period February–April in relation to 2015 but no change if further data are considered (category D), and high variability within LFDs in reference periods and in relation to 2015 (category E). Significant changes in LFDs between 1966 and 1971 in relation to 2015 appeared for 17 (C + D + E) out of 21 tested combinations considering reference period February–April of the historical records, and in 20 out 28 cases (A + C + E− 1) considering reference period January–May (Table 4, hypotheses III.9a and IV.9b). Hypotheses III.9a and IV.9b were significantly associated considering all species–region combinations (IV.10), but not when considering combinations with an inclusion index >0.75 (on the basis of analysis block IV inclusion index values). There was no regional effect, i.e. no association between regional affiliation (tropics, subtropics) and significant changes in LFDs (Table 4, III.11 and IV.12); i.e. for instance for reference period February–April, 13 significant changes for the tropics were contrasted by 4 non-significant changes when compared with 4 significant changes in the subtropics and zero non-significant changes. There was no clear relationship between changes in LFDs and changes in maximum or minimum sizes (Table 4, III.13–IV.16); the test for the HA reference period February–April (III.13) resulted in $P = 0.08$ but could not be re-evaluated with regard to combinations with an inclusion index >0.75. Changes in size class structure between 1966−1971 and 2015 were not significant (IV.17), i.e. in nine species, younger size classes increased in dominance, whereas in nine cases older size classes increased. In two species, a shift in modal length was observed. For the sternoptychid *A. hemigymnus* (subtropics), the myctophid *C. warmingii* (Figure 5, tropics), and the phosichtyid *Vinciguerria nimbaria*, younger additional size classes were found, whereas for *Diretmoides pauciradiatus* considerably larger specimens were indicated (increase of maximum size from 72 to 118 mm). Whereas no significant relationships were indicated for changes in LFD in relation to other size metrics (Table 4, III.11–IV.16), a significant association was indicated between region and changes in size class structure, with the increase in younger size classes linked to the subtropical and for older size classes in the tropical region (IV.18); i.e. for six species additional younger size classes were indicated in the subtropics with zero additional older size classes when compared with nine species with additional older size classes in the tropics accompanied by three species with additional younger size classes. This relationship remained valid considering combinations with an inclusion index >0.75 ($p = 0.02$).

Time-averaging (Table 4, hypothesis 19) was not directly observable because only in five species–region combinations HA size ranges were simultaneously smaller and larger when

Table 3. Comparison of length frequency distributions by species in selected ocean regions from 1966–71 to 2015, corresponding size ranges and changes in population structure with Engel MT 1600 and "Aal"-net and literature data.

Family	Species	Region	Cate-gory	Block II: CvM	Block III: CvM	Block IV: CvM	Block III: inclusion index	Block IV: inclusion index	Size range reference period February–April 1966–1971 (mm)	Size range reference period January–May 1966–1971 (mm)	Size range March–April 2015 (mm)	Changes in size structure in 2015	Reported maximum size (mm)
Myctophidae	*Ceratoscopelus maderensis*	TSUB	A	–	–	n.s.	–	0.35	–	32–81	26–69.9	–	81
Bathylagidae	*Bathylagichthys greyae*	TSUB	A	–	–	$p > 0.95$	–	0.24	–	47–147	32–135	Increased dominance of younger size classes	160
Myctophidae	*Hygophum macrochir*	T	A	–	–	$p > 0.95$	–	0.29	–	23–54	22.9–65	Shift in modal size	60
Myctophidae	*Lepidophanes gaussi*	TSUB	A	–	–	$p > 0.95$	–	0.72	–	29–47	18–51	Additional younger size classes	50
Myctophidae	*Myctophum affine*	T	A	–	–	$p > 0.95$	–	0.39	–	13–47	22.5–51	Increased dominance of older size classes	60
Myctophidae	*Notoscopelus caudispinosus*	TSUB	A	–	–	$p > 0.95$	–	0.75	–	38–130	35–140	Shift in modal size	140
Phosichthyidae	*Vinciguerria nimbaria*	TSUB	A	–	–	$p > 0.95$	–	0.82	–	25.2–50	17–42	Additional younger size classes	48
Myctophidae	*Lepidophanes guentheri*	T	B	n.s.	n.s.	n.s.	0.26	0.35	34–71	30–76	24.9–78		78
Stomiidae	*Malacosteus niger*	T	B	n.s.	n.s.	n.s.	0.29	0.37	62–175	38–175	100.7–155.8	–	240
Myctophidae	*Hygophum taaningi*	T	B	n.s.	n.s.	n.s.	0.06	0.06	25–52	25–52	11.7–59	–	61.2
Stomiidae	*Astronesthes richardsoni*	T	B	n.s.	n.s.	n.s.	0.37	0.45	26–185	26–185	22.9–172	–	145
Myctophidae	*Ceratoscopelus warmingii*	T	C	n.s.	$p > 0.95$	$p > 0.95$	0.68	0.84	20–80	20–80	16.6–75.9	Additional younger size classes	81
Diretmidae	*Diretmoides pauciradiatus*	T	C	n.s.	$p > 0.95$	$p > 0.95$	0.54	0.78	16–72	16–72	24.7–118.2	Additional older size classes	370
Gonostomatidae	*Bonapartia pedaliota*	T	C	n.s.	$p > 0.95$	$p > 0.95$	0.2	0.29	36–77	32–77	28–78.2	Increased dominance of older size classes	69
Gonostomatidae	*Gonostoma denudatum*	T	C	n.s.	$p > 0.95$	$p > 0.95$	0.73	0.78	43–140	43–140	73.2–146.3	Increased dominance of older size classes	140
Myctophidae	*Electrona risso*	T	C	n.s.	$p > 0.95$	$p > 0.95$	0.17	0.29	21–82	21–82	36.2–84.1	Increased dominance of older size classes	82
Myctophidae	*Nannobrachium isaacsi*	T	C	n.s.	$p > 0.95$	$p > 0.95$	0.34	0.34	36–126	36–126	53.1–158	Additional older size classes	133.4
Myctophidae	*Notoscopelus resplendens*	TSUB	C	n.s.	$p > 0.95$	$p > 0.95$	0.21	0.75	60–73	21–85	18–84	Increased dominance of younger size classes	95
Myctophidae	*Notoscopelus resplendens*	T	C	n.s.	$p > 0.95$	$p > 0.95$	0.74	0.98	29–86	29–91	16.1–95.5	Increased dominance of older size classes	95

Continued

Table 3. Continued

Family	Species	Region	Cate-gory	Block II: CvM	Block III: CvM	Block IV: CvM	Block III: inclusion index	Block IV: inclusion index	Size range reference period February–April 1966–1971 (mm)	Size range reference period January–May 1966–1971 (mm)	Size range March–April 2015 (mm)	Changes in size structure in 2015	Reported maximum size (mm)
Sternoptychidae	*Argyropelecus affinis*	T	C	n.s.	$p > 0.95$	$p > 0.95$	0.05	0.05	35–72	31–75	25.6–78	Increased dominance of younger size classes	72
Sternoptychidae	*Argyropelecus sladeni*	T	C	n.s.	$p > 0.95$	$p > 0.95$	0.44	0.65	15–72	15–72	19.9–83.5	Increased dominance of older size classes	70
Stomiidae	*Chauliodus sloani*	T	C	n.s.	$p > 0.95$	$p > 0.95$	0.59	0.62	60–235	60–235	98–248.1	Decrease in dominance of older size classes	>300
Gonostomatidae	*Diplophos taenia*	T	D	$p > 0.95$	$p > 0.95$	n.s	0.29	0.81	65–130	46–136	55.5–147		276
Myctophidae	*Ceratoscopelus warmingii*	TSUB	D	$p > 0.95$	$p > 0.95$	n.s	0.3	0.87	37–68	17–77	21–73		81
Phosichthyidae	*Vinciguerria nimbaria*	T	D	$p > 0.95$	$p > 0.95$	n.s	0.43	0.78	23–48	21–56	18–54.5		48
Diretmidae	*Diretmus argenteus*	T	E	$p > 0.95$	$p > 0.95$	$p > 0.95$	0.1	0.19	12–80	12–190	24.6–98.9	Increased dominance of younger size classes and decline in max. size	125
Myctophidae	*Diaphus rafinesquii*	TSUB	E	$p > 0.95$	$p > 0.95$	$p > 0.95$	0.28	0.93	40–74	30–92	23–84	Increased dominance of younger size classes	90
Sternoptychidae	*Argyropelecus hemigymnus*	TSUB	E	$p > 0.95$	$p > 0.95$	$p > 0.95$	0.81	0.82	17–33	12–44	18.8–39.2	Change in size classes structure: two modal lengths instead of one with younger size classes increased	39

Analysis blocks II to IV refer to the following analysed combinations: Block II - HA Feb-Apr to HA Jan-May, block III - HA Feb-Apr 1966/71 to PA 2015, block IV – HA Jan-May to PA 2015. CvM – Cramér-von Mises test on length frequency distributions. Reported maximum size based on Gibbs (1964), Baird (1971), Nafpaktitis *et al.* (1977), Hulley (1981) and Whitehead *et al.* (1984). Category refers to grouped results from analysis blocks II to IV, see text. TSUB – subtropical region, T – tropics

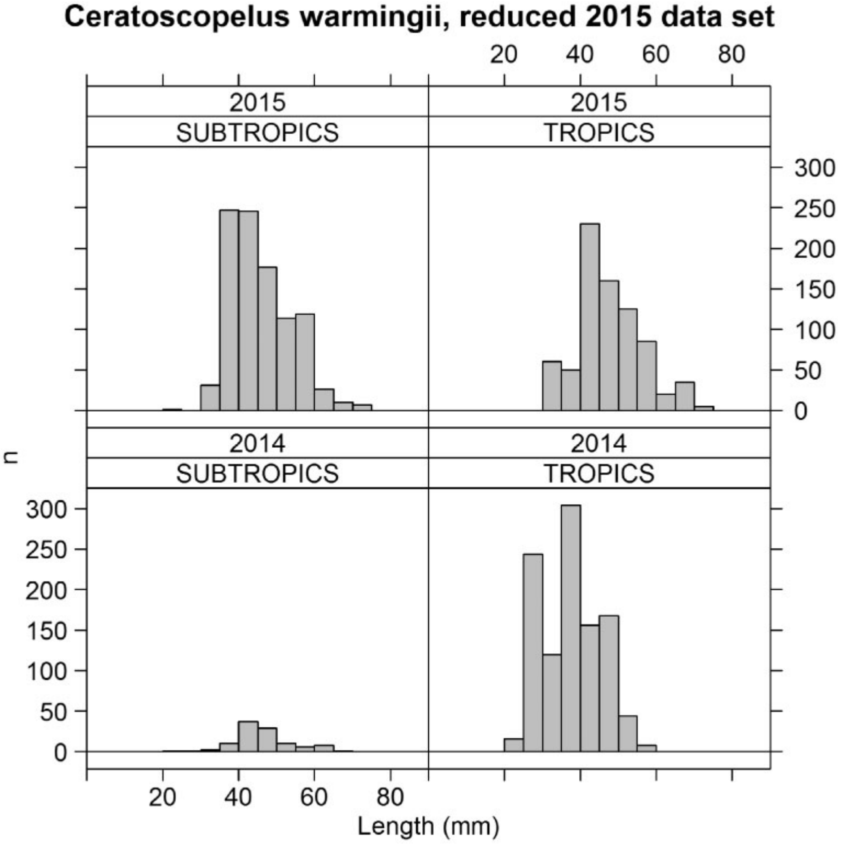

Figure 3. LFD of the myctophid *Ceratoscopelus warmingii* in the tropics and subtropics in July 2014 and March/April 2015. Numbers refer to measured specimens of the measurement categories "fd" and corresponding "rge" records, but are not raised to total population abundance. For analysis, numbers were transformed into proportions of LFD composition. Owing to the low sample coverage in 2014, the number of stations and sampling depths in 2015 was adjusted to a "reduced 2015 dataset."

compared with PA size ranges. However, hypothesis IV.10 (Table 4) shows that similarities between HA and PA differences with regard to both HA reference periods become insignificant considering species–region combinations with an inclusion index >0.75. This would indicate either increased variability in HA as one possible indicator for time-averaging or the artefact of under-sampling, when small samples are compared with larger ones.

Community level LFDs and biomass spectra

Log difference plots for the three regions (Figure 6) were consistent with plots after excluding taxa to account for sampling and behavioural bias (Stomiidae, Paralepididae, and Anguilliformes; Supplementary Material S8). For the subtropics and tropics, it is indicated that smaller length classes increased in relative abundances in 2015, leading to negative log differences. The opposite is indicated for the temperate region. The high negative log difference values for the subtropics for smaller size classes correspond to the significant change in size classes' structure for the subtropics (Table 4, IV.18) but the increase in older length classes indicated for the tropics is not reflected.

For the comparison with OMZ data (Figure 7), negative log differences in particular between the 90 and 220 mm length classes indicate that in the OMZ relative abundances of smaller specimens were higher than in the corresponding tropics.

The biomass size distribution shows in five cases a clear curvilinear pattern with well-defined upward and downward legs, i.e. spectra (Figure 8). Only the temperate region in 2015 appears data deficient (Figure 8c, closed circles), given that only two stations were sampled with overall low abundances, and neither the upward nor the downward leg are well defined. In the other five cases, biomass per size classes peaked at 2° g for the tropics and subtropics in the historical data, and at 2^1 g in the 2015 data, respectively. In the temperate region, the peak was indicated at 2^{-1} g for the historical dataset. This indicates variability from 2^{-1} to 2^0 g for the historical dataset, and presumably 2^0 to 2^1 g for the 2015 data indicative of almost no difference in selectivity pattern. Slopes for the biomass spectra were steeper for the 2015 data, i.e. −0.59 (1966–1971) when compared with −1.03 (2015) in the tropics, and −1.04 (1966–1971) when compared with −1.28 (2015) in the subtropics. The HA slope for the temperate region was −0.50. The HA and PA biomass size spectra were clearly intersecting for the tropics, with higher values in the PA spectrum from 2° to 2^2 g and lower PA values from 2^4 g upward (Figure 8a).

Discussion

Methodological aspects

Size-based criteria in different analytical combinations were applied in this long-term comparison to distinguish between

Table 4. Association tests for present (PA) and historic assemblages (HA), and combinations thereof.

Hypothesis	**Test statistics and *p*-values**	***p*-Values only for data with inclusion index ≥0.75**
Analysis block Ia : PA–PA comparisons, seasons March–April vs. July		
I.1 : Differences in LFDs	$\chi^2 = 2$, df $= 1$, p-value $= 0.15$	–
I.2: Differences in maximum sizes	$\chi^2 = 8$, df $= 1$, p-value $= 0.004$	–
I.3: Differences in size class structure	$\chi^2 = 0.5$, df $= 1$, p-value $= 0.48$	–
Analysis block Ib : PA–PA comparisons, regions tropics vs. OMZ		
I.4: Differences in LFDs	$\chi^2 = 4.5$, df $= 1$, p-value $= 0.03$	–
I.5: Differences in maximum sizes	$\chi^2 = 14$, df $= 1$, p-value $= 0.0001$	–
I.6: Differences in minimum sizes	$\chi^2 = 2.5$, df $= 1$, p-value $= 0.11$	–
I.7: Differences in size classes structure	$\chi^2 = 0.09$, df $= 1$, p-value $= 0.76$	–
Analysis block II : HA–HA comparisons, aggregation effect		
II.8 : Similarity between LFDs for reference periods HA February–April and HA January–May (Table 4 categories B + C vs. D + E)	$\chi^2 = 3.8$, df $= 1$, p-value $= 0.049$	–
Analysis blocks III AND IV: HA–PA comparisons, HA reference periods indicated		
III.9a : Differences in LFDs, reference period February–April 1966–1971	$\chi^2 = 8.9$, df $= 1$, p-value $= 0.004$	–
IV.9b : Differences in LFDs, reference period January–May 1966–1971	$\chi^2 = 5.1$, df $= 1$, p-value $= 0.02$	$p = 0.08$
IV.10 : Similarity between 9a and 9b	Odds ratio = Inf, p-value $= 0.005$	$p = 0.19$
III.11 : Association between regions for significant LFD changes, months February–April, 1966–1971	Odds ratio = 0, p-value $= 0.53$	–
IV.12 : Association between regions for significant LFD changes, months January–May, 1966–1971	Odds ratio = 0.62, df $= 1$, p-value $= 1$	–
III.13 : Association between significant LFD changes and increases in maximum size in 2015, reference period February–April, 1966–1971	Odds ratio = 13.53, p-value $= 0.08$	–
IV.14 : Association between significant LFD changes and increases in maximum size, reference period January–May, 1966–1971	Odds ratio = 3.68, p-value $= 0.19$	$p = 1$
III.15 : Association between significant LFD changes and decreases in minimum size, reference period February–April, 1966–1971	Odds ratio = 0.43, p-value $= 0.61$	–
IV.16 : Association between significant LFD changes and decreases in minimum size, reference period January–May, 1966–1971	Odds ratio = 0.82, p-value $= 1$	–
IV.17 : Increase in presence of older size classes in either year, reference period January–May, 1966–1971	$\chi^2 = 0$, df $= 1$, p-value $= 1$	–
IV.18 : Association between changes in size classes structure and region, reference period January–May, 1966–1971	Odds ratio = Inf, p-value $= 0.009$	$p = 0.02$
Time-averaging[a]		
Hypothesis 19 No joint changes in minimum and maximum sizes in relation to 1966–1971	$\chi^2 = 11.5$, df $= 1$, p-value < 0.001	$p = 0.003$

[a] III.10 for species–region combinations with inclusion index >0.75 (from analysis block IV) indicates a difference between HA reference periods February–April and January–May, which can be either interpreted as effect of under-sampling and subsequently high type II errors or time-averaging, see Discussion.

Tests are applied against H_0 with a uniform distribution, equivalent to an odds ratio of 1 in Fisher's exact test. For odds ratio values = Inf, the 95% confidence limits was >>1 . In each case, H_0 may be formulated as "No. . ." and the hypothesis text pasted.

sampling and environmental effects on mesopelagic historical (HA) and present fish assemblages (PA). Size-based criteria have been applied in paleobiological studies to indicate changes in ecological "fidelity" (see Miller *et al.*, 2014). Four major sources of uncertainty were considered (Table 1), i.e. under-sampling, time-averaging, collection bias, and environmental change. The major analytical trade-off was between under-sampling and time-averaging, i.e. to reduce type II error susceptibility of the analysis as evidenced by inclusion index values while probably increasing HA variability owing to including more historical sampling months and years. One sign for time-averaging is increased variability in size metrics owing to environmental influences, i.e. minima, maxima, and LFDs. The climate indicator North Atlantic Oscillation index (NAO, Supplementary Figure S10) was low for the period 1965–1971 and 1977–1979, so it can be concluded that similar oceanic conditions were prevailing in that period. Time-averaging as simultaneous changes in minima and maxima was not evident (Table 4, hypothesis 19), whereas changes in LFDs were significant with all species–region combinations considered and marginally significant in analysis block IV taking into account the 0.75-criterion combinations (IV.9b). Another way to elucidate time-averaging effects is to split HA into several subunits and to repeat the HA–PA analysis with each HA subunit (Terry, 2010). In this study, two different HA reference periods are analysed in analysis blocks III and IV (Figure 2). Time-averaging could only be potentially inferred from the performance of the two tests for hypothesis IV.10 (Table 4), indicating that similarity in HA–PA comparisons disappears between the two HA reference periods when the 0.75-criterion is applied. Time-averaging and hypothesis IV.10 can be further evaluated in light of analysis block Ia, showing that a seasonal effect was associated with significant changes in size metrics, whereas for analysis blocks III and IV these changes were not significantly associated with LFD structure (Table 4, III.13–IV.16), except for a marginal value of $P = 0.08$ obtained for a HA–PA increase in maximum size with regard to the HA reference period

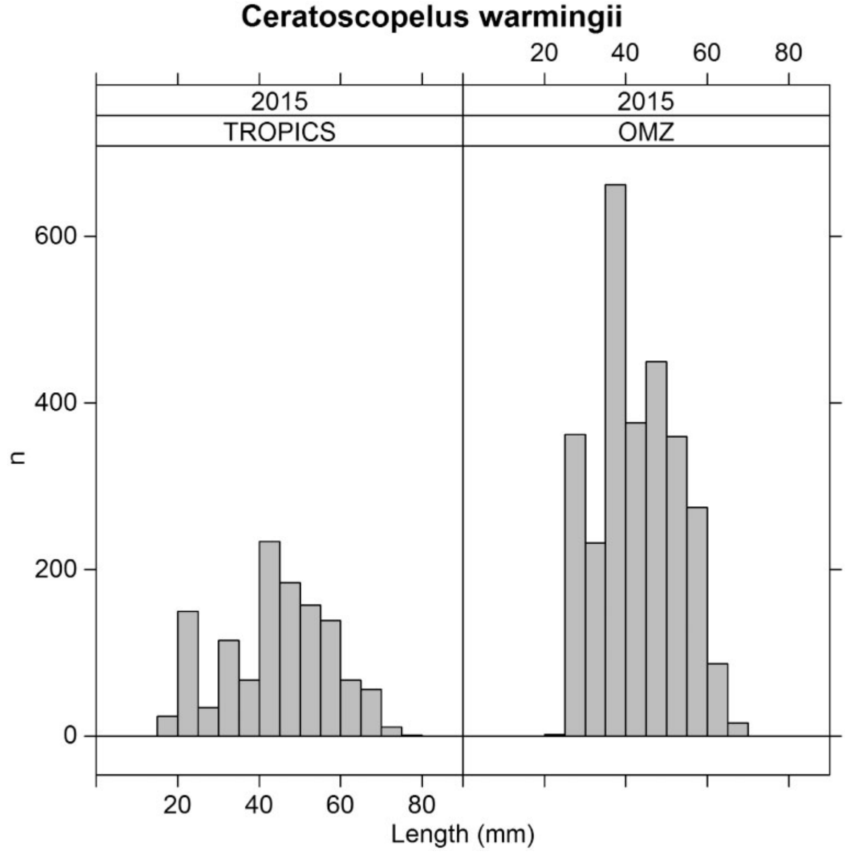

Figure 4. LFD of the myctophid *Ceratoscopelus warmingii* in the tropics and the OMZ region for 2015 (see Figure 1). Numbers refer to measured specimens of the measurement categories "fd" and corresponding "rge" records, but are not raised to total population abundance.

February–April (III.13). No association was evident in hypothesis IV.14 when considering combinations satisfying and non-satisfying the 0.75-criterion of the inclusion index. Because hypotheses IV.10 and III.13 are only significant including the combinations with low inclusion index values, the interpretation is equivocal either in terms of under-sampling creating spurious contrasts or in terms of time-averaging creating more variability and random structure comparing from III.13 ($P = 0.08$) to IV.14 ($P = 0.19$). All comparisons in analysis block III referring to HA reference period February–April are subject to smaller sample size as evidenced by the low average inclusion index (see Table 3). Only one species–region combination met the 0.75-criterion for the inclusion index. In turn, in analysis block IV for the HA reference period January–May, 11 out of 28 combinations passed the 0.75-criterion, as did 4 out of 8 in analysis block I. This indicates that analysis blocks IV were more robust than analysis blocks III. This robustness and the results for hypothesis 19 and IV.14 let us conclude that with regard to minimum and maximum sizes HA and PA selectivity patterns are not considered different and time-averaging is not likely to confound results with regard to a pooled PA. This is further corroborated by the low number of category D species in Table 3; with a significant effect of time-averaging this group should have been more pronounced.

With regard to collection bias and thus gear operations, trawling speed and type of tow must be considered. The probability of capture is positively linked to trawling speed (Pearcy, 1983), but no difference in average trawling speed between 1966–1979 and 2015 was indicated (Supplementary Material S2). In the case of double oblique tows for HA and horizontals tows for PA, patterns were analysed at community level with respect to different groups of species being subsequently excluded from the analysis to take account for the hypothesis that behavioural traits could confound the analysis of differently operated trawls (see discussion on swimming behaviour in Harrison, 1967; Gjoesaeter and Kawaguchi, 1980). The patterns did not change with the exclusion of vertically orientated species (Figure 6; Supplementary Figure S8), indicating that the pattern in the size range analysed (20–250 mm) was likely not biased from vertically orientated species.

In turn, the methodological approach is capable of indicating environmental change. Thus the differences in analysis block IV, i.e. the regional affiliation of change in population structure (Table 4, IV.18), and the subsequent changes in slopes of the biomass size spectra are likely attributed to environmental influences. Analysis block I shows that changes in LFDs and maximum sizes at species level were associated with environmental, i.e. OMZ, and temporal gradients, i.e. season. Unexpectedly, for the species investigated in the seasonal comparison maximum sizes during summer were smaller, indicating high mortality of older size classes in that season. For *Nannobrachium isaacsi* (Myctophidae), maximum size in July 2014 was 174 mm SL in the subtropics (no LFD analysis owing to low samples size), indicating that not all species showed a decline in maximum size.

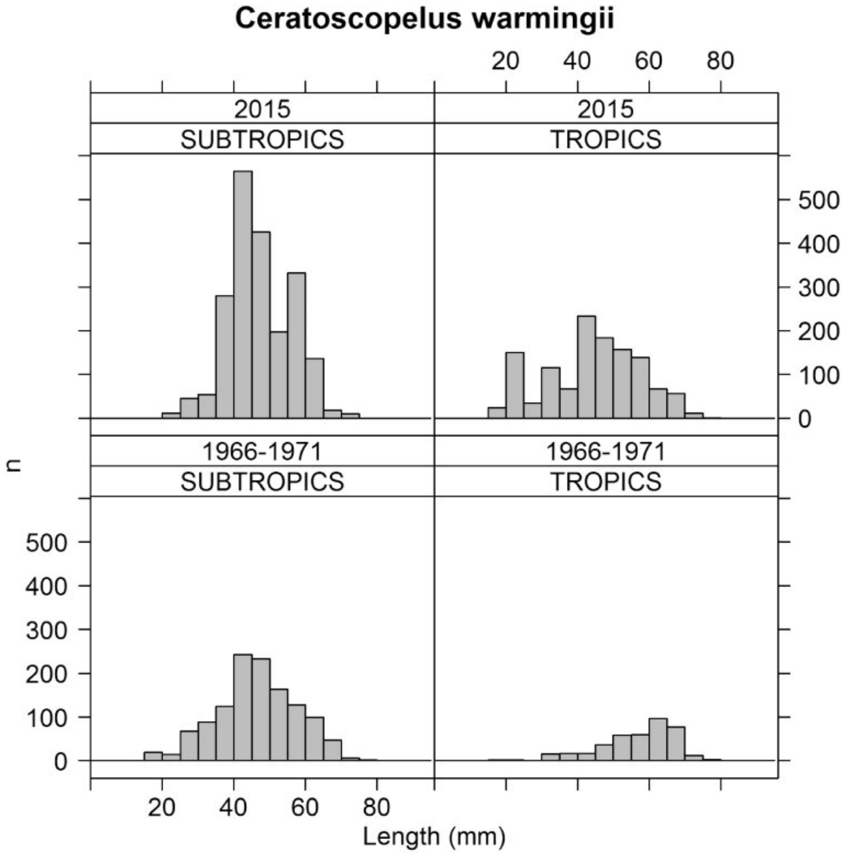

Figure 5. LFD of the myctophid *Ceratoscopelus warmingii* in the subtropics and tropics for 1966–1971 (reference period January–May) and 2015. Numbers refer to measured specimens of the measurement categories "fd" and corresponding "rge" records, but are not raised to total population abundance.

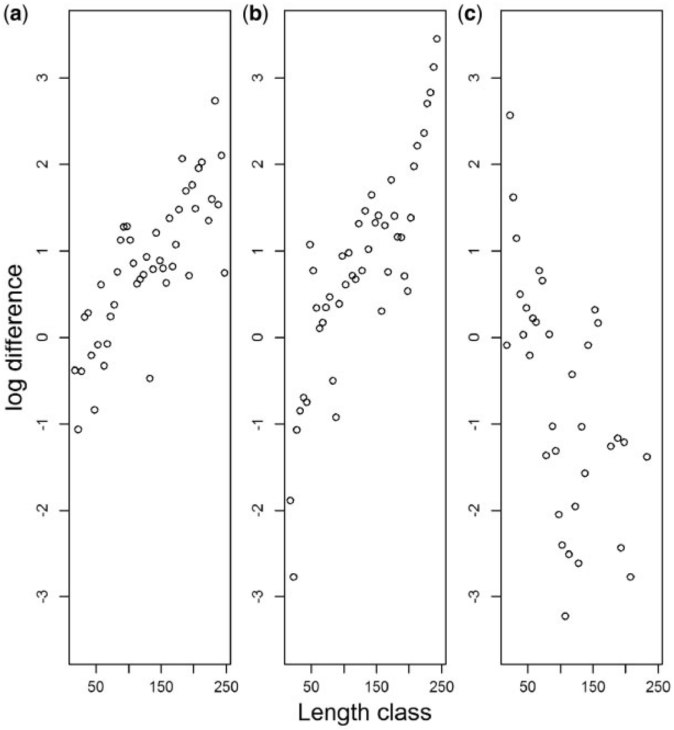

Figure 6. Log difference 1966–1971 to 2015 of LFD proportions by length classes. (a) Tropics, (b) subtropics, (c) temperate region (including 1979 data). Negative difference—proportion in 2015 greater than in 1966–1971.

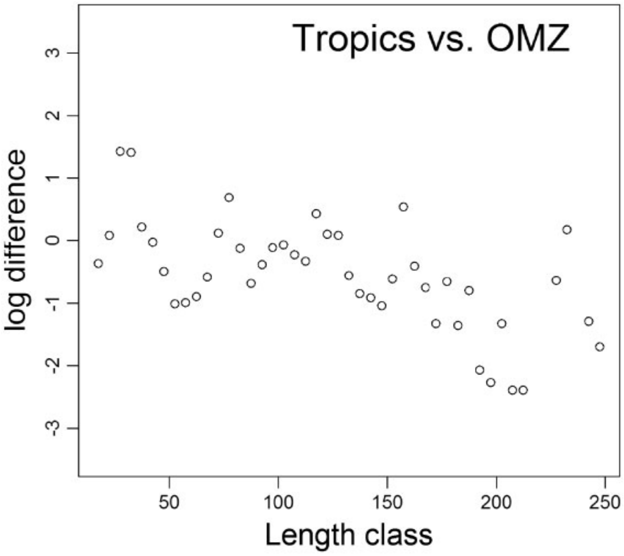

Figure 7. Log difference of LFD proportions by length classes for tropics and OMZ (see Figure 1). Negative difference—proportion in tropics greater than in OMZ.

Size-based criteria and gear selectivity in mesopelagic assemblages

On the basis of published evidence, size-based criteria prove successful to indicate differences in selectivity with regard to smaller nets. Examples applying a 5 ×7 m net in March–April 2015 in the central Eastern Atlantic ("Mesopelagos" net, 4 mm codend mesh size; Olivar *et al.*, 2017) show that in 12 out of the 15 cases maximum sizes were smaller than in this study, indicating a gear effect. Although surface migrators and certain small species (e.g. myctophids *Diogenichthys atlanticus*, *Notolychnus valdiviae, Gonichthys cocco*) are not well represented in Engel trawls (Hulley and Krefft, 1985), for smaller species not included in Table 4 maximum sizes differed only very little between the "Mesopelagos" and the "Aal"-trawl catches, e.g. myctophids *D. atlanticus* (24–24.3 mm SL) and *Benthosema suborbitale* (34–33.4 mm SL). In a comparative study of two midwater trawls (2.6 and 5.3 m^2), Gartner *et al.* (1989) showed that in all investigated species gear-correlated changes in size-based metrics occurred, i.e. smaller size classes (<35 mm) were enhanced in the smaller trawl, the larger net was more effective in size classes 35–65 mm, and maximum sizes were larger in the large net but never in the smaller net.

Reported maximum sizes for the species considered differed in most cases only little from the maximum sizes indicated in this

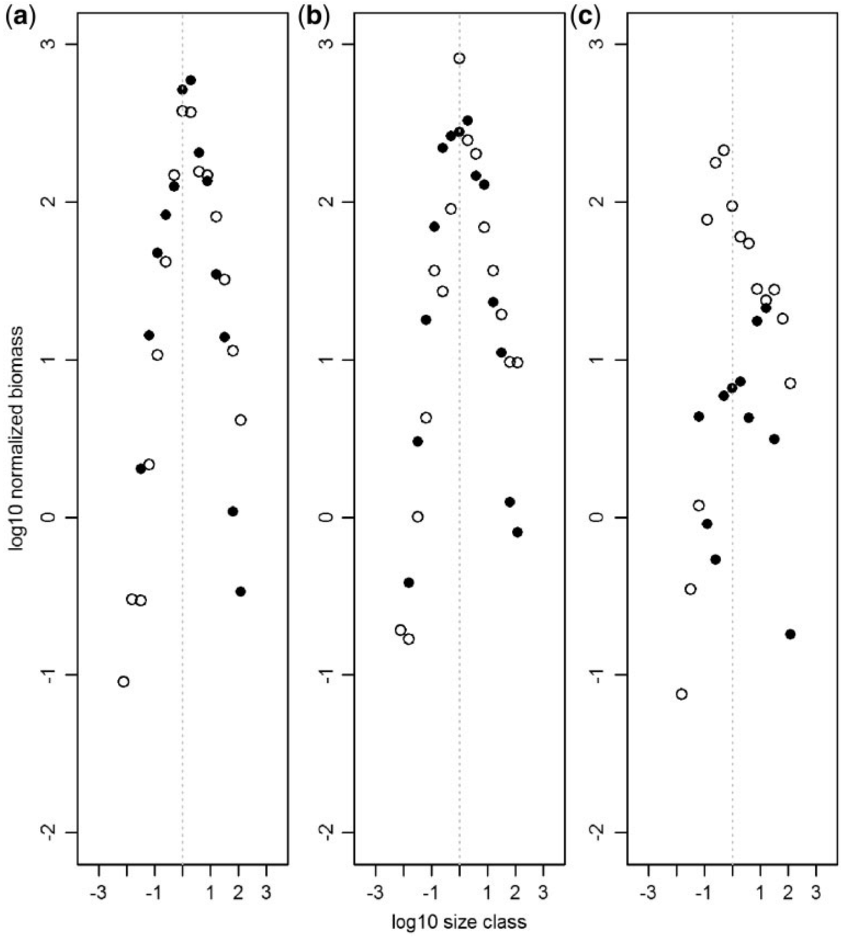

Figure 8. Normalized biomass size distribution plots for historical (open circles) and 2015 data (closed circles) by region, (a) tropics, (b) subtropics, (c) temperate region. Values are standardized to 30 min twos but not to different trawl openings. Vertical line indicates size classes 2°g.

study for the respective regions (Table 3), indicating that an almost representative upper size range was sampled in both historical reference periods and in 2015. For the lower size range, Gartner *et al.* (1989) point out that nets with meshes >2 mm likely underestimate the lower size range (<30 mm SL) considerably. A specimen of 30 mm SL has an approximate weight of 2^{-1} g, so that this observation conforms to the inflection point of the biomass size distributions (see below, Figure 8). Accordingly, Olivar *et al.* (2017) showed that sampling efficiency for *Cyclothone* spp. in MOCNESS1 plankton nets with 0.2 mm mesh size was significantly higher than for the "Mesopelagos" net.

Community metrics and biomass size spectra

We expected that a change in the inflection point of the biomass size spectrum would indicate a change in selectivity as can be seen in the example of Trenkel *et al.* (2004). The peak of the biomass size distribution in this study was observed at ca. 2° g, which was fairly the same as for Gartner *et al.* (1989) with nets <10 m^2. It can be concluded, that the increasing susceptibility of small specimens to smaller mesh sizes probably has a trade off in the necessarily smaller physical dimensions of trawls with smaller meshes, so that reaction distances are still sufficient to avoid trawls despite smaller and more effective mesh sizes.

At community level, patterns in the log difference figures need to be interpreted in line with biomass size distributions. For the temperate region, the biomass size distribution showed that this region was likely data deficient in 2015, so that different patterns in the log difference plot (Figure 6C) are considered spurious when compared with respective figures for the subtropics and tropics (Figure 6a and b).

Slopes of the biomass size spectra were steeper in 2015 than in 1966–1979. The highest value of −0.5 was indicated for HA in the temperate region. The range of the other values was −0.59 to −1.28. Applying the model framework of Jennings and Blanchard (2004), scaling of the biomass size spectrum is dependent on trophic efficiency (TE) and predator–prey mass ratio (PPMR) as $M^{\log 10(\mathrm{TE})/\log 10(\mathrm{PPMR})+0.25}$ for un-normalized spectra. They calculated a slope of −0.1 for an unfished assemblage in the North Sea, equivalent to −1.1 for a normalized spectrum, and of −1 for a strongly fished assemblage corresponding to −2 for a normalized slope, on the basis of basic assumptions of TE = 0.125 and PPMR = 390. This indicates that our slopes correspond to the case of unfished assemblages. Normalized slopes greater than −1 would require a re-parameterization of TE and PPMR probably in the direction of higher TE, which would be affected by the productivity regime and or habitat. Heymans *et al.* (2014) showed that TE increases with depth of habitat shown for habitats from 5 to >200 m depth, where in shallow bays and lagoons much production at all trophic levels is lost to detritus. Considering the depth of the mesopelagic zone, high variability in TE must be expected. Results for zooplankton indicate that slopes become steeper with increasing productivity and thus show strong seasonality (San Martin *et al.*, 2006; Zhou *et al.*, 2009). The interpretation of changes in biomass size spectra slopes in line with productivity corresponds to results from Haedrich (1986), where an increase in ocean primary production was correlated with a shift in the biomass size spectrum of mesopelagic fishes towards an increase in the number of smaller specimens. The clear intersection of HA and PA biomass spectra for the tropics (Figure 8a) conforms to model results of trophic spectra from Gascuel *et al.* (2005) after reduction of top-down control. Apparently this effect was less pronounced in the subtropics, indicating a potential impact of fisheries for large migratory species on mesopelagic biomass, knowing that small mesopelagics constitute a major prey for juvenile tuna in the eastern tropical Atlantic (Ménard *et al.*, 2000).

Alternatively, temperature aspects might be considered. Brandt (1981) showed that with increasing water temperature myctophid size distributions shifted towards smaller specimens. These *in situ* findings are congruent with theoretical considerations suggesting changes in size as an effect of increasing oxygen demand with increasing water temperatures (e.g. Cheung *et al.*, 2012). The results of this study may be interpreted in line with these results, indicating that observed changes in community LFDs between OMZ and tropical region were similar to changes between historical and 2015 samples after a period of warming (see Figure 1), indicating a relative increase in smaller specimens in both cases.

However, the potential response of pelagic fishes to temperature changes must be weighed against their capability to inhabit a wide range of thermal habitats by means of their daily vertical migration (DVM). Mesopelagic fishes may be thus better adapted to strong temperature gradients and may be able to find their optimum along this gradient (Jennings and Collingridge, 2015). In case of combined effects of warming and decline in oxygen availability, a suite of responses are possible that would lead to a decrease in maximum sizes (Ekau *et al.*, 2010): changes in growth owing to higher metabolic demands of respiration, avoidance of OMZ regions by larger specimens, and changes in spatial patterns including DVM so that they are not captured. Differences in DVM characteristics are evident between the tropical Atlantic and the OMZ region, indicating increased fluxes in the latter as indicated by hydroacoustics (Klevjer *et al.*, 2016). Regarding a possible long-term trend, these increased fluxes could be linked to increased productivity, given that trade winds have increased (Polyakov *et al.*, 2010) likely influencing coastal upwelling.

Supplementary data

Supplementary material is available at the *ICESJMS* online version of the manuscript.

Acknowledgements

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SYNOPTIC DISCUSSION

Regional patterns in mesopelagic fish communities of the tropical North Atlantic

Biogeographic composition

As part of **articles 1 and 2**, we investigated the biogeographic composition of mesopelagic fish communities in three different ecoregions of the tropical North Atlantic. Our results confirm that depth occurrence and migration behaviour are important factors of biogeographic distribution patterns in mesopelagic fish species. Significantly distinct communities of diel migratory species were found in epipelagic layers during night-time between stations bordering ecoregion (ER) 26 'Mauritania/Cape Verde' and ER 27 'Tropical & West Equatorial Atlantic' (**article 1**), while at greater depths, regional variations diminished and species assemblages shared a greater number of species. In species clusters sampled during night-time between 200 and 500 m, regional patterns were still apparent in the community analysis, reflecting a response to regional surface productivity patterns and variations in sinking flux to deep sea ecosystems. Based on limited sampling of only four stations, the deeper mesopelagic fish community (below 500 m) sampled during day- and night-time in ER 26 and ER 27 in the secondary mesopelagic SSL was regionally even more homogenous, in response to the decrease in environmental variation and turbulence (Krefft, 1976). Nevertheless, vertical plasticity in the spatial domain has been demonstrated in deeper mesopelagic and bathypelagic species due to competitive effects and local heterogeneity in environmental conditions, e.g. water masses or prey availability (Angel and Fasham, 1975; Krefft, 1976; Marshall, 1979). The platytroctid *Searsia koefoedie* is e.g. described as a species with subtropical distribution pattern that shows comparatively shallow main occurrences ~500–600 m at its northern and southern distributional borders, whereas it is found deeper than 1000 m in the centre of its range related to warm saline water masses (Krefft, 1976). Considering that present mesopelagic fish biogeographic schemes represent only a few of the 200 taxonomic families and + 2000 species of meso- and bathypelagic fishes; most of which are non-migratory and occur at greater depths (Priede, 2017), increased knowledge about these deeper occurring species and their biogeographic patterns is expected to add to the complexity of the existing mesopelagic biogeographic schema.

Table 1: Dominant mesopelagic fish species composition in different ecoregions of the tropical Atlantic by different authors. Distribution patterns according to Hulley (1981) and Backus (1970)

Ecoregion	*Study*	*Dominant Species*	*Pattern*	*Rel. contrib.*
ER 24	**Article 2 - all samples**	*Scopelogadus mizolepis*		19%
Central North		*Ceratoscopelus warmingii*	BT	13%
Atlantic		*Nannobrachium cuprarium*	ST	12%
		Bolinichthys photothorax	T	6%
		Hygophum cf. taaningi/macrochir	BT/T	4%
		Melamphaes gen. sp.		4.5%
		Lepidophanes guentheri	T-BT	3%
		Lampanyctus photonotus	BT	3%
	Article 2 - epipelagic SSL	*Ceratoscopelus warmingii*	BT	
	(#316, 27° N, 52 °W)	*Hygophum cf. taaningi/macrochir*	T/BT	
		Lepidophanes guentheri	T-BT	
		Lampanyctus photonotus	BT	
	Hulley and Krefft (1985)	*Ceratoscopelus warmingii*	BT	
		Hygophum hygomii	ST	
		Lobianchia gemellari	BT	
		Hygophum benoiti	T	
		Lobianchia dofleini	W	
		Diaphus mollis	BT	
	Sutton et al. (2010)	*Cyclothone spp.*		
	(station 3)	*Lampanyctus photonotus*	BT	
		Ceratoscopelus warmingii	BT	
	Backus (1970)	*Lepidophanes gaussi*	ST	
	Sargasso Sea Pattern	*Diaphus effulgens*	ST	
		Chauliodus danae		
		Eustomias cf. obscurus		
		Idiacanthus fasciola		
	Porteiro (2005)	*Chauliodus danae*		46%
	(North Atlantic tropical Gyre – West (‘NATR-W’), only stomiids considered)	*Idiacanthus fasciola*		12%
		Photostomias guernei		12%
ER 26	**Article 1**	*Diaphus vanhoeffeni*	T	26%
Mauritania/		*Lepidophanes guentheri*	T-BT	11%
Cape Verde		*Vinciguerria nimbaria*	T	10%
		Notoscopelus resplendens	BT	8%
		Hygophum macrochir	T	7%
		cf. Hygophum macrochir/taaningi	T/BT	3%
	Olivar et al. (2017)	*Myctophum affine*	T	total of 57%
	(cluster B;	*Lampanyctus alatus*	BT	
	stations #7 to #10)	*Notolychnus valdiviae*	W	

		Hygophum macrochir	T	
		Lobianchia dofleini	W	
	Backus et al. 1977	*Diaphus holti*	E	16%
		Lepidophanes guentheri	T-BT	15%
		Lampanyctus pusillus	Temp-SST	10%
		Ceratoscopelus maderensis	Temp-SST	9%
		Diaphus vanhoeffeni	T	8%
	Porteiro (2005)	*Stomias affinis*		10%
	(eastern tropical Atlantic	*Stomias lampropeltis*		9%
	(ETRA); only stomiids)	*Chauliodus schmidti*		8%
ER 27 Tropical and West Equatorial Atlantic	**Article 1**	*Diaphus dumerilii*	BT	6%
		Hygophum taaningii	BT	14%
		Diaphus fragili	T	6%
		Diaphus perspicillatus	BT	6%
		Lepidophanes guentheri	T-BT	6%
		Benthosema suborbitale	BT	5%
	Olivar et al. (2017)	*Diaphus brachycephalus*	BT	total of 55%
	(group A;	*Ceratoscopelus warmingii*	BT	
	stations from #3 to #6)	*Lepidophanes guentheri*	BT	
		Lampanyctus nobilis	T	
		Diaphus mollis	BT	
	Eduardo et al. (2021)	*Bolinichthys distofax*	ST	Total of 66%
		Diaphus brachycephalus	BT	
		Diaphus perspicillatus	BT	
		Diaphus splendidus	BT	
		Electrona risso	W	
		Hygophum taaningi	BT	
		Lampanyctus nobilis	T	
	Porteiro (2005)	*Chauliodus sloani*		22%
	(western tropical Atlantic	*Astronesthes ricardsoni*		23%
	(WTRA); only stomiids)			
ER 28 Guinea Basin and East Equatorial Atlantic'	**Kobyliansky et al. (2010)**	*Diogenichthys atlanticus*	T	Myctophidae Total of 81%
	(polygon 2, #2170, #2172)	*Benthosema suborbitale*	T	
		Lampanyctus sp.		
		Diaphus vanhoeffeni	T	
		Hygophum macrochir	T	
		Vinciguerria nimbaria	T	25%
	Backus (1970)	*Vinciguerria nimbaria*	T	
		Notolychnus valdiviae	W	
		Lepidophanes guentheri	T-BT	
		Diaphus vanhoeffeni	T	
		Ceratoscopelus warmingii	BT	

T = tropical, BT = broadly tropical; ST = subtropical; SST = semi-subtropical; temp = temperate; W = widespread.

The relative contribution of myctophid species with a tropical distribution pattern (Hulley, 1981) to the dominant myctophid species composition decreased in our study from ER 26 'Mauritania/Cape Verde' (5 tropical, 2 broadly tropical) to ER 27 'Tropical & West Equatorial Atlantic' (4 tropical, 4 broadly tropical, 1 widespread) to ER 24 'Central North Atlantic' (2 (3) tropical, 4 (5) broadly tropical, 2 subtropical). This was unrelated to regional patterns in surface and midwater temperatures, which were lower in ER 26 compared to ER 24 at the time of our sampling. According to Backus et al. (1977), the northern limit of the tropical region in the eastern Atlantic is defined by the 14°C isotherm at 200 m depth, but lower temperatures of 13 °C at 200 m depth were measured in ER 26 and north of 2 °N in ER 27. These data support the concept that in regions with high seasonal variability, as our study regions between ER 26 and ER 27, biogeographic boundaries seasonally diverge from static lines based on mean annual oceanographic characteristics (Sutton et al., 2017).

The biogeographic composition presented in **article 2** for ER 24 was based on a sampling scheme which differed from ER 26 and ER 27, in that we predominantly targeted depths between 100–300 m during night-time, including only one night-time tow in the epipelagic SSL. The dominant mesopelagic fish species composition in ER 24 suggest a stronger influence of tropical species to the community composition of the southern part of the Sargasso Sea compared to its northern part (Table 1). In comparison, the study by Hulley and Krefft (1985), sampling with an EMT 1600 commercial midwater trawl and an intermediate sized IKMT (Isaacs Kidd Midwater Trawl) in a more north-eastern geographical area of the Sargasso Sea, reported numerical dominance of subtropical, temperate and widespread species in addition to the myctophid *N. cuprarium* (subtropical, gyral-eye subpattern), that was dominant in both studies. Sampling with a 10-m^2 mouth-area MOCNESS (Midwater Opening/Closing Net and Environmental Sensing System), Sutton et al. (2010) reported very low catches of fish species other than the gonostomatids *Cyclothone spp*. in comparison. Backus (1970) identified the 'Sargasso Sea pattern', to which they assigned migratory species that were uncommon in the previous studies, but further the non-diel migratory stomiids *Chauliodus danae*, *Eustomias cf. obscurus* and *Idiacanthus fasciola.* Of all of these, only *C. danae* was collected regularly between 200–300 m in our study. This conforms to the typical stomiid species assemblage (with average abundances of 46% for *C. danae*) identified by Porteiro (2005) for the province North Atlantic Tropical Gyral – Western part ('NATR-W'; sensu Longhurst, 2007). Further important stomiids in his study were *I. fasciola* and *Photostomias guernei* (both contributing each 12%), which we only caught in single numbers, likely related to shallower sampling depths.

In ER 26 and ER 27, the dominant species composition was driven by largest catches in the epipelagic SSL (between 45–85 m) during night-time. Except for *H. macrochir*, our results of the most abundant species in ER 26 deviated in relative contribution from those reported by Olivar et al. (2017) for their cluster B (stations #7 to #10; Table 1). Olivar et al. (2017) sampled with a comparatively smaller-sized net ('Mesopelagos trawl', mean mouth opening of 5 × 7 m, total length of 58 m, 30 mm body mesh, 4 mm cod-end mesh size) between the surface and 1000 m during the same season and year at partly matching locations (#7–#318 and #8–#337), but including more northern stations (#9 and #10). The differences in community composition likely partly reflect characteristics connected to the gear and trawling operations, i.e. presumably predominantly mesh size selectivity and contiguous *vs*. non-contiguous sampling, but geographical influence of northern *vs*. southern locations seems further important. Inadequate sampling of *Notolychnus valdiviae* by the Aalnet used in our study was shown earlier (Hulley and Krefft, 1985). Compared to these two studies, increased occurrences of temperate, temperate-subtropical and subpolar-temperate species were reported in studies covering the northern parts of ER 26 (Backus et al., 1977). This strengthens the notion that ER 26 hosts distinct mesopelagic fish species communities in a transition from northern to southern waters, as well as from inshore slope, through the upwelling region to offshore waters (Badcock, 1981; Priede, 2017; Sutton et al., 2017). The dominant species community in ER 26 in our study showed in fact larger resemblance to communities reported as representative for ER 28 'Guinea Basin and East Equatorial Atlantic' (sensu Sutton et al., 2017) by Priede (2017; citing Kobyliansky et al. (2010)), as well as by Backus (1970) for their 'Guinean Province' (which differs from Sutton et al. (2017) by extending uninterruptedly in the eastern tropical Atlantic). ER 28 (Sutton et al., 2017) is characterised by increased productivities due to intensification of the Southeast trade winds, as well as an oxygen minimum zone (OMZ) and high species richness; all of which conditions apply equally to the southern part of ER 26 during the time of our sampling (March/April). Regional similarity in biogeochemical aspects between ER 26 and ER 28 was also demonstrated by Reygondeau (2018).

Our dominant species community in ER 27 shows overlaps in composition with findings by Olivar et al. (2017) and Eduardo et al. (2021), but relative abundances and dominance vary considerably. The dominant species in Olivar et al. (2017)'s group A (stations from #3 to #6), — sampling partly matching (#5–#333 and #6–#324), but also partly more south-western stations, — were also caught in the present study, albeit in lower numbers and *vice versa*. Eduardo et al. (2021) sampled the north-eastern Brazilian Coast at 3 °S, using a micronekton trawl (body mesh: 40 mm, cod-end mesh: 10 mm, estimated opening area: 120 m^2). Compared to both studies, low abundances of *Diaphus brachycephalus, D. splendidus* and *Lampanyctus nobilis,* that are known to occur also in our sampling region (Hulley, 1981; Nafpaktitis et al., 1977)*,* were caught in our study. This likely results from the discrete sampling scheme during our study, that apparently missed the vertical abundance maxima of these species at lower epipelagic (*D. brachycephalus*, *D. splendidus)* and upper mesopelagic depths (*L. nobilis*). Our data confirm the distributional gap of *D. dumerilii* and *D. fragilis* in productive upwelling waters (Hulley, 1981) for latitudes between ~8.5° N–12.3° N, corresponding to our OMZ stations.

Key constituents of the community at upper mesopelagic depths in ER 26 and ER 27 during day- and night-time were the sternoptychids *Argyropelecus affinis* and *A. sladeni,* the myctophid *Electrona risso* and the stomiids *Chauliodus schmidti/sloani/sp.* Despite this resident population of limited and non-migratory species, results from clustering and nMDS analyses (**article 1)** suggested that daytime tows were significantly distinct from night-time tows at corresponding layers, due to varying contributions of other species. These findings correspond with results from off southern California, in which factor analysis of the catches of deep midwater fishes revealed a complex of four resident communities, which interact with a number of transitory, presumably less stable groups (Ebeling et al. 1970). Our results of these key upper mesopelagic species are in line with studies from the western tropical Atlantic that suggested the functional importance of sternoptychids and *Chauliodus sloani* in tropical ecosystems (Eduardo et al., 2020a, 2020b). Porteiro (2005) equally reported *C. sloani* (22%)

and further *Astronesthes richardsoni* (23%) as most numerous in the region 'Western tropical Atlantic' (WTRA), corresponding largely to ER 27 and further encompassing our study area in ER 26. In the eastern tropical Atlantic (ETRA, both sensu (Longhurst, 2007)), which borders ER 26 in the eastern part, the stomiid *C. schmidti* (8 %) ranked only third, following *Stomias affinis* (10 %) and *S. lampropeltis* (9 %), whereas in our study *C. schmidti* was the dominant stomiid in ER 26. Daytime tows in the secondary mesopelagic SSL were not significantly different from night-time tows in the principal mesopelagic SSL in ER 26 and 27, suggesting likely ubiquitous occurrence of a lower mesopelagic community at these depths. This community consisted in both regions of the sternoptychids *Sternoptyx diaphana*, the stomiids *Chauliodus schmidti/sloani,* the gonostomatid *Cyclothone spp.* and *the myctophids Lampanyctus tenuiformis.* Only in ER 26 we caught comparatively high abundances of the platytroctid *Searsia koefodie,* the melanostomiid *Malacosteus niger* and the sternoptychid *Argyropelecus gigas*. This suggests an impact of environmental conditions on vertical distribution patterns and/or regional densities in these species. Krefft (1974) mentions the, what he called 'pretentious' food requirements of *A. gigas*, that cause its absence in nutrient-poor regions, which may equally apply to other species. We caught *S. koefoedi* at the southernmost position of 4 °N, which is further south than reported by Krefft (1976) and suggests a possible seasonal shift in distribution patterns in this species related to the southern position of the ITCZ during the time of our sampling. *M. niger* reportedly has a widespread pattern and possibly shows regionally varying depth distributions between the equatorial and the OMZ region in response to local heterogeneity in environmental conditions.

Functional composition and hydroacoustic structure

In functional terms, our results from **article 1** emphasise the important contribution of non-diel migratory fishes to tropical SSLs. At all stations in both, ER 26 and ER 27, non-diel migratory fishes made up the largest proportions of total tow community composition (abundance and biomass) in the principal and secondary mesopelagic SSL during night-time (375–680 m) and during most daytime tows (low-oxygen region: 390–555 m, equatorial region: 325–500 m). This corresponds with results of Badcock and Merret (1977) who sampled 100 m depth strata with an RMT8 at a location near station 309 (day)/311 (night), and demonstrated substantially larger proportions of swimbladderless fishes below 400 m. In terms of species, our study, that was based on comparatively larger size-spectra, indicated higher species numbers of non-diel migratory species at all investigated depths including the epipelagic layer, whereas in the study by Badcock and Merret (1977) the numbers of swimbladderless species was comparable below 200 m becoming larger below 500 m. The differences in size spectra caught by the RMT8 and the Aalnet are important factors to notice, as these authors discuss themselves that pronounced differences in vertical occurrence may be encountered in different life stages of the same species. In addition the assignment of species between 'swimbladderless' and 'non-diel migratory' may vary between the two studies. Due to their general lack of a gas-filled swimbladder, non-diel migratory species likely do not contribute much to overall backscattering of the main SSLs at operating frequencies of 38 kHz widely used in mesopelagic fish biomass assessments (Davison, 2011; Irigoien et al., 2014). They, therefore, go unnoticed as to their quantitative contribution to mesopelagic fish biomass and ecosystem fluxes, which is an important unknown (Klevjer et al., 2020; Koslow et al., 1997). In addition, we demonstrate that considerable biomass of fishes with likely regressed swimbladders (e.g. the melamphaid *Scopelogadus mizole*pis and the myctophids *Lampanyctus cuprarius* and *L. isaacsi* (Marshall, 1960)) existed in the comparatively low-backscatter epi-meso transition zone (between c. 100–300 m) in ER 24 and ER 26. In that regard, another important aspect is the increase in relative weighting of the rather large-sized myctophids *L. isaacsi, L. ater, L. lineatus* and *L. tenuiformis* when using biomass instead of abundances in our community analyses (**article 1)**. Since in terms of ecosystem functioning, biomass is the more important currency regarding metabolism, trophic level, species interactions and other factors (Andersen et al., 2016; Brown et al., 2004; Peters, 1983; Romero-Romero et al., 2016; Saint-Germain et al., 2007), these findings suggest the potentially important functional roles of these species. Relating SSLs to their resonant components is not trivial, especially in diverse tropical ecosystems (e.g. Davison, 2011; Davison et al., 2015). In our study, the incomplete availability of taxonomic data of all micronekton groups, as well as sampling limitations of the Aalnet regarding fish body sizes < c. 30 mm do not allow a direct comparison of catch biomass *vs.* backscattering strength, because a significant source of scatter is lacking.

Hydroacoustic profiles (38 kHz) investigated in **articles 1 and 2** showed strong variation in the formation, amplitude and backscattering strength of SSLs between the three ERs, as well as between eastern and western oxygen minimum zone (OMZ) stations in ER 26. The main backscattering (38 kHz) in the principal and secondary mesopelagic SSL deepened progressively on a productivity gradient from the eastern OMZ (principal SSL: 300–450 m/secondary SSL: 500–550 m) to the western OMZ (350–450 m/550–650 m) in ER 26, to ER 27 (350–500 m/600–700 m) and further to ER 24 (450–700 m/750–850 m). This implies a concomitant regional gradient in migration amplitude of the underlying mesopelagic community, which seemed to be particularly reduced in ER 26. These data are in line with results from larger-scale studies that demonstrated regional differences in daytime main SSL depths between the eastern equatorial and the central part of the Atlantic ocean (Bianchi and Mislan, 2016; Klevjer et al., 2016). The differences were related to an impact of physico-chemical properties on the vertical functional processes in mesopelagic communities, whereby sub-surface oxygen concentration and turbidity were the most important parameters identified. This is in line with low-oxygen and productive conditions in ER 26 compared to ER 27 and ER 24. Coastal upwelling off West Africa reaches its southernmost location in boreal spring (Van Camp et al., 1991) and was also indicated from satellite chlorophyll data for the months February/March 2015. A relationship to productivity is supported by a study conducted at 20 °N during March/April 1982, which equally demonstrated pronounced differences in SSL daytime depth and structure on a gradient from near-coastal upwelling (18 °W) to offshore areas (36 °W) (Schalk, 1988). In the study by Schalk (1988) the principal and the secondary mesopelagic SSL seemed merged during night-time in the upwelling area at 18 °N, and a generally shallower located principal mesopelagic SSL was observed; contrary to offshore stations. This is similar to our results that show merging of the principal and secondary mesopelagic SSL to one layer at 350–450 m at the eastern OMZ station 309/311, whereas in ER 24, ER 27 and the western part of ER 26 continuous bands of comparable mean backscattering strength were observable in the principal and secondary mesopelagic SSL during day- and night-time. Generally differing vertical migration patterns under upwelling conditions were suggested by the authors, as e.g. demonstrated for *Benthosema glaciale* (cf. discussion in Schalk, 1988).

Vertical community and trophic structure between the equatorial and OMZ region

Based on clustering and nMDS ordination (**Article 1**), as well as using stable isotope analysis (**Article 3**), regional differences in mesopelagic fish functional community composition and trophic structure were indicated between ER 26 and ER 27, as well as between the eastern and the western OMZ region. Our results from these analyses overall support the hypothesis of vertically restructured mesopelagic communities and food webs in the eastern OMZ compared to the other regions in agreement with the observed hydroacoustic patterns based on 38 kHz. Firstly, community analysis indicated increased mixing between diel migrators and non-diel migrators in ER 26 compared to ER 27, based on several results: (i) Tows in the epi-meso transition zone at eastern OMZ stations 306 and 311 were clustered together with comparatively deeper tows. (ii) In addition, only the dominant diel migratory species of the LO (i.e., *N. isaacsi, C. warmingii, N. resplendens, L. guentheri and H. macrochir*) also showed consistent presence in the principal mesopelagic SSL during night-time. It needs to be mentioned here, that because of vertically separated discrete sampling in our study, these findings may possibly be spurious, since in ER 27, diel migratory species that were caught in the epipelagic SSLs may have been present also at mesopelagic depths, albeit at different strata than sampled in our study. (iii) Moreover, stable isotope analysis suggested increased niche overlap between the feeding-migrator guilds epi and mesopelagic copepod feeders in the eastern OMZ, contrary to the equatorial region, where the isotopic niches of epi- and mesopelagic copepod feeders were clearly separated. Secondly, our analysis indicated also differences in the vertical ecology of generally deeper occurring non-diel migratory and predatory members of the mesopelagic fish community in ER 26, especially in the eastern OMZ. This was indicated by (i) increased proportions of non-diel migratory species in the principal epi- and mesopelagic SSL, and the largest proportions of predatory species in these SSLs at the eastern OMZ stations. (ii) Contrary to the equatorial region and previous findings from the oligotrophic Pacific near Hawaii (Choy et al., 2015; Romero-Romero et al., 2019), there clearly was no depth-related increase in $\delta^{15}N$ values in the species observed in the eastern OMZ. This was reflected by a comparatively reduced $\delta^{15}N$ enrichment relative to baseline values in the OMZ in all trophic levels higher than epipelagic copepod feeders.

Although a variety of aspects could be responsible, the combined data from hydroacoustics, community and trophic analyses suggest that these deeper occurring non-diel migratory species feed at shallower depths on prey with lower $\delta^{15}N$ signatures. Alternatively, or additionally, feeding on lower trophic prey, that would equally be expected to have reduced $\delta^{15}N$ values, could be an explanation. Our analyses suggested increased niche competition in the OMZ and relative shifts in trophic niches in some species between the equatorial region and the OMZ, which fits both hypotheses. These results agree with an influence of upwelling conditions, while in addition, increased vertical biogeochemical gradients due to the presence of the OMZ could be partly influential by altering vertical food availability (Maas et al., 2014; Williams et al., 2014; Wishner et al., 2013). In addition, a correlation between hypoxia-threshold and hyperbaric threshold has been demonstrated in shallow water fish species (Brown and Thatje, 2015), which might potentially also be of relevance in certain mesopelagic species at their environmental niche boundaries. Due to the lack of comparative data from other OMZ regions for larger-sized mesopelagic fishes, and of more detailed vertical data at OMZ depths in our study, the relative impact of increased productivity *vs*. low-oxygen conditions on the vertical structure of mesopelagic communities could not be assessed in the present study.

Regional and temporal variation in relative condition and size structure

The analysis of condition factors among sub-regions in ER 26 and ER 27 in nine species in **article 4** supported the notion of particular conditions in the eastern OMZ compared to ER 27 and the western part of ER 26. In the eastern OMZ, the major part of analysed species showed the strongest increase in relative condition from small to large specimens. Relative condition is an indicator of a variety of individual or population physiological and nutritional aspects, that can be interpreted in terms of energy reserves, but further with respect to life history parameters e.g. reproduction and growth (Gubiani et al., 2020; Jakob et al., 1996). A possible explanation in our study, therefore, involves specific life history patterns in the mesopelagic fish species investigated, which are likely synchronised to the pulse of nutrient flux from the Mauritanian upwelling. In support of this, we demonstrate seasonal changes in length-frequency distributions (LFD) in the more northern located subtropical region in **article 5,** with smaller maximum sizes and increases in younger size classes in summer compared to spring. This is in line with results of the reproductive cycle in the myctophid *Notoscopelus resplendens* off the Canary Islands, that indicated a spawning season between January and April in the Canary Current region (Sarmiento-Lezcano et al., 2018). In the eastern OMZ region, random sampling revealed mature individuals of *L. isaacsi* and *S. koefoedi*, which suggests late mature stages in these species in this more southern location during the months March/April. Further indicative of this regional variation in life history patterns were higher abundances of smaller size classes in the OMZ compared to the equatorial region in the analysis of size structure in **Article 5**. Alternatively, this result may reflect the larger productivity in ER 26 with concomitant increases in smaller size spectra (Haedrich, 1986). Our observation, that all 14 investigated species had smaller maximum sizes in the OMZ compared to the equatorial region could alternatively be related to higher oxygen demands in the former region, since low-oxygen conditions favour smaller sizes due to advantageous body-mass-oxygen consumption ratios (Audzijonyte et al., 2019; Burleson et al., 2001). Although reproductive patterns cannot be ruled out in the mesopelagic limited migrators *A. sladeni, E. risso* and *S. mizolepis*, overall higher condition in the eastern OMZ is also in line with the earlier mentioned hypothesis of increased feeding opportunities at these stations, related to either, or a combination of, upwelling-induced increases in general productivity or particular feeding opportunities related to the OMZ. The fact that this pattern in relative condition was not observed in the ubiquitously encountered *A. affinis,* might be related to its specific adaptation of yellow lenses; possibly offering competitive advantage only under more oligotrophic conditions (Somiya, 1976). The observed decrease in relative condition in the majority of species sampled in the northern equatorial region in ER 27 suggests profound variability in overall life history patterns and/or food supply on rather small scales in these biogeographic boundary regions.

In **article 5** we further studied long-term changes in mesopelagic communities, using size-based indicators at the species (size class structure, extreme values and LFDs) and the community level (relative community LFD and biomass size distributions). Based on several analyses, robust results gave sufficient confidence to allow the conclusion that no severe influence of time-averaging was evident; neither of an obvious gear bias related to double oblique vs. horizontal towing. These indicators thus proved overall suitable to disentangle sampling from environmental effects, thereby supporting their usefulness in the study of ecosystem changes and environmental status (dos Santos et al., 2017; Jennings and Blanchard, 2004; Petchey and Belgrano, 2010; Shin et al., 2005; Trenkel et al., 2004). We observed smaller body sizes between the periods 2014/15 and 1966–79 in tropical and subtropical regions, corresponding to steeper slopes for the biomass size spectra. This possibly reflects long-term changes in mesopelagic fish communities of the eastern tropical and subtropical Atlantic in response to multiple coupled climate variations amplified by anthropogenic warming, and human fishing pressure on high trophic level and commercial fish species (Foltź et al., 2019; Yang et al., 2021). Smaller body sizes may be an adaptive response to temperature-related changes operating at the cellular, physiological and/or ecological organismal level, and are thereby strongly connected to food-web structure and oxygen supply (Audzijonyte et al., 2019). However, an additional influencing factor in our study are catching depths, which in present assemblages more often sampled biomass-rich epipelagic layers compared to historical assemblages (1966–79). Because mean body sizes increase with depth, a respective higher weighting of smaller-sized specimens in present assemblages compared to historical assemblages, could possibly additionally impact the perceived community size spectra.

Our perception of mesopelagic communities depends on the sampling method

The pelagic ocean basically is a black box which yields variable impressions of its inhabiting community depending on the sampling method employed to dip in. Each method has a specific "window of discrimination", allowing relatively sound estimates of community parameters in one place at point in time, outside of which specific sampling characteristics bias and distort natural patterns (Angel, 1977). This concerns all important community aspects, i.e. overall abundances and biomass, the relative contribution of broad taxonomic groups and the species and functional composition per taxon and size ranges, that all vary under the influence of spatio-temporal environmental and ecological conditions (e.g. Badcock and Merret, 1976; Heino et al., 2011). In that respect, no sampling method is superior to another, but each offers insights on specific taxonomic and size spectra of the mesopelagic community and its respective ecology. The particular advantage of large midwater trawls, such as the 'Aalnet' used in this study, lies in their improved ability to catch more sparsely distributed fish species by sampling much larger volumes of water compared to smaller sized gear. This may further level out local horizontal and vertical patchiness more effectively compared to e.g. an Isaacs-Kidd Midwater trawl (IKMT) or an RMT8 (mouth openings of c. 8 m^2) often used in mesopelagic studies. Additionally, large mesh sizes allow sufficient speed to catch faster swimming adult sizes also of larger species (Heino et al., 2011; Porteiro, 2005; Priede, 2017). Our knowledge regarding larger-sized species is very restricted due to generally low sample sizes collected as a result of major operational difficulties (Priede, 2017; Webb et al., 2010). The disadvantage of large commercial trawls is that due to their variable net geometry, mouth opening and unknown escapement, quantitative comparisons of catches by larger midwater trawls are not straightforward (Pearcy, 1983). Also the fact, that in our study we collected samples from specific and vertically separated strata, prevents an adequate quantitative analysis (see discussion in Badcock and Merret (1977)). Even though we sampled comparable depth horizons during similar daytimes per station in ER 26 and ER 27, this implies a static vertical biological situation per day and per night, which is an assumption that may not be met in reality due to variable light conditions affecting migration depth. Regarding these limitations, our biogeographic and community analysis is truly restricted to the specific SSLs sampled, and any generalisations drawn beyond these limits have to be considered with due caution.

In the early days of mesopelagic fish research, its fauna has been described as ‘Lilliputian fauna’ due to the apparent dominance of small-sized fishes less than 10 cm (Murray and Hjort, 1912). The repeated affirmation of this view based on gear and methodologies that are limited in accessing the larger size spectra of its community has framed our perception. Anecdotal evidence suggests that large-sized species and even “prize-sized” fish are likely more common, than apparent from trawl catches (Beebe, 1934; Harrisson, 1967; Heino et al., 2011). In addition, we are aware that much larger pelagic species and life stages, despite their capital sizes, went unnoticed for a long time and are hardly ever seen again, e.g. the megamouth shark *Megachasma pelagios*, the large pelagic ray *Hexatrygon bickelli* (Haedrich, 1997) or the giant phantom jelly in the Gulf of California *Stygiomedusa gigantean*. But the scarcity of opportunities of these observations and the consequent lack of quantitative assessments give them low credit in our perception as to be truly widespread phenomena (Harrisson 1967).

Although quantitative community parameters are important aspects of mesopelagic community analyses (McGowan, 1974), true species abundances are very difficult, if impossible, to determine, due to the multitude of sampling limitations (e.g. Heino et al., 2011). Therefore, increased efforts to study gear effectiveness and catchability seem much needed to advance our knowledge on true relative abundances of mesopelagic species. In addition, an inter-institutional agreement on consistent sampling protocols would allow spatio-temporal comparisons of data collected and the acquisition of long-term data series (Haedrich, 1997). Considering the multitude of limitations in the assessment of overall community composition, future studies may preferably focus on particular indicator species and try to sample these as comprehensively as possible. Moreover, theoretical considerations on effective population sizes could provide additional perspectives on the real composition of mesopelagic communities (Marandel et al., 2019). In addition, integrated sampling using various techniques may offer a more synoptic view on mesopelagic communities, even though data comparisons from multiple sources, that show large spatio-temporal variations and differences in accuracies, are often difficult (Merten et al., 2021). In that regard, as we demonstrate also in **article 5**, advancing statistical and analytical approaches may offer solutions to use these data from multiple sources efficiently (Fock et al., 2002; Heino et al., 2011; Porteiro, 2005). The development of novel techniques, like environmental DNA, may add additional insights on community compositions, unrestricted by size-based and behavioural limitations, as well as patchiness (Merten et al., 2021; Taberlet et al., 2012). Overall, the special quality of the pristine deep-sea habitats, hosting communities whose ecologies remain largely enigmas to us, caution scientists to use sampling approaches guided by conservation principles (Priede, 2017; Webb et al., 2010).

Conclusions

By providing an integrative view on mesopelagic fish communities and their functional structure under varying productivity and oxygen environments in the tropical North Atlantic, the present study contributes importantly to the existing mesopelagic fish research. To be able to monitor responses of the mesopelagic fish community to global climate and anthropogenic changes, we need to increase our understanding of the influence of environmental heterogeneity on spatio-temporal scales on these communities. Our study offers crucial insights on mesopelagic fish community and trophic structure under the influence of an oxygen minimum zone, which is little investigated so far. By demonstrating that larger-sized non-diel migratory mesopelagic species contribute importantly to the mesopelagic community of the main mesopelagic sound scattering layers, this study points out a crucial unknown in our estimates of mesopelagic fish biomass and thereby, their contribution to global ecosystem fluxes. In addition, we demonstrate the usefulness of size-based indicators in studies of community change and point out the tight ecological and physiological adaptations of mesopelagic communities on small spatial and temporal scales to their respective environment.

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Declaration on oath

(according to § 7 (4) doctoral degree regulations of the MIN Faculty)

I hereby declare upon oath that I have written the present dissertation independently and have not used further resources and aids than those stated.

Eidesstattliche Versicherung

Hiermit erkläre ich an Eides statt, dass ich die vorliegende Dissertationsschrift selbst verfasst und keine anderen als die angegebenen Quellen und Hilfsmittel benutzt habe.

Hamburg, 18.01.2022