



Influencing factors for microplastic intake in abundant deep-sea lanternfishes (Myctophidae)

Guilherme V.B. Ferreira^{a,*}, Anne K.S. Justino^{a,b}, Leandro N. Eduardo^{a,c}, Natascha Schmidt^d, Júlia R. Martins^e, Frédéric Ménard^d, Vincent Fauvelle^f, Michael M. Mincarone^{g,h}, Flávia Lucena-Frédou^a

^a Universidade Federal Rural de Pernambuco (UFRPE), Departamento de Pesca e Aquicultura (DEPAQ), Rua Dom Manuel de Medeiros, s/n, Recife, PE 52171-900, Brazil

^b Université de Toulon, Aix Marseille Univ., CNRS, IRD, Mediterranean Institute of Oceanography, Toulon, France

^c MARBEC, Univ. Montpellier, CNRS, Ifremer, IRD, Sète, France

^d Aix Marseille Univ., Université de Toulon, CNRS, IRD, Mediterranean Institute of Oceanography, Marseille, France

^e Universidade Federal do Rio de Janeiro (UFRJ), Instituto de Biodiversidade e Sustentabilidade (NUPEM), Programa de Pós-graduação em Ciências Ambientais e Conservação (PPG-CIAC), Av. São José do Barreto, 764, Macaé, RJ 27965-045, Brazil

^f Université de Toulouse, LEGOS (CNES/CNRS/IRD/UPS), Toulouse, France

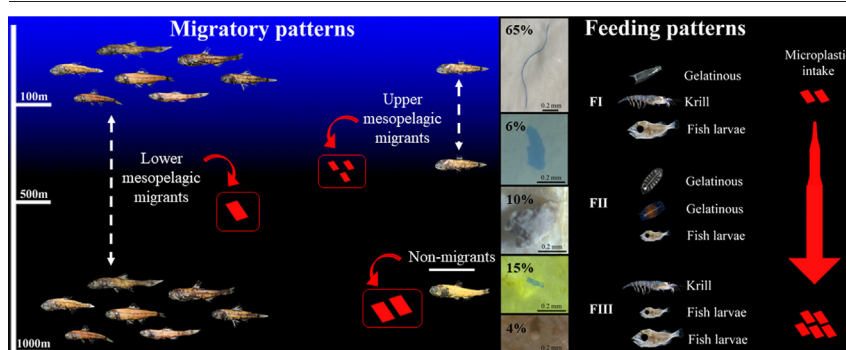
^g Universidade Federal do Rio de Janeiro (UFRJ), Instituto de Biodiversidade e Sustentabilidade (NUPEM), Av. São José do Barreto, 764, Macaé, RJ 27965-045, Brazil

^h Chapman University, Schmid College of Science and Technology, 1 University Drive, Orange, CA 92866, USA

HIGHLIGHTS

- High-density microplastics were more abundant in mesopelagic fishes.
- The size of microplastics was inversely associated with the continental distance.
- Biological mediated transport of plastic debris to the deep sea was evinced.
- Niche partitioning was the primary predictor of the microplastic intake rates.
- The jaw length of lanternfishes was positively correlated to microplastic intake rates.

GRAPHICAL ABSTRACT



ARTICLE INFO

Editor: Damià Barceló

Keywords:

Plastic debris
Vertical distribution
Mesopelagic
Microplastic ingestion
Hazardous waste

ABSTRACT

Plastic debris is ubiquitous in the hydrosphere. Yet, we lack an understanding of contamination among deep-sea species and primarily how each trait can influence microplastic intake. We investigated microplastic contamination in the digestive tract of hyper-abundant mesopelagic lanternfishes ($n = 364$ individuals) from the Southwestern Tropical Atlantic, captured from 90 to 1000 m depth. Overall, microplastics were detected in most individuals analysed (frequency of occurrence = 68 %). Large microplastics, mostly of a filamentous shape were the most frequent, followed by smaller fragments and foams. Microplastics made of high-density polymers (PET, PVC, PA, SBR rubber) were more prevalent than low-density ones (PE, EVA and PBD rubber), especially under deeper layers. Larger microplastics were detected in lanternfishes captured off the northeastern Brazilian coast (mean $0.88 \pm SE 0.06$ mm) compared to those from around the Rocas Atoll and Fernando de Noronha Archipelago (0.70 ± 0.07 mm; $p \leq 0.05$), ~350 km from the continent. Moreover, lanternfishes that migrate from the upper mesopelagic (200–500 m) to the epipelagic layers (<200 m) had simultaneously the highest intake and the smallest particles (1.65 ± 0.17 particles individual⁻¹ and 0.55 ± 0.07 mm; $p \leq 0.05$). Biological mediated transport of microplastics from the epipelagic to the mesopelagic waters was evinced, but fishes foraging in shallower layers had the lowest intake (1.11 ± 0.10 part. ind.⁻¹; $p \leq 0.05$). Furthermore, the jaw length was positively associated with an increment

* Corresponding author.

E-mail address: guilherme.vbf@gmail.com (G.V.B. Ferreira).

in microplastic intake (Incidence Rate Ratio = 1.1; $p \leq 0.05$). The lanternfishes that preferably prey upon fish larvae are more prone to microplastic intake than their counterparts, which forage mostly on crustaceans and gelatinous zooplankton ($p \leq 0.05$).

1. Introduction

The mesopelagic ocean zone (200–1000 m) encompasses habitats where solar radiation does not support primary production. Despite being one of the most remote environments in the biosphere, organisms inhabiting the mesopelagic zone are vulnerable to several anthropogenic impacts. For instance, mesopelagic fishing activity and deep-sea mining are emerging alternatives to satisfy the growing demand for animal protein and minerals (Drazen et al., 2020; Gillard et al., 2019; Morato et al., 2006). In addition, as most plastics are fossil carbon-based, the world energy matrix is associated with substantial plastic waste production (Hopewell et al., 2009), menacing even to the deep sea.

Of the 400 million metric tons of plastics manufactured yearly, only 9 % are estimated to be recycled (Geyer et al., 2017; PlasticsEurope, 2020), which makes the circular economy of plastics far from being achieved. Although plastics are mainly used in land-based applications, plastic residues can undergo long-range transport (Mishra et al., 2019; Onink et al., 2019). Between 1 and 12 million metric tons of mismanaged plastic waste (particles >5 mm) are estimated to be introduced into the ocean annually (Boucher and Friot, 2017; Geyer et al., 2017; Jambeck et al., 2015; Lebreton et al., 2017), although these estimates have recently been questioned and are suspected to be several orders of magnitude lower than presumed (Weiss et al., 2021). Regardless of the high durability, plastics are susceptible to weathering by environmental and biological factors, continuously fragmenting into ever smaller particles (microplastics, MPs < 5 mm; nanoplastics, NPs < 1 µm), favouring dispersion (Enfrin et al., 2020; Gewert et al., 2015).

More than half of the manufactured polymers are positively buoyant (Andrady, 2011). However, MPs are estimated to remain in surface waters for up to a few years (~2.4 years) (Weiss et al., 2021). Then MPs are dispersed downward to the ocean layers (e.g., increased density through oxidation and transfer by marine biota) or fragmented below the typical cut-off of sampling devices (150–300 µm) (Karlsson et al., 2018; Justino et al., 2022). Additionally, biofouling and incorporating marine snow (aggregates larger than 200 µm) increase the sinking rates of particles, including those of positively buoyant polymers (Kvale et al., 2020; Möhlenkamp et al., 2018; Porter et al., 2018).

Marine snow mainly consists of particulate organic matter (POM), including fecal pellets, phytoplankton, bacteria, and protists, which increase sinking rates due to increased aggregation (Newell et al., 2005; Porter et al., 2018). This mechanism associated with the bottom currents has been acknowledged as the main pathway for the final fate of MPs in the seabed (Courteney-Jones et al., 2017; Egger et al., 2020; Kane et al., 2020; Kanhai et al., 2018; Liu et al., 2020). Likewise, allochthonous sources are the main energy supply to the mesopelagic layers through the advective transport of organic matter from surface waters (Davison et al., 2013).

Marine biota is highly susceptible to ingesting MPs (Savoca et al., 2021; Wootton et al., 2021), and contamination has been reported throughout the ocean basins in deep-sea species (Choy and Drazen, 2013; Pereira et al., 2020; Sathish et al., 2020; Esposito et al., 2022). MP intake is linked to the development of several sub-lethal effects and can result in the uptake of chemical additives and pollutants adsorbed from the water column (Bhagat et al., 2020; Lei et al., 2018; Rochman et al., 2014; Senko et al., 2020; Wang et al., 2020). The environmental abundance (particles.m⁻³) of MPs and the ecological behaviour (migratory and feeding strategy) of species influence the intake of MPs (Ferreira et al., 2019; Fossi et al., 2018; McNeish et al., 2018; Pazos et al., 2017; Wootton et al., 2021).

MPs are abundant throughout the deep sea (Vega-Moreno et al., 2021), and species can intake particles while foraging and drinking water for

homeostatic regulation (Roch et al., 2020). In addition, many species residing at mesopelagic depths are also susceptible to MP intake from the epipelagic layers when ascending to feed in near-surface waters at night (Ferreira et al., 2022; Justino et al., 2022; Wieczorek et al., 2018). The diel variability in light intensity triggers indeed a vertical migratory response in several deep-sea organisms, inducing them to swim upwards to the productive shallow waters and forage at nighttime (Eduardo et al., 2020, 2021; Sutton, 2013). This diel vertical migration of zooplankton and fishes can contribute up to half of the carbon from the passive sinking to the deep sea (Davison et al., 2013; Steinberg and Landry, 2017).

Biomass of about 10 billion metric tons is estimated for mesopelagic fishes (Irigoien et al., 2014). Among these, the family Myctophidae (lanternfishes) includes some of the most abundant species, regardless of the ocean basin and vertical mesopelagic strata (Catul et al., 2011; Eduardo et al., 2021; Irigoien et al., 2014). These species play a significant role in energetic pathways by consuming zooplankton and providing forage for numerous epipelagic (e.g., tuna, mammals, squids, and diving seabirds) and deep-sea (e.g., viperfish, lancetfish, and moonfish) predators (Eduardo et al., 2021; Gjøsæter, 1973; Hernandez-Gonzalez et al., 2018; Olaso et al., 2005).

Lanternfishes are crucial for connecting epipelagic and deep-sea ecosystems, acting as a potential vector of carbon and MPs. Therefore, several species were investigated for MP contamination (Bernal et al., 2020; Boerger et al., 2010; Davison and Asch, 2011; Justino et al., 2022; Lusher et al., 2016; McGoran et al., 2021; Romeo et al., 2016; Wieczorek et al., 2018). However, most of these surveys focus on the species level, often lacking replicates and quality assurance procedures. Moreover, the influence of the ecological roles and niches of lanternfishes in MP intake has been overlooked so far. This study aims to improve knowledge of the relationship between plastic and the poorly known deep-sea biota, by studying MP intake in one of the most abundant fish taxa in mesopelagic waters. We tested the hypothesis that MP contamination in Myctophidae from the Southwestern Tropical Atlantic (SWTA) is associated with (i) niche partitioning and (ii) spatial variability.

2. Methods

2.1. Study area

Data collection was performed along the SWTA during the austral autumn of 2017 (Fig. 1). Samplings were conducted off the northeastern Brazilian coast, including oceanic islands (Rocas Atoll and Fernando de Noronha Archipelago), ~350 km from the coastal zone, and seamounts of the Fernando de Noronha Ridge, which is considered an Ecological and Biological Significant Area (CBD, 2014). The seamounts and off northeastern Brazil surface layers (0 to 70 m) are controlled by the North Brazil Current (NBC) and North Brazil Undercurrent (NBUC), whereas the Rocas Atoll and Fernando de Noronha Archipelago surface layers are controlled by the South Equatorial Undercurrent (SEUC) and the central branch of the South Equatorial Current (cSEC) (Assunção et al., 2020; Costa da Silva et al., 2021).

2.2. Sample collection and preparation

The lanternfishes were collected by micronekton trawls (30 min at 2–3 kt, 40 mm body mesh and 10 mm cod-end mesh) during the multidisciplinary research cruise ABRACOS2 (Acoustics along the BRAZILIAN COast 2) on-board the French RV *Antea* (Bertrand, 2017). The micronekton net (colour: wheat) has a 24 × 24 m size mouth composed of 40 mm thermoplastic

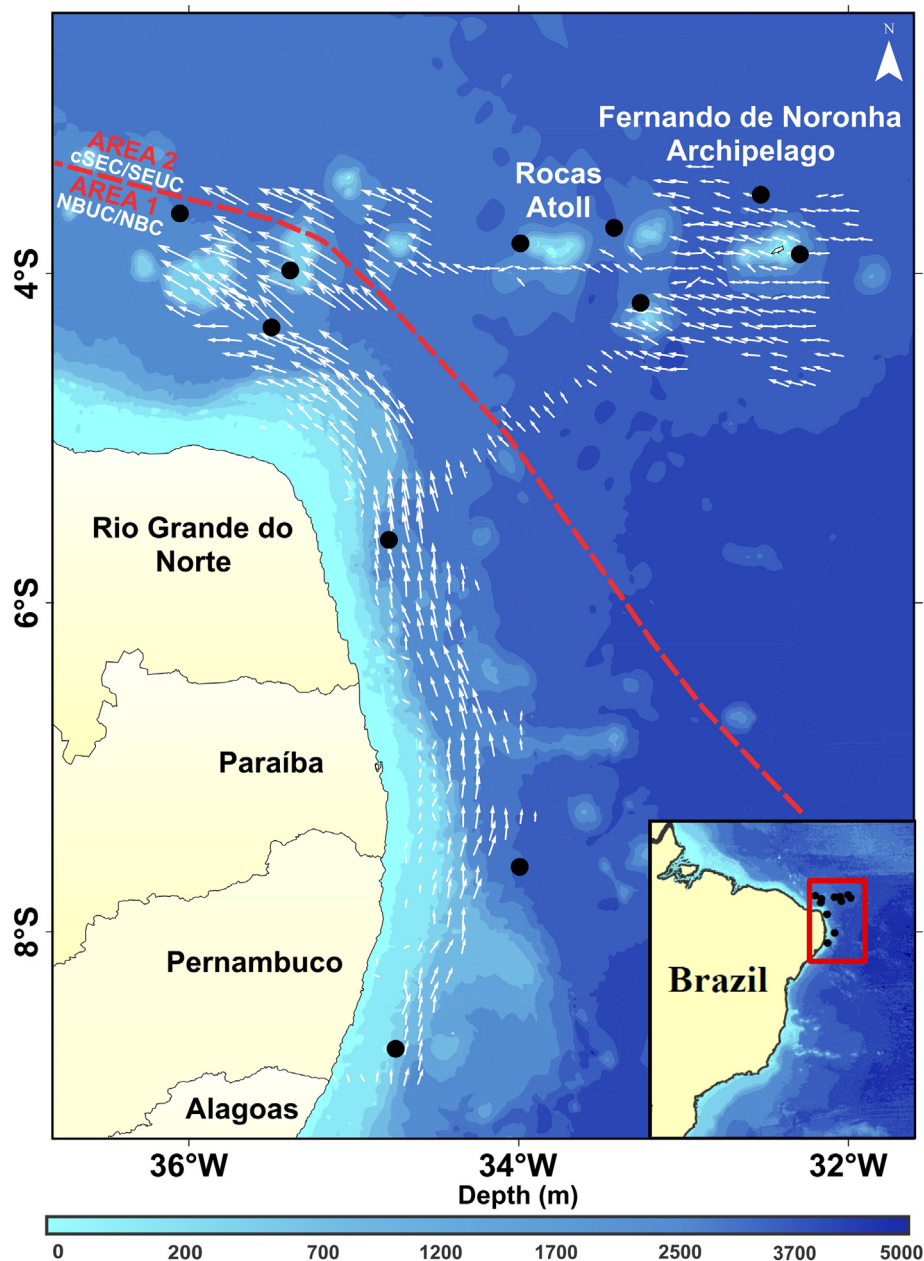


Fig. 1. Sampling stations (black dots) of lanternfishes (Myctophidae) off northeastern Brazil, Southwestern Tropical Atlantic. Red dashed line divides the study area according to the thermohaline structure and current systems: cSEC– central branch of the South Equatorial Current; SEUC– South Equatorial Undercurrent; NBC– North Brazil Current; NBUC– North Brazil Undercurrent (adapted from Assunção et al., 2020; Eduardo et al., 2021). Area 1 encompasses sampling stations off northeastern Brazil and seamounts. Area 2 encompasses sampling stations around the Rocas Atoll and Fernando de Noronha Archipelago. White arrows indicate the direction and strength of ocean currents between 0 and 75 m.

polyamide elastomer (TPA) body mesh and 10 mm polyamide (PA) cod-end mesh, to increase the size range of captured specimens (Bertrand, 2017; Eduardo et al., 2022).

Samplings were carried out between 9th April and 6th May 2017 (autumn) during day and night, encompassing different depth strata (90 to 1000 m), and 11 stations were selected for the study due to the abundance of individuals (Fig. 1, Table S1). Daytime samplings occurred between one hour after sunrise to one hour before sunset, and nighttime samplings were performed one hour after sunset until one hour before sunrise. Conductivity, temperature, depth and dissolved oxygen profiles were acquired by a CTD Seabird SBE911plus and auxiliary sensors (Bertrand, 2017; Eduardo et al., 2020).

On board the cruise, the lanternfishes were firstly fixed in a 4 % formalin solution and then preserved in a 70 % ethanol solution. In the

laboratory, species were identified according to Nafpaktitis et al. (1977). Voucher specimens from the survey were deposited in the Fish Collection of the Instituto de Biodiversidade e Sustentabilidade, Universidade Federal do Rio de Janeiro (NPM, Macaé, Brazil). The most dominant Myctophidae species in the study area were selected for MP contamination (Eduardo et al., 2021).

For each specimen, weight (nearest 0.0001 g) and morphological features (nearest 0.01 mm of total length, jaw length, eye diameter and the longest axis of the dorso-nasal photophore) were registered. All measurements were taken from the left side. Stomach-inverted specimens were excluded from the analysis to avoid airborne contamination and/or loss of particles. All methods were conducted following the Brazilian Ministry of Environment under authorization number SISBIO: 47270–5.

2.3. Microplastic analysis

In the research cruise precautionary measurements to avoid airborne MP contamination were not implemented. Therefore, at the laboratory specimens were meticulously rinsed with filtered (0.7 µm pore size glass fibre filters) distilled water to remove any particles attached to the outermost tissue. Specimens were eviscerated, and their digestive tracts (stomach and intestine) were removed and thoroughly washed with filtered distilled water. Then, the digestive tracts were submitted to chemical digestion through sodium hydroxide (NaOH 1 mol L⁻¹) to decompose proteins, easing the identification of MPs (Ferreira et al., 2022; Justino et al., 2021, 2022). The use of NaOH is a cost-effective method and does not imperil plastic integrity for polymer investigation (Budimir et al., 2018).

Each sample (digestive tract of a given individual: 1.66 ± 0.07 g) was placed into a 50 mL beaker, filled with sodium hydroxide solution, covered by a glass lid and placed into a laboratory oven (60 °C) for 24 h to increase the reaction rate. Samples were mixed with a glass stick two times during the incubation period to homogenise the solution. The outputs of the chemical digestion were filtered through glass fibre filters (Whatman: GF/F 0.7 µm pore size) using a laboratory vacuum set-up. The glass fibre filters with the digestion residues were then placed in covered Petri dishes and oven-dried at 60 °C for 24 h.

The resulting samples were then visually examined using a stereomicroscope (Zeiss Stemi 508) coupled to a camera device (AxioCam 105 Color), under the highest magnification available, with a detection limit of 0.02 mm. Particles suspected to be made of plastic were photographed, counted and measured (length of the longest axis) using digital microscopy software (Zeiss ZEN 3.2).

Particles ≤ 5 mm were considered microplastics (MPs) and categorised according to morphological and optical characteristics into five different shapes: fibres (filamentous shape), fragments (thick with an irregular shape), film (flat with an irregular shape), foam (soft with an irregular shape), and beads (spherical shape); and five colours (black, blue, green, red, and white) (Lusher et al., 2017). Additional colours of the visible spectrum and unsaturated colours were included close to their bands (e.g., purple was included in the blue category, and orange and yellow were included in the red category).

A random sub-sample (10.8 %; 50 particles) of the detected particles was identified through Laser Direct Infrared analysis (LDIR) to access the polymer composition, following the recommendations proposed by Hanke (2013). An Agilent 8700 LDIR Chemical Imaging System was used to perform at least 7 scans for each particle in the wavelength ranging from 975 to 1800 cm⁻¹ (Ourgaud et al., 2022). The outputs were compared with the Microplastics Starter 1.0 library reference spectra, and the polymer of a given particle was asserted when the polymer identification match was superior to 70 % (Eo et al., 2021; Ferreira et al., 2022; Justino et al., 2022). Since the polymer composition was accessed in a sub-sample of the detected particles, it is important to notice that, to a certain degree, non-plastic particles could also have been accounted for as MPs.

2.4. Laboratory quality assurance/quality control

The protocol implemented for MP extraction followed methodological steps to mitigate airborne contamination of samples (Song et al., 2021). Analyses were conducted in an isolated subsection of the main laboratory to limit flow in the workstation. Disposable latex gloves and 100 % cotton lab coats were used during all procedures. All work surfaces were thoroughly cleaned with 70 % filtered ethanol, and handling equipment was made exclusively of metal and glass. Before use, handling equipment, beakers and Petri dishes were rinsed with filtered distilled water and checked for adhered particles under a stereomicroscope.

To avoid airborne contamination, reagent preparation and sample handling were performed under a fume hood cabinet. Any solution used for MP extraction (distilled water and sodium hydroxide) was filtered over a 47 mm glass fibre filter (GF/F 0.7 µm Whatman). Two observers

performed MP identification to reduce identification variance (overestimation and/or underestimation).

A procedural blank was run for each sample batch, which consisted of an average of 15 samples (sample = stomach and intestine of a given individual). Procedural blanks were submitted to the same procedures as samples. Whenever MPs were observed within blanks, particles with the same characteristics (shape and colour) were removed from the corresponding sample batch. Four contaminations were registered out of the thirty procedural blanks implemented during the analysis: two green fragments, one green film and one black fibre identified as cellulosic.

2.5. Data analysis

To investigate the regional scale of MP contamination in lanternfishes (frequency of occurrence, number and size of particles), the sampling stations were divided according to the main surface currents and thermohaline structure into Areas 1 and 2. Area 1 encompasses the sampling stations off northeastern Brazilian coast and seamounts northward in the study area, whereas Area 2 represents the sampling stations around the oceanic islands (Rocas Atoll and Fernando de Noronha Archipelago) (Fig. 1) (Assunção et al., 2020; Eduardo et al., 2021). The vertical scale of MP contamination was investigated through the main depth strata where fishes were captured [epipelagic layer (0–200 m), upper mesopelagic layer (200–500 m) and lower mesopelagic layer (500–1000 m)].

MP contamination was also investigated according to species and from an ecological perspective. To investigate the influence of ecological patterns on MP intake, nine sampled species (*Bolinichthys distofax*, *Diaphus brachycephalus*, *D. garmani*, *D. fragilis*, *D. perspicillatus*, *D. splendidus*, *Hygophum taaningi*, *Lampanyctus nobilis*, and *Lepidophanes guentheri*) were categorised into different niches based on migration behaviour and feeding strategy, according to carbon and nitrogen isotopes proposed by Eduardo et al. (2021) in the study area (Table S2).

The migratory behaviour comprised species that inhabit mainly (i) the upper mesopelagic (UM.Mig; 200–500 m) and (ii) the lower mesopelagic (LM.Mig; 500–1000 m) layers and perform diel vertical migration towards the epipelagic waters to forage, and (iii) non-vertical migrant (Non.Mig), which forage in the lower mesopelagic waters. The feeding strategy of lanternfishes included three main zooplanktivore patterns [F I: species foraging mainly on *Abylopsis tetragona*, *Euphausia gibboides* and fish larvae ranging from 15 to 20 mm; F II: species foraging mostly on *Soestia zonaria*, *Salpa* spp. and fish larvae ranging from 5 to 10 mm; F III: species foraging mainly on *E. gibboides*, two groups of fish larvae, ranging from 5 to 10 mm and 15 to 20 mm] (Eduardo et al., 2021) (Table S2).

Only the vertical migrants were selected to investigate the influence of the feeding strategy on MP ingestion (species that forage in the epipelagic zone). Therefore, the non-migrants were not included in the feeding strategy analysis. Additionally, MP polymer densities correspond to pristine particles from Osswald and Oberbach (2006). One-way analyses of variance were performed to assess whether the number (particles individual⁻¹) and size (particle length individual⁻¹) of detected MPs (regardless of shape and colour) varied among categorical variables (depth strata, area, diel period, species, migration behaviour, and feeding strategy).

Since only the lower mesopelagic migrants were captured in the epipelagic waters, this group was omitted from the ANOVA regarding the migratory behaviour. Hence, the migratory behaviour analysis included only fish captured within mesopelagic waters (including non-migrants and upper and lower mesopelagic migrants).

Two-way analyses of variance allowed us to investigate the interaction between habitat features (area vs. depth strata and diel period vs. depth strata). Data were previously Box-Cox transformed (Box and Cox, 1964) and normality was tested using Levene's and Bartlett's tests (Table S3) (Levene, 1960; Underwood, 1997). Whenever significant differences were observed, the post hoc Tukey test was applied to detect the source of variance.

Generalised Linear Models were proposed to investigate the influence of morphological features of fish, environmental drivers, and ecological patterns (categorical and continuous variables) on the number of detected

MPs (response variable). Firstly, collinearity was checked and exploratory data analyses were performed on the response variables to propose the fit distribution and link function of the models. The number of detected MPs (particles individual⁻¹) was analysed through the Poisson distribution (log link). The Akaike Information Criterion was used to check the goodness of fit of models, while stepwise procedures (backwards method) were performed in the full model. All exploratory variables were included (with interactions), and non-significant variables were progressively excluded to achieve the model with the best fit (Table S4) (McCullagh and Nelder, 2019). To validate the selected model, the null and residual deviance were evaluated, as well as the normal probability plot of the residual components of the deviance, and the chi-squared value of the deviance was assessed to verify whether the models provided an adequate fit (Fig. S1, Tables S4 and S5) (McCullagh and Nelder, 2019). All statistical analyses were carried out using R 3.6 (R Core Team, 2022) and performed at a significance level of 0.05.

3. Results

From the 11 trawls, 364 individuals from nine species of Myctophidae were investigated for MP intake. The standard length of specimens ranged from 25.18 to 92.74 mm and jaw length from 4.85 to 19.26 mm. A total of 462 MP particles were detected in 248 contaminated individuals (digestive tract), representing a frequency of occurrence of 68 % (Fig. 2, Table S2). MPs were detected in all depths of capture, regardless of species. On average, 1.27 MP particles per individual (Standard error \pm 0.07) were detected in lanternfishes with an average particle size of 0.81 mm (SE \pm 0.04) (Table 1). The size of particles ranged from 0.044 mm (blue film) to

Table 1

Detected microplastics in lanternfishes (Myctophidae) from the Southwestern Tropical Atlantic according to spatial-temporal variability expressed in frequency of occurrence (FO%), number (particles individual⁻¹) and size (mm) of particles (mean \pm SE). [No sampling (-)].

		FO%	Number of MPs	Size of MPs
Day trawl	Epipelagic	–	–	–
	Upper mesopelagic	84.61	1.81 \pm 0.25	0.54 \pm 0.12
	Lower mesopelagic	76.59	1.29 \pm 0.15	0.99 \pm 0.15
Night trawl	Epipelagic	63.35	1.11 \pm 0.10	0.82 \pm 0.07
	Upper mesopelagic	–	–	–
	Lower mesopelagic	71.43	1.54 \pm 0.17	0.76 \pm 0.09
Area 1	Epipelagic	63.92	1.15 \pm 0.13	0.85 \pm 0.07
	Upper mesopelagic	–	–	–
	Lower mesopelagic	78.84	1.52 \pm 0.17	0.98 \pm 0.09
Area 2	Epipelagic	62.91	1.01 \pm 0.15	0.74 \pm 0.14
	Upper mesopelagic	84.61	1.81 \pm 0.25	0.54 \pm 0.12
	Lower mesopelagic	69.23	1.38 \pm 0.16	0.75 \pm 0.13
Myctophidae		68.13	1.27 \pm 0.07	0.81 \pm 0.04

4.991 mm (white fragment), particles larger than 5 mm were not detected. Additionally, up to 15 foam particles were detected in a single individual of *D. splendidus*, captured in the epipelagic waters.

3.1. Environmental characterisation

The environmental features showed moderate variability between off the northeastern Brazilian coast and the oceanic islands (Area 1 and 2, respectively). The mixed layer where floating MPs can sink due to surface

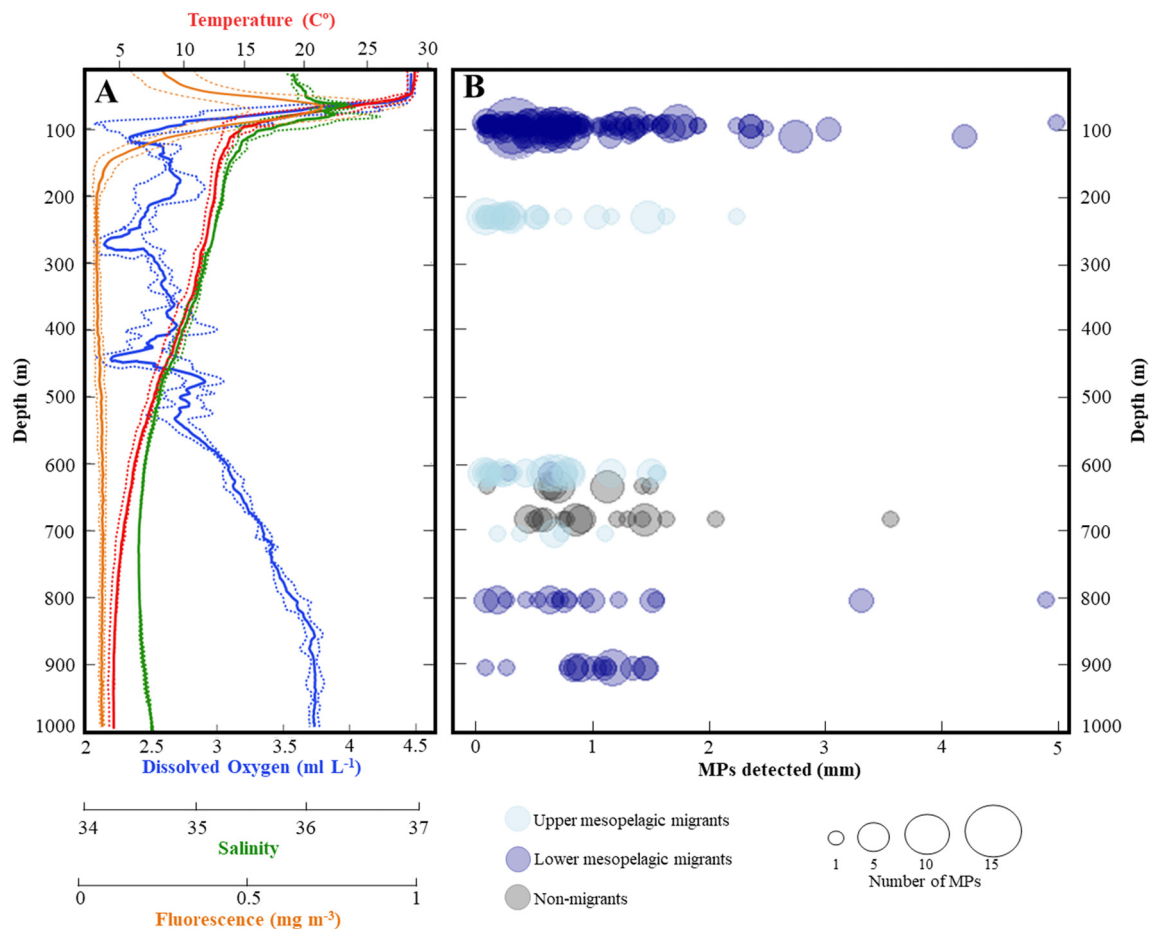


Fig. 2. A) Mean and standard deviation of vertical profiles of temperature, dissolved oxygen, salinity, and fluorescence; (B) number and size of detected microplastics (MPs) in lanternfishes, according to capture depth, from the Southwestern Tropical Atlantic.

forcing extended up to 50 m. Salinity and fluorescence increased (36.00 to 36.25, and 0.25 to 0.60 mg m⁻³, respectively) from the surface towards the upper thermocline limit (~ 40 m). On the other hand, temperature and dissolved oxygen (DO) slightly decreased from 29 to 25 °C and from 4.5 to 4.25 mg L⁻¹ (Fig. 2).

Environmental drivers had the greatest variability within the thermocline (~ 40 to 150 m), where the lanternfish from the epipelagic waters were captured (Table S1). Salinity, temperature, and fluorescence progressively decreased towards the lower thermocline limit (35.25; 13 °C; 0.1 mg m⁻³, respectively) (Fig. 2). Dissolved oxygen sharply decreased from 4.25 to 2.75 mg L⁻¹, but at 100 m depth, DO oscillated. Likewise, DO fluctuated within the upper mesopelagic waters (200–500 m) and increased within the lower mesopelagic water (500–1000 m) from 2.75 to 3.75 mL L⁻¹. Temperature and salinity progressively decreased from the lower thermocline limit to the lowest capture depth (from 35.25 to 34.50 and from 13.0 to 4.4 °C; 900 m, respectively), whereas fluorescence remained roughly steady (Fig. 2, Table S1).

3.2. Microplastic contamination and niche partitioning

Whatever their shape and colour, the number of detected MPs in lanternfishes did not vary significantly depending on the sampling area (Area 1: 1.24 ± 0.11 part. ind.⁻¹, and Area 2: 1.31 ± 0.1 part. ind.⁻¹). However, MPs detected in fishes from Area 1 were larger (0.88 ± 0.06 mm; $F = 5.223$; $p \leq 0.05$) than those from Area 2 (0.70 ± 0.07 mm) (Fig. 3, Tables S6 and S7). Regarding the depth strata, lanternfishes sampled from the epipelagic zone had the lowest number of MPs (1.11 ± 0.10 part. ind.⁻¹; $F = 9.155$; $p \leq 0.05$), but the size of those particles did not vary significantly (epipelagic: 0.81 ± 0.06 mm; upper mesopelagic: 0.54 ± 0.12 mm; lower mesopelagic: 0.86 ± 0.08 mm) (Fig. 3, Tables S6 and S7).

MP contamination according to the diel period showed that fishes trawled during the daytime had the highest number of MPs (1.48 ± 0.14 part. ind.⁻¹; $F = 5.68$; $p \leq 0.05$). However, the diel period did not influence the size of detected particles (daytime: 0.81 ± 0.11 mm; nighttime: 0.80 ± 0.05 mm) (Fig. 3, Tables S6 and S7).

Interactions between diel period vs. depth strata and area vs. depth strata indicated significant effects on the number of MPs ingested but not on their size (Table 1 and S7). The number of detected MPs was lowest in fishes captured in the epipelagic layer during nighttime (1.11 ± 0.10 part. ind.⁻¹; $F = 6.128$; $p \leq 0.05$) and in the epipelagic layer within Area 2 (1.01 ± 0.15; $F = 5.886$; $p \leq 0.05$) (Tables 1 and S7).

All the Myctophidae species evaluated depicted high rates of contamination (FO%), ranging from 55 % in *L. guentheri* to 93 % in *D. perspicillatus* (Table S2). Of the nine species studied, *L. nobilis* exhibited the lowest number of detected MPs (0.71 ± 0.11 part. ind.⁻¹; $F = 3.088$; $p \leq 0.05$), whereas in *D. brachycephalus* and *B. distofax* the smallest and largest MPs were detected, respectively (0.4 ± 0.06 mm, and 1.09 ± 0.13 mm; $F = 3.618$; $p \leq 0.05$) (Tables S2 and S7).

The analyses of detected MPs according to the vertical migratory behaviour of Myctophidae species indicated that the upper mesopelagic migrants had the highest MP intake (1.65 ± 0.17 part. ind.⁻¹; $F = 4.673$; $p \leq 0.05$) and the smallest size of particles (0.55 ± 0.07 mm; $F = 7.212$; $p \leq 0.05$) (Fig. 3, Tables S6 and S7). The feeding strategy of lanternfishes is also reflected in the number of detected MPs; specimens belonging to the feeding strategy III had the highest number of particles (1.69 ± 0.15 part. ind.⁻¹; $F = 5.306$; $p \leq 0.05$), followed by feeding strategy II (1.23 ± 0.16 part. ind.⁻¹) and I (0.97 ± 0.09 part. ind.⁻¹) (Fig. 3, Table S7).

The generalised linear model results indicated that the feeding strategy, depth of capture and jaw length were the best predictors of the number of detected MPs in lanternfish from the SWTA (Table S4). The analysis of deviance of the fitted generalised linear model suggested that the variations observed in the number of detected MPs with the depth of capture were significant (Table S5). Likewise, the number of detected MPs varied significantly between feeding strategies of lanternfishes, which explained 14.8 % of data variability (Table S5).

The lanternfish species grouped into feeding strategies I and II were negatively related to the number of detected MP in the digestive tract (stomach and intestine). Both groups had respectively, 82 % and 51 % (Incidence Rate Ratio = 0.18 and 0.49; 95 % Confidence Interval = 0.08–0.37 and 0.33–0.71, respectively; $p \leq 0.05$) fewer chances of MP intake than lanternfishes from feeding strategy III (Table 2). The jaw length of lanternfishes was positively correlated with the number of detected MPs; thus, each one-unit increase in the size of the jaw was associated with a 10 % increase in the incidence rate ratio of MP intake (IRR = 1.1; 95 % CI = 1.05–1.16; $p \leq 0.05$) (Table 2). The depth of capture had a slightly positive influence on the number of detected MPs ($p \leq 0.05$) (Fig. 4, Table 2). Similarly, the predicted number of MPs in the digestive tract increased more rapidly towards greater capture depths and in fish with longer jaws (Fig. 4).

3.3. Microplastic characterisation

A myriad of colours was identified among the detected MPs, but blue was the most prevalent, representing 49 % of particles, followed by white (35 %), red (8 %), black (7 %) and green (1 %). Moreover, blue and white particles prevailed throughout the spatial (depth strata and area) and temporal scale (Fig. S1). Of the different shapes of detected particles, fibres were the most prevalent accounting for 65 % of particles (0.83 ± 0.05 part. ind.⁻¹), followed by fragments (15 %; 0.19 ± 0.02 part. ind.⁻¹), foam (10 %; 0.12 ± 0.05 part. ind.⁻¹), film (6 %; 0.06 ± 0.01 part. ind.⁻¹) and beads (4 %; 0.05 ± 0.01 part. ind.⁻¹) (Fig. S1, Table S8).

Regarding the size of MP shapes, fibres were the largest particles identified in the digestive tracts of lanternfishes (1.03 ± 0.05 mm) and ranged from 0.05 to 4.99 mm, prevailing among all size ranges (0.5 mm break interval), except between the smallest interval (range: 0.1–0.5 mm) and from 2 to 2.5 mm (Fig. 5). Fragments (0.35 ± 0.11 mm) had the broadest size range (from 0.03 to 4.99 mm) and were followed by foams (range: 0.1–1.2 mm; mean: 0.46 ± 0.06 mm), films (0.04–0.34 mm; 0.09 ± 0.01 mm) and beads (0.07–0.37 mm; 0.05 ± 0.01 mm) (Fig. 5, Table S9).

The polymer composition was accessed in a subsample that comprehended 10.8 % of the detected particles (50 particles) Fig. 6. Within the analysed subset, LDIR successfully identified the plastic polymer composition of 53 % of particles, including twelve different plastic polymers (Fig. S2). Biopolymers comprehended 11 % of tested particles, including cellulose acetate. Non-identified particles included two groups, 15 % of the total analysed resembled plastic polymers but were below the cutoff point (scoring between 60 and 69.9 % of similarity with the reference spectrum), and 21 % of particles did not resemble any spectra from the accessed library (Fig. S2). As the LDIR is still a novel technique used to identify MP, the number of available reference spectra for virgin and weathered polymers constantly increases, reducing the rate of non-identified particles in future studies.

Within the successfully identified plastic polymers, polyethylene (PE) and polyethylene terephthalate (PET) were the most abundant (17 %, each), followed by polyamide (PA: 14 %), styrene-butadiene (SBR rubber: 14 %), polyvinyl chloride (PVC: 10 %), acrylonitrile butadiene styrene (ABS: 7 %), alkyd varnish (7 %), ethylene-vinyl acetate (EVA: 3 %), polycarbonate (PC: 3 %), and polybutadiene rubber (PBD rubber: 3 %). Two additional subclasses were identified within the PE particles: low-density polyethylene (LDPE) and chlorinated polyethylene (Figs. 6 and S2).

The theoretical (relative to pristine material) high-density polymers (> 1.02 g cm⁻³) prevailed over the low-density materials (75 % and 25 %, respectively). LDPE (0.92–0.96 cm⁻³) was identified in fishes captured in the epipelagic zone, except for a blue fibre extracted from an upper mesopelagic migrant captured at 230 m (Figs. 6 and S2). On the other hand, the higher density polymers PET (1.34 cm⁻³; 95–800 m depth), SBR (0.94–1.04 cm⁻³; sampling depth: 95–680 m), PA (1.02–1.14 cm⁻³; 95–800 m depth), PVC (1.42–2.2 cm⁻³; 90–900 m depth) and alkyd varnish (1.42–2.22 cm⁻³; 95–630 m depth) were identified throughout the water column. Furthermore, concerning the non-migrant lanternfish solely, three high-density polymers were identified (SBR, PET, and alkyd varnish) (Fig. 6).

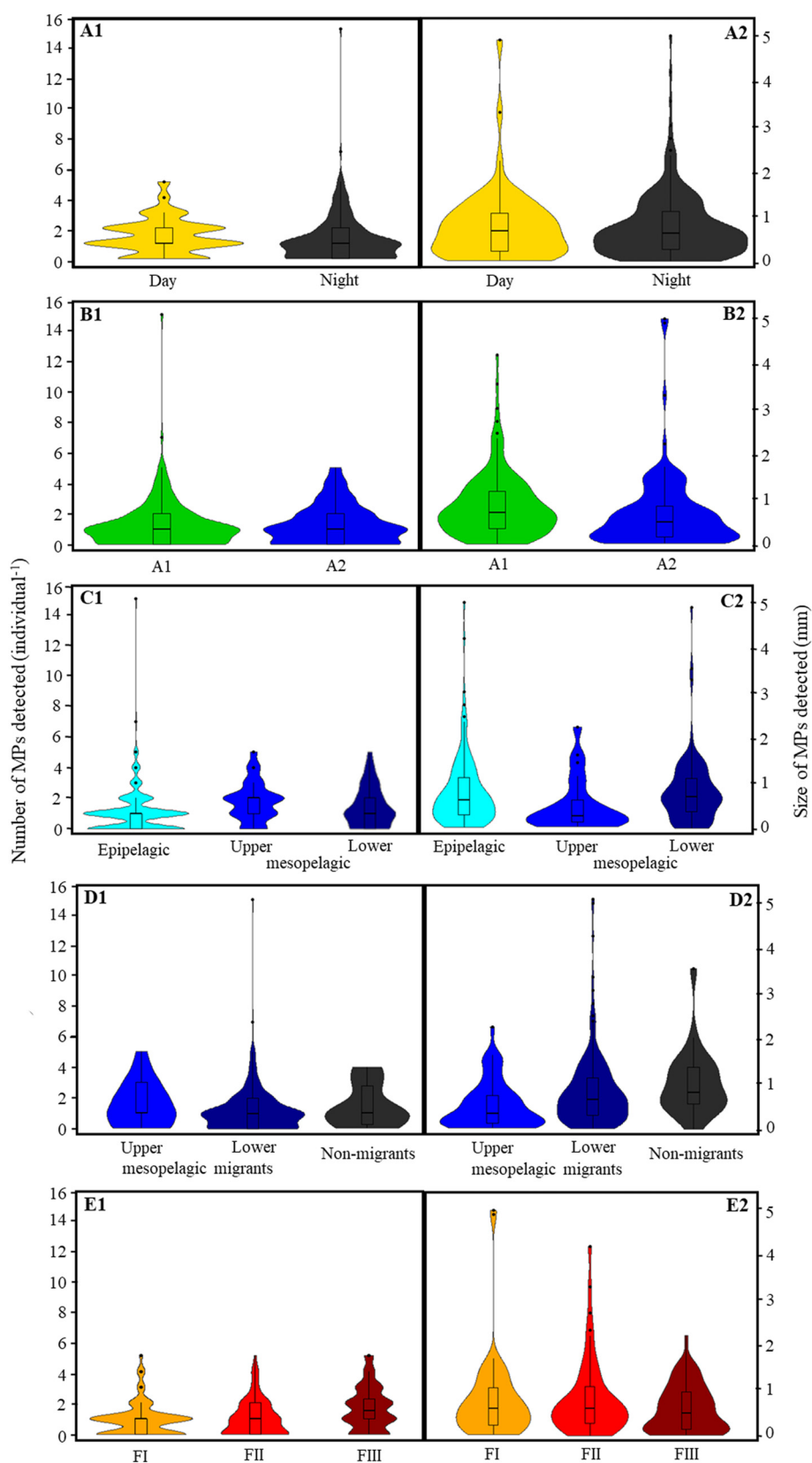


Fig. 3. (1) Number and (2) size of detected microplastics in lanternfishes from the Southwestern Tropical Atlantic according to (A1 and A2) diel period, (B1 and B2) area and (C1 and C2) depth strata of capture, (D1 and D2) migratory behaviour, and (E1 and E2) feeding strategy. The violin plots show kernel density estimation as a representation of data distribution. The horizontal line within the box plots shows the inter-quartile range, the whiskers show the $1.5 \times$ interquartile range, and the dots represent outliers.

Table 2

Coefficients from the generalised linear models fitted to the number of detected microplastics in lanternfishes (Myctophidae) from the Southwestern Tropical Atlantic. SE– standard error; IRR– Incidence Rate Ratio; CI– 95 % Confidence Interval; * $p < 0.05$.

Coefficient	Estimate	SE	z-value	IRR	CI	p-Value
Microplastics						
Intercept	−0.7276	0.3199	−2.27			* 0.0229
Depth of capture	0.0013	0.0004	2.71	1	1–1	* 0.0067
Jaw length	0.0952	0.0251	3.78	1.1	1.05–1.16	* 0.0001
Feeding Strategy I	−1.7193	0.3999	−4.29	0.18	0.08–0.37	* 0.0001
Feeding Strategy II	−0.7111	0.1927	−3.69	0.49	0.33–0.71	* 0.0001
Null deviance	286.55 on 189 df					
Res. deviance	242.89 on 185 df					
R ² Nagelkerke	0.264					
AIC	528.08					

4. Discussion

Deep-sea species are presumably less vulnerable to MP contamination than those inhabiting surface waters (Fossi et al., 2018; Pereira et al., 2020; Sathish et al., 2020) due to the buoyant characteristic of most plastic polymers and the greater distance from the major input sources, where surface currents and wind friction generate accumulation zones (Lima et al., 2021; van Sebille et al., 2015) in the uppermost layers (Kanhai et al., 2018; Reisser et al., 2015). Greater MP abundance in the water leads to higher contamination and intake rates (occurrence and quantity of particles) in fish, but this association has been evinced mostly in semi-enclosed water bodies (Ferreira et al., 2018; Pazos et al., 2017; Savoca et al., 2021; Wootton et al., 2021; Wright et al., 2013). Nevertheless, our findings showed a high frequency of occurrence of MPs in every species evaluated throughout the regional and vertical scales.

Regardless of species, the intake rates were at least an order of magnitude higher than measured in lanternfishes from other basins, including

those from areas beneath major accumulation zones (Bernal et al., 2020; Davison and Asch, 2011; Lusher et al., 2016; Romeo et al., 2016). Our intake rates data were, however, comparable to those measured in lanternfishes from the North Atlantic (1.8 vs. 1.27 particles individual^{−1} detected in this study) (Wieczorek et al., 2018), where higher abundances of floating MPs are estimated when compared to our study area (Lebreton et al., 2012; Lima et al., 2021).

Within the mesopelagic zone, deep-sea currents are the main factor inducing MP dispersion (Kane et al., 2020; Liu et al., 2020; Vega-Moreno et al., 2021) and the abundance of particles in deeper layers is not straightforwardly correlated to the abundance in surface waters (Liu et al., 2020; Zhao et al., 2022). Moreover, the feeding strategy of species might be more prominent than the abundance of particles to explain MP contamination in the deep layers (Ferreira et al., 2022; Wootton et al., 2021).

Overall, the number of detected MPs in lanternfish from the study area did not differ on a regional scale. Yet, regardless of depth, the area in which fishes were captured significantly affected the size of detected particles, with larger particles being detected in individuals inhabiting waters off the northeastern Brazilian coast and seamounts (Area 1). The continental vicinity of Area 1 might influence the size of available MPs and consequently lead to the intake of larger fractions. Indeed, continental distance also negatively influenced the size of MPs ingested by lanternfishes in the subtropical Indian Ocean (Bernal et al., 2020).

Regardless of the sinking rate, MPs are also transported offshore by the ocean currents, the horizontal dispersion varies according to the current speed. MPs likely have a higher horizontal dispersion within the surface ocean whereas the wind-driven currents are stronger than the thermohaline circulation in the deep sea (Kane et al., 2020; Lima et al., 2021). The Area 1 surface waters are controlled by the western boundary current system (Assunção et al., 2020), which is an important transport route for MPs from South America, acknowledged as the main input source to the south Atlantic (Lebreton et al., 2012). On the other hand, Area 2 surface waters (Rocas Atoll and Fernando de Noronha Archipelago) are influenced by

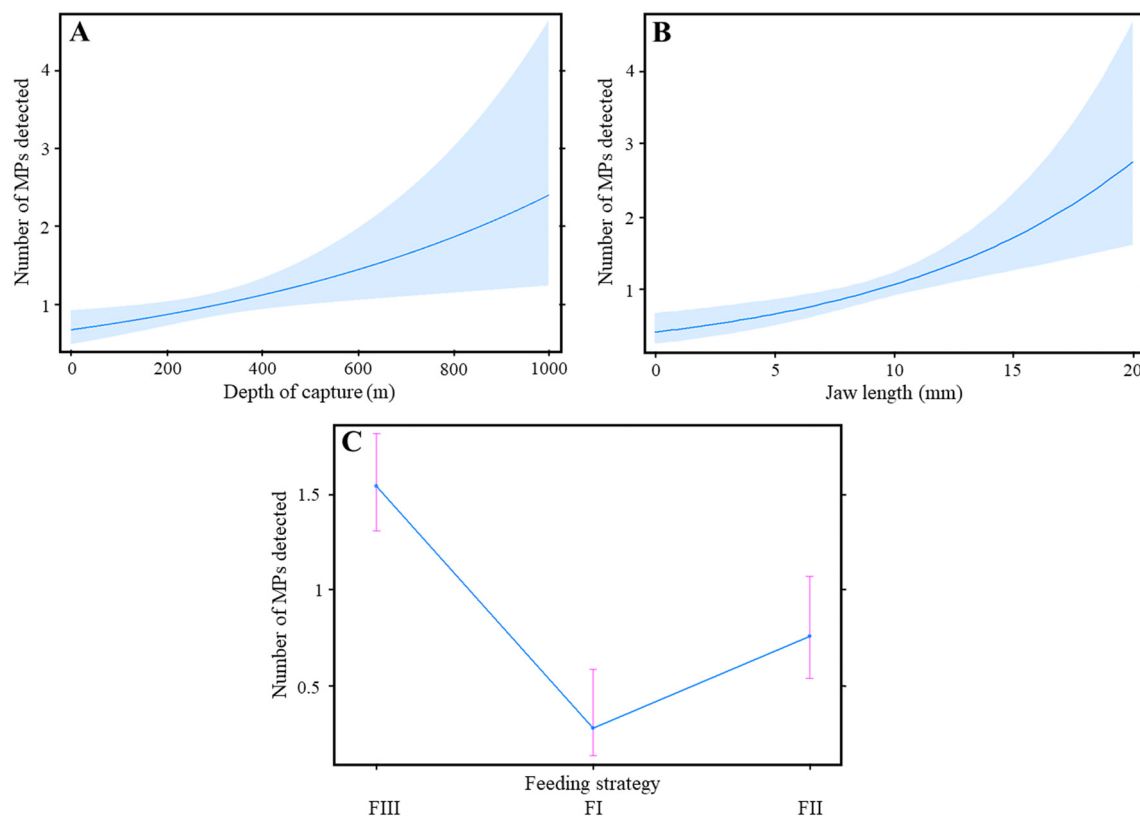


Fig. 4. Effect display for the interaction of (A) depth of capture, (B) jaw length, and (C) feeding strategy of lanternfishes in the logit model fit to microplastic intake rates. The vertical axes are labelled on the probability scale (rescaled from log transformation) and 95 % pointwise confidence interval (hatched blue) around the estimated effect.

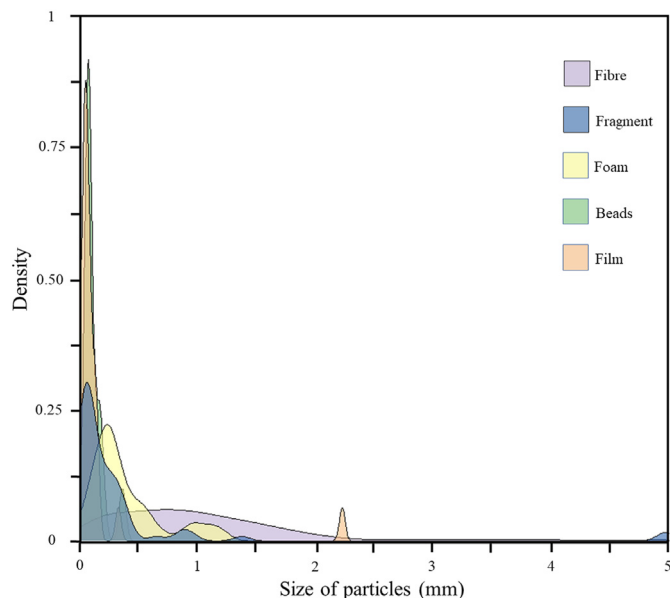


Fig. 5. Size distribution of detected microplastics in lanternfishes from the Southwestern Tropical Atlantic according to the shape of particles.

the SEUC and cSEC that transport MPs from offshore sources (Assunção et al., 2020; Costa da Silva et al., 2021; Lebreton et al., 2019). We assume that MPs from offshore are most likely to have a longer residence time in the environment and thus are more prone to fragmentation due to a longer weathering time (Meides et al., 2021; Qin et al., 2022).

The diel cycle and depth of capture influenced the number of detected MP but not their size. During daytime, lanternfishes have a higher MP intake rate due to different foraging depths (vertical migration) and distinct prey uptake. For instance, Tanaka et al. (2013) pointed out that *Diaphus chrysorhynchus* increased the contribution of fish over euphausiids in their

diet during daytime. Surveys on MP abundance within mesopelagic waters are scarce worldwide, and the study area has not been evaluated to date. Within epipelagic waters (nighttime), lanternfishes forage preferably in the fluorescence peak within the thermocline, which has been revealed a contrasting role in MP retention regarding the different size fractions (Choy et al., 2019; Eo et al., 2021; Kanhai et al., 2018; Vega-Moreno et al., 2021).

Interestingly, the notorious ascension of lanternfishes to the epipelagic waters during nighttime towards greater prey availability is associated with the lowest MP frequency of occurrence and intake rates observed in this survey. Particularly for fishes captured within the epipelagic waters (nighttime) around the Rocas Atoll and Fernando de Noronha Archipelago (Area 2), which might be associated with a lower abundance of plastic particles and/or better prey detection, resulting in MP avoidance. Higher prey availability may diminish active ingestion of MPs (Santos et al., 2021) since fish tend to have lower MP intake rates when food is supplied under controlled laboratory environments (Roch et al., 2020).

MPs float on the surface and gradually disperse through deeper layers (Cozar et al., 2014; Pabortsava and Lampitt, 2020; Weiss et al., 2021), increasing the likelihood of intake by marine biota. Biological mediated transport has been evidenced in various taxa (Choy et al., 2019; Ferreira et al., 2022; Justino et al., 2022; Katija et al., 2017; Lusher et al., 2016); we verified that lanternfishes from the SWTA can intake MPs while foraging in the epipelagic layers (nighttime) and possibly transport particles to the mesopelagic zone (daytime).

Indeed, given the great biomass of this group, Savoca et al. (2021) estimated that lanternfishes could transport up to 10^9 particles (worldwide) to the deep layers daily. Given that the most abundant mesopelagic vertical migrants (Eduardo et al., 2021, 2020; Irigoien et al., 2014) alongside marine snow enhance the sinking of contaminants (Justino et al., 2022; Kvale et al., 2020a, b; Lusher et al., 2016; Porter et al., 2018), the ocean carbon cycle might be a key factor for MPs dispersion in the deep sea, in conjunction with the physical forcings (Kane et al., 2020). However, the intake rates were considerably lower among fish captured in the upper layer. Hence, vertical transport is not straightforwardly correlated with increased MP intake.

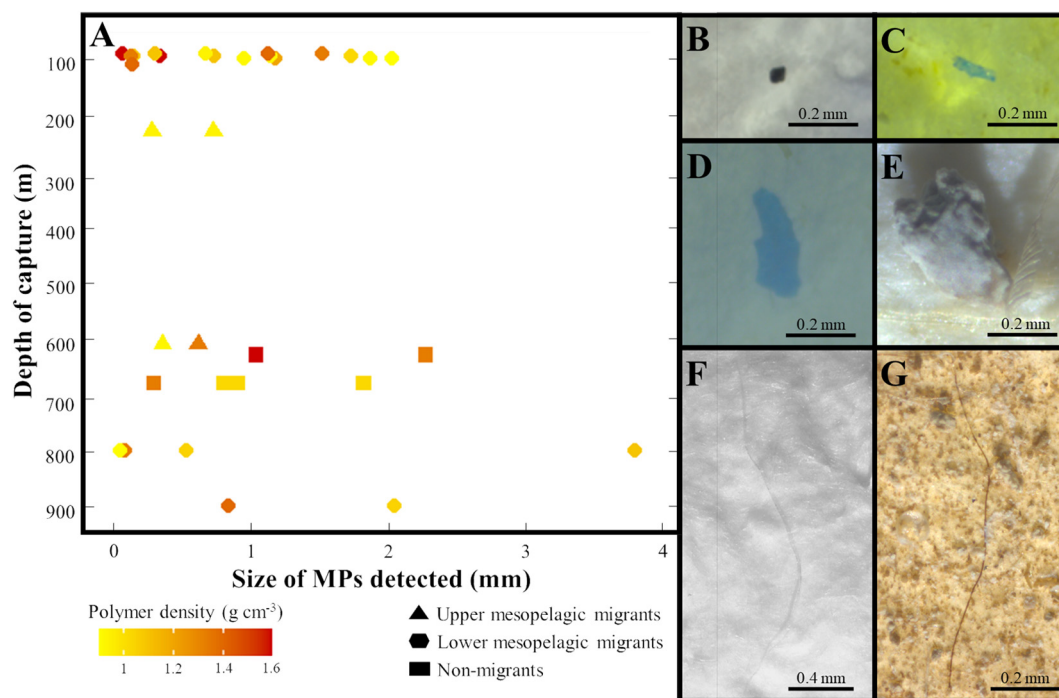


Fig. 6. Detected microplastics (MP) in lanternfishes from the Southwestern Tropical Atlantic. (A) Microplastic polymers identified by LDIR analysis according to the depth of capture, polymer density and migratory behaviour of lanternfishes; (B) styrene-butadiene rubber black fragment (680 m); (C) polyethylene terephthalate blue fragment (630 m); (D) alkyd varnish blue film (95 m); (E) polyamide white foam (95 m); (F) polyethylene terephthalate white fibre (630 m); and (G) polyamide red fibre (800 m).

Despite the fish from the oceanic islands' (Area 2) epipelagic waters (90 m) having the lowest MP intake rates, a considerable number of particles were detected in the digestive tracts of this group, averaging one particle per individual. Even though depicting much lower concentrations than in the accumulation zones (Mountford and Morales Maqueda, 2019), remote environments have been reported with relevant MP abundances in the water column, which can even exceed the most abundant fish larvae species (Lima et al., 2016), increasing the likelihood of MP intake by local biota (Eriksson and Burton, 2003; Garnier et al., 2019).

It is important to address that for vertical migrant species, the comparison between day and night trawls may not accurately reflect prey uptake within the circadian cycle and the precise depth where they were assimilated, especially regarding MPs. The higher MP intake observed during daytime and on individuals captured in mesopelagic depths may be associated with a momentary build-up of particles. Knowledge of MP behaviour within the digestive tract of species evaluated here is absent, but for other myctophids, the evacuation rate (i.e. digested amount of the consumed food in a certain time) has been estimated between 0.1 and 0.52 h⁻¹ (Clarke, 1978; Tanaka et al., 2013).

Laboratory studies on model species (e.g., *Danio rerio* and *Carassius auratus*) evinced that small MPs (< 0.1 mm) had a considerable residence time within the digestive tract, remaining for up to two days before egestion (Hoang and Felix-Kim, 2020; Lu et al., 2016). Moreover, larger particles remain longer in the digestive tract and may even surpass prey retention since the passage of larger MPs can be hindered through the pyloric sphincter (Grigorakis et al., 2017; Ory et al., 2018).

Most lanternfish species ascend vertically, seeking greater prey availability within epipelagic waters. However, to avoid interspecific competition, species adapted to perform distinct migratory patterns, including those with similar feeding strategies (Catul et al., 2011; Eduardo et al., 2021; Sutton, 2013). Additionally, lanternfishes are asynchronous migrants; hence the entire population does not migrate at once (Eduardo et al., 2021), and individuals that remain in the deep also forage, which results in different prey compositions (Tanaka et al., 2013).

Among the specimens captured within the mesopelagic zone (below 200 m depth), the upper mesopelagic migrants had the highest MP intake rates. In contrast, those inhabiting the deep sea (non-migrants and lower mesopelagic migrants) had fewer particles in the digestive tract. In our study area, Justino et al. (2022) observed a similar pattern in hatchetfishes (Sternoptychidae), where species that preferably inhabit the upper mesopelagic waters (Eduardo et al., 2020) exhibited the highest MP intake. In addition, the smallest particles were detected in the upper mesopelagic migrants, mostly on those captured below the lower thermocline limit, which had a higher contribution of small microplastics (< 0.1 mm). Indeed, larger particles are more prone to be retained within density gradients; on the other hand, small microplastics seem to be less influenced by water stratification (Zhao et al., 2022).

The feeding strategy of lanternfishes plays an important role in MP contamination, which might be associated with prey composition and the foraging approach (Ferreira et al., 2016; McGoran et al., 2021; McNeish et al., 2018; Peters et al., 2017). Euphausiids, for instance, are one of the most important resources for all the Myctophidae species evaluated (Eduardo et al., 2021). In the North Pacific upper mesopelagic waters, euphausiids ingested MPs within the same size range as detected herein (Desforges et al., 2015), but the number of particles identified was up to orders of magnitude higher in fishes evaluated in this study.

The size range of detected MPs in our samples, including the non-migrant *B. distofax*, was similar to the one reported for lanternfishes in the North Atlantic (Lusher et al., 2016; Wieczorek et al., 2018) and for fish with similar body sizes (Cheung et al., 2018; Herrera et al., 2019). Moreover, the majority of particles overlapped with the main size distribution of lanternfish prey (Battaglia et al., 2016; Figueiredo et al., 2020; Pusch et al., 2004) and the MPs from deep waters (Eo et al., 2021), where particles smaller than 1.5 mm represented half of the MPs (Egger et al., 2020).

The different feeding strategies did not influence the size of particles but led to distinct intake rates. Lanternfishes that preferably prey upon fish

larvae are more prone to MP intake than their counterparts, principally while using deeper water resources. Among zooplankton, fish larvae are more prone to ingest MPs (Amin et al., 2020). Therefore, the trophic transfer might be a meaningful pathway for particles intake, similarly to the Myctophidae from the northwest Atlantic (Wieczorek et al., 2018) and fishes from shallower ecosystems (Au et al., 2017; Eriksson and Burton, 2003; Ferreira et al., 2016; Nelms et al., 2018). Nonetheless, the bioaccumulation and biomagnification concepts describing the body burden of persistent pollutants could not be applied to the size range of particles detected herein.

The mouth size is a crucial factor to outline the feeding strategy of fish, setting prey upper limit and regulating the volume of water sucked during prey capture (Alexander, 1967; Dabrowski and Bardega, 1984). Indeed, we observed that the intake rates of MPs increased towards specimens with longer jaws. Fish can take MPs actively in through ingestion when they are mistaken for prey but also passively, especially fibres, while protruding the mouth to feed or breathe (Hoang and Felix-Kim, 2020; Li et al., 2021; Roch et al., 2020). Laboratory experiments suggest that planktivorous fish are more prone to take MPs in passively when particles are in the vicinity of prey aggregates. Moreover, when MPs are co-captured with the prey, they are less likely to be spit out by the fish (Ory et al., 2018).

Fibres accounted for two-thirds of the detected particles in this study and are the prevailing MP shape detected in fish regardless of the ecosystem evaluated (Acharya et al., 2021; Müller, 2021), likely due to being the most abundant MP shape on the shorelines, seafloor, surface and deep ocean (Barrows et al., 2018; Browne et al., 2011; Vega-Moreno et al., 2021; Liu et al., 2020; Ross et al., 2021; Woodall et al., 2014). Ultimately, the input rate coupled with sinking rate reflect MPs abundance within different depth strata, in addition to the water and polymer density, the sinking rate is mainly influenced by particle size and shape. Spheroids particles (beads), for instance, have a considerably faster sinking velocity than the cylindrical-elongated (fibres) due to a smaller surface area to volume ratio, hence are more prone to settle on the seabed (Khatmullina and Isachenko, 2017; Kowalski et al., 2016).

In particular, fishing lines are estimated to represent the largest share of marine litter (from micro- to megaplastics) floating in the open ocean worldwide, although the continents are still addressed as the main source of litter to the aquatic ecosystems (Morales-Caselles et al., 2021). Land-based fibres mostly originate from the abrasion of textiles during domestic laundry (de Falco et al., 2019; Jones, 1995; Napper and Thompson, 2016; Ross et al., 2021). The primary fibre colour (blue) and plastic polymers (PE, PA and PET) identified in fishing gear and textiles (Int-Veen et al., 2021; Morishige and McElwee, 2012) prevailed in the digestive tract of lanternfishes. However, Wieczorek et al. (2018) detected only PE, and McGoran et al. (2021) identified mostly biopolymers fibres in deep-sea biota, including lanternfish. Nonetheless, both PA and PET are also commonly applied to manufacture textile products (Acharya et al., 2021), and a single laundry cycle can generate from a thousand to a million fibres depending on the garment specificities (de Falco et al., 2019; Sillanpää and Sainio, 2017).

Although PE and PP account for more than half of the world's plastic production (Geyer et al., 2017), the low-density polymers represented only one-quarter of the identified particles. The high-density MPs, specifically PET, PVC, PA, and Alkyd, were the most abundant in the lanternfishes from the SWTA. Similarly, high-density polymers overcome the low-density ones in surveys encompassing the MPs abundance in the mesopelagic zone (Eo et al., 2021; Zhao et al., 2022). Therefore, the deep-sea biota might be more susceptible to intake high-density MPs due to the faster sinking rates of those particles.

Weathering is enhanced in the surface layer due to photooxidation (Meides et al., 2021), but even under absent UV conditions MPs can fragment into nanoplastics and release plasticisers, metal, and other plastic additives, as well as impurities incorporated during the manufacturing (Fauvelle et al., 2021; Qin et al., 2022). Differently from larger plastics that can lead to death due to gut perforation or impaction (Wilcox et al., 2018), MPs are mostly linked to sub-lethal effects, impairing swimming

capabilities, growth, and reproduction rates (Bhagat et al., 2020; Malafaia et al., 2022; Salerno et al., 2021).

We emphasise that the diel vertical migrant biota should be considered in models estimating the MP dispersion pathways within the epipelagic/mesopelagic interface. In that sense, the lanternfishes are excellent to be used as marine litter sentinels, since these species fit the criteria proposed by Fossi et al. (2018) displaying important ecological and sampling logistical advantages. First, lanternfishes consume zooplankton and provide forage for numerous epipelagic and deep-sea predators, acting as a proxy for other important trophic levels in pelagic ecosystems (Catul et al., 2011). Second, lanternfishes perform massive vertical migrations and are among the most abundant and widespread fish groups in the world ocean (Irigoiien et al., 2014). Therefore, the collection of lanternfishes can be done in shallow oceanic waters and are much easier than for most other deep-sea groups. Nonetheless, given that several ecological aspects may diverge among lanternfishes (Eduardo et al., 2021), we reinforce that for accurate comparisons these species should not be treated as a homogeneous group regarding MP intake. Further works should cluster lanternfishes by ecological features such as feeding and migratory strategies, rather than traditional taxonomic categories such as the genus.

5. Conclusion

Lanternfishes from the SWTA exhibited high levels of MP contamination (frequency of occurrence of particles), regardless of habitat and species evaluated. The size of detected particles decreased from nearshore waters (off northeastern Brazil) to oceanic islands (Rocas Atoll and Fernando de Noronha Archipelago). Moreover, niche partitioning (feeding strategy and migratory behaviour) was the primary predictor of the MP intake rates. Lanternfishes that forage on fish larvae are more prone to MP intake, whereas the upper mesopelagic migrants had the highest MP intake, consisting of the smallest MP size fraction. Our findings corroborate the hypothesis of vertical transport of MPs through a biological route, although even non-migratory lanternfishes are susceptible to MP contamination.

Data availability

The authors do not have permission to share data.

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.

Acknowledgements

All the authors thank the members of the BIOIMPACT laboratory (UFRPE) for their constant support. This study was also supported by the LMI TAPIOCA program CAPES/COFECUB (88881.142689/2017-01) and MicroplastiX project/JPI-Oceans/CONFAP/FACEPE (APQ-0035-1.08/19). We thank the FACEPE (Fundação de Amparo à Ciência e Tecnologia de Pernambuco) for providing grants to Guilherme Ferreira (BFP-0049-5.06/20 and BFP-0107-5.06/21); CAPES (Coordenação de Aperfeiçoamento de Pessoal de Nível Superior) for granting doctoral and masters scholarships to Anne Justino and Júlia Martins, respectively; and CNPq (Conselho Nacional de Desenvolvimento Científico e Tecnológico), for providing research grants to Michael M. Mincarone and Flávia Lucena-Frédou (314644/2020-2 and 305014/2016-1, respectively). We wish to thank Christos Panagiotopoulos and Richard Sempéré (MIO) for providing access to the LDIR Chemical Imaging System.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.scitotenv.2023.161478>.

References

- Acharya, S., Rumi, S.S., Hu, Y., Abidi, N., 2021. Microfibers from synthetic textiles as a major source of microplastics in the environment: a review. *Text. Res. J.* 91, 2136–2156. <https://doi.org/10.1177/0040517521991244>.
- Alexander, R.McN., 1967. The functions and mechanisms of the protrusible upper jaws of some acanthopterygian fish. *J. Zool.* 151, 43–64. <https://doi.org/10.1111/j.1469-7998.1967.tb02865.x>.
- Amin, R., Sohaimi, E.S., Anuar, S.T., Bachok, Z., 2020. Microplastic ingestion by zooplankton in Terengganu coastal waters, southern South China Sea. *Mar. Pollut. Bull.* 150, 110616. <https://doi.org/10.1016/j.marpolbul.2019.110616>.
- Andrady, A.L., 2011. Microplastics in the marine environment. *Mar. Pollut. Bull.* 62, 1596–1605. <https://doi.org/10.1016/j.marpolbul.2011.05.030>.
- Assunção, R.V., Silva, A.C., Roy, A., Bourlès, B., Silva, C.H.S., Ternon, J.F., Araujo, M., Bertrand, A., 2020. 3D characterisation of the thermohaline structure in the southwestern tropical Atlantic derived from functional data analysis of in situ profiles. *Prog. Oceanogr.* 187, 102399. <https://doi.org/10.1016/j.pocean.2020.102399>.
- Au, S.Y., Lee, C.M., Weinstein, J.E., van den Hurk, P., Klaine, S.J., 2017. Trophic transfer of microplastics in aquatic ecosystems: identifying critical research needs. *Integr. Environ. Assess. Manag.* 13, 505–509. <https://doi.org/10.1002/ieam.1907>.
- Barrows, A.P.W., Cathey, S.E., Petersen, C.W., 2018. Marine environment microfiber contamination: global patterns and the diversity of microparticle origins. *Environ. Pollut.* 237, 275–284. <https://doi.org/10.1016/j.envpol.2018.02.062>.
- Battaglia, P., Andaloro, F., Esposito, V., Granata, A., Guglielmo, L., Musolino, S., Romeo, T., Zagami, G., 2016. Diet and trophic ecology of the lanternfish *Electrona risso* (Cocco 1829) in the strait of Messina (central Mediterranean Sea) and potential resource utilization from the deep scattering layer (DSL). *J. Mar. Syst.* 159, 100–108. <https://doi.org/10.1016/j.jmarsys.2016.03.011>.
- Bernal, A., Tøresen, R., Riera, R., 2020. Mesopelagic fish composition and diets of three myctophid species with potential incidence of microplastics, across the Southern Tropical Gyre. *Deep-Sea Res. II*, 104706. <https://doi.org/10.1016/j.dsr2.2019.104706>.
- Bertrand, A., 2017. ABRACOS 2 cruise. RV Antea <https://doi.org/10.17600/17004100>.
- Bhagat, J., Zang, L., Nishimura, N., Shimada, Y., 2020. Zebrafish: an emerging model to study microplastic and nanoplastic toxicity. *Sci. Total Environ.* 728, 138707. <https://doi.org/10.1016/j.scitotenv.2020.138707>.
- Boerger, C.M., Lattin, G.L., Moore, S.L., Moore, C.J., 2010. Plastic ingestion by planktivorous fishes in the North Pacific Central Gyre. *Mar. Pollut. Bull.* 60, 2275–2278. <https://doi.org/10.1016/j.marpolbul.2010.08.007>.
- Boucher, J., Friot, D., 2017. Primary Microplastics in the Oceans: a Global Evaluation of Sources. IUCN, Gland, Switzerland <https://doi.org/10.2305/IUCN.CH.2017.0>.
- Box, G.E.P., Cox, D., 1964. An analysis of transformations. *J. R. Stat. Soc.* 26, 211–252.
- Browne, M.A., Crump, P., Niven, S.J., Teuten, E., Tonkin, A., Galloway, T.S., Thompson, R., 2011. Accumulation of microplastic on shorelines worldwide: sources and sinks. *Environ. Sci. Technol.* 45, 9175–9179. <https://doi.org/10.1021/es201811s>.
- Budimir, S., Setälä, O., Lehtiniemi, M., 2018. Effective and easy to use extraction method shows low numbers of microplastics in offshore planktivorous fish from the northern Baltic Sea. *Mar. Pollut. Bull.* 127, 586–592. <https://doi.org/10.1016/j.marpolbul.2017.12.054>.
- Catul, V., Gauns, M., Karuppasamy, P.K., 2011. A review on mesopelagic fishes belonging to family Myctophidae. *Rev. Fish Biol. Fish.* 21, 339–354. <https://doi.org/10.1007/s1160-010-9176-4>.
- CBD, S. of the C. on B.D., 2014. Ecologically or Biologically Significant Marine Areas (EBSAs). *Special Places in the World's Oceans: Volume 2: Wider Caribbean and Western Mid-Atlantic Region*. 2nd ed. Ecologically or Biologically Significant Marine Areas (EBSAs). Special places in the world's oceans.
- Cheung, L.T.O., Lui, C.Y., Fok, L., 2018. Microplastic contamination of wild and captive flat-head grey mullet (*Mugil cephalus*). *Int. J. Environ. Res. Public Health* 15 (4), 597. <https://doi.org/10.3390/ijerph15040597>.
- Choy, C.A., Drzen, J.C., 2013. Plastic for dinner? Observations of frequent debris ingestion by pelagic predatory fishes from the central North Pacific. *Mar. Ecol. Prog. Ser.* 485, 155–163. <https://doi.org/10.3354/meps10342>.
- Choy, C.A., Robison, B.H., Gagne, T.O., Erwin, B., Firl, E., 2019. The vertical distribution and biological transport of marine microplastics across the epipelagic and mesopelagic water column. *Sci. Rep.* 9, 7843. <https://doi.org/10.1038/s41598-019-44117-2>.
- Clarke, T.A., 1978. Diel feeding patterns of 16 species of mesopelagic fishes from Hawaiian waters. *Fish. Bull.* 76, 495–513.
- Costa da Silva, A., Chaigneau, A., Dossa, A.N., Eldin, G., Araujo, M., Bertrand, A., 2021. Surface circulation and vertical structure of Upper Ocean variability around Fernando de Noronha Archipelago and Rocas Atoll during spring 2015 and fall 2017. *Front. Mar. Sci.* 8, 598101. <https://doi.org/10.3389/fmars.2021.598101>.
- Courteney-Jones, W., Quinn, B., Gary, S.F., Mogg, A.O.M., Narayanaswamy, B.E., 2017. Microplastic pollution identified in deep-sea water and ingested by benthic invertebrates in the rockall trough, North Atlantic Ocean. *Environ. Pollut.* 231, 271–280. <https://doi.org/10.1016/j.envpol.2017.08.026>.
- Cozar, A., Echevarria, F., Gonzalez-Gordillo, J.I., Irigoien, X., Ubeda, B., Hernandez-Leon, S., Palma, A.T., Navarro, S., Garcia-de-Lomas, J., Ruiz, A., Fernandez-de-Puelles, M.L., Duarte, C.M., 2014. Plastic debris in the open ocean. *Proc. Natl. Acad. Sci.* 111, 10239–10244. <https://doi.org/10.1073/pnas.1314705111>.
- Dabrowski, K., Bardega, R., 1984. Mouth size and predicted food size preferences of larvae of three cyprinid fish species. *Aquaculture* 40, 41–46. [https://doi.org/10.1016/0044-8486\(84\)90214-X](https://doi.org/10.1016/0044-8486(84)90214-X).
- Davison, P., Asch, R.G., 2011. Plastic ingestion by mesopelagic fishes in the North Pacific Sub-tropical Gyre. *Mar. Ecol. Prog. Ser.* 432, 173–180. <https://doi.org/10.3354/meps09142>.
- Davison, P.C., Checkley, D.M., Koslow, J.A., Barlow, J., 2013. Carbon export mediated by mesopelagic fishes in the Northeast Pacific Ocean. *Prog. Oceanogr.* 116, 14–30. <https://doi.org/10.1016/j.pocean.2013.05.013>.

- de Falco, F., di Pace, E., Cocca, M., Avella, M., 2019. The contribution of washing processes of synthetic clothes to microplastic pollution. *Sci. Rep.* 9, 6633. <https://doi.org/10.1038/s41598-019-43023-x>.
- Desforges, J.P.W., Galbraith, M., Ross, P.S., 2015. Ingestion of microplastics by zooplankton in the Northeast Pacific Ocean. *Arch. Environ. Contam. Toxicol.* 69, 320–330. <https://doi.org/10.1007/s00244-015-0172-5>.
- Drazen, J.C., Smith, C.R., Gjerd, K.M., Haddock, S.H.D., Carter, G.S., Anela Choy, C., Clark, M.R., Dutrieux, P., Goetze, E., Hauton, C., Hatta, M., Anthony Koslow, J., Leitner, A.B., Pacini, A., Perelman, J.N., Peacock, T., Sutton, T.T., Watling, L., Yamamoto, H., 2020. Midwater ecosystems must be considered when evaluating environmental risks of deep-sea mining. *Proc. Natl. Acad. Sci. U. S. A.* 117, 17455–17460. <https://doi.org/10.1073/pnas.2011914117>.
- Eduardo, L.N., Bertrand, A., Lucena-Frédou, F., Villarins, B.T., Martins, J.R., Afonso, G.V.F., Pietsch, T.W., Frédo, T., di Dario, F., Mincaroni, M.M., 2022. Rich and underreported: first integrated assessment of the diversity of mesopelagic fishes in the Southwestern Tropical Atlantic. *Front. Mar. Sci.* 9. <https://doi.org/10.3389/fmars.2022.937154>.
- Eduardo, L.N., Bertrand, A., Mincaroni, M.M., Martins, J.R., Frédo, T., Assunção, R.V., Lima, R.S., Ménard, F., le Loc'h, F., Lucena-Frédo, F., 2021. Distribution, vertical migration, and trophic ecology of lanternfishes (Myctophidae) in the Southwestern Tropical Atlantic. *Prog. Oceanogr.* 199, 102695. <https://doi.org/10.1016/j.pcean.2021.102695>.
- Eduardo, L.N., Bertrand, A., Mincaroni, M.M., Santos, L.V., Frédo, T., Silva, A., Ménard, F., Schwamborn, R., le Loc'h, F., Lucena-Frédo, F., Assunção, R.V., 2020. Hatchetfishes (Stomiiformes: Sternoptychidae) biodiversity, trophic ecology, vertical niche partitioning and functional roles in the western Tropical Atlantic. *Prog. Oceanogr.* 187, 102389. <https://doi.org/10.1016/j.pcean.2020.102389>.
- Egger, M., Sulu-Gambari, F., Lebreton, L., 2020. First evidence of plastic fallout from the North Pacific garbage patch. *Sci. Rep.* 10, 7495. <https://doi.org/10.1038/s41598-020-64465-8>.
- Enfrin, M., Lee, J., Gibert, Y., Basheer, F., Kong, L., Dumée, L.F., 2020. Release of hazardous nanoplastic contaminants due to microplastics fragmentation under shear stress forces. *J. Hazard. Mater.* 384. <https://doi.org/10.1016/j.jhazmat.2019.121393>.
- Eo, S., Hong, S.H., Song, Y.K., Han, G.M., Seo, S., Shim, W.J., 2021. Prevalence of small high-density microplastics in the continental shelf and deep sea waters of East Asia. *Water Res.* 200, 117238. <https://doi.org/10.1016/j.watres.2021.117238>.
- Eriksson, C., Burton, H., 2003. Origins and biological accumulation of small plastic particles in fur seals from Macquarie Island. *Ambio* 32, 380–384. <https://doi.org/10.1579/0044-7447-32.6.380>.
- Esposito, G., Prearo, M., Renzi, M., Anselmi, S., Cesarani, A., Barcelò, D., Dondo, A., Pastorino, P., 2022. Occurrence of microplastics in the gastrointestinal tract of benthic by-catches from an eastern Mediterranean deep-sea environment. *Mar. Pollut. Bull.* 174, 113231. <https://doi.org/10.1016/j.marpolbul.2021.113231>.
- Fauvel, V., Garel, M., Tamburini, C., Nerini, D., Castro-Jiménez, J., Schmidt, N., Paluselli, A., Fahs, A., Papillon, L., Booth, A.M., Sempéré, R., 2021. Organic additive release from plastic to seawater is lower under deep-sea conditions. *Nat. Commun.* 12, 4426. <https://doi.org/10.1038/s41467-021-24738-w>.
- Ferreira, G.V.B., Barletta, M., Lima, A.R.A., 2019. Use of estuarine resources by top predator fishes. How do ecological patterns affect rates of contamination by microplastics? *Sci. Total Environ.* 655, 292–304. <https://doi.org/10.1016/j.scitotenv.2018.11.229>.
- Ferreira, G.V.B., Barletta, M., Lima, A.R.A., Dantas, D.V., Justino, A.K.S., Costa, M.F., 2016. Plastic debris contamination in the life cycle of *Acoupa weakfish (Cynoscion acoupa)* in a tropical estuary. *ICES J. Mar. Sci.* 73, 2695–2707. <https://doi.org/10.1093/icesjms/fsw108>.
- Ferreira, G.V.B., Barletta, M., Lima, A.R.A., Morley, S.A., Justino, A.K.S., Costa, M.F., 2018. High intake rates of microplastics in a Western Atlantic predatory fish, and insights of a direct fishery effect. *Environ. Pollut.* <https://doi.org/10.1016/j.envpol.2018.01.095>.
- Ferreira, G.V.B., Justino, A.K.S., Eduardo, L.N., Lenoble, V., Fauvel, V., Schmidt, N., Junior, T.V., Frédo, T., Lucena-Frédo, F., 2022. Plastic in the inferno: microplastic contamination in deep-sea cephalopods (*Vampyroteuthis infernalis* and *Aburria veranyi*) from the southwestern Atlantic. *Mar. Pollut. Bull.* 174, 113309. <https://doi.org/10.1016/j.marpolbul.2021.113309>.
- Figueiredo, G.G.A.A., Schwamborn, R., Bertrand, A., Munaron, J.M., le Loc'h, F., 2020. Body size and stable isotope composition of zooplankton in the western tropical Atlantic. *J. Mar. Syst.* 212, 103449. <https://doi.org/10.1016/j.jmarsys.2020.103449>.
- Fossi, M.C., Pedà, C., Compà, M., Tsangaris, C., Alomar, C., Claro, F., Ioakeimidis, C., Gagliani, F., Hema, T., Deudero, S., Romeo, T., Battaglia, P., Andaloro, F., Caliani, I., Casini, S., Panti, C., Baini, M., 2018. Bioindicators for monitoring marine litter ingestion and its impacts on Mediterranean biodiversity. *Environ. Pollut.* 237, 1023–1040. <https://doi.org/10.1016/j.envpol.2017.11.019>.
- Garnier, Y., Jacob, H., Guerra, A.S., Bertucci, F., Lecchini, D., 2019. Evaluation of microplastic ingestion by tropical fish from Moorea Island, French Polynesia. *Mar. Pollut. Bull.* 140, 165–170. <https://doi.org/10.1016/j.marpolbul.2019.01.038>.
- Gewert, B., Plassmann, M.M., MacLeod, M., 2015. Pathways for degradation of plastic polymers floating in the marine environment. *Environ. Sci. Process. Impacts* 17, 1513–1521. <https://doi.org/10.1039/C5EM00207A>.
- Geyer, R., Jambeck, J.R., Law, K.L., 2017. Production, use, and fate of all plastics ever made. *Sci. Adv.* 3, 25–29. <https://doi.org/10.1126/sciadv.1700782>.
- Gillard, B., Purkiani, K., Chatzievangelou, D., Vink, A., Iversen, M.H., Thomsen, L., 2019. Physical and hydrodynamic properties of deep sea mining-generated, abyssal sediment plumes in the Clarion clipperton fracture zone (eastern-Central Pacific). *Elementa (Wash. D.C.)* 7. <https://doi.org/10.1525/elementa.343>.
- Gjøsæter, J., 1973. The food of the myctophid fish, *benthosema glaciale* (reinhart), from Western Norway. *Sarsia* 52, 53–58. <https://doi.org/10.1080/00364827.1973.10411231>.
- Grigorakis, S., Mason, S.A., Drouillard, K.G., 2017. Determination of the gut retention of plastic microbeads and microfibers in goldfish (*Carassius auratus*). *Chemosphere* 169, 233–238. <https://doi.org/10.1016/j.chemosphere.2016.11.055>.
- Hanke, G., 2013. Guidance on Monitoring of Marine Litter in European Seas: A Guidance Document Within the Common Implementation Strategy for the Marine Strategy Framework Directive. European Commission, Joint Research Centre, Luxembourg <https://doi.org/10.25607/OBP-725.128pp>.
- Hernandez-Gonzalez, A., Saavedra, C., Gago, J., Covelo, P., Santos, M.B., Pierce, G.J., 2018. Microplastics in the stomach contents of common dolphin (*Delphinus delphis*) stranded on the Galician coasts (NW Spain, 2005–2010). *Mar. Pollut. Bull.* 137, 526–532. <https://doi.org/10.1016/j.marpolbul.2018.10.026>.
- Herrera, A., Stindlova, A., Romero-kutzner, V., Montoto, T., 2019. Microplastic ingestion by Atlantic Chub Mackerel (*Scomber colias*) in the Canary Islands Coast. *Mar. Pollut. Bull.* 139, 127–135. <https://doi.org/10.1016/j.marpolbul.2018.12.022>.
- Hoang, T.C., Felix-Kim, M., 2020. Microplastic consumption and excretion by fathead minnows (*Pimephales promelas*): influence of particles size and body shape of fish. *Sci. Total Environ.* 704, 135433. <https://doi.org/10.1016/j.scitotenv.2019.135433>.
- Hopewell, J., Dvorak, R., Kosior, E., 2009. Plastics recycling: challenges and opportunities. *Philos. Trans. R. Soc. Lond. Ser. B Biol. Sci.* 364, 2115–2126. <https://doi.org/10.1098/rstb.2008.0311>.
- Int-Veen, I., Nogueira, P., Isigkeit, J., Hanel, R., Kammann, U., 2021. Positively buoyant but sinking: polymer identification and composition of marine litter at the seafloor of the North Sea and Baltic Sea. *Mar. Pollut. Bull.* 172, 112876. <https://doi.org/10.1016/j.marpolbul.2021.112876>.
- Irgoien, X., Klejver, T.A., Røstad, A., Martinez, U., Boyra, G., Acuña, J.L., Bode, A., Echevarria, F., Gonzalez-Gordillo, J.I., Hernandez-Leon, S., Agusti, S., Aksnes, D.L., Duarte, C.M., Kaartvedt, S., 2014. Large mesopelagic fishes biomass and trophic efficiency in the open ocean. *Nat. Commun.* 5, 3271. <https://doi.org/10.1038/ncomms4271>.
- Jambeck, J.R., Geyer, R., Wilcox, C., Siegler, T.R., Perryman, M., Andrady, A., Narayan, R., Law, K.L., 2015. Plastic waste inputs from land into the ocean. *Science* 347, 768–771. <https://doi.org/10.1126/science.1260352>.
- Jones, M.M., 1995. Fishing debris in the Australian marine environment. *Mar. Pollut. Bull.* 30, 25–33. [https://doi.org/10.1016/0025-326X\(94\)00108-L](https://doi.org/10.1016/0025-326X(94)00108-L).
- Justino, A.K.S., Ferreira, G.V.B., Schmidt, N., Eduardo, L.N., Fauvel, V., Lenoble, V., Sempéré, R., Panagiotopoulos, C., Mincaroni, M.M., Frédo, T., Lucena-Frédo, F., 2022. The role of mesopelagic fishes as microplastics vectors across the deep-sea layers from the Southwestern Tropical Atlantic. *Environ. Pollut.* 300, 118988. <https://doi.org/10.1016/j.envpol.2022.118988>.
- Justino, A.K.S., Lenoble, V., Pelage, L., Ferreira, G.V.B., Passarone, R., Frédo, T., Frédo, F.L., 2021. Microplastic contamination in tropical fishes: An assessment of different feeding habits. *Reg. Stud. Mar. Sci.* 45, 101857. <https://doi.org/10.1016/j.rsma.2021.101857>.
- Kane, I.A., Clare, M.A., Miramontes, E., Wogelius, R., Rothwell, J.J., Garreau, P., Pohl, F., 2020. Seafloor microplastic hotspots controlled by deep-sea circulation. *Science* 369, 1–8. <https://doi.org/10.1126/science.aba5899>.
- Kanhai, L.D.K., Gärdfeldt, K., Lyashevskaya, O., Hasselöv, M., Thompson, R.C., O'Connor, I., 2018. Microplastics in sub-surface waters of the Arctic Central Basin. *Mar. Pollut. Bull.* 130, 8–18. <https://doi.org/10.1016/j.marpolbul.2018.03.011>.
- Karlsson, T.M., Hasselöv, M., Jakubowicz, I., 2018. Influence of thermooxidative degradation on the in-situ fate of polyethylene in temperate coastal waters. *Mar. Pollut. Bull.* 135, 187–194. <https://doi.org/10.1016/j.marpolbul.2018.07.015>.
- Katija, K., Choy, C.A., Sherlock, R.E., Sherman, A.D., Robison, B.H., 2017. From the surface to the seafloor: How giant larvaceans transport microplastics into the deep sea. *Sci. Adv.* 3, 1–6. <https://doi.org/10.1126/sciadv.1700715>.
- Khatmullina, L., Isachenko, I., 2017. Settling velocity of microplastic particles of regular shapes. *Mar. Pollut. Bull.* 114, 871–880. <https://doi.org/10.1016/j.marpolbul.2016.11.024>.
- Kowalski, N., Reichardt, A.M., Waniek, J.J., 2016. Sinking rates of microplastics and potential implications of their alteration by physical, biological, and chemical factors. *Mar. Pollut. Bull.* 109, 310–319. <https://doi.org/10.1016/j.marpolbul.2016.05.064>.
- Kvale, K., Prowe, A.E.F., Chien, C.T., Landolfi, A., Oschlies, A., 2020. The global biological microplastic particle sink. *Sci. Rep.* 10, 16670. <https://doi.org/10.1038/s41598-020-72898-4>.
- Kvale, K.F., Friederike Prowe, A.E., Oschlies, A., 2020. A critical examination of the role of marine snow and zooplankton fecal pellets in removing ocean surface microplastic. *Front. Mar. Sci.* 6, 1–8. <https://doi.org/10.3389/fmars.2019.00808>.
- Lebreton, L., Egger, M., Slat, B., 2019. A global mass budget for positively buoyant macroplastic debris in the ocean. *Sci. Rep.* 9, 1–10. <https://doi.org/10.1038/s41598-019-49413-5>.
- Lebreton, L.C.M., Greer, S.D., Borrero, J.C., 2012. Numerical modelling of floating debris in the world's oceans. *Mar. Pollut. Bull.* 64, 653–661. <https://doi.org/10.1016/j.marpolbul.2011.10.027>.
- Lebreton, L.C.M., van der Zwet, J., Damsteeg, J.-W., Slat, B., Andrady, A.L., Reisser, J., 2017. River plastic emissions to the world's oceans. *Nat. Commun.* 8, 15611. <https://doi.org/10.1038/ncomms15611>.
- Lei, L., Wu, S., Lu, S., Liu, M., Song, Y., Fu, Z., Shi, H., Raley-Susman, K.M., He, D., 2018. Microplastic particles cause intestinal damage and other adverse effects in zebrafish *Danio rerio* and nematode *Caenorhabditis elegans*. *Sci. Total Environ.* 619–620, 1–8. <https://doi.org/10.1016/j.scitotenv.2017.11.103>.
- Levene, H., 1960. Robust test for equality of variances. In: Olkin, I., Ghurye, S.G., Hoeffding, W., Madow, W.G., Mann, H.B. (Eds.), *Contributions to Probability and Statistics: Essays in Honour of Harold Hotelling*. Stanford University Press, Palo Alto, pp. 278–292.
- Li, B., Liang, W., Liu, Q.-X., Fu, S., Ma, C., Chen, Q., Su, L., Craig, N.J., Shi, H., 2021. Fish ingest microplastics unintentionally. *Environ. Sci. Technol.* 55, 10471–10479. <https://doi.org/10.1021/acs.est.1c01753>.
- Lima, A.R.A., Barletta, M., Costa, M.F., 2016. Seasonal-Dial Shifts of Ichthyoplankton Assemblages and Plastic Debris around an Equatorial Atlantic Archipelago. *Front. Environ. Sci.* 4, 56. <https://doi.org/10.3389/fenvs.2016.00056>.
- Lima, A.R.A., Ferreira, G.V.B., Barrows, A.P.W., Christiansen, K.S., Treinish, G., Toshack, M.C., 2021. Global patterns for the spatial distribution of floating microfibers: Arctic Ocean as a potential accumulation zone. *J. Hazard. Mater.* 403, 123796. <https://doi.org/10.1016/j.jhazmat.2020.123796>.

- Liu, K., Courtene-Jones, W., Wang, X., Song, Z., Wei, N., Li, D., 2020. Elucidating the vertical transport of microplastics in the water column: A review of sampling methodologies and distributions. *Water Res.* 186. <https://doi.org/10.1016/j.watres.2020.116403>.
- Lu, Y., Zhang, Y., Deng, Y., Jiang, W., Zhao, Y., Geng, J., Ding, L., Ren, H., 2016. Uptake and accumulation of polystyrene microplastics in zebrafish (*Danio rerio*) and toxic effects in liver. *Environ. Sci. Technol.* 50, 4054–4060. <https://doi.org/10.1021/acs.est.6b00183>.
- Lusher, A.L., Holliman, P., Mandoza-Hill, J., 2017. *Microplastics in Fisheries and Aquaculture*. 1st ed. Food and Agriculture Organization of the United Nations, Rome.
- Lusher, A.L., O'Donnell, C., Officer, R., O'Connor, I., 2016. Microplastic interactions with North Atlantic mesopelagic fish. *ICES J. Mar. Sci.* 73, 1214–1225. <https://doi.org/10.1093/icesjms/fsv241>.
- Malafaia, G., Nóbrega, R.H., Luz, T.M.da, Araújo, A.P.da C., 2022. Shedding light on the impacts of gestational exposure to polystyrene nanoplastics on the reproductive performance of *Poecilia reticulata* female and on the biochemical response of embryos. *J. Hazard. Mater.* 427, 127873. <https://doi.org/10.1016/j.jhazmat.2021.127873>.
- McCullagh, P., Nelder, J.A., 2019. *Generalized Linear Models*. Routledge <https://doi.org/10.1201/9780203753736>.
- McGoran, A.R., MacLaine, J.S., Clark, P.F., Morritt, D., 2021. Synthetic and semi-synthetic microplastic ingestion by mesopelagic fishes from Tristan da Cunha and St Helena, South Atlantic. *Front. Mar. Sci.* 8, 633478. <https://doi.org/10.3389/fmars.2021.633478>.
- McNeish, R.E., Kim, L.H., Barrett, H.A., Mason, S.A., Kelly, J.J., Hoelllein, T.J., 2018. Microplastic in riverine fish is connected to species traits. *Sci. Rep.* 8, 1–12. <https://doi.org/10.1038/s41598-018-29980-9>.
- Meides, N., Menzel, T., Poetschner, B., Löder, M.G.J., Mansfeld, U., Strohriegel, P., Altstaedt, V., Senker, J., 2021. Reconstructing the environmental degradation of polystyrene by accelerated weathering. *Environ. Sci. Technol.* 55, 7930–7938. <https://doi.org/10.1021/acs.est.0c07718>.
- Mishra, S., Rath, C., Charan, Das, A.P., 2019. Marine microfiber pollution: A review on present status and future challenges. *Mar. Pollut. Bull.* 140, 188–197. <https://doi.org/10.1016/j.marpolbul.2019.01.039>.
- Möhlenkamp, P., Purser, A., Thomsen, L., 2018. Plastic microbeads from cosmetic products: an experimental study of their hydrodynamic behaviour, vertical transport and resuspension in phytoplankton and sediment aggregates. *Elementa* 6. <https://doi.org/10.1525/elementa.317>.
- Morales-Caselles, C., Viejo, J., Martí, E., González-Fernández, D., Pragnell-Rasch, H., González-Gordillo, J.L., Montero, E., Arroyo, G.M., Hanke, G., Salvo, V.S., Basurko, O.C., Mallos, N., Lebreton, L., Echevarría, F., van Emmerik, T., Duarte, C.M., Gálvez, J.A., van Sebille, E., Galgani, F., García, C.M., Ross, P.S., Bartual, A., Ioakeimidis, C., Markalain, G., Isoabe, A., Cózar, A., 2021. An inshore-offshore sorting system revealed from global classification of ocean litter. *Nat. Sustain.* 4, 484–493. <https://doi.org/10.1038/s41893-021-00720-8>.
- Morato, T., Watson, R., Pitcher, T.J., Pauly, D., 2006. Fishing down the deep. *Fish Fish* 7, 24–34. <https://doi.org/10.1111/j.1467-2979.2006.00205.x>.
- Morishige, C., McElwee, K., 2012. At-sea detection of derelict fishing gear in the North Pacific: An overview. *Mar. Pollut. Bull.* 65, 1–6. <https://doi.org/10.1016/j.marpolbul.2011.05.017>.
- Mountford, A.S., Morales Maqueda, M.A., 2019. Eulerian modeling of the three-dimensional distribution of seven popular microplastic types in the Global Ocean. *J. Geophys. Res.* 124, 8558–8573. <https://doi.org/10.1029/2019JC015050>.
- Müller, C., 2021. Not as bad as it seems? A literature review on the case of microplastic uptake in fish. *Front. Mar. Sci.* 8. <https://doi.org/10.3389/fmars.2021.672768>.
- Nafpaktitis, B.G., Backus, R.H., Craddock, J.E., Haedrich, R.L., Robison, B.H., Karmela, C., 1977. *Family Myctophidae*. In: Gibbs, R.H. (Ed.), *Fishes of the Western North Atlantic. Part seven. Order Inimomi (Myctophiformes): Neoscolecidae and Myctophidae, and Atlantic Mesopelagic Zoogeography*. Sears Foundation for Marine Research, Memoir 1. Yale University Press, pp. 13–265.
- Napper, I.E., Thompson, R.C., 2016. Release of synthetic microplastic plastic fibres from domestic washing machines: Effects of fabric type and washing conditions. *Mar. Pollut. Bull.* 112, 39–45. <https://doi.org/10.1016/j.marpolbul.2016.09.025>.
- Nelms, S.E., Galloway, T.S., Godley, B.J., Jarvis, D.S., Lindeque, P.K., 2018. Investigating microplastic trophic transfer in marine top predators. *Environ. Pollut.* 238, 1–9. <https://doi.org/10.1016/j.envpol.2018.02.016>.
- Newell, C.R., Pilskaln, C.H., Robinson, S.M., MacDonald, B.A., 2005. The contribution of marine snow to the particle food supply of the benthic suspension feeder, *Mytilus edulis*. *J. Exp. Mar. Biol. Ecol.* 321, 109–124. <https://doi.org/10.1016/j.jembe.2005.01.006>.
- Olaso, I., Gutiérrez, J.L., Villamor, B., Carrera, P., Valdés, L., Abaunza, P., 2005. Seasonal changes in the North-Eastern Atlantic mackerel diet (*Scomber scombrus*) in the north of Spain (ICES division VIIIc). *J. Mar. Biol. Assoc. U. K.* 85, 415–418. <https://doi.org/10.1017/S0025315405011343h>.
- Onink, V., Wichmann, D., Delandmeter, P., van Sebille, E., 2019. The role of Ekman currents, geostrophy, and Stokes drift in the accumulation of floating microplastic. *J. Geophys. Res.* 124, 1474–1490. <https://doi.org/10.1029/2018JC014547>.
- Ory, N.C., Gallardo, C., Lenz, M., Thiel, M., 2018. Capture, swallowing, and egestion of microplastics by a planktivorous juvenile fish. *Environ. Pollut.* 240, 566–573. <https://doi.org/10.1016/j.envpol.2018.04.093>.
- Osswald, T.A., Oberbach, S., 2006. *International Plastics Handbook: The Resource for Plastics Engineers*. 4th ed. Hanser Gardner Publications, Ohio.
- Ourgaud, M., Phuong, N.N., Papillon, L., Panagiotopoulos, C., Galgani, F., Schmidt, N., Fauvel, V., Brach-Papa, C., Sempéré, R., 2022. Identification and quantification of microplastics in the marine environment using the laser direct infrared (LDIR) technique. *Environ. Sci. Technol.* 56, 9999–10009. <https://doi.org/10.1021/acs.est.1c08870>.
- Pabortsava, K., Lampitt, R.S., 2020. High concentrations of plastic hidden beneath the surface of the Atlantic Ocean. *Nat. Commun.* 11, 1–11. <https://doi.org/10.1038/s41467-020-17932-9>.
- Pazos, R.S., Maiztegui, T., Colausti, D.C., Paracampo, A.H., Gómez, N., 2017. Microplastics in gut contents of coastal freshwater fish from Río de la Plata estuary. *Mar. Pollut. Bull.* 122, 85–90. <https://doi.org/10.1016/j.marpolbul.2017.06.007>.
- Pereira, J.M., Rodríguez, Y., Blasco-Monleon, S., Porter, A., Lewis, C., Pham, C.K., 2020. Microplastic in the stomachs of open-ocean and deep-sea fishes of the north-east Atlantic. *Environ. Pollut.* 265, 115060. <https://doi.org/10.1016/j.envpol.2020.115060>.
- Peters, C.A., Thomas, P.A., Rieper, K.B., Bratton, S.P., 2017. Foraging preferences influence microplastic ingestion by six marine fish species from the Texas Gulf Coast. *Mar. Pollut. Bull.* 124, 82–88. <https://doi.org/10.1016/j.marpolbul.2017.06.080>.
- PlasticsEurope, 2020. *Plastics-the Facts 2020: An Analysis of European Plastics Production, Demand and Waste Data*.
- Porter, A., Lyons, B.P., Galloway, T.S., Lewis, C., 2018. Role of marine snows in microplastic fate and bioavailability. *Environ. Sci. Technol.* 52, 7111–7119. <https://doi.org/10.1021/acs.est.8b01000>.
- Pusch, C., Schnack-Schiel, S., Mizdalski, E., von Westernhagen, H., 2004. Feeding ecology of three myctophid species at the great meteor seamount (North-East Atlantic). *Arch. Fish. Mar. Res.* 51, 251–271.
- Qin, J., Zeng, S., Wang, X., Lin, C., 2022. Generation of micro(nano)plastics and migration of plastic additives from Poly(vinyl chloride) in water under radiation-free ambient conditions. *Chemosphere* 299, 134399. <https://doi.org/10.1016/j.chemosphere.2022.134399>.
- R Core Team, 2022. *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria.
- Reisser, J., Slat, B., Noble, K., du Plessis, K., Epp, M., Proietti, M., de Sonnevill, J., Becker, T., Pattiaratchi, C., 2015. The vertical distribution of buoyant plastics at sea: An observational study in the North Atlantic Gyre. *Biogeosciences* 12, 1249–1256. <https://doi.org/10.5194/bg-12-1249-2015>.
- Roch, S., Friedrich, C., Brinker, A., 2020. Uptake routes of microplastics in fishes: Practical and theoretical approaches to test existing theories. *Sci. Rep.* 10. <https://doi.org/10.1038/s41598-020-06030-1>.
- Rochman, C.M., Hentschel, B.T., The, S.J., 2014. Long-term sorption of metals is similar among plastic types: implications for plastic debris in aquatic environments. *PLoS ONE* 9, 85433. <https://doi.org/10.1371/journal.pone.0085433>.
- Romeo, T., Pedà, C., Fossi, M.C., Andaloro, F., Battaglia, P., 2016. First record of plastic debris in the stomach of Mediterranean lanternfishes. *Acta Adriat.* 57, 115–124.
- Ross, P.S., Chastain, S., Vassilenko, E., Etemadifar, A., Zimmermann, S., Quesnel, S.-A., Eert, J., Solomon, E., Patankar, S., Posacka, A.M., Williams, B., 2021. Pervasive distribution of polyester fibres in the Arctic Ocean is driven by Atlantic inputs. *Nat. Commun.* 12, 106. <https://doi.org/10.1038/s41467-020-20347-1>.
- Salerno, M., Berlino, M., Mangano, M.C., Sarà, G., 2021. Microplastics and the functional traits of fishes: A global meta-analysis. *Glob. Chang. Biol.* 27, 2645–2655. <https://doi.org/10.1111/gcb.15570>.
- Santos, R.G., Machovsky-capuska, G.E., Andrades, R., 2021. Plastic Ingestion as an Evolutionary Trap: Toward a Holistic Understanding. 60, pp. 56–60.
- Sathish, M.N., Jayasanta, I., Patterson, J., 2020. Occurrence of microplastics in epipelagic and mesopelagic fishes from tuticorin, southeast coast of India. *Sci. Total Environ.* 720, 137614. <https://doi.org/10.1016/j.scitotenv.2020.137614>.
- Savoca, M.S., McInturf, A.G., Hazen, E.L., 2021. Plastic ingestion by marine fish is widespread and increasing. *Glob. Chang. Biol.* 27, 2188–2199. <https://doi.org/10.1111/gcb.15533>.
- Senko, J., Nelms, S., Reavis, J., Witherington, B., Godley, B., Wallace, B., 2020. Understanding individual and population-level effects of plastic pollution on marine megafauna. *Endanger. Species Res.* 43, 234–252. <https://doi.org/10.1038/s41354-esr01064>.
- Sillanpää, M., Sainio, P., 2017. Release of polyester and cotton fibers from textiles in machine washings. *Environ. Sci. Pollut. Res.* 24, 19313–19321. <https://doi.org/10.1007/s11356-017-9621-1>.
- Song, Z., Liu, K., Wang, X., Wei, N., Zong, C., Li, C., Jiang, C., He, Y., Li, D., 2021. To what extent are we really free from airborne microplastics? *Sci. Total Environ.* 754, 142118. <https://doi.org/10.1016/j.scitotenv.2020.142118>.
- Steinberg, D.K., Landry, M.R., 2017. Zooplankton and the ocean carbon cycle. *Annu. Rev. Mar. Sci.* 9, 413–444. <https://doi.org/10.1146/annurev-marine-010814-015924>.
- Sutton, T.T., 2013. Vertical ecology of the pelagic ocean: classical patterns and new perspectives. *J. Fish Biol.* 83, 1508–1527. <https://doi.org/10.1111/jfb.12263>.
- Tanaka, H., Sassa, C., Ohshimo, S., Aoki, I., 2013. Feeding ecology of two lanternfishes *Diaphus garmani* and *Diaphus chrysorhynchus*. *J. Fish Biol.* 82, 1011–1031. <https://doi.org/10.1111/jfb.12051>.
- Underwood, A.J., 1997. *Experiments in Ecology: Their Logical Design and Interpretation Using Analysis of Variance*. 1st ed. Cambridge University Press, Cambridge.
- van Sebille, E., Wilcox, C., Lebreton, L., Maximenko, N., Hardesty, B.D., van Franeker, J.A., Eriksen, M., Siegel, D., Galgani, F., Law, K.L., 2015. A global inventory of small floating plastic debris. *Environ. Res. Lett.* 10, 124006. <https://doi.org/10.1088/1748-9326/10/12/124006>.
- Vega-Moreno, D., Abaroa-Pérez, B., Rein-Loring, P.D., Presas-Navarro, C., Fraile-Nuez, E., Machín, F., 2021. Distribution and transport of microplastics in the upper 1150 m of the water column at the Eastern North Atlantic Subtropical Gyre, Canary Islands, Spain. *Sci. Total Environ.* 788, 147802. <https://doi.org/10.1016/j.scitotenv.2021.147802>.
- Wang, Y., Wang, X., Li, Y., Li, J., Wang, F., Xia, S., Zhao, J., 2020. Biofilm alters tetracycline and copper adsorption behaviors onto polyethylene microplastics. *Chem. Eng. J.* 392, 123808. <https://doi.org/10.1016/j.cej.2019.123808>.
- Weiss, L., Ludwig, W., Heussner, S., Canals, M., Ghiglione, J.-F., Estoumel, C., Constant, M., Kerhervé, P., 2021. The missing ocean plastic sink: Gone with the rivers. *Science* 373 (6550), 107–111. <https://doi.org/10.1126/science.abc0290>.
- Wieczorek, A.M., Morrison, L., Croft, P.L., Allcock, A.L., MacLoughlin, E., Savard, O., Brownlow, H., Doyle, T.K., 2018. Frequency of microplastics in mesopelagic fishes from the Northwest Atlantic. *Front. Mar. Sci.* 5, 39. <https://doi.org/10.3389/fmars.2018.00039>.
- Wilcox, C., Puckridge, M., Schuyler, Q.A., Townsend, K., Hardesty, B.D., 2018. A quantitative analysis linking sea turtle mortality and plastic debris ingestion. *Sci. Rep.* 8, 12536. <https://doi.org/10.1038/s41598-018-30038-z>.
- Woodall, L.C., Sanchez-Vidal, A., Canals, M., Paterson, G.L.J., Coppock, R., Sleight, V., Calafat, A., Rogers, A.D., Narayanaswamy, B.E., Thompson, R.C., 2014. The deep sea is a major sink for microplastic debris. *R. Soc. Open Sci.* 1. <https://doi.org/10.1098/rsos.140317>.

- Wootton, N., Reis-Santos, P., Gillanders, B.M., 2021. Microplastic in fish – a global synthesis. *Rev. Fish Biol. Fish.* 31. <https://doi.org/10.1007/s11160-021-09684-6>.
- Wright, S.L., Thompson, R.C., Galloway, T.S., 2013. The physical impacts of microplastics on marine organisms: a review. *Environ. Pollut.* 178, 483–492. <https://doi.org/10.1016/j.envpol.2013.02.031>.
- Zhao, S., Zettler, E.R., Bos, R.P., Lin, P., Amaral-Zettler, L.A., Mincer, T.J., 2022. Large quantities of small microplastics permeate the surface ocean to abyssal depths in the South Atlantic Gyre. *Glob. Chang. Biol.* 28, 2843–2845. <https://doi.org/10.1111/gcb.16089>.