Main Manuscript for

Microplastic Ingestion by Deep-Pelagic Crustaceans and Fishes

Ryan P. Bos[1,2]*, Shiye Zhao[3], Tracey T. Sutton[2], Tamara M. Frank[2]

Affiliations
[1]Harbor Branch Oceanographic Institute, Florida Atlantic University, Fort Pierce, Florida 34946, USA.

[2]Guy Harvey Oceanographic Research Center, Halmos College of Arts and Sciences, Nova Southeastern University, 8000 North Ocean Drive, Dania Beach, Florida 33004, USA

[3]Japan Agency for Marine-Earth Science and Technology, 2-15 Natsushimacho, Yokosuka 237-0061, Japan

*Corresponding author: Ryan P. Bos

Email: rbos2019@fau.edu

Author Contributions: R. P. B., T. M. F., and T. T. S. conceptualized the research; T. M. F. and T. T. S. collected samples; R. P. B. and S. Z. processed the samples; R. P. B. processed the data; R. P. B. and T. M. F. analyzed the data. R. P. B. wrote the first draft of the manuscript. All authors edited and approved the final version of the manuscript.

Keywords: deep-pelagic | diel vertical migration | ingestion | marine snow | microplastics

This PDF file includes:
Main Text
Figures 1 to 5
Tables 1 to 3

Abstract

A size-selective loss of smaller microplastics (<1 mm) from surface pelagic waters has been reported, yet few surveys have studied biological ingestion by deep-pelagic organisms as a sink for the 'missing' plastic. Here, 557 individuals representing 35 species of vertically migrating and non-migrating mesopelagic crustaceans and fishes were collected in the Gulf of Mexico from discrete-depth intervals (0-200 m; 200-600 m; 600-1000 m; 1000-1200 m; 1200-1500 m) and analyzed for microplastic ingestion. We observed that 29% and 26% of crustacean and fish individuals, respectively, ingested microplastics, with an average plastic length of 0.59 ± 0.2 mm. A subsample of ingested polymers was identified using Fourier Transform Infrared Spectroscopy, revealing that alkyd resin (density 1.6 g cm^{-3}) and cellophane (density 1.42 g cm^{-3}) were mainly consumed. Our data indicate that non-migratory crustaceans had significantly higher levels of microplastic ingestion than migratory crustaceans at all depths available for comparison. While migratory fishes ingested microplastics at higher frequencies (0.28) than non-migratory fishes (0.23), the frequency of microplastic ingestion by non-migratory fishes increased with depth and was highest at depths of 1200-1500 m (0.40). Paired with the data for crustaceans, these observations suggest that plastic ingestion may be higher at deeper depths. Feeding strategy also appeared correlated to microplastic ingestion, as species that rely on gelatinous materials and marine snow for energy had the highest levels of ingestion. Altogether, our data highlight a largely undescribed temporary reservoir and implicate important biological transport pathways for the smaller plastic size fractions in the open ocean.

Introduction

Plastic debris, now ubiquitous in the marine environment, is a serious threat to global aquatic ecosystems. Plastic field surveys by Cózar et al. (2014) and Eriksen et al. (2014) reported that more than five trillion plastic particles with a combined mass of over 250,000 tons were afloat in the surface ocean alone, with greater than 90% of particles falling under the microplastic size classification (<5 mm). Projected increases in human population size are anticipated to be accompanied by an increase in global plastic production, which is forecasted to rise to 1,500 million tons annually (Bergmann et al. 2015). Current model predictions estimate that as many as 23 million metric tons, equaling 11% of annual plastic production, is input to the global ocean each year (Borelle et al. 2020), increasing the need for infrastructure and policies for mitigating plastic pollution.

Cózar et al. (2014) and Eriksen et al. (2014) observed a size-selective loss of the smaller size fractions of microplastics (<1 mm) from the surface ocean, and this observation brings the fate of plastic into question. Since these reports, field surveys and numerical models have made substantial progress towards understanding plastic's fate in the marine environment due to physical oceanographic processes and chemical and physical properties of polymers (Isobe et al. 2014; Hardesty et al. 2017; Choy et al. 2019; Kane et al. 2019; Lobelle et al. 2021; Moralles-Caselles et al. 2021; Klink et al. 2022; Zhao et al. 2022). Indeed, hotspots of the smaller size fractions of microplastics in the ocean's interior have been shown to accumulate in areas with slower current flow (Kane et al. 2019; Zhao et al. 2022), generally collecting in higher abundances along isopycnals (Choy et al. 2019; Zobkov et al. 2019; Uurasjärvi et al. 2021). Further differences in residence times of plastic polymers in the pelagic water column are driven largely by settling velocity, where retention times increase quadratically with particle size

(Kindler et al. 2010), and the ultimate fate of plastics thought to be deep-sea sediments (Van Cauwenberge et al. 2013; Woodall et al. 2014; Martin et al. 2022).

Biological variables, which can alter the sinking behavior of microplastics, however, are generally poorly represented in plastic distribution models (Clark et al. 2016; rev. in Van Sebille et al. 2020). The model simulations by Kvale et al. (2020) revealed that biologically-mediated pathways, including aggregation with marine snow and sinking, or ingestion by zooplankton and subsequent sinking, could account for a substantial portion of the so-called 'missing' plastic size fraction. While microplastics have been documented in marine aggregates (Zhao et al. 2017) and ingested by gelatinous zooplankton (Katija et al. 2017; Choy et al. 2019; Wieczorek et al. 2019), empirical support for Kvale's 2020 simulations is still limited due to the logistical constraints of mid-water sampling.

Deep-pelagic crustaceans and fishes make significant contributions to global food webs and total biomass in all deep-sea assemblages (Gjosaeter and Kawaguchi, 1980; Kaartvedt et al. 2012; Irigoien et al. 2014). These predominantly micronektonic animals (2-20 cm) serve as crucial trophic intermediates, as they are dominant zooplanktivores that are consumed by a variety of cephalopods, larger fishes, mammals, and seabirds (Borodulina, 1972; Hopkins et al. 1994; Beamish et al. 1999). Many of these meso- and bathypelagic crustaceans and fishes also undergo extensive diel vertical migrations into shallow epipelagic waters to forage at night (Longhurst, 1976; Cohen and Forward, 2005; rev. in Bos et al. 2021). Upon reaching satiation, these animals sink or swim back to deeper waters while digesting and defecating and therefore serve as a

vector for the transport of materials from shallow to deep-pelagic waters (Dam et al. 1995; Hidaka et al. 2001; Pearre, 2003).

Vertical migration has been hypothesized to enhance the flux of microplastics to deep-pelagic waters, although verification for this postulate does not currently exist. There are an increasing number of studies that have demonstrated that migratory mesopelagic fishes ingest high amounts of microplastics from various bodies of water, with variable ingestion patterns (Boerger et al. 2010; Davison and Asch, 2011; Choy and Drazen, 2013; Lusher et al. 2016; Wieczorek et al. 2018; Bernal et al. 2020; Hamilton et al. 2021; Justino et al. 2022; Ferreira et al. 2023). Few studies have included migratory midwater crustaceans for microplastic ingestion analyses, although these studies revealed that microplastics have infiltrated deep-pelagic food webs (Bordbar et al. 2019; Choy et al. 2019). However, when and where microplastics are ingested by vertical migrators is not known, as stomach fullness data suggest that some deep-dwelling species apparently feed exclusively in surface waters during their migrations, while other species feed throughout their entire depth distributions (Donaldson, 1975; Hu, 1978; Roe, 1984). While microplastic ingestion has also been reported in deep-sea benthic crustaceans (Taylor et al. 2016; Courtene-Jones et al. 2017; Carreras-Colom et al. 2018; Jamieson et al. 2019), few investigations have sampled targeted depth intervals and included non-migratory, midwater species for comparative analyses of microplastic ingestion alongside migratory species. Consequently, this remains an open-ended question that needs to be addressed to inform plastic distribution models.

Using the modelled global mesopelagic fish biomass of 1 Gt (Gjosaeter and Kawaguchi 1980), Lusher et al. (2016) calculated that the number of mesopelagic fishes ingesting microplastics

could range from 2.1×10^{12}–5.5×10^{14} individuals, and no estimates are currently available for mesopelagic crustaceans. Recent acoustic field surveys indicate that the global mesopelagic fish biomass is at least 10-fold higher than previous model estimates (Irigoien et al. 2014), which suggests that the actual biomass of global mesopelagic fishes ingesting microplastics is higher than previously thought. Of equal interest, there is a historic underestimation of bathypelagic crustacean and fish biomass, due to limited acoustic and trawl surveys (Drazen and Sutton, 2017). Taken together, these observations highlight the importance of evaluating biological entrainment, specifically in deep-pelagic organisms as a potentially important temporary reservoir in the pelagic realm.

In the current study, we leveraged previously collected meso- and bathypelagic crustaceans and fishes (collected during the Offshore Nekton Sampling and Analysis Program [ONSAP] and Deep Pelagic Nekton Dynamics of the Gulf of Mexico [DEEPEND] expeditions [Cook et al. 2020]) from discrete-depth intervals in the pelagic Gulf of Mexico to study microplastic ingestion. The Gulf of Mexico is a semi-enclosed body of water with fresh and saltwater inputs from the Mississippi River and Loop Current, respectively. The Gulf of Mexico has been referred to as a two-layer system with respect to seawater dynamics, with the dynamics of the upper layer (0 – 1200 m) controlled by meso- and submesoscale features spinning off from the Loop Current, and the lower layer (>1200 m) being semi-isolated containing water with residence times of 250 years (Rivas et al. 2005). The goals of the present study were to 1) characterize the abundance, polymer type, and size of ingested microplastics in the diets of deep-pelagic micronekton; 2) evaluate the relationship between vertical migration behavior and microplastic ingestion; and 3) compare levels of microplastic ingestion with feeding strategy and prey preference.

Materials and Methods

Sample Collection and Processing and Contamination Control

Deep-pelagic crustacean and fish samples were gathered from the Gulf of Mexico aboard the MV *Meg Skansi* and RV *Point Sur* as part of the ONSAP and DEEPEND programs, respectively (Figure 1). Samples were collected using a 10-m^2 Multiple Opening and Closing Net and Environmental Sensing System (MOCNESS; 3-mm mesh; Wiebe et al. 1976). Five discrete-depth intervals were targeted in the present study: 0-200 m, 200-600 m, 600-1000 m, 1000-1200 m, and 1200-1500 m. Stations were sampled twice a day, with trawls deployed between 1000 h - 1600 h and 2200 h - 0400 h. Samples were fixed in 10% formalin:seawater and sent to the Deep-Sea Biological Laboratory (crustaceans) and the Oceanic Ecology Laboratory (fishes) at Nova Southeastern University for identification and analysis. Species abundance, diet, and distribution data, including the published data on nocturnal and diurnal distributions of micronektonic crustaceans and fishes (Donaldson, 1975; Roe, 1984; Hopkins et al. 1994, 1996; Burghart et al. 2007; Burdett et al. 2017; Frank et al. 2020; rev in. Bos et al. 2021), were used to classify taxa as migratory or non-migratory and assign them to feeding guilds. The biomass of each species group from each net sample was measured with a P114 balance (Denver Instruments) to the nearest 0.01g. The carapace length of crustaceans and standard length of fishes were measured with a digital caliper (CO030150 electronic digital caliper, Marathon Management®) to the nearest 0.1 mm. Prior to excision of crustacean and fish stomachs, each organism was thoroughly rinsed with type I ultrapure water and dipped into a filtered acetone rinse (0.7 μm), to remove potential contamination on the exterior of the animal, and stored in a flamed (inverted and held over a flame for five minutes), acetone-sterilized covered glass petri dish until ready for dissection following methods by Jamieson et al. (2019). Further precautions

to avoid airborne contamination included processing samples in a HEPA filtration hood in the Microbial Genomics Laboratory and wearing non-plastic clothing coupled with a 100% cotton laboratory coat (Enders et al. 2015; Lusher et al. 2015; Zhao et al. 2017). Flamed forceps and surgical tools were used to directly handle all samples. Process blanks served as internal controls and were examined at the end of each dissection series under a dissecting microscope for potential contamination. Procedural blanks were processed in the same manner that all samples were processed: 1) digestion; 2) visual inspection of filters; and 3) hot-needle test on particles on filter to confirm presence of plastic.

The excised stomachs were placed individually into sterile, flamed (inverted and held over a flame for five minutes) borosilicate glass vials, covered with aluminum foil, and digested using one of two digestive solutions. Fish stomachs were digested using 1:1 KOH:NaClO following protocols described by Enders et al. (2017). While Enders et al. (2017) suggested that the proposed basic digestion could be effective at digesting flocculent, biogenic materials, results from the present study demonstrated that this basic digestion was inefficient for digesting crustacean stomach contents. The products of basic digestion resulted in a greasy slurry, which made it challenging to sort through for microplastics. For this reason, crustacean stomachs were digested with a 4:1 nitric (70%) and perchloric acid (70%) solution in individual borosilicate vials following protocols described in De Witte et al. (2014). Tissues were left to digest overnight in the HEPA filtration hood. The digestive solution inside the glass vials was then diluted with type I ultrapure water, and heated (>80 ℃) for 10 minutes. The products of acid and basic digestion were filtered through a 0.7-µm Whatman GF/F glass microfiber filter in the HEPA filtration hood and prepared for polymer identification. All specimens were individually

processed except for the two euphausiid species *Nematobranchion boopis* and *Thysanopoda acutifrons*, which were batch processed due to their small size.

Polymer Identification

Particles that withstood digestion were photographed using a camera (Canon DS126571) mounted on a stereomicroscope (Meiji Techno). Along with visual identification, these particles were subsequently subjected to the 'hot-needle' or 'burn' test to determine if they were plastic. Upon being probed with a hot needle, plastic fragments stick to the needle, and the needle may leave a burn mark or slight charring on the plastic. In the case of fibers, these plastics are repelled by the needle, begin to curl up, and in some cases melt (Devriese et al. 2015; Karlsson et al. 2017; Lusher et al. 2017). Chitinous material, which can be visually confused with plastic, did not exhibit any sign of charring or melting when probed with a hot needle. Images of particles that were verified to be plastic particles were uploaded into the free software *ImageJ* for analysis of dimensions (Schneider et al. 2012).

A random subsample of 25 ingested polymers was chosen for chemical identification by an FTIR Spectroscopy instrument (Thermo Scientific, Nicolet iN10MX, USA) using Attenuated Total Reflectance in the spectral range of 3600-1200 cm^{-1}. All identifications were done in a HEPA filtration hood in the Marine Plastic and Pollutants Laboratory at Harbor Branch Oceanographic Institute. The Hummel Polymer Sample Library, available in OMNIC Picta (Thermo Scientific), was used for chemically identifying ingested polymer particles. Spectra were preprocessed with auto baseline correction and normalization, followed by atmospheric peak removal. Predicted chemical identities based on software interpretation were validated (>60% match with reference spectra) or rejected (<60% match with reference spectra, with absence of clear diagnostic

polymer peaks). Chemical spectra between 50-60% match similarity were reevaluated as being a potential plastic polymer by spectral interpretation (i.e., the presence of diagnostic polymer peaks), and were considered to be a plastic polymer if the presence of diagnostic polymer peaks was confirmed. Thin ingested fibers were difficult to identify using transmission mode, so for some fibers, spectra were collected using reflectance mode with a gold-plated slide (Brahney et al. 2020).

Data Analysis

Microplastic ingestion was quantified separately for crustaceans and fishes for each depth range and solar cycle (day, night). The mean proportion of microplastic ingestion for each species was calculated as the number of individuals containing plastic divided by the total number of processed individuals for that species. The proportion of plastic ingestion between depth intervals and number of individuals that ingested plastic based on their migration pattern was compared using Chi-squared frequency analysis or Fisher's exact test.

Results

Contamination Controls

After visual inspection of the process blanks, only one out of 38 total control filters possessed contamination (three small clear fibers), so the samples associated with this filter were excluded from analyses. Airborne microplastic contamination was considered negligible as contamination was not observed on 97.3% of process blanks. While polyamide 6.6 was identified in our samples, no identified polymers resembled the color of the 3-mm nylon mesh used for sampling, so net feeding of plastics was also considered negligible.

Characteristics of Ingested Polymers

Crustaceans collectively ingested 128 plastic particles, whereas 95 plastic particles were consumed by fishes. The most abundant colors of microplastics were blue (37%), red (17%), clear (12%), black (9%), and other (24%). The ingested microplastic particles ranged in size from 0.27 mm to 3.97 mm, with an average size of 0.59 mm ± 0.2 mm. The composition of ingested microplastics was 69% fibers (n = 154) and 31% fragments (n = 69; Figure 2A). In terms of length, 78% of microplastics were less than 1 mm along their longest dimension, and this category was chiefly composed of fibers. The 1.01-2.00 mm category encompassed 15.6% of the microplastics and was composed mainly of fragments (57%). The 2.01-3.00 mm category accounted for 4.4% of all particles and was made up of only fragments, and the least prevalent size class was the larger size class (3.01- 4.00 mm), composed of only four fragments (1.7% of all plastics). No particles were found in the 4.01-5.00 length category. Crustaceans consumed predominantly fibers (78%), whereas fishes ingested a slightly higher percentage of fragments relative to fibers (54%, Figure 2B). Examples of chemically identified fibers and fragments found in the present study are displayed in Figure 3.

Of the 25 particles randomly chosen for chemical identification (>10% of all particles detected), 100% of the particles were confirmed to be plastic polymers (Table 1). In total, nine distinct polymer types were identified, with the four most abundant polymers being cellophane (n = 8), alkyd resin (n = 3), polyethylene-polypropylene copolymer (n = 3), and polyethyl acrylate acrylamide copolymer (n = 3).

Assessment of Microplastic Ingestion

A total of 557 individuals (300 crustaceans and 257 fishes) from a combined 35 species and 9 families were assessed for microplastic ingestion (Tables 2-3). Of the crustacean species analyzed, 12 species are vertical migrators while five species are non-migrators, whereas for the fishes, 13 species are vertical migrators, and five species are not. At least one microplastic particle was found in the digestive tract of 29% and 26% of crustaceans and fishes collected from the Gulf of Mexico, respectively. As the migratory euphausiids *Nematobranchion boopis* and *Thysanopoda acutifrons* individuals were batch digested, they were excluded from Table 2. Of 22 *N. boopis* individuals, no microplastics were found on filters after digestion and filtration, whereas 15 microplastics were isolated from *T. acutifrons* (n = 96).

Vertical Migration and Microplastic Ingestion

There was no observed difference in the mean plastic-positive proportion of crustaceans and fishes collected during daytime (0.29) vs. nighttime (0.28, Figure 4A). After disaggregating crustacean and fish taxa, the mean proportion of crustaceans that ingested microplastics was slightly higher during the day (0.32) than at night (0.26), but this difference was not statistically significant (Chi-squared, $p = 0.320$, Figure 4B). For the fishes, a slightly higher mean proportion of individuals ingested plastic at night (0.29) than during the day (0.24), but again, this difference was not statistically significant (Chi-squared, $p = 0.235$, Figure 4B).

Vertically migrating taxa of fishes had a higher mean proportion of individuals that ingested microplastics (0.28) than non-migratory taxa (0.23), but these differences were not statistically

significant (Chi-squared, p = 0.270, Figure 4C). The opposite was true for crustaceans, where non-migratory taxa had a significantly higher mean proportion of individuals ingesting microplastics (0.37) than migratory taxa (0.23, Chi-squared, p = 0.0120, Figure 4C).

Microplastic Ingestion with Depth

When grouping crustacean and fish taxa together, the highest mean proportion of individuals containing plastic was found at depths of 600-1000 m both during the day and at night. The mean proportion of plastic-positive specimens decreased to its lowest frequency between depths of 1000-1200 m and was highest at depths of 1200-1500 m (Figure 5A).

The mean proportion of migratory crustacean taxa that ingested microplastics was relatively consistent, ranging between 0.24-0.28 across nearly all depths, except for depths of 1000-1200 m where the lowest mean proportion (0.08) of migrators containing plastic was found (Figure 5B). The proportion of non-migratory crustacean taxa containing microplastics was also consistent, fluctuating narrowly between 0.33-0.35, except for depths of 600-1000 m where the highest mean proportion of individuals ingesting microplastics (0.44) was found. When comparing migratory and non-migratory crustacean taxa, significantly more non-migrators contained microplastics at all depths where comparisons were possible. The largest difference was observed at depths of 1000-1200 m, and this depth range had the lowest mean proportion of individuals ingesting microplastics for both taxa groupings (Figure 5B).

The mean proportion of individuals of migratory fish taxa that ingested microplastics was inconsistent across depths, with no apparent trend (Figure 5B), while the proportion of

non-migratory fish taxa ingesting microplastics appeared to progressively increase with depth, with the highest frequency of ingestion occurring at depths of 1200-1500 m (Figure 5B). Like the migratory crustaceans, migratory fish taxa had the highest mean proportion of individuals with microplastics at depths of 600-1000 m and the lowest proportion at depths of 1000-1200, while the non-migratory fish taxa exhibited the highest and lowest mean proportions of individuals containing microplastics at depths of 1200-1500 m and 600-1000 m, respectively.

Discussion

This is the first assessment of microplastic ingestion for deep-pelagic crustaceans and fishes in the Gulf of Mexico. Data collected in this study demonstrate the presence of microplastics in 29% of crustaceans and 26% of fishes and expand our understanding of the fate of smaller microplastics (<1 mm) with comparisons between migratory and non-migratory crustaceans and fishes from meso- and bathypelagic depths (Figure 3 and Tables 2 and 3). Visual identification, paired with the hot-needle test, although rapid and cost-effective, is only viable with plastic particles that are greater than ~250 microns in length (De Witte et al. 2014; Devriese et al. 2015; Vandermeersch et al. 2015; Bellas et al. 2016; Kapp and Yeatman, 2018). Consequently, the two-step polymer verification process used to identify microplastics herein (hot-needle test followed by FTIR) likely underrepresents the smallest size fractions of microplastics (<200 micron) that have been reported to be highly abundant in mesopelagic fishes (Wieczorek et al. 2018). Moreover, although still used as a viable plastic extraction technique, the acidic digestion used for digestion of recalcitrant crustacean stomachs could degrade plastic particles and misrepresent the true extent of microplastic ingestion in crustaceans. Therefore, our estimates for microplastic ingestion in the present study should be considered conservative, as the smallest

particle reported here was 270 µm, and it is reasonable to hypothesize that the extent of microplastic ingestion is substantially higher than the values we report.

Chemical Identification of Polymers

There is a growing number of observations in the literature that suggest that negatively buoyant polymers, especially polyamides and polyesters, are predominantly consumed by deep-pelagic organisms (Courtene-Jones et al. 2017, 2019; Choy et al. 2019; Justino et al. 2022). Choy et al. (2019) hypothesized that the predominance of negatively buoyant polymers ingested by deep-pelagic organisms could mean that these dense plastics are ingested directly from the water column (see below), which have been shown to be in high abundance in deep-pelagic waters (La Daana et al. 2017; Ross et al. 2021) In the present study, greater than 60% of chemically identified polymers were theoretically negatively buoyant in seawater, and cellophane (1.42 g cm^{-3}), followed by alkyd resin (1.6 cm^{-3}), were the dominant ingested polymers (Table 1). Alkyd resin is potentially linked to the degradation and shedding of marine paints from metal ships (Song et al. 2015; Lacerda et al. 2019), as well as land-based inputs of paints via rivers (Turner et al. 2022), which may be transported to the pelagic environment. Given the prevalence of commercial fishing activities and shipping in the Gulf of Mexico, ships are a plausible sea-based source for alkyd resin in this body of water, but because of riverine inputs via the Mississippi River, coastal origins of alkyd resins cannot be discounted. Cellophane is a cellulose-based polymer that has great utility in packaging of cosmetics, foods, and textiles and is also used as a coating for synthetic polymers (Yang et al. 2015). When using FTIR spectroscopy, it is difficult to differentiate artificial and natural cellulose particles. For example, alginic acids and methyl cellulose were highly ingested by mesopelagic fishes, and this result could arise from insufficient

removal of sodium hydroxide used for removal of organic matter (Wieczorek et al. 2018). However, the authors argue that thorough cleaning of plastic particles with filtered, ultrapure water after digestions could prevent skewed absorbance spectra. After digestions in the present study, however, type 1 ultrapure water was passed through the filters containing particles, so it is not immediately clear if residual caustic solutions remained on these particles and skewed spectra, or if these particles are of anthropogenic or natural origin.

Vertical Migration and Microplastic Ingestion

An increasing number of studies have investigated microplastic ingestion by deep-pelagic fishes (Boerger et al. 2010; Davison and Asch, 2011; Choy and Drazen, 2013; Lusher et al. 2016; Wieczorek et al. 2018; Justino et al. 2022), yet few exist for midwater crustaceans (Choy et al. 2019), as previous crustacean-centric studies have focused on deep-sea benthic or benthopelagic samples (Taylor et al. 2016; Courtene-Jones et al. 2017, 2019; Carreras-Colom et al. 2018; Jamieson et al. 2019). This is the first instance of non-migratory midwater taxa, that almost always dwell deeper than 600 m, being represented in high volume, as the previous studies that did include non-migrators were characterized by small sample sizes insufficient for analyses with depth (Davison and Asch, 2011; Lusher et al. 2016). In the current study, vertically migrating taxa of fishes had a higher (0.28), yet not significantly different proportion of individuals ingesting microplastics than non-migratory taxa of fishes (0.23, Figure 4C). This result is consistent with findings from Davison and Asch (2011), where the authors reported that 11.6% and 4.8% of migratory and non-migratory fish taxa, respectively ingested microplastics, but again these comparisons are limited due to smaller sample sizes of non-migrators. Crustaceans exhibited the opposite behavior, with non-migratory taxa ingesting a significantly higher

proportion microplastics (0.37) than vertically migrating taxa (0.23) (Figure 4C). As this is the first comparison of migratory and non-migratory decapod crustaceans ingesting microplastics, comparison with previous studies is not possible. More data on microplastic ingestion by midwater decapod crustaceans are necessary to verify the plastic ingestion trend observed in the present study.

The data presented here do not support the model predictions from Kvale et al. (2020), or field surveys by Choy et al. (2019) and Justino et al. (2022), that the proportion of individuals ingesting microplastics decrease with depth (Figure 5). Two critical distinctions between the current study and previous field surveys that may explain these differences in microplastic ingestion are 1) greater resolution, with inclusion of targeted depth intervals using a MOCNESS (0-200 m; 200-600 m; 600-1000 m; 1000-1200 m; 1200-1500 m); and 2) comparisons between non-migratory crustacean and fish taxa alongside migratory taxa. Expanding the total sampling depths included in analyses, with targeted sampling bins from day and night, and inclusion of non-migratory biomass may facilitate a more comprehensive understanding of microplastic ingestion trends. The proportion of non-migratory crustacean taxa that ingested microplastics was significantly higher than migratory crustacean taxa at all depths greater than 600 m, and the proportion of non-migratory fish taxa that ingested microplastics increased with depth and was highest at 1200-1500 m (Figure 5B). These observations, that would have otherwise been missed by prior sampling schemes, suggest that microplastic ingestion may potentially be more frequent in deeper waters, and the same may be true for plastic concentrations, although more data from other regions are required to verify these findings.

We hypothesize that non-migratory, pelagic organisms are at higher risk for microplastic ingestion due to their life history characteristics and may have longer plastic retention times due to their slower metabolisms (Childress and Theusen, 1992). Stemming from reduction in downwelling light intensity and therefore reduced visual predation pressure (Childress and Thuesen, 1992), the non-migratory taxa studied here spend most of their life in a quiescent state in colder waters and have evolved buoyancy adaptations (Morris, 1972; Sanders and Childress, 1988; Kelly and Yancey, 1999) to counteract passive sinking to conserve energy. For example, when compared with shallow-living crustaceans, the deep-pelagic mysid *Gnathophausia ingens* has a lower metabolic rate due reduced musculature resulting from reduced swimming capability (Cowles and Childress, 1988) and the lower metabolic rates of deep-pelagic fishes are a byproduct of decreased locomotory capacity (Childress and Thuesen, 1992) for energy conservation purposes. While the gut evacuation rates of non-migratory species are largely unknown, it could be expected that they are substantially slower than for migratory species. Non-migratory, midwater species may represent a heretofore important temporary reservoir for microplastics, whereby plastics can be entrained for long time periods. While the proportion of non-migratory crustaceans ingesting plastics was significantly greater than migratory crustaceans, the proportion of migratory fishes ingesting plastics was higher than non-migratory fishes, although the differences were not statistically significant, and a bigger sample size is needed to verify that this difference is real. The residence times of microplastics in the digestive tract of marine organisms is unknown and should remain at the forefront of discussion for understanding the ultimate fate of plastics in the marine environment.

Despite the differences in microplastic ingestion based on migration behavior (Tables 2 and 3), time and depth of sampling (Figures 4 and 5), and theoretical densities of ingested polymer types (Table 1), these data cannot be used to determine when or where microplastics were ingested for migratory species. However, the data for non-migratory taxa can be used to determine that plastics were ingested at depths greater than 600 m. There are limited data available for complete stomach evacuation for decapod crustaceans, but those existing range from 1-13 hours under normal environmental conditions, to 2-3 days in controlled laboratory settings with starved animals (Omori, 1974; Murtaugh, 1984). The study by Mincks et al. (2000) suggested that an average stomach evacuation time of six hours could be applied to deep-pelagic organisms, but these estimates must be used with caution because they are based on the coastal mysid *Neomysis mercedis*. When applying this evacuation estimate to our data, these data suggest that migratory crustaceans and fishes could potentially have consumed microplastics in shallower waters during their migrations. The presence of microplastics in the digestive tract of day samples may be an artifact from feeding during the previous night's migration, or feeding at depth during the day, but this remains to be determined.

Feeding Strategy May Partly Explain Differences in Microplastic Ingestion

While some deep-pelagic crustaceans and fishes co-occur in the water column (Hopkins et al. 1994), these animals occupy different ecological niches and represent an opportunity to study how feeding strategies and life history characteristics may explain microplastic ingestion trends. The shapes (fiber, fragment) of polymers ingested presents a stark contrast between deep-pelagic crustaceans and fishes, and this may be partly explained by feeding strategies and prey preference. While many micronekton crustaceans and fishes are zooplanktivorous, crustaceans

use the gastric milling process and mandibles to macerate their prey items, whereas micronekton fishes are selective particle feeders, swallowing whole prey items. In the present study, the crustaceans ingested predominantly fibers (78%), whereas the fishes consumed primarily fragments (54%; Figure 2B). The data for the crustaceans corroborate previous findings that fibers appear to be the major polymer shape ingested (Taylor et al. 2016; Courtene-Jones et al. 2017; Jamieson et al. 2019). However, our data on microplastic ingestion by deep-pelagic fishes conflict with previous observations that these fishes ingest mainly fibers (Lusher et al. 2016; Wieczorek et al. 2018; McGoran et al. 2021; Justino et al. 2022). In addition to feeding strategies, Wieczorek et al. (2018) proposed an alternative explanation for trends in ingested polymer shapes. In that study, the authors collected samples from a warm-core eddy and proposed that types of ingested microplastics reflect the hydrodynamics of the environment from which organisms are sampled. It is plausible that the unique flow regime of the Gulf of Mexico, with the upper layer (0-1200 m) of seawater dynamics being controlled by the Loop Current and associated eddies, and the lower layer (>1200 m) being semi-isolated, containing water with residence times of 250 years (Rivas et al. 2005), may play a role in controlling the distribution of bioavailable polymer shapes.

Marine snow has been hypothesized to be an export mechanism of microplastics from shallow waters to deeper waters (Van Cauwenberge et al. 2013; Cozar et al. 2014; Eriksen et al. 2014; Woodall et al. 2014; Turner, 2015). Laboratory studies demonstrated that microplastics increase the rate at which organic aggregates form (Long et al. 2015; Michels et al. 2018; Porter et al. 2018) and Zhao et al. (2017) reported that natural, coastal marine aggregates contained microplastics that were on average ~500 microns in diameter. Omori (1974), Roe (1984),

Alldredge and Silver (1988), and Hopkins et al. (1994) have documented the presence of an olive-green material present in the foreguts of many deep-pelagic crustaceans, which is purported to be marine snow. This observation suggests that midwater crustaceans that ingest marine snow may be important sinks for microplastics. In Hopkin's 1994 study, the authors reported that within the family Benthesicymidae, 87% of *Gennadas capensis* and *G. valens* ingested this material. *Bentheogenemma intermedia*, a predominantly bathypelagic species that was included in the current study, was not included in Hopkins study. All members of Benthesicymidae are morphologically equipped with head appendages that are thought to facilitate the sieving of small particles from the water column, so it could be expected that *B. intermedia* individuals also contain large amounts of olive-green material in their stomachs. In the present study, the observation that Benthesicymidae and non-migratory crustacean taxa had the highest levels of microplastic ingestion suggest a correlation between scavenging and microplastic ingestion (Table 2). However, there are potential caveats to this generalization such as the observation that 57% of the migratory piscivore, *Notostomus elegans,* ingested microplastics. This observation implies that piscivory could also result in higher amounts of plastic ingestion. Another feeding modality that unites many of the benthesicymids and non-migratory crustacean taxa is piscivory, and a notable switch from crustacean to fish prey between meso- and bathypelagic depths has been noted (Burghart et al. 2010). Taken together, these observations suggest plausible correlations between scavenging (marine snow consumption), a common feeding strategy in the deeper layers of the ocean, as well as piscivory, and microplastic ingestion, although this remains to be determined. More controlled laboratory mesocosm experiments to study aggregate formation and ingestion by organisms with different feeding strategies could be productive avenues for future research.

The observed differences between feeding strategy and microplastic ingestion by the two euphausiid species in this study, *Nematobranchion boopis* and *Thysanopoda acutifrons,* is of equal interest. *Nematobranchion boopis* and *T. acutifrons* individuals were not dissected individually like the other micronekton in this study, but batch processed due to their small size. For *N. boopis* (n = 22) no microplastics were found on the filter after bulk digestion, whereas 15 microplastics were found on the filter after digestion for *T. acutifrons* (n = 96). Although the data presented in this study are not for individual euphausiids, and the difference in number of microplastics left on the filter after bulk digestion may be due to having approximately four times as many *T. acutifrons* individuals relative to *N. boopis*, it is interesting that zero microplastics were found from bulk digestion of 22 *N. boopis* individuals. In all other crustacean species processed, those with sample sizes greater than seven had at least one ingested microplastic, and the same was true for fish species. Therefore, the difference in microplastic ingestion between *T. acutifrons*, a known herbivorous species that filters seawater with a basketlike apparatus and *N. boopis*, an actively hunting, omnivorous species with a high critical flicker fusion frequency and elongated 2nd and 3rd pleopods with claws for capturing prey from the water column (Mauchline, 1967; Suh et al. 1996; Frank, 2003) is likely real. This evidence suggests that filter-feeding species may be at greater risk for microplastic ingestion. Microplastic ingestion by euphausiids, or animals with similar digestion strategies could result in generation of billions of additional nanoplastic particles worldwide. For example, Dawson et al. (2018) demonstrated that *Euphausia superba* is capable of fragmenting microplastics into nanoplastics with the gastric milling process, which could make nanoplastics bioavailable at every trophic level.

The migratory fishes *Benthosema suborbitale*, *Ceratoscopelus warmingii, Lampanyctus alatus*, *L. lineatum,* and *Lepidophanes guentheri* display diel feeding patterns, and primarily consume calanoid copepods sized ~1 mm (Hopkins and Baird, 1985). As plastic has been hypothesized to be confused with natural prey items (Boerger et al. 2010), and the former fish species are selective particle feeders, it is possible that a portion of ingested microplastics is mistaken as preferred copepod prey and directly consumed from the water-column in low-ambient light conditions. Indeed, Hopkins et al. (1996) demonstrated that a large portion of myctophid diets comprise shallow-living copepod species, and the majority of microplastic fibers and fragments ingested in the current study overlaps with the size fraction of preferred prey (Figure 2A). Atkinson (1996) reported that copepods ingested prey items with an equivalent spherical diameter of <60 microns, so, based on the observed size classes of microplastics ingested analyzed in the present study, it is unlikely that these extracted plastics were biomagnified through consumption of copepod prey. Similar observations have been reported in prior studies of deep-pelagic fishes (Lusher et al. 2016; Justino et al. 2022), as the size fraction of ingested microplastics were substantially larger than prey items of copepods. Like the present study, both of the former studies did not have the capability of identifying the smaller size fractions of microplastics (<250 microns). However, Wieczorek et al. (2018) showed that the smallest recorded microplastic ingested by deep-pelagic fishes was 42 microns, so it is also possible that these smaller microplastics can be biomagnified by copepod prey.

The deepest dwelling gonostomatid in the Gulf of Mexico, *Cyclothone obscura,* accounts for roughly 22% of the micronekton biomass in the bathypelagic (Burghart et al. 2010), with its diet

being composed of calanoid copepods, ostracods, and a large portion of unidentifiable prey (DeWitt and Cailliett, 1972; Burghart et al. 2010). Although *C. obscura* is thought to eat infrequently (Burghart et al. 2010), greater than 30% of these non-migratory fish ingested microplastics (Table 3), suggesting that, like the non-migratory crustaceans, microplastics may have a longer residence time in fishes with slower metabolisms, such as these deep-living non-migrators (Childress, 1975; Childress et al. 1980). As stomach contents were digested and not analyzed for prey composition in the current study, it is difficult to determine what mechanism directly contributes to higher levels of microplastic ingestion for this species. However, it is thought that *Cyclothone* may also consume a large amount of gelatinous material and marine snow (McClain-Counts et al. 2017), and gelatinous prey are purported to be an important energy source for bathypelagic organisms (Kaartvedt et al. 2015). Katija et al. (2017), Choy et al. (2019), and Wieczorek et al. (2019) reported that larvaceans expedite the flux of smaller size classes of microplastics through sinking fecal pellets and discarded mucus houses. The stable isotope analysis by Gloeckler et al. (2017) demonstrated that *Cyclothone* fed primarily on suspended particles, and that reliance on sinking particles increased with depth. Therefore, it is plausible that *Cyclothone* and other bathypelagic fishes that rely on gelatinous material for energy may be prone to inadvertently consuming microplastics.

We are only beginning to understand the distribution and fate of microplastics in the marine environment. Our dataset describes a largely understudied microplastic sink in the deep-pelagial and implicates sinking particles such as marine snow and senescent gelatinous materials as important pathways for microplastic flux. The observations made here underscore the significance of biological parameters in plastic distribution models. In addition to vertical

migration behavior, feeding strategies, life history characteristics, and prey preference may be useful for explaining trends in microplastic ingestion in other environments. To obtain a clearer illustration of temporary plastic reservoirs in the midwater, future inquiry should include not only non-vertical migrators collected from different depths and geographic locations, but also organisms with diverse migration patterns and anatomical and physiological traits. It is plausible that an element of species specificity and combination of traits exists that is conducive for plastic ingestion, and these observations may be important for understanding the connectivity of marine food webs.

Acknowledgements

We thank the crews of the MV *Meg Skansi* and RV *Point Sur* for assistance with sampling, as well as Devan Nichols, Michael Novotny, Nathan LaSpina, Nina Pruzinsky, Richard Hartland, and Ronald Sieber for taxonomic identifications and sample processing assistance. We are grateful for permission from Dr. Jose Lopez to use the HEPA filtration hood in the Microbial Genomics Laboratory at Nova Southeastern University. We also thank Dr. Tracy Mincer in the Marine Plastics and Pollutants Laboratory at Harbor Branch Oceanographic Institute for assistance and facilities for chemical identification of polymers.

Funding

This research was made possible in part by a grant from The Gulf of Mexico Research Initiative, and in part by the National Oceanic and Atmospheric Administration's RESTORE Science Program under award NA19NOS4510193 to Nova Southeastern University. Data are publicly available through the Gulf of Mexico Research Initiative Information & Data Cooperative

(GRIIDC) at https://data.gulfresearchinitiative.org (doi: 10.7266/N7VX0DK2, 10.7266/N70P0X3T, 10.7266/N7XP7385, and 10.7266/N7902234).

References

Atkinson, A. (1996). Subantarctic copepods in an oceanic, low chlorophyll environment: ciliate predation, food selectivity and impact on prey populations. *Marine Ecology Progress Series*, 130, 85-96.

Alldredge, A. L., Silver, M. W. (1988). Characteristics, dynamics and significance of marine snow. *Progress in Oceanography*, 20(1), 41-82.

Beamish, R. J., Leask, K. D., Ivanov, O. A., Balanov, A. A., Orlov, A. M., et al. (1999). The ecology, distribution, and abundance of midwater fishes of the Subarctic Pacific gyres. *Progress in Oceanography*, 43(2), 399-442.

Bellas, J., Martínez-Armental, J., Martínez-Cámara, A., Besada, V., Martínez-Gómez, C. (2016). Ingestion of microplastics by demersal fish from the Spanish Atlantic and Mediterranean coasts. *Marine Pollution Bulletin*, 109(1), 55-60.

Bergmann, M., Gutow, L., Klages, M. (2015). Marine anthropogenic litter (p. 447). Springer Nature.

Bernal, A., Toresen, 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 Research Part II: Topical Studies in Oceanography*, 179, 104706.

Boerger, C. M., Lattin, G. L., Moore, S. L., Moore, C. J. (2010). Plastic ingestion by planktivorous fishes in the North Pacific Central Gyre. *Marine Pollution Bulletin*, 60(12), 2275 227.

Bordbar, L., Kapiris, K., Kalogirou, S., Anastasopoulou, A. (2018). First evidence of ingested

plastics by a high commercial shrimp species (*Plesionika narval*) in the eastern Mediterranean. *Marine Pollution Bulletin*, 136, 472-47.

Borodulina, O. D. (1972). The feeding of mesopelagic predatory fish in the open ocean. *Journal of Ichthyology*, 12, 692-70

Brahney, J., Hallerud, M., Heim, E., Hahnenberger, M., Sukumaran, S. (2020). Plastic rain in protected areas of the United States. *Science*, 368(6496), 1257-1260.

Borrelle, S. B., Ringma, J., Law, K. L., Monnahan, C. C., Lebreton, L., McGivern, A., et al. (2020). Predicted growth in plastic waste exceeds efforts to mitigate plastic pollution. *Science*, *369*(6510), 1515-1518.

Bos, R. P., Sutton, T. T., Frank, T. M. (2021). State of Satiation Partially Regulates the Dynamics of Vertical Migration. *Frontiers in Marine Science*, 8, 143.

Brunner, K., Kukulka, T., Proskurowski, G., Law, K. L. (2015). Passive buoyant tracers in the ocean surface boundary layer: 2. Observations and simulations of microplastic marine debris. *Journal of Geophysical Research: Oceans*, 120(11), 7559-7573.

Burdett, E. A., Fine, C. D., Sutton, T. T., Cook, A. B., Frank, T. M. (2017). Geographic and depth distributions, ontogeny, and reproductive seasonality of decapod shrimps (Caridea: Oplophoridae) from the northeastern Gulf of Mexico. *Bulletin of Marine Science*, 93(3), 743 767.

Burghart, S. E., Hopkins, T. L., Torres, J. J. (2007). The bathypelagic Decapoda, Lophogastrida, and Mysida of the eastern Gulf of Mexico. *Marine Biology*, 152(2), 315-327.

Burghart, S. E., Hopkins, T. L., Torres, J., (2010). Partitioning of food resources in bathypelagic micronekton in the eastern Gulf of Mexico. *Marine Ecology Progress Series*, 399, 131140.

Carreras-Colom, E., Constenla, M., Soler-Membrives, A., Cartes, J. E., Baeza, M. et al. (2018).

Spatial occurrence and effects of microplastic ingestion on the deep-water shrimp *Aristeus antennatus*. *Marine Pollution Bulletin*, 133, 44-52.

Childress, J. J. (1975). The respiratory rates of midwater crustaceans as a function of depth of occurrence and relation to the oxygen minimum layer off Southern California. Comparative *Biochemistry and Physiology Part A: Physiology*, 50(4), 787-799.

Childress, J. J., Taylor, S. M., Cailliet, G. M., Price, M. H. (1980). Patterns of growth, energy utilization and reproduction in some meso- and bathypelagic fishes off Southern California. Marine Biology. 61(1), 27-40

Childress, J. J., Thuesen, E. V. (1992). Metabolic potential of deep-sea animals: regional and global scales. *Deep-sea Food Chains and the Global Carbon Cycle* (pp. 217-236). Springer, Dordrecht.

Choy, C. A., Drazen, J. C. (2013). Plastic for dinner? Observations of frequent debris ingestion by pelagic predatory fishes from the central North Pacific. *Marine Ecology Progress Series*, 485, 155-163.

Choy, C. A., Robison, B. H., Gagne, T. O., Erwin, B., Firl, E., Halden, R. U., et al. (2019). The vertical distribution and biological transport of marine microplastics across the epipelagic and mesopelagic water column. *Scientific reports*, 9(1), 1-9.

Clark, J. R., Cole, M., Lindeque, P. K., Fileman, E., Blackford, J., Lewis, C., et al. (2016). Marine microplastic debris: a targeted plan for understanding and quantifying interactions with marine life. *Frontiers in Ecology and the Environment*, 14(6), 317-324.

Cohen, J. H., Forward, R. B. (2005). Diel vertical migration of the marine copepod Calanopia americana. II. Proximate role of exogenous light cues and endogenous rhythms. *Marine Biology*, 147(2), 399-410.

Cook, A. B., Bernard, A. M., Boswell, K. M., Bracken-Grissom, H., D'Elia, M., DeRada, S., et al. (2020). A Multidisciplinary approach to investigate deep-pelagic ecosystem dynamics in the Gulf of Mexico following Deepwater Horizon. *Frontiers in Marine Science*, 1122.

Courtene-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. *Environmental Pollution*, 231, 271-280.

Courtene-Jones, W., Quinn, B., Ewins, C., Gary, S. F., Narayanaswamy, B. E. (2019). Consistent microplastic ingestion by deep-sea invertebrates over the last four decades (1976 2015), a study from the North East Atlantic. *Environmental Pollution*, 244, 503-512.

Cowles, D. L., Childress, J. J. (1988). Swimming speed and oxygen consumption in the bathypelagic mysid *Gnathophausia ingens*. *The Biological Bulletin*, *175*(1), 111-121.

Cózar, A., Echevarría, F., González-Gordillo, J. I., Irigoien, X., Úbeda, B., Hernández-León, S., et al. (2014). Plastic debris in the open ocean. *Proceedings of the National Academy of Sciences*, 111(28), 10239-10244.

Dam, H. G., Roman, M. R., Youngbluth, M. J. (1995). Downward export of respiratory carbon and dissolved inorganic nitrogen by diel-migrant mesozooplankton at the JGOFS Bermuda time series station. *Deep-Sea Research I*, 42(7), 1187–1197.

Davison, P., Asch, R. G. (2011). Plastic ingestion by mesopelagic fishes in the North Pacific Subtropical Gyre. *Marine Ecology Progress Series*, 432, 173-180.

Dawson, A. L., Kawaguchi, S., King, C. K., Townsend, K. A., King, R., Huston, et al. (2018). Turning microplastics into nanoplastics through digestive fragmentation by Antarctic krill. *Nature communications*, 9(1), 1-8.

DeWitt, F. A., Cailliet, G. M. (1972). Feeding habits of two bristlemouth fishes, *Cyclothone acclinidens* and *C. signata* (Gonostomatidae). *Copeia*, 1972(4), 868-871.

Devriese, L. I., van der Meulen, M. D., Maes, T., Bekaert, K., Paul-Pont, I., et al. (2015). MP contamination in brown crustaceans (*Crangon crangon*, Linnaeus 1758) from coastal waters of the Southern North Sea and Channel area. *Marine Pollution Bulletin*, 98(1), 179-187.

De Witte, B., Devriese, L., Bekaert, K., Hoffman, S., Vandermeersch, G., et al. (2014). Quality assessment of the blue mussel (*Mytilus edulis*): Comparison between commercial and wild types. *Marine Pollution Bulletin*, 85(1), 146-155.

Donaldson, H. A. (1975). Vertical distribution and feeding of sergestid shrimps (Decapoda: Natantia) collected near Bermuda. *Marine Biology*, *31*(1), 37-50.

Drazen, J. C., Sutton, T. T. (2017). Dining in the deep: the feeding ecology of deep-sea fishes. *Annual Review of Marine Science*, 9: 337-366.

Egger, M., Sulu-Gambari, F., Lebreton, L. (2020). First evidence of plastic fallout from the North Pacific Garbage Patch. *Scientific Reports*, 10(1), 7495.

Enders, K., Lenz, R., Stedmon, C. A., Nielsen, T. G. (2015). Abundance, size and polymer composition of marine microplastics ≥ 10 μm in the Atlantic Ocean and their modelled vertical distribution. *Marine pollution bulletin*, *100*(1), 70-81.

Enders, K., Lenz, R., Beer, S., Stedmon, C. A. (2017). Extraction of MP from biota: recommended acidic digestion destroys common plastic polymers. *ICES Journal of Marine Science*, 74(1), 326-331.

Eriksen, M., Lebreton, L. C., Carson, H. S., Thiel, M., Moore, C. J., et al. (2014). Plastic pollution in the world's oceans: more than 5 trillion plastic pieces weighing over 250,000 tons afloat at sea. *PloS one*, 9(12), e111913.

Ferreira, G. V., Justino, A. K., Eduardo, L. N., Schmidt, N., Martins, J. R., Ménard, F., et al. (2023). Influencing factors for microplastic intake in abundant deep-sea lanternfishes (Myctophidae). *Science of The Total Environment*, 867, 161478.

Frank, T. M. (2003). Effects of light adaptation on the temporal resolution of deep-sea crustaceans. *Integrative and Comparative Biology*, 43(4), 559-570.

Frank, T. M., Fine, C. D., Burdett, E. A., Cook, A. B., Sutton, T. T. (2020). The vertical and horizontal distribution of deep-sea crustaceans in the Order Euphausiacea in the vicinity of the Deepwater Horizon oil spill. *Frontiers in Marine Science*, 7, 99.

Gjøsaeter, J., Kawaguchi, K. (1980). A review of the world resources of mesopelagic fish: Food and Agriculture Org.

Gloeckler, K., Choy, C. A., Hannides, C. C., Close, H. G., Goetze, E., Popp, B. N., et al. (2018). Stable isotope analysis of micronekton around Hawaii reveals suspended particles are an important nutritional source in the lower mesopelagic and upper bathypelagic zones. *Limnology and Oceanography*, 63(3), 1168-1180.

Hamilton, B. M., Rochman, C. M., Hoellein, T. J., Robison, B. H., Van Houtan, K. S., Choy, C. A. (2021). Prevalence of microplastics and anthropogenic debris within a deep-sea food web. *Marine Ecology Progress Series*, 675, 23-33.

Hardesty, B. D., Harari, J., Isobe, A., Lebreton, L., Maximenko, et al. (2017). Using numerical model simulations to improve the understanding of micro-plastic distribution and pathways in the marine environment. *Frontiers in marine science*, *4*, 30.

Hidaka, K., Kawaguchi, K., Murakami, M., Takahashi, M. (2001). Downward transport of organic carbon by diel migratory micronekton in the western equatorial Pacific: its quantitative and qualitative importance. *Deep Sea Research I*, 48(8), 1923-1939.

Hopkins, T. L., Baird, R. C. (1985). Feeding ecology of four hatchetfishes (Sternoptychidae) in 60 the eastern Gulf of Mexico. *Bulletin of Marine Science*, 36(2), 260-277.

Hopkins, T. L., Flock, M. E., Gartner Jr, J. V., Torres, J. J. (1994). Structure and trophic ecology of a low latitude midwater decapod and mysid assemblage. *Marine Ecology Progress Series*, 143-156.

Hopkins, T. L., Sutton, T. T., Lancraft, T. M. (1996). The trophic structure and predation impact of a low latitude midwater fish assemblage. *Progress in Oceanography*, 38(3), 205-239.

Hu, V. J. (1978). Relationships between vertical migration and diet in four species of euphausiids 1. *Limnology and Oceanography*, *23*(2), 296-306.

Irigoien, X., Klevjer, T. A., Røstad, A., Martinez, U., Boyra, G., et al. (2014). Large mesopelagic fishes biomass and trophic efficiency in the open ocean. *Nature Communications*, 5:3271.

Isobe, A., Kubo, K., Tamura, Y., Nakashima, E., Fujii, N. (2014). Selective transport of microplastics and mesoplastics by drifting in coastal waters. *Marine Pollution Bulletin*, *89*(1-2), 324-330.

Jamieson, A. J., Brooks, L. S. R., Reid, W. D. K., Piertney, S. B., Narayanaswamy, B. E., et al. (2019). Microplastics and synthetic particles ingested by deep-sea amphipods in six of the deepest marine ecosystems on Earth. *Royal Society Open Science*, 6(2), 180667.

Justino, A. K., Ferreira, G. V., Schmidt, N., Eduardo, L. N., Fauvelle, et al. (2022). The role of mesopelagic fishes as microplastics vectors across the deep-sea layers from the Southwestern Tropical Atlantic. *Environmental Pollution*, 118988.

Kaartvedt, S., Staby, A., Aksnes, D. L. (2012). Efficient trawl avoidance by mesopelagic fishes causes large underestimation of their biomass. *Marine Ecology Progress Series*, 456, 1-6.

Kaartvedt, S., Ugland, K. I., Klevjer, T. A., Røstad, A., Titelman, J., et al. (2015). Social

behaviour in mesopelagic jellyfish. *Scientific Reports*, 5, 11310.

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*, 368(6495), 1140-1145.

Kapp, K. J., Yeatman, E. (2018). Microplastic hotspots in the Snake and Lower Columbia rivers: A journey from the Greater Yellowstone Ecosystem to the Pacific Ocean. *Environmental Pollution*, 241, 1082-1090.

Karlsson, T. M., Vethaak, A. D., Almroth, B. C., Ariese, F., van Velzen, M., et al. (2017). Screening for microplastics in sediment, water, marine invertebrates and fish: Method development and microplastic accumulation. *Marine Pollution Bulletin*, 122(1), 403-408.

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. *Science Advances*, 3(8), e1700715.

Kelly, R. H., Yancey, P. H. (1999). High contents of trimethylamine oxide correlating with depth in deep-sea teleost fishes, skates, and decapod crustaceans. *The Biological Bulletin*, *196*(1), 18-25.

Kindler, K., Khalili, A., Stocker, R. (2010). Diffusion-limited retention of porous particles at density interfaces. *Proceedings of the National Academy of Sciences*, 107(51), 22163-22168.

Klink, D., Peytavin, A., Lebreton, L. (2022). Size Dependent Transport of Floating Plastics Modeled in the Global Ocean. *Frontiers in Marine Science*, 9, 903134.

Koelmans, A. A., Kooi, M., Law, K. L., Van Sebille, E. (2017). All is not lost: deriving a top down mass budget of plastic at sea. *Environmental Research Letters*, 12(11), 114028.

Kukulka, T., Law, K. L., Proskurowski, G. (2016). Evidence for the influence of surface heat

fluxes on turbulent mixing of microplastic marine debris. *Journal of Physical Oceanography*, 46(3), 809-815.

Kvale, K., Prowe, A. E. F., Chien, C. T., Landolfi, A., Oschlies, A. (2020). The global biological microplastic particle sink. *Scientific Reports*, *10*(1), 1-12.

Lacerda, A. L. D. F., Rodrigues, L. D. S., Van Sebille, E., Rodrigues, F. L., Ribeiro, L., et al. (2019). Plastics in sea surface waters around the Antarctic Peninsula. *Scientific Reports*, *9*(1), 1-12.

La Daana, K. K., Gårdfeldt, K., Lyashevska, O., Hassellöv, M., Thompson, R. C., O'Connor, I. (2018). Microplastics in sub-surface waters of the Arctic Central Basin. *Marine Pollution Bulletin*, 130, 8-18.

Lobelle, D., Kooi, M., Koelmans, A. A., Laufkötter, C., Jongedijk, C. E., Kehl, C., van Sebille, E. (2021). Global modeled sinking characteristics of biofouled microplastic. *Journal of Geophysical Research: Oceans*, 126(4), e2020JC017098.

Long, M., Moriceau, B., Gallinari, M., Lambert, C., Huvet, A., et al. (2015). Interactions between microplastics and phytoplankton aggregates: impact on their respective fates. *Marine Chemistry*, 175, 39-46.

Longhurst, A. R. (1976, August). Interactions between zooplankton and phytoplankton profiles in the eastern tropical Pacific Ocean. In *Deep Sea Research and Oceanographic Abstracts* (Vol. 23, No. 8, pp. 729-754). Elsevier.

Lusher, A. (2015). Microplastics in the Marine Environment: Distribution, Interactions and Effects. In M. Bergmann, L. Gutow, and M. Klages (Eds.), *Marine Anthropogenic Litter* (pp. 45 307). Cham: Springer International Publishing.

Lusher, A. L., O'Donnell, C., Officer, R., O'Connor, I. (2016). Microplastic interactions with

North Atlantic mesopelagic fish. *ICES Journal of Marine Science*, 73 (4):1214-1225.

Lusher, A. L., Welden, N. A., Sobral, P., Cole, M. (2017). Sampling, isolating and identifying microplastics ingested by fish and invertebrates. *Analytical Methods*, *9*(9), 1346-1360.

Martin, C., Young, C. A., Valluzzi, L., Duarte, C. M. (2022). Ocean sediments as the global sink for marine micro‐and mesoplastics. *Limnology and Oceanography Letters*, 7(3), 235-243.

Mauchline, J. (1967). Feeding appendages of the Euphausiacea (Crustacea). *Journal of Zoology*, 153(1), 1-43.

McClain‐Counts, J. P., Demopoulos, A. W., Ross, S. W. (2017). Trophic structure of mesopelagic fishes in the Gulf of Mexico revealed by gut content and stable isotope analyses. *Marine Ecology*, *38*(4), e12449.

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. *Frontiers in Marine Science*, *8*, 78.

Michels, J., Stippkugel, A., Lenz, M., Wirtz, K., Engel, A. (2018). Rapid aggregation of biofilm-covered microplastics with marine biogenic particles. Proceedings of The Royal Society B, 285(1885), 20181203.

Mincks, S. L., Bollens, S. M., Madin, L. P., Horgan, E., Butler, M., et al. (2000). Distribution, abundance, and feeding ecology of decapods in the Arabian Sea, with implications for vertical flux. *Deep Sea Research Part II: Topical Studies in Oceanography*, 47(7-8), 1475-1516.

Morales-Caselles, C., Viejo, J., Martí, E., González-Fernández, D., Pragnell-Raasch, H., González-Gordillo, J. I., et al. (2021). An inshore–offshore sorting system revealed from global classification of ocean litter. *Nature Sustainability*, 4(6), 484-493.

Morris, R. J. (1972). The occurrence of wax esters in crustaceans from the North-east Atlantic

Ocean. *Marine Biology*, *16*(2), 102-107.

Murtaugh, P. A. (1984). Variable gut residence time: problems in inferring feeding rate from stomach fullness of a mysids crustacean. *Canandian Journal of Fisheries and Aquatic Sciences*, 41: 1287–1293.

Omori, M. (1974). The biology of Pelagic shrimps in the ocean. *Advances in Marine Biology*, 12, 233324.

Pearre, S. (2003). Eat and run? The hunger/satiation hypothesis in vertical migration: history, evidence and consequences. *Biological Reviews*, 78(1), 1-79.

Podeswa, Y. (2012). Active carbon transport and feeding ecology of pelagic decapods in the North Pacific Subtropical Gyre. University of British Columbia.

Porter, A., Lyons, B. P., Galloway, T. S., Lewis, C. (2018). Role of marine snows in microplastic fate and bioavailability. *Environmental Science and Technology*, 52(12), 7111-7119.

Rivas, D., Badan, A., Ochoa, J. (2005). The ventilation of the deep Gulf of Mexico. *Journal of Physical Oceanography*, 35, 1763–178.

Roe, H. S. J. (1984). The diel migrations and distributions within a Mesopelagic community in the North East Atlantic. 2. Vertical migrations and feeding of Mysids and decapod crustacea. *Progress in Oceanography*, 13(3), 269-318.

Ross, P. S., Chastain, S., Vassilenko, E., Etemadifar, A., Zimmermann, S., Quesnel, S. A., et al. (2021). Pervasive distribution of polyester fibres in the Arctic Ocean is driven by Atlantic inputs. *Nature Communications*, 12(1), 106.

Sanders, N. K., Childress, J. J. (1988). Ion replacement as a buoyancy mechanism in a pelagic deep-sea crustacean. *Journal of Experimental Biology*, *138*(1), 333-343.

Schneider, C. A., Rasband, W. S., Eliceiri, K. W. (2012), "NIH Image to ImageJ: 25 years of image analysis", *Nature methods*, 9(7): 671-675.

Song, Y. K., Hong, S. H., Jang, M., Han, G. M., Shim, W. J. (2015). Occurrence and distribution of microplastics in the sea surface microlayer in Jinhae Bay, South Korea. *Archives of Environmental Contamination and Toxicology*, 69, 279–287.

Suh, H. L. (1996). The gastric mill of euphausiid crustaceans: a comparison of eleven species. *Hydrobiologia*, 321(3), 235-244.

Taylor, M., Gwinnett, C., Robinson, L., Woodall, L. (2016). Plastic microfibre ingestion by deep-sea organisms. *Scientific Reports*, 6

Turner, J. T. (2015). Zooplankton fecal pellets, marine snow, phytodetritus and the ocean's biological pump. *Progress in Oceanography*, 130, 205-248.

Uurasjärvi, E., Pääkkönen, M., Setälä, O., Koistinen, A., Lehtiniemi, M. (2021). Microplastics accumulate to thin layers in the stratified Baltic Sea. *Environmental Pollution*, 268, 115700.

Van Cauwenberghe, L., Vanreusel, A., Mees, J., Janssen, C. R. (2013). MP pollution in deep-sea sediments. *Environmental Pollution*, 182, 495-499.

Van Sebille, E., Aliani, S., Law, K. L., Maximenko, N., Alsina, et al. (2020). The physical oceanography of the transport of floating marine debris. *Environmental Research Letters*, 15(2), 023003.

Ward, J. E., Kach, D. J. (2009). Marine aggregates facilitate ingestion of nanoparticles by suspension-feeding bivalves. *Marine Environmental Research*, 68(3), 137-142.

Wiebe, P. H., Burt, K. H., Boyd, S. H., Morton, A. W. (1976). A multiple opening/closing net and environmental sensing system for sampling zooplankton. *Journal of Marine Research*, 34:313-326.

Wieczorek, A. M., Morrison, L., Croot, P. L., Allcock, A. L., MacLoughlin, E., et al. (2018). Frequency of Microplastics in Mesopelagic Fishes from the Northwest Atlantic. *Frontiers of Marine Science*, 5(39).

Wieczorek, A. M., Croot, P. L., Lombard, F., Sheahan, J. N., Doyle, T. K. (2019). Microplastic ingestion by gelatinous zooplankton may lower efficiency of the biological pump. *Environmental Science and Technology*, *53*(9), 5387-5395.

Woodall, L. C., Sanchez-Vidal, A., Canals, M., Paterson, G. L. J., Coppock, R., et al. (2014). The deep sea is a major sink for MP debris. *Royal Society Open Science*, 1(4), 140317.

Yang, D., Shi, H., Li, L., Li, J., Jabeen, K., Kolandhasamy, P. (2015). Microplastic pollution in table salts from China. *Environmental Science and Technology*, *49*(22), 13622-13627.

Zhao, S., Ward, E. J., Danley, M., Mincer, T. J. (2017). Field-Based Evidence for Microplastic in Marine Aggregates and Mussels: Implications for Trophic Transfer. *Environmental Science and Technology*, 52 (19), 11038–11048.

Zhao, S., Zettler, E. R., Bos, R. P., Lin, P., Amaral-Zettler, L. A., et al. (2022). Large quantities of small microplastics permeate the surface ocean to abyssal depths in the South Atlantic Gyre. *Global Change Biology*.

Zobkov, M. B., Esiukova, E. E., Zyubin, A. Y., Samusev, I. G. (2019). Microplastic content variation in water column: The observations employing a novel sampling tool in stratified Baltic Sea. *Marine Pollution Bulletin*, 138, 193-205.

Main Text Figures and Tables

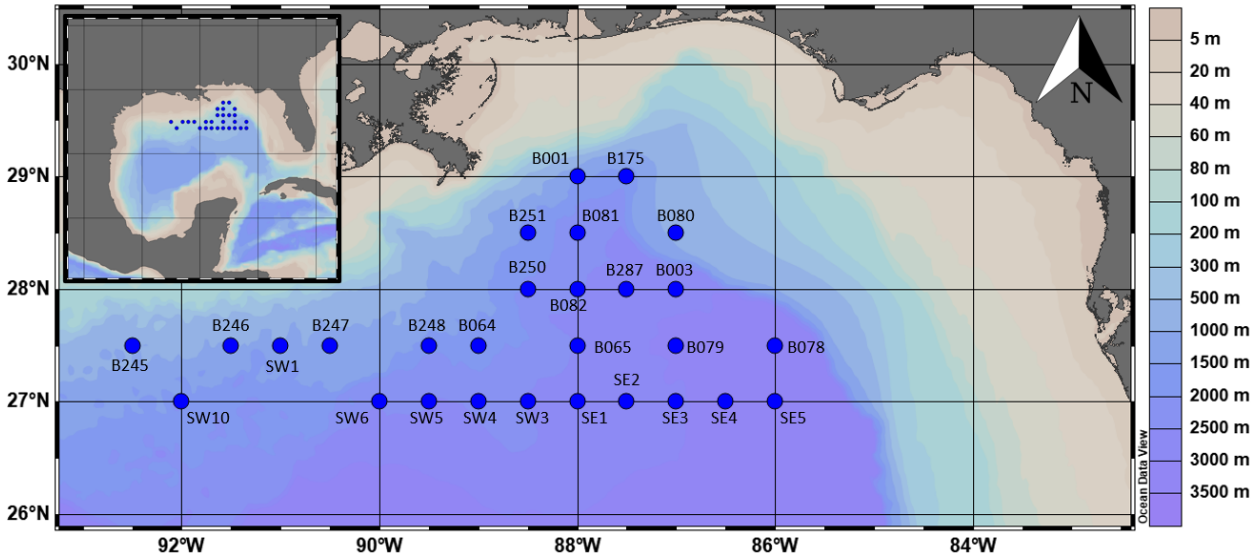

Figure 1. Trawl deployment locations in the Gulf of Mexico for collections of deep-pelagic crustaceans and fishes.

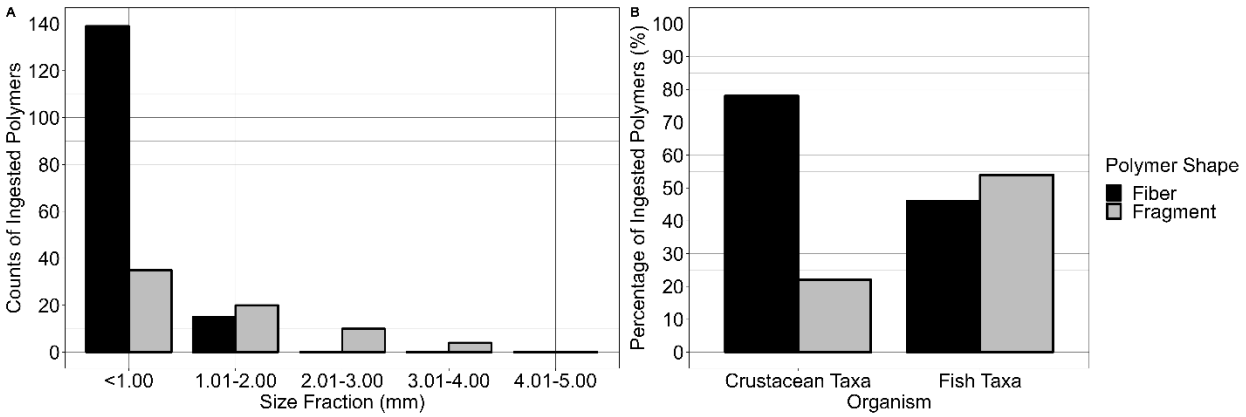

Figure 2. (A) The aggregated size fractions and composition of polymer shapes (fibers, fragments) ingested by deep-pelagic crustaceans and fishes and **(B)** the polymer shapes disaggregated for crustaceans and fishes.

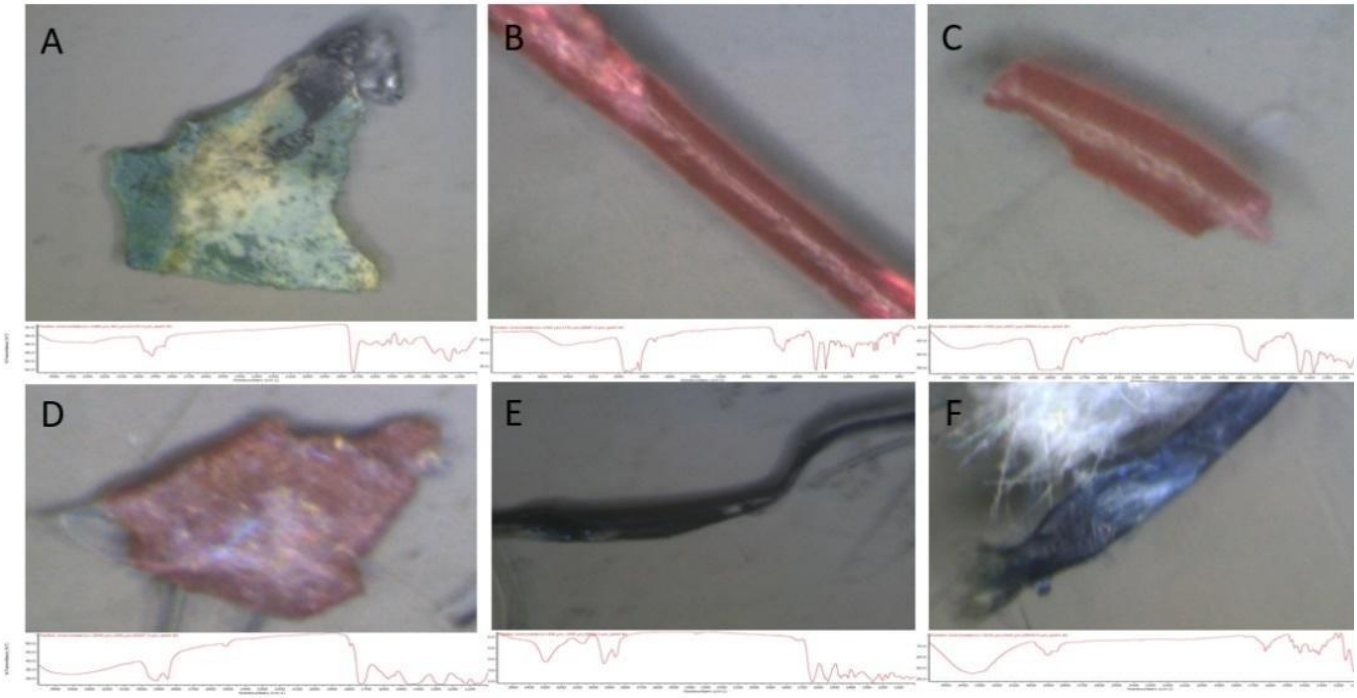

Figure 3. Example of chemically verified polymers ingested by deep-pelagic crustaceans and fishes. **(A)** polymethyl methacrylate; **(B-C)** polypropylene; **(D)** polyethylene; **(E)** polyamide 6.6; **(F)** cellophane. Chemical spectra, with characteristics plastic polymer peaks, are displayed below images of microplastics.

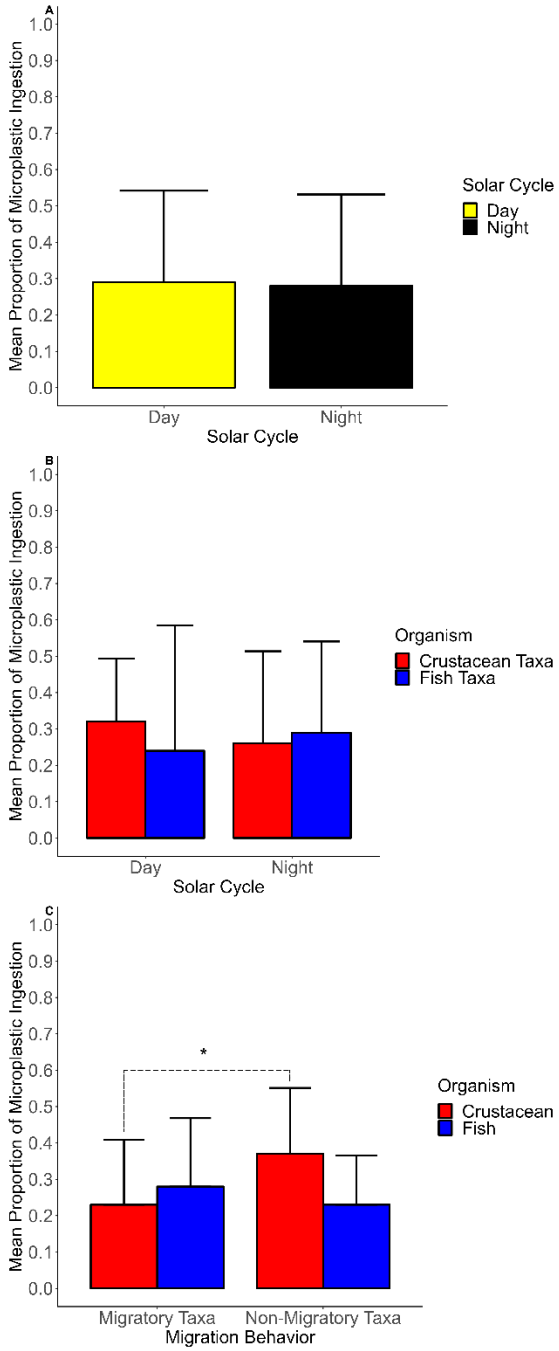

Figure 4. (A) The mean proportion of microplastics ingestion by crustacean and fishes (aggregated daytime- and nighttime-collected specimens) **(B)** microplastic ingestion proportion as a function of time of collection (daytime or nighttime) and **(C)** microplastic ingestion

proportion as a function of vertical migration behavior. Error bars are standard errors. * denotes statistical significance between groups.

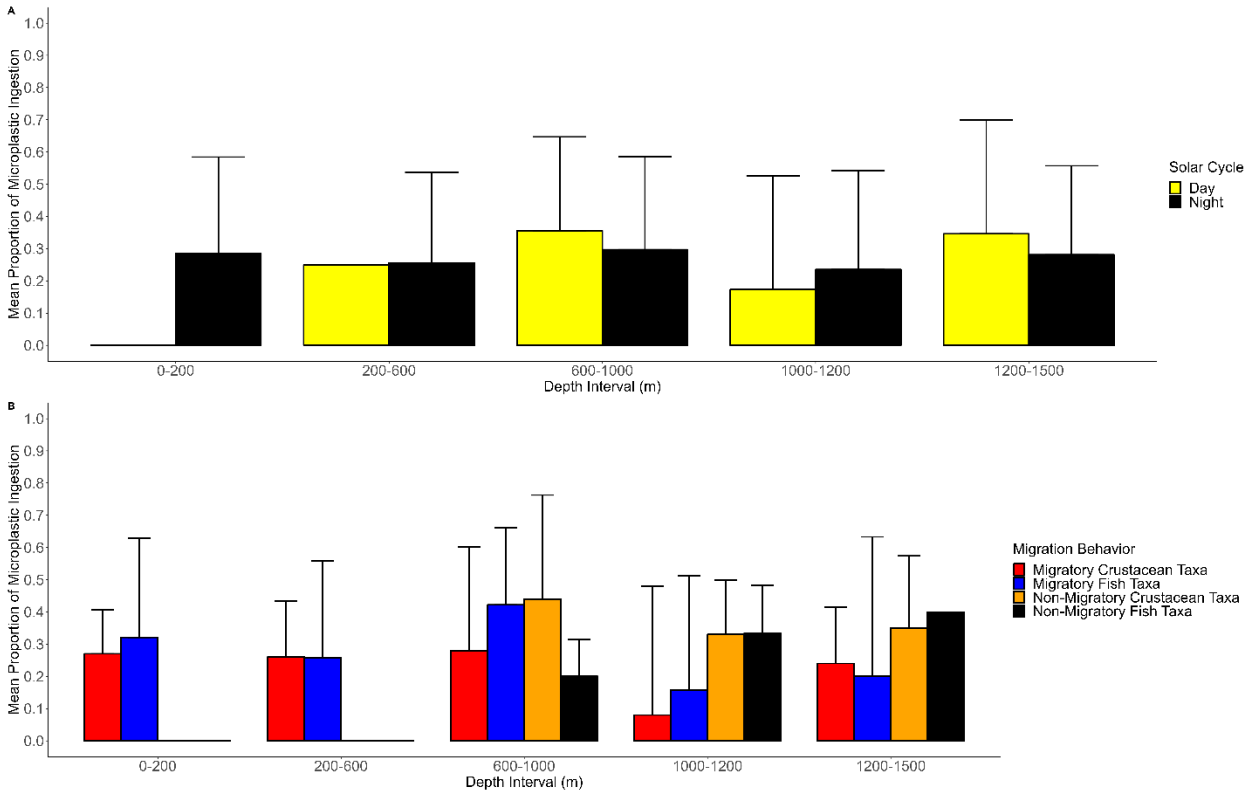

Figure 5. (A) The proportion of migratory and non-migratory crustacean and fish taxa that ingested microplastics, with discrete-depth intervals separated by day and night and **(B)** by migration behavior/taxa. Error bars are standard errors.

Table 1. Subsample of ingested polymers chemically identified by Fourier Transform Infrared spectroscopy. Theoretical densities were sourced from the Polymer Database (https://polymerdatabase.com/).

Species	Vertical Migration Behavior	Depth	Chemical Identity	Theoretical Density (g cm^{-3})	Polymer Shape	Animal Type
Acanthephyra curtirostris	NVM	1000-1200 m	Polyethyl acrylate acrylamide copolymer	0.93	Fragment	Crustacean
Acanthephyra curtirostris	NVM	1200-1500 m	Polyethylene-Polypropylene copolymer	0.95	Fragment	Crustacean
Acanthephyra purpurea	SVM	600-1000 m	Alkyd resin	1.6	Fiber	Crustacean
Bentheogenemma intermedia	NVM	1200-1500 m	Polyethyl acrylate acrylamide copolymer	0.93	Fragment	Crustacean
Bentheogenemma intermedia	NVM	1200-1500 m	Polyethyl acrylate acrylamide copolymer	0.93	Fragment	Crustacean
Benthosema suborbitale	SVM	200-600 m	Polymethyl methacrylate	1.18	Fragment	Fish
Benthosema suborbitale	SVM	0-200 m	Cellophane	1.42	Fiber	Fish
Ceratoscopelus warmingii	SVM	0-200 m	Polyamide 6.6	1.14	Fiber	Fish
Cyclothone obscura	NVM	1000-1200 m	Polyethylene-Polypropylene copolymer	0.95	Fragment	Fish
Gennadas capensis	SVM	1000-1200 m	Cellophane	1.42	Fiber	Crustacean
Gennadas capensis	SVM	200-600 m	Cellophane	1.42	Fiber	Crustacean
Gennadas valens	SVM	1200-1500 m	Alkyd resin	1.6	Fiber	Crustacean
Gennadas valens	SVM	1200-1500 m	Polyurethane	1.15	Fiber	Crustacean
Gennadas valens	SVM	200-600 m	Cellophane	1.42	Fiber	Crustacean
Gennadas valens	SVM	200-600 m	Cellophane	1.42	Fiber	Crustacean
Gennadas valens	SVM	0-200 m	Polyethylene	0.94	Fragment	Crustacean

Gennadas valens	SVM	1000-1200 m	Alkyd resin	1.6	Fiber	Crustacean
Lampanyctus alatus	SVM	200-600 m	Polymethyl methacrylate	1.18	Fragment	Fish
Lampanyctus alatus	SVM	200-600 m	Polyamide 6.6	1.14	Fiber	Fish
Notolychnus valdiviae	SVM	0-200 m	Cellophane	1.42	Fiber	Fish
Notostomus gibbosus	NVM	600-1000 m	Cellophane	1.42	Fiber	Crustacean
Plesionika richardi	SVM	0-200 m	Polypropylene	0.86	Fragment	Crustacean
Systellaspis debilis	SVM	0-200 m	Polyethylene-Polypropylene copolymer	0.95	Fragment	Crustacean
Systellaspis debilis	SVM	0-200 m	Polypropylene	0.94	Fragment	Crustacean
Systellaspis debilis	SVM	600-1000 m	Cellophane	1.42	Fiber	Crustacean

Table 2. Crustacean species from the Gulf of Mexico that were utilized for microplastic ingestion analyses. SVM = strong vertical migrator; WVM = weak vertical migrator; NVM = nonvertical migrator. Refer to Bos et al. (2021) for more information regarding migration classifications.

Species	Migratory Behavior	# of Individuals	Mean Carapace Length ± SD (mm)	Range of microplastics ingested (mean number of microplastics ingested) [% individuals ingesting microplastics]	Feeding Guild
Benthesicymidae					
Bentheogenemma intermedia	NVM	15	13.2 ± 2.19	0-3 (0.73) [40 %]	Detritivore, piscivore
Gennadas capensis	SVM	15	8.6 ± 1.5	0-4 (0.87) [47 %]	Detritivore, piscivore
Gennadas valens	SVM	21	9.2 ± 2.2	0-6 (0.62) [33 %]	Detritivore, piscivore
Oplophoridae					
Acanthephyra acanthitelsonis	WVM	2	18.2 ± 1.13	0-1 (0.5) [50 %]	Piscivore
Acanthephyra acutifrons	NVM	15	25.1 ± 11	0-2 (0.6) [53 %]	Detritivore, piscivore
Acanthephyra curtirostris	NVM	16	14.1 ± 4.34	0-3 (0.88) [50 %]	Detritivore, piscivore
Acanthephyra purpurea	SVM	43	10.7 ± 4.71	0-2 (0.30) [28 %]	Mixed zooplanktivore
Acanthephyra stylorostratis	NVM	28	9.3 ± 2.33	0-4 (0.39) [21 %]	Detritivore, piscivore
Notostomus elegans	SVM	7	18.3 ± 6.33	0-3 (1.0) [57 %]	Piscivore
Notostomus gibbosus	NVM	15	34.3 ± 10	0-3 (0.53) [33 %]	Detritivore, mixed zooplanktivore
Systellaspis debilis	SVM	46	9.96 ± 3.34	0-3 (0.26) [20 %]	Mixed zooplanktivore
Pandalidae					
Plesionika richardi	SVM	46	7.6 ± 1.9	0-5 (0.32) [24 %]	Piscivore
Pasiphaeidae					

Pasiphaea merriami	SVM	4	18.0 ± 3.76	0 (0) [0 %]	Mixed zooplanktivore
Sergestidae					
Gardinerosergia splendens	SVM	12	9.7 ± 2.1	0-1 (0.08) [8 %]	Mixed zooplanktivore
Sergia tenuiremis	SVM	15	17.2 ± 2.8	0-1 (0.13) [13 %]	Mixed zooplanktivore
Total		**300**		**128**	

Table 3. Fish species from the Gulf of Mexico that were utilized for microplastic ingestion analyses. SVM = strong vertical migrator; WVM = weak vertical migrator; NVM = non-vertical migrator. Refer to Bos et al. (2021) for more information regarding migration classifications.

Species	Migratory Behavior	# of Individuals	Average Standard Length ± SD (mm)	Range of microplastics ingested (mean number of microplastics ingested) [% individuals ingesting microplastics]	Feeding Guild
Gonastomatidae					
Cyclothone acclinidens	NVM	15	27.7 ± 1.5	0-1 (0.13) [13 %]	Mesozooplanktivore
Cyclothone obscura	NVM	15	39.1 ± 5.2	0-3 (0.47) [33 %]	Detritivore, Mesozooplanktivore
Cyclothone pallida	NVM	15	35.0 ± 6.1	0-1 (0.06) [7 %]	Mesozooplanktivore
Sigmops elongatus	SVM	6	39.0 ± 5.2	0-2 (0.63) [17 %]	Mixed zooplanktivore
Myctophidae					
Benthosema suborbitale	SVM	17	24.1 ± 3.4	0-1 (0.53) [53 %]	Mixed zooplanktivore
Ceratoscopelus warmingii	SVM	18	53.8 ± 9.1	0-2 (0.27) [19 %]	Generalist
Diaphus dumerilii	SVM	1	52.9 [NA]	4 (4) [100 %]	Mixed zooplanktivore
Diaphus lucidus	SVM	5	66.4 ± 13.6	0 (0) [0 %]	Mixed zooplanktivore
Lampanyctus alatus	SVM	57	37.4 ± 3.7	0-4 (0.56) [39 %]	Mixed zooplanktivore
Lampanyctus lineatus	SVM	18	61.6 ±15.8	0-4 (0.55) [18 %]	Mixed zooplanktivore
Lepidophanes guentheri	SVM	11	35.3 ± 9.9	0-1 (0.28) [28 %]	Mixed zooplanktivore
Notolychnus valdiviae	SVM	25	16.8 ± 1.3	0-2 (0.20) [12 %]	Mixed zooplanktivore
Notoscopelus resplendens	SVM	14	35.4 ± 7.3	0-1 (0.07) [7 %]	Mixed zooplanktivore
Sternoptychidae					
Argyropelecus aculeatus	SVM	2	30.5 ± 15.5	0 (0) [0 %]	Generalist
Argyropelecus hemigymnus	WVM	8	13.5 ± 2.4	0-1 (0.5) [50 %]	Mixed zooplanktivore
Sternoptyx diaphana	NVM	27	11.7 ± 3.6	0-5 (0.52) [33 %]	Copepodivore
Sternoptyx pseudobscura	NVM	3	14.1 ± 1.7	0 (0) [0 %]	Generalist
Stomiidae					
Chauliodus sloani	SVM	1	129.0 [NA]	0 (0) [0 %]	Piscivore
Total		**257**		**95**	