



Contribution to the Themed Section: 'Mesopelagic resources—potential and risk' Original Article

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

Thünen Institute of Sea Fisheries, Marine Ecosystems Working Group, Herwigstr 31, D-27572 Bremerhaven, Germany

*Corresponding author: tel: + 49 471 94460366; fax: + 49 40 38905 263 e-mail: Heino.fock@thuenen.de.

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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 of 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 Ehrlich*, 2010; *Irigoién 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. $40 \mu\text{mol l}^{-1}$ were measured (0.9 ml l^{-1} , *Supplementary Material S1*), which according to *Ekau et al.* (2010) meet criteria for hypoxic conditions of $<60 \mu\text{mol}$.

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

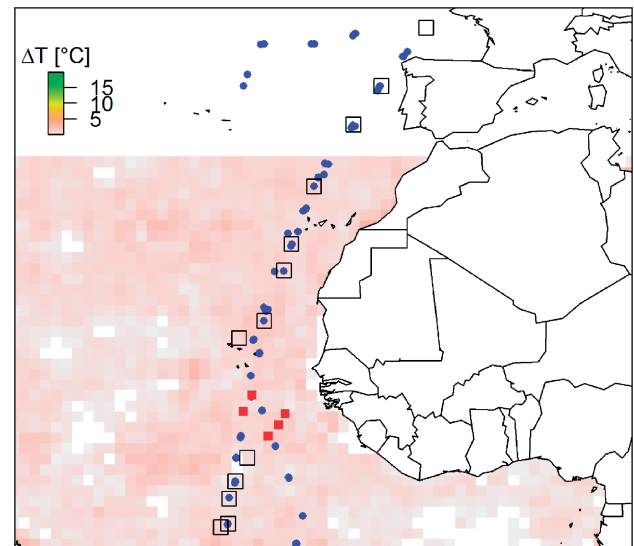


Figure 1. Changes in water temperature 1965/1974 to 2005/2012 and sampling stations 1966–1971, 1979, and 2015. Blue—sampling 1966–1971 and 1979 (stations west of Bay of Biscay), black—sampling stations in 2015, red—OMZ stations 2015. Changes in water temperature calculated from World Ocean Atlas data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

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*).

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

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 \ll 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 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).

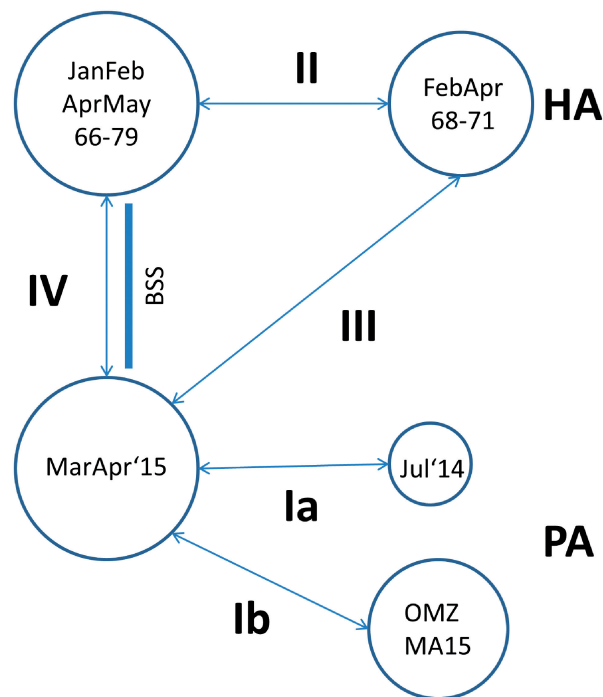


Figure 2. Defining four analysis blocks I–IV with regard to HA and PA data. Circle sizes represent availability of data. Subsets in terms of time or region are indicated. BSS, biomass size spectra analysis; OMZ, oxygen minimum zone.

depend on growth and thus could depend on the time of sampling indicating a seasonal effect, whereas size class structure is assumed 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, parapleidids, 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 (Figure 1; 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 m², 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 [$>40^{\circ}\text{N}$, 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 melamphids 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 :

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

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.

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

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):

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

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 Ehrlich, 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 \times 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 \times 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		Analysis block		Changes in	
				la: LFD differences [CvM]	la: inclusion index	Size range Jul 2014	Size range Mar/April 2015	LFD characteristics in 2014	
Myctophidae	<i>Ceratoscopelus warmingii</i>	TROPICS	July–Mar/April	$p > 0.95$	0.62	21.14–56.29	31.1–73.5	–	
Myctophidae	<i>Ceratoscopelus warmingii</i>	SUBTROPICS	July–Mar/April	n.s.	0.79	22.98–67	21–71.9	Increase in younger size class	
Myctophidae	<i>Diaphus rafinesquii</i>	SUBTROPICS	July–Mar/April	$p > 0.95$	0.65	54.26–79.57	57–84	–	
Gonostomatidae	<i>Diplophos taenia</i>	TROPICS	July–Mar/April	n.s.	0.54	64.6–126.56	55.5–131.8	–	
Myctophidae	<i>Lepidophanes guentheri</i>	TROPICS	July–Mar/April	$p > 0.95$	0.2	29.21–70.7	34.3–77	–	
Myctophidae	<i>Notoscopelus resplendens</i>	SUBTROPICS	July–Mar/April	$p > 0.95$	0.96	23–55	22–84	–	
Myctophidae	<i>Notoscopelus resplendens</i>	TROPICS	July–Mar/April	$p > 0.95$	0.84	21.08–89.53	19.9–95.5	Increase in younger size class	
Phosichthyidae	<i>Vinciguerrria nimbaria</i>	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 of 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 phosichthyid *Vinciguerrria nimbaria*, younger additional size classes were found, whereas for *Directmoides 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	<i>Ceratospelus maderensis</i>	TSUB	A	-	-	n.s.	-	0.35	-	32–81	26–69.9	-	81
Bathylagichthys	<i>Bathylagichthys greyae</i>	TSUB	A	-	-	$p > 0.95$	-	0.24	-	47–147	32–135	Increased dominance of younger size classes	160
Myctophidae	<i>Hygophum macrochir</i>	T	A	-	-	$p > 0.95$	-	0.29	-	23–54	22.9–65	Shift in modal size	60
Myctophidae	<i>Lepidophanes gaussi</i>	TSUB	A	-	-	$p > 0.95$	-	0.72	-	29–47	18–51	Additional younger size classes	50
Myctophidae	<i>Myctophum affine</i>	T	A	-	-	$p > 0.95$	-	0.39	-	13–47	22.5–51	Increased dominance of older size classes	60
Myctophidae	<i>Notoscopelus caudispinosus</i>	TSUB	A	-	-	$p > 0.95$	-	0.75	-	38–130	35–140	Shift in modal size	140
Phosichthyidae	<i>Vinciguerria nimbaria</i>	TSUB	A	-	-	$p > 0.95$	-	0.82	-	25.2–50	17–42	Additional younger size classes	48
Myctophidae	<i>Lepidophanes guentheri</i>	T	B	n.s.	n.s.	n.s.	0.26	0.35	34–71	30–76	24.9–78	-	78
Stomiidae	<i>Malacosteus niger</i>	T	B	n.s.	n.s.	n.s.	0.29	0.37	62–175	38–175	100.7–155.8	-	240
Myctophidae	<i>Hygophum taaningi</i>	T	B	n.s.	n.s.	n.s.	0.06	0.06	25–52	25–52	11.7–59	-	61.2
Stomiidae	<i>Astronesthes richardsoni</i>	T	B	n.s.	n.s.	n.s.	0.37	0.45	26–185	26–185	22.9–172	-	145
Myctophidae	<i>Ceratospelus warmingii</i>	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	<i>Diretmoides pauciradiatus</i>	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	<i>Bonapartia pedaliota</i>	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	<i>Gonostoma denudatum</i>	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	<i>Electrona risso</i>	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	<i>Nannobranchium isaaci</i>	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	<i>Notoscopelus resplendens</i>	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	<i>Notoscopelus resplendens</i>	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:		Block III:		Block IV:		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)
				II: CvM	III: CvM	Block III: inclusion index	Block IV: CvM	IV: CvM							
Sternoptychidae	<i>Argyropelecus affinis</i>	T	C	n.s.	$p > 0.95$	$p > 0.95$	0.05	$p > 0.95$	0.05	35–72	31–75	25.6–78	Increased dominance of younger size classes	72	
Sternoptychidae	<i>Argyropelecus sladeni</i>	T	C	n.s.	$p > 0.95$	$p > 0.95$	0.44	$p > 0.95$	0.65	15–72	15–72	19.9–83.5	Increased dominance of older size classes	70	
Stomiidae	<i>Chauliodus sloani</i>	T	C	n.s.	$p > 0.95$	$p > 0.95$	0.59	$p > 0.95$	0.62	60–235	60–235	98–248.1	Decrease in dominance of older size classes	> 300	
Gonostomatidae	<i>Diplophos taenia</i>	T	D	$p > 0.95$	$p > 0.95$	n.s.	0.29	n.s.	0.81	65–130	46–136	55.5–147		276	
Myctophidae	<i>Ceratospelus warmingii</i>	TSUB	D	$p > 0.95$	$p > 0.95$	n.s.	0.3	n.s.	0.87	37–68	17–77	21–73		81	
Phosichthyidae	<i>Vincigueria nimbaria</i>	T	D	$p > 0.95$	$p > 0.95$	n.s.	0.43	n.s.	0.78	23–48	21–56	18–54.5		48	
Dirietmidae	<i>Dirietmus argenteus</i>	T	E	$p > 0.95$	$p > 0.95$	$p > 0.95$	0.1	$p > 0.95$	0.19	12–80	12–190	24.6–98.9	Increased dominance of younger size classes and decline in max. size	125	
Myctophidae	<i>Diaphus rafinesquii</i>	TSUB	E	$p < 0.95$	$p < 0.95$	$p < 0.95$	0.28	$p < 0.95$	0.93	40–74	30–92	23–84	Increased dominance of younger size classes	90	
Sternoptychidae	<i>Argyropelecus hemigygnus</i>	TSUB	E	$p > 0.95$	$p > 0.95$	$p > 0.95$	0.81	$p > 0.95$	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 1966/71 to PA 2015, block III - HA Jan-May, block IV - HA Jan-May 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

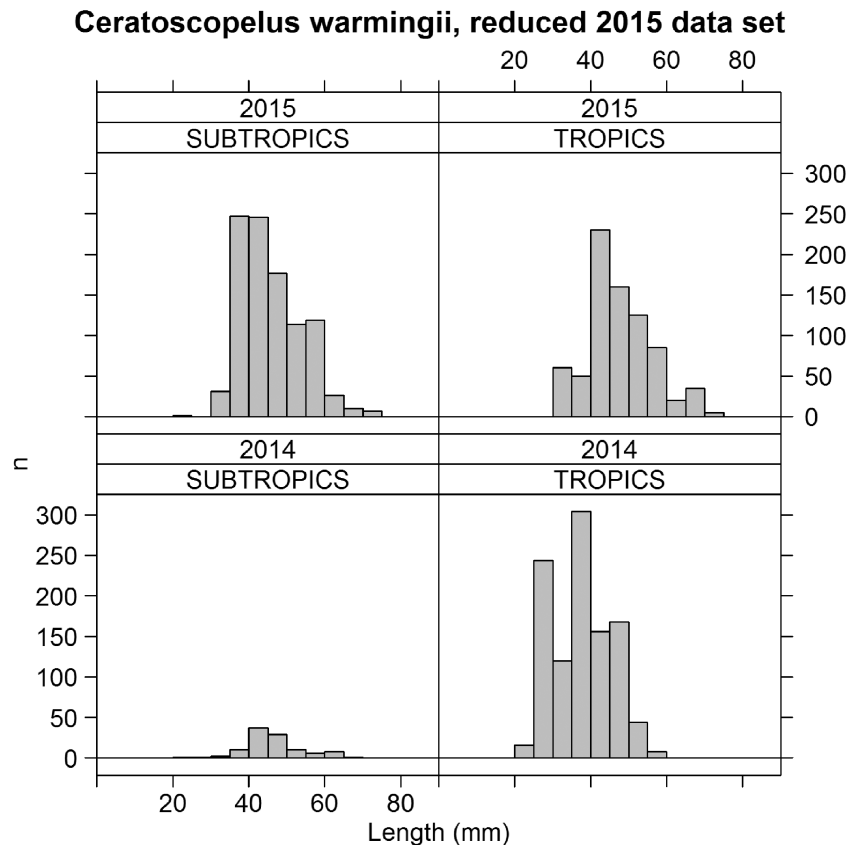


Figure 3. LFD of the myctophid *Ceratoscopelus warmingii* in the tropics and subtropics in July 2014 and March/April 2015. Numbers refer to measured specimens of the measurement categories “fd” and corresponding “rge” records, but are not raised to total population abundance. For analysis, numbers were 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 2^0 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, 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 2^0 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 <i>p</i> -values	<i>p</i> -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	$\chi^2 = 2$, <i>df</i> = 1, <i>p</i> -value = 0.15	–
I.2: Differences in maximum sizes	$\chi^2 = 8$, <i>df</i> = 1, <i>p</i> -value = 0.004	–
I.3: Differences in size class structure	$\chi^2 = 0.5$, <i>df</i> = 1, <i>p</i> -value = 0.48	–
Analysis block Ib : PA–PA comparisons, regions tropics vs. OMZ		
I.4: Differences in LFDs	$\chi^2 = 4.5$, <i>df</i> = 1, <i>p</i> -value = 0.03	–
I.5: Differences in maximum sizes	$\chi^2 = 14$, <i>df</i> = 1, <i>p</i> -value = 0.0001	–
I.6: Differences in minimum sizes	$\chi^2 = 2.5$, <i>df</i> = 1, <i>p</i> -value = 0.11	–
I.7: Differences in size classes structure	$\chi^2 = 0.09$, <i>df</i> = 1, <i>p</i> -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)	$\chi^2 = 3.8$, <i>df</i> = 1, <i>p</i> -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	$\chi^2 = 8.9$, <i>df</i> = 1, <i>p</i> -value = 0.004	–
IV.9b : Differences in LFDs, reference period January–May 1966–1971	$\chi^2 = 5.1$, <i>df</i> = 1, <i>p</i> -value = 0.02	<i>p</i> = 0.08
IV.10 : Similarity between 9a and 9b	Odds ratio = Inf, <i>p</i> -value = 0.005	<i>p</i> = 0.19
III.11 : Association between regions for significant LFD changes, months February–April, 1966–1971	Odds ratio = 0, <i>p</i> -value = 0.53	–
IV.12 : Association between regions for significant LFD changes, months January–May, 1966–1971	Odds ratio = 0.62, <i>df</i> = 1, <i>p</i> -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, <i>p</i> -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, <i>p</i> -value = 0.19	<i>p</i> = 1
III.15 : Association between significant LFD changes and decreases in minimum size, reference period February–April, 1966–1971	Odds ratio = 0.43, <i>p</i> -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, <i>p</i> -value = 1	–
IV.17 : Increase in presence of older size classes in either year, reference period January–May, 1966–1971	$\chi^2 = 0$, <i>df</i> = 1, <i>p</i> -value = 1	–
IV.18 : Association between changes in size classes structure and region, reference period January–May, 1966–1971	Odds ratio = Inf, <i>p</i> -value = 0.009	<i>p</i> = 0.02
Time-averaging^a		
Hypothesis 19 No joint changes in minimum and maximum sizes in relation to 1966–1971	$\chi^2 = 11.5$, <i>df</i> = 1, <i>p</i> -value < 0.001	<i>p</i> = 0.003

^aIII.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

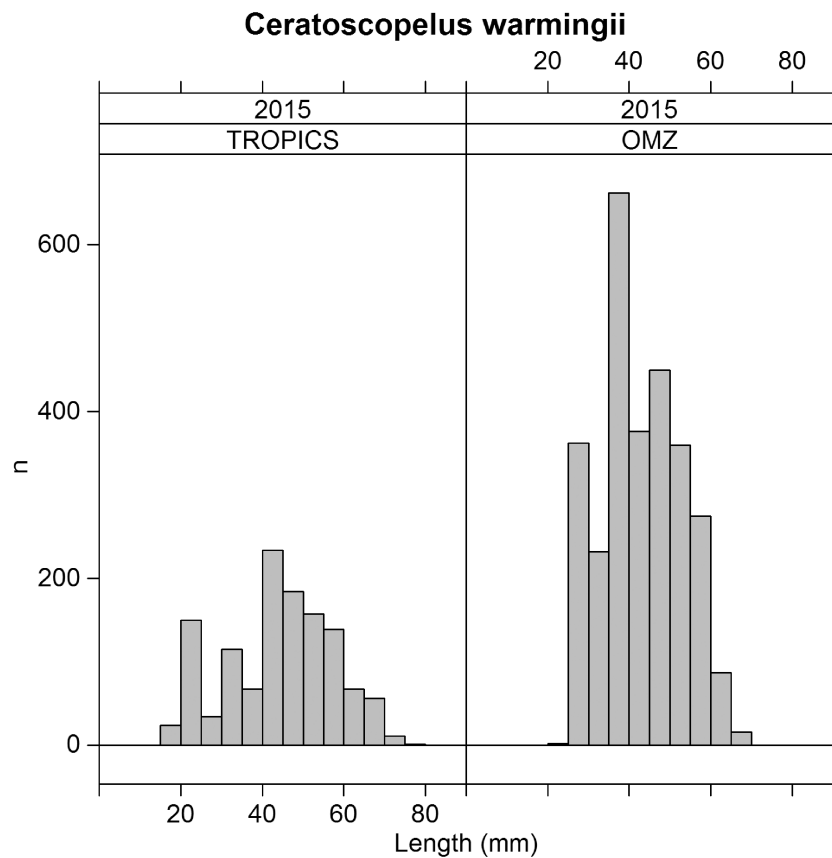


Figure 4. LFD of the myctophid *Ceratoscopelus warmingii* in the tropics and the OMZ region for 2015 (see Figure 1). Numbers refer to measured specimens of the measurement categories “fd” and corresponding “rge” records, but are not raised to total population abundance.

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 horizontal 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 *Nannobranchium isaaci* (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.

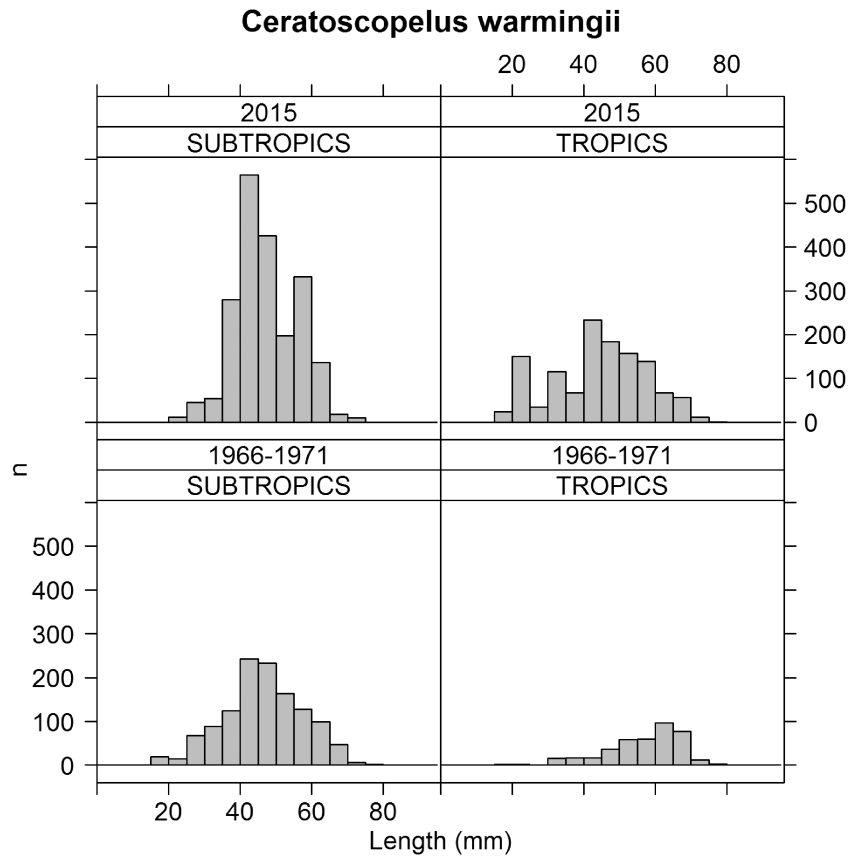


Figure 5. LFD of the myctophid *Ceratoscopelus warmingii* in the subtropics and tropics for 1966–1971 (reference period January–May) and 2015. Numbers refer to measured specimens of the measurement categories “fd” and corresponding “rge” records, but are not raised to total population abundance.

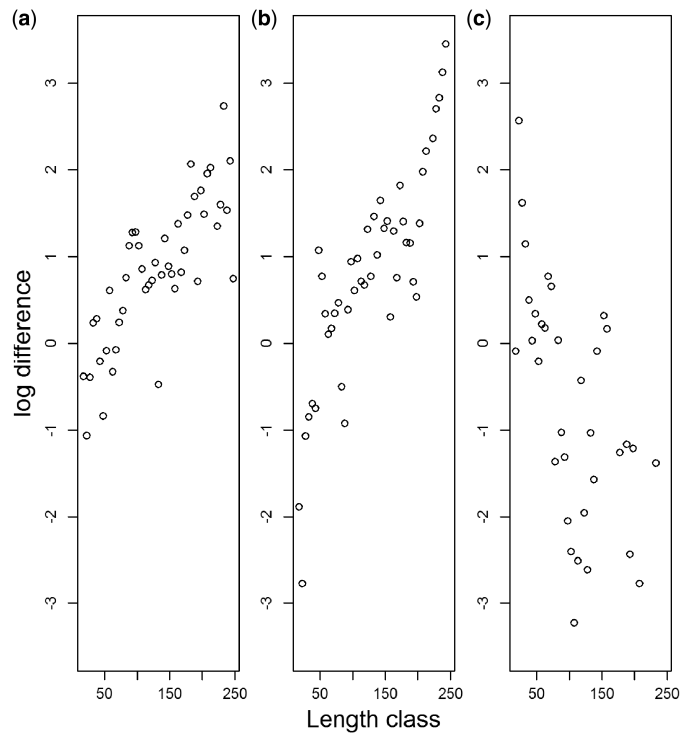


Figure 6. Log difference 1966–1971 to 2015 of LFD proportions by length classes. (a) Tropics, (b) subtropics, (c) temperate region (including 1979 data). Negative difference—proportion in 2015 greater than in 1966–1971.

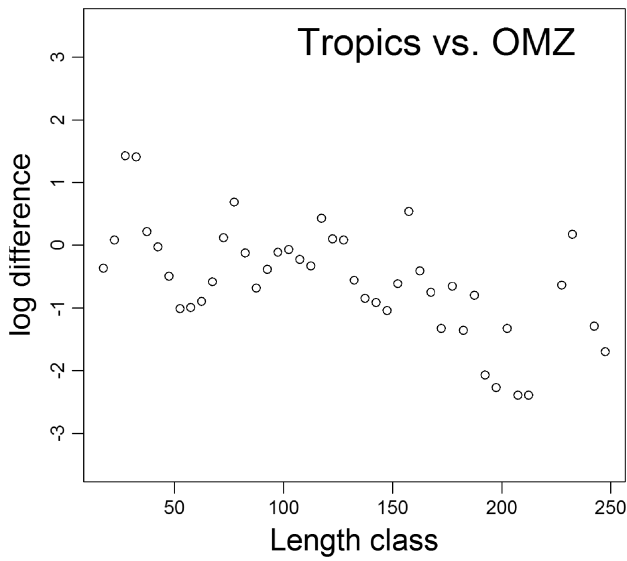


Figure 7. Log difference of LFD proportions by length classes for tropics and OMZ (see Figure 1). Negative difference—proportion in tropics greater than in OMZ.

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 *Benthoosema suborbitale* (34–33.4 mm SL). In a comparative study of two midwater trawls (2.6 and 5.3 m²), [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

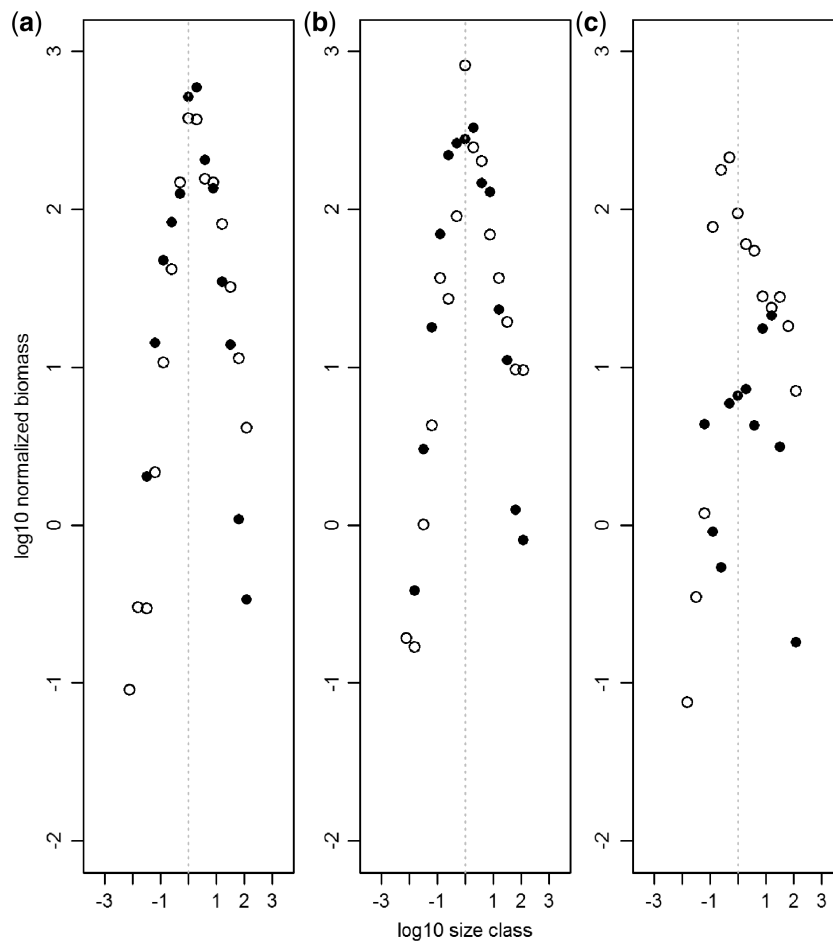


Figure 8. Normalized biomass size distribution plots for historical (open circles) and 2015 data (closed circles) by region, (a) tropics, (b) subtropics, (c) temperate region. Values are standardized to 30 min twos but not to different trawl openings. Vertical line indicates size classes 2° g.

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 m². 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 $M^{\log_{10}(TE)/\log_{10}(PPMR)+0.25}$ 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.

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