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Lanternfish as bioindicator of microplastics in the deep sea: A spatiotemporal analysis using museum specimens

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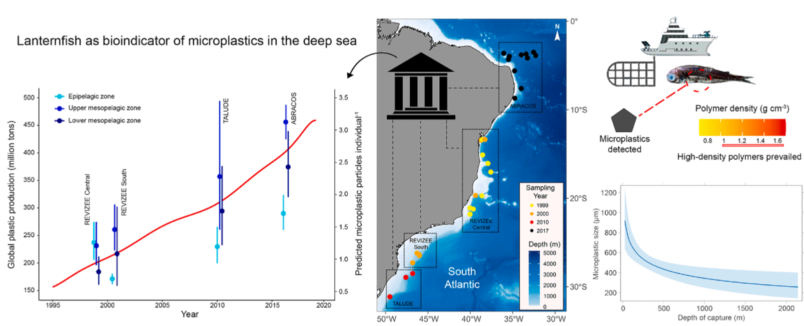
HIGHLIGHTS

- Lanternfishes had a 44 % lower probability of MP ingestion in 1999 than in 2017.
- The size of ingested MPs was negatively correlated with depth.
- Lanternfishes were generally more likely to ingest high-density polymers.
- The detected polymer concentration was 445.4 ± 526.4 μg g^{-1} Gastrointestinal tract.
- Museum collections can be invaluable tools for time series analysis.

GRAPHICAL ABSTRACT



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ABSTRACT

We investigated MP ingestion in lanternfishes (Myctophidae), one of the most abundant vertebrates in the world, using archived specimens from museum collections from 1999 to 2017. Microplastics were detected in 55 % of the 1167 specimens analysed (0.95 ± 1.22 MP $individual^{-1}$). Global plastic production has increased by about 53 % during this period. Interestingly, almost half of the lanternfishes analysed contained at least one particle in the gastrointestinal tract in the earliest data. In contrast, the incidence increased to two-thirds in the most recent data available. Although the shape and colour composition of MPs followed a similar proportion, the model considering the sampling year and migration patterns showed that specimens collected in 1999, 2000, and 2010 had a 44 %, 23 % and 20 % lower probability of MP ingestion than those collected in 2017. However, migration was the most robust predictor of MP contamination. Further analysis of specimens collected in 1999–2000

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revealed that fish caught in the bathypelagic zone had the lowest number of particles, while those caught just below the thermocline had an eightfold higher probability of MP ingestion. Lanternfishes were generally more likely to ingest high-density polymers, although polyethylene had the highest concentration (445.5 ± 526.4 μg g^{-1} gastrointestinal tract).

1. Introduction

Microplastics (MPs: <5000 μm) represent the largest share of plastic waste on the ocean surface, with an estimated abundance of 5–51 trillion particles, corresponding to a mass of 14.4–236 thousand tonnes [1-3]. Global plastic production surged from 202 to 400 million tonnes between 1999 and 2022 [4,5]. During this period, waste management infrastructure lagged significantly behind production, particularly in the Global South [6,7]. Current estimates indicate that rivers export approximately 0.5 million tonnes of plastics annually, remarkably, the mass of MPs is equivalent to that of meso and macroplastics (<5000 μm) [8].

Despite the increasing abundance (particles m^{-3}) in some regions, monitoring surveys have not revealed clear temporal trends [9]. Notwithstanding, studies examining interannual variability are largely limited to surface and coastal environments [9]. Even in well-sampled regions, data lack the spatial resolution required to adequately support models [3,9,10]. On a global scale, only 1–16 % of the estimated annual plastic input to the ocean is found in the surface layer [2,3, 11–13]. The remaining fraction is likely transported to the deep waters by physical processes [14,15] and the biologically driven "plastic pump" [16], contributing to seafloor storage of MPs [17].

Although the water column below 200 m represents over 90 % of the Earth's biosphere, this region remains one of the least studied in terms of MP abundance and biota contamination [18-20], leaving significant gaps in our understanding of the fate of MPs in the deep ocean. For example, while the global prevalence of fish ingesting MPs has doubled [21], raising concerns about the sublethal effects of hazardous chemical compounds released by MPs [22], the temporal and spatial dynamics of MP contamination in the deep ocean remain largely unknown.

In this context, sentinel species can provide key information on the environmental MP concentration across different spatial scales over time while providing valuable insights into how the biota responds to such rapid changes. Selecting an effective bioindicator species requires evaluating several criteria [23-25]. Lanternfishes represent one of the largest vertebrate biomasses in the ocean [26,27] and can be captured in surface waters at night using standard nets. They play a crucial ecological role [27,28] and are among the best-studied groups in the deep ocean, although much remains to be learned about them. They are exposed to MP ingestion when ascending to the nutrient-rich epipelagic zone (< 200 m depth) [29,30], where they feed on fish larvae, krill and gelatinous plankton [28], organisms that also ingest MPs [31]. Moreover, their return to the mesopelagic (200–1000 m) and bathypelagic (>1000 m) zones during the day to avoid pelagic predators increases the likelihood of MP contamination [32]. Thus, among the deep-sea organisms, lanternfish emerge as promising candidates for use as bioindicators of MP.

Museum collections provide extensive geographical and historical records of biological samples. The analysis of preserved specimens can provide baseline levels and spatiotemporal trends of MP contamination using up-to-date techniques that were unavailable at the time of sample collection [33-35]. Here, we provide the earliest record of MP ingestion by lanternfish in the Atlantic Ocean through a comprehensive sample set, considering biological and environmental aspects, which are usually overlooked in the literature. We tested the hypothesis that ecological patterns and depth variability influence MP contamination in lanternfishes. Additionally, we compared samples collected in different campaigns in the Southwestern Atlantic (SWA) over time to evaluate temporal trends in MP ingestion.

2. Methods

2.1. Study area and sampling procedures

The uppermost northern layers of the study area are influenced by the North Brazilian Current (NBC). South of 10 °S, the Brazilian Current (BC) becomes the predominant oceanographic feature, flowing south-southwestward down to depths of 450–500 m, with temperatures of 22–27°C and salinity of 36.5–37, transporting Tropical Waters (TW: >20°C and 36.2 psu) ([36,37]. At 21°S, near the Vitória–Trindade Ridge, the South Atlantic Central Waters (SACW: 5–18 °C and 34.3–35.8 psu), which flows between 400 and 700 m depth bifurcates. The BC transports the SACW south of this latitude, while the northern branch flows northward with the North Brazilian Undercurrent (NBUC) [38,39] (Fig. 1).

Below the BC lies the Intermediate Western Boundary Current (IWBC), which flows in the opposite direction (N-NE). The IWBC extends down to 1150 m depth, transporting the South Atlantic Central Waters (SACW: 5–18 °C and 34.3–35.8 psu) between 400 and 700 m [40], the Antarctic Intermediate Waters (AAIW: 2.6 °C and 33.8–34.8 psu) between 800 and 900 and the North Atlantic Deep Water (NADW: 1.5–4 °C and 34.8–35.0) down to 3500 m depth [41].

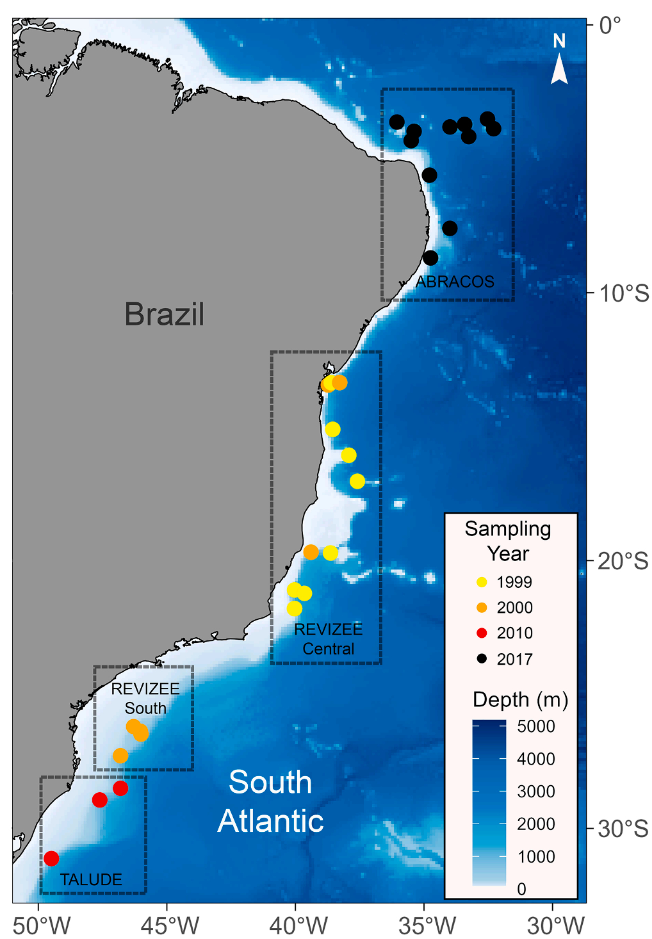

Fig. 1. Lanternfish (Myctophidae) sampling stations performed by oceanographic campaigns from 1999 to 2017 off Brazil, Southwestern Atlantic.

Data and specimen collections were performed at 28 stations by four sampling campaigns from 1999 to 2017 within the SWA, by midwater and bottom trawl nets, both day and night (Fig. 1, Table S1). The diurnal categorisation was established as those samplings performed from one hour after sunrise to one hour before sunset [42]. Conversely, nocturnal trawls occurred from one hour after sunset to one hour before sunrise. For sampling details see the Supplementary Material.

2.2. Laboratory procedures

Voucher specimens from the research cruises, stored in glass jars filled with 70 % ethanol were selected from the Fish Collection of the Instituto de Biodiversidade e Sustentabilidade, Universidade Federal do Rio de Janeiro (NPM, Macaé, Brazil). A minimum of 15 individuals from each species were selected to represent a given station to enhance results reliability and to represent MP contamination within the populations more accurately (Table S1). Species identification was performed according to Nafpaktitis et al. [43].

Under a laminar flow cabinet, individuals underwent a thorough cleaning process with filtered (glass fibre filters GF/F, 0.7 μm pore size; Whatman), distilled water. Specimen mass was measured with an analytical balance (0.0001 g), and the morphological features, including eye diameter, jaw length, standard, and total length, were measured through an electronic calliper (0.01 mm).

Specimens were dissected to remove the gastrointestinal tracts (GITs), which were weighed, rinsed with filtered distilled water, and submerged entirely in 50 mL beakers filled with NaOH (1 mol L^{-1}). Each beaker containing the digestive tract of a given individual (sample) was sealed with a glass cover and submitted to heating with the oven set at 60 °C for 24 h. The resulting material was filtered through glass fibre filters using a laboratory vacuum system, and filters were transferred to glass Petri dishes and oven-dried at 60 °C for 24 h. All particles retained on the filters were visually inspected under a stereomicroscope (Zeiss Stemi 508), with a magnification range of 50x and the suspected plastic particles [32,44,45] were photographed with a coupled camera device (Axiocam 105 Color). Then, particles were measured in the longest axis (Zeiss Zen 3.2), with a detection limit of 20 μm, classified according to shape (fibres, fragments, films, foams, and beads) [46], colour (black, blue, green, red, and white), and size (mesoplastics: 5–20 mm and microplastics: 1–5000 μm) [47].

2.3. Polymer analysis

Two different methods were applied to assess the polymer composition of particles detected from REVIZEE Central campaign samples, following a subsample threshold proposed by harmonised marine litter monitoring frameworks [46]. Due to the large sample size in the data set, a random sub-sample of 56 particles (15 % of particles) was screened through Laser Direct Infrared analysis (LDIR). The selected sub-sample followed particle shape and depth of capture as the main criteria, covering a size range from 46 to 1712 μm. The Agilent 8700 LDIR Chemical Imaging System was employed to conduct at least seven scans on each particle in manual mode, within the spectral range of 975–1800 cm^{-1} [48]. The spectral data obtained were cross-referenced with the library data from Microplastics Starter 1.0, and a polymer type was conclusively identified when the matching score was superior to 70 % [49]. The LDIR analysis was also applied to a subsample of particles (11 %) detected in the ABRACOS campaign [32].

Additionally, a random subsample based on the depth strata (discrete depth) criteria of 21 samples (4 % of specimens; each glass fibre filter corresponding to one individual) from the REVIZEE Central was selected for analysis by Pyrolysis Gas Chromatography Tandem Mass Spectrometry (Py-GC–MS/MS). Filters were ground using a mini-grinder, Pulverisette 23 (Fritsch, Idar-Oberstein, Germany), in a zirconium bowl with 3 zirconium oxide beads (10 mm diameter) with a grinding time of 60 s at 2100 rpm. Quartz pyrolysis tubes (from Quad Service, France) were freshly precalcined at 1000 °C. A sub-sample of 2 mg (± 0.01) was weighed with a Sartorius microbalance (MCE225P-2S00-A Cubis®-II Semi) [50]. Online derivatization was performed by adding 5 μL of aqueous tetramethylammonium hydroxide solution (Sigma—Aldrich, 97 %) at 25 wt% in ethanol, which was directly added to the pyrolysis tubes with a glass microsyringe (VWR, Pennsylvania, USA).

The samples were placed in an inox sample holder under a glass bell to dry for one hour before they were placed into the pyrolysis autosampler equipped with a metallic cover. A total of four polymers were targeted: polyethene (PE), polyethene terephthalate (PET), polypropylene (PP) and polystyrene (PS). Pyrolysis analyses were performed with a CDS Analytical Pyroprobe® Model 6150 (QUAD SERVICE, Achères, France) interfaced with a GC-MS/MS triple quadrupole TSQ® 9000 Thermo Fisher Scientific (Villebon sur Yvette, France). The gas chromatography column was a 60 m TraceGOLD TG-5SilMS (Thermo Fisher Scientific). The pyrolysis of samples was conducted at 600 °C for 30 s. The polymer contents were determined via external calibration, which preparation was described previously [51].

Briefly, all polymers were first cryo-milled using the SPEX® cryogenic grinder. The cryo-milling programme was as follows: precool 2 min; run 1 min; cool 2 min; cycles 15; cps 15. The ground polymers were diluted in an inert glass fibre matrix (prepared from glass fibre filters that were cryo-milled with a precooled for 1 min; cooled for 1 min; cycled 6; cps 15). The ground inert matrix was calcinated at 500 °C before use. Standards were initially prepared at 1–5 mg g^{-1} concentrations, depending on the polymer. Standards were obtained by dilution to establish a calibration range in the nanogram range (see range details by polymer in Table S4). The external standards were systematically analysed to calibrate the instruments, enabling accurate sample quantification. The validation criteria to proceed to quantification were as follows: (i) the retention time of the sample peak must be within a 0.04 min window compared to the external standard, (ii) quantification and confirmation peaks were to be within a 0.01 min window, (iii) the confirmation to quantification ratio deviation was less than 30 % compared to the externals standards, and (iv) the sample signal had to be 5 times greater than the procedural blanks signal. A procedural blank was performed for each group of 5–10 samples with similar features (sampling station and species); see QA/QC for procedural blank preparation. The procedural blanks were analysed under the same conditions as the samples and the polymer content was only determined if the sample signal was 5 times higher than that of the procedural blank. The total polymer content in each sample was determined by calculating the ratio between (i) the polymer content detected in the subsample, which was corrected for its respective blank and extrapolated to the total filter weight, and (ii) the fish's GIT weight. The details of Py-GC-MS/MS conditions are given in Tables S2, S3 and S4.

2.4. Quality assurance and quality control

During MP analysis, several procedures outlined by Song et al. [52] were implemented to avoid airborne and glassware contamination. Particle extraction and analysis took place in a dedicated section of the laboratory to minimise air circulation, and the workflow was limited to two people. Additionally, all the extraction procedures were performed under a laminar flow cabinet. Operators used 100 % cotton laboratory coats and disposable latex gloves during all laboratory stages. All the solutions used in the process, including distilled water, NaOH and ethanol, were pre-filtered through glass fibre filters (GF/F, 0.7 μm pore size). Preliminary measures included extensive cleaning of workstations with 70 % ethanol, and all glassware was rinsed with filtered distilled water, followed by an inspection for residual particles using a stereomicroscope.

Petri dishes were kept closed throughout the stereomicroscope identification process to avoid airborne contamination of samples. A procedural blank was processed for each batch of samples, typically consisting of between 10 and 15 samples. This blank was subjected to identical handling as the samples. Whenever MPs were detected within the blanks, any particles sharing similar features (shape and colour) were subsequently excluded from the corresponding batch of samples.

2.5. Data analysis

Sampling stations were inspected as continuous (depth of capture) and categorical data (depth strata) to investigate the vertical scale of MP contamination. The depth strata were grouped into epipelagic (0–200 m), upper mesopelagic (200–500 m), lower mesopelagic (500–1000 m) and bathypelagic zones (1000–2000 m). To analyse the influence of lanternfish's migratory behaviour on MP contamination, species were grouped into two categories. The upper mesopelagic and lower mesopelagic migrants, consisting of species that predominantly reside within the upper mesopelagic and lower mesopelagic zone, respectively, and engage in diel vertical movements to the epipelagic waters during night-time to forage [28].

To investigate the MP contamination in the lanternfishes from the SWA caught between 1999 and 2017, a total of 1122 individuals representing 14 species from the REVIZEE Central, REVIZEE South, TALUDE, and ABRACOS campaigns were analysed (Table S1). The specimens included the most abundant Myctophidae species in the SWA [28,53].

Simple General Linear Models (GLMs) were used to elaborate temporal variability (sampling campaigns), interactions between time and depth strata, period of the day and migratory patterns were involved. Lanternfishes in the bathypelagic zone and non-migratory species were excluded due to irrepresentability.

Furthermore, samples from the REVIZEE Central campaign were selected for a detailed characterisation of the MP contamination in the lanternfishes from the SWA during the late 1990s. This campaign was selected due to its robust sampling design and representation of the earliest available data (Table S5). General Linear Models were used to investigate the best predictors of MP ingestion. The models investigated the influence of environmental factors, regional scale, morphological features and migratory behaviour (predictors: explanatory variables) on the number and size of MPs detected (response variables) in the REVIZEE Central campaign (Tables S6 and S7). For a detailed description of the model selections, see the Supplementary Material.

Kruskal-Wallis tests, followed by the post-hoc Dunn's tests for pairwise comparisons, were applied to explore the variability in the number and size of detected MPs according to the species from the REVIZEE Central campaign. This statistical procedure investigated differences among the polymer-type concentrations quantified by Py-GC-MS/MS.

All the statistical tests were performed at a significance level of 0.05 in R v.4.4.1 (R [54]), packages deployed included Effects [55], FSA [56], MASS [57], performance [58], see [59], and sjPlot [60]. Data visualisation was performed with the packages circlize [61], ggplot2 [62] and ggOceanMaps [63].

3. Results

3.1. Campaign comparisons

Microplastics were detected in 55 % (FO: frequency of occurrence) of the 1167 lanternfishes, with an average of 0.95 ± 1.22 microplastics per individual (MP individual^{-1}). Among these, 508 specimens from the 1999–2000 REVIZEE Central campaign, 120 specimens from the 2000 REVIZEE South campaign, 165 specimens from the 2010 TALUDE campaign and 344 specimens from the 2017 ABRACOS campaign were analysed, with total lengths of 56.4 ± 16.5, 60.6 ± 12.2 mm, 67.4 ± 24.3 mm and 57.2 ± 12.6 mm, respectively. On average, 0.75 ± 1.08 MP ind.$^{-1}$ (FO: 67 %) was detected in the REVIZEE Central, 0.97 ± 1.08 MP ind.$^{-1}$ (FO: 56 %) in the REVIZEE South, 0.84 ± 1.05 MP ind.$^{-1}$ (FO: 52 %) in the TALUDE and 1.26 ± 1.43 MP ind.$^{-1}$ (FO: 68 %) in the ABRACOS (detection limit of 20 μm) (Fig. 2).

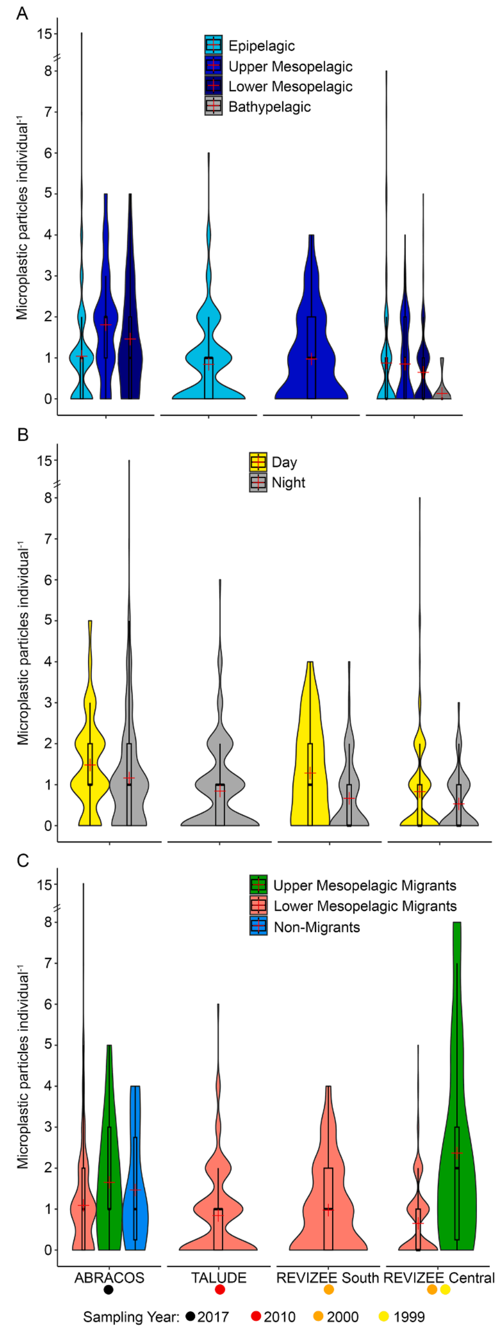

Fig. 2. Number of microplastics detected in lanternfishes (Myctophidae) from the Southwestern Atlantic, collected in the ABRACOS (2017), TALUDE (2010), REVIZEE South (2000) and REVIZEE Central (1999–2000) campaigns, according to (A) depth strata, (B) period of day, and (C) migratory behaviour of species. The horizontal line within the box plots shows the interquartile range, the whiskers show the 1.5 × interquartile range, and the red cross indicates the mean value.

The generalised model fitted to the data from the four campaigns, which included 1137 specimens, revealed significant variations in the number of MPs detected according to the migratory patterns, period of day, depth strata of capture and their respective interactions (Fig. 2, Table S8). Across all campaigns, the specimens collected in the upper and lower mesopelagic zones had, respectively, 64 % and 33 % more chances of MP ingestion than those captured in the epipelagic zone (Incidence Rate Ratio = 1.33 and 1.64, respectively; $p \leq 0.05$) (Table S8). Moreover, the lanternfishes captured in the REVIZEE Central (years 1999–2000), REVIZEE South (2000) and TALUDE (2010) campaigns were negatively related to MP ingestion. These groups had, respectively, 20 %, 46 % and 23 % fewer chances of MP ingestion when compared to the ABRACOS campaign (2017) (IRR = 0.8, 0.54 and 0.77, respectively; $p \leq 0.05$). Considering the epipelagic waters from the ABRACOS as a reference point, lanternfishes from the upper and lower mesopelagic zone from the REVIZEE Central campaign were 44 % and 41 % less likely to ingest MPs (IRR = 0.59 and 0.56, respectively; $p \leq 0.05$) (Fig. 3, Table S8).

Similarly, lanternfishes from the REVIZEE Central, REVIZEE South, and TALUDE campaigns exhibited a negative correlation with MP ingestion in the model including the interaction between the sampling campaign and the period of day (IRR = 0.58, 0.87, and 0.71, respectively; $p \leq 0.05$). Lanternfishes captured during the nighttime showed a 20 % lower likelihood of MP ingestion than those captured during the daytime (IRR = 0.8; $p \leq 0.05$).

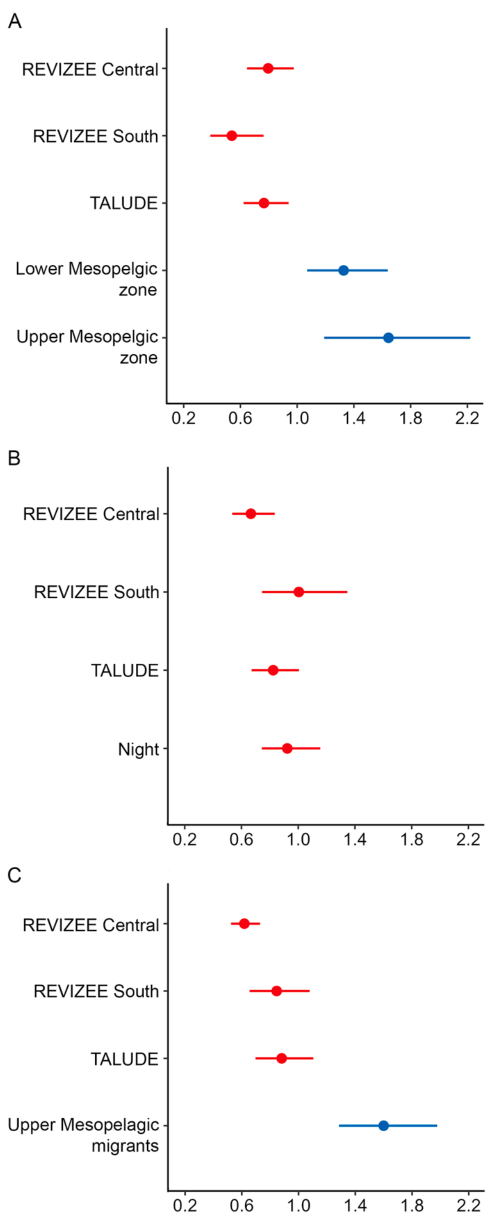

Fig. 3. Incidence Rate Ratios (IRR) from the generalised linear model fitted to the number of detected microplastics, considering the interaction between sampling campaigns and (A) depth strata, (B) period of day, and (C) migratory behaviour. The red (negative IRR values) and blue (positive IRR values) bars indicate a 95 % pointwise confidence interval around the Incidence Rate Ratio.

The migratory patterns significantly influenced MP ingestion, with upper mesopelagic migrant species exhibiting a 45 % higher likelihood of MP ingestion compared to lower mesopelagic migrants (IRR = 1.45; $p \leq 0.05$) (Fig. 3, Table S8). Notably, lanternfishes from the REVIZEE Central campaign demonstrated a 44 % lower probability of MP ingestion than those from the ABRACOS campaign (IRR = 0.56; $p \leq 0.05$). However, within the REVIZEE Central campaign, upper mesopelagic migrants had a 53 % higher probability of ingesting MPs compared to the lower mesopelagic migrants from the ABRACOS campaign (IRR = 1.53; $p \leq 0.05$) (Fig. 3, Table S8).

3.2. REVIZEE central campaign (1999–2000)

The specimens ranged from 24.5 to 107 mm SL (standard length) with a mean total weight of 2.01 ± 1.89 g (Table S5). In general, MPs were systematically detected in the REVIZEE Central samples; from the 508 specimens analysed, 242 were contaminated (Frequency of Occurrence = 47 %). In total, 383 MPs were detected across investigated species, averaging 0.75 ± 1.08 MPs individual^{-1} (Table S5).

Considering the MP shapes and colours altogether, the number of detected MPs per individual ranged from 0 to 8. *Diaphus brachycephalus* (2.36 ± 2.37 MPs ind.$^{-1}$; *p*-value <0.001) showed the highest ingestion among the lanternfishes (Fig. 4, Table S9). The GLM models indicate that the best predictors for the number of ingested MPs were the depth strata where samples were captured, followed by the migratory patterns and the digestive tract weight of lanternfishes (*p*-value <0.03) (Fig. 5, Table S10). The lanternfishes captured in the bathypelagic zone had the lowest number of detected particles among the groups (0.13 ± 0.35 MPs ind.$^{-1}$) and were thus negatively correlated with MP ingestion. Indeed, the fishes captured in the epipelagic zone (0.87 ± 1.4 MPs ind.$^{-1}$) had fourfold more chances of MP ingestion, whereas those captured in the upper mesopelagic (0.85 ± 0.96 MPs ind.$^{-1}$) and lower mesopelagic zone (0.65 ± 0.84 MPs ind.$^{-1}$) had an eightfold and sixfold higher probability, respectively, when compared to those captured in the bathypelagic zone (IRR = 4.79, 8.2 and 5.9; Confidence Interval = 1.49–29.30, 2.56–50.10, and 1.87–35.82, respectively) (Fig. 5, Table S10).

The migratory pattern of lanternfishes explained 10.5 % of data variability, indicating that the upper mesopelagic migrants (2.36 ± 2.41 MPs ind.$^{-1}$) have fourfold more chances of MP ingestion compared to the lower mesopelagic migrants (0.65 ± 0.84 MPs ind.$^{-1}$) (IRR = 4.75; CI = 3.4–6.65). Furthermore, the digestive tract weight of fish was slightly positively correlated to the number of detected MPs, in a way that each one-unit (grams) increase in this organ weight corresponded to 19 % more chances of MP ingestion (IRR= 1.19; CI = 1.05–1.34) (Fig. 5, Tables S10 and S11).

The detected MPs included a wide range of sizes, averaging 645 ± 931 μm. The smallest particles were two black fragments measuring 21 μm in the longest axis, whereas the largest was a 4982 μm white fibre. Mesoplastics (> 5000 μm) were not detected. *Diaphus dumerilii* registered the smallest MPs (275 ± 598 μm; *p*-value <0.001) among the lanternfishes (Fig. 5, Table S9).

The GLM model fitted for the size of MPs indicated that the lanternfish species, accounting for 12 % of data variability, along with the depth of capture, were the best predictors. The depth in which fishes were captured showed a negative correlation with the size of MPs (Estimate: −3.35) (Fig. 7, Tables S11 and S12). Assuming *C. warmingii* as a reference point, the remaining species showed a negative correlation with MP size, highlighting *D. lucidus* and *D. dumerilii* with the strongest negative effect (Estimate: −14.05 and −18.91, respectively) (Fig. 5, Table S12).

Considering the categorisation of MP shapes, fibres were the most abundant, corresponding to 54 % of the particles, followed by fragments at 25 %, foams at 12 %, films at 5 % and beads at 3 %. (Fig. 6). In terms of colour, blue was the most abundant, comprising 43 % of the total, which was succeeded by white at 26 %, black at 22 %, red at 7 %, and

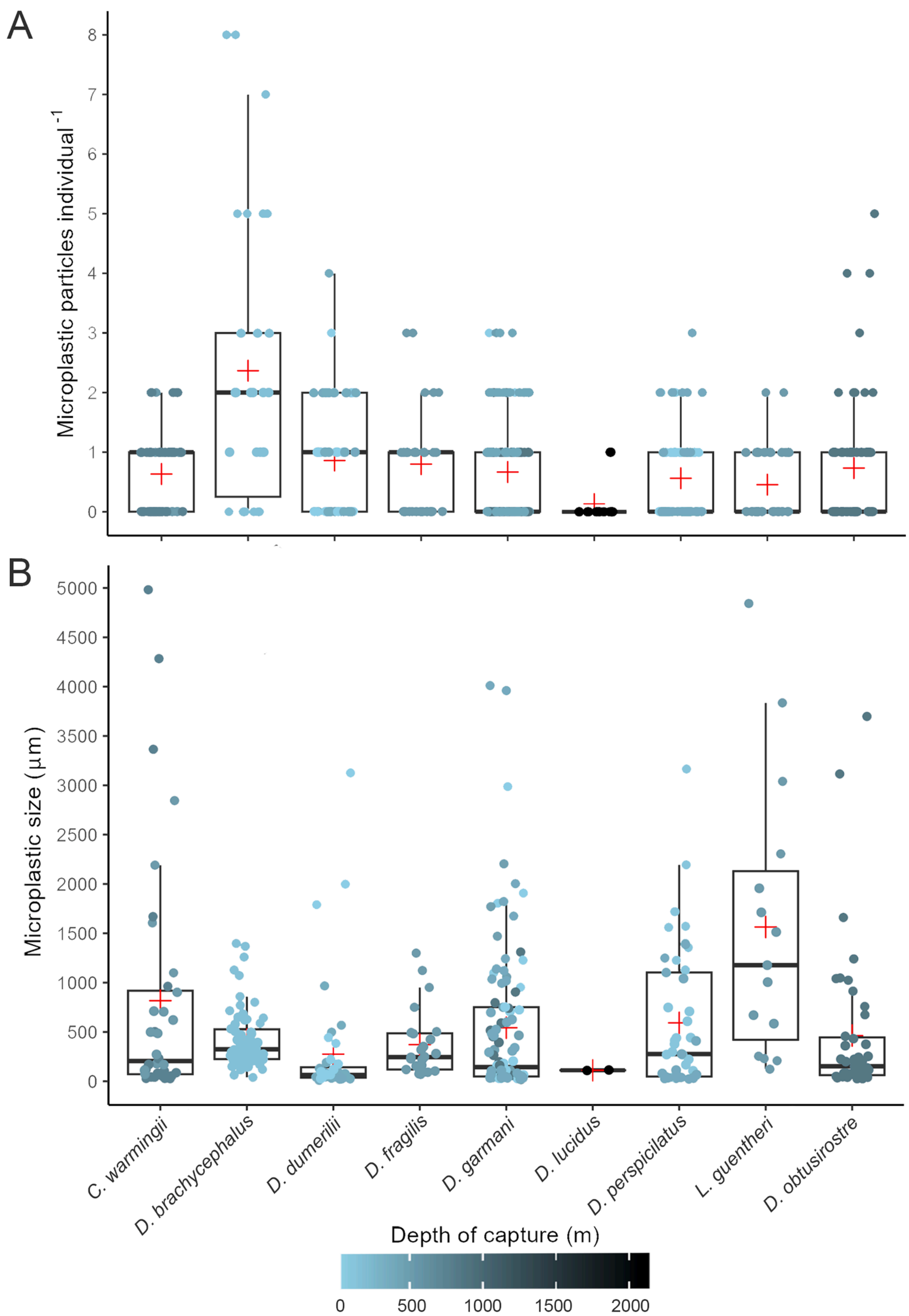

Fig. 4. (A) Number and (B) size of microplastics detected in lanternfishes (Myctophidae) from the Southwestern Atlantic, collected in the REVIZEE Central campaign (1999–2000), according to depth of capture. The horizontal line within the box plots shows the interquartile range, the whiskers show the 1.5 × interquartile range and the red cross indicates the mean value.

green at 1 %. The MP shapes and colours remained relatively homogenous across the depth strata, except for foams and films that decreased more than fivefold and elevenfold, respectively, from the epipelagic and upper mesopelagic to the lower mesopelagic zone. Only two MPs were detected from the 15 specimens analysed in the bathypelagic zone, one black and one blue fragment.

The LDIR analysis successfully identified 30 out of the 56 particles screened, detecting 10 different plastic polymers corresponding to 83 % of the subsample analysed, whereas 17 % corresponded to cellulose (CE) fibres. Considering the plastic polymers, polyamide (PA) was the most prevalent, constituting 36 % of the identified MPs. This was succeeded by cellulose acetate (CA) at 16 %, styrene-butadiene rubber (SBR) at 12 %, polyurethane (PU), and PE at 8 % (Fig. 7).

Between the four polymers investigated by Py-GC-MS/MS analysis, PE showed the highest mean concentration (445.47 ± 526.42 µg g^{-1} Gastrointestinal Tract) (p-value <0.001), with a FO of 100 % among the samples subjected to analysis. Furthermore, we detected 53.7 ± 101.5 PP µg g^{-1} GIT (FO= 59 %), 32.4 ± 54.5 PS µg g^{-1} GIT and a marginal concentration of PET (1.56 ± 1.48 µg g^{-1} GIT). In each analysed sample, the detected polymer composition ranged from one to three distinct polymer types, and the total polymer concentration (polymers altogether) detected was 102.5 ± 279.2 µg g^{-1} GIT (Fig. 7, Table S9).

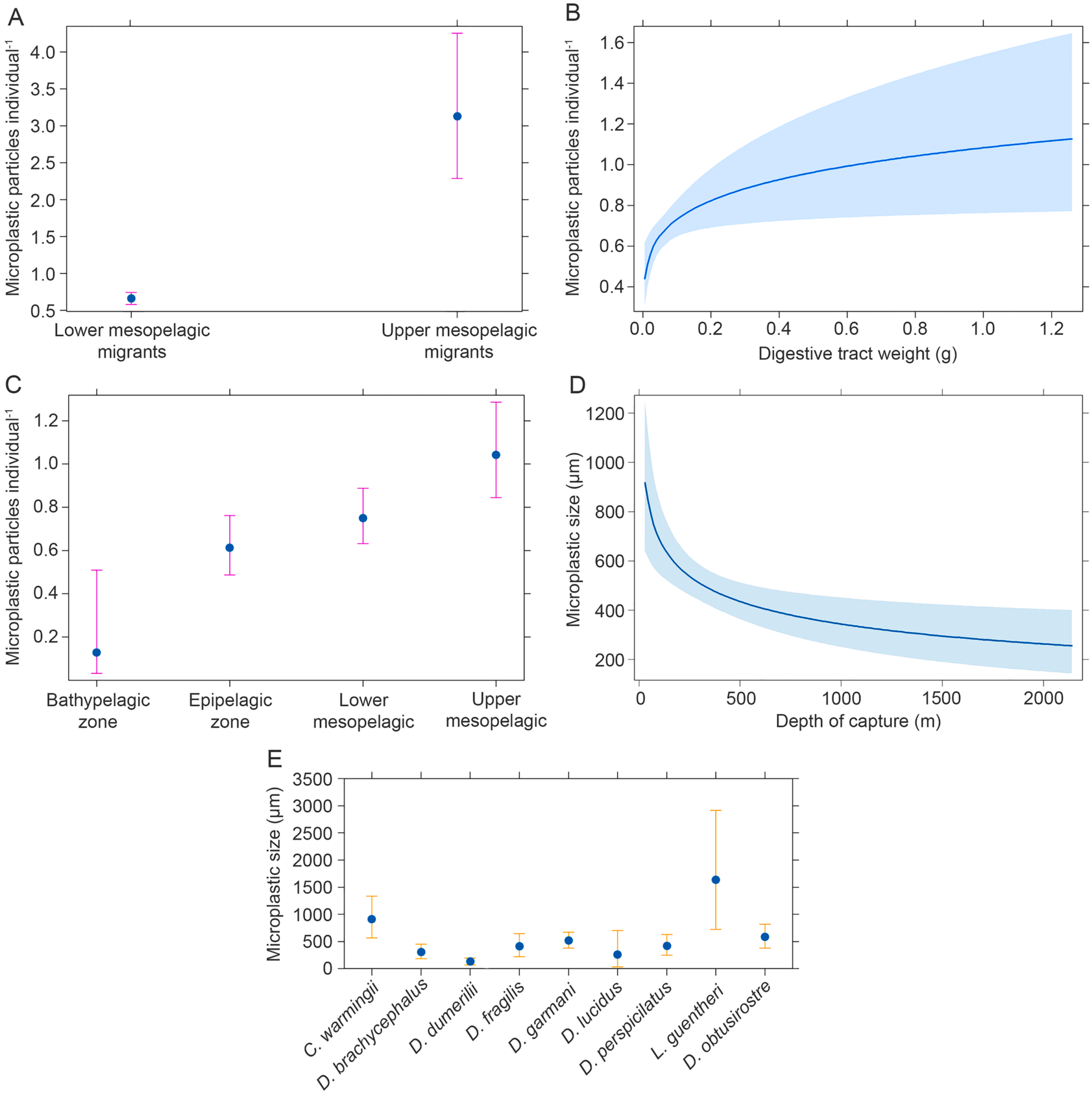

Fig. 5. Effect display for the best predictors fitted by the GLM models on the number (A, B and C) and size (D and E) of microplastic detected in lanternfishes (Myctophidae) from the Southwestern Atlantic, collected in the REVIZEE Central campaign (1999–2000). The horizontal axes are labelled on the probability of microplastic ingestion according to the (A) migratory patterns, (B) digestive tract weight and (C) depth strata, (D) depth of capture, and (E) species. The hatched blue indicates a 95 % pointwise confidence interval around the estimated effect.

4. Discussion

Regardless of the considerable distance of the study area from the main input sources of plastic waste to the ocean [64], MPs were detected in all sampling stations and investigated species. Considering the REVIZEE Central (1999–2000) and ABRACOS (2017) campaigns, which sampled comprehensive depth profiles, almost half of the lanternfishes analysed contained at least one particle in the GIT in the earliest data, whereas the incidence increased to two-thirds in the latest data available. Although the shape and colour compositions of MPs followed a similar proportion.

The increase in plastic production during the study period was mainly influenced by the packaging industry, which contributed to 36 % of production, while the textile industry is the third-largest sector, accounting for 14 % [5]. Despite this, synthetic fibres account for one-third of MPs entering the ocean [65], primarily due to domestic laundering activities [66]. Moreover, they are usually the most common MP shape ingested across various ecosystems [67].

The cylindrical shape of the fibres results in a low settling velocity, which promotes their dispersal [68,69], leading to a higher abundance than other shapes in all ocean layers [70]. As a result, these fibres remain suspended in the water column for longer periods of time, increasing

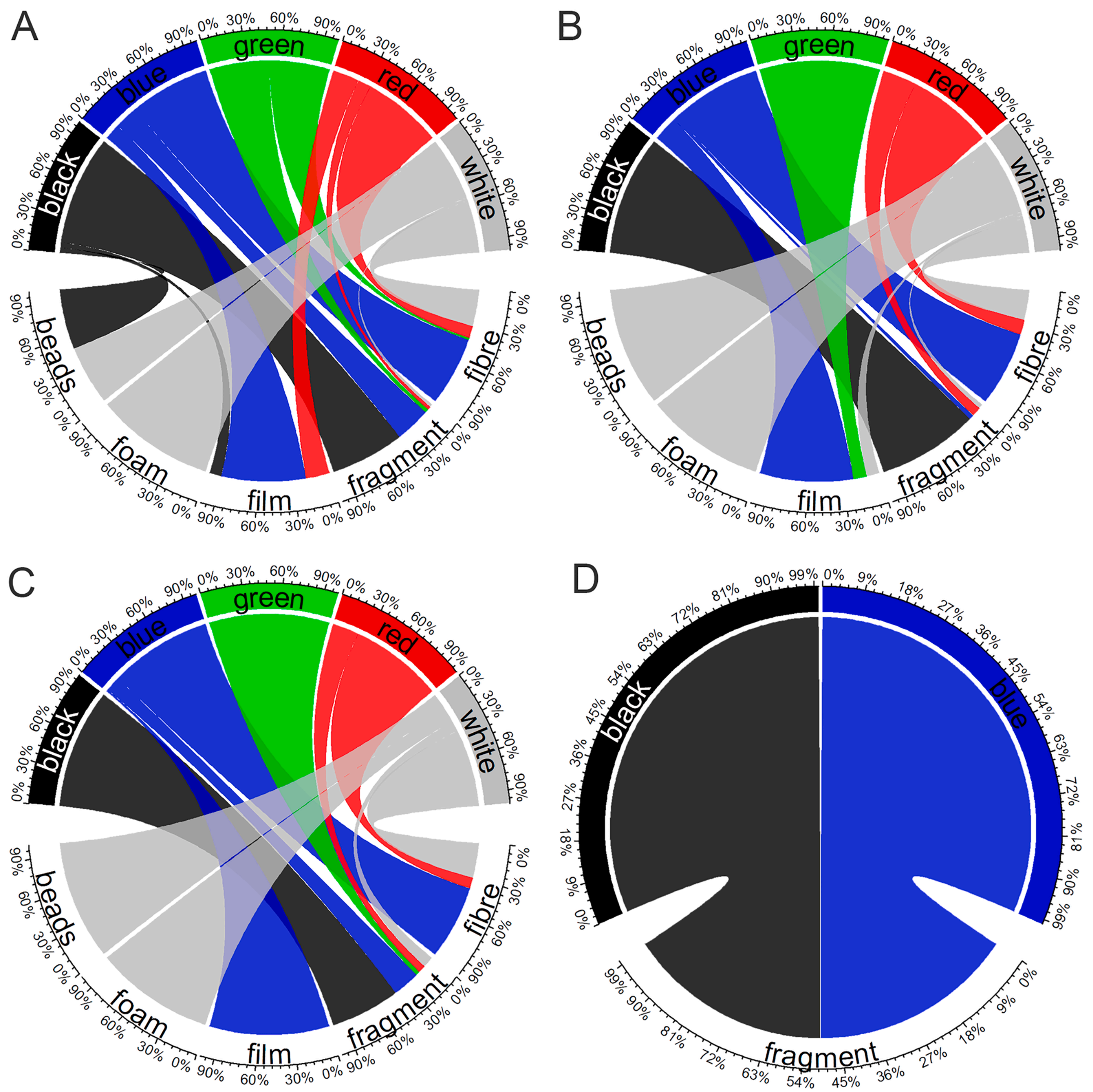

Fig. 6. Chord diagram for the shape and colours of microplastics detected in lanternfishes (Myctophidae) from the Southwestern Atlantic, collected in the REVIZEE Central campaigns in 1999–2000, according to depth strata [(A) epipelagic; (B) upper mesopelagic; (C) lower mesopelagic and (D) bathypelagic waters].

their potential for ingestion by marine organisms. It is unclear whether lanternfishes selectively ingest MP particles based on their colour, primarily due to the lack or limited availability of light in their feeding environment. Notably, the predominant ingested colour (blue) is often reported to be the most prevalent across ocean layers and in the GIT of marine biota, including this group [20,33,71].

The specimens captured during 1999, 2000 and 2010 (REVIZEE Central, REVIZEE South, and TALUDE campaigns) were less prone to MP ingestion than those from 2017 (ABRACOS campaign). Although the campaigns sampled different areas off the Brazilian coast, these boundary current areas are not predicted to be MP accumulation zones [72,73]. This suggests that geographic variation is less important than temporal factors, as the absence of known MP accumulation zones suggests that changes in MP ingestion are more likely driven by shifts in plastic pollution levels and ocean dynamics over time, rather than site-specific influences.

Moreover, the migratory patterns and the depth where specimens were captured had a stronger effect size on MP ingestion than the temporal variability. Likewise, studies have consistently shown stable or minor increases in MP contamination in marine biota [74-77]. In the Baltic Sea, a 30-year time series of the planktivorous Atlantic herring (*Clupea harengus*), European sprat (*Sprattus sprattus*) and the filter-feeders blue mussels (*Mytilus edulis*) showed no increase in MP ingestion [74,76], whereas *M. edulis* from the North Sea exhibited a 0.11 µg increase per year [76]. Interestingly, the only time series on MP contamination in lanternfishes revealed no significant increase in

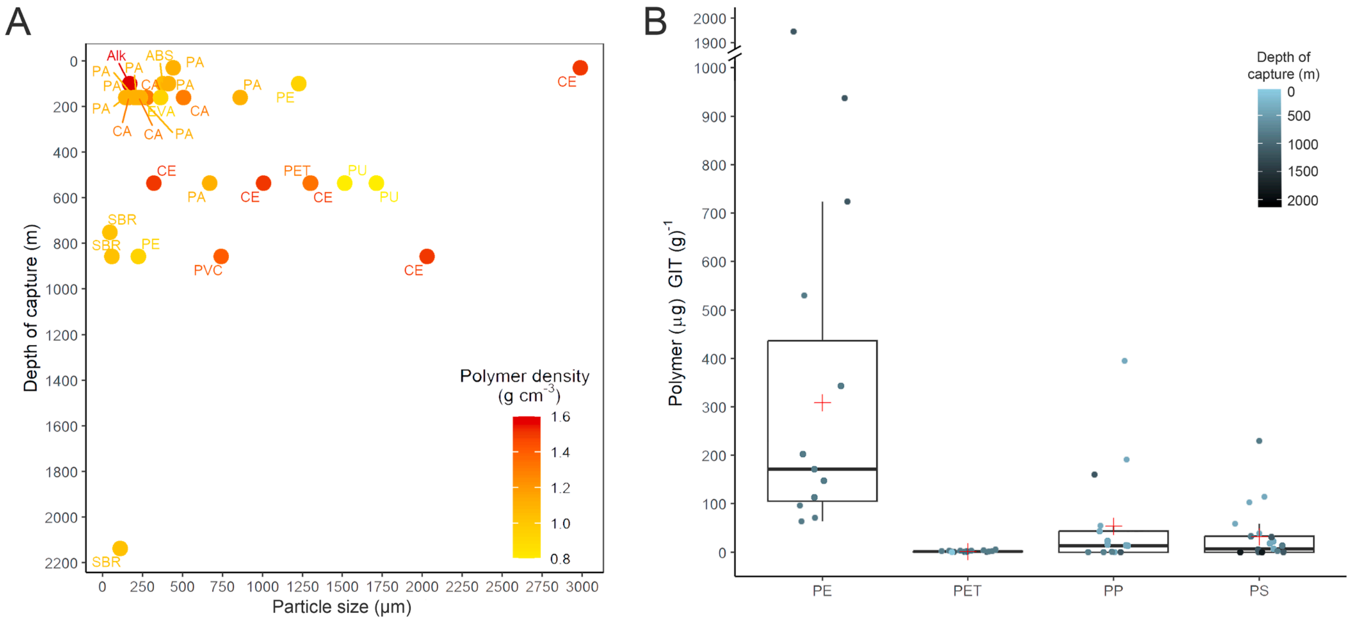

Fig. 7. Polymers detected in lanternfishes (Myctophidae) from the Southwestern Atlantic, collected in the REVIZEE Central campaign (1999–2000). (A) Microplastic polymers identified by LDIR analysis according to depth of capture, particle size, and theoretical polymer density. (B) Microplastic polymer content per gastrointestinal tract (GIT) of lanternfishes quantified by Py-GC-MS. The horizontal line within the box plots shows the interquartile range, the whiskers show the 1.5 × interquartile range, the dots represent outliers, and the red cross indicates the mean value.

contamination levels in the Northeastern Pacific [33]. However, when samples from off the western coast of the United States were analysed separately a slight increase was observed in the proportion of fish that had ingested MP, despite the authors addressing that the sample size was insufficient to draw more definitive conclusions.

The total polymer concentration detected by Py-GM-MS/MS was at ppm levels; this concentration was one order of magnitude higher than the amount detected in *M. edulis* from the North Sea in the same period (1999–2000) [76]. Invertebrate deposit feeders from the Northwestern Mediterranean registered similar levels to orders of magnitude higher [50]. However, caution is warranted in such comparisons due to taxonomic and methodological constraints, as analyses in shellfish focus on soft tissues, in echinoderms on the entire body, and fish on the gastrointestinal tract.

While Py-GM-MS/MS has not yet been applied to deep-sea fish, spectroscopy analysis (e.g. FTIR, Raman and LDIR) are the main tools used for polymer characterisation in lanternfishes (Table S13). Studies have consistently shown that this group is more prone to ingest theoretical (relative to pristine materials) high-density polymers, including PA, PET and SBR [30,32,78], which differs markedly from shallow-water fishes [79]. High-density polymers are more likely to increase abundance in deeper layers, whereas low-density polymers tend to accumulate at the sea surface for longer periods [80].

Polyethene terephthalate showed the lowest concentration among the 1999 and 2000 samples, contrasting with the 2017 samples, where PET was among the top three polymers identified [32]. Similarly, the PET contribution over other polymers increased in fish larvae [75] and two water snakes (*Natrix natrix* and *Natrix tessellata*) [81] along decades time series. Since the 1990s, the production of non-cellulosic fibres, consisting mainly of PET [5], has surpassed the production of natural fibres and has been growing steadily, while the production of natural fibres has remained relatively stable [67,82].

Polyethene was ranked fifth in polymer prevalence according to the LDIR analysis but exhibited the highest concentration in the Py-GC-MS/MS analysis. This discrepancy was likely due to considerable differences in the shapes of the evaluated MPs since fragments have a mass of at least ten times greater than fibres [83]. We found that the highest PE concentrations were associated with samples containing MP fragments.

One of the main limitations of spectroscopic analysis is that particle size and degree of degradation strongly influence the detection limit and spectra comparisons with the reference polymer type. The degradation potential of MPs in the GIT of fish stored for decades in 70 % ethanol remains uncertain. However, studies of museum-preserved specimens generally assume that ethanol has a minimal effect on MPs, largely due to the inherent stability of long-chain plastic polymers [33,84]. While Py-GC-MS/MS has no size-related limitations, the targeted particle must exceed the critical mass of the detection and quantification limits [85,86], which herein ensured the detection of the smallest MP size fractions. The size of ingested particles was negatively correlated with depth, and we assume that the MPs detected in lanternfishes are more likely to have a higher degree of degradation than those from shallower water fish. Therefore, integrating spectroscopy and Py-GC-MS/MS analyses could improve the comprehension of MP composition in deep-sea biota.

Through a global assessment of 555 fish species, Savoca et al. [21] identified five families (including lanternfishes) warranting special attention due to the extensive sampling efforts and recurrent documented plastic ingestion. Biologically mediated transport of MPs to the deep sea has been recognised as an important pathway for plastic dispersion to the final reservoir on the seafloor [17,87]. Marine snow is likely to provide the largest fraction of the global budget, but vertically migrating species are also hypothesised to play a crucial role [30,88–91]. Indeed, the lanternfish group alone has an estimated daily capacity to ingest up to 10^9 MPs in the epipelagic zone during vertical migrations and to excrete these particles within faecal pellets in the deep sea [21,91].

The high susceptibility of lanternfishes to MP ingestion, consistent with several features of this group, makes them effective candidates for serving as bioindicators in deep-sea ecosystems [23]. They are globally distributed, comprise one of the largest vertebrate biomass in the ocean [27], and provide an important link between basal and upper trophic levels [92]. Moreover, unlike most deep-sea biota, they are easier to collect and can be sampled in shallow waters at night. However, as with other taxonomic groups [93], the use of lanternfishes as bioindicator species for MP contamination presents several unresolved challenges that require attention, such as the selective ingestion of particles and retention time in the GIT, which remain poorly understood for most fish species to date [94,95].

Although trophic transfer has been evidenced in lanternfish predators [44], studies have not demonstrated bioaccumulation or biomagnification of MPs [96-98]. This suggests that while MPs are being transferred from prey to predator, they do not appear to concentrate or increase in quantity as they move up the trophic levels. Given the particularities of transient MP retention compared to persistent pollutants, monitoring this contaminant class in marine biota is even more challenging. Nevertheless, MP bioindicator species should be used as a comparable tool with other trophic levels considering sympatry and between their peers (e.g. same taxa or trophic niches) from different ocean basins or intervals of time.

The mean number of MPs detected in the 1999 and 2000 (REVIZEE Central) samples (0.75 ± 1.08 MPs ind.$^{-1}$) and the FO (47 %) were lower than those reported for lanternfishes from the South Atlantic in the second half of the 2010 decade [30,99] (Table S13). In the Southeast Atlantic, off the Tristan da Cunha Island, a mean of 1 ± 0.8 MP was reported in four individuals of *Lampanyctus australis* (75 % FO) caught in the upper mesopelagic layer in 2019 [99]. Likewise, in specimens collected in the Southwestern Tropical Atlantic in 2017, Justino et al. [30] detected 1.63 ± 1.41 and 1.07 ± 1.2 MPs ind.$^{-1}$ in *Diaphus brachycephalus* (75 % FO; N = 69) and *Hygophum taaningi* (62 % FO; N = 53), respectively. Although the sampling areas of the above-mentioned studies are on opposite margins of the South Atlantic, they are predicted to have similar MP abundances in the surface and subsurface waters [72].

The MP abundance along the boundary currents is relatively low when compared to accumulation zones, such as the North Pacific Central Gyre [73], which is estimated to contain 38 % of the meso- and microplastic abundance from the surface oceans [2]. In this region, lanternfishes collected from the surface layer in 2008 were reported with the highest MP contamination to date, ranging from one particle in the two least contaminated species to up to nine in *Myctophum aurolanternatum* (9 ± 8.99 MPs ind.$^{-1}$) and *Symbolophorus californiensis* (7.2 ± 8.39 MPs ind.$^{-1}$) [29]. It is important to address that these samples were collected in the shallowest layer considering the other studies on lanternfishes, which collected samples above 20 m depth (Table S13). Indeed, the plastic abundance in the upper 5 m decreases exponentially with depth [100], which could also be linked to the high ingestion rates observed in the lanternfishes from the North Pacific Central Gyre. Likewise, lanternfishes collected in the mesopelagic zone above MP accumulation zones, such as the Mediterranean Sea (2017) and an eddy region in the Northwest Atlantic (2015), exhibited high ingestion rates [101,102].

Studies on lanternfishes assessing MP contamination by evaluating the fish's diet contents (ingested prey) detected the lowest MP ingestion but did not implement either polymer analysis or QA/QC procedures [103,104]. To ensure accurate detection, acid or alkali digestion steps have been widely recommended for MP extraction from different matrixes [46]. Additionally, Wieczorek et al. [102] underscored the importance of employing a low detection limit for accurate MP contamination assessments in lanternfishes which may explain the low values detected in lanternfish studies (Table S13).

Most studies on MP contamination in lanternfishes have not accounted for the depth of capture in data analysis, which may introduce bias in interpreting general patterns. For instance, when MP ingestion is evaluated considering depth variability, the differences observed among campaigns investigated herein become even more pronounced. Generally, the highest MP contamination in pelagic fish is observed in intermediate waters [21]. We found a pronounced depth-related pattern in samples from all the evaluated campaigns, with a particularly high MP ingestion below the thermocline limit [105,106]. For instance, the likelihood of lanternfishes captured in the REVIZEE Central campaign ingesting MPs increased from the shallower layers of the TW, in the epipelagic zone, towards a peak in the lower limit of this water mass in the upper mesopelagic zone [30,32]. Depth profiles on MP abundance in the water column indicate a concentration increase within the upper mesopelagic zone [18,107]; thus, the contaminant availability might reflect higher ingestion odds.

Conversely, the likelihood of MP ingestion decreased in fishes captured in the SACW and AAIW, in the lower mesopelagic zone to a minimum in the NADW, in the bathypelagic zone. Meanwhile, the size of ingested MP showed a sharp decrease in the TW, especially in the first hundred meters of sampling. Furthermore, the MP ingested by the lanternfishes captured in the deep-water masses were more likely to correspond to the smallest size fractions detected herein. Indeed, the low geostrophic velocities in the deeper layers of the study area [40] associated with the remarkably low settling velocity of MPs smaller than 300 μm suggest a higher residence time of this size fraction in the water column [108]. Hence, there is a higher ingestion odd for small MPs at these depths.

Furthermore, the ecological traits of fish can significantly influence MP contamination [109]. The migratory patterns of lanternfishes were one of the most important factors influencing MP ingestion [32]. Similarly, the smallest particles were more likely to be detected in *D. brachycephalus* and *D. dumerilii*. These species systematically migrate from the upper mesopelagic to the epipelagic zone. *Diaphus lucidus* caught at the study's deepest station (2217 m depth) also showed a higher probability of ingesting the smallest MPs. At this depth, MPs of a similar size to those detected in *D. lucidus* prevailed at the edge of the North Atlantic Subtropical Gyre [110].

In addition to the standard protocols for MP extraction and identification, there are several critical considerations when using bioindicators for MP contamination in the deep sea to ensure comparability. Firstly, when planning the field cruise, the vertical behaviour of the species must be considered and specified, and the vertical range of sampling must be adapted accordingly. Secondly, the optimal sample size should be defined in order to detect a realistic abundance in the different ocean layers. Protocols and guidelines have established minimum sample sizes [46,111], but we recommend sampling a higher number of individuals, especially for abundant species, to ensure statistical power given the great variability of discrete variables such as the number of ingested particles, which are often zero-inflated. Nevertheless, sampling designs can differ significantly from studies as they need to be tailored to provide insights into a specific hypothesis [111,112].

Attention should also be paid to the size of detected MPs, which may significantly underestimate the number of particles ingested by specimens if the adopted detection limit is relatively high. For instance, 46 % and 32 % of particles detected herein were smaller than 200 and 100 μm, respectively, a threshold above those often implemented (Table S13). A detailed analysis of MP size fractions can provide valuable insights into particle selectivity [93], comparability with prey size [32], and further insights into adverse effects linked to MP ingestion, which depend upon particle size [113,114].

5. Conclusion

Despite the relatively short temporal gap between the sampling years and the present, global plastic production has increased by about 53 % over this period, with an estimated 60 % of all plastic materials produced now stored in landfills or the environment [4,5]. As such, our samples are valuable snapshots of the past, providing comparisons with samples collected at the present time. Interestingly, the ecological and environmental drivers responsible for MP ingestion in lanternfishes have remained consistent over time.

Lanternfishes from the SWA showed a slight increase in MP ingestion over the years, but a greater size effect was observed for the migratory patterns and depth at which specimens were captured. Microplastic composition (shape, colour) remained relatively homogenous across depths and sampling campaigns, with blue fibres of high-density polymers being the most prevalent. Finally, lanternfishes are valuable bioindicators of deep-sea environments, and museum collections can serve as essential tools for monitoring efforts.

Environmental implication

Global plastic production surged from 202 to 400 million tonnes between 1999 and 2022, and a considerable amount of mismanaged plastic waste is introduced into the ocean. In addition to the additives included during the manufacturing process, plastics can adsorb hydrophobic pollutants available in the environment that are persistent and bioaccumulative. Yet, there is a great knowledge gap on the microplastic contamination in the deep sea species. Here, we evaluated microplastic ingestion in one of the most abundant groups of the deep ocean using data from multiple sampling campaigns (from 1999 to 2017) enabling temporal comparisons.

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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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.jhazmat.2025.137125.

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